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On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids

With a taxonomic appendix

By Harry Mutvei

With 20 plates and 24 figures in the text

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Introductory remarks

The present paper, which represents a part of the writer's studies on the shell structure and systematics of fossil nautiloids, deals with the functional areas of origin of the retractor muscles, longitudinal mantle-musculature and sub-epithelial musculature in the dorsal portion of the body proper in certain fossil nautiloids. In order to interpret these areas of origin in the fossil forms a general survey of the corresponding structures in recent *Nautilus* is also made. This survey is based on the literature, but since the statements in the literature often are rather obscure

and incomplete the present writer has made some complementary investigations on *N. pompilius* L. (one specimen preserved in alcohol and several dried shells). The shell terminology in *Nautilus* has also been revised and several misleading and erroneous terms have been replaced by new and more suitable ones. This new terminology is, of course, wholly applicable to the shells of fossil nautiloids.

In addition to material in the possession of the Palaeozoological Department of the Swedish Museum of Natural History, Stockholm (below abbreviated to RM) I have also had at my disposal specimens belonging to the following institutes and museums: the Paleontological Institute, Uppsala (below abbreviated to UPI); the Geological Survey of Sweden, Stockholm; the Paleontological Institute, Lund; and the British Museum (Natural History), London. I would like to express my very sincere gratitude to the authorities of these institutes and museums for generously lending their material. I wish to record also my best thanks to Dr. V. Jaanusson, Uppsala, who suggested this paper, and to Dr. L. F. Spath, London, who assisted with the correct identification of several Mesozoic nautiloids.

The orientation of the nautiloid shells figured in the following text-figures and plates is in most cases the reverse of their anatomical orientation; on every plate and text-figure, therefore, the ventral and dorsal directions are given.

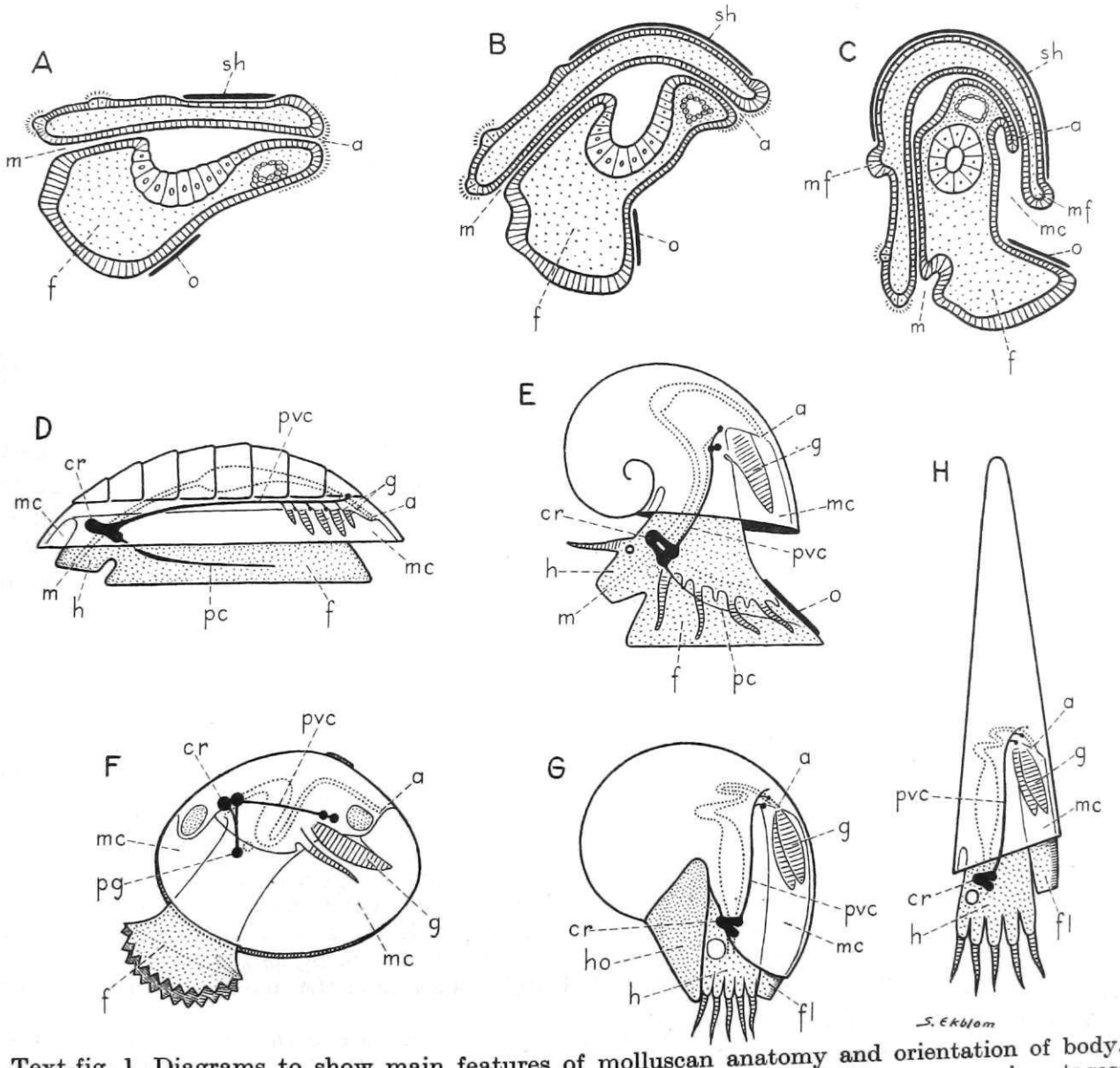
Nautilus

1. Anatomic ground-plan and body orientation

The main outlines in the anatomy of molluscs are, according to Hescheler (1900), Pelseneer (1906) and Naef (1926), briefly as follows. The anterior portion of the molluscan body is formed into a head (*h*, text-fig. 1 D, E, G, H) and the ventral portion of the body into a powerful, muscular foot (*f*, text-fig. 1 A–F). Around the periphery of the body there exists a downwardly hanging fold, the mantle fold (*mf*, text-fig. 1 C), which constitutes the external wall of a cavity, the mantle cavity (*mc*, text-fig. 1 C–H). The posterior portion of the mantle cavity, which is considerably dilated, houses the pallial organ-complex which includes the gills (*g*, text-fig. 1 D–H) and the anal (*a*, text-fig. 1 A–H), reproductive and excretory apertures. The dorsal portion of the body is enclosed by a shell which is secreted by the epithelium of the dorsal surface of the body and by the external and marginal epithelium of the mantle fold. The powerful foot contains, *inter alia*, a special retractor muscle which has its functional origin on the inside of the shell (see below). The nervous system is composed of (1) a circumoesophageal nerve-ring (*cr*, text-fig. 1 D–H) along which, in most cases, the nerve cells are localised in three pairs of ganglia (cerebral, pedal and pleural), and (2) two paired nerve cords, a ventral pedal cord (*pc*, text-fig. 1 D, E) and a dorsal pleuro-visceral cord (*pvc*, text-fig. 1 D–H), both of which issue from the circumoesophageal ring whence they run backwards. The pedal cord innervates the foot, whilst the pleuro-visceral cord innervates the dorsal integument, including the mantle fold, the viscera and gills.

Huxley (1853), Balfour (1880), Hescheler (loc. cit.), Pelseneer (loc. cit.), Plate (1922) and Naef (loc. cit.) have correctly pointed out that in cephalopods the mantle fold, the pallial organ-complex and the shell are developed in accordance with these principles of molluscan anatomy. In connection with the transition from a creeping to a largely drifting way of life the cephalopods acquired a high, conical shape

(text-fig. 1 H). The head, together with the mouth, secondarily moved downwards to the ventral side of the body, whilst the foot was modified into the funnel (*fl*, text-fig. 1 G, H) and into the tentacles around the head (text-fig. 1 G, H). That the nautiloids have undergone such an evolution is proved by the following facts: (1) the nerves of the tentacles must be derived from the original pedal nerve cord (THORE 1939); (2) the tentacles originate embryologically between the mouth and the anus on the ventral side of the body, and it is fairly late, during ontogeny, that they take up a position around the head; and (3) the original retractor muscle of the molluscan foot persists and is inserted on the cartilages in the head and in the anterior portion of the funnel; in dibranchiates it is differentiated into both the retractor capitis and the depressor infundibuli.



Text-fig. 1. Diagrams to show main features of molluscan anatomy and orientation of body. A, B, C, median-sagittal sections through an embryo of *Paludina* at three successive stages; these figures show retroflexion of rectum, development of mantle fold and of shell; D, prototype of chitonid; E, prototype of gastropod; F, prototype of lamellibranch; G, *Nautilus*; H, straight-shelled fossil nautiloid (figs. A–F after Naef 1926).

a, anus; *cr*, circumoesophageal nerve-ring; *g*, gills; *f*, foot; *fl*, funnel; *h*, head; *ho*, hood; *m*, mouth; *mc*, manle cavity; *mf*, mantle fold; *o*, operculum; *pc*, pedal nerve-cord; *pvc*, pleuro-visceral nerve-cord.

The shell in dibranchiates is more or less secondarily reduced and lies embedded in the soft tissues, whilst the shell in tetrabranchiates, i.e. *Nautilus*, is unreduced and external. Since the shell in the latter form bends into a forwardly directed spiral the dorso-ventral axis of the shell also is twisted into a corresponding spiral (text-figs. 1 G, 2 A), The morphologically posterior side of the shell is the peripheral side of the whorl and the morphologically anterior side of the shell the central side of the whorl.

In relation to the orientation of the animal in the water the morphological dorso-ventral axis of the body in certain primitive, fossil nautiloids, with slightly coiled shells (e.g. *Orthoceros, Michelinoceras, Kionoceras*), was vertical, but in the majority of the fossil and recent cephalopods this axis has secondarily acquired a more or less horizontal position. This situation has arisen in connection with the adoption by the cephalopods of a more mobile manner of living either by the coiling of the shell, as in the many fossil nautiloids, ammonoids and in the living *Nautilus*, or by the reduction of the shell, as in dibranchiates. In both cases the body became streamlined and the funnel acquired a horizontal position which is more suited to its function. Due to the fact that the morphological dorso-ventral axis of the body of many cephalopods lies secondarily horizontally or approximately so many writers (e.g. Owen 1832, Keferstein 1860, Barrande 1877, Appellöf, 1893, Griffin 1900, Willey 1902) have considered it to be the antero-posterior axis of the body, but such an interpretation is based on a misunderstanding of the principles of molluscan anatomy.

2. The shell and its relations to the soft parts

From a descriptive point of view the *Nautilus*-shell may be regarded as composed of two divisions: (1) the *domiciliary division* ("dwelling chamber", Owen; "grande chambre", Barrande; "domicilium", Holm; "body chamber", Griffin, Flower, Miller; "living chamber", Hyatt; "animal chamber", Willey; "Wohnkammer", Appellöf, Keferstein, Teichert; etc.) and (2) the *septate division* ("partie cloisonne", Barrande; "phragmocone", Teichert, Foerste; "phragmocone + protoconch", Owen, Holm, Flower, Miller; etc.).[1]

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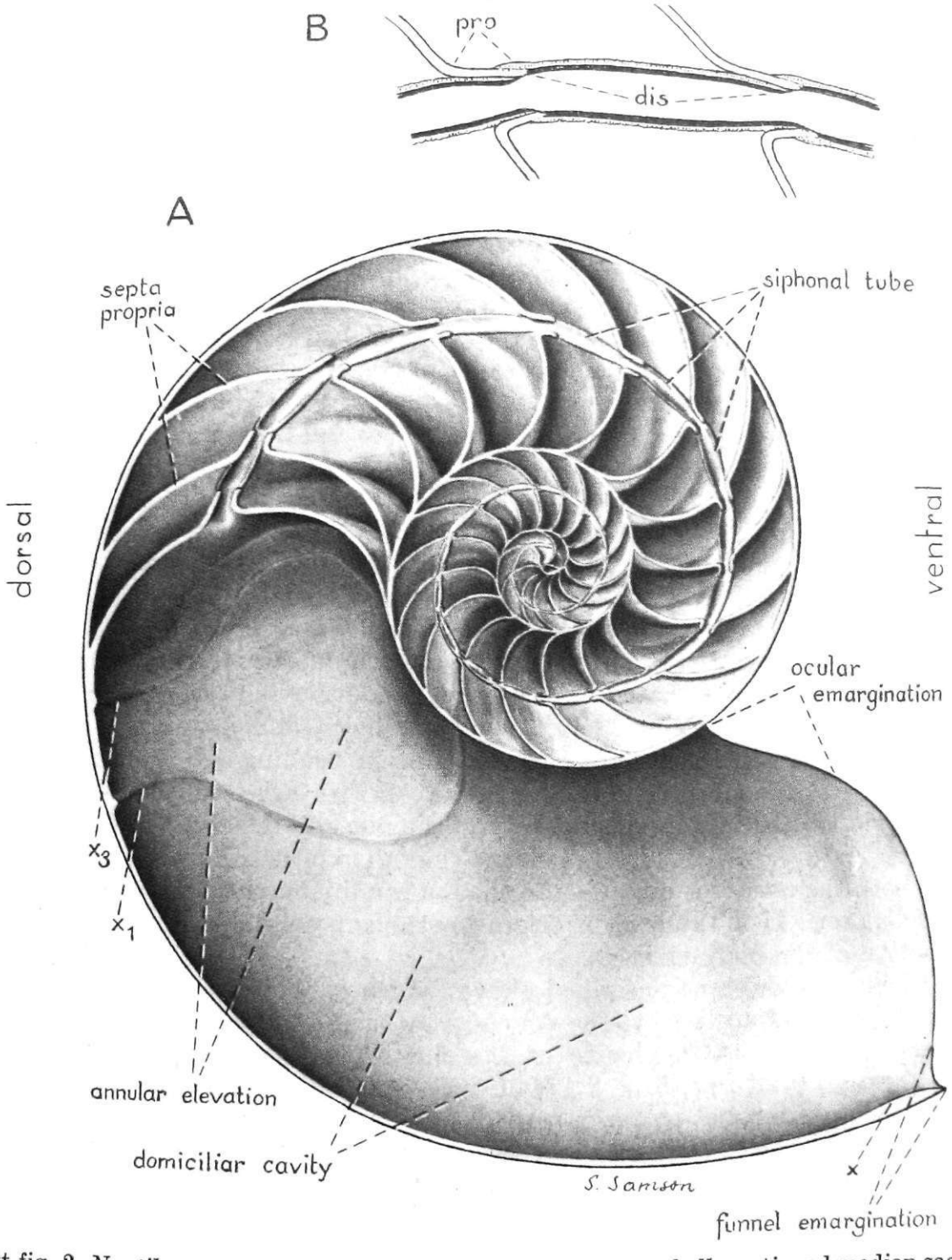
[1] The term "phragmocone" was introduced by Owen (1832) for a certain division of the belemnoid shell, which, according to Owen (1844), is composed of three divisions: "1st. The terminal spathose body called the 'guard', sheath or rostrum. ... 2nd. The chambered or siphonated part of the shell which I have called the 'phragmocone', and which is lodged in the conical alveolus or cavity at the base of the 'guard'. 3rd. The conical, thin, but dense, corneo-nacreous case, which immediately invests the phragmocone, and lines the alveolus of the guard; commencing at the bottom or apex of that cavity, and continued beyond the thin margins of the basal aperture of the alveolus, and beyond the last septum of the phragmocone, to form, as Dr. Buckland rightly describes, the large anterior chamber of the Belemnite containing the ink-bag and some other viscera."

The "phragmocone" in this original sense represents the septa and the internal layer of the septate division in the nautiloid shell (cf. Naef 1922), whilst Owen's third division, which was called the "conotheca" by Huxley (1864), corresponds to the external shell layer in nautiloids. Since the belemnoid shell was entirely embedded in soft parts its domiciliary division is strongly reduced and its septate division enclosed by the "guard" or the "rostrum", which is a secondary formation, without any corresponding structure in nautiloids.

From these facts it is evident that the terms "phragmocone" and "conotheca" are misleading and superfluous and must therefore be rejected.

a) Domiciliary division

The domiciliary division which is the lowermost, youngest portion of the shell encloses a large continuous cavity, the *domiciliary cavity* (text-fig. 2 A; pl. 1). This cavity, which contains the head, the mantle fold and the greater portion of the body proper ("visceral hump"), is defined dorsally by the youngest septum and opens



Text-fig. 2. *Nautilus pompilius* L. A, Left side of a full grown shell, sectioned median sagittally, × $\frac{4}{5}$; B, diagram to show the structure of siphonal tube in median-sagittal section, × 3. *dis*, distal division of siphonal funnel; *pro*, proximal division of siphonal funnel; x, apertural ridge; x_1, ventral annular ridge; x_3, mural ridge.

downwards and outwards through the shell aperture. The margin of the shell aperture shows two emarginations: an antero-lateral paired *ocular emargination* and a posterior unpaired *funnel emargination* (text-fig. 2 A; "hyponomic sinus", Hyatt), separated from each other on either side by a downwardly projecting portion of the margin of the shell aperture.

The relations between the soft parts and the wall of the domiciliary division were first discussed by Owen (1832) who stated that the greater part of body proper lies free in the domiciliary cavity, but is attached by means of a horisontal, annular zone of epithelium on the inside of the shell somewhat below the youngest septum. For reasons which are more evident from the following description, this zone is here named the *epithelial zone I*, whilst for its corresponding zone of attachment on the shell wall the term *conchial zone I* is suggested (text-fig. 3). Owen stated, moreover, that the epitehlial zone I is composed of three portions: a narrow, unpaired posterior portion, a likewise narrow, unpaired anterior portion, and a broad, paired lateral portion, the latter being the area of origin for the retractor muscle of either side. The conchial zone I was described by Owen as a thin layer of "brown horny matter" which in fact is conchin.[1] Keferstein (1860) introduced the name "annulus" for the anterior and the posterior portions of the epithelial zone I. Waagen (1870) established that the thin conchin layer, which, according to Owen, was to be found only on the conchial zone I, actually extends upwards as far as to the youngest septum. From this fact Waagen, and later also Dewitz (1879a, b, c) and Schröder (1881), concluded that the entire conchin-covered surface ("Haftfläche", Waagen; "Verwachsungsband," Dewitz, Schröder) is an area of attachment for a continuous epithelial zone. It is, however, evident from the investigations of Appellöf (1893) that this interpretation is wrong. Appellöf found, rather, that the body proper is attached on the inside of the shell not only by means of the epithelial zone I but also by means of another, upper annular epithelial zone, here called the *epithelial zone II*, whose area of attachment, the *conchial zone II* (text-fig. 3), is situated immediately below the youngest septum. Griffin (1900) designated this epithelial zone the "posterior ventral aponeurotic band + dorsal aponeurotic band", whilst Willey (1902) named this the "septal aponeurosis". Both these terms are erroneous and misleading and must be discarded (the real aponeuroses are mesodermal structures). Rauther (1925) has investigated the histology of epithelial zones I and II, and the muscles lying just internal to these zones. From his investigations it is evident that the epithelial zone I is the area of origin for both the retractor muscles and the longitudinal mantle-musculature, whilst the epithelial zone II is the area of origin for the sub-epithelial musculature in the upper portion of the body proper.

The conchin-covered area described above, which extends from the lower margin of the conchial zone I upwards to the youngest septum, appears as a slight horizontal, ring-shaped elevation of the inside of the shell. This elevation, here named the *annular elevation* (text-figs. 2 A, 3), is of different widths in its different portions. The unpaired anterior and posterior portions are both narrow, especially the latter, whilst the paired lateral portion is, on the contrary, wide. This latter portion is so strongly produced dorso-ventrally that it forms an upper and a lower lobe. The

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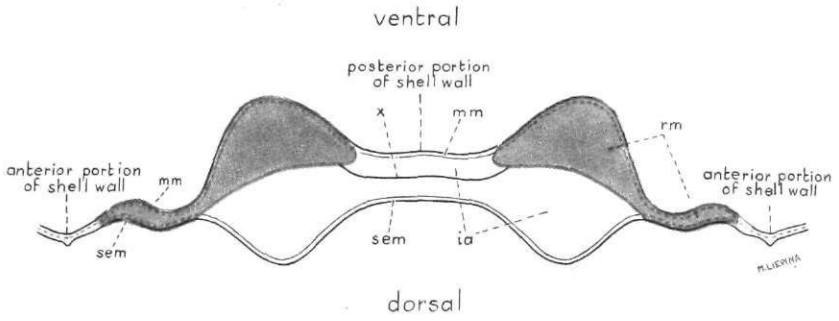
[1] Conchin (Simroth 1897; "Epikutikula", "Konchyliolin", "Konchyolin") is a chitin-like, organic substance which generally occurs in the mollusc shell.

annular elevation is composed of two thin layers: an external calcareous layer[1] which is attached on the internal shell wall, and an internal conchin layer.

It is evident from the above description that the annular elevation topographically corresponds to the areas of origin of the retractor muscles, of the longitudinal mantle-musculature and of the sub-epithelial musculature in the dorsal portion of the body proper. These muscles do not, however, take their origin directly from the elevation under discussion, but from epithelial zones I and II which lie on the elevation and which secrete its calcareous and conchin layers. As in lamellibranchs and gastropods (Brück 1913, 1914; Röchling 1922), the epithelium at the origins of the muscles in *Nautilus* is probably crossed by special "epithelial" fibres, running in a basalo-superficial direction, which are directly continuous with the muscle fibres. These "epithelial" fibres in lamellibranchs and gastropods, and presumably in *Nautilus*, form together a sort of pseudo-tendon between the muscle fibres and the shell. The presence of this epithelium, called "Haftepithel" (Brück), accordingly, results in the muscles of molluscs reaching only indirectly the shell wall.



