

# Restudy of the Lower Carboniferous Scaphopoda described by DE KONINCK (1843, 1883)

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## Abstract

The fossils which DE KONINCK described and illustrated as members of the molluscan Class Scaphopoda have been reexamined. For the first time, photographs of these specimens are presented. Scaphopod shells show only a limited number of morphologic features and for most of these species, the details are lacking which would indicate that the fossils belong undoubtedly in the Scaphopoda. The study suggests that most of the named species may not be Scaphopoda; these species are assigned to informal groupings, ranging from *Incertae sedis*, through "worm tubes" to "probably Scaphopoda". Only one specimen may be identified without question as a member of the scaphopods.

**Key words:** Scaphopoda, Lower Carboniferous, Belgium.

## Résumé

Les fossiles que DE KONINCK décrit et figura comme membres de la classe des mollusques Scaphopoda ont été réexaminés. Pour la première fois, des photographies de ces spécimens sont présentées. Les coquilles de scaphopodes possèdent qu'un nombre limité de caractères morphologiques et pour la plupart de ces espèces, les détails qui indiqueraient que les fossiles appartiennent sans discussion aux Scaphopoda manquent. L'étude suggère que la plupart des espèces ne sont pas des Scaphopoda; ces espèces sont placées dans des groupes informels allant d'*Incertae sedis* à «tubes de vers» et «probablement Scaphopoda». Un seul spécimen peut être identifié avec certitude comme membre des Scaphopoda.

**Mots-clefs:** Scaphopoda, Carbonifère inférieur, Belgique.

## Introduction

Scaphopoda have been variously described as a "minor" or "lesser" class within the Mollusca. This group is best exemplified by the late Mesozoic to Recent genus *Dentalium* LINNAEUS, 1758.

Actually, that name was mentioned by LINNAEUS more than two decades before it entered into formal zoological nomenclature, and other authors used it in still earlier literature. As discussed below, the curved shell has two

openings, at the aperture and at the apex. Because of their curious shape, the Recent shells were part of the cabinets of many of the classic mollusc collections. Despite the striking difference between the trochiform shape of a typical gastropod, and the slight curve of *Dentalium*, for more than a century after the Phylum Mollusca was proposed, the scaphopods were included within the Class Gastropoda. Following the accepted classification of the time, DE KONINCK (1883) placed them as a subclass within the Gastropoda.

The Palaeozoic Scaphopoda constitute a little-studied group of fossils. As part of his monographic effort in 1883, DE KONINCK named or redescribed more species of Lower Carboniferous scaphopods than any other author known to us. Indeed, there has been no other study of any age which included Palaeozoic Scaphopoda that can be considered monographic for the class. Following DE KONINCK's comprehensive study, the investigation of Early Carboniferous taxa has been scant, as the later limited use of his specific names demonstrates.

In keeping with the available technology, DE KONINCK illustrated his species with drawings, and like all scientific drawing some are more accurate than others. Coordinate with improvement in illustration has come more information from both the fossil record and the living representatives of the group. In honesty, one must admit that Palaeozoic Scaphopoda are fossils of slight interest, in part because of their rarity and in part because of their restricted range of morphology. Nevertheless, it does seem appropriate, after a century and a quarter, to reconsider the Belgian material.

## DE KONINCK's investigations of Carboniferous Scaphopoda

The first general description of the Carboniferous faunas of Belgium by DE KONINCK was published in several fascicles between 1842 and 1844. Conventionally, these parts are found in libraries as a bound volume and are cited with this combined date. By reference to synonymy given in later publications of DE KONINCK, the year when the various fascicles were printed can be determined. It is

with a high degree of confidence that we cite 1843 for his earlier work on Scaphopoda. SHERBORN (1925, p. 1287; 1927, p. 3195; 1929, p. 4620) confirms this date.

In 1843 (pp. 314-319), the author redescribed *Dentalium priscum* MÜNSTER in GOLDFUSS, 1842 [= *Dentalium priscum* GOLDFUSS, 1841 (ex Münster MS) according to STEINER & KABAT (2004, p. 633)] and described two new species which he assigned to *Dentalium*. DE KONINCK also described a third new species as *D. cinctum*, but on pp. 514 and 635 (erratum), he placed this taxon in the synonymy of *Orthoceras subcentrale* DE KONINCK, 1844. Later (1880, p. 29), DE KONINCK placed *D. cinctum* and *O. subcentrale* in the synonymy of *Cyrtoceras cinctum* MÜNSTER.

Forty years later (1883), in his monograph on Gastropoda, DE KONINCK devoted six pages (pp. 214-219) and one plate (pl. 49) of this work to scaphopods. He again discussed *D. priscum*, redescribed the two species named in 1843, and added four new species. He also considered a species described by DE RYCKHOLT (1847). The three species named by DE KONINCK in 1843 were also transferred by him to *Entalis*; presumably this was done because none of Belgian forms showed the prominent longitudinal lirae characteristic of typical *Dentalium*. Although DE KONINCK credited that generic name to Sowerby, as indicated in the synonymy compiled by EMERSON (1962, p. 469), authorship is an exceedingly complex matter which included homonymy with an annelid worm. The details of authorship and correct generic name for the concept used by DE KONINCK (1883) are not germane to this study.

The fossils studied by DE KONINCK and reexamined herein were originally part of different old collections housed at the "Institut royal des Sciences naturelles de Belgique", where they are numbered IRScNB a4263 to IRScNB a4275 (in the course of this work, IRScNB will be omitted). As might be expected, for some taxa it has been difficult to recognize what specimens were illustrated by DE KONINCK in 1843, as a number of the drawings were idealized. Moreover, labels related to the determination in the work of 1843 are missing. In a sense, the extreme rarity of the fossils which were considered scaphopods has been of help in identifying those specimens, for there was essentially no choice. We are confident that the material from this first publication (1843) has been as correctly identified as possible; details are given in the appropriate sections below. Additional material has been discovered in the old collections of the Department of Palaeontology of the University of Liège.

The drawings of 1883 are superior to those published four decades earlier, and the figured specimens are easily recognized. In addition, labels indicate this information and provide an example of improvement in curatorial practice. It is also appropriate to mention that while searching for illustrated material in the DE KONINCK collection and other appropriate collections, we also looked for additional unfigured fossils that might assist in the present study. With the exception of a small collection

from Liège University, this search was essentially fruitless and one must conclude that in the Lower Carboniferous strata of Belgium, tubular fossils, whether authentic scaphopods or scaphopod-like, are among the rarest of forms.

### Stratigraphic and geographic data (Fig. 1)

Since the 1843 and 1883 studies of DE KONINCK, considerable progress has been made in precision and interpreting Carboniferous stratigraphy. In particular, publications from the last fifty years devoted to the litho-, bio- and chronostratigraphy of the Tournaisian and Viséan of Belgium refined the generalizations provided by DE KONINCK.

The information as it pertains to the taxa considered in this study is discussed here and summarized in graphic form on Figure 1.

Even with a better understanding of the rock sequences, the precise locality or localities from which the DE KONINCK fossils were obtained is not known. Outcrops and quarries were not designated on the labels. This uncertainty applies to specimens from all the listings below. It may be helpful to note that all specimens studied are silicified, and that point is discussed in more detail in the systematic section.

The lithological units from which the studied material has been collected are as follows, from the older to the younger:

"*Argile carbonifère de Tournay*" (1843), "*Calcschiste de Tournai*" (1883)

The investigation of DEMANET (1958, pp. 124, 140) indicated that the material studied by DE KONINCK was collected from the "Calcaire d'Allain" and the "Calcaire de Providence", but mainly came from the "Calcaire de Première"; later literature has designated this last as the "Calcaire de Pont à Rieux". These units are now considered as three of the six members into which the Tournai Fm. has been subdivided (see POTY *et al.*, 2002, p. 79, fig. 6). In the geological literature of Belgium these three units are cited by the symbols Tn2c, Tn3a, and Tn3b or only Tn3a and Tn3b (see SARTENAER & PŁODOWSKI, 1996, fig. 2). The units mentioned by DE KONINCK are now considered to be Ivorian in age, the second subdivision of the Tournaisian. It is to be noted that POTY *et al.* (2002, fig. 5) considered the Tournaisian as a series, whereas METCALF *et al.* (2000, pp. 5-7) considered it as a stage.

"*Calcaire de Waulsort*", "*Calcaire des Pauquys*", "*Calcaire de Dréhance*" (1883)

These units correspond to the Waulsort Fm. of the upper Tournaisian (see POTY *et al.* 2002, pp. 80-81, fig. 5). The localities where fossils were collected are indicated with a reference number on the set of reference maps housed at the IRScNB. These are: "Calcaire de Waulsort" or "Waulsortien de Waulsort" – Hastière 608; "Calcaire

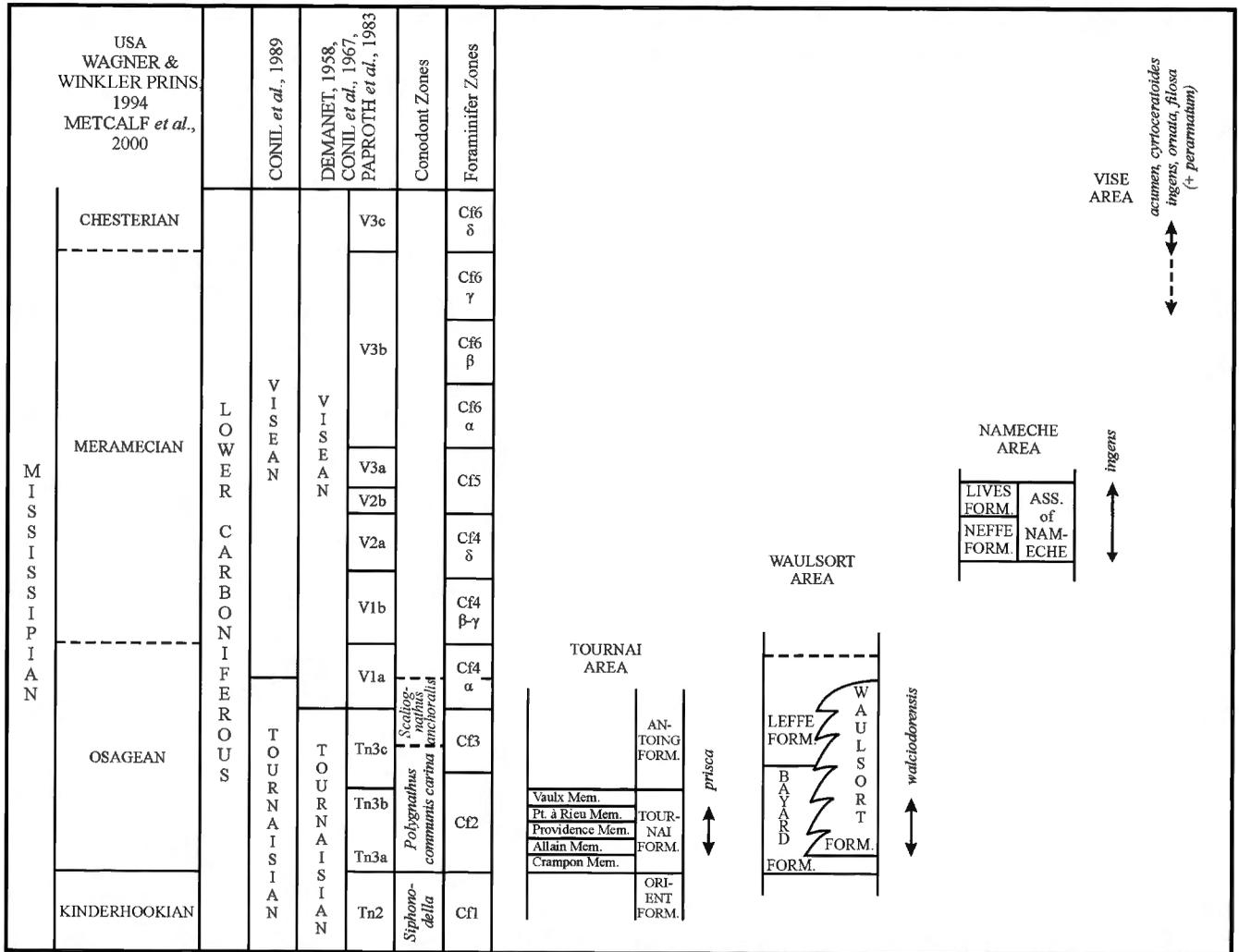


Fig. 1 — Distribution of the Scaphopoda described by DE KONINCK (1843, 1883). Lithological units, Foraminifer and Conodont Zones from the synthesis of POTY *et al.* (2002).

de Pauquys” or “Waulsortien des Pauquys” – Dinant 605 & 606 (see also DELEPINE, 1940, pp. 13-15, fig. 3); “Calcaire de Dréhance” – Dinant 810 (see also DELEPINE, id., pp. 16-17, fig. 3). According to CONIL (1968, p. 700), the material described by DE KONINCK from the Pauquys at Waulsort, comes probably from the unit *r1* (= “récif inférieur”) (see also DEHANTSCHUTTER & LEES, 1996, pp. 125-129).

“Calcaire carbonifère de Visé” (1843), “Calcaire de Visé” (1883)  
 According to DEMANET (1958, p. 32) most of the specimens studied by DE KONINCK were collected south of Visé on the east side of the Meuse River valley. They were from quarry G (DEMANET, 1958, p. 29, unnumbered figure) in beds which are currently designated by the symbols V3b and V3c. PAPROTH *et al.* (1983, p. 228) write: “The most famous faunas from the Visé Limestone are from the lower Cf6d Zone (PIRLET, 1976b)”. The Cf6d Zone based on Foraminifera corresponds, more or less, to the V3c beds (see also POTY, 1981, pp. 78-80).

“Calcaire de Namèche” (1883)  
 The “Assise de Namèche” as delimited by DEMANET (1923, p. 49; 1958, p. 93) is subdivided into two units: the “V2a, Calcaire de Neffe” below and the “V2b, Calcaire de Lives” above. CONIL *et al.* (1967) adopted the same divisions, though the denomination of the upper unit was modified to “Calcaire de Namèche et de Lives”. In PAPROTH *et al.* (1983) and POTY *et al.* (2002) the names “Assise de Namèche” and “Calcaire de Namèche” are abandoned. Presently, we consider that the fossils reported by DE KONINCK as collected from the “Calcaire de Namèche” are from an undifferentiated V2a-V2b sequence.

**General remarks**

Among the present-day classes of shelled Mollusca, the Scaphopoda are the least taxonomically diverse and show a limited range of morphologies, the Polyplacophora show greater diversity and there are so few genera within the shell-less Aplaco-

phora that no meaningful comparison can be made. Scaphopods are informally known as elephant tusk shells, because the bilaterally symmetrical shell has a slight curvature, the curvature following a wide logarithmic spiral. The shell itself differs from that of all other Mollusca in that the apical area is also open in addition to the apertural opening. This is a consequence of lack of fusion at each end of the lateral margins of the early shell. The original opening is then modified by bioerosion. In some taxa, there is also a short notch or slit at one place around the circumference of the apical inclined opening. Whereas a number of different kinds of tubular fossils may be broken at both ends, and some even have hard parts constructed with two openings, the apical bioerosion and especially the apical notch are features of the shell that seemingly are unique to this class.

There are two principal groups within the class which have been variously treated as distinct taxa, ranging in assignment from family level to subclass level (LUDBROOK, 1960). In a current classification (REYNOLDS, 2002, pp. 143-144), two orders are used, Dentaliida and Gadilida. The Dentaliida, that is those described above, may be characterized, somewhat inaccurately, as shallow water forms. Thirty one genera are included by REYNOLDS (2002) in the order, of which 11 are marked as fossil forms. The Gadilida are more obscure forms, occur in deeper water, are smaller shells in general, and are swollen rather than expanding uniformly. Twenty eight genera are included in the classification, of which four are marked as fossil forms. One of these fossil genera has been described from the Palaeozoic, but it is open to other interpretations. In any event, none of DE KONINCK'S specimens are considered to be related to the Gadilida and that order will not be considered further.

