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A preliminary report on the structure of the siphonal tube and on the precipitation of lime in the shells of fossil Nautiloids

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With 1 plate and 4 figures in the text

Introduction

The present paper communicates some of the results of the writer's recent investigations into the shell structure of Paleozoic Nautiloids. In order to explain the structure of the siphonal tube in these Nautiloids a general survey of the structure of the siphonal tube in *Nautilus* and *Spirula* is also included. This latter survey is based, in part, on new investigations carried out by the writer.

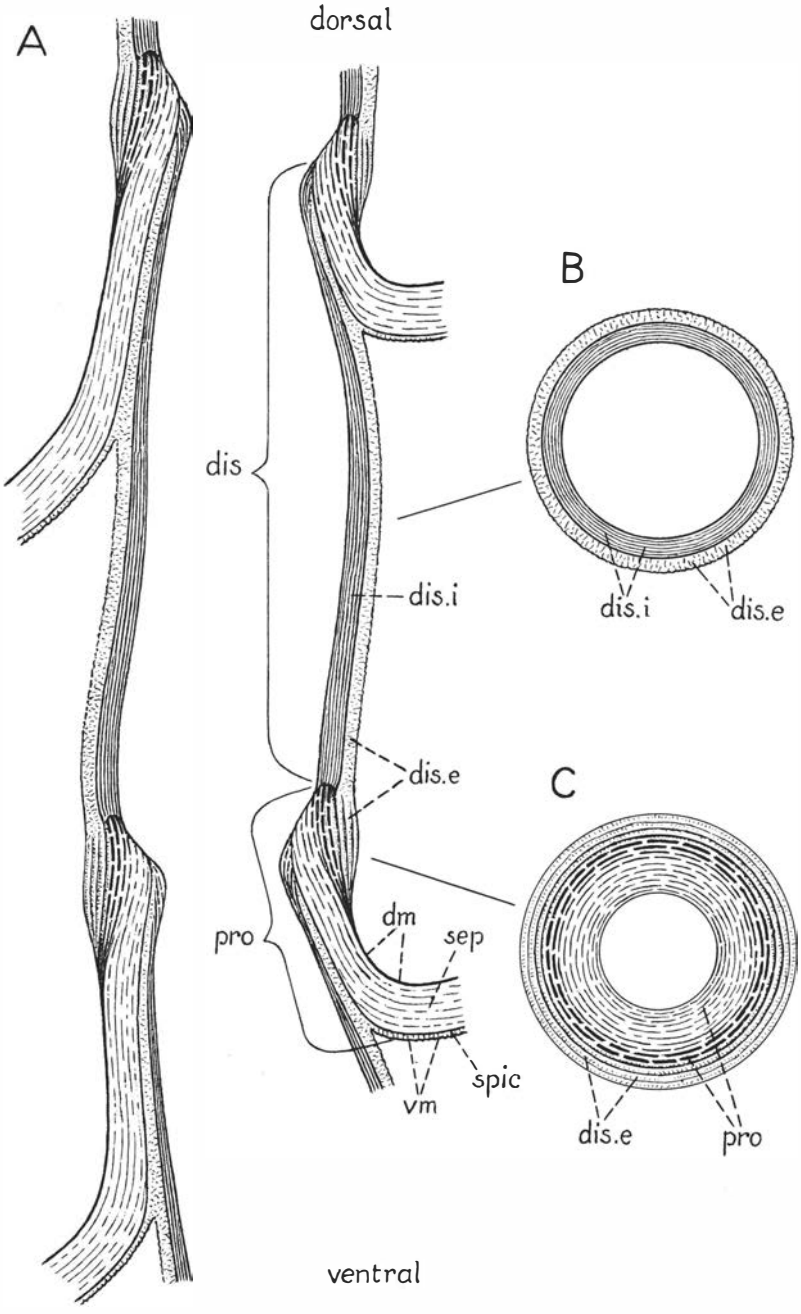
Many previous writers (Huxley 1853, Balfour 1880, Hescheler 1900, Pelseneer 1906, Plate 1922, Naef 1926, and Mutvei 1956) have pointed out that the Cephalopod body must be orientated on the basis of comparative anatomy and with due regard to conditions in molluscs in general. Thus the head and the funnel then lie ventral and the dilated portion of the mantle cavity, with the pallial organ-complex, postero-ventral. Since the shell is secreted by the epithelium on the dorsal surface of the body proper, it lies, morphologically, with the aperture of the shell directed downwards and its apex upwards. In the following description the shell is orientated in this way.