Text-fig. 3. *Nautilus pompilius* L. Diagram of annular elevation of shell projected in one plane × ½ (pl. 1).
ia, intermediate area; *mm*, functional area of origin of longitudinal mantle musculature (conchial zone I); *rm*, functional area of origin of retractor muscles (conchial zone I); *sem*, functional area of origin of sub-epithelial musculature of dorsal portion of body proper (conchial zone II); *x*, functional area of attachment of pallio-visceral ligament.

On the basis of the above one may say, therefore, that the retractor muscles, the longitudinal mantel-musculature and the sub-epithelial musculature in the dorsal portion of the body proper take their origin functionally on the annular elevation. More precisely, the functional origins of these muscles are situated as follows: (1) the area of origin for the retractor muscle of either side (*rm*, text-fig. 3; pl. 1) occupies the ventral lobe of the lateral portion of the annular elevation and, in addition, the adjacent half of the posterior portion of that elevation; (2) the area of origin of the longitudinal mantle-musculature (*mm*, text-fig. 3; pl. 1) is a narrow, ring-shaped zone along the lower margin of the elevation, whilst (3) the area of origin of the sub-epithelial musculature in the dorsal portion of the body proper (*sem*, text-fig. 3;

[1] This layer probably corresponds to the "helle Schicht", which Tullberg (1882) described in the lamellibranchiate-shell. According to Schmidt (1924) this "helle Schicht" differs only slightly from the nacreous layer of the shell.

pl. 1) is a, likewise, narrow, ring-shaped zone along the upper margin of the same elevation. Both these marginal zones lie far apart from each other posteriorly and laterally, but are close together antero-medially, where they merge with each other without any definite boundary. Moreover, the lower marginal zone merges both laterally and antero-laterally, without any boundary, with the area of origin of the retractor muscle, whilst the upper marginal zone is united antero-laterally only with it. The origins of the retractor muscles and the longitudinal mantle musculature on the one hand and the area of origin for the sub-epithelial musculature in the dorsal portion of the body proper on the other hand are separated laterally and posteriorly from each other by an *intermediate area* (*ia*, text-fig. 3; pl. 1) on which only the pallio-visceral ligament is attached.

It is well known that as the soft parts of the animal grow in size they shift downwards in the domiciliary cavity[1] causing a corresponding growth downwards of the shell at the margin of its aperture. *Pari passu* the annular elevation also grows slowly downwards by a gradual deposition of calcareous and conchin substance on its ventral side. Owing to the gradual shifting downwards of the soft parts, there arises in the upper portion of the domiciliary cavity a vacuity, which, in agreement with the shell chambers, is filled with gas. When this vacuity attains a certain size it is divided from the domiciliary cavity by a septum which is secreted by the epithelium on the dorsal surface of the body proper, and this process is repeated as long as the animal grows in size. The annular elevation is covered dorsally by the mural part of each new septum and is in this way gradually embedded in the shell wall. After the growth of the animal has ceased, the soft parts and the annular elevation also assume a fixed position in the domiciliary cavity. Simultaneously, of course, the formation of new septa ceases. The epithelium of the body immediately above the margin of the shell aperture, along the lower margin of the annular elevation and along the lower margin of the mural part of the youngest septum continues, however, in some cases to secrete shell substance for a period. Thereby horizontal, ridge-like thickenings are formed on the three corresponding places on the internal surface of the domiciliary division. These ridge-like thickenings are here called in succession from below upwards the *apertural ridge*, the *lower annular ridge*[2] and the *mural ridge* (x, x_1, x_2, text-fig. 2 A), respectively.

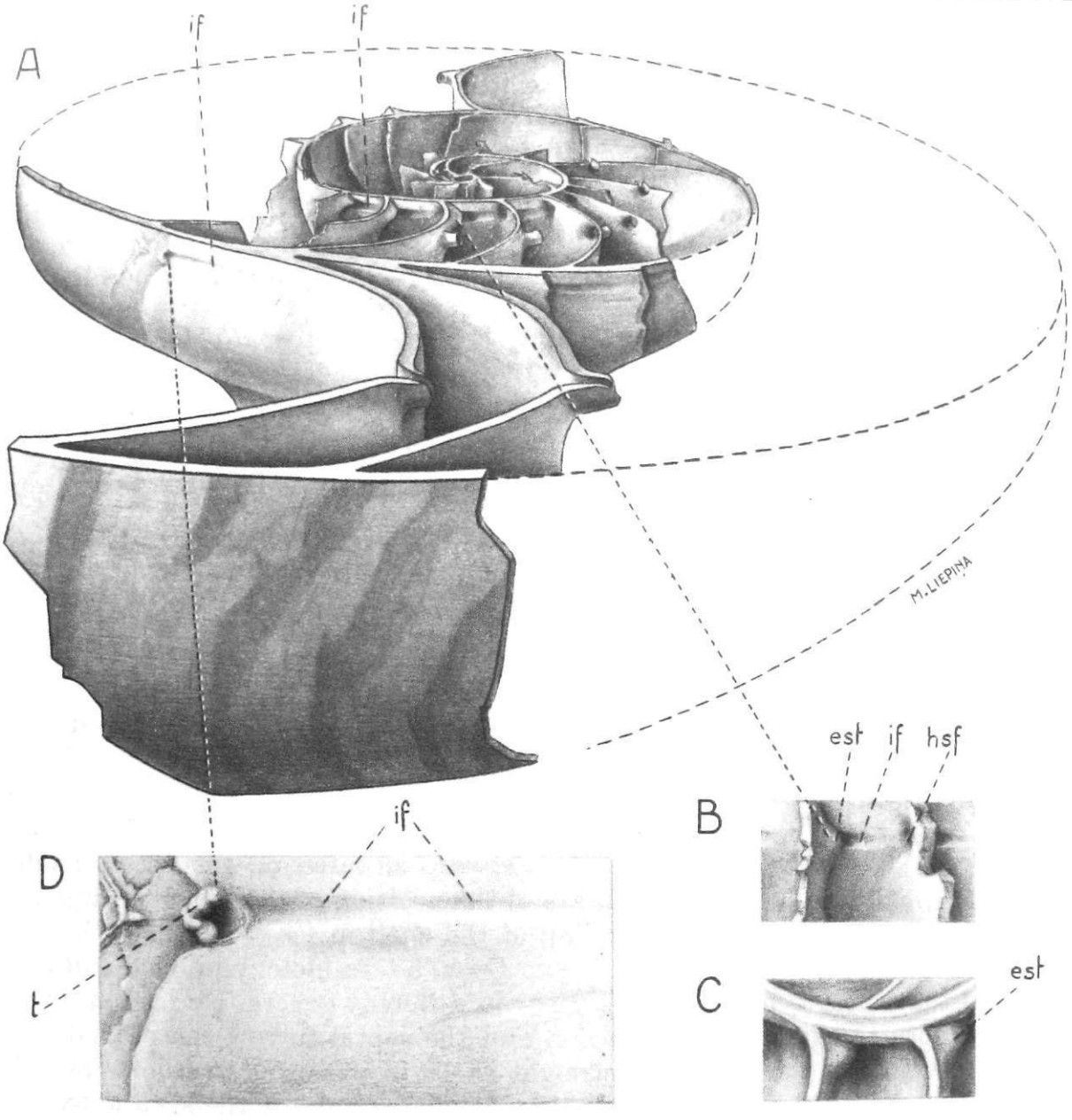
b) Septate division

The septate division of the shell will be more fully described in a forthcoming paper. Since, however, this division is important from the taxonomic point of view (e.g. the new terms, which are introduced for certain portions of the septum, are used in the taxonomic appendix to this paper) it is necessary here to discuss briefly this division.

The division of the shell in question here extends from the domiciliary division upwards to the apex of the shell and its cavity is divided by the septa into numerous chambers. In each septum two divisions may be distinguished: (1) the *septum proper*

[1] It is not quite clear at present how the "Haftepithel" during growth of the animal moves downwards on the inside of the domiciliary cavity. According to Keferstein (1861) and Appellöf (1893) the downward movement of the retractor muscle origin takes place in such a way that new muscle-substance is added to the ventral side of the muscle, whilst, simultaneously, the dorsal portion of the muscle is resorbed to a corresponding degree.

[2] In certain fossil nautiloids there occurs also an upper annular ridge (p. 231).



Text-fig. 4. *Nautilus pompilius* L. A, parts of right shell wall to show position of septal furrows and episeptal tubercles, $\times\frac{4}{5}$; B, details of septal furrows; hyposeptal fossae and episeptal tubercles in anterior view, $\times\frac{8}{5}$; C, details of episeptal tubercle from left side. $\times\frac{8}{5}$; D, details of septal furrow of the youngest septum, with a tubercle (*t*), $\times\frac{8}{5}$.
if, septal furrow; *est*, episeptal tubercle; *hsf*, hyposeptal fossa.

("free part of septum" Foerste & Teichert) and (2) the *siphonal funnel* ("siphonal segment"; text-fig. 2 B.).

The septum proper, which, corresponding to the internal shell layer, is composed of nacreous substance, is slightly arched with its convex face directed upwards. The individual septa have, on their ventral side close to the antero-medial margin, a little depression, the *hyposeptal fossa* (*hsf*, text-fig. 4 B; Appellöf 1893, pl. 10:3). On the dorsal side of the septum this depression is marked by an elevation, the *episeptal tubercle* ("dorsal lobe"; *est*, text-fig. 4 A, B, C; Appellöf loc. cit., pl. 10:2, 3). The hyposeptal fossa is distinct on the oldest septa, but becomes more and more shallow

on the succeeding younger ones and is entirely lacking on the youngest septa. The septum proper is composed of several nacreous lamellae; the more dorsal of these lamellae are well defined peripherically on the inside of the shell wall, whilst the ventral lamellae, on the contrary, continue downwards and merge with the shell wall without any distinct boundary (Appellöf, loc. cit.). In this way the lateral, mural parts of the latter lamellae ("mural part of septum") effects a fusion between each individual septum and the shell wall. The narrow zone, where every septum is thus fused on to the shell wall, is here called the *systegnosis* ("suture", "Lobenlinie").[1] The mural portion of each septum is very thin or absent entirely along the very antero-median line of the shell wall, where, accordingly, there arises a longitudinal septal furrow [Flower; "Normallinie", Sandberger (partim)] for each septum (*if*, text-fig. 4 A, B, D). In the older portion of the septate division this furrow extends from the hyposeptal fossa of each septum downwards to the episeptal tubercle of the septum next below. It should be noted that in certain full grown shells the septal furrow of the youngest septum ends ventrally in a little tubercle (*t*, text-fig. 4 D), which is not an episeptal tubercle.

The siphonal funnel and its terminology (text-fig. 2 B) has been already discussed by the present author (Mutvei 1956).

Fossil nautiloids

1. Coiling of the shell

It is well known that the posterior margin of the shell aperture in most fossil nautiloids is characterized by a distinct funnel emargination. In some shells there is, in addition, the septal furrow which is always situated on the anterior side of the shell (Flower 1939). With the guidance of the position of the funnel emargination Owen (1860) pointed out that the coiling of the shell in fossil nautiloids is of two kinds, forward and backward (according to Owen's terminology upward and downward), and that these types of coiling occur in different genera. By reference to the position of both the funnel emargination and the septal furrow the present writer was able to establish that so-called straight shells in paleozoic nautiloids are often also slightly coiled either along their entire height or only at the shell apex (text-fig. 5); this coiling is always backward.

Among the 9 genera discussed in the present paper 5 (*Uranoceras* (?), *Discoceras*, *Estonioceras*, *Eutrephoceras*, *Apheleceras*) have the shell coiled forwards and 4 (*Lyecoceras*, *Orthoceros*, *Geisonoceras*, *Baltoceras*) backwards.

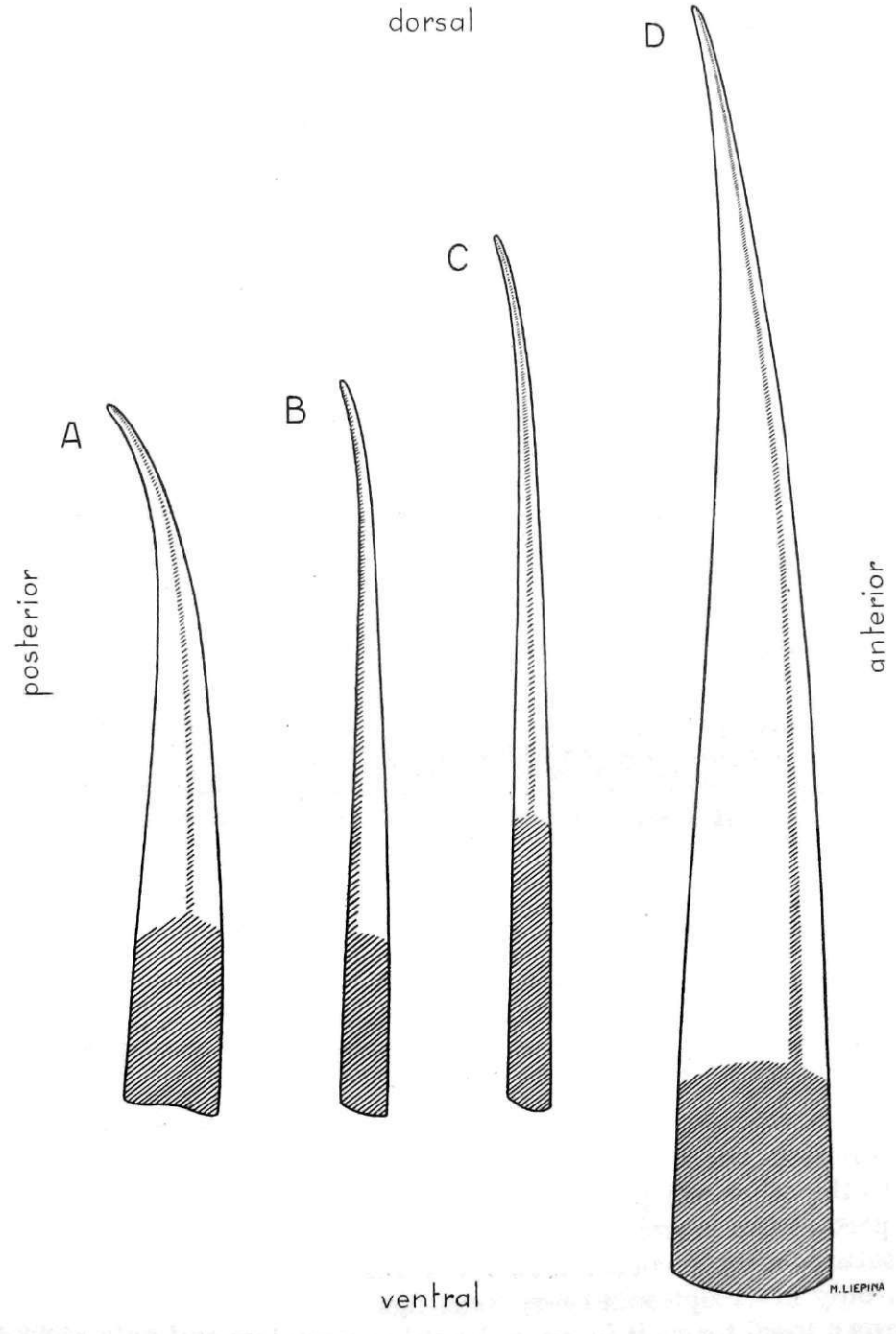
2. Annular elevation

The annular elevation in fossil nautiloids has been described by many writers (Mojsisovics 1873; 1882; Dames 1879; Dewitz 1879a, b, c; 1880; Schröder 1881; 1882; Noetling 1882; Rüdiger 1889; Foord & Crick 1889, 1890; Remelé 1890; Hyatt 1894; Crick 1898b; 1904; 1905; Loesch 1914; Kessler 1923), who stated that the posterior, anterior or lateral portion of the elevation generally broadens downwards as a

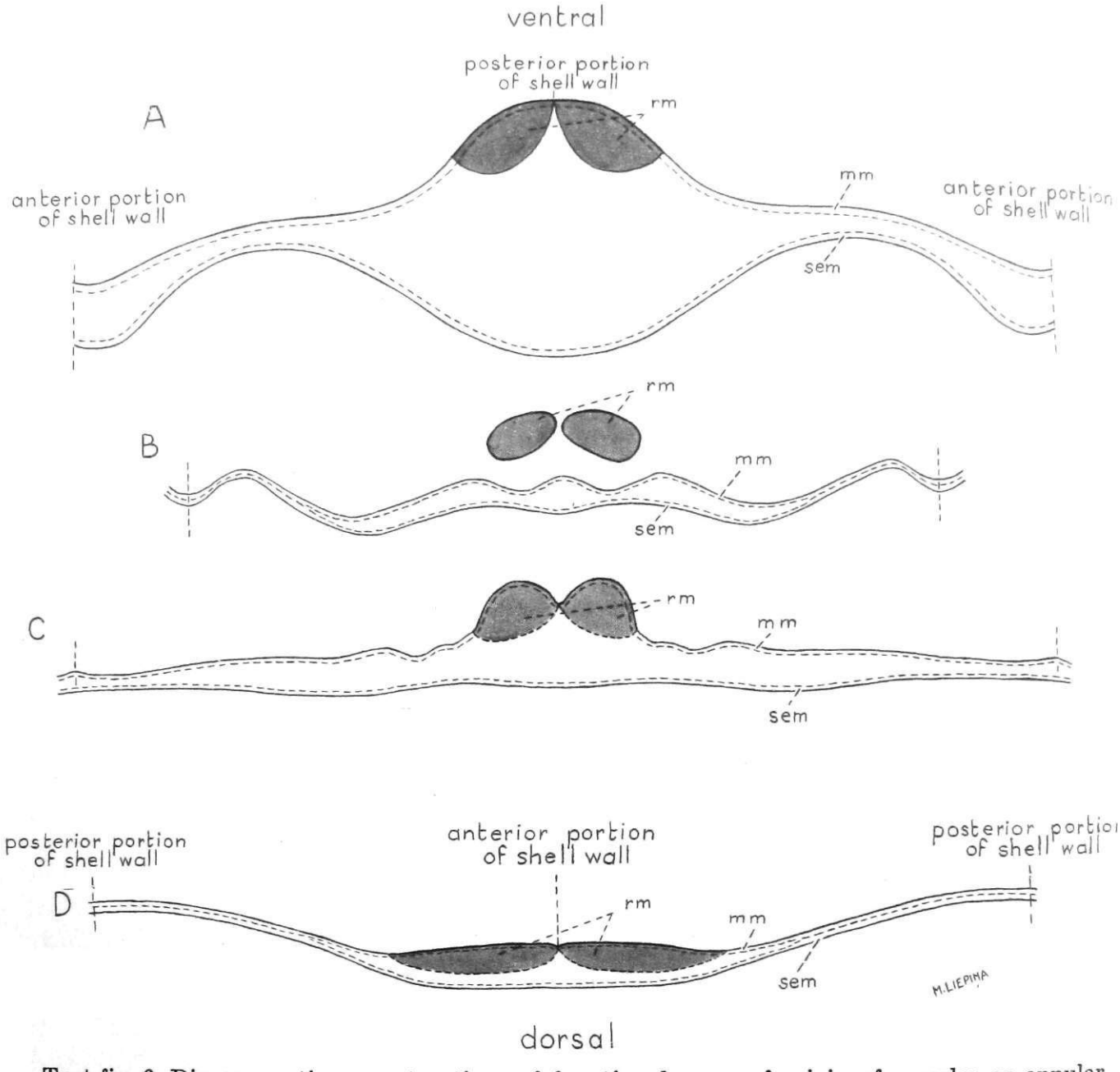
[1] The term "suture" has been used with reference to vertebrates, arthropods, gastropods, cephalopods, and plants, but in each case with a different meaning. Its usage, referring to cephalopods, may therefore be misleading and an alternative term has been adopted in the present paper.

lobe, the *ventral lobe*. From this lobe, in spite of its position, the main portion of the retractor muscle took its functional origin, in a way similar to *Nautilus*. This muscle was probably paired in all nautiloids so far investigated (*rm*, text-fig. 6). The longitudinal mantle-musculature and the sub-epithelial musculature in the dorsal portion of the body proper certainly had, as in *Nautilus*, their functional origin on a narrow zone along the lower and the upper margin of the annular elevation, respectively (*mm*, *sem*, text-fig. 6).