In spite of their limited diversity, the Scaphopoda are distinct and fully deserving of the rank of a class within the Mollusca.

The animal lives with the shell mostly buried in sediment with the open anterior protruding into water. Living specimens are fierce predators, preying predominately on foraminifers which they collect from adjacent sediments by the captacula, an apparatus of many thin tentacles. The anterior of the mantle cavity soft part contains a radula adjacent to the captacula, but no eyes. An outstanding summary of anatomy and ecology of living scaphopods has recently been published (REYNOLDS, 2002).

There is evidence that Jurassic forms were also predatory (PALMER, 1975) and since the morphology of living and fossil forms is so similar, it is reasonable to assume that Palaeozoic scaphopods had a comparable habitat and mode of feeding. To place this in broader terms, the scaphopods seem to have exploited a narrow ecologic niche and have remained essentially unchanged to any significant degree since they first appeared in the fossil record.

Because of some similarities in early larval development, and other features, including lack of a "head", in the classic zoological literature the Scaphopoda were linked to the Bivalvia, despite the lack of a radula in the latter class. From the study of Palaeozoic Rostroconchia, POJETA & RUNNEGAR (1979) have suggested that they arose in the Ordovician, a view subsequently repeated (POJETA & RUNNEGAR, 1985). STEINER (1992) reviewed the earlier literature on phylogenetic relationship to other Mollusca and concluded "Even though the connecting links between the Rostroconchia and Scaphopoda are missing and the shifts of the body and shell axes are neither explained nor documented, it is considered most likely the scaphopod ancestor was of rostroconch origin" (p. 386).

YOCHELSON (1978) was dubious of the Ordovician reports of Scaphopoda and suggested a Devonian age for the oldest scaphopods; he appealed to an unknown soft-bodied ancestor to resolve the issue of the presence of a radula in scaphopods. Subsequently, ENGESER & RIEDEL (1996) suggested the Scaphopoda appeared in the Devonian, but derived them from a different group of the Rostroconchia. They also noted, correctly, "The idea of ... an unknown non-shelled ancestor is readily rejected ..." (p. 121). In part because of the presence of a radula in scaphopods, a few authors suggested a closer relationship to the Gastropoda and Cephalopoda. Still more recently, using molecular data, STEINER & DREYER (2003) have suggested a relationship to the Cephalopoda. Such disparate views, reinforce the view that the relationships of Scaphopoda within the Mollusca remain obscure.

### Summary geologic history

The fossil scaphopods have a long but uncertain geologic history. In general, a new species is proposed as a member of the Scaphopoda and then remains in the literature without further comment or restudy by subsequent investigators. As a result, the issue of when the oldest representatives of the class occur in the fossil record is subject to different interpretations.

Part of the difficulty in studying the older scaphopods is that material is both scanty and often fragmentary. More often than not, specimens consist of part of a tube with both the anterior and the posterior portions broken away. Compounding this difficulty, Scaphopoda are not the only fossils with a tube-like form. PILSBRY & SHARP (1898) removed from the class a number of species that they considered to be serpulid worms. The process of removing fossil species which were incorrectly identified as Mollusca continues, as for example in PALMER (2001) and PALMER *et al.* (2004).

Among Palaeozoic forms, a recent development has been the realization of external homeomorphy of certain scaphopods with slightly curved orthoconic cephalopods (YOCHELSON & HOLLAND, 2004). Already DE KONINCK (1883, p. 218) commented on this external similarity, but his views were forgotten. Still further compounding the problem of what is a fossil scaphopod within the Palaeozoic there are fossils which develop tube-like hard parts, and need not be curved orthocones nor serpulid worms. The coleolid "worm tubes" and the tentaculitids immediately come to mind.

As a result, one cannot be certain that a curved tubular fossil is a scaphopod or even a member of the Mollusca. Some named species now judged not to be Scaphopoda show enough detail to be readily assigned elsewhere in the Kingdom Animalia, and some do not. It is our view that to begin to make sense of the development of the class through geologic history, a more rigorous morphologic standard should be applied. Unless fossil specimens show morphologic features which are unique to the class – admittedly a difficult criterion to determine – they should not be placed in that class, but rather transferred to *Incertae sedis*, pending discovery and study of better specimens. This generalized assignment can be used at all levels, but is more common at higher taxonomic levels.

To return to the issue of first occurrence in the geologic record: some Permian species show a small notch at the apical opening. Likewise, some Upper Carboniferous (Pennsylvanian) forms have this feature. One aim of this inquiry is to determine whether Lower Carboniferous forms can be assigned to the class without question.

Several Devonian species have been removed from the Class (YOCHELSON & GOODISON, 1999; YOCHELSON, 2002; YOCHELSON & HOLLAND, 2004) and it seems doubtful that any Devonian specimens are scaphopods. As far as we know, no Silurian species have been described. One Ordovician report from Russia has been reinterpreted as the infilling (steinkern) of the body chamber of orthoconic cephalopods (KISELEV, 2001).

There have been three reports from the USA of material originally described or later referred to the scaphopods. For one a refutation and reassignment has been published (YOCHELSON, 1968); a second also has been refuted (YOCHELSON, 2004). This leaves only the report of POJETA & RUNNEGAR (1979) as the earliest putative representative of the class. In the view of one of us (YOCHELSON, 2004) this material is not properly assigned to the Phylum Mollusca; indeed, it does not show morphologic features which could be interpreted as showing without question that it belongs to the class.

If these reinterpretations are upheld by others, Scaphopoda cannot be considered as first occurring in the Ordovician. Thus, it becomes critical to determine whether all, some, or none of the DE KONINCK specimens are Scaphopoda. The descriptions and measurements of DE KONINCK are generally accurate and need not be repeated. However, there is an old saying that "The eye beholds what the mind perceives". At the time of his publication, there was no clear notion among those who described fossil molluscs that curved tube-like fossils need not necessarily be Scaphopoda.

In the same spirit, it should be noted that two events of about the same time need not be "cause and effect". Even allowing for that caution, we find it of interest that authentic scaphopods appear in the fossil record at about the same time that calcareous foraminifers abound.

### History of this investigation

In 1997, Yochelson and Godefroid spent one day examining the material figured by DE KONINCK and stored in the Palaeontology Department at the "Institut royal des Sciences naturelles de Belgique" in Brussels. Time did not permit searching the museum collections for additional material. Subsequently, one of us (ELY) has examined tubular Lower Carboniferous fossils of the same age from Scotland and must assume principal responsibility for provisional reassignments presented in the first draft for consideration by the other two authors.

During the same interval, one of us (JG) has photographed DE KONINCK material. In some instances, the published drawings on plate 49 of DE KONINCK (1883) are accurate, but in others some features are different. The publication of museum catalogue numbers herein (IRScNB a) will also facilitate the work of future investigators. Finally one of us (BM) has undertaken the work of final editing, rechecking of specimens and resolving the rare differences in interpretation of the specimens as the work progressed. We all concur on the formal and informal suggestions for further placement of DE KONINCK's taxa, discussed below.

When the material was examined in 1997, the views which ELY held as to morphology of members of the class were discussed. Circumstances have prevented us from jointly re-examining the specimens, though there has been exchange of ideas through the mechanism of e-mail. However, nothing can replace mutual discussion while examining specimens.

For each species, we have reproduced in the Figures, the illustrations of DE KONINCK (1843, 1883) with their original

numbering and added photographs of the specimens. The photographs are designated by the original numbering in DE KONINCK (1883) followed by one or two asterisk(s). Further, for each species we only cite the references to DE KONINCK (1843, 1883) and the original references anterior to the works of DE KONINCK.

We include herein, the references subsequent to DE KONINCK (1883) which mention the specific names included in that work. These are all from the remarkable, but unpublished catalogue of T. Engeser. Most of these references simply consist of a mention of the name or rarely a transfer to another genus. A synonymy is considered to be an evaluation of earlier published literature and an acceptance or rejection of the taxonomic conclusions and specimens of each of the authors cited. We have not examined any of the few species illustrated by other authors than DE KONINCK assigned to the Early Carboniferous taxa discussed herein and thus choose not to provide any formal synonymy. Although the informal mention given of post-1883 publications is of limited value, it does provide a starting place for another investigator. Perhaps, equally importantly, it is a measure of how little attention the Palaeozoic scaphopods have received during more than a century of palaeontologic investigations.

As the first step we have photographed and described the considered specimens of 1883; as the second step, the specimens are informally assigned and reassigned and finally those considered member of the Scaphopoda are considered in more detail.

### Discussion of specimens

Remarks below on species follow the order used by DE KONINCK (1883) in his systematic descriptions (all specimens were illustrated on plate 49 of his work and, accordingly, we have only cited his figure numbers). We have not written any descriptions or made formal reassignments here, for though we judge our comments on the specimens to be accurate, it is important to emphasize the preliminary nature of those views. Accordingly, interpretations of our observations are not in this section, but are considered elsewhere in this work. It is evident that a search for more and better specimens is necessary as the next step in any more comprehensive study and formal reassignment of these taxa.

#### *Entalis prisca* (MÜNSTER in GOLDFUSS, 1841)

##### Plate I

- \* 1841 *Dentalium priscum* MÜNSTER – GOLDFUSS, p. 2, pl. 166, fig. 3.
- 1843 *Dentalium priscum* – DE KONINCK, pp. 316-317, pl. 22, fig. 1.
- 1883 *Entalis prisca*, G. zu MÜNSTER – DE KONINCK, p. 215, pl. 49, figs. 1, 2, 3, 20, 21, unnumbered text-fig.

#### INFORMAL SYNONYMY

Following the original publication of this species as a *Dentalium*, DE KONINCK (1883, p. 215) provided the synonymy from 1843 onward, and transferred the species to *Entalis*. According to the compilation of Engeser, following that 1883 publication,

LEYH (1897, p. 538) mentioned a specimen as *Dentalium* cf. *priscum* and the following year, PILSBRY & SHARP (1898, p. 232) reassigned the species to *Dentalium* without question. CRAMER (1914, p. 65, pl. 3, fig. 30) questionably assigned a specimen to this taxon. Next, REED (1925, p. 94) in discussion came up with the combination of *Plagiogypta* cf. *prisca*. GARWOOD (1930, pl. 10, fig. 1) illustrated a specimen identified as *D. priscum*. Following that identification, RAZKUSZ (1932, p. 190, pl. 9, figs. 21, 22) described a specimen as *Laevidentalium* cf. *priscum*. In what may be the latest transfer, HABE (1964, p. 24) mentioned the species in passing and once again transferred it to *Plagiogypta*.

#### MATERIAL

Three specimens (a4263, Piret collection; a4264, a4265, Cantraine collection).

#### COMMENTS

In his 1843 publication (pl. 22), DE KONINCK had four drawings. One is of an essentially complete specimen (fig. 1a) and attached to it by a dashed line is a cross-section (fig. 1d) indicating a thicker shell wall along part of the circumference. Also attached by a dashed line, presumably to indicate relative position on the complete specimen is an enlarged view (fig. 1c) showing gently inclined growth lines on what may be a fragment. In turn, this is attached by another dashed line to another fragment (fig. 1b), indicated in the caption as showing an inclined aperture.

In 1883, DE KONINCK illustrated three specimens by drawings. Because, as noted by DE KONINCK in 1843, the species had been described in 1842, no type material is involved and determining whether any of the specimens were illustrated twice is not critical. We think it likely that fig. 1a of 1843 and fig. 1 of 1883 (a4263) represent the same specimen. It is to be noted that the apertural margin is broken so that inclination of the margin does not follow that of the growth lines. This specimen actually consists of three pieces (I-III). The upper and medial section very likely fit together, and show extremely slight curvature. Curvature of the smallest, apical piece is slightly more obvious, though in keeping with the curvature of the larger pieces above. The upper part of this fragment does not have a good match to the next wider piece; the 1883 drawing does indicate a discontinuity at about this point.

Closely spaced growth lines are prominent on the highest piece and are clear, though slightly reduced on the medial piece; they are inclined at slightly less than 10 degrees to the axis of the shell. The lowest piece lacks any indication of growth lines, but this may be consequence of silicification of the surface. If the smallest apical fragment does not actually belong to those above, at least it seems to be conspecific.

The 1843 drawing (fig. 1d) indicated part of the circumference thickened near the aperture, but this specimen apparently is missing. A cross-section of the apical region in 1883 (fig. 3) shows a circular cross-section without any inner thickening. It is impossible to confirm or deny this drawing because the three pieces constituting the specimen a4263 are glued to a card and are extremely fragile. The thickened circumference figured in 1843 could be a drawing error. DE KONINCK's figure 2 (1883) suggests a groove, but it is a result of the artistic rendering and not a real feature.

DE KONINCK illustrated two more specimens in 1883 and these are not definitely related to his earlier drawings. Figure 20 (a4264) shows a specimen distinctly curved at the apical portion. The specimen illustrated lacks the apical portion,

though the lower portion of the tube does show slight curvature. Actually two pieces have been assembled at the apical end, but their fit together and to the larger portion is moderately good. No growth lines have been noted through the length.

The third specimen (a4265) is accurately drawn in figure 21. It is broken longitudinally, as well as at the apertural and apical ends. It appears to be slightly more strongly curved than a comparable portion of the most complete 1843 specimen, but it may be an optical illusion from comparing a shorter fragment to a longer piece. No septation is evident. Near the apertural portion of this hollow tube another tubular piece is also present. Three interpretations are possible. The first one is that it is some sort of internal feature preserved by silicification. The second possibility is that this is a separate tubular specimen moved by water current within an open tube and then cemented in place by silicification which was DE KONINCK's interpretation. The third one is that the small tube corresponds to the apical portion of the larger one but was broken and moved within the larger one.

There is nothing to suggest that the second and third specimens of 1883, discussed above, are necessarily the same taxon as the first. Apart from being "tubular" in general shape, they convey little morphologic information.

DE KONINCK's figure 20 (a4264) shows a curved apertural area coming to a point. This may have been restored for the specimen lacks an apex and has been broken and glued. The original of figure 21 (a4265) also lacks the apical area. Both specimens are curved. Because the angle of tangency of the logarithmic spiral is so slight in scaphopods it is very difficult to measure and harder to interpret. Having that caveat, it appears that the curvature of the two is somewhat different. For a4264, one interpretation is that the upper two-thirds of the specimens is straight and expands at a lower rate than the lower portion of the tube. As one can determine from the photograph a4265 is broken longitudinally and shows an internal feature. DE KONINCK interpreted this as a shell secondarily moved into a larger one, a not uncommon phenomenon of tubular fossils. Although a smaller tubular shell may have moved into a larger one, one difficulty is that the smaller shows less curvature to the enclosing one. They need not be related.

The Yale Peabody Museum, New Haven (Connecticut, USA) has one specimen labeled as this species in its collections from Tournai. YPM 36823 is a minimized fragment not quite 3 cm long. At the broken apertural end, approximately half the circumference shows an exceedingly thick shell and the remainder is thin. Within this broken aperture, the surface appears curved and one possible interpretation is that this is a septum, with the shell thickened on the ventral side. Most of the thinner part of the specimen is eroded away.

Another specimen in the National Museum of Natural History, Washington D.C., USNM 63130, is about 2 1/2 cm in length. It too is silicified and may have been naturally eroded from limestone. The fragment shows growth lines which seem to be at right angles to the shell axis; the fragment is too short to allow certainty, but the specimen may be straight, rather than curved.

The two are not congeneric and reinforce the view that several different kinds of tubular fossils may be identified as this species.

#### OCCURRENCE

In 1883, DE KONINCK reported this species from "le calcschiste des environs de Tournai (assise I), où elle n'est pas rare" (p. 215). This is the only species that the author indicated as being at all common. DE KONINCK mentioned reports of

this species from Scotland by Armstrong and by Young and Roberston, but indicated that these were misidentifications.