The structure of the septum in Nautilus and Spirula

a) The septum proper

It is well known that two main divisions can be distinguished in each individual septum of *Nautilus* and *Spirula:* (a) the *septum proper*, and (b) the *siphonal funnel* ("septal segment", Flower).

The septum proper is, in *Nautilus*, composed of the following four layers: (a) a dorsal chitinous membrane (*dm*, Fig. 1 A; Appellöf 1893, *mb*, pl. 11:1; 12:1); (b) a nacreous layer, made up of numerous lamellae (*sep*, Fig. 1 A; Appellöf loc. cit., *sp*, pl. 11:1; 12:1); (c) a thin layer of needle-shaped calcareous elements, the *spicular layer* (*spic*, Fig. 1 A; Appellöf loc. cit., *pf*, pl. 12:1, 3); and (d) a ventral chitinous membrane (*vm*, Fig. 1 A; Appellöf loc. cit., *mb*, pl. 12:3). The spicular layer is fairly thick in the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proximity of the siphonal funnel, but probably thins out and disappears towards the shell wall.

In *Spirula* the septum proper has a simpler structure than in *Nautilus*; it is composed only of a nacreous layer (*sep*, Fig. 2 A; Appellöf loc. cit., *sp*, pl. 8:1; 9:1, 2, 5, 6) and a spicular layer; the latter is, however, to be found only in close proximity to the siphonal funnel (*spic*, Fig. 2 A, C; Appellöf loc. cit., *pf*, pl. 8:1; *d*, pl. 9:1). According to the writer's own observations the spicular layer in *Spirula* is not continuous but is represented by radiating ridges (*spic*, Fig. 2 C).

b) The siphonal funnel

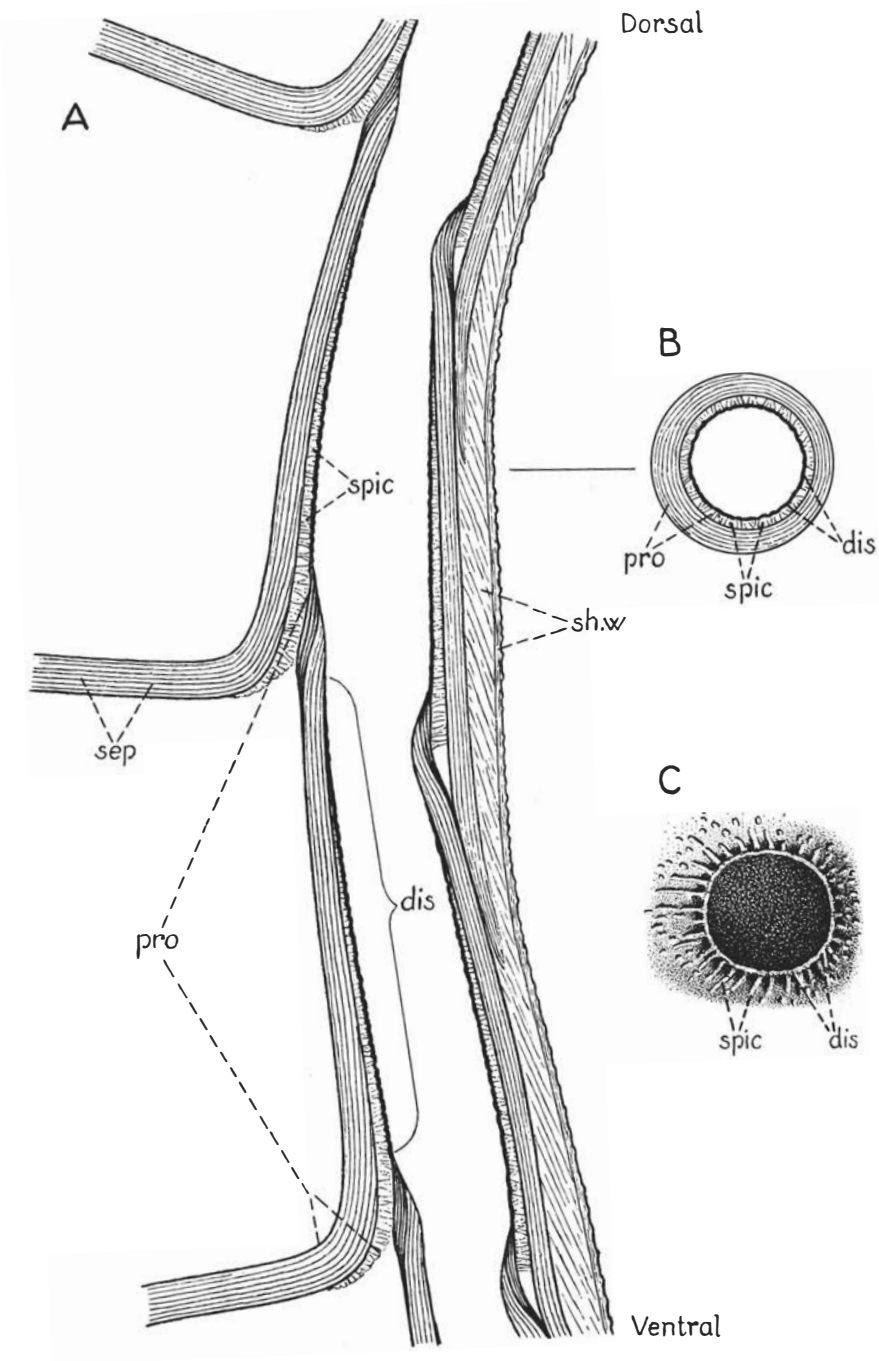
The septum proper in *Nautilus* and *Spirula* is produced upwards into a siphonal funnel, which extends to the next older siphonal funnel, to the inside of which it is attached (Barrande 1877 a, Brooks 1888, Appellöf loc. cit.). Consequently the siphonal funnels form a continuous tube. This tube, the *siphonal tube* ("siphuncle", Owen, Hyatt; "siphon", Barrande, Griffin; "Sifo", Appellöf; etc.), encloses the *siphonal cord* ("siphuncle", Griffin, Willey; "siphon", Owen, Hyatt; "fleischiger Sifo", Appellöf; etc.), i.e. the dorsal, narrow portion of the body extending up towards the shell apex. In the siphonal funnel of both forms one can distinguish two structurally different divisions: (a) a *proximal* (*pro*, Figs. 1, 2; "funnel", Hyatt, Brooks; "goulot", Barrande; "Siphonaldute", Sandberger, Appellöf; etc.); and (b) a *distal* (*dis*, Figs. 1, 2; "sheath", Hyatt; "enveloppes siphonales", Barrande; "Siphonalhülle", Appellöf; "connecting ring", Flower; etc.).