Owing to the varying position of its origin and to the varying curvature of the



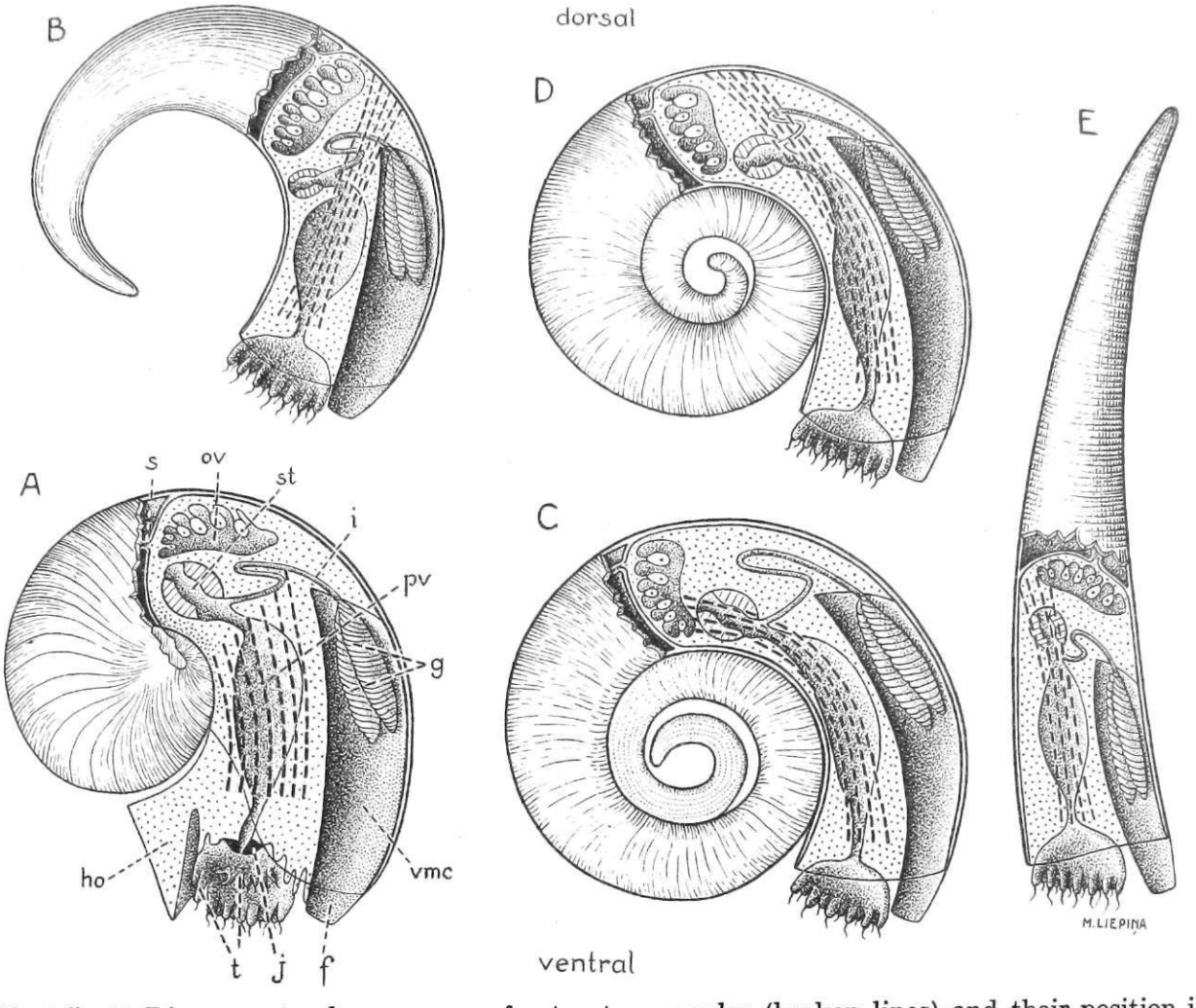
Text-fig. 5. Diagrammatic sketches of some backwarldy coiled shells of fossil nautiloids; A, *Lyecoceras gotlandense* n. sp.; B, *Baltoceras burchardi* (DEWITZ); C, "*Geisonoceras*" *scabridum* (ANGELIN); D, "*Orthoceras*" *angulatum* WAHL. All figures × $\frac{1}{3}$.



Text-fig. 6. Diagrammatic reconstructions of functional areas of origin of muscles on annular elevation of shell in four fossil nautiloids; annular elevation projected in one plane, nat. size. A, *Estonioceras perforatum* (SCHRÖDER); B, *Discoceras angulatum* (SAEMANN); C, *Uranoceras* (?) *longitudinale* (ANGELIN); D, *Lyecoceras gotlandense* n. sp.
mm, functional area of origin of longitudinal mantle musculature; *rm*, functional area of origin of retractor muscles; *sem*, functional area of origin of sub-epithelial musculature of dorsal portion of body proper.

domiciliary division, the retractor muscle in fossil nautiloids had different positions in relation to the other soft parts (text-fig. 7).

With respect to the morphology of the annular elevation in fossil nautiloids the following features must be pointed out. The annular elevation is prominent over its whole area only in exceptional cases (text-figs. 12; 15 A, B, C; pl. 2:4, 5, 6), but in most full-grown fossil forms it is, as in *Nautilus*, very low and only along its inferior margin is it clearly marked by a ridge, the *lower annular ridge* (x_1, text-figs. 8 A, B, C, E; 9 A, B; 10; 13 A, B, C; 14 A, B, C, E; 16 A–E; 17 A, B, C; 18 A, B, C). Immedi-



Text-fig. 7. Diagrams to show course of retractor muscles (broken lines) and their position in relation to other soft parts in *Nautilus* and in four fossil nautiloids. Soft parts in fossil forms, other than retractor muscles, reconstructed after *Nautilus*. A, *Nautilus pompilius* L.; B, *Uranoceras* (?) *longitudinale* (ANGELIN); C, *Apheleceras hibernicum* (FOORD & CRICK); D, *Estonioceras perforatum* (SCHRÖDER); E, *Lyecoceras longistriatum* n. sp.
f, funnel; *g*, gills; *ho*, hood; *i*, intestine; *j*, jaw; *ov*, ovarium; *pv*, proventriculus; *s*, siphonal cord; *st*, stomach; *t*, tentacles; *mc*, mantle cavity.

ately below the upper margin of the annular elevation there occurs also, in some forms, an *upper annular ridge* (x_2, text-figs. 8 A, B, C, E; 13 B, C; 16 A, B, C; 17 A, B, C) which has no corresponding structure in *Nautilus*. Apart from these two ridges, the surface of the annular elevation is mostly even and smooth. In certain cases, however, it shows more or less delicate vertical striae (text-figs. 8 A; 10 A; 13 A, C; 16 A, D; 17 A, B), or is divided into low tuberosities of varying form (text-figs. 10 D; 12 A, B, E; 15 A, B, C).

The functional area of origin of the paired retractor muscle, i.e. the ventral lobe of the annular elevation, is lateral in *Nautilus* and in Mesozoic nautiloids, but mainly anterior or posterior in Paleozoic nautiloids.[1] According to the position of the ventral lobe one may therefore distinguish in nautiloids three different types of annular

[1] In ammonites the area of origin for the retractor muscle is always situated dorsally (Waagen 1870; Mojsisovics 1873, 1882; Crick 1898a).

elevation, here named (1) the *Nautilus* type, (2) the *Estonioceras* type, and (3) the *Lyecoceras* type.[1]

(1) The annular elevation of the *Nautilus* type, which is characterized by the laterally situated ventral lobe, is so far known only in the following 9 fossil genera: *Eutrephoceras* (text-fig. 18; pl. 15:4, 5, 6), *Apheleceras* (pl. 16:1, 2, 3; Foord 1900), *Vestinautilus* (Foord & Crick 1889), *Solenocheilus* (Foord & Crick 1890), *Cenoceras* (Foord & Crick 1890; Crick 1898 b), *Pleuronautilus* (Mojsisovics 1873), *Syringoceras* (Mojsisovics ibid.), *Germanonautilus* (Mojsisovics 1882), *Grypoceras* (Mojsisovics ibid.), and in some undetermined genera [*"Bisiphytes" polygonalis* (SOW.) Foord & Crick 1890; *"Nautilus" rogeri* LOESCH, Loesch 1914; *"Nautilus" rotundus* CRICK, Crick 1898 b].

(2) The annular elevation of the *Estonioceras* type, characterized by the posteriorly situated ventral lobe, is, at present, known in the following four genera: *Estonioceras* (text-figs. 6 A; 8; 9 A, B, C; pls. 2:1, 2, 3; 3; 4:1, 2; Hyatt 1894), *Planctoceras* (text-fig. 9 D, E; pl. 5; Dewitz 1879b), *Uranoceras* (?) (text-figs. 6 C; 10; 11; pls. 4:3; 6; 7:4, 5), *Discoceras* (text-figs. 6 B; 12; 14; pls. 8; 9:1, 2, 3).

(3) The anteriorly situated ventral lobe is characteristic of the annular elevation of the *Lyecoceras* type which at the present time has been observed in the following four genera: *Lyecoceras* (text-figs. 6 D; 13; 16 A, B, C, G; pls. 9:4, 5; 10; 11; 12), *Orthoceros* (pl. 2:4, 5, 6; Dewitz 1879a, b; 1880; Schröder 1881; Remelé 1890), *Baltoceras* (text-fig. 16 D–F; pl. 14:1–6; Dewitz 1879c; 1880; Schröder 1881), *Lituites* (Schröder 1881; Noetling 1882), and in two undetermined genera [*"Geisonoceras" scabridum* (ANGELIN) text-fig. 15; pls. 13; 14:7, 8, 9; Rüdiger 1889; and *"Orthoceras" angulatum* WAHL., text-fig. 17; pl. 15:1, 2, 3].

Particular attention should be drawn to the fact that the annular elevation of the *Lyecoceras* type is to be found only in the backwardly coiled shells[2], whilst the annular elevations of the *Estonioceras* and the *Nautilus* types occur in the forwardly coiled shells. In spite of the fact that the annular elevation is so far known only in a small number of fossil nautiloids, it is already possible to foresee its great importance to nautiloid taxonomy.

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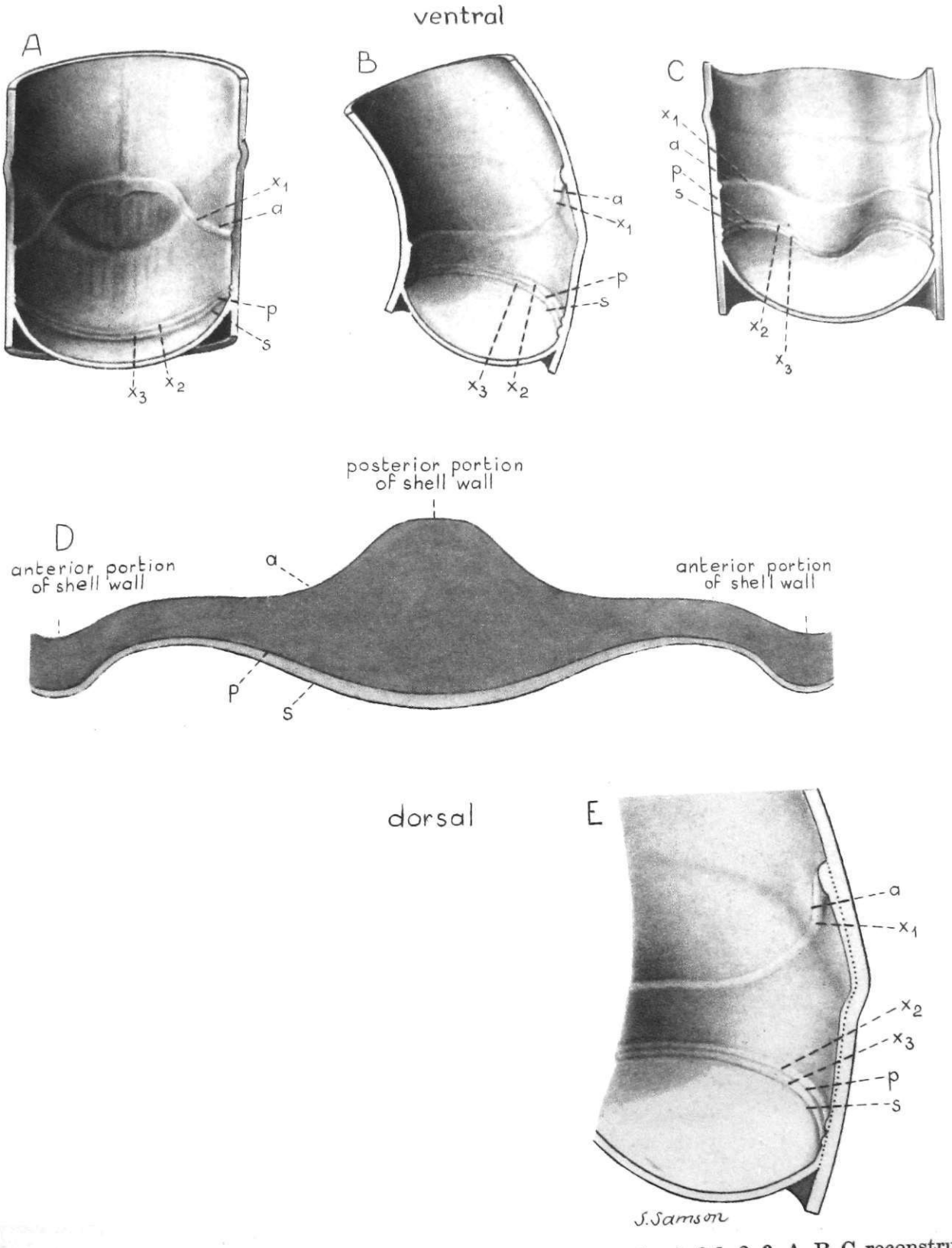
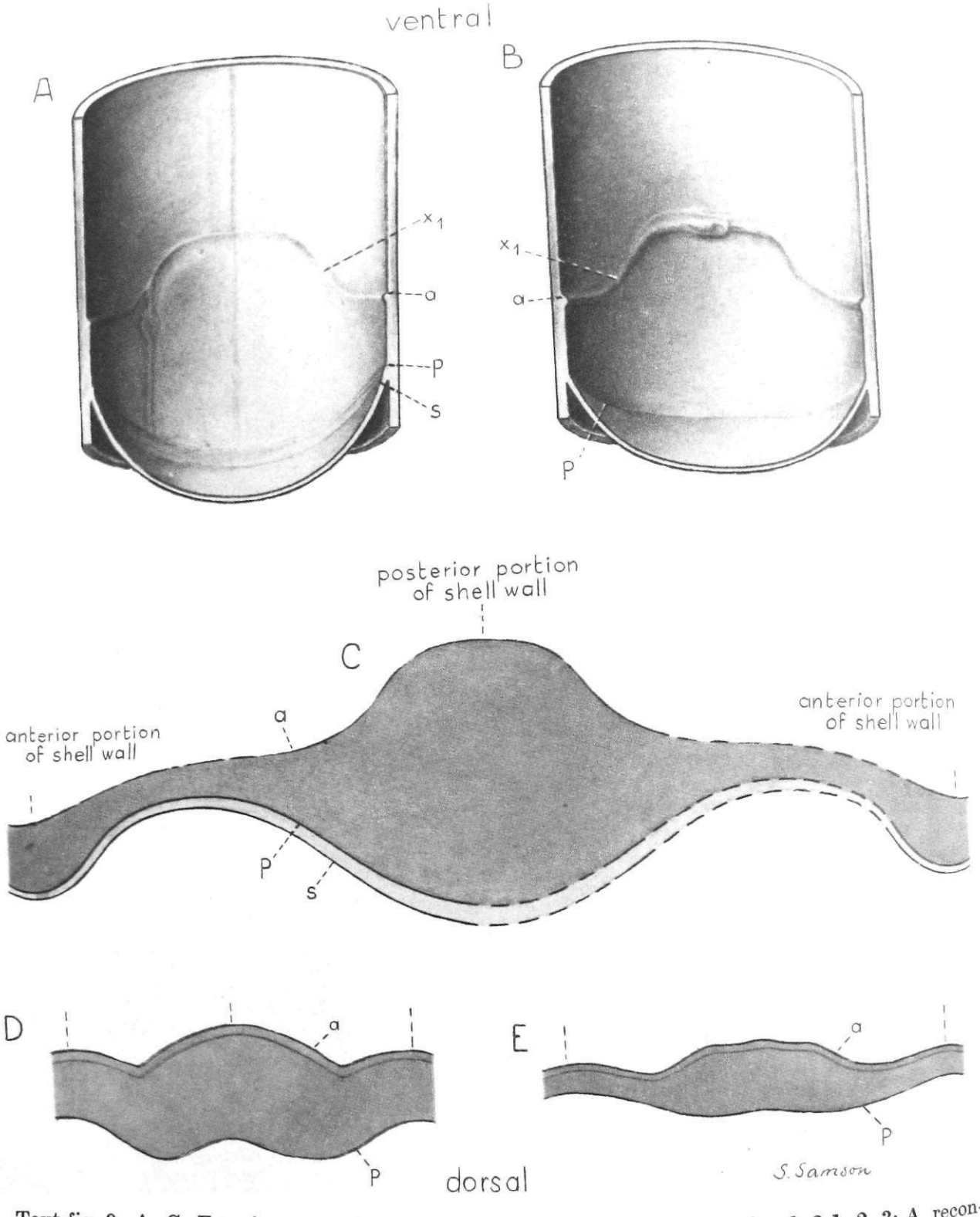
[1] In the following review only those genera in which the annular elevation is reliably described are included [not *Endoceras* (Schröder 1881), *Clinoceras* (Mascke 1876; Dewitz 1880), *Rhynchorthoceras* (Schröder 1881), *"Meloceras"* (Crick 1905), Amphereopsis (Crick 1904)].

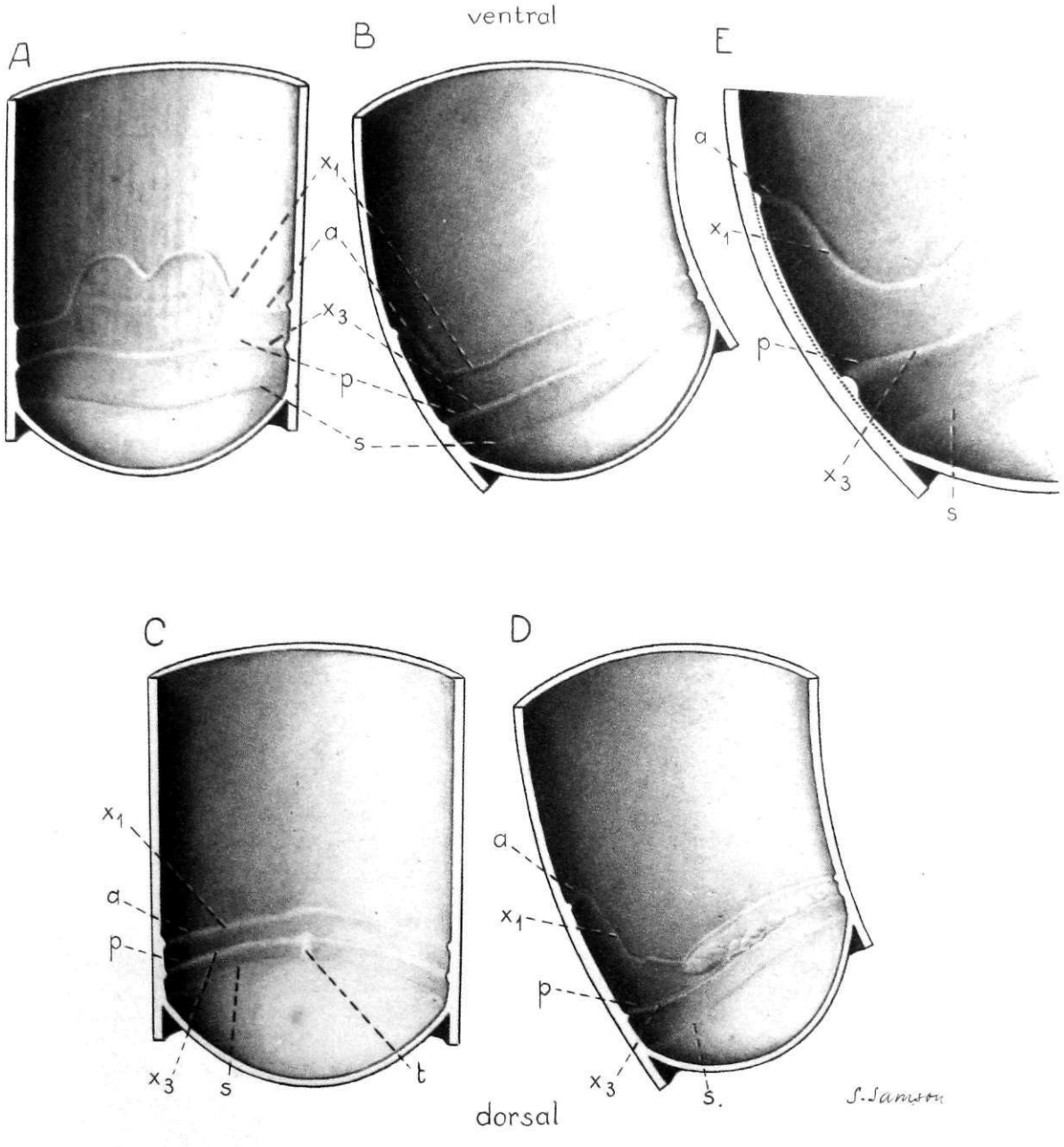
[2] In the genus *Lituites*, however, only the ventral portion of the shell is coiled backwards, whilst the dorsal portion forms a forwardly directed spiral.



Text-fig. 8. *Estonioceras impressum* (HYATT), same specimen as in pl. 2:1, 2, 3. A, B, C, reconstruction of annular elevation on posterior, lateral, and anterior portions of shell wall, respectively, $\times \frac{6}{5}$; D, annular elevation projected in one plane, $\times \frac{6}{5}$; E, details of fig. B, $\times \frac{12}{5}$.
a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part; x_1, ventral annular ridge; x_2, dorsal annular ridge; x_3, mural ridge.