*Entalis walciodorensis* DE KONINCK, 1883

Figure 2

\* 1883 *Entalis walciodorensis* – L.G. DE KONINCK, pp. 215–216, pl. 49, figs. 16, 17.

INFORMAL SYNONYMY

In a listing, PILSBRY & SHARP (1898, p. 233) transferred the species to *Dentalium*. In a footnote, KITTL (1903, p. 696) returned the species to *Entalis*.

MATERIAL

Two specimens of which one figured (a4266A, Dupont collection).

COMMENTS

The species is illustrated by a specimen in three pieces (fig. 16) (a4266), supplemented (fig. 17) by a cross section near the

midlength. The three pieces are separate, though there is no reason to question their original assignment as they closely resemble the drawing. Both the apertural and apical areas are broken. Insofar as one can tell, the specimen is straight and none of the pieces give even a hint of curvature; if any curvature was present, it would be more obvious in the two smaller pieces closer to the apical area.

In the principal drawing, growth lines are suggested on the central piece, but there is no evidence of them. Growth lines are prominent and closely spaced on the largest piece. Several show minor irregularities, though the course of most seems to be uniform and circular around the shell. A shell irregularity is on one side toward the aperture where the circumference narrows abruptly, but even here the growth lines appear uniform; this irregularity is not shown in DE KONINCK's illustration.

The drawing of the cross section shows a uniform thickness around the circumference and insofar as this can be determined all three fragments demonstrate uniform shell thickness.

The three pieces were originally glued to a cardboard, but were removed for closer examination. The anterior opening of the smallest fragment is distinctly oval, being 0.47 cm in one diameter and 0.64 cm in the other. For the middle fragment, the smaller end is oval, measuring 0.5 cm and 0.6 cm, respectively, whereas the larger end is circular with a diameter of 0.76 cm. Interestingly enough, the smaller end of the largest fragment is again nearly circular, with diameters of 0.70 cm and 0.71 cm. It is evident that at least the middle and upper fragments do not match the segment closest to the aperture. Growth lines are exceedingly faint on the two lower fragments and it is possible that their course is slightly different from that on the largest fragment.

The evidence suggests the drawing is of an artificial assemblage. To avoid any future confusion as to what this species name represents, we designate the largest and widest fragment as the lectotype (a4266A). The two fragments of lesser diameter cannot be assigned with any degree of certainty are numbered a4266B.

OCCURRENCE

The illustrated specimen (a4266) is from Waulsort (Assise IV) and is from the Dupont collection. DE KONINCK mentioned another occurrence in Assise III at Dréhance, but did not illustrate material. The occurrence is "très rare", presumably at both localities. The second specimen has not been located in the collections.

One unnumbered fragment is in the DE KONINCK collection, and a fairly recent locality label indicates "calcaire des Pauquys". In his discussion, DE KONINCK mentions a fragment having a diameter of 1.6 cm, which is far larger than this fossil. This specimen contributes no additional information and does not warrant further discussion or illustration.

*Entalis? acumen* DE KONINCK, 1883

Figure 3

\* 1883 *Entalis? acumen*, L.-G. DE KONINCK – DE KONINCK, p. 216, pl. 49, fig. 22.

INFORMAL SYNONYMY

Following the original description in 1883, the specific name, under *Dentalium* was listed in the catalogue of PILSBRY & SHARP (1898, p. 229). In a footnote, KITTL (1903, p. 696) returned the species to *Entalis*. As the last reported nomen-

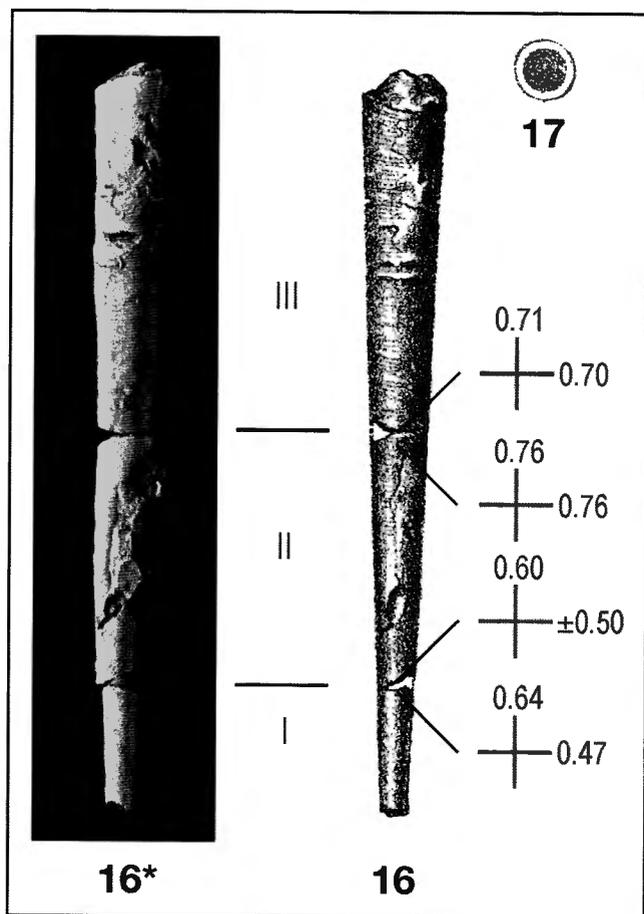


Fig. 2 — *Entalis walciodorensis* DE KONINCK, 1883. Specimens IRScNB a4266A (= III) and a4266B (= I + II) (16, 16\*). Reproduction of the illustration in DE KONINCK (1883) with its original numbering and photograph of the specimen. Same remark as in Pl. 1 concerning the fragments and the measurements of the axis. Natural size.

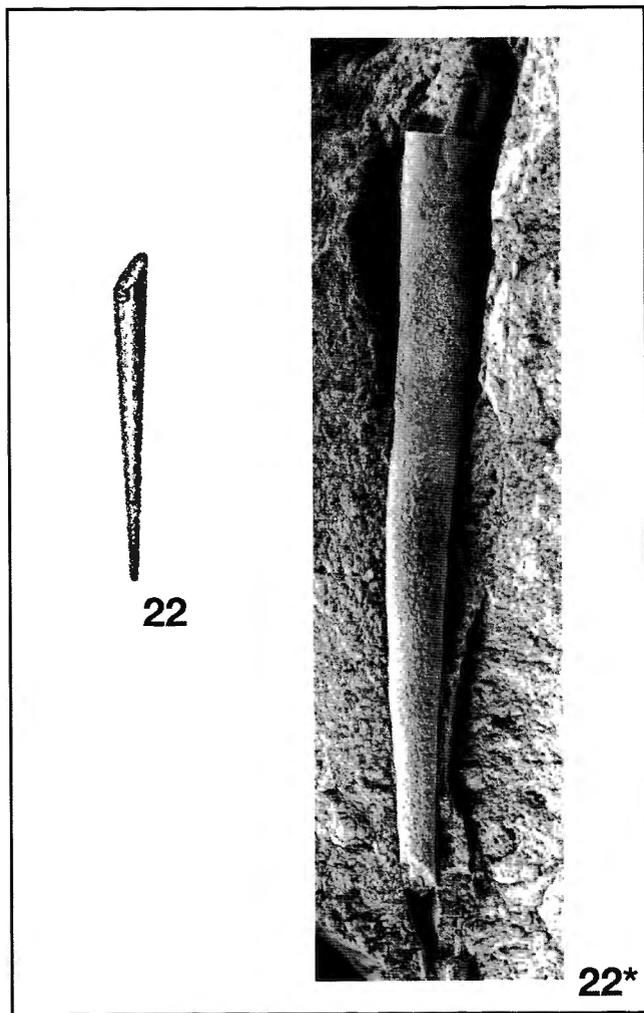


Fig. 3 — *Entalis? acumen* DE KONINCK, 1883. Specimen IRScNB a4267 (22, 22\*). Reproduction of the illustration in DE KONINCK (1883) with its original numbering and photograph of the specimen. Same remark as in Pl. 1 concerning the measurements of the axis. 22: natural size; 22\*:  $\times 3$ .

clatural action, under the heading of *D. (Antalis) acumen* (KONINCK), WANG (1987, p. 319, pl. 1, fig. 4) described and illustrated a specimen. The one exception to the statement that no identifications subsequent to 1883 have been checked against specimens is that of WANG mentioned above. The material on which this report was based actually is an orthoconic cephalopod (WANG, 1988).

#### MATERIAL

One specimen (a4267, de Ryckholt collection).

#### COMMENTS

There is a striking difference between the published drawing of DE KONINCK which shows the illustration of a free specimen and the type specimen (a4267) which is attached to matrix. Inasmuch as only one specimen is known, it becomes the holotype, rather than lectotype. The illustration indicates a straight specimen, preserving the apex and expanding at a uniform rate. In fact, it is broken at the apical area, but beyond the break the specimen extends straight and expands uniformly for about half the length. Near the midpoint, the specimen is bent slightly and

then seems to show almost no further expansion of the tube. Indeed, near the broken apertural end, the tube appears to narrow, though this is an optical illusion as a result of shadows from a depression in the matrix on the sides of the specimen, the shallow depression is accentuated by the lighting used for the photograph. No growth lines are evident. The specimen is mineralized, and is not a steinkern, as indicated by examination of the external impression in the apical area. Whether the specimen contained a cavity or was solid during life cannot be determined.

#### OCCURRENCE

The species is reported as "se trouve rarement dans le calcaire de Visé (assise VI)".

#### *Entalis cyrtoceratoides* DE KONINCK, 1883

##### Figure 4

\* 1883 *Entalis cyrtoceratoides*, L.-G. DE KONINCK — DE KONINCK, p. 216, pl. 49, figs. 13, 14, 15.

#### INFORMAL SYNONYMY

In their catalogue of Scaphopoda, PILSBRY & SHARP (1898, p. 230) transferred this species to *Dentalium*. It was mentioned under that genus by CRAMER (1914, p. 65).

#### MATERIAL

One specimen (a4268, de Ryckholt collection).

#### COMMENTS

The specimen illustrated by DE KONINCK (fig. 13) (a4268) is composed of seven fragments with both apical and apertural areas broken. These are attached to a cardboard and some of the fragments fit closely, but others do not. In our considered judgment, these fragments are best interpreted as forming three groups. The smallest diameter piece may show a slightly different rate of expansion than the higher pieces, but all other fragments seem to expand at a uniform rate. The piece closest to the apex is actually two fragments with a hairline crack to be seen. The most troubling aspect of this species is that the illustrated specimen is drawn as exhibiting a smooth curvature.

That cannot be reconciled with the fragments, all of which appear straight. The cross section at the broken apical end (fig. 14) is circular and the shell appears to be of uniform thickness around the circumference. The lowest fragment of the middle section shows uniformly spaced, fine rings or coarse growth lines, having an essentially circular course as indicated by the drawing (fig. 15). That this ornament is not distinctly inclined relative to the axis of the shell, reinforces the observation that it may have grown essentially straight rather than curved. These rings are less obvious on the two fragments which fit closely, but whether this is the result of less satisfactory preservation is not certain. This ornament cannot be seen on the two widest fragments above, but again the absence may be a consequence of incomplete silicification, rather than biologic change.

In view of the apparently composite nature of the "type", we designate the medial three fragments as the lectotype.

These pieces all fit closely and all show growth lines. We cannot be certain that the pieces above and below this central portion belong to the same organism nor are growth lines present to link them to even the same taxon. Viewed indepen-

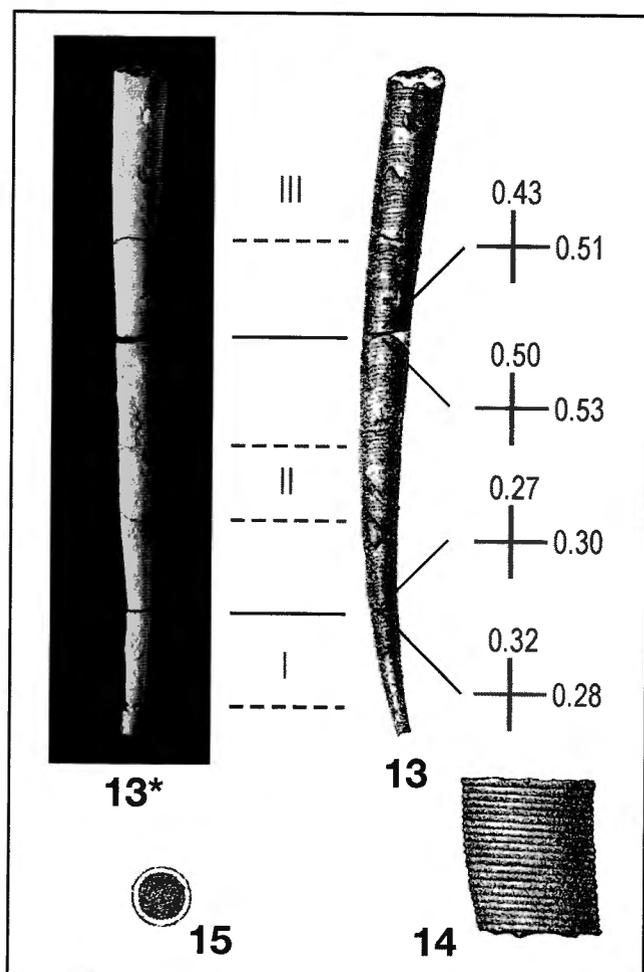


Fig. 4 — *Entalis cyrtoceratoides* DE KONINCK, 1883. Specimen IRScNB a4268. Reproduction of the illustrations in DE KONINCK (1883) with their original numbering and photograph (13\*) of the specimen. Same remark as in Pl. 1 concerning the fragments and the measurements of the axis. 13, 13\*, 15: natural size; 14 ( $\times 3$ ).

dently both sets of fragments are simply indeterminate tubular fossils and in our judgment they should not be designated as paralectotypes.

#### OCCURRENCE

The form is considered as "très rare" in assise VI of Visé.

#### *Entalis ingens* (DE KONINCK, 1843)

Plate 2

- \* 1843 *Dentalium ingens* — DE KONINCK, p. 317, pl. 22, fig. 2a-c.
- 1847 *Dentalium ingens* DE KONINCK — DE RYCKHOLT, p. 68.
- 1883 *Entalis ingens*, L.-G. DE KONINCK — DE KONINCK, p. 217, pl. 49, figs. 10, 11, 12, 18, 19.

#### INFORMAL SYNONYMY

This species was first described in 1843 by DE KONINCK as a *Dentalium*; the subsequent synonymy was listed by DE KONINCK (1883, p. 216). KITTL (1903, pp. 697-698, pl. 22, fig. 26) men-

tions this species and illustrates a specimen tentatively referred to it. Engeser (in manuscript) indicates that this name may be a subjective synonym of *Dentalium inaequale* DE RYCKHOLT, 1851. However, he also indicates that DE RYCKHOLT's name is preoccupied; we have not investigated or resolved that nomenclatural issue.

#### MATERIAL

Three specimens (a4269A, de Ryckholt collection; a4269B, Nyst collection; a4270, unnamed collection).

#### COMMENTS

This species is illustrated by three drawings in the 1843 work, with the illustration of an entire specimen (pl. 22, fig. 2a) indicated as being at natural size. If it is assumed that there is an error in the caption for half natural size, there is an approximate match to figure 10 of DE KONINCK, 1883. Despite differences in the two drawings, there is no evidence from investigations of the other earlier named DE KONINCK species to suggest that the 1843 specimens were lost and that other material was illustrated in its place for the later publication. The problem is further complicated in that more specimens were illustrated in 1883 than in 1843.

One approach is to begin with specimen a4269A of 1883 (fig. 10, 10\*, 12). The drawing shows a gently curved, reconstructed specimen of at least eight pieces. This may be evaluated in three separate sections. The aperture is broken, but a larger and smaller piece of this upper segment are interconnected and can be safely judged to be parts of one individual. The medial portion consists of five fragments with the two widest and the two narrowest again reasonably well interconnected. The lower edge of the central fragment matches the one directly below better than the upper edge matches the overlying piece of the tube. Still, it is a reasonable assumption that these five pieces probably are from one individual.