With regard to its structure, the proximal division in *Spirula* is similar to the septum proper, i.e. it is composed of two layers, the nacreous layer and the spicular layer (*pro*, Fig. 2 A, B; Appellöf loc. cit., *dt*, *pf*, pl 8:1, 3; 9:5). In *Nautilus* this division is made up of three of the four layers present in the septum proper, or, more precisely, the dorsal chitinous membrane, the nacreous layer, and the spicular layer (*pro*, Fig. 1; Appellöf loc. cit., pl. 12:1), whilst the ventral chitinous membrane is lacking. It may also be noted that the proximal division has a considerably greater height in *Spirula* than in *Nautilus*. Its height is, in the former, as much as $\frac{3}{5}$ and in the latter as much as $\frac{1}{4}$ to $\frac{1}{3}$ of the total height of the siphonal funnel.

The distal division in *Nautilus* is composed of two layers, (a) an external, porous, calcareous layer, which is largely made up of small, needle-shaped calcareous elements (*dis.e*, Fig. 1 A, B, C; Appellöf loc. cit., *pf*, pl. 11:2, 4; 12:1; Brooks 1888, *a*, *ax*, pl. 1, 2); and (b) an internal chitinous layer (*dis.i*, Fig. 1 A, B); the latter contracts on drying and appears, therefore, in the dried shells as a chitinous membrane only (Appellöf loc. cit., *chm*, pl. 11:2, 3; 12:1; Brooks loc. cit., *f*, *fx*, pl. 1, 2). In *Spirula*, on the contrary, the division under discussion is composed of a thin calcareous layer only (*dis*, Fig. 2 A, B, C; Appellöf loc. cit., *hü*, pl. 8:1, 3), made up of small, rounded calcareous

Fig. 1. Diagram to show the structure of the siphonal tube in *Nautilus pompilius*, L. from several thin-sections of a shell preserved in alcohol and plastic embedded. *A*, lower portion of the siphonal tube in median-sagittal section; *B*, *C*, cross-section through the distal division of the siphonal funnel and the upper portion of the proximal division. × 8.

dis, distal division of the siphonal funnel; *dis.e*, external calcareous layer of the distal division; *dis.i*, internal chitinous layer of the distal division; *dm*, dorsal chitinous membrane of the septum proper; *pro*, proximal division of the siphonal funnel; *sep*, nacreous layer of the septum proper; *spic*, spicular layer of the septum proper; *vm*, ventral chitinous membrane of the septum proper.


Dorsal
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elements, and which in *Nautilus* corresponds to the external calcareous layer of the distal division. The internal chitinous layer of the distal division in *Nautilus* is, therefore, entirely lacking in *Spirula*.