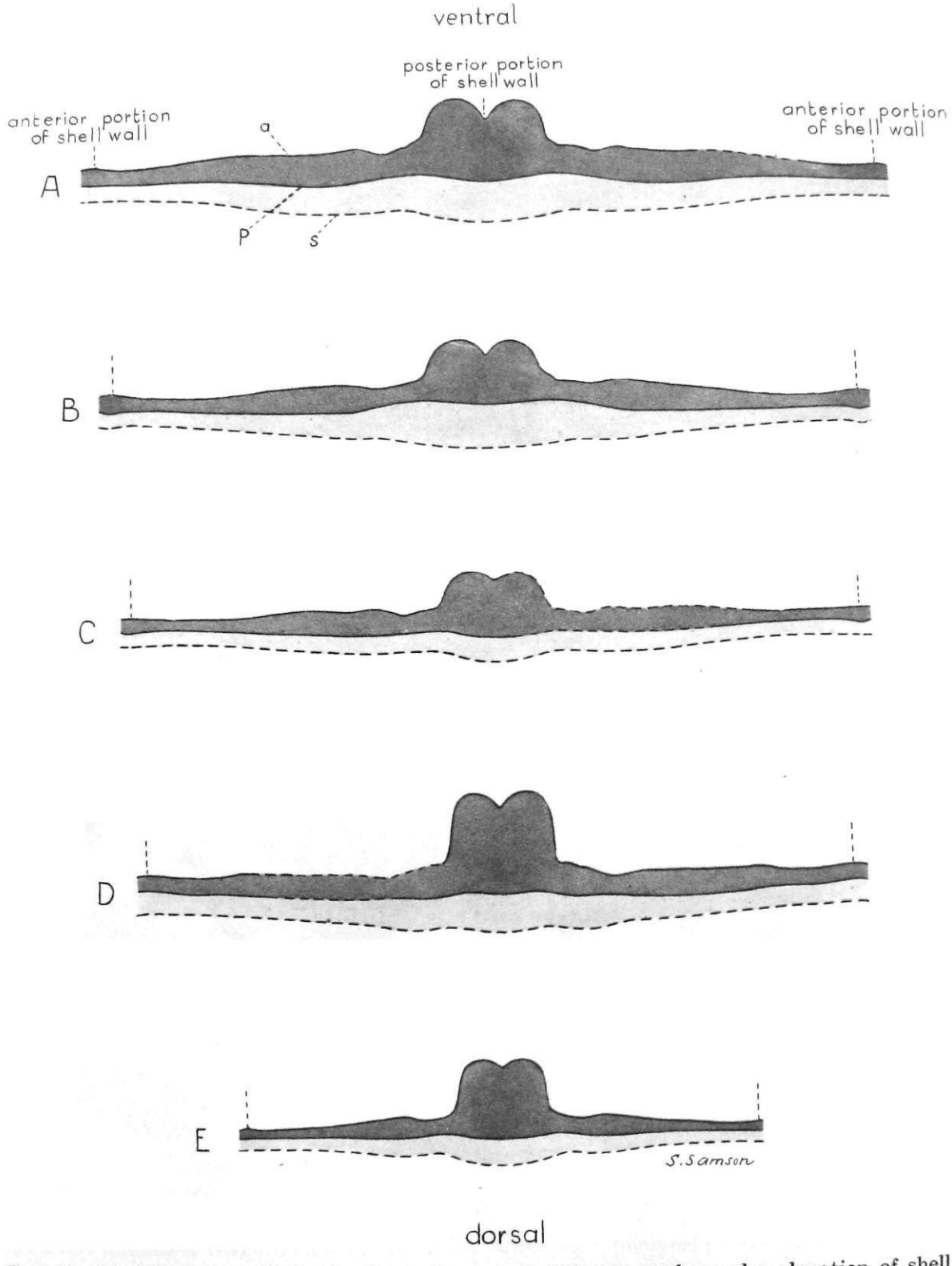


Text-fig. 9. A, C, *Estonioceras perforatum* SCHRÖDER, same specimen as in pl. 3:1, 2, 3; A, reconstruction of annular elevation on posterior portion of shell wall, $\times\frac{6}{5}$; C, diagram of annular elevation projected in one plane, $\times\frac{6}{5}$; B, *Estonioceras imperfectum* (QUENSTEDT), same specimen as in pl. 3: 4, 5; reconstruction of annular elevation on posterior portion of shell wall, $\times\frac{6}{5}$; D, E, *Planoceras falcatum* (SCHLOTH.), two diagrams of annular elevation projected in one plane, $\times\frac{6}{5}$; same specimens as in pl. 5:4, 5, 6, and pl. 5:1, 2, 3.
a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part.



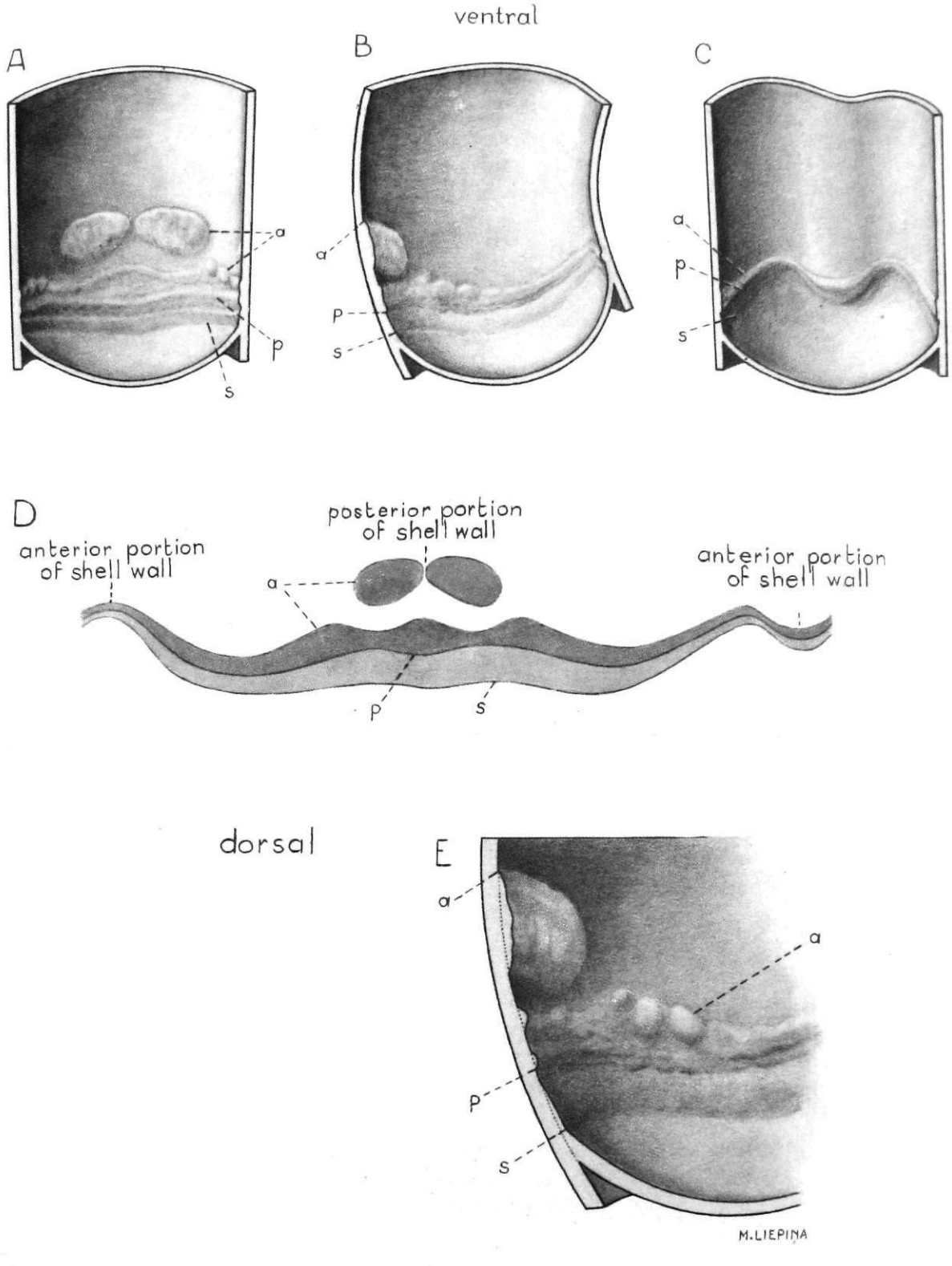
Text-fig. 10. *Uranoceras* (?) *longitudinale* (ANGELIN). A, B, C, reconstruction of annular elevation on posterior, lateral, and anterior portions of shell wall, respectively; same specimen as in pl. 6, $\times\frac{3}{4}$; E, details of fig. B, $\times\frac{3}{2}$; D, reconstruction of annular elevation on lateral portion of shell wall, same specimen as in pl. 4:3, $\times\frac{3}{4}$.

a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part; *t*, tubercle of septal furrow of youngest septum; x_1, ventral annular ridge; x_2 mural ridge.

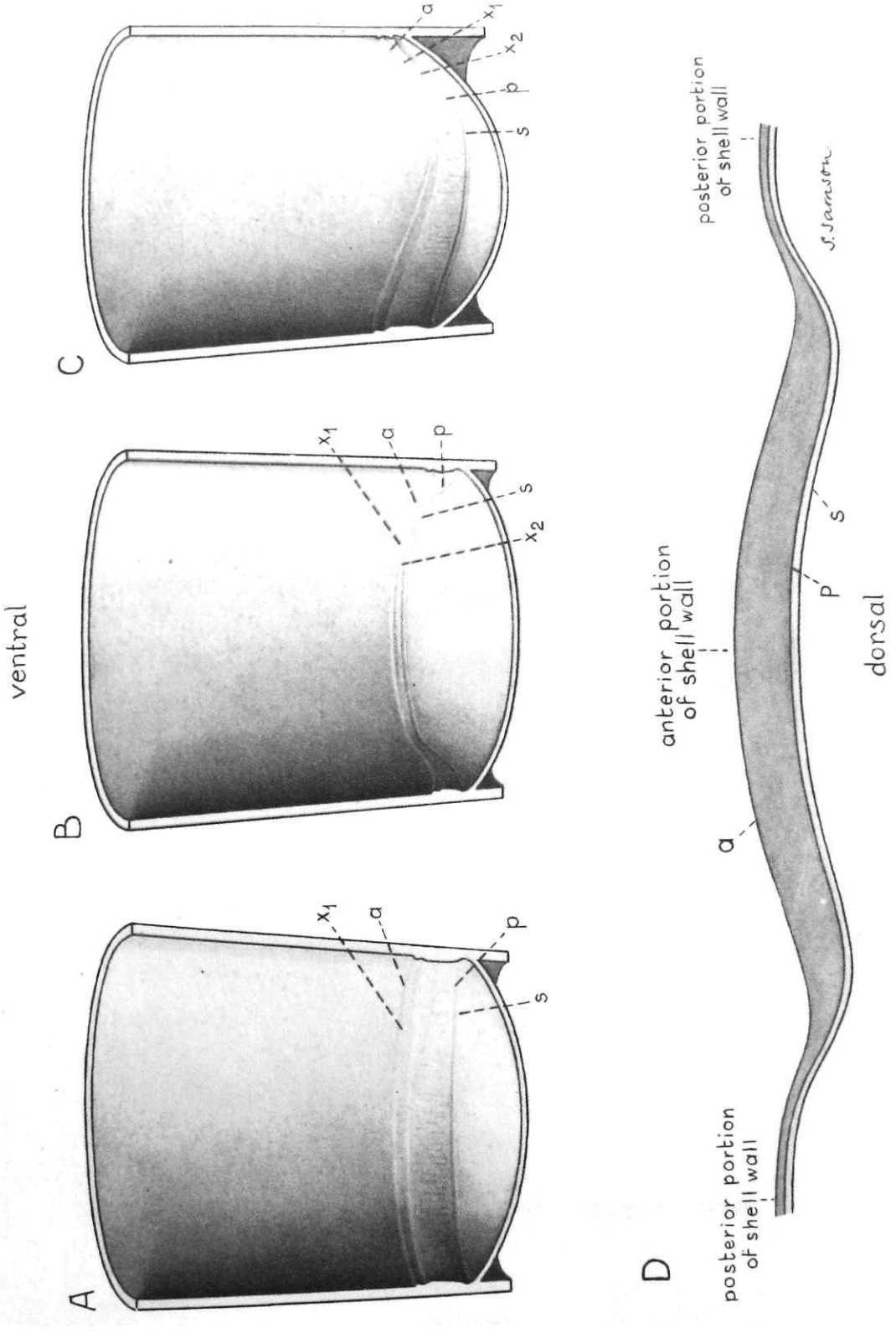


Text-fig. 11. *Uranoceras* (?) *longitudinale* (ANGELIN). Diagrams of annular elevation of shell in five specimens; annular elevations projected in one plane; × ⅔; A, same specimen as in pl. 6; B, specimen UPI, No. D 437; C, specimen UPI, No. D 436; D, same specimen as in pls. 4:3; 7:5; E, same specimen as in pl. 7:4.

a, ventral margin of annular elevation of shell ; p. dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part.

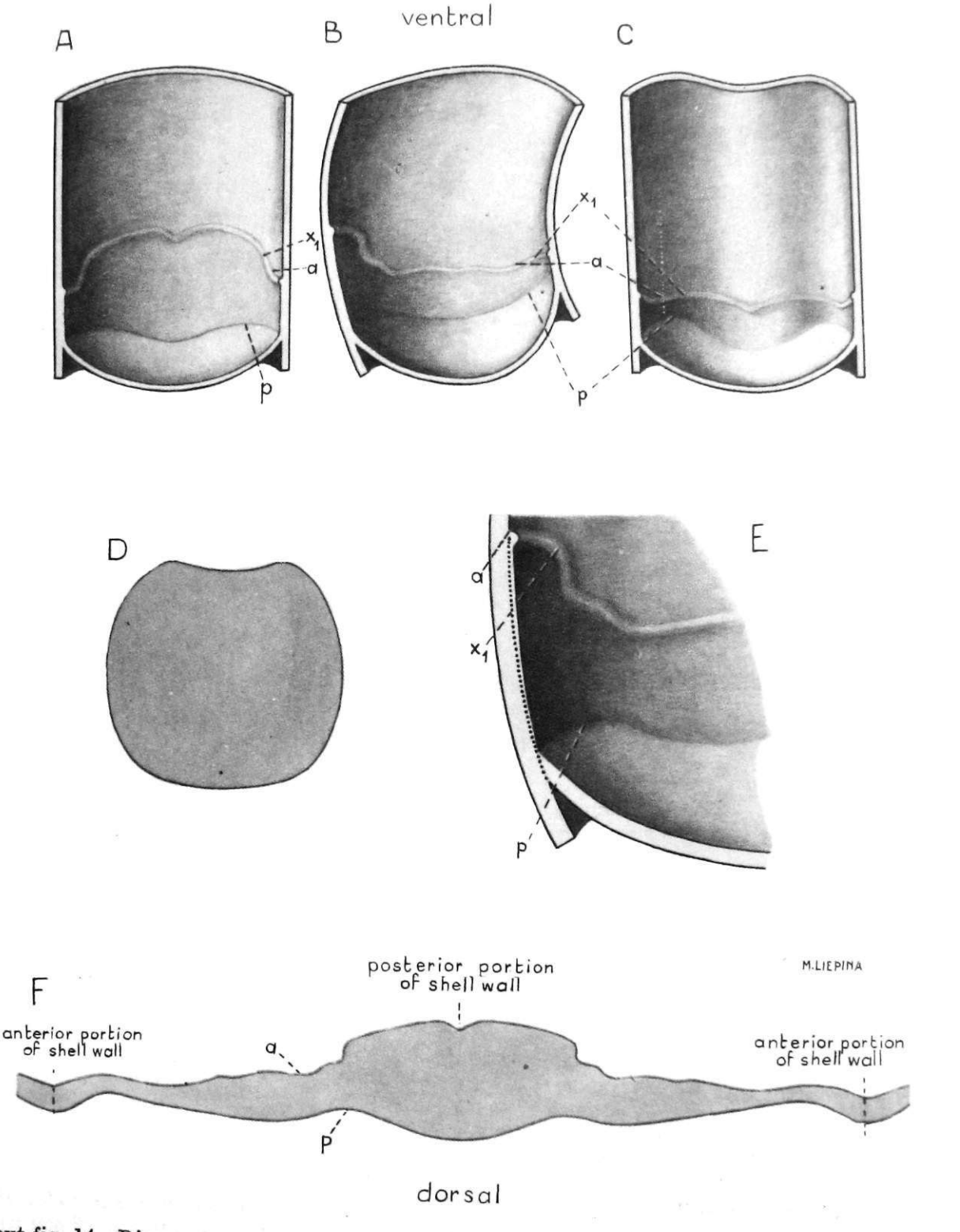


Text-fig. 12. *Discoceras angulatum* (SAEMANN), same specimen as in pl. 8. A, B, C, reconstruction of annular elevation on posterior, lateral, and anterior portions of shell wall, respectively, $\times\frac{6}{5}$; D, diagram of annular elevation projected in one plane, $\times\frac{6}{5}$; E, details of fig. B, $\times\frac{12}{5}$.
a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part.



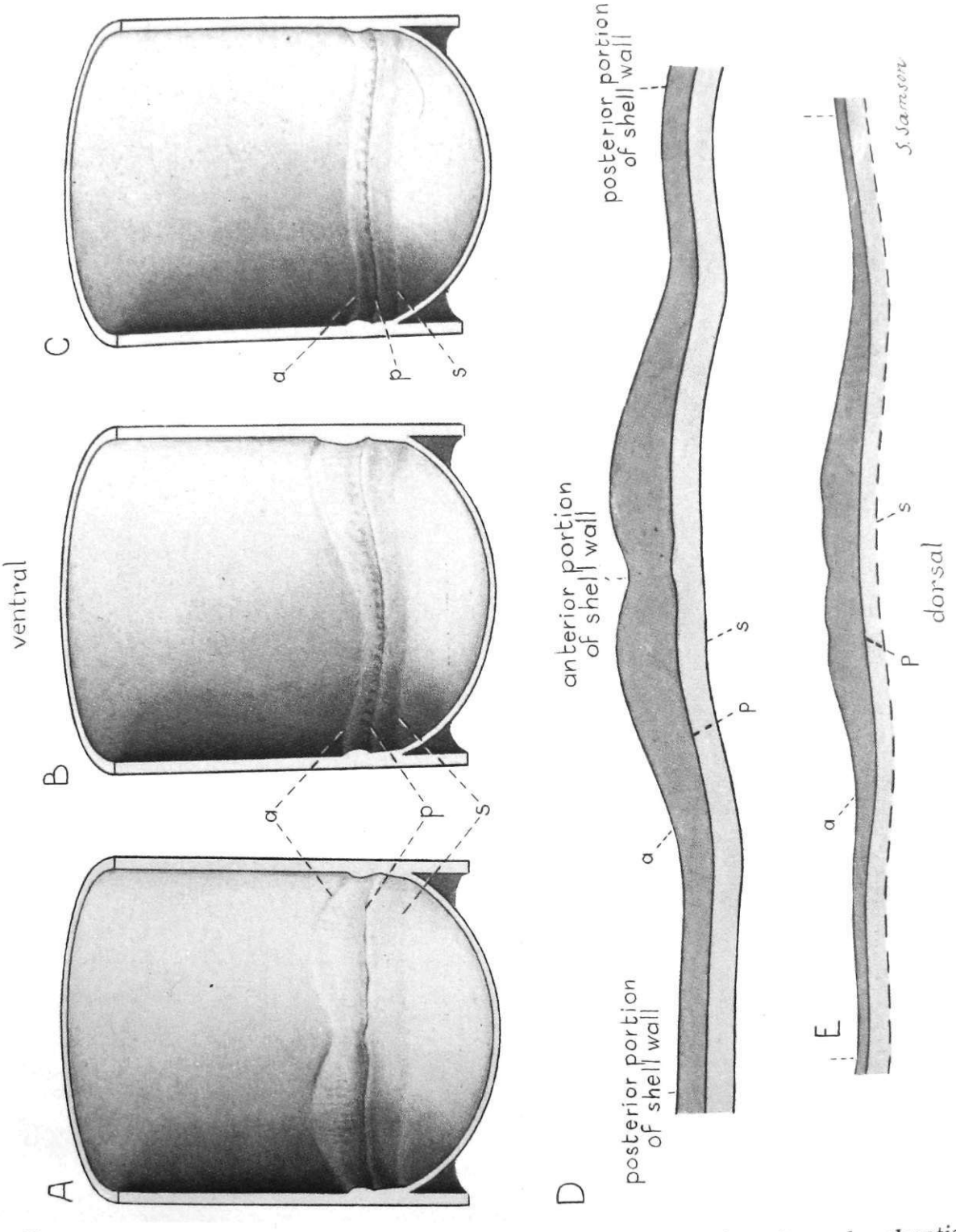
Text-fig. 13. *Lyecoceras* (?) sp., same specimen as in pl. 12. A, B, C, reconstruction of annular elevation on anterior, posterior, and lateral portions of shell wall, respectively, × $\frac{4}{5}$; D, diagrams of annular elevation of shell projected in one plane, × $\frac{4}{5}$.

a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part; x_1, ventral annular ridge; x_2 dorsal annular ridge.