One of the 1843 drawings (fig. 2c) is of a cross-section showing the cross-section as oval rather than circular. An oval cross-section was again illustrated in 1883 (fig. 12), though it is shown as less compressed than the earlier one and it is at right angles to the earlier drawing. Deviation from a circular cross-section to one that is bilaterally symmetrical may be a biologic feature or it may be taphonomic, caused by compression of the tube after death. We cannot be certain, but suggest that in this instance it is more likely that this is a bilaterally symmetrical form rather than one which has been deformed.

Measurements of the cross-section taken at the apertural end are about 1.42 cm  $\times$  1.70 cm. At the lower end of this segment, they are 1.07 cm  $\times$  1.30 cm. The ratio of the two measurements at both ends is essentially the same. At the upper end of the medial section, these measurements are about 0.98 cm  $\times$  1.30 cm. The ratio is about 10% different, and matching a diameter of 1.35 cm below to a diameter of 1.30 cm above seems unlikely, though it could be the result of slight taphonomic distortion on a bilateral cross-section; if the maximum and minimum diameters of each set of measurement is added together, the difference is slight.

Growth lines having an oval outline and slightly inclined to the axis of growth occur near the base of the median segment and near the upper fragment of this group, as indicated in DE KONINCK's drawing. Likewise, as indicated in this drawing, similar growth lines occur near the lower part of the apertural segment. All the growth lines are exceedingly faint. We cannot be certain that the medial and apertural segments are from the same individual, but in our judgment they are similar enough to be conspecific.

The smallest apical piece (a4269B) does not connect to the fragment above (a4269A); it demonstrates features which mark it as an unquestioned scaphopod. The apical area of the 1843 drawing (fig. 2a) ends abruptly with a line at right angles to the axis of the tube and, accordingly does not match this fragment.

To continue a conservative course, we designate the most mature segment (the one with the widest diameter and closest to the aperture) of the specimen a4269A as the lectotype of this species. The medial segment is considered as a paralectotype; the apical part of DE KONINCK's figure 10 should be considered as a paralectotype (see also discussion in the systematic palaeontology section).

The drawing of DE KONINCK (fig. 11) is accurate in most features. The bioeroded apical area is straight and strongly inclined relative to the growth lines. Because of silicification, clear evidence of bioerosion on the flattened surface cannot be observed. However, at the base of the inclined apical surface, a short notch-like depression is present. The only difference from the drawing is that it suggests the growth lines as essentially circular, whereas they are oval, inclined about 15-20 degrees from the axis of the shell. The cross-section is oval with a maximum diameter of about 1.00 cm and a minimum diameter of 0.88 cm. The fragment bearing this modified apical area is short and it is difficult to determine the position of the notch relative to a more mature shell. It is our interpretation that the notch is probably lateral. Despite its small diameter, the shell of this fragment is relatively thick and the direction of bilateral symmetry on this piece shows no indication of being affected by post-mortem compression.

In regard to figures 18-19 (a4270), the indication is of two pieces with only a minor gap between them and uniform expansion. In fact, the lower part shows almost no expansion. In contrast, the higher piece expands at a fairly rapid rate and this seems to increase still more near the broken apertural region. No growth lines can be observed. The cross-section is circular and the specimen appears to be straight.

#### OCCURRENCE

The species was obtained by DE KONINCK from Visé (assise VI) and he also reported it "dans le calcaire de Namèche, près Namur (assise VI)". He further indicated two reports of its occurrence in Scotland, but we have not investigated these reports. No indication of relative abundance was given.

#### *Entalis ornata* (DE KONINCK, 1843)

Plate 3

- \* 1843 *Dentalium ornatum* – DE KONINCK, pp. 318-319, pl. 22, fig. 3a-c.
- 1883 *Entalis ornata*, L.-G. DE KONINCK – DE KONINCK, p. 218, pl. 49, figs. 4-9.

#### INFORMAL SYNONYMY

This was originally described as a species of *Dentalium* by DE KONINCK in 1843. Subsequent synonymy is given by DE KONINCK (1883, p. 218) and this included the subjective synonymy of *Dentalium dentalioideum* PHILLIPS in DE RYCKHOLT (1847, pp. 68-69). The year after the republication of the species, QUENSTEDT (1884, p. 817, pl. 217, figs. 130-131) returned it to *Dentalium* and reproduced one of the original figures. In the catalogue of PILSBRY & SHARP (1898, p. 232) it was listed under that generic name.

#### MATERIAL

Three specimens (a4271, de Ryckholt collection; a4272, de Koninck collection; a4273, de Ryckholt collection).

#### COMMENTS

In 1843, DE KONINCK illustrated this species with three drawings. Despite some difference in size, his figure 3a accords fairly well with the lower part of the 1883 figure 5 (a4272). His figure 3b, again matches reasonably well with the 1883 figure 7 (a4273); whereas the former two figures differed in length, these two differ in width. In 1843, both pieces were shown with a strongly compressed bilaterally symmetrical oval cross-section, a cross-section (fig. 9) from some unknown position on figure 5 is widely bilaterally symmetrical and is more accurate. Approximate dimensions of the axis in the widest measurable part: 2.05 cm and 2.10 cm. These dimensions are not measured at the extremity of the shell because it is irregularly broken).

Because there are two specimens in the original lot, a lectotype should be designated. Accordingly we designate the specimen figured as 3a in 1843 and the lower part of figure 5 in 1883 as the lectotype (a4272). The lectotype is slightly curved, expands at a low rate and bears closely spaced longitudinal lirae.

DE KONINCK's figure 5 consists of two isolated pieces with a portion missing in the middle. As restored, it is at least 20 cm long and this exceeds the length of almost all known living scaphopods, though far larger ones have been reported from the Palaeozoic. The upper piece bears closely spaced longitudinal lirae closely comparable to the lectotype. This ornament fades out abruptly toward the broken aperture. The ornament on both these pieces is more closely spaced than shown in DE KONINCK's enlargement (fig. 6), for the interstices are narrower than the lirae. Although this fragment might only be considered an assigned specimen we are confident that it is conspecific with the lectotype, and designate it as a paralectotype.

Another specimen (a4273), as illustrated in figure 7, is a shorter fragment than the lectotype whose greatest width is slightly larger than that of the lectotype. In contrast to the lectotype, this fossil shows no evidence of curvature, such as is depicted in figure 7. In addition, the longitudinal ornament is not as depicted by DE KONINCK in figure 8, but is irregularly bent into narrow segments, each segment ended at a growth line. The growth lines are closely spaced so that at first glance the ornament appears sinuous. The growth lines are close to circular, reinforcing the interpretation that this piece is essentially straight.

In light of these differences, we cannot assign specimen a4273 to the species typified by the lectotype. For the moment at least, it will remain without a name.

The third specimen illustrated in figure 4 (a4271) is from the de Ryckholt collection. It is a steinkern which lacks the apical portion and the apertural area is broken. The photograph clarifies a feature only hinted at in the drawing, namely an expansion of the tube below the broken aperture. We interpret this as a relatively abrupt thinning of shell thickness near the apertural rim. As another unexpected feature, the steinkern shows a narrow groove on the convex side of the specimen. Approximate dimensions of the axis of the widest measurable part: 1.33 cm, 1.44 cm. Because the specimen may not have been part of the type lot it does not have any nomenclatural status, but more importantly it cannot be compared to either of the two specimens discussed above. It too will remain unsigned.

## OCCURRENCE

The species is reported as rare in "le calcaire de Visé (assise VI)". Under DE RYCKHOLT's specific name it was also reported from the United Kingdom, but we have not investigated that assignment.

*Entalis? filosa* DE KONINCK, 1883

Figure 5

\* 1883 *Entalis? filosa*, L.-G. DE KONINCK – DE KONINCK, p. 219, pl. 49, figs. 23, 24.

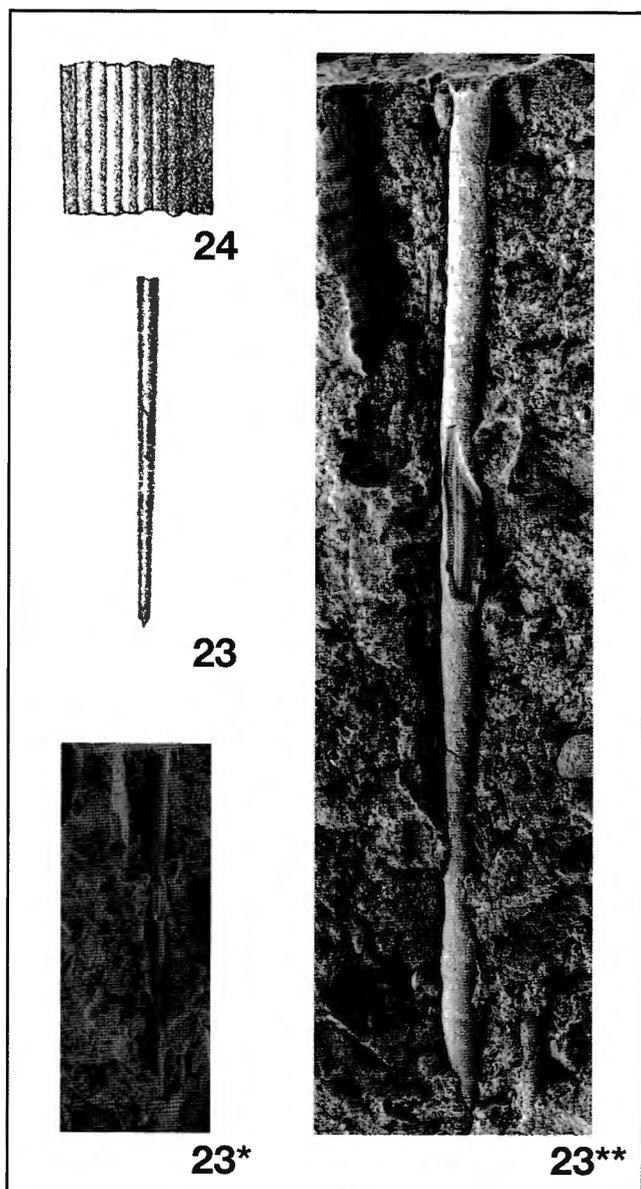


Fig. 5 — *Entalis? filosa* DE KONINCK, 1883. Specimen IRScNB a4274 (23, 23\*, 23\*\*, 24). Reproduction of the illustrations in DE KONINCK (1883) with their original numbering, and photograph of the specimen. Same remark as in Pl. 1 concerning the fragments and the measurements of the axis. 23, 23\* (natural size), 23\*\* ( $\times 3$ ), 24 (non specified).

## INFORMAL SYNONYMY

No significance should be assigned to the different spacing of the question mark between this species and that of *E? acumen*. There is however, one formal systematic action which cannot be ignored. At one point *Entalis* had been placed in synonymy of *Dentalium*. As a consequence, the specific name became a junior homonym of *D. filosa* BRODERIP & SOWERBY, 1830. The homonymy was corrected by a replacement name. Thus, the correct designation for this taxon is *Dentalium orthoceras* PILSBRY & SHARP, 1898. KITTL (1903, p. 696) mentions this species in a footnote but did not note the synonymy.

## MATERIAL

One specimen (a4274, old, unnamed collection).

## COMMENTS

This is a straight tube expanding at an exceedingly slow rate and it is attached to a block of matrix, though the 1883 drawing (fig. 23) suggests that it a free specimen.

The apical area of a4274 is concealed by matrix and the apertural area is broken away. In a supplementary drawing (fig. 24) DE KONINCK indicated closely spaced, rounded longitudinal ornament on the exterior, there is no evidence of such ornament or of growth lines. A small area near the midlength is excoriated and shows the shell thickness. Although this is a subjective observation, the shell seems relatively thick in relation to the small diameter.

## OCCURRENCE

The species is from the "calcaire de Visé (assise VI)", but there is no indication of its relative abundance.

## "Appendix" of DE KONINCK

Following the description of seven species, DE KONINCK (1883, p. 219) mentioned *Dentalium perarmatum* DE RYCKHOLT (1847, p. 67, pl. 2, figs. 39, 40) and repeated the original description. Figure 25 of DE KONINCK is of a specimen from the "calcaire de Visé (assise VI)". On the figure caption, number a4275 is listed as the "spécimen type" and the original label is with this specimen in the de Ryckholt collection (Fig. 6).

The type appears to be composed completely of solid silica. It is curved and near the apical area are several short spines extending from the outer surface. In the drawing they are more prominent and it is possible that some handling in the collections may have worn them slightly.

## Informal assignment based on restudy

With the exception of one additional specimen found in the collections of the Royal Belgian Institute of Natural Sciences and the small collection from Liège University this examination has been confined to the fossils illustrated by DE KONINCK in 1883. Most were indicated in his text with varying degrees of rarity, but in the absence of additional material there is no way to check this data. Several of the species are known from single individuals, several are known from material which may be a composite of more than one specimen; for those species which are illustrated by more than one individual, there is no reason to assume that the specimens are related. To simplify the efforts of future investigators we have designed lectotypes and paralect-

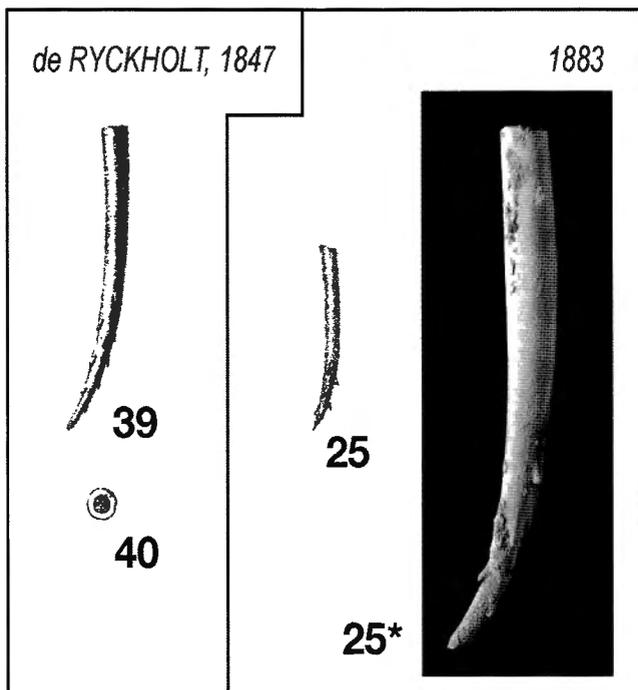


Fig. 6 — *Dentalium perarmatum* DE RYCKHOLT, 1847. Specimen IRScNB a4275. Specimen illustrated in DE RYCKHOLT (39, 40) and in DE KONINCK (25, 25\*). 39, 40 ( $\pm \times 1.5$ ), 25 (natural size), 25\* ( $\times 3$ ).

totypes where there is uncertainty as to what was the type specimen.

The eight species discussed above may be divided among five informal groups. We judge that most of the material is not correctly assigned to the Scaphopoda. In light of the limited number of fossils available, we therefore do not consider it appropriate to make formal reassignment of these taxa.

If in the future additional specimens are collected and a comprehensive study is made, a more appropriate biological placement of these “*Entalis*” and “*Dentalium*” species might then be made.

Incertae sedis and not a member of the Mollusca

*Dentalium perarmatum* — The type specimen of the DE RYCKHOLT species seems to be a solid structure, rather than solidification of a tube. As such, it appears so clearly to be a spine, probably of an echinoderm, that it may with question eventually be moved to the Echinodermata by a specialist is that phylum and class. The short spines near the apical area further reinforce this interpretation (Fig. 6).

Not a member of Scaphopoda, but possibly a “worm tube”

*Entalis? filosa* = *Dentalium orthoceras* — Because the specimen shows such a slight increase in diameter despite its relative long length and because it shows no curvature throughout its length we are satisfied that it could be related to the “worms”. So few features are shown that we suggest usage for the name be limited to the type specimen.