The two divisions of the siphonal funnel in *Nautilus* are connected with each other in such a way that the external calcareous layer of the distal division encloses the upper half of the proximal division and merges into it without any distinct boundary (Fig. 1 A; Appellöf loc. cit., *ds*, pl. 12:1; Brooks loc. cit., pl. 1), whilst the internal chitinous layer of the distal division has, on the contrary, a clearly defined boundary at the upper margin of the proximal division (Fig. 1 A). In *Spirula* the distal division of the siphonal funnel is connected with the upper portion of the proximal division (Fig. 2 A; Appellöf loc. cit., pl. 8:1) in a manner similar to that of the external calcareous layer of the distal division in *Nautilus* just described.

The individual siphonal funnels in *Nautilus* are joined in such a way that the upper half of the distal division in each siphonal funnel extends upwards into the next older one and invests the inside of the proximal division of it. The external calcareous layer of the distal division therefore connects with, and merges into, the spicular layer of the next older septum (Fig. 1 A; Appellöf loc. cit., pl. 12:1; Brooks loc. cit., pl. 1, 2). In *Spirula* the individual siphonal funnels join each other, in principally the same way as in *Nautilus*. Owing to the fact that the proximal division of the siphonal funnel in this form is very high, the entire distal division invests the proximal division of the next older siphonal funnel (Fig. 2 A; Appellöf loc. cit., pl. 8:1).

The structure of the siphonal tube in fossil Nautiloids

The siphonal tube in all fossil Nautiloids, as in *Nautilus* and *Spirula*, is composed of successive siphonal funnels, each of which is composed of two structurally different divisions, a proximal and a distal. Owing to the fact that the fossil Nautiloid-shells are always more or less recrystallized the siphonal funnel shows little or nothing of its original structure (Barrande 1877 a).

It is well known that the two divisions of the siphonal funnel vary considerably in height in different fossil Nautiloids. The height of these divisions in many fossil forms (e.g. *Orthoceros*, *Michelinoceras*, *Estonioceras*) corresponds to those in *Nautilus*, whilst some other fossil forms (e.g. *Endoceras*, *Piloceras*, *Aturia*) resemble *Spirula* in this respect. Moreover, the distal division of the siphonal funnel varies in thickness (Holm 1899; Flower 1941 a, 1943 b, 1946, 1947, 1950; Ulrich, Foerste, Miller & Unklesbay 1944; Cecioni 1953; Teichert & Glenister 1954), but the variations in this character are considerably smaller than has been previously stated. According to Holm (loc. cit.) this division of the siphonal funnel in *Bathmoceras* is so thick that it forms a very prominent ridge on the inside of the siphonal tube. *Bathmoceras* would in this respect differ from all remaining Nautiloids. It is, however, quite clear that this ridge does not belong to the division under discussion, but is a later secondary thickening on the

Fig. 2. Diagram to show the structure of the siphonal tube in *Spirula spirula* (L), from several thin-sections of shells preserved in dried condition and plastic embedded. *A*, lower portion of the siphonal tube in median-sagittal section; *B*, cross-section of the siphonal tube; *C*, spicular layer, represented by radiating ridges, at the passage between the septum proper and the siphonal funnel; the distal division of the next older siphonal funnel (*dis*) broken off. × 28.

dis, distal division of the siphonal funnel; *pro*, proximal division of the siphonal funnel; *sep*, nacreous layer of the septum proper; *sh.w*, shell wall; *spic*, spicular layer of the septum proper.

inside of the siphonal tube (see p. 186). Again in *Eothinoceras* (Ulrich, Foerste, Miller & Unklesbay loc. cit.; Teichert & Glenister loc. cit.) and in *Cyrtocerina* (Flower 1943 b, 1946) the inside of the distal division in every siphonal funnel would form a prominent ridge, but in the opinion of the present writer this ridge is also probably of the same nature as in *Bathmoceras*, i.e. a later thickening on the inside of the siphonal tube.

Flower (1939 b, 1941 a, 1946, 1947) states that the distal division of the siphonal funnel is, in all Nautiloids, a mesodermal structure. This interpretation is quite incompatible with an anatomical point of view. Further, according to Flower (1941 a, b, 1943 b, 1946, 1947, 1950), the upper portion of the distal division, the "eyelet", has in certain fossil Nautiloids, e.g. *Tarphyceratidae* and *Endoceratidae*, a different structure from the rest of this division. It is, however, very doubtful if this is actually the case. To judge from Flower's figures the shells of the illustrated Nautiloids are strongly recrystallized and it could, therefore, be difficult to establish what the original structure of the siphonal funnel really was. The writer's close study of the structure of the siphonal funnel in a large, and well preserved, collection of material, e.g. *Endoceratidae*, did not confirm Flower's observations.