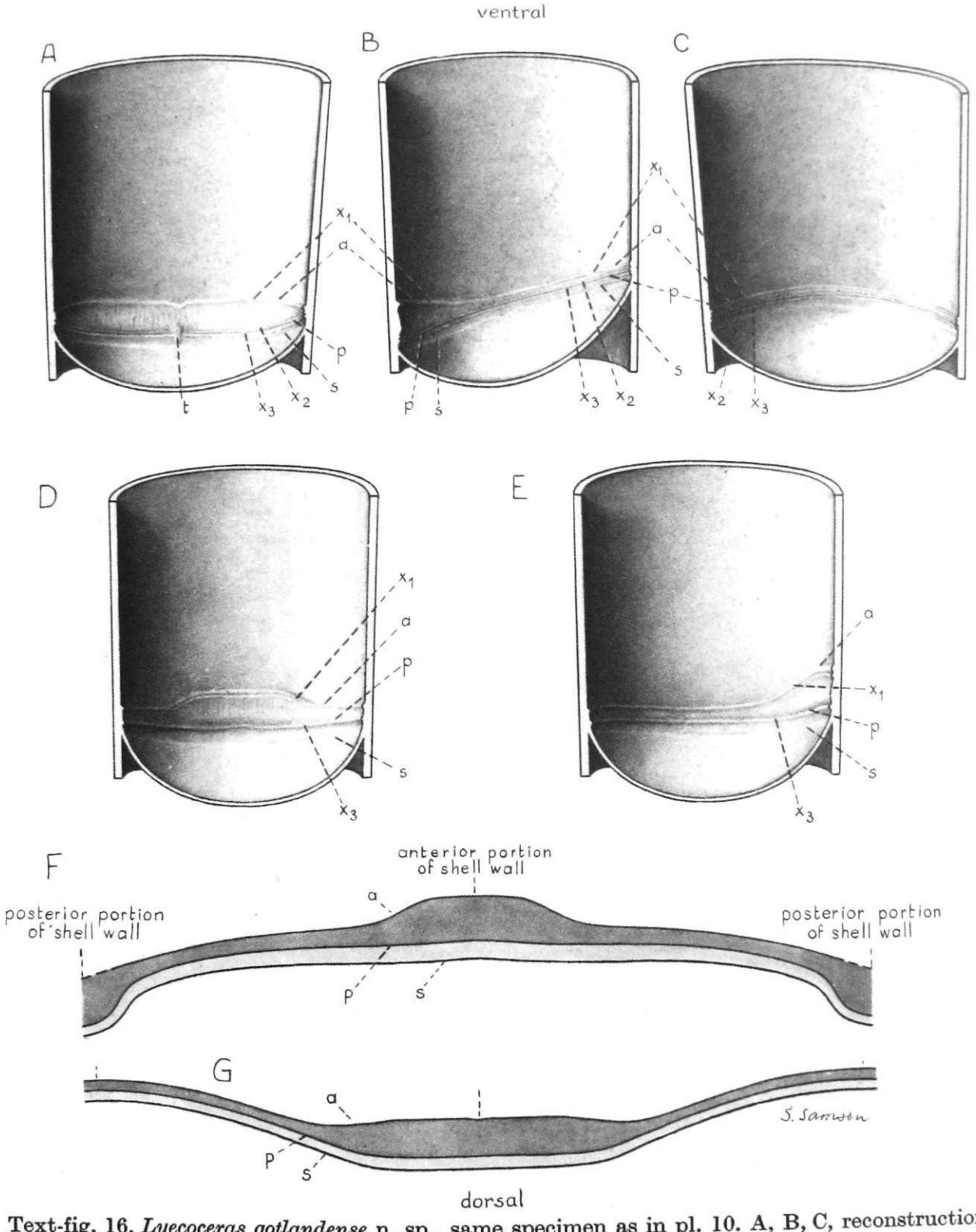
Text-fig. 14. *Discoceras* sp., same specimen as in pl. 9:1, 2, 3. A, B, C, reconstruction of annular elevation on posterior, lateral, and anterior portions of shell wall, respectively, $\times \frac{6}{5}$; D, horizontal section of domiciliary division of shell, $\times \frac{6}{5}$. E, details of fig. B, $\times \frac{12}{5}$; F, diagram of annular elevation projected in one plane, $\times \frac{6}{5}$.

a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; x_1, ventral annular ridge.



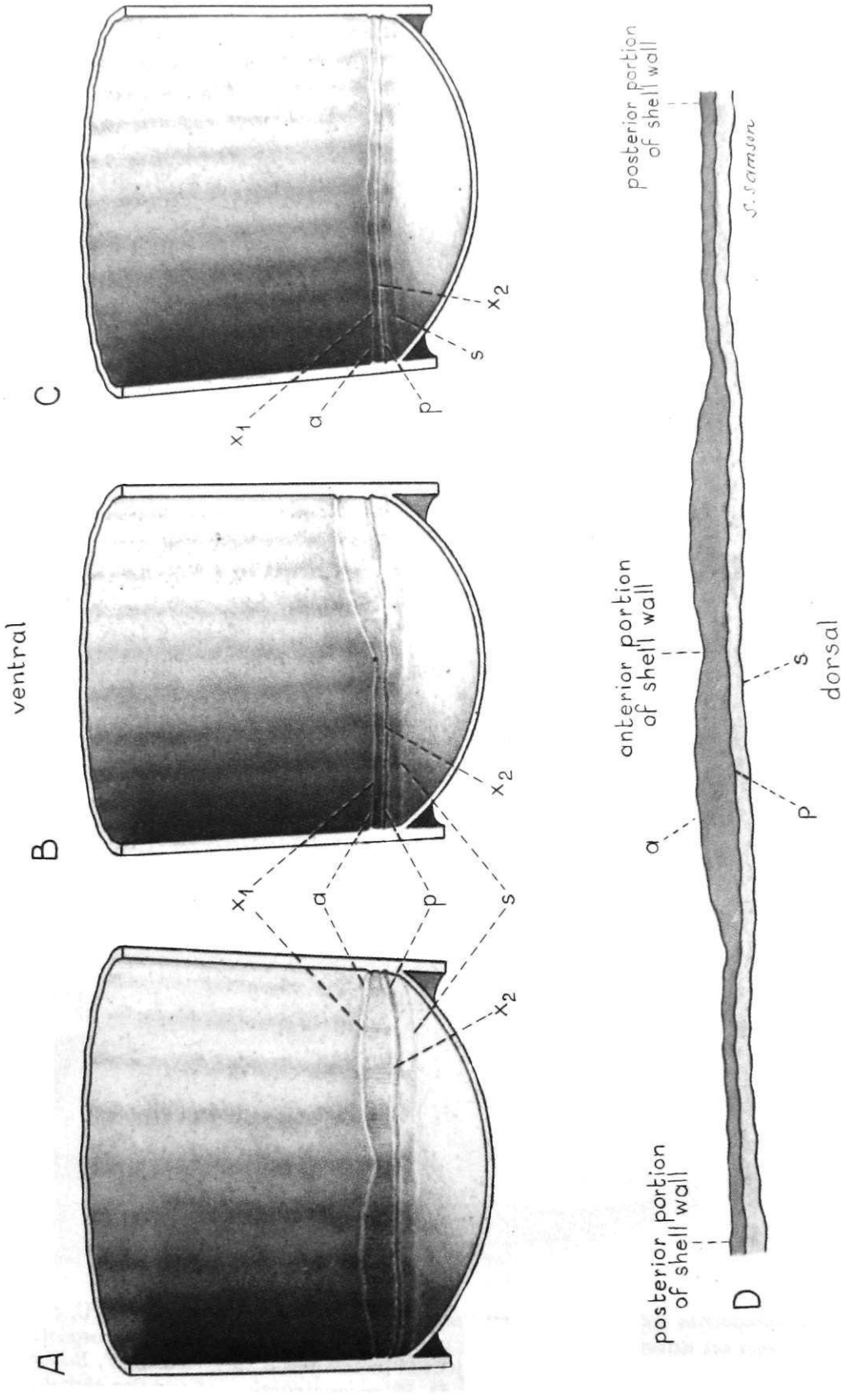
Text-fig. 15. "*Geisonoceras*" *scabridum* (ANGELIN). A, B, C, reconstruction of annular elevation on anterior, lateral, and posterior portions of shell wall, respectively, × 3, same specimen as in pl. 13:1–6; D, diagram of annular elevation of shell in same specimen projected in one plane, × $\frac{12}{5}$; E, diagram of annular elevation of shell in same specimen as in pl. 14: 7, 8 projected in one plane, × $\frac{12}{5}$.

a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part; *t*, tubercle of septal furrow of the youngest septum.

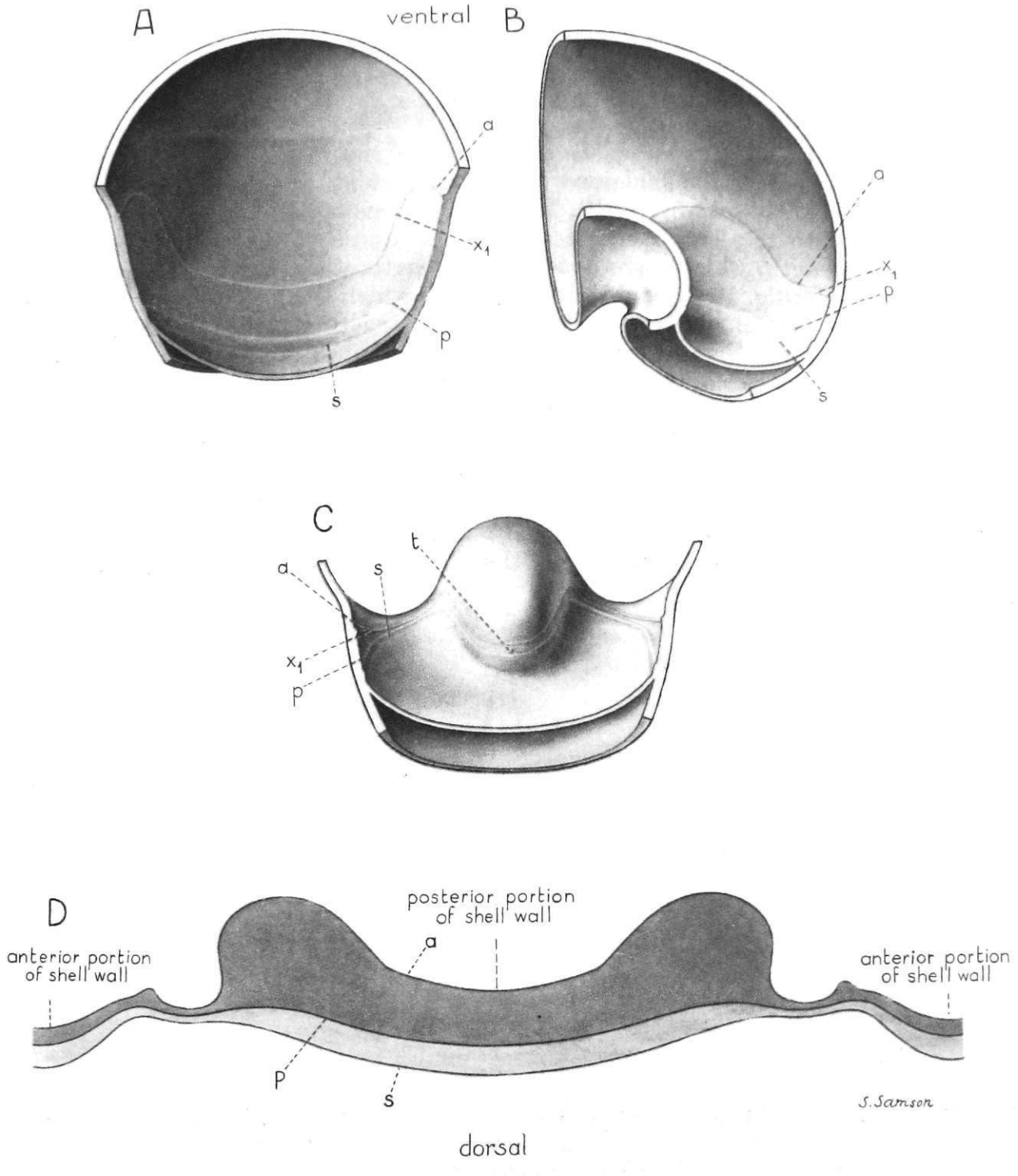


Text-fig. 16. *Lyecoceras gotlandense* n. sp., same specimen as in pl. 10. A, B, C, reconstruction of annular elevation on anterior, lateral, and posterior portions of shell wall, respectively, nat. size; G, diagram of annular elevation of shell projected in one plane, nat. size. D–F, *Baltoceras burchardi* (Dewitz), same specimen as in pl. 14:1–6. D, E, reconstruction of annular elevation on anterior and lateral portions of shell wall, respectively, × 2; F, diagram of annular elevation of shell projected in one plane, × 2.

a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part; *t*, tubercle of septal furrow of youngest septum; x_1, ventral annular ridge; x_2, dorsal annular ridge; x_3, mural ridge.



Text-fig. 17. "*Orthoceras*" *angulatum* WAHLENBERG, same specimen as in pl. 15:1, 2, 3. A, B, C, reconstruction of annular elevation on anterior, lateral, and posterior portions of shell wall, respectively, × ¾; D, diagram of annular elevation of shell projected in one plane, × ¾.
a, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation; *s*, angle between the youngest septum proper and its mural part; x_1, ventral annular ridge; x_2 dorsal annular ridge.



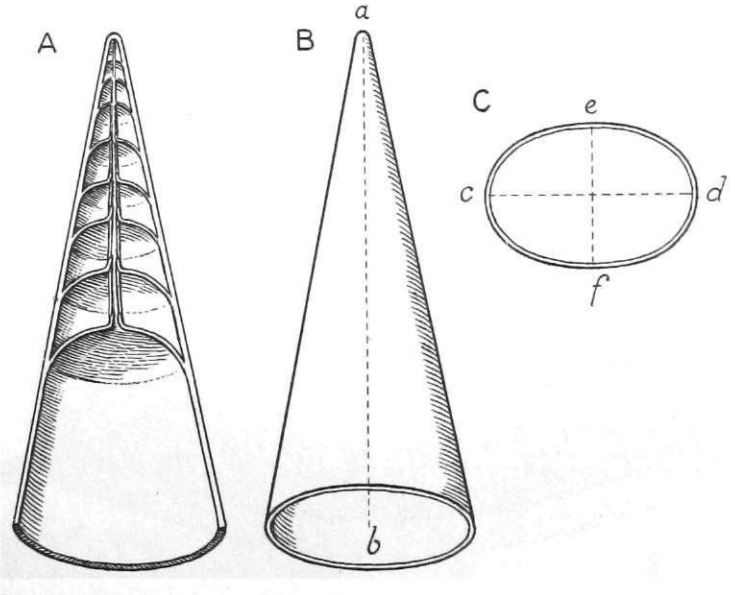
Text-fig. 18. *Eutrephoceras bellerophon* (LUNDEGREN), same specimen as in pl. 15:4, 5, 6. A, B, C reconstruction of annular elevation on posterior, lateral, and anterior portions of shell wall respectively, nat. size; D, diagram of annular elevation of shell projected in one plane, nat. size *a*, ventral margin of annular elevation of shell; *p*, dorsal margin of annular elevation of shell; *s* angle between the youngest septum proper and its mural part; *t*, tubercle of septal furrow of the youngest septum; x_1, ventral annular ridge.

Taxonomic appendix

Measurements

The dimensions used in measuring the shells of the fossil nautiloids dealt with below can be most easily explained by reference to a hypothetical, generalized, straight-shelled form (text-fig. 19 B). These dimensions are as follows: (1) the height, which is equal to the length of the dorso-ventral axis of the shell (*a-b*, text-fig. 19 B); (2) the length, which corresponds to the length of the antero-posterior axis of the shell (*c-d*, text-fig. 19 C); and (3) the breadth, which is equal to the length of the transverse axis of the shell (*e-f*, text-fig. 19 C). The structure of the septa and siphonal tube were suitably studied in a median-sagittal section of the shell (text-fig. 19 A), whilst the circumference of the shell was studied in horizontal sections (text-fig. 19 C) lying at right angles to the dorso-ventral axis of the shell. The distance between two succeeding septa is conveniently given in proportion to the morphological length of the shell, measured midway between the two septa.

The coiled shells were measured in the same manner as the straight ones having regard to their anatomical orientation. The height of the shell is thus equal to the length of the coiled dorso-ventral axis of the shell and the other dimensions are given in relation to this coiled axis.



Text-fig. 19. Diagram of hypothetical, generalized straight-shelled nautiloid. A, median-sagittal section; B, external aspect; C, horizontal section.
***a–b*, height; *c–d*, length; *e–f*, breadth.**

A. *Uranoceras* HYATT 1883

The genus *Uranoceras* was erected by Hyatt (1883) on a Bohemian species, "*Cyrtoceras*" *uranum* (Barrande 1866; 1867; 1877) and was later revised by Foerste (1925). On the basis of the descriptions of these three writers the following diagnosis may be given for this genus: shell coiled in an open whorl; morphological length of shell somewhat greater than breadth; circumference of shell elliptical, or somewhat quadrangular; shell ornamentation consisting of delicate, vertical ridges; systegnoses

turn upwards in a paired curve on lateral portion of shell wall, but downwards in an unpaired curve on anterior and posterior portions of shell wall; siphonal tube situated slightly posterior to dorso-ventral axis of shell; proximal division of siphonal funnel short, distal division long; siphonal tube narrow in the former division, but widens in the latter; on the inside of siphonal tube slight annular ridges in some cases.

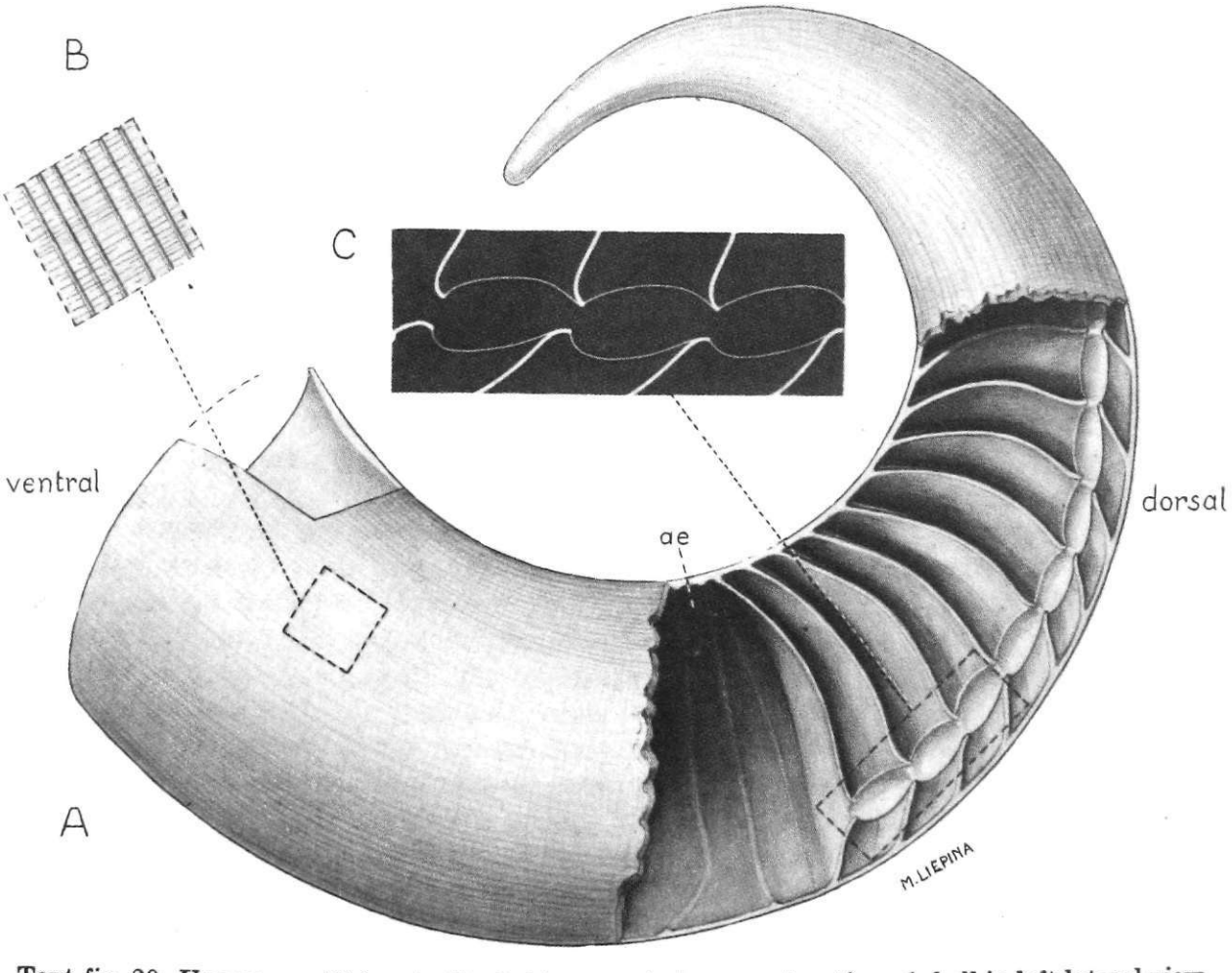
According to Foerste (loc. cit.) the genus *Uranoceras* includes the following three species: the genotype *"Cyrtoceras" uranum* (Barrande, loc. cit.) from the Silurian of Bohemia; *U. hercules* (Winchell & Marcy) and *U. dyeri* (Hyatt), both from U.S.A., Racine dolomite, Middle Silurian. In addition, a fourth species, *U.* (?) *longitudinale* (Angelin) is here included in this genus.