*Entalis? acumen* — The slight, but distinct bend in the tube, in contrast to logarithmic curvature should be sufficient to remove this species from the Scaphopoda. The portion of the tube

between the bend and the broken apertural area shows less of an increase in diameter with length than the apical portion.

There is no reason to assume that this species is a member of the Mollusca, and while it may be related to the “worms” it is a different taxon than the species mentioned above. We suggest that usage of the name be limited to the type specimen, for it is poorly preserved and there is little merit in assigning better material to this taxon.

Not a member of the Scaphopoda, but probably different taxa of “worm tubes”

*Entalis ingens* (part) — The specimen illustrated on figure 18 (a4270) is in two pieces. Both appear to be straight rather than curved. If they are correctly associated, there is a dramatic increase in the rate of the expansion near the aperture. Even if the two pieces are not associated, it is difficult to find a feature on either which would suggest that these are scaphopods. As they are not part of the type lot, there is no reason to use the specific name and there are not reassigned.

*Entalis walciodorensis* — Apart from some minor irregularities near the base of the largest fragment of the specimen, the growth lines appear circular, rather than oval, even at the prominent growth stoppage near the broken apertural area. Their course reinforces the view that the specimen is not curved. Without cutting the specimen it is impossible to determine whether septa are present, though we would guess that this is not a cephalopod. Within the Devonian, the genus *Coleolus* (a “worm tube”) occurs sporadically. That genus or closely related forms are also present in younger rocks, though seldom reported. We suggest that with further study this DE KONINCK species might be readily accommodated within the coleolids.

Because the three fragments of the type specimen seem to be an artificial assemblage, this further limits what is known of this species. We suggest that usage of this specific name be confined to the lectotype (a4266A).

*Entalis cyrtoceratoides* — If, as suggested, the various pieces are straight rather than curved, this would argue against assignment to the scaphopods. The rate of expansion seems somewhat less than one might expect in a specimen of this length, but that is a weak criterion for assignment. Because of the diameter at the widest end, the lowest piece may not actually be part of the same specimen. It seems to lack the ring-like growth lines present on the wider pieces above. These rings are similar to those seen in the unnamed specimens from the Devonian (Givetian) of southern Germany (YOCHELSON, 2002).

*Entalis ornata* (part) = *Dentalium ornatum* — The specimen of this species illustrated in figure 4 (a4271) is a steinkern (Plate 3) and cannot be compared to the other two specimens. We question whether it is even closely related. No septation is visible along the preserved length. Orthoconic cephalopods have a long body chamber, though this would seem to be of exceptional length if the specimen is interpreted as a nautiloid. Although the apertural area is broken, enough remains to show that the tube has a distinct increase in the diameter, after maintaining essentially a uniform rate of expansion along most of its length. The gradual inward thickening of a shell from a knife-edge thin apertural rim would produce a change in the rate of expansion preserved on a steinkern. In the scaphopods, the shell thickens so gradually backward from the aperture that it would not produce such an abrupt change in diameter. Another unusual feature of the specimen is a groove on one side

along most of the length of the specimen. Few steinkerns are known that can be attributed to scaphopods, but none of them show such a feature. A similar groove has been illustrated on the type specimen of *Dentalium illinoisensis* WORTHEN, 1883, a steinkern, from beds of approximately the same age in the United States.

Not a member of the Scaphopoda but probably a member of Mollusca

*Entalis ornata* (part) = *Dentalium ornatum* – The two pieces in the type lot and the specimen illustrated in figure 7 are disparate and as noted may well represent different taxa. When the type lot, the most scaphopod-like (a4272) of the two, is compared to DE KONINCK's illustrations of specimens which we interpret as more likely being scaphopods, there may be a slightly more rapid rate of expansion and a slightly larger degree of curvature, but these are highly subjective observations. The longitudinal lirae are comparable to that of some scaphopods, but their relatively rapid disappearance near the apertural area is not typical.

The second specimen (a4273) shows no obvious curvature and the ornament pattern is strange, quite unlike that of lirate scaphopods, and suggests that this might be an orthoconic cephalopod. It is not generally recognized that a few "orthocone" nautiloids are slightly curved. When the apertural and apical areas are broken away on such specimens, they mimic scaphopods, especially if the fragment is part of the body chamber. In the absence of longitudinally-cut sections to demonstrate whether segmentation is present, neither of these two can be assigned to the Cephalopoda, but we suggest that these may well belong in that class as two distinct genera. In his discussion DE KONINCK (1883, p. 218) noted similarity to species which had been assigned to *Cyrtoceras*. Indeed, in the "rapports et différences" DE KONINCK writes that: 1 – he does not agree with DE RYCKHOLT and MCCOY who consider that *Entalis ornata* is synonym of *Orthoceras dentaloideum* PHILLIPS. 2 – *Orthoceras dentaloideum* PHILLIPS represents a species of *Cyrtoceras* close to *C. gesneri* MARTIN, rather than a species of *Entalis*. Thus the external homeomorphy between Palaeozoic scaphopods and curved "orthocones" was recognized more than a century and a half ago, but was ignored in the interval (YOCHELSON & HOLLAND, 2004).

The two specimens showing prominent ornament may well be molluscs. Regardless of whether any or all of these three are accepted as possible members of the Cephalopoda, none of the specimens show features by which they could be readily placed in the Scaphopoda.

#### Scaphopoda and probably Scaphopoda

*Entalis prisca* (part) – In the photographs of the specimen illustrated by figures 1-3, (a4263) the closely spaced, simple, uniformly growth lines may be seen; as noted, the apparent central ridge shown in figure 2 may only be an example of the artist attempting to convey the convex curvature as the growth lines pass the "dorsum" of the shell. The course of the growth lines, combined with the slight uniform logarithmic curvature and the uniform expansion are sufficient to demonstrate that this is almost certainly a scaphopod.

*Entalis prisca* (part) – Interpretation of two specimens in this taxon, as Scaphopoda is more speculative than those mentioned above. If the broken specimen illustrated by DE KONINCK (1883) as figure 21 (a4265) was a curved "orthoceroid" cephalopod

one might expect to observe septa. On the other hand the degree of curvature and rate of expansion accord with that of the largest specimens.

The specimen illustrated in figure 20 (a4264) shows no distinguishing features apart from a slight curvature. The strongest reason, and it is admittedly weak, to consider the two together is the surface appearance. The process of silicification is complex and not understood in detail. The texture of the replacement varies with the group of fossils, so that, for example, otherwise unidentifiable fragments of pelecypods may be differentiated from fragments of brachiopods. The difference may be a reflection of original mineralogy, the features of the organic matrix of the shell, or both. At the same time, subtle difference in seemingly similar beds influence silicification such that in some instances, formations may be identified by the character of the surface of the fossil rather than its taxonomic position. To add to this, regional replacement of fossils by silica and surface solidification may produce different textures.

The only reason to suggest that these specimens are related to Scaphopoda is the similar surface texture; the only reason to suggest that they may be molluscan rather than "worms" is based on even weaker speculation.

*Entalis ingens* (part) – As discussed above figure 10 of DE KONINCK (1883) (a4269A) may be based on a reconstruction of two individuals. Thus a lectotype and paralectotype have been designated. Their preservation is not particularly good.

*Entalis ingens* (part) – The presence of the bioeroded apical area, and the short slit demonstrate conclusively that the original of figure 11 (a4269B) is indeed a scaphopod! Among the publications on Palaeozoic Scaphopoda, this Viséan specimen is the oldest unquestioned fossil representative of the class.

This specimen could correspond to the figure 2b of 1843.

## Systematic palaeontology

### Discussion

There is general agreement from what is known of the fossil record, that the Scaphopoda first appeared later than representatives of the other shell-bearing extant classes. There is no agreement, however, on how much "later". Thus, POJETA & RUNNEGAR (1979) have considered a Middle Ordovician tubular fossil to be a scaphopod. In contrast, YOCHELSON (2004) has argued that there are no Ordovician specimens which are certainly scaphopods, there have been no reports from the Silurian, and the most likely of the Devonian reports is, at best, uncertain. The oldest authentic members of the Scaphopoda are several illustrated by DE KONINCK in his 1883 work. By authentic, we mean specimens which show clear evidence of an open, unbroken, bioeroded apical area. Other specimens, which lack the apex but show similar growth, may be presumed to be scaphopods and this judgment is strengthened when the mature specimens possess a relatively thick shell. These few comments deserve amplification, given below.

### Morphology and morphometrics

The overall simplicity of the scaphopod shell presents serious difficulties in presenting accurate descriptions of taxa. One morphometric feature is the rate of expansion of the tube-like shell. This may be determined by measuring the diameter at two points and the distance between them; the data might be

expressed in the form of a ratio. It is based on the assumption that once the earliest growth stages are passed, the shell expands at a uniform rate. Little data of this sort exists as yet. Informal examination of living scaphopods which expand "rapidly" and those which expand "slowly" suggests there is relatively little interspecific variation in this feature, though it might be useful for characterizing genera.

The logarithmic curvature of the shell is so small that virtually all species are "hardly curved" or "slightly curved". Traditional methods to measure the angle of tangency of a logarithmic spiral require that one begins at the point of origin of the spiral. One can measure this angle in gastropod shells by beginning at the protoconch, but the earliest portion of a scaphopod shell is lost once modification of the apical area begins. Without the point of origin, measuring the angle of tangency is a formidable problem. Just as the rate of expansion of the shell appears to be constant, the angle of tangency of the logarithmic spiral appears to remain constant. Because the angle is so low, the longer the shell, the less obvious to the eye is the curvature.

There is one less complication in the geometry of the scaphopod shell compared to that of the gastropod. Whereas typically gastropods also grow following a logarithmic pattern, they are again, typically, coiled in a three-dimensional spiral. As far as known, the scaphopod shell is limited to two dimensions and in that sense is symmetrical. Whether the cross-section is circular or elliptical is a difficult issue. Most shells appear to have a circular cross-section. It is possible that some are oval, and therefore bilaterally symmetrical. Such bilateral symmetry is slight, at best, even when seen in relatively large shells. Giant specimens of *Prodentulum raymondi* YOUNG, 1942 from the Upper Carboniferous of Texas (USA), suggest that the cross-section of this species may not be circular. As a further complication, post-mortem modification of the cross-section from slight compaction of the matrix cannot be ruled out.

#### *Orientation and life habit*

The terms dorsal and ventral are difficult to apply to many of the groups of molluscs. When a specimen is seen in lateral view, one edge is concave and one is convex. From what is known of the life habit of living scaphopods, the concave side is upward, which most of the length of the shell buried in the sediment. If the concave side is "dorsal", one can then refer to the right lateral side and the left lateral side. As with so many features of a seemingly simple shell, such terminology is more difficult to apply than one might assume, for curvature of a fragment of a relatively mature shell may be imperceptible.

A more subtle issue is whether the symmetry of the shell is "radial", ignoring the effect of logarithmic curvature, or whether it is bilaterally symmetrical. Most specimens at most growth stages appear to be "radial". If bilateral symmetry is present among Palaeozoic species, it is slight. On the other hand, some of the measurements taken of fragments in the de Koninck collection suggest a bilateral cross-section. Whether taphonomic processes could compress a shell slightly is not known. In the present state of lack of information, one can only mention this as additional feature to be considered by future investigators.

Several collections of silicified Permian molluscs have yielded abundant specimens of Scaphopoda. It may be a fair generalization that during life specimens were gregarious, as indeed are some Recent species. One cannot obtain from the DE KONINCK types, which are more than a century old, any data bearing on the issue of abundance. The small collection from

Liège does include a number of specimens from Tournai, and provides weak support for this generalization. In the Permian collections cited above, another point is that bellerophonacean gastropods are common in the beds which have yielded scaphopods. It would be interesting to dissolve some Tournaisian limestones in the laboratory to see if this association is present in the Lower Carboniferous.

If there is any overall aspect to the notion of gregariousness, it is that if a single curved tubular fossil is recovered from an outcrop or a silicified collection, caution is dictated, rather than automatically assuming it is a scaphopod. This caution is of limited utility since many "worms" have a gregarious habitat.

#### *Growth lines*

Growth lines are not unique to the Mollusca, and a curved shell showing such episodic growth need not necessarily be a mollusc. Extremely closely spaced, relatively fine growth lines, consistently inclined in the same direction are a feature seen on well-preserved scaphopod shell. In gastropods, it is not evident that the inclination of the aperture – that is in effect the latest growth line – bears any obvious relationship to the degree of logarithmic coiling of the shell. One may measure the angle of the growth lines to the axis of the shell, making the simplifying assumption that it is vertical, rather than curved logarithmically, but there is no reason to assume that this angle bears any direct relationship to the curvature. Indeed, some scaphopods which show relatively strong curvature, have an apertural rim that is essentially at right angles to the axis of the shell, whereas others in which the logarithmic curvature is less, have the aperture distinctly inclined. As with both the expansion of the shell and the angle of curvature, the amount of interspecific variation in the inclination of the growth lines appears to be quite limited.

All this may be something of an *apologia* for providing only a qualitative description of species. At best such writing is of limited use as delineation of species becomes more precise. Until someone sufficiently skilled to model scaphopod shells on a computer and thereby providing the detailed information to compare one specimen with another, the definition of species and the distinction between species will contain a degree of uncertainty. If any prediction or guess is needed as a reason to test this speculation, it is that such effort would probably reduce the number of named fossil species of scaphopods and might also place a few Recent specific names into synonymy.

#### *Preservation*

Many Palaeozoic scaphopods, and all of those which are the subject of this work, are silicified. The process of silicification provides a tremendous advantage to the palaeontologist in that specimens are released from limestone and might never be obtained lose by breaking the rock. At the same time, there are some disadvantages with this form of preservation, as there are with all forms of preservation of fossils. Thus f.i. the quality of silicification varies, primarily between localities, so that exceptionally well-preserved specimens may be recovered from one locality, whereas another locality will yield only coarsely-preserved material lacking fine detail, but otherwise probably the same species.

The quality and degree of silicification varies among taxonomic groups; fortunately, molluscs seem to be particularly apt candidates for this kind of replacement. Not all of a specimen need be silicified, for unbroken but incomplete specimens are known. Perhaps the most complex process is that of replacement throughout the thickness of the shell. In some examples, the original shell fabric may be reproduced, and conversely not

all shell layers need be replaced by silica. This phenomenon has been documented among Permian silicified gastropods (YOCHELSON, 1956). In extreme cases only the inner surface of the shell may be silicified, resulting in fragile specimens showing no exterior detail. In other cases, surplus silica may aggregate on the exterior and mask details, or provide spurious ones. It is also possible to have extra silica deposited within the shell.

Silicified specimens may be naturally etched free from limestone or they may be dissolved out by acid under laboratory conditions. The texture of the silicification often is different for each condition. The specimens in the de Koninck collection were probably weathered free on the outcrop and picked up on the surface. This might account for the incorrect assemblage of fragments documented for some of the species named by de Koninck. The small collection from Liège (ULg) reinforces the interpretation that specimens were naturally weathered out. In particular, several retain an inner filling (steinkern) of limestone.

#### Shell thickness

In some localities in the Upper Carboniferous (Pennsylvanian) of the southwestern USA where specimens are preserved in shale, body chambers of orthoconic cephalopods are compressed, and associated scaphopods are not. Laboratory solution of Permian scaphopod-rich limestones from a variety of localities has not yielded any obviously compressed scaphopods. Quite surprisingly, the small collection from Liège University includes two relatively small specimens, which seem to have a relatively thicker shell than cephalopods from the same general area, but the specimens are crushed along part of the length. This is yet another complication in attempting to determine whether incomplete tubular specimens are correctly assigned to the Scaphopoda. With all the above considerations in mind, we are satisfied that the specimens assigned below are authentic members of the class.