It is well known that the septum proper in all Nautiloids is secreted by the epithelium on the dorsal surface of the body proper. The siphonal funnel, on the contrary, is formed by the epithelium of the siphonal cord, or more exactly, on the newly formed part which results from the elongation of the siphonal cord. After having formed the siphonal tube the epithelium of the siphonal cord generally ceased entirely the secretion of shell substance. In certain Paleozoic Nautiloids (e.g. *Endoceratidae*, *Piloceratidae*, *Actinoceratidae*, *Trimeroceratidae*, etc.) the epithelium on the upper portions of the siphonal cord began, however, after an interval to secrete again. Thus there arose in these forms a new calcareous deposit on the inside of the siphonal tube, the *secondary endosiphonal deposit* ("dépôt organique dans le siphon", Barrande; "endosiphonal deposit", Hyatt; "endosiphuncular deposit", Ruedemann; "endosiphonal stereoplasmic deposit", Kobayashi; "siphonal deposit", Flower). This appears in three different types: (a) *conical* ("dépôt conique", Barrande); (b) *radial* ("actinosiphonate deposit", Flower); and (c) *annular* ("annulosiphonate deposit", Flower). It must therefore be presumed that the secondarily lime-secreting epithelium was differentiated in three ways. The conical endosiphonal deposit (Fig. 3 C), which from my findings is a continuous layer, was in all probability secreted by a horizontal epithelial zone, the height of which corresponded to several siphonal funnels. The radial endosiphonal deposit (Fig. 3 A) is composed of a great number of vertical, radially arranged, lamellar cristae ("lamelles rayonnantes", Barrande; "rays", "longitudinal lamellae", Flower; "radiating laminae", "internal calcareous septa", "radiating lamellae", "actiniform lamellae", Hyatt; etc.). These must have been formed by corresponding vertical epithelial bands (Barrande 1855, 1877b), which probably extended through at least one siphonal funnel. The annular endosiphonal deposit (Fig. 3 B) is made up of a series of horizontal ring-shaped ridges, the *annular ridges* ("anneaux obstructeurs", Barrande; "rosettes", "rings", Hyatt; "annuli", Foerste, Teichert, Flower; "bulettes", Strand; "obstruction rings", Kobayashi, Teichert; etc.), one of which is present on the inside of each siphonal funnel. The epithelium which secreted these ridges must therefore have been composed of a small number of horizontal zones, one to each ridge (Barrande 1855, 1877b).

Due to the continued lime-secretion the three types of secondary endosiphonal deposits grew in thickness, and consequently the cavity of the siphonal tube was correspondingly reduced which brought about a similar decrease in the diameter of the