Uranoceras (?) *longitudinale* (Angelin)

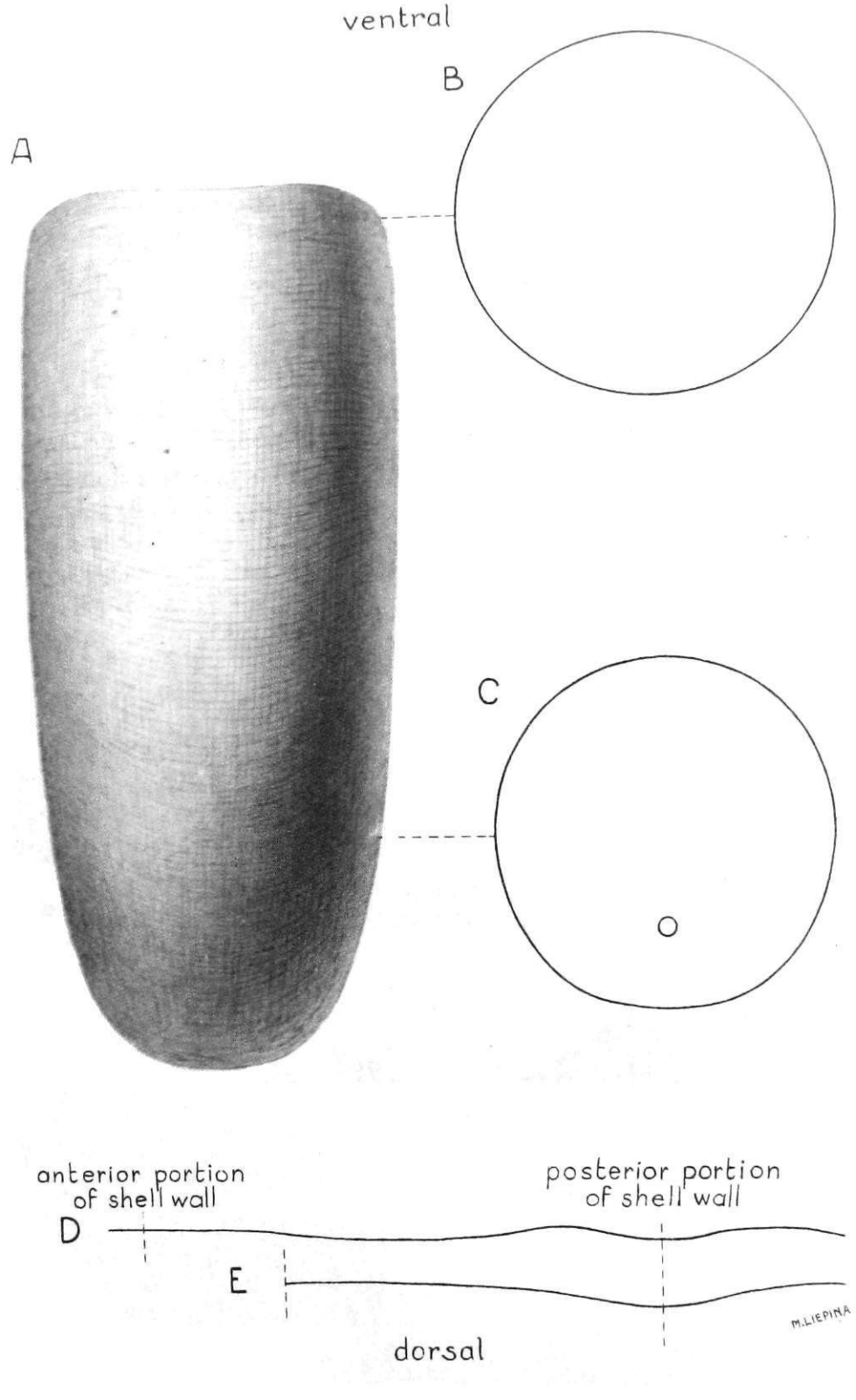
Text-figs. 6 C; 7 B; 10; 11; 20; 21; pls. 4:3; 6; 7; 17; 18.

1880 *Cyrtoceras longitudinale* n. sp. — Angelin, Fragm. Silurica, p. 11, pl. 16:5.

Material.—A great number of specimens which show the domiciliary division of the shell and the ventral portion of the septate division. Only few specimens are, however, sufficiently well preserved for description.



Text-fig. 20. *Uranoceras* (?) *longitudinale* (Angelin). A, reconstruction of shell in left lateral view, with shell wall and sections of septa removed at one place, × $\frac{4}{5}$; B, details of shell ornamentation, × $\frac{8}{5}$; C, part of siphonal tube in median-sagittal section, × $\frac{8}{5}$.
ae, annular elevation of shell.



Text-fig. 21. *Uranoceras* (?) *longitudinale* (ANGELIN). A, reconstruction of shell in posterior view, × ⅔; B, C, two horizontal sections of shell at the levels indicated; D, E, diagrams of two systegnoses projected in one plane, × ⅔.

LECTOTYPE: RM, No. Mo 149998 (pl. 17:2, 3; Angelin 1880, pl. 16:5).

STRATUM AND LOCALITIES.—Boda Limestone, which belongs to the uppermost Ordovician; Dalecarlia: Kallholn, Osmundsberget and Solberga (?).

DIAGNOSIS.—Morphological length of shell equal to breadth, or slightly greater; circumference of shell circular, or broadly elliptical; shell ornamentation consisting of delicate, vertical ridges separated by broad and smooth intervals; systegnoses practically horizontal on anterior portion of shell wall, but turn upwards in an unpaired curve on posterior portion of shell wall and in some cases in a slight, paired curve on lateral portion of shell wall; distance between septa in ventral portion of septate division equal to $\frac{1}{4}$–$\frac{1}{5}$ of the morphological length of shell; distance between siphonal tube and posterior portion of shell wall corresponds to $\frac{1}{5}$–$\frac{1}{6}$ of equal length.

DESCRIPTION.—A reconstruction based on several incomplete specimens shows that the shell must have formed a loose whorl (text-fig. 20 A), the coiling of which decreased slightly with the proceeding growth of the animal. The morphological length of the shell, which attains up to 60 mm at the shell aperture, is equal to the breadth, or slightly greater. Consequently, the circumference of the shell is circular, or broadly elliptical (text-fig. 21 B, C). The increase of the morphological length and breadth is, as a rule, greater in the dorsal portion of the shell than in the ventral portion, but in some specimens it is also quite considerable in the latter portion (pl. 4:3). The height of the domiciliary division in the full-grown shell is somewhat greater than $\frac{1}{3}$ of the whole morphological height of the shell. A slight antero-median tubercle (*t*, text-fig. 10 C) on the inside of the domiciliary cavity immediately below the youngest septum belongs, in all probability, to the septal furrow of the youngest septum.

The shell ornamentation is made up of delicate, vertical ridges separated by rather broad and smooth intervals (text-fig. 20 B; pl. 18). In certain places in the lectotype these ridges are replaced by furrows (pl. 18:1); the furrows, but not the ridges, are mentioned in Angelin's diagnosis.

The septa in the ventral portion of the septate division of the shell are practically horizontal (text-fig. 20 A; pls. 4:3; 6:2; 7:2). The distance between the septa in the ventral portion of the septate division corresponds to $\frac{1}{4}$–$\frac{1}{5}$ of the morphological length of the shell. The systegnoses are almost horizontal on the anterior portion of the shell wall (text-fig. 21 D, E; *s*, pls. 6:3; 7:3), but turn upwards in an unpaired curve of varying dimensions on the posterior portion of the shell wall (text-fig. 21 D, E; *s*, pls. 6:1; 7:1, 4, 5) and, in some cases, also in a slight paired curve on the lateral portion of the shell wall (text-fig. 21 D; *s*, pls. 4:3; 6:2). The distance between the siphonal tube and the posterior portion of the shell wall is equal to $\frac{1}{5}$–$\frac{1}{6}$ of the morphological length of the shell. The proximal division of the siphonal funnel is very short compared with the distal division (text-fig. 20 A, C; *pro*, *dis*, pl. 17:1); the siphonal tube narrows in the former division, but widens in the latter.

The annular elevation of *U.* (?) *longitudinale* has been discussed on pp. 230–232.

REMARKS.—*U.* (?) *longitudinale* differs from the other species of the genus *Uranoceras* mainly in the fact that the systegnoses on the posterior portion of the shell wall turn upwards, and not downwards, in an unpaired curve. Owing to this difference it is not quite certain that this species belongs to the genus *Uranoceras*.

B. *Lyecoceras* n. gen.

GENOTYPE: *Lyecoceras gotlandense* n. sp.

DIAGNOSIS.—Shell slightly coiled in posterior direction; morphological breadth of shell equal to length, or rather greater; circumference of shell circular, or broadly elliptical; margin of shell aperture projects somewhat further down anteriorly than laterally and posteriorly; septa lie obliquely to morphological dorso-ventral axis of shell in such a way that posterior margin is more ventral than anterior; according to this position of septa systegnoses are almost horizontal on anterior portion of shell wall, but turn downwards in a broad, unpaired curve on lateral and posterior portions of shell wall; siphonal tube situated slightly anterior to morphological dorso-ventral axis of shell; proximal division of siphonal funnel short, distal division long; siphonal tube narrow in the former division, but widens slightly in the latter; septal furrow conspicuous; annular elevation forming an anteriorly situated ventral lobe.

In the genus *Lyecoceras* are included the following three species: *L. gotlandense* n. sp., *L. longistriatum* n. sp. and *Lyecoceras* (?) sp. The latter species, represented by only one incomplete specimen (text-fig. 13; pl. 12), differs from the other two species by a considerably larger size and at least by the fact also that the systegnoses on the anterior portion of the shell wall are not horizontal, but turn downwards in an unpaired curve.

At present the genus *Lyecoceras* is known only in the Hemse-Group of the Silurian, Isle of Gotland.

Lyecoceras gotlandense n. sp.

Text-figs. 5 A; 6 D; 16 A, B, C, G; 22; pls. 9:4,5; 10; 16:4,5,6; 19:2; 20.

MATERIAL: a large number of specimens (about 50).

HOLOTYPE: RM, No. Mo 149991 (pl. 10).

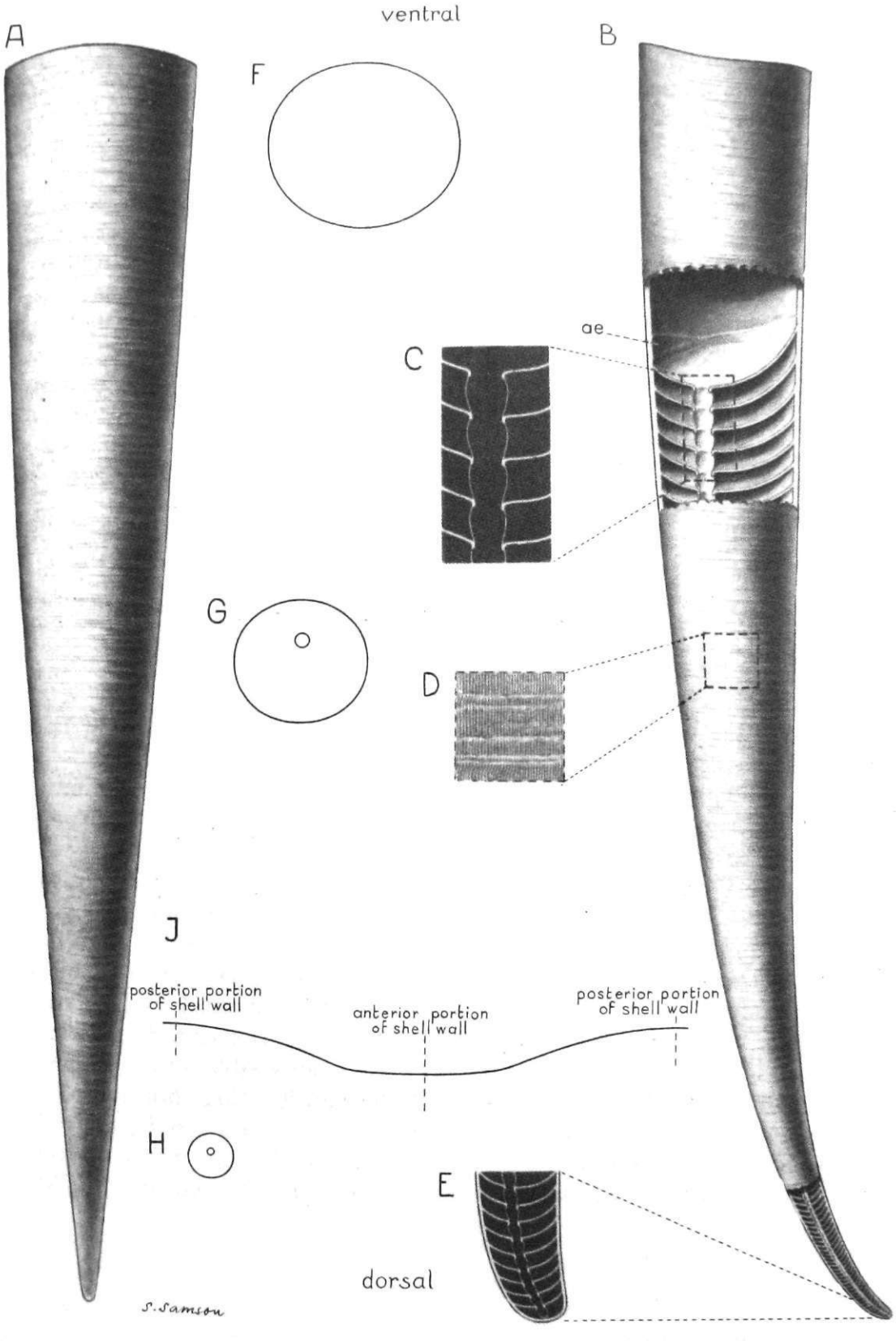
STRATUM AND LOCALITIES: Hemse-Group, Lower Ludlow, Silurian; Isle of Gotland: Mannagårda, Lye; Sandarve kulle; Ethelhem and Linde klint.

DIAGNOSIS.—Morphological breadth of shell slightly greater than length; circumference of shell broadly elliptical; external surface of shell ornamented only in dorsal portion of septate division with delicate, vertical striae; distance between siphonal tube and anterior portion of shell wall equal to $\frac{1}{3}$–$\frac{2}{5}$ of morphological length of shell.

DESCRIPTION.—The shell is very slightly coiled in its ventral portion, but its coiling lincreases a little towards the apex (text-fig. 22 B; pls. 16:5; 20:1, 2). The morphoogical breadth and length increase rather more in the septate division of the shell than in the domiciliary division (text-fig. 22 A, B). The circumference of the shell is broadly elliptical (text-fig. 22 F, G, H). The apertural margin of the shell projects somewhat further down anteriorly than laterally and posteriorly (text-fig. 22 A, B; pl. 10:2).

The external surface of the shell shows growth lines and also, in the dorsal portion of the septate division, delicate, vertical striae (text-fig. 22 D; pl. 19: 2). The internal surface of the shell has delicate, undulating, horizontal striae, similar to those in *L. longistriatum* (pl. 19:3).

The septa lie obliquely to the morphological dorso-ventral axis of the shell in such a way that the posterior margin is more ventral than the anterior. The younger



Text-fig. 22. *Lyecoceras gotlandense* n. sp. A, reconstruction of shell in anterior view, $\times\frac{3}{5}$; B, reconstruction of shell in right lateral view, with shell wall and sections of septa removed at two places, $\times\frac{3}{5}$; C, part of siphonal tube in median-sagittal section, $\times\frac{6}{5}$; D, details of shell ornamentation, $\times\frac{6}{5}$; E, details of shell apex cut in a median-sagittal plane, $\times\frac{12}{5}$; F, G, H, three horizontal sections of shell; $\times\frac{3}{5}$; J, diagram of systegnosis of the youngest septum projected in one plane, $\times\frac{3}{5}$. *ae*, annular elevation of shell.

septa are more oblique than the older ones (text-fig. 22 B; pls. 10:2; 20). Moreover, the distance between the younger septa is greater than between the older ones, relative to the morphological length of the shell. More exactly, this distance corresponds to $\frac{1}{4}$–$\frac{1}{10}$ of the morphological length of the shell. The septal furrow is conspicuous (*if*, pl. 9:5). In the domiciliary cavity of the full-grown shell this furrow terminates ventrally in a little tubercle (*t*, text-fig. 16 A; pl. 10:1). The systegnoses are almost horizontal on the anterior portion of the shell wall (text-fig. 22 J; *s*, pls. 9:4, 5; 10:1), but turn downwards in a broad unpaired curve on the lateral and posterior portions of the shell wall (text-fig. 22 J; *s*, pl. 10:2, 3). The siphonal tube is situated a little anterior to the morphological dorso-ventral axis of the shell (text-fig. 22 B; pl. 20) and its distance from the anterior portion of the shell wall corresponds to $\frac{1}{3}$–$\frac{2}{5}$ of the morphological length of the shell. The dorsal end of the siphonal tube is hemispherical and probably lies in contact with the inside of the shell apex (text-fig. 22 E; pl. 20:2). The proximal division of the siphonal funnel is very short compared with the distal division (text-fig. 22 C, E; pl. 20), the siphonal tube is slightly narrower in the former division than in the latter.

The annular elevation in *L. gotlandense* has already been discussed (pp. 230–232).

Lyecoceras longistriatum n. sp.

Text-figs. 7 E; 23; 24; pls. 11; 19:1,3.

MATERIAL: 4 specimens.

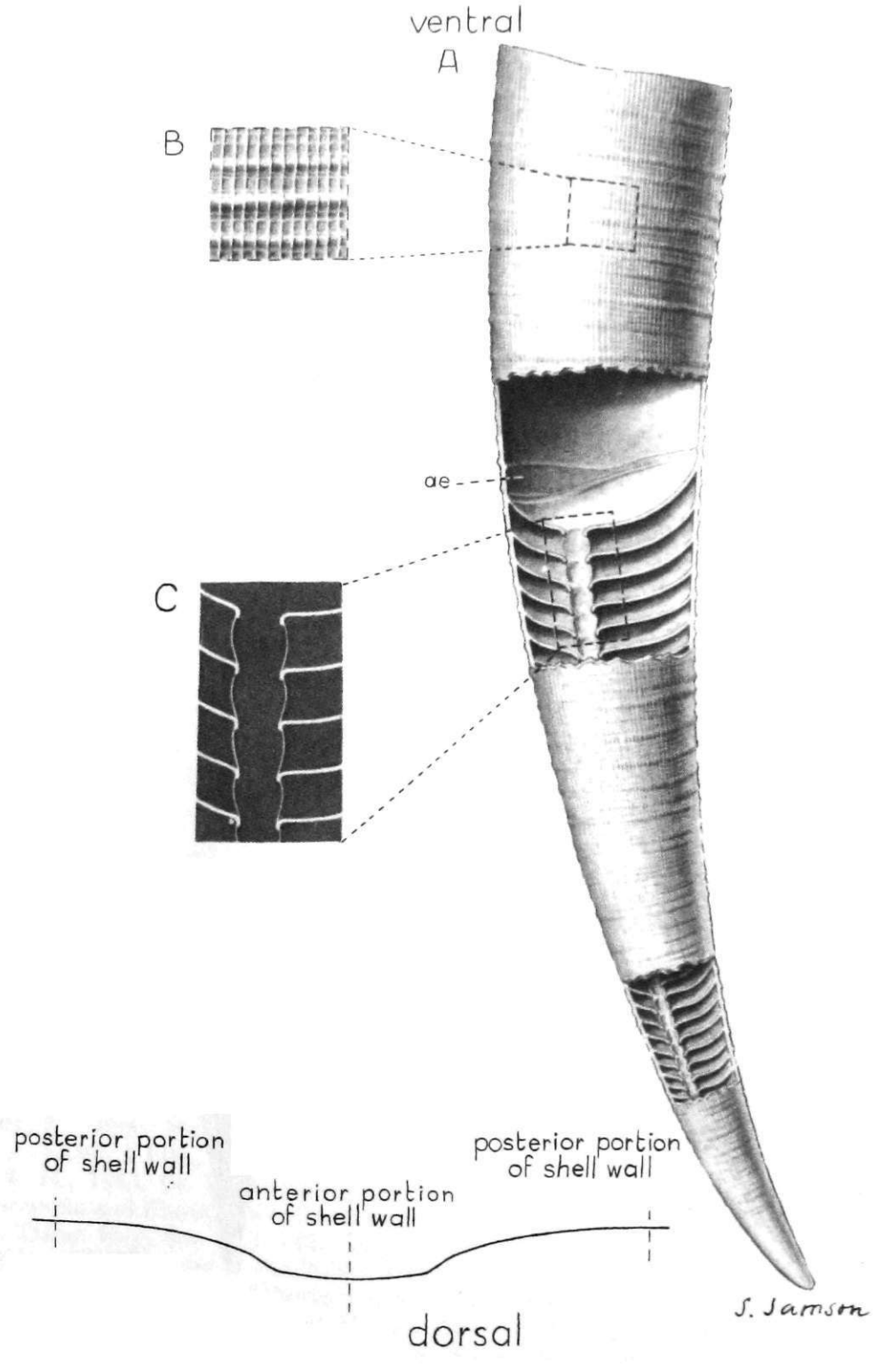
HOLOTYPE: RM, No. Mo 149992 (pl. 11).

STRATUM AND LOCALITIES: Hemse-Group, Lower Ludlow, Silurian; Isle of Gotland: Mannagårda, Lye; Tänglings hällar, Lye; Etlehem.