Even though emphasis has been placed on shell thickness, in that a relatively thick shell is one criterion to distinguish a fragment of a scaphopod shell from a broken slightly curved orthoconic cephalopod, it is a generalization which must be used with caution. As mentioned above a result of differential silicification there may be some fossil scaphopods which are thin. These show no evidence of growth lines. The phenomenon of silicification is poorly understood, but there may be some relationship between organic matter and deposition of silica. One may speculate that the thin shell is silicified only on the inner surface of a recently dead animal with fragments of the mantle clinging to the shell, but this is simply a wild guess.

Two other aspects of shell thickness deserve comment. The first concerns inward thickening of the shell; one need only observe a bioeroded apical area to see a shell that is relatively thick when compared to about the same growth stage as a gastropod. The growing edge of the aperture in both gastropods and scaphopods is paper thin so there may be some merit in determining the relative distance to the thickest part of the shell, that is: does it thicken gradually or abruptly? To obtain data requires the cutting of a number of specimens, and it is not likely that enough collections of abundant fossil scaphopods are available to even consider this approach.

A second aspect of shell thickness more readily studied, at least perhaps in theory, is whether the shell is of uniform thickness around the circumference or is thickened at one quadrant. One may speculate that forms which have the aperture at right angles to the axis of curvature, and thus have essentially straight growth lines would have uniform shell

thickness. Forms in which the aperture is inclined, have the portion of the aperture on the convex side extended forward. For an organism digging into sediment, strengthening this part of the shell might be advantageous. Cutting cross-sections might provide information on this morphologic detail. Once again, the problem of taphonomic effects must be considered. For example, the process of silicification might result in additional replacement silica being deposited in one part of the circumference, but not the other.

#### Phylum Mollusca

Class Scaphopoda BRONN, 1862

Order Dentalida DA COSTA, 1776

Family unassigned

Genus *Plagioglypta* PILSBRY & SHARP, 1898

Type species: *Dentalium undulatum* GOLDFUSS, 1841

In the earlier literature most fossil Scaphopoda were referred to *Dentalium*. This Linnean name appeared in the literature long before 1758 and for most of a century or more was conventionally used for most Palaeozoic species. Almost all Palaeozoic genera which have been transferred out of that genus are placed in *Plagioglypta*. To the best of our knowledge the only other generic name used for Palaeozoic scaphopods is *Prodentalium* YOUNG, 1942. One feature of that genus is the presence of fine closely spaced longitudinal lirae during early growth stages. Despite the potential theoretical problems cited above in regard to silicification, we are convinced that none of the Lower Carboniferous scaphopods examined bear any ornamentation apart from growth lines. YOUNG's generic name is therefore inappropriate.

The 1897-1898 catalogue of Scaphopoda by PILSBRY & SHARP is an impressive publication. Both authors were zoologists-cataloguers and naturally were concerned primarily with Recent taxa. In an effort to better understand *Dentalium*, they recognized a number of subgenera including the new subgenus *Plagioglypta* PILSBRY & SHARP (1898, p. xxxi). Although it is credited in that monograph to PILSBRY and another publication is cited, this 1898 work has priority.

The type species of *Plagioglypta* is Triassic and it is most unlikely that either author examined the original material of this MÜNSTER IN GOLDFUSS species. Preliminary study of several topotype specimens suggests that there is considerable individual variation and that, accordingly, the type species might actually be a "worm tube" (A. Nützel, unpublished). Until this matter is clarified, the generic name is used below in a questionable sense.

*Entalis*, the generic name adopted by DE KONINCK in his 1883 study and to which he transferred his 1843 specimens and species of *Dentalium* has an incredibly complex nomenclatural history. It has been replaced and the replacement name is employed only with Recent species. To recount the history of this name would add obscure references not germane to this study (for details, see STEINER & KABAT, 2001).

*Plagioglypta? prisca* (MÜNSTER in GOLDFUSS, 1841)

Figures 7-9

- 1841 *Dentalium priscum* MÜNSTER – GOLDFUSS, p. 2, pl. 166, fig. 3.  
 1843 *Dentalium priscum* – DE KONINCK, pp. 316-317, pl. 22, fig. 1.  
 1883 *Entalis prisca*, G. zu MÜNSTER – DE KONINCK, p. 215, pl. 49, figs. 1, 2, 3, 20 (?), 21 (?), unnumbered text-fig.

*Description*

Very slightly curved, uniformly expanding shells, probably with a circular cross-section, and with closely spaced growth lines inclined about 15 degrees from the axis of the shell.

*Discussion*

*Dentalium priscum* was illustrated by two specimens in the publication of GOLDFUSS (1841) on plate 166 as figures 3 and a, b, c. The Goldfuss collection is kept in the Institut für Paläontologie, Rheinische Friedrich-Wilhelms-Universität, Bonn, Germany. It does not include this material. The Münster collection is housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany. At our request, the curator, Dr. W. Werner has kindly examined the type lot. Two specimens and two drawings from plate 166 were glued to a plate and assigned recently number BSPG AS VII 1437. The accompanying legend repeats the GOLDFUSS locality data of "Tournay". The specimens are silicified and are too fragile to be removed from the plate or to be sent to another institution.

The specimen to the right may be matched with GOLDFUSS figure 3. This individual was later assigned number BSPG AS VII 1720. It is here designated as the lectotype. Growth lines are closely spaced and are inclined at about 15 degrees from the axis of the shell. Because of the mounting on the plate, the curvature of the lectotype cannot be determined but, judging from the GOLDFUSS illustration, it is very slight.

The specimen to the left may be matched with figure 3a; the GOLDFUSS illustration shows both the broken apertural area and a hole in the shell. It is here designated as the paralectotype. Figure 3c of GOLDFUSS is a cross-section, drawn as slightly oval and connected by a dotted line to the base of 3a. It, in turn, is connected by a dotted line to a fragment, indicated as 3b, showing growth lines; both 3b and 3c are enlarged views. Because of the dotted lines, presumably these views are from the largest segment of the specimen to the left. According to Dr. Werner, the apertural portion of this specimen was broken and reglued at an angle, as shown in the photograph. Thus one cannot check whether the oval cross-section is accurate, though in view of the rendering of the hole and the broken apical area delineated, one may place some confidence in that illustration. As recounted earlier, the Münster species is the most widely cited Lower Carboniferous species in subsequent literature, yet to the best of our knowledge this is the first time that the type lot has been illustrated photographically.

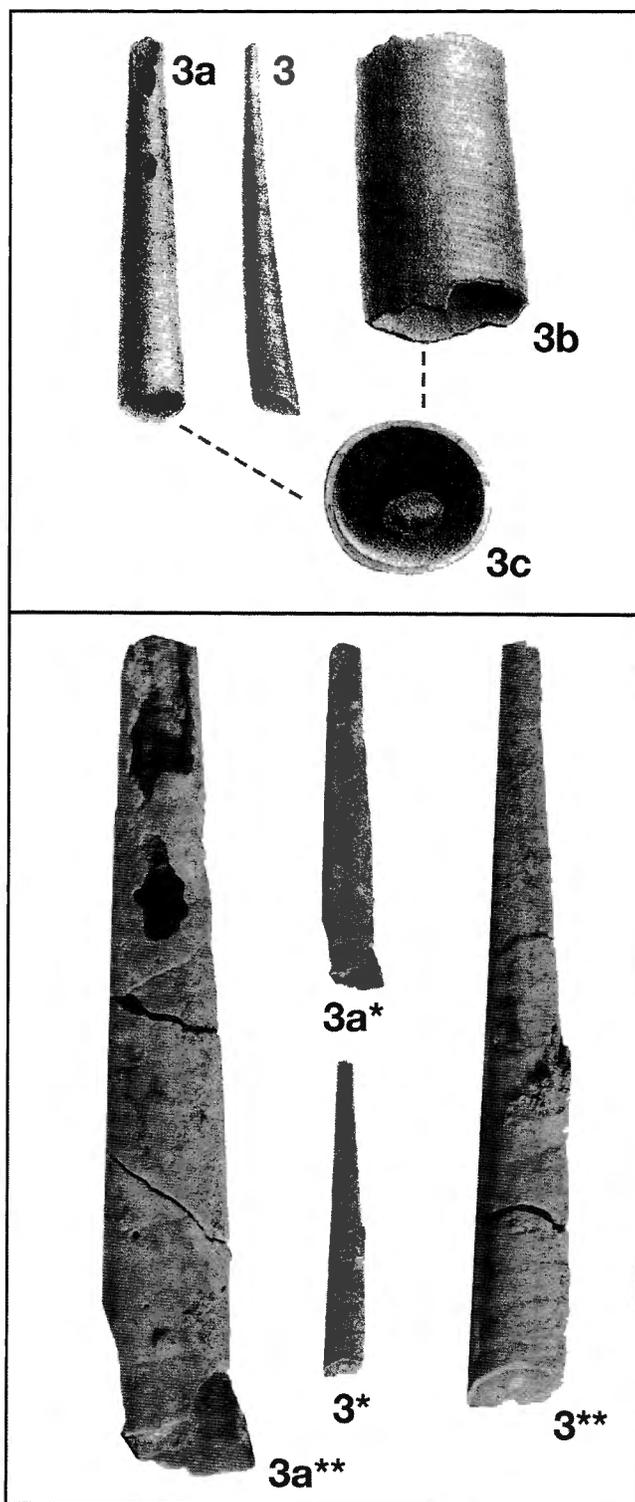


Fig. 7 — *Plagioglypta? prisca* (MÜNSTER in GOLDFUSS, 1841). Specimens BSPG AS VII 1437 (Munich). Reproduction of the illustrations in GOLDFUSS (1841) with their original numbering, and photographs of the specimens. 3, 3a [natural size according to GOLDFUSS], 3b, 3c (non specified), 3\*, 3a\* (natural size), 3\*\*, 3a\*\* ( $\pm \times 2.4$ ).

Figures 20 and 21 of DE KONINCK, as mentioned, provide limited information bearing on whether they are correctly assigned to the scaphopods, but probably they

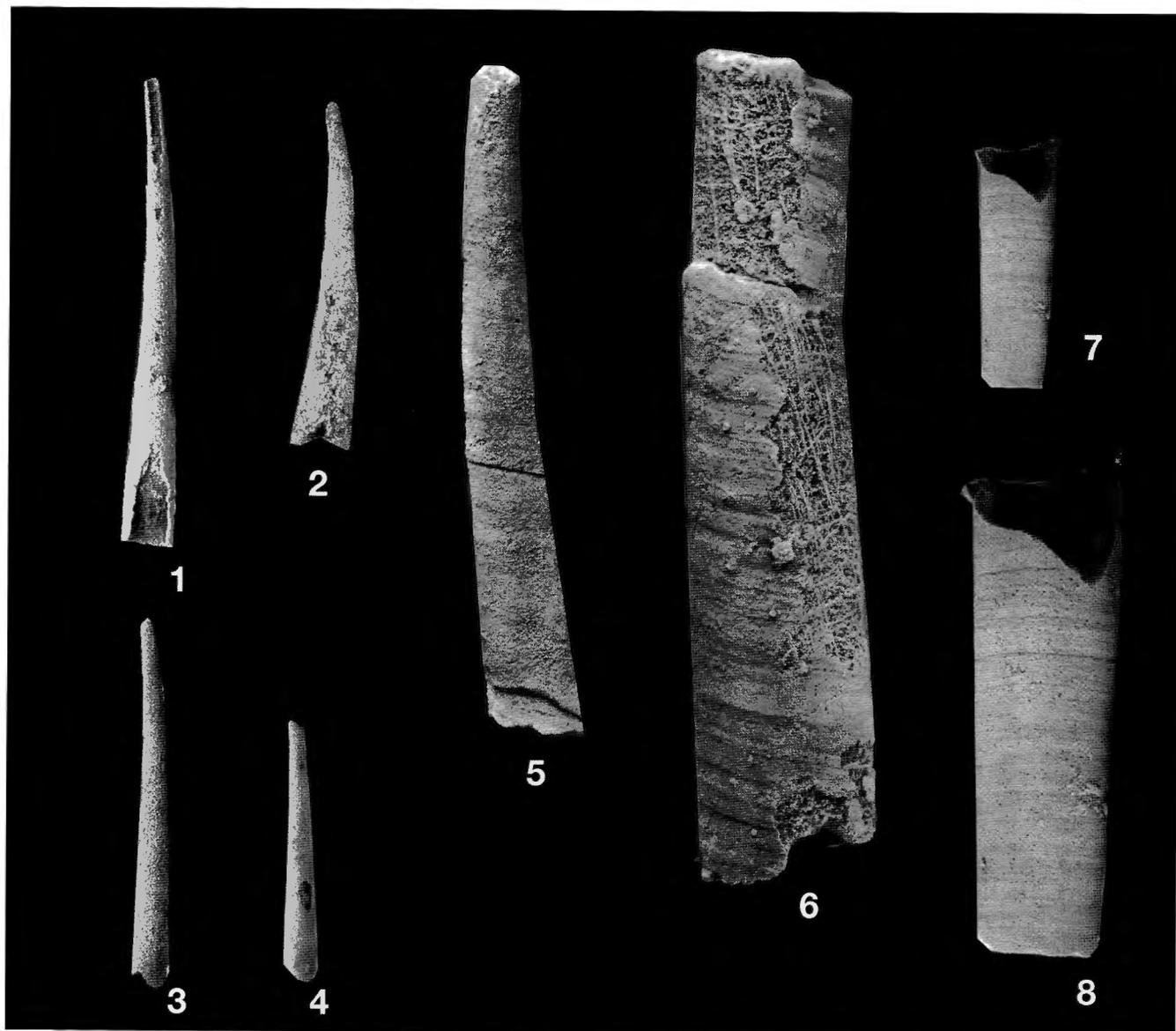


Fig. 8 — *Plagioglypta? prisca* (MÜNSTER in GOLDFUSS, 1841). 1-4. Four juvenile shells showing the slight degree of curvature (1, 2: right lateral view; 3-4: left lateral view). 5. Right lateral view of a moderate sized specimen in which the log curvature is clearly seen. 6. Right lateral view of an incomplete specimen showing inclination of growth lines and several phenomena of the silicification process. 7-8. Views of a specimen showing closely spaced growth lines (orientation is uncertain, but this may be the concave side of the shell). 1. ULg 6/06/05-1 (Liège University), 2. ULg 6/06/05-2, 3. ULg 6/06/05-3, 4. ULg 6/06/05-4, 5. ULg 6/06/05-5, 6. ULg 6/06/05-6, 7-8. ULg 6/06/05-7. All  $\times 2$  except 7 ( $\times 1$ ).

belong to this species. The originals of figures 1 and 2 can be matched well with the growth lines and rate of expansion of the lectotype. DE KONINCK specimens were also from Tournai and therefore are topotypes.

The species concept is further reinforced by additional specimens from Tournai in a small collection from Liège University (ULg). All of the material is silicified. Several small specimens (ULg 6/06/05-1, 2, 3, 4) are present and give an indication of how slight is the logarithmic curvature of this species (Figs. 8.1-8.4).

Another slightly larger specimen further reinforces the low degree of curvature (ULg 6/06/05-5, Fig. 8.5). A still larger specimen (ULg 6/06/05-6, Fig. 8.6) shows several interesting features of the silicification process. The

extremely close spacing of growth lines is indicated by another fragment (ULg 6/06/05-7, Figs. 8.7-8.8). Comparing the course of the growth lines in these three figures, from straight to oblique emphasize the need for precise orientation of a lateral view.

Perhaps the most interesting specimen is the largest (ULg 6/06/05-8, Fig. 9). From examination of the diameter of the smaller specimens and on the basis of this largest piece, it is probable that during life this individual was in excess of 20 cm in length. The fossil was originally in three pieces, allowing examination of the circumference at several growth intervals. The apertural margin seems to be unbroken and at a relatively short distance within the shell, it is greatly thickened.