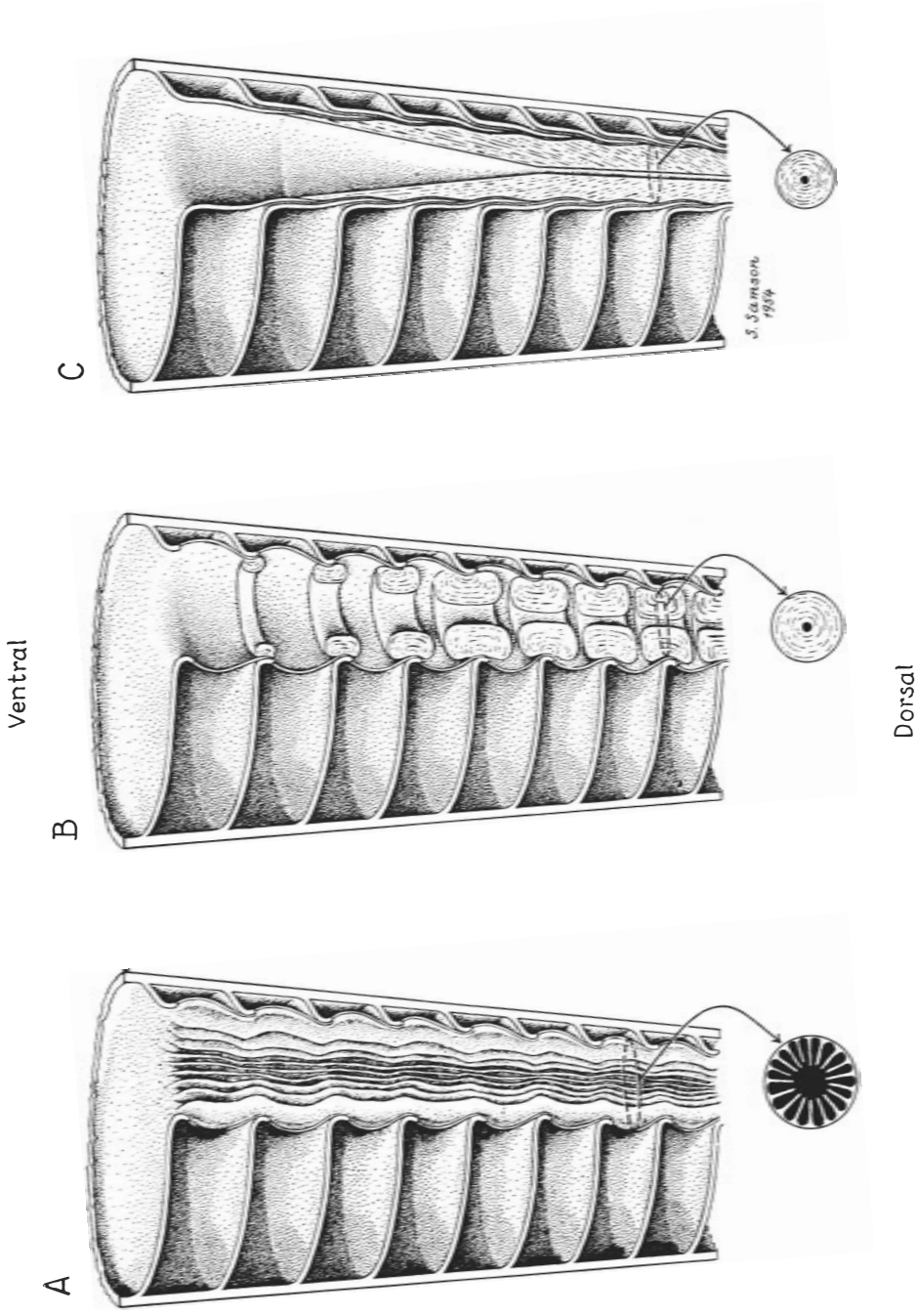

Fig. 3. Schematic representation of the three types of the secondary endosiphonal deposits. *A*, radial; *B*, annular; and *C*, conical.

siphonal cord in the locality of the lime secreting epithelium (Barrande 1855, 1877 b). The siphonal cord in the conical endosiphonal deposit became, therefore, distinctly narrower along its whole height (Fig. 4 C), whilst the siphonal cord internal to the annular and the radial endosiphonal deposits showed deep depressions, which in the former case were horizontal (Fig. 4 B; Barrande 1855, pl. 6:10–14) and in the latter case vertical (Fig. 4 A).

The secondarily lime-secreting region of the epithelium of the siphonal cord arose, in my opinion, on the upper portions of the siphonal cord and then moved successively downwards during the growth of the animal. In certain cases the movement continued as far as the lowermost portion of the siphonal cord in the full-grown animal. This downward movement occurred in such a way that the epithelium below the lime-secreting region regained the capacity for secreting lime, whilst the upper portion of this region at the same time lost this function. Simultaneously the endosiphonal deposit grew downwards, either by the continuous secretion of lime on its lower margin as in the conical and radial types, or by the upgrowth of new ring-shaped ridges below the next older one, as in the annular type.

With regard to its structure, the conical endosiphonal deposit agrees with the septum proper. When the conical endosiphonal deposit is only slightly recrystallized it has distinct growth lamellae which have arisen through smaller variations in the composition of the secretion. These growth lamellae have been misinterpreted by all previous writers (e.g. Barrande 1855, 1877b; Hyatt 1883, 1900; Holm 1885, 1895; Ruedemann 1903; Kobayashi 1934, 1936 b, 1947; Flower 1941 a, 1950, 1955 b) as a series of separate calcareous walls ("gaines coniques", Barrande; "sheaths", Hyatt; "endocones", Hyatt, Ruedemann, Foerste, Holm, Flower; "endosiphosheaths", Ruedemann; "endosipholining", Ruedemann, Flower; "holoendosheaths", "endosiphuncular endosheaths", "interendosheaths", "subsheaths", Kobayashi; "Endosiphonalscheiden", Schindewolf; etc.), which according to Holm and Ruedemann would be attached to each other by means of a small number of radially arranged lamellae, called by Holm "endosiphoblades". To the number and position of these "endosiphoblades", Flower (1950) attaches great taxonomic value. From my own investigations it is evident that the "endosiphoblades", described by Holm, are only vertical fissures in the endosiphonal deposits, formed after the death of the animals. In all probability most of the "endosiphoblades", which Ruedemann and Flower have described, are similar post mortem fissures.