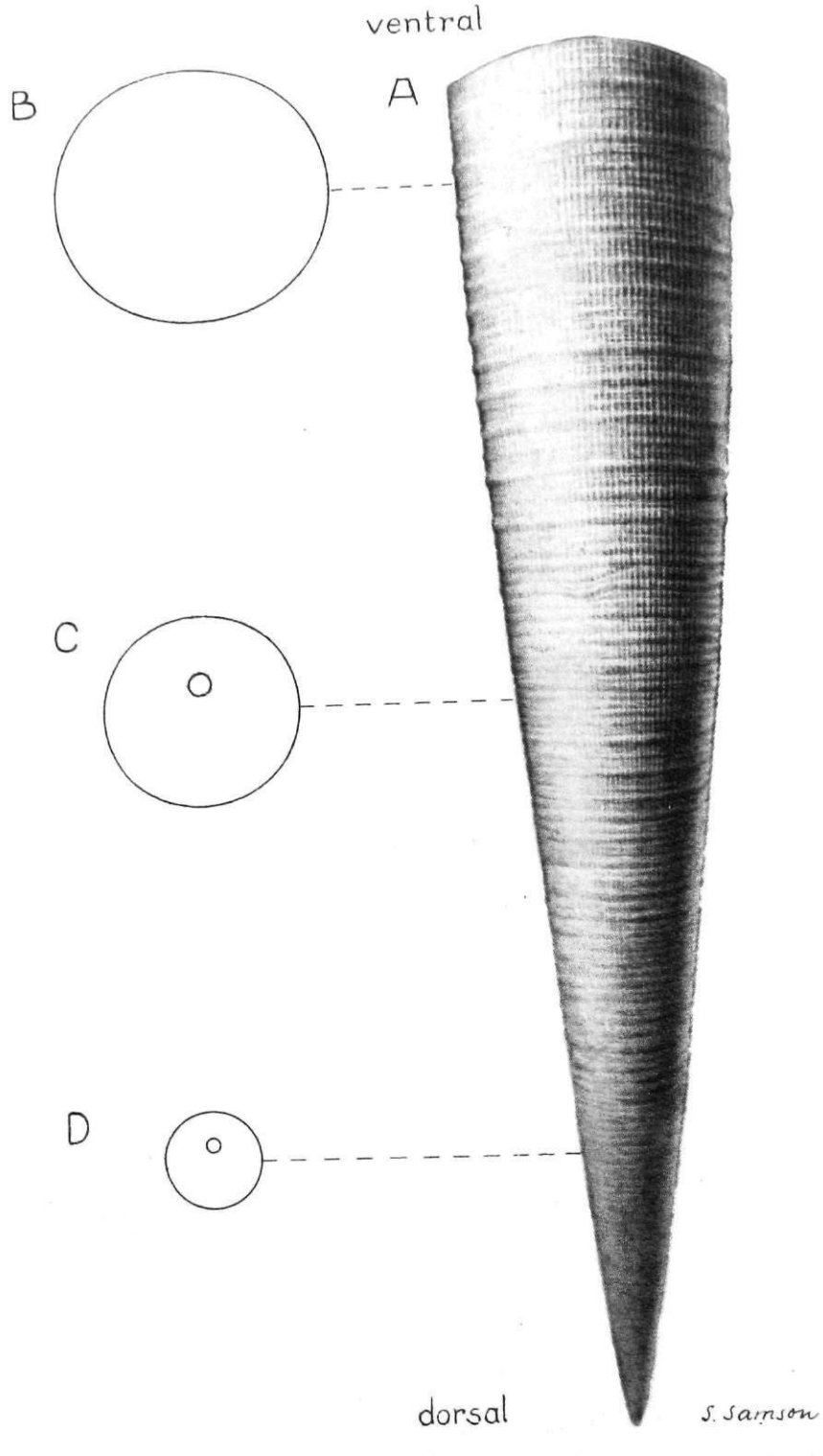
DIAGNOSIS.—Morphological length of shell equal to breadth; circumference of shell circular; external surface of shell ornamented with horizontal ridges, irregular in spacing and size and with, in addition, delicate, vertical ridges.

DESCRIPTION.—This species can be easily distinguished from *L. gotlandense* by the following three characters: (1) a greater increase of the morphological length and breadth of the shell in relation to the height (cf. text-figs. 22 A and 23 A); (2) the circular circumference of the shell (text-fig. 24 B, C, D); and (3) the ornamentation of the external shell surface, consisting of horizontal ridges, irregular in spacing and size and also of delicate, vertical ridges (text-fig. 23 B; pls. 11; 19:1). The horizontal ridges are so distinct that they are even visible on the internal surface of the shell which, in addition, reveals delicate, undulating, horizontal striae (pl. 19:3). The distance between the septa is about the same as in *L. gotlandense*, and the siphonal tube has approximately the same position as in the latter species.

The annular elevation of *L. longistriatum* has been mentioned on pp. 230–232.



Text-fig. 23. *Lyecoceras longistriatum* n. sp. A, reconstruction of shell in right lateral view, with shell wall and sections of septa removed at two places, $\times\frac{4}{5}$; B, details of shell ornamentation, $\times\frac{8}{5}$; C, details of siphonal tube in median-sagittal section, $\times\frac{8}{5}$; D, diagram of systegnosis of the youngest septum projected in one plane, $\times\frac{4}{5}$.
ae, annular elevation of shell.



Text-fig. 24. *Lyecoceras longistriatum* n. sp. A, reconstruction of shell in anterior view, $\times\frac{4}{5}$; B, C, D, three horizontal sections of shell at the levels indicated, $\times\frac{4}{5}$.

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Tryckt den 22 mars 1957

Uppsala 1957. Almqvist & Wiksells Boktryckeri AB

Plate 1

Nautilus pompilius L.

Ventral view of shell, preserved in alcohol, to show domiciliary cavity, with functional area of origin of muscles on lateral and posterior portions of annular elevation (text-figs. 2 A, 3), nat. size.

ia, intermediate area; *mm*, functional area of origin of longitudinal mantle-musculature; *rm*, functional area of origin of retractor muscles; *s*, youngest septum; *sem*, functional area of origin of sub-epithelial musculature of dorsal portion of body proper; *x*, functional area of attachment of pallio-visceral ligament.

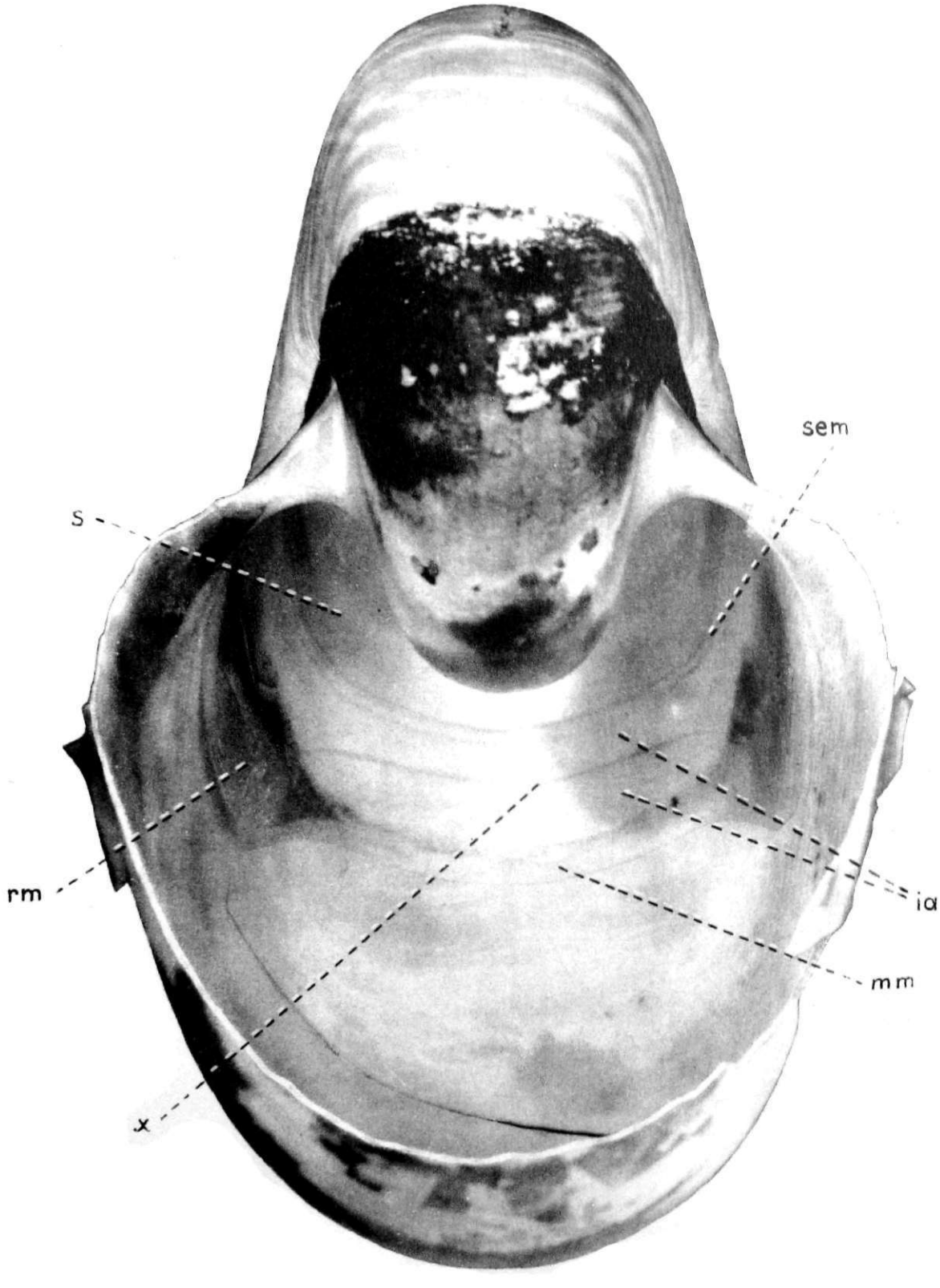

sem
S
rm
ia
mm
x

Plate 2

Estonioceras impressum (HYATT).

Figs. 1, 2, 3. Cast of domiciliary cavity of shell in posterior, lateral, and anterior views, respectively (text-fig. 8), $\times \frac{4}{3}$; Möthlitz, Germany, B III, from a Diluvial boulder of Lower Ordovician.

Orthoceros regulare (SCHLOTHEIM).

Figs. 4, 5, 6. Cast of domiciliary cavity of shell in anterior, lateral, and posterior views, respectively; $\times \frac{4}{3}$; specimen RM, No. Mo 149996, Sjönhem, Kellinge, Isle of Gotland, from a Diluvial boulder of Middle Ordovician.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part.

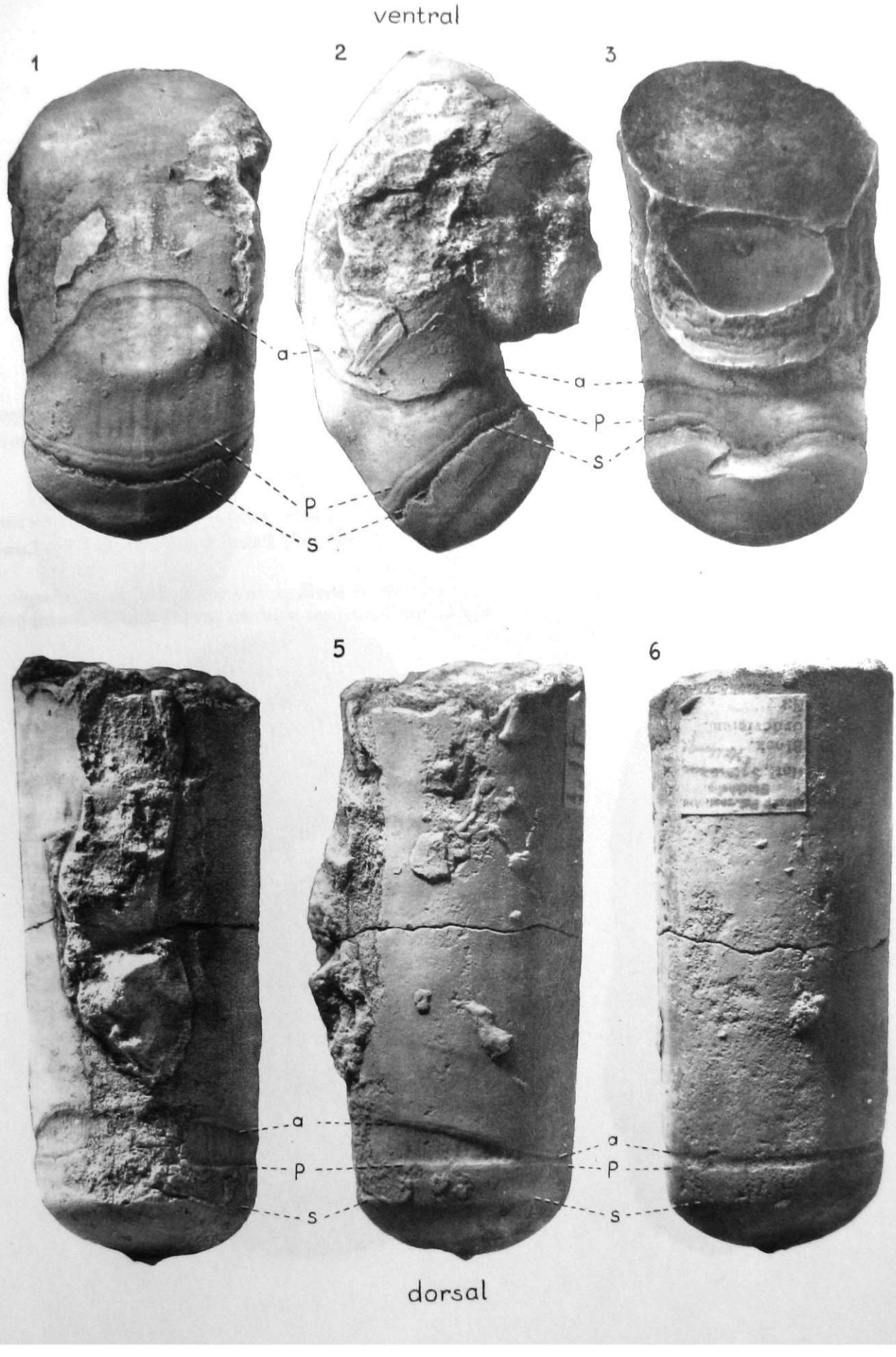

ventral
1
2
3
a
p
s
a
p
s
4
5
6
a
p
s
a
p
s
dorsal

Plate 3

Estonioceras perforatum SCHRÖDER.

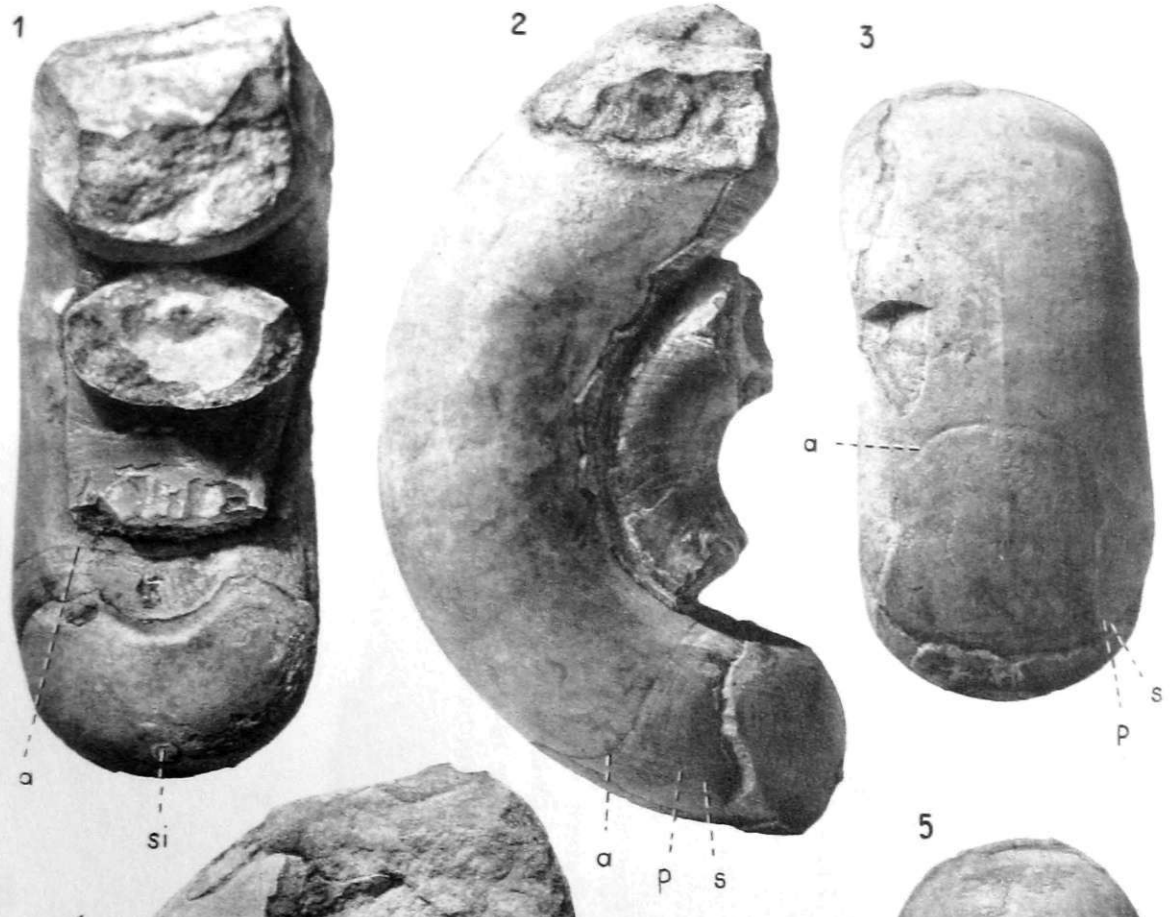
Figs. 1, 2, 3. Cast of domiciliary cavity of shell in anterior, lateral, and posterior views, respectively (text-fig. 9 A, C,), $\times \frac{9}{10}$; specimen RM, No. Mo 149983, Tallinn, Estonia, B III γ, Lower Ordovician.

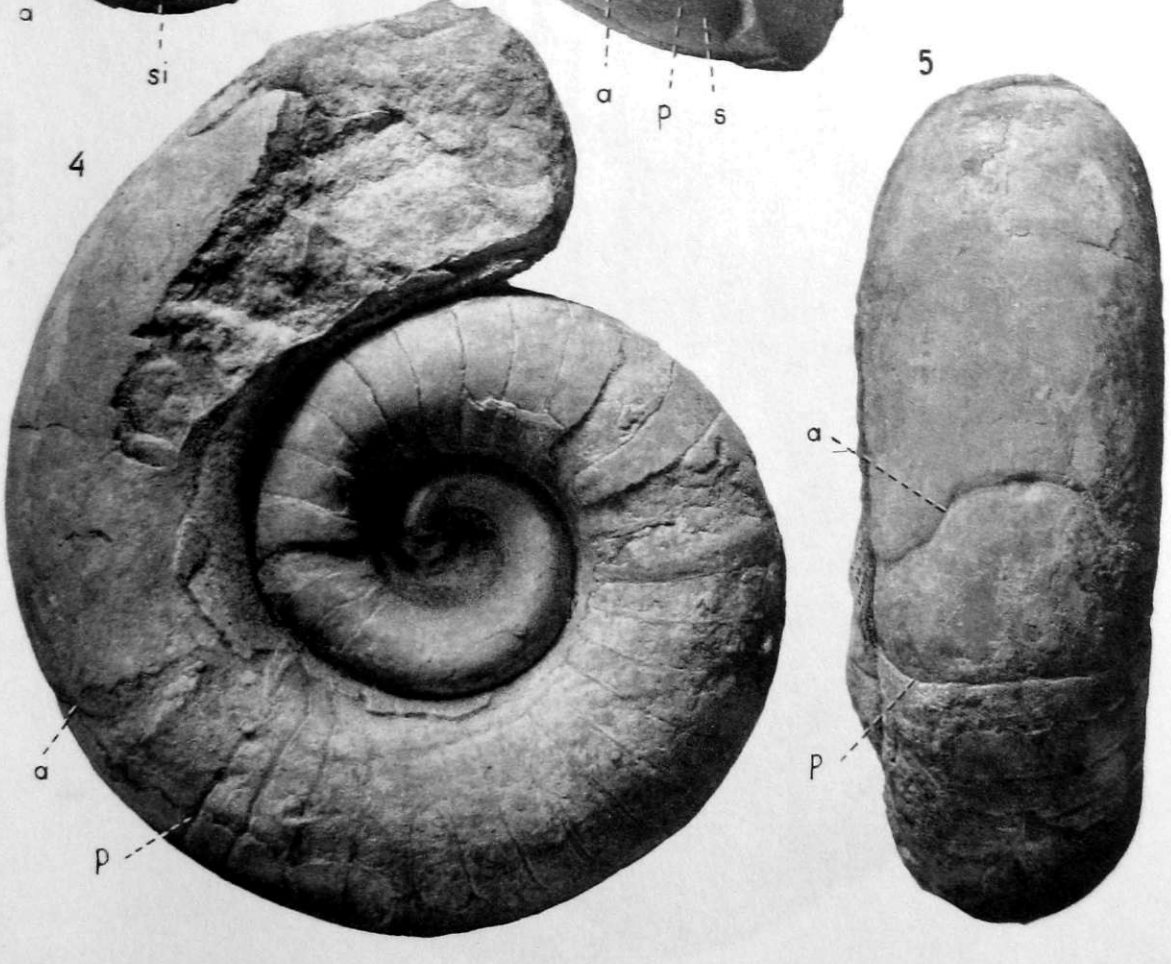
Estonioceras imperfectum (QUENSTEDT).

Figs. 4, 5. Cast of domiciliary cavity of shell and shell chambers in lateral and posterior views, respectively (text-fig. 9 B), $\times \frac{9}{10}$; specimen RM, No. Mo 149982, Tallinn, Estonia, B III γ, Lower Ordovician.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *si*, siphonal tube.

ventral





dorsal

Plate 4

Estonioceras perforatum SCHRÖDER.

Figs. 1, 2. Cast of domiciliary cavity of shell, and septate division of shell in lateral and posterior views, respectively, nat. size; specimen No. C. 15223, British Museum (Nat. Hist.), Tallinn, Estonia, B III γ, Lower Ordovician.

Uranoceras (?) *longitudinale* (ANGELIN).

Fig. 3. Cast of domiciliary cavity of shell in lateral view (text-fig. 10 D), nat. size; uncatalogued specimen, Geological Survey of Sweden, Kallholn, Dalecarlia, Boda Limestone.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part.

ventral
dorsal
1
2
3
a
p
p
s
a
p

Plate 5

Planctoceras falcatum (SCHLOTHEIM).

Two casts of domiciliary cavity of shell and of some shell chambers in posterior, lateral, and anterior views, respectively, nat. size; specimen No. C. 4074, British Museum (Nat. Hist,) (text-fig. 9 E) and specimen RM, No. Mo 149984 (text-fig. 9 D); both specimens from Tallinn, Estonia, B III γ, Lower Ordovician.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation.