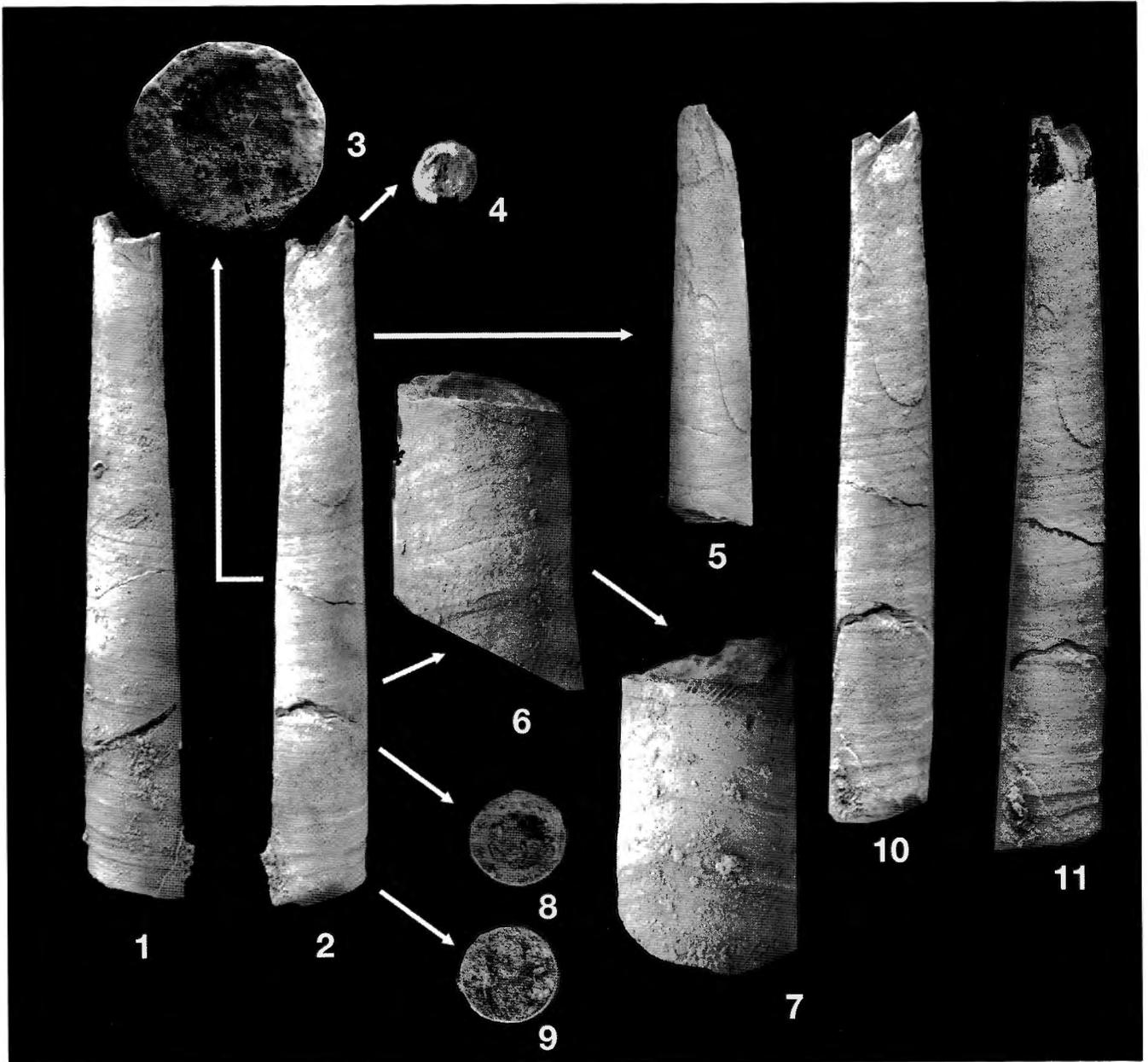


Fig. 9 — *Plagioglypta? prisca* (GOLDFUSS, 1841). Specimen ULg 6/06/05-8. 1. Left lateral view. 2. Right lateral view. 3. Shell thickness at approximately the middle of the restored specimen. 4. Cross section at broken apical end of the shell. 5. Right lateral view. 6. Right lateral view. 7. Left lateral view. 8. Cross section at first "break" above the aperture showing the apical thickening of shell. 9. Apertural view showing thin margin of growing shell. 10-11. Convex side of shell (not perfectly aligned). All  $\times 1$  except 3 ( $\times 4$ ), 6, 7 ( $\times 2$ ).

Perhaps most interesting is the cross-section near the middle of the specimen. It suggests, but does not conclusively demonstrate, a slightly greater thickening of the shell on the convex side.

This specimen also emphasizes the caution needed in measuring the angle of growth lines, particularly if one measures from a photograph. Two lateral views show their true course, whereas two other views of the presumed concave and convex sides are not perfectly oriented and thus suggest less inclination of the growth lines than is observed on the specimen.

#### *Plagioglypta? ingens* (DE KONINCK, 1843)

- \* 1843 *Dentalium ingens* — DE KONINCK, p. 317, pl. 22, fig. 2a-c.
- 1847 *Dentalium ingens* DE KONINCK — DE RYCKHOLT, p. 68.
- 1883 *Entalis ingens*, L.-G. DE KONINCK — DE KONINCK, p. 217, pl. 49, figs. 10, 11, 12, non 18, non 19.

#### Description

Uniformly expanding, slightly slender and slightly curved shells, having a broadly oval, bilaterally symmetrical, cross-section.

### Discussion

In 1843, DE KONINCK did not designate a type. We presume, though cannot be totally certain, that figure 10 of 1883 may be based on the same specimen as figure 2 of 1843. The specimen is in several pieces with gaps between them. To avoid any future misunderstanding the most mature fragment, that is the one with the widest diameter and closest to the aperture is here designated as the lectotype. Most of the remainder of this specimen as reconstructed in figure 10 are designated as paralectotypes, even though several pieces seem to fit well.

The most interesting specimen which DE KONINCK illustrated in 1883 is figure 11. It shows the apical area and it has the attribute of a bioeroded surface; a short slit might be present, but it could have been modified by incomplete silicification. This is irrefutable evidence that the specimen is a member of the Scaphopoda. Even though much of the length of the specimen is broken away, some growth lines may be seen, and these form one of the features for concluding that other specimens in the DE KONINCK collection are correctly assigned to the class.

The apical part of figure 10 suggests that in DE KONINCK's drawing this piece was part of the larger specimen. There is a gap between it and the next larger piece. Despite this uncertainty, we conclude that it also should be a paralectotype. Part of this decision is based on the importance of this piece as conclusively the oldest known representative of the class.

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- The species has been transferred to *Plagioglypta* by WATERHOUSE (1980, pp. 198-199).
- Plagioglypta? ingens* seems to differ from *P? prisca* in being slightly more curved, and perhaps having a lower rate of expansion. The angle of the growth lines in both species seems to be similar. DE KONINCK illustrated an oval cross-section in both 1843 and 1883 and measurements of the type lot confirm this difference between the two species. Because so little material from the Viséen is available, we suggest that this specific name be limited to use with the type lot, until it can be better characterized.

### Acknowledgments

ELY thanks the National Geographic Society for a grant which allowed him to visit museums in Germany and Belgium to examine the collections of Palaeozoic scaphopods. T. Engeser (Institut fuer Palaeontologie, FU Berlin) kindly supplied his unpublished bibliography of Scaphopoda and this has been invaluable for searching the literature and for constructing the synonyms given. E. Poty gave us access to the old collections of the Department of Palaeontology of Liège University. W. Werner and G. Janssen (Munich) supplied respectively comments concerning type material of *Dentalium priscum* MÜNSTER in GOLDFUSS and photographs of this species. M. Amler (Marburg) provided useful data. C. MacClintock (Yale Peabody Museum, New Haven, Connecticut, USA) lent specimens under his care as did P. Wagner (Field Museum of Natural History, Chicago, USA). Photographs of Liège specimens were made by J. Steiner (Imaging Laboratory, National Museum of Natural History, Washington D.C.) and W. Miseur (Brussels) printed the photographs of DE KONINCK's specimens.

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## APPENDIX

## Comments on American Mississippian (Lower Carboniferous) scaphopod species

by Ellis L. YOCHELSON

It seemed appropriate to examine collections of presumed scaphopods from North America of broadly the same age as those from Belgium. As with the DE KONINCK investigation, this is an informal inquiry and no formal systematic decisions have been made. Several small lots of Mississippian fossils are in the Palaeozoic Scaphopoda collection of the National Museum of Natural History, Washington, DC. Though the kindness of Peter Wagner, Field Museum of Natural History, Chicago, I have also had the opportunity to examine the Mississippian specimens under his charge. Likewise, C. MacClintock, Yale Peabody Museum, New Haven, lent the three specimens under this charge. When combined with the holdings of the National Museum of Natural History, one obvious conclusion is that Mississippian fossils which earlier investigators assumed to be scaphopods are quite rare.

Ms. B. Husani searched the data base of the American Museum of Natural History, but found no specimens in their collections.

A species catalogue of several classes North American Late Palaeozoic Mollusca (YOCHELSON & SAUNDERS, 1967) lists twenty named species of scaphopods, plus the published reports of unnamed species. The necessary literature references are given in that work and need not be repeated here. No special attempt has been to search the subsequent literature, but as far as I know, subsequent to this work only one Permian form has been named from North America.

Of these twenty species, eight are certainly or probably Mississippian in age. Among them, three are best allowed to lapse into obscurity. Thus, *Dentalium missouriensis* from Missouri was named and described, but never illustrated. The type material was lost in a fire at the University of Missouri. Only one other author has mentioned this specific name and that was more than 11 decades ago. Likewise *Dentalium grandvillensis* was not illustrated. The only subsequent usage, more than a century ago was to transfer the species to *Plagioglypta*. The type material was lost in a fire at Denison University. Finally, *Dentalium? barquense* from Michigan, was also described, but never illustrated. The only other reference is one several years later by the author of the species who questioned whether it was a mollusc; the type may be at the University of Michigan.

***Dentalium grandaevum* WINCHELL, 1863**

Collection in the Museum of Paleontology, Natural History Museum, University of Michigan, include three specimens labeled as the type lot of *Dentalium grandaevum*. The label bears two numbers 2154 and 1447. They are from Burlington, Iowa, and a later addition to the label is "*Chonopectus* sandstone". Two specimens are about four cm long and appear nearly complete; a fragment is about one and one-half cm long. All three specimens are straight with no indication of curvature. All expand at a low rate. For the longest and narrowest specimen, the early growth stages near the broken apex expand at an

even slower rate than the majority of the length of the tube. All the specimens are steinkerns of sandstone in a sandstone matrix. The shell may have been thin, but nothing can be gleaned as to its composition. These specimens probably should be referred to *Coleolus?*, the uncertainty being based on the lack of data on shell composition.

Illustrations of topotypical material published in the early 1900s provide no additional data. A topotype, Field Museum 19273, is a specimen 33 mm long attached to matrix. Insofar as one can tell, the specimen is straight, not curved and expands at a uniform, quite low rate. Growth lines are closely spaced and are at right angles to the axis of the tube. The earliest part of the apical area cannot be seen, but if it is open, the opening must be quite small. Material identified as this species (Field Museum 10619) from another locality consists of six loose fragments from about 1.5 to about 2.5 cm in length and of varying widths. No growth lines may be seen and several are partially crushed. A complete tube may have been more than 9 cm in length. In addition, attached to matrix is an incomplete tube more than 5 cm in length. This is straight, not curved, and shows a uniform, quite low rate of expansion. If one combines the two lots, a complete specimen must have been more than 12 cm in length.

These additional specimens confirm the view that this species should be removed from the Palaeozoic Scaphopoda.

***Plagioglypta illinoisensis* (WORTHEN, 1883)**

A few years after its first description, that material was repeated, accompanied by an illustration. The type was deposited in the Illinois State Museum. WORTHEN wrote: "This species differs from *D. missouriensis* of SWALLOW, in its larger size, smooth surface, and straight former; the illustration of the type is nearly 15 cm long". A century ago the species was transferred from *Dentalium* (For details see YOCHELSON & SAUNDERS, 1967, p. 17).

Field Museum 26612, from 4 miles northwest of Chester, and presumably a topotype collection, contains two specimens. One specimen is a tubular fossil, nearly 9 cm in length, attached to a piece of limestone. It is a steinkern showing virtually no taper, surrounded by a relatively thick recrystallized shell; this may not be congeneric with the second specimen.

This second specimen is a loose steinkern broken into two pieces but approximately 9.5 cm long. It is straight, not curved and expands at a uniform rate. A feature of the Field Museum specimen is that at the break, some calcium carbonate is present which may not be part of the infilling. Although this is inconclusive, it is suggestive of the presence of a septum.

***Plagioglypta primaria* (HALL, 1858)**

Following the original description and illustration, one other comment was made on occurrence, and subsequently the species was transferred from *Dentalium* (For details, see YOCHELSON & SAUNDERS, 1967, p. 18).

USNM 67587 consists of a rectangular plaster cast, also bearing "CU 22181" – possibly Chicago University; a label indicates "plastoholotype". USNM 50118 is a gutta percha mould labeled as plastotype which matches the part of the cast showing a specimen. Whether these two were made independently is unknown.

The cast is slightly more than 5.5 cm long. It is gently and seemingly uniformly curved. It also seems to expand at a uniform rate. The outer surface is smooth, and the absence of any cross-section of shell suggests that this is not a steinkern. The apical area cannot be observed.

The Field Museum has two collections labeled as this species, but neither are from the type locality. Number 38622 is a silicified specimen showing growth lines, suggestive of a scaphopod, but the preservation is atypical of that at Spergen Indiana, the reported locality.

Number 38623-32 are more typical in preservation, but consist of short fragments of a tubular fossil, providing essentially no useful data.

The Yale Peabody Museum collection contains a silicified specimen, YPM 34622, from the St. Louis Limestone at Spergen Hill, Indiana. It is slightly less than 2.5 cm in length, broken at both apertural and apical ends and appears straight. The shell is thin at both ends, and the apical portion contains sparry calcite.

One possible interpretation is that this was a geode, suggestive of a chamber, and therefore septate, but admittedly this is based on quite weak evidence. Ten other specimens YPM 38623-38632 are all fragments of varying diameter but less than 1 cm in length. Several are filled with matrix and others are inconclusive on this point, but three specimens, YPM 38424, 38625, and 38631 show sparry calcite at both ends. Again, this is possibly suggestive, but not conclusive that septation might be present.

#### *Plagioglypta subannulata* EASTON, 1962

USNM 118878 consists of a limestone block upon whose surface are fragments of three tubular fossils. The shortest and widest is designated as holotype and the longest as paratype.

Curiously enough, a third specimen on the same piece of matrix is not mentioned. Other specimens mentioned by the author as being in the collections of the U.S. Geological Survey are not currently available for examination. (For details see YOCHELSON & SAUNDERS, 1967, p. 18).

The age of this species is not precisely known, but it is either quite late in the Mississippian or is Pennsylvanian. The only feature which may be of significance is the presence of closely spaced growth lines inclined at an angle of 15° to the axis of the tube.

#### *Dentalium (Laevidentalium) venustum* MEEK & WORTHEN, 1861

This species was described from near Waterloo, Illinois. It was transferred to *Plagioglypta* and subsequently to *Laevidentalium*. The last work to consider topological material was in 1916. (For details see YOCHELSON & SAUNDERS, 1967, p.16). The types of MEEK & WORTHEN may be at the Illinois State Museum; the published illustration is of a short length of a broken tube, which shows no critical features.

USNM 68348 contains five pieces of limestone coquina bearing tubular specimens varying in length from 8 mm to 18 mm. This material from near Waterloo may have been donated by Stuart Weller of the University of Chicago. Several tubes are gently curved and several appear straight. All are slender and none show growth lines or other ornament.

An unnumbered Field Museum collection from near Waterloo, Illinois, consists of 7 relatively slender limestone fragments ranging from 3-6 mm long and a wider, slightly crushed fragment 1 cm long; the larger piece has a thinner shell than the others and may not be related. Most of the fragments are filled with limestone, but one piece shows a sparry infilling, suggestive of a geode, and another seems to have a thicker shell at one end, possible indication of a break at the point of a septum. Neither of these observations is compelling evidence.