As a rule, every individual annular ridge in the annular endosiphonal deposit arose on the inside of the proximal division of the siphonal funnel (Barrande 1855, 1877 b; Hyatt 1900; Teichert 1933). An exception is, however, constituted by some few forms (*Bathmoceras* and probably also *Eothinoceras* and *Cyrtocerina*), in which every such ridge was, instead, formed on the inside of the distal division of the siphonal funnel. In the former case the annular ridges have the same structure as the septum proper, whilst in the latter case, on the contrary, they correspond structurally to the distal division of the siphonal funnel.

The structure of the radial endosiphonal deposit is at present unknown.

The origin of the endosiphonal deposit was discussed by Teichert (1933, 1935) and Flower (1941 a, 1942, 1943 b, 1946, 1955 b) who both arrived at conclusions which are quite erroneous from an anatomical point of view. Teichert states that the annular endosiphonal deposit was formed by a calcification of the tissues of the siphonal cord around an "endosiphuncular vascular system" in the siphonal cord. According to Flower all endosiphonal deposits were formed in the mesoderm.

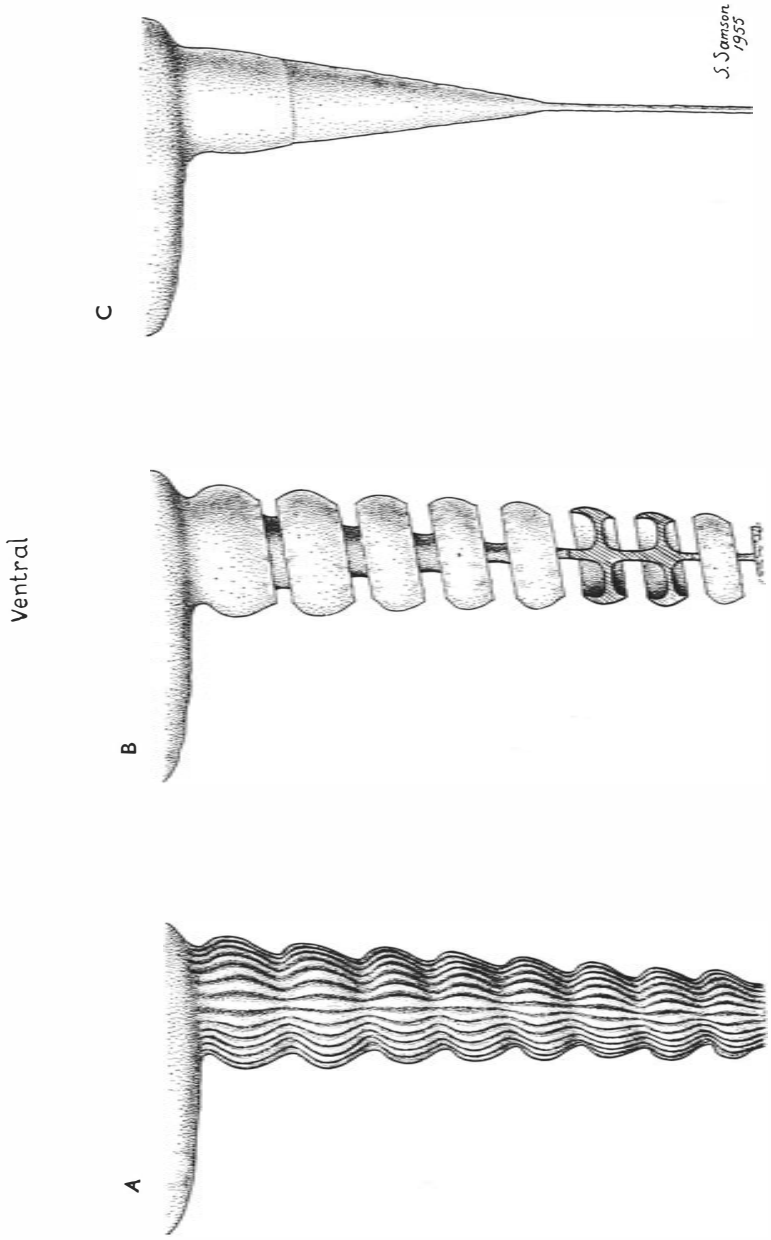

Fig. 4. Schematized reconstruction of the reduced siphonal cord in the three types of the secondary endosiphonal deposits. *A*, in the radial (Fig. 3 A); *B*, in the annular (Fig. 3 B); and *C*, in the conical (Fig. 3 C).

Precipitation of lime in the shell chambers of the fossil Nautiloids

In *Nautilus* and *Spirula* the shell chambers are filled by gas (Vrolik 1843; Willey 1902; Bruun 1943). As the majority of the writers have pointed out, this was certainly true also in fossil Nautiloids. When, after the death of the animal, the shells of these Nautiloids sank down on to a calcareous bottom sediment and were gradually embedded in it, the lime-satured water above and about this sediment would percolate through the distal division of the siphonal funnel into the shell chambers. Thereafter the lime crystallized out on the inside of the shell wall and on the dorsal and ventral surface of the septum proper. Such a crystallization could under certain physico-chemical conditions produce lime precipitations of very peculiar form and structure, as e.g. the lamellar filling of the shell chambers in "*Lamelloceras*" spp. (Pl. 1; see Le Maitre 1950; Termier 1950 a, b), which I have investigated more closely.[1] The lime precipitations, formed in the way just described, have been misinterpreted by numerous writers (e.g. Barrande 1859, 1877 a; Blake 1882; Hyatt 1900; Ruedemann 1906; Grabau 1922; Croneis 1926; Teichert 1933, 1934 a, b, 1935; Teichert & Glenister 1952, 1953; Schindewolf 1935, 1942; Miller, Dunbar & Corda 1933; Kobayashi 1936 a, b, 1937; Flower 1936, 1939 a, b, 1940, 1942, 1943a, 1946, 1950, 1955 a; Ulrich, Foerste, Miller & Unklesbay 1944; Termier 1950 a, b) as secretions of the tissues of the animal. More exactly, these precipitations, which have been called "dépôt organique dans les loges aériennes" (Barrande), "intrakamerale Ablagerung" (Teichert, Schindewolf), "intracameral stereoplasmic deposit" (Kobayashi), "cameral deposit" (Flower) etc., should have been formed either by the epithelium on the dorsal surface of the body proper (Barrande) or by special tissues in the shell chambers which were completely separate from the tissues of the rest of the body and called by Flower "cameral mantle" (Teichert and Flower). Both these interpretations are, however, quite erroneous and have arisen owing to the imperfect knowledge of the above-mentioned writers of the anatomy of Cephalopods and of Molluscs in general. This is also true of Teichert's (1933) and Flower's (1939 b, 1946, textfig. 2) statements that living tissue would be found in the shell chambers of *Nautilus*.

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[1] These forms belong to a large collection of material of Paleozoic Nautiloids which I had opportunity of collecting in French North Africa through the generous support of "Centre de Recherches Sahariennes", "Service Géologique du Maroc" and "Direction générale des Relations culturelles du Ministère des Affaires étrangères", and I would like here to express my very sincere gratitude to the Directors of these Institutes. I wish also to record my best thanks to Prof. P. Pruvost and to Dr J.-P. Lehman who helped in every possible way.

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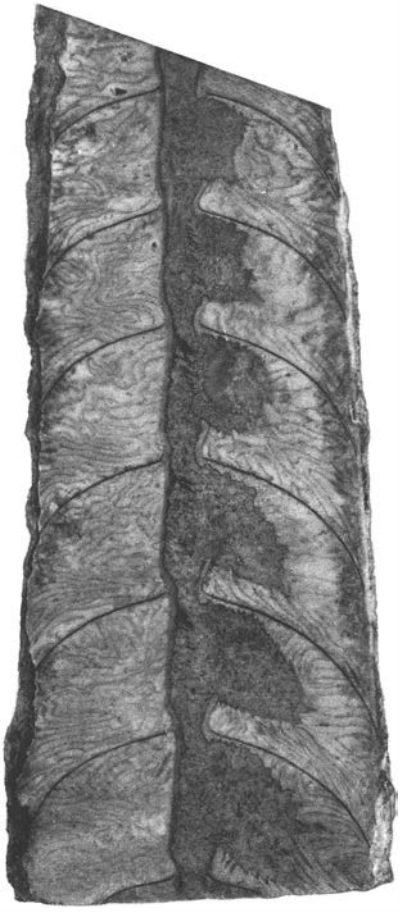
Plate I

Figs. 1, 2, 3, 4. Sagittal section through the septate division of the shell in four undetermined Nautiloids, probably of the same genus and species (="*Lamelloceras*"). These figures illustrate the variation of the post-mortem lime precipitation in the shell chambers. N. Africa, N. Sahara, Marhouma (Saoura), Eifélien, Devonian. × 5/4 of the natural size.

Tryckt den 5 december 1956

Uppsala 1956. Almqvist & Wiksells Boktryckeri AB

1



2



3



4