Topotype specimens provide no firm data to suggest that this species is correctly assigned to the Scaphopoda. At least two lots in the Field Museum collection identified as this species – but not topotypes – may be orthoconic nautiloids.

In passing it may be mentioned that a specimen from Oklahoma was illustrated by GIRTY (1909) as this species (USNM 120756).

It is a 1.5 cm long fragment of a straight, exceedingly slender tube showing virtually no expansion along its length and is a steinkern.

### Summary

It is most unlikely that any of the species discussed above are correctly assigned to *Dentalium* or *Plagioglypta*, as these genera are currently understood, but there is insufficient information to transfer species to other taxa with any degree of confidence. One can only hold the slight hope that eventually better material will be collected from the appropriate type localities or will be discovered in other repositories. Nothing significant enough to warrant illustration, formal description, or reassignment has been discovered among the handful of specimens available.

In their Palaeozoic scaphopods collections, both the National Museum and Field Museum have a number of fragments from the Spergen Limestone of southern Indiana, ranging from about 0.5 cm to 2 cm in length. The variation in width among the fragment is sufficient to suggest that specimens of 10 cm or longer are not implausible. The shell is relatively thin. No septation has been noted, but likewise no morphologic features suggest that this material might be related to the Scaphopoda.

Among the five species considered above, the oblique growth lines of *P. subannulata* suggest that it could be a scaphopod. For what little it may be worth, the geologic horizon is probably younger than Viséan where an authentic scaphopod is known. Even if this species is correctly assigned at the class level, the type material is so incomplete as to make comparison to other described species virtually impossible.

The remaining four species are even more problematic. The oldest among them is *D. grandaevum* from the Kinderhookian and near the base of the Mississippian. If the topotype is correctly identified, from it and the original description there is no reason to assume that this species is a member of the Scaphopoda. There is no information on presence or absence of septa, but the exceedingly slow rate of expansion may argue against assignment to Cephalopoda. "Worm tube" cannot be supported, nor can it be ruled out.

*Plagioglypta primaria* was described from the Warsaw Limestone that is the basal formation of the Meramecian. Based on the plaster cast, the only material available for this study, it is impossible to refute that this species is not a scaphopod. By the same token there is no basis for assuming that it is correctly assigned to the Scaphopoda, or necessarily even to the Mol-

lusca. A little more is known of *Dentalium* (*Laevidentalium*) *venustum* from the St. Louis Limestone of mid-Chesterian age, but it is equally enigmatic. Nothing supports assignment to either Scaphopoda or Cephalopoda. The notion of a calcareous "worm tube" such as *Coleolus* cannot be ruled out and should be considered by a later investigator.

In contrast to the uncertainty associated with the two Meramecian species, features of the younger Chesterian *P. illinoisensis* are not so vague. It has a straight shell and a relatively large size, both of which suggest that it should be carefully considered by a specialist in Palaeozoic Cephalopoda as an orthoconic nautiloid.

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## Explanations of the Plates

### PLATE 1

*Entalis prisca* (MÜNSTER IN GOLDFUSS, 1841). Specimens IRScNB a4263 (1-3, 1\*, 1\*\*, 2\*), a4264 (20, 20\*), a4265 (21, 21\*). Reproduction of the illustrations in DE KONINCK (1843, 1883) with their original numbering, and photographs of the specimens. The fragments are indicated by roman numerals. Concerning the measurements of the sections, the horizontal lines correspond to the axis parallel to the sheet, the vertical lines to the axis perpendicular to the sheet. Natural size except 1\*\*, 20\* and 21\* ( $\times 3$ ).

### PLATE 2

*Entalis ingens* (DE KONINCK, 1843). Specimens IRScNB a4269A (10, 10\*, 12), a4269B (11, 11\*), a4270 (18, 18\*, 19). Reproduction of the illustrations in DE KONINCK (1843, 1883) with their original numbering, and photographs of the specimens. Correspondence between the illustrations of 1883 and 1843 are discussed in the text. Same remark as in Pl. 1 concerning the fragments and the measurements of the axis. Natural size except 11\* ( $\times 4$ ) and 1b, c (non specified).

### PLATE 3

*Entalis ornata* (DE KONINCK, 1843). Specimens IRScNB a4271 (4, 4\*), a4272 (5, 5\*, 6, 9), a4273(7, 7\*, 8). Reproduction of the illustrations in DE KONINCK (1843, 1883) with their original numbering, and photographs of the specimens. Correspondence between the illustrations of 1883 and 1843 are discussed in the text. Same remark as in Pl. 1 concerning the fragments and the measurements of the axis. Natural size except 6, 8, 9 (non specified) and 7\* ( $\times 3$ ).

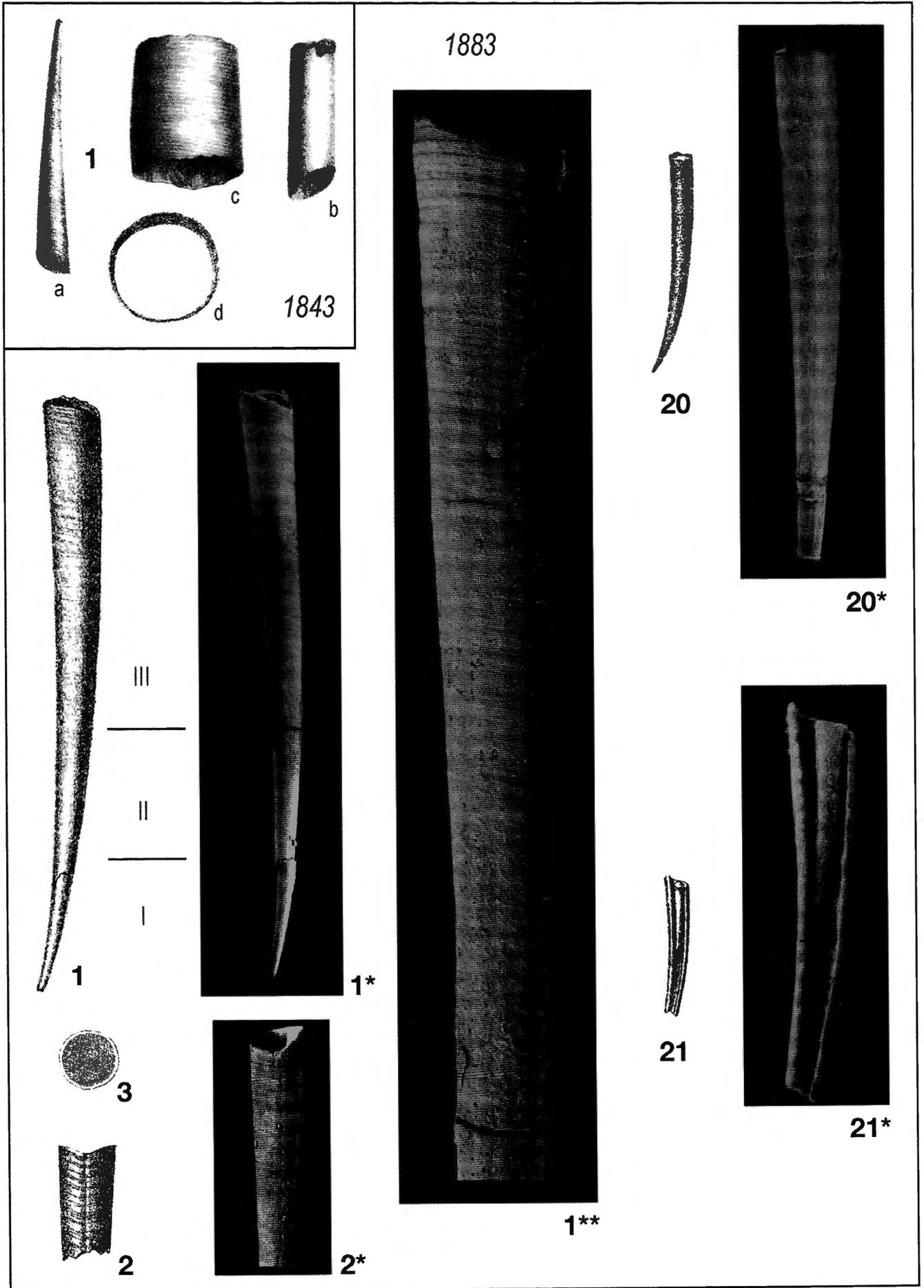


PLATE 1

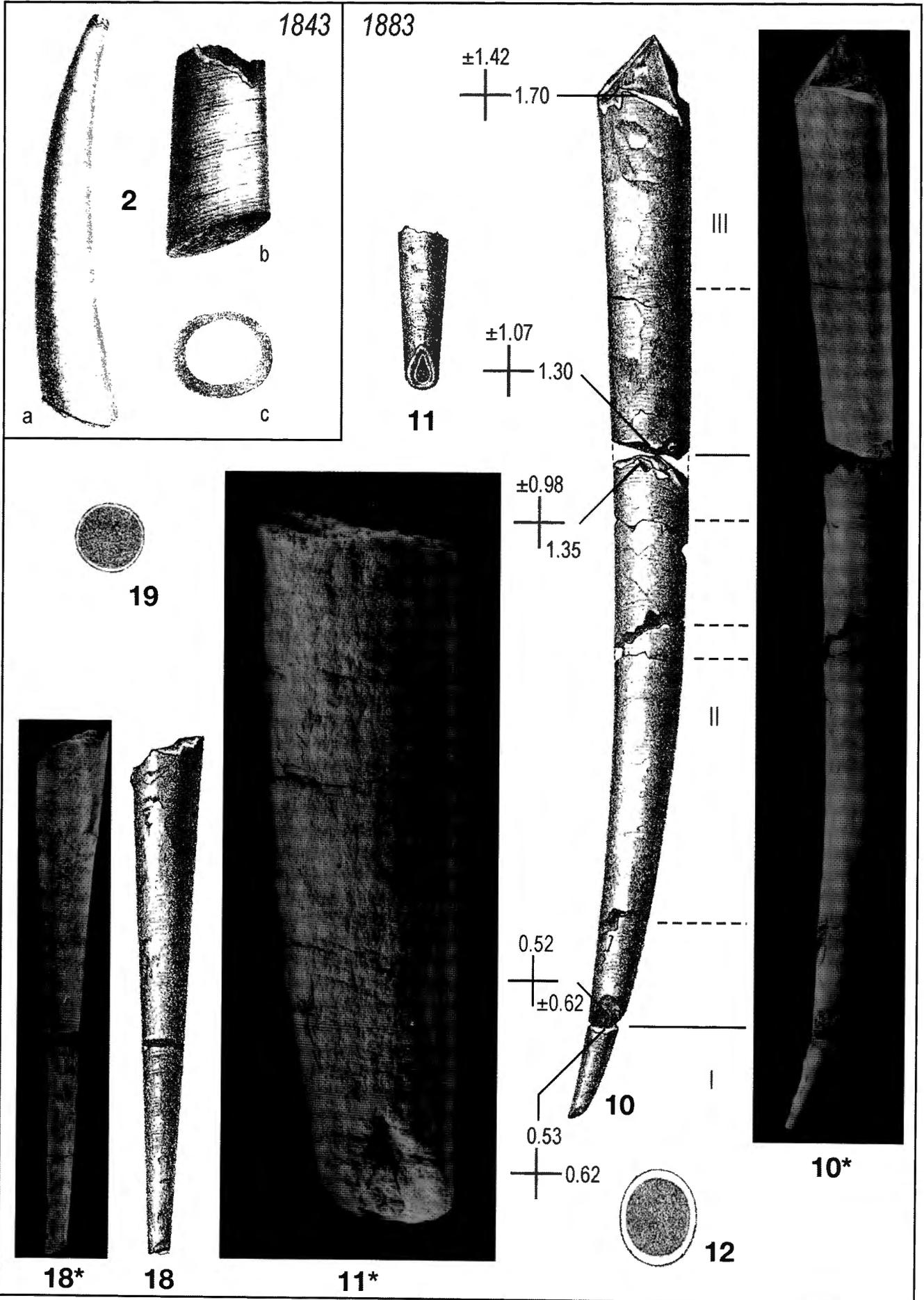


PLATE 2

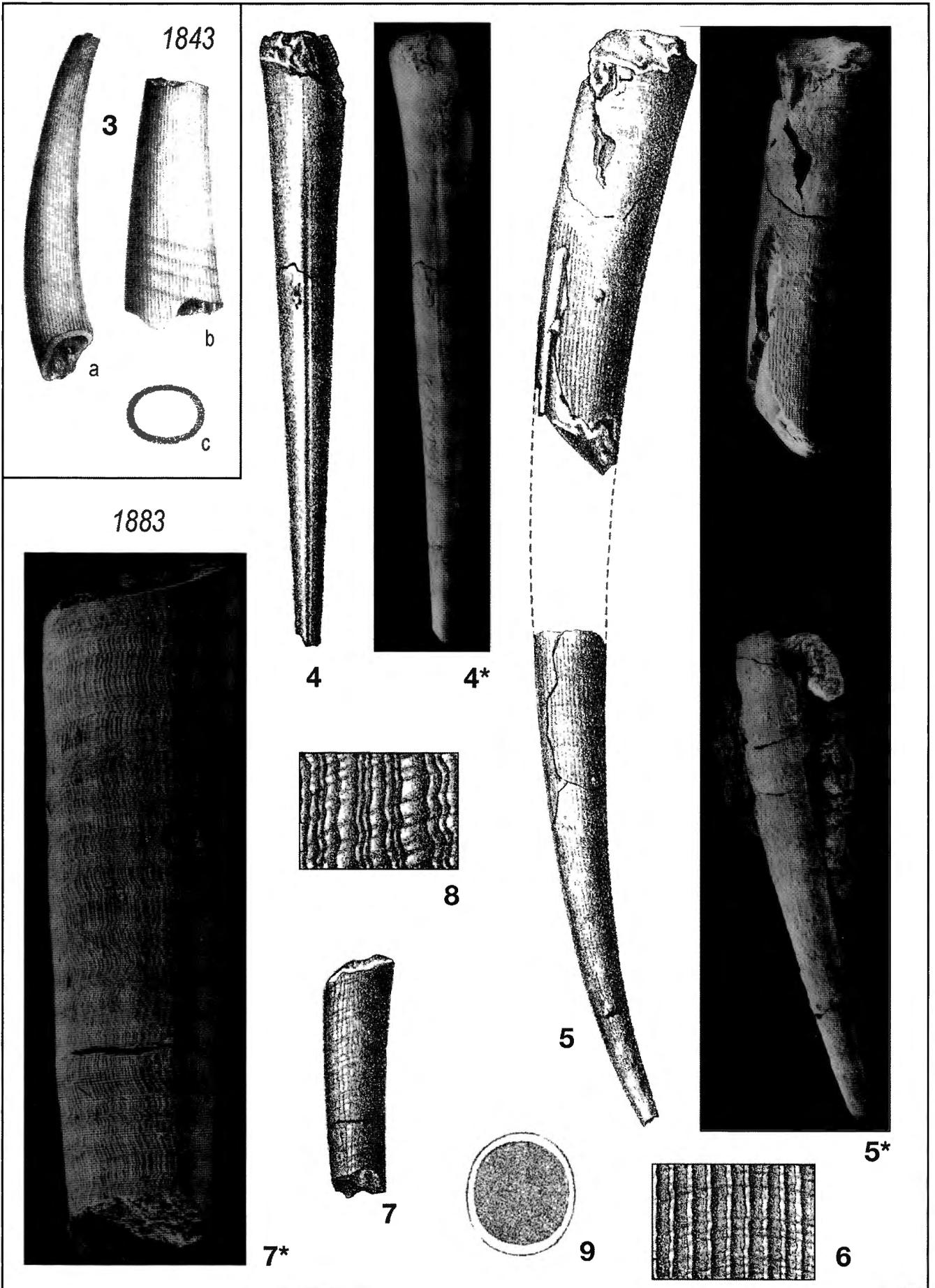


PLATE 3