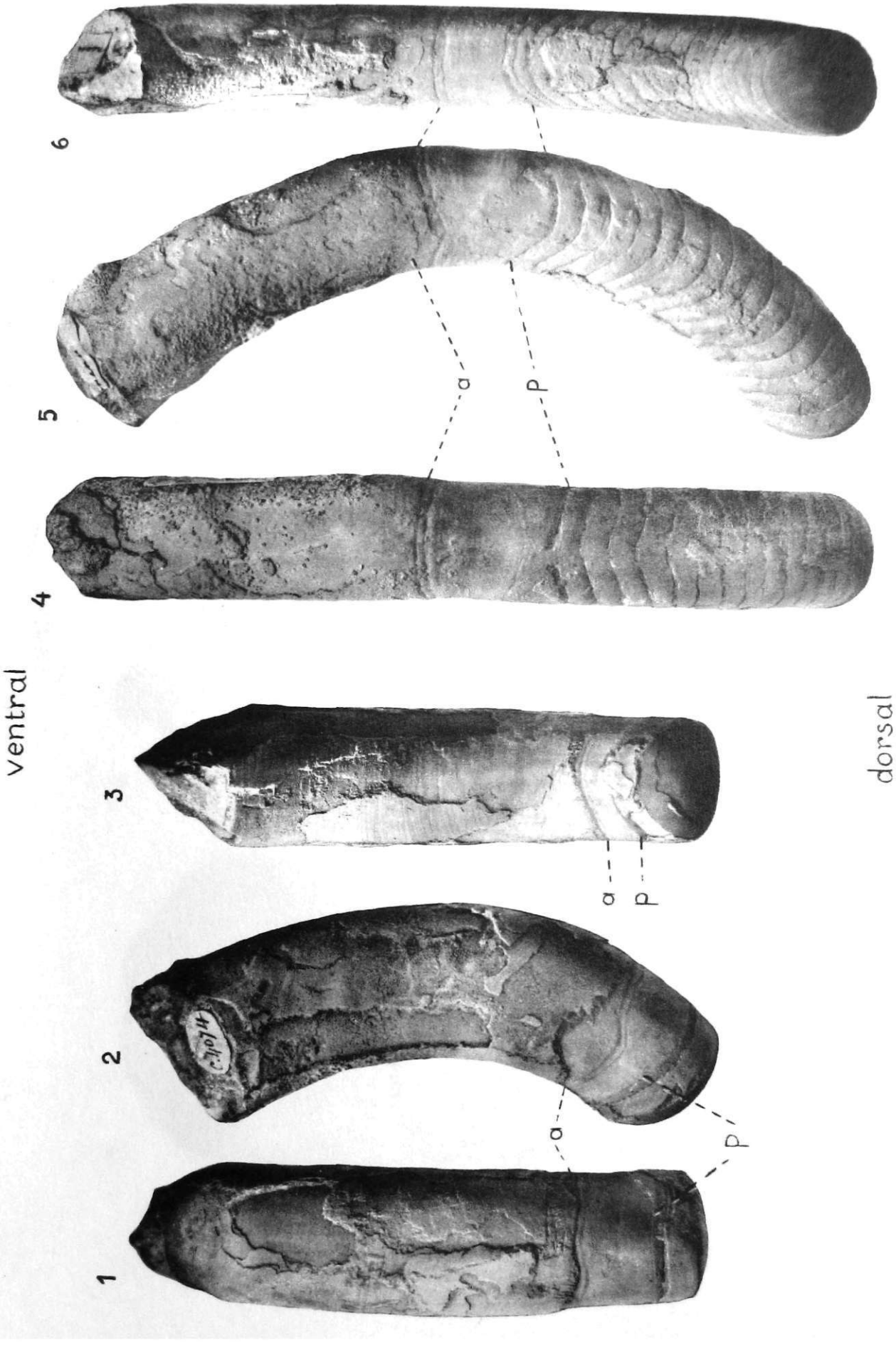

6
5
4
3
2
1
a
p
a
p
a
p
ventral
dorsal

Plate 6

Uranoceras (?) *longitudinale* (ANGELIN).

Figs. 1, 2, 3. Cast of domiciliary cavity of shell in posterior, lateral, and anterior views, respectively (text-figs. 10 A, B, C, E; 11 A), × $\frac{4}{5}$; specimen UPI, No. D 435, Osmundsberget, Dalecarlia, Boda Limestone.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *t*, impression of tubercle of septal furrow of the youngest septum.

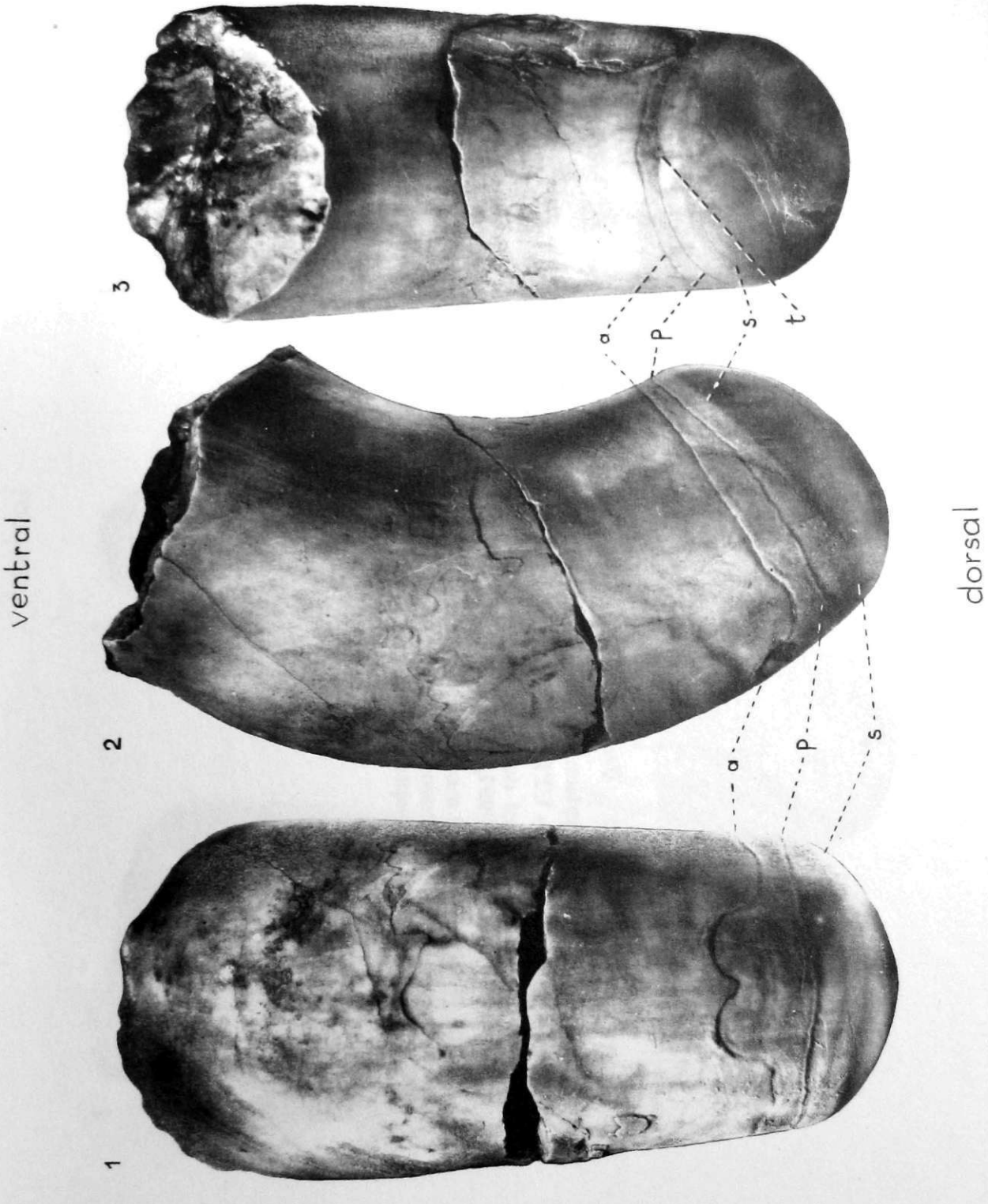

ventral
dorsal
1
2
3
a
p
s
t

Plate 7

Uranoceras (?) *longitudinale* (ANGELIN).

Figs. 1, 2, 3. Ventral portion of septate division of shell in posterior, lateral, and anterior views, respectively, $\times \frac{4}{5}$; specimen UPI, No. D 434, Kallholn, Dalecarlia, Boda Limestone.

Figs. 4, 5. Two casts of domiciliary cavity of shell in posterior view (text-fig. 11 D, E), $\times \frac{4}{5}$; specimen RM, No. Mo 149997, Solberga (?), Dalecarlia, and same specimen as in pl. 4:3.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *sep*, peripheral portion of septum proper; *si*, siphonal tube.

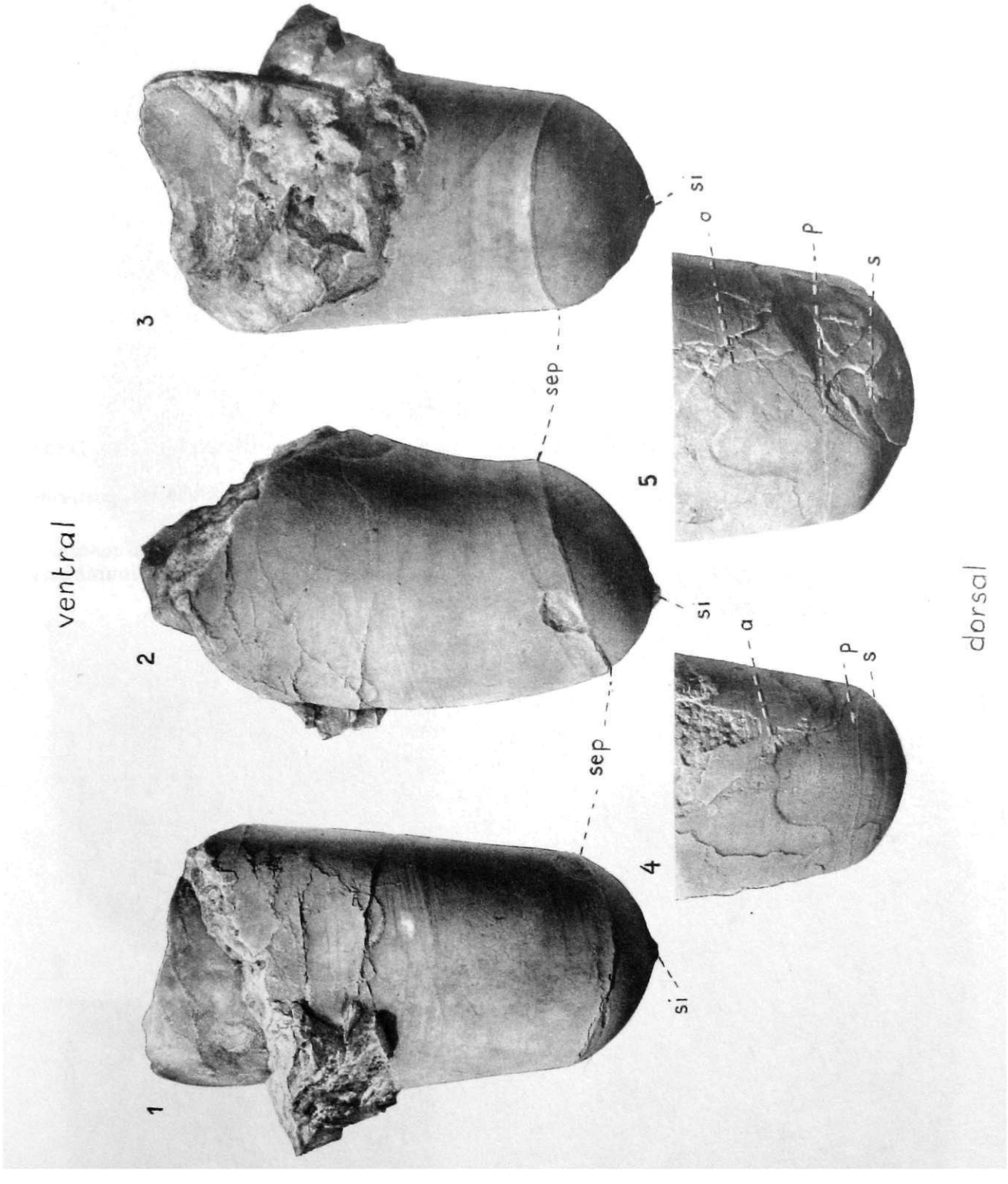

ventral
dorsal
1
2
3
4
5
sep
sep
si
si
si
a
a
p
p
s
s

Plate 8

Discoceras angulatum (SAEMANN).

Figs. 1, 2. Shell in posterior and lateral views, respectively, nat. size; specimen UPI, No. D 432, Osmundsberget, Dalecarlia, Boda Limestone.

Figs. 3, 4, 5. Details of same specimen to show cast of domiciliary cavity of shell in posterior, lateral, and anterior views, respectively (text-fig. 12), × 2.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part.

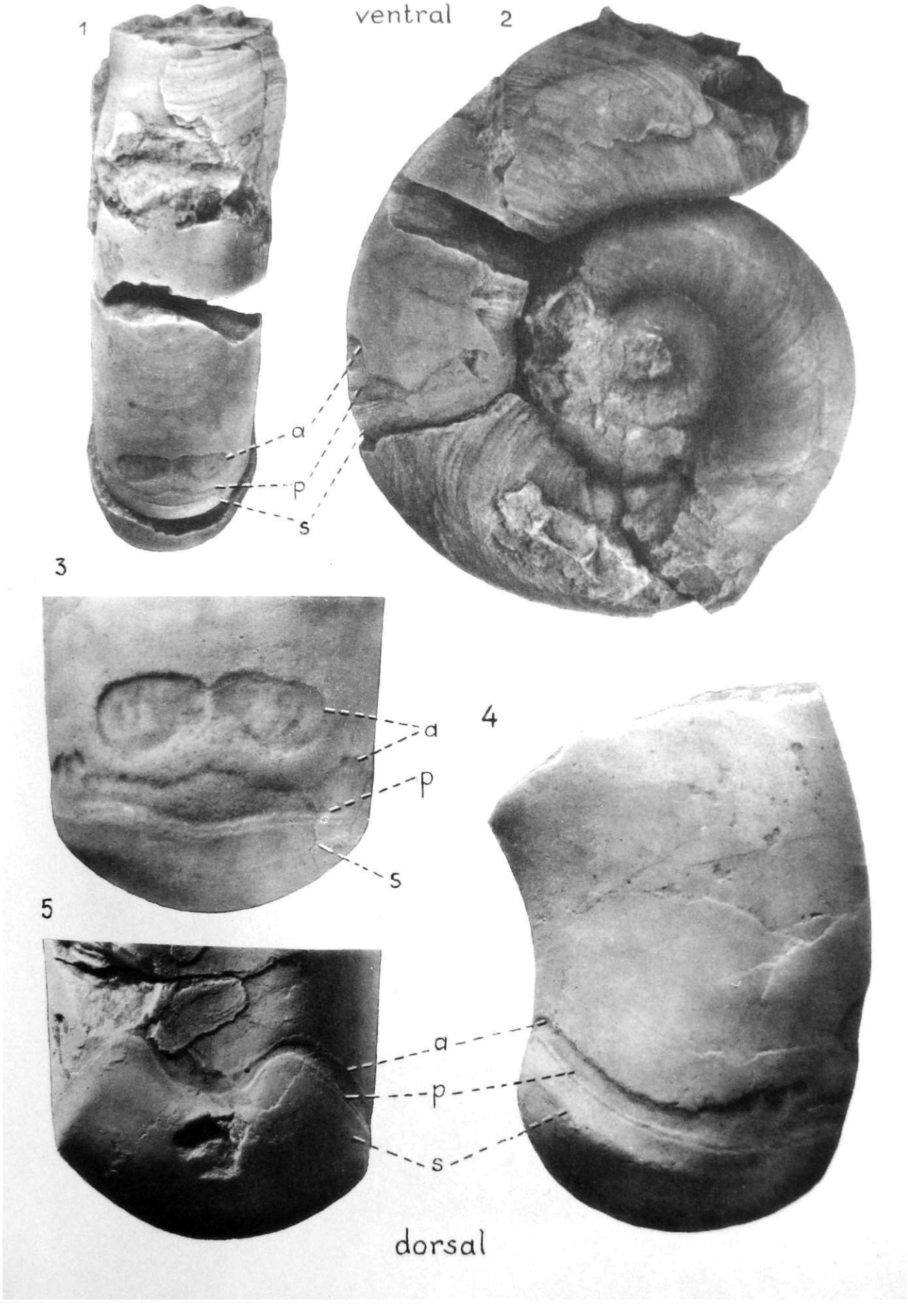

1
ventral
2
a
p
s
3
a
p
s
4
5
a
p
s
dorsal

Plate 9

Discoceras sp.

Figs. 1, 2, 3. Cast of domiciliary cavity of shell and of several shell chambers in posterior, lateral, and anterior views, respectively (text-fig. 14), nat. size; specimen RM, No. Mo 149985, Idavere, Estonia, Idavere stage, Middle Ordovician.

Lyecoceras gotlandense n. sp.

Figs. 4, 5. Two casts of domiciliary cavity of shell in anterior view, $\times \frac{4}{3}$; specimen RM, No. Mo 44442 and RM, No. Mo 149990, both from Mannagårda, Lye, Isle of Gotland, Hemse-Group, Silurian.

a, impression of ventral margin of annular elevation of shell; *if*, impressions of septal furrows; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *si*, siphonal tube.

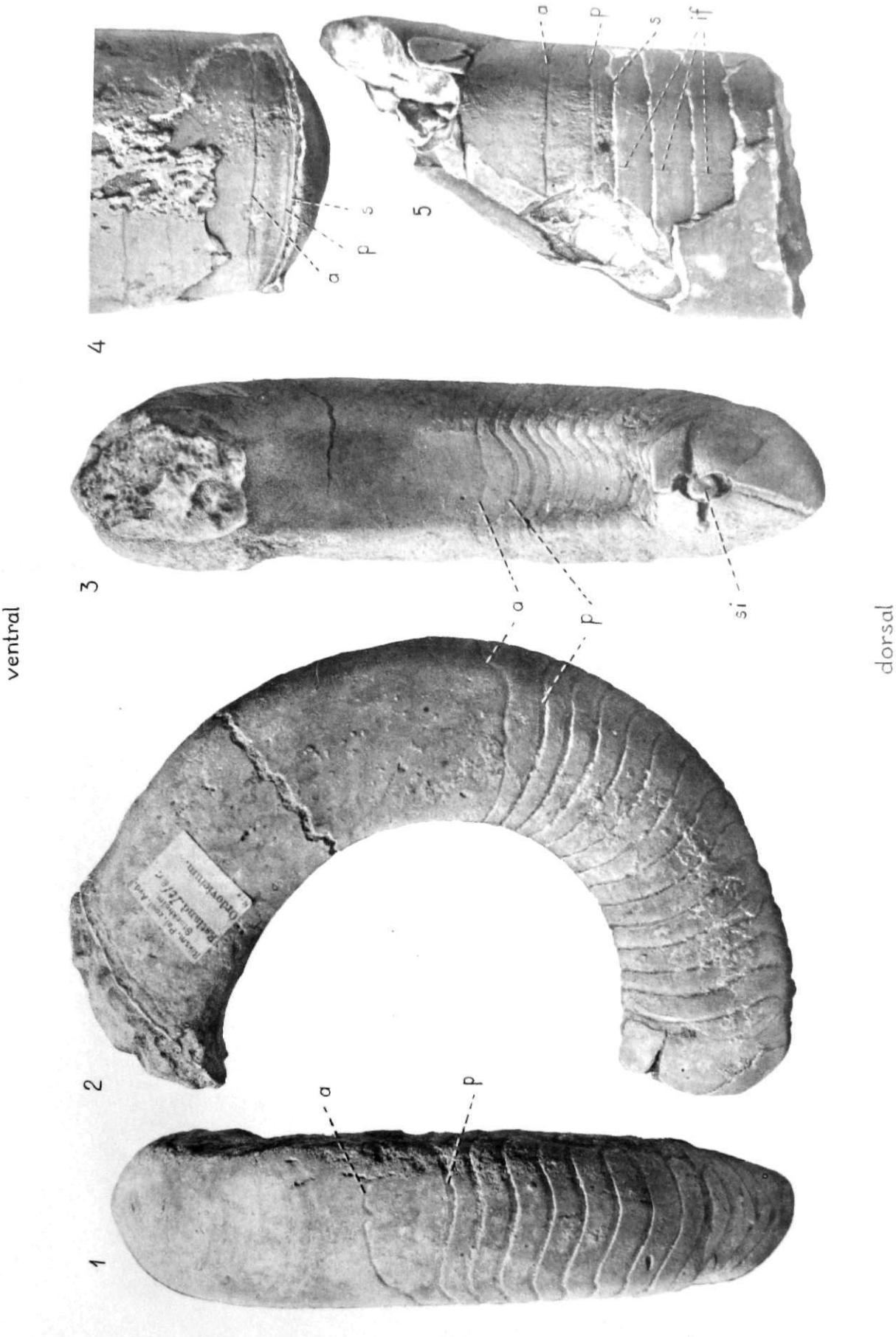

ventral
dorsal
1
2
3
4
5
a
p
si
s
if

Plate 10

Lyecoceras gotlandense n. sp.

Figs. 1, 2, 3. Shell in anterior, lateral, and posterior views, respectively (text-fig. 16 A, B, C, G), $\times\frac{4}{5}$; specimen RM, No. Mo 149991 (holotype), Mannagårda, Lye, Isle of Gotland, Hemse-Group, Silurian.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *t*, impression of tubercle of septal furrow of the youngest septum.

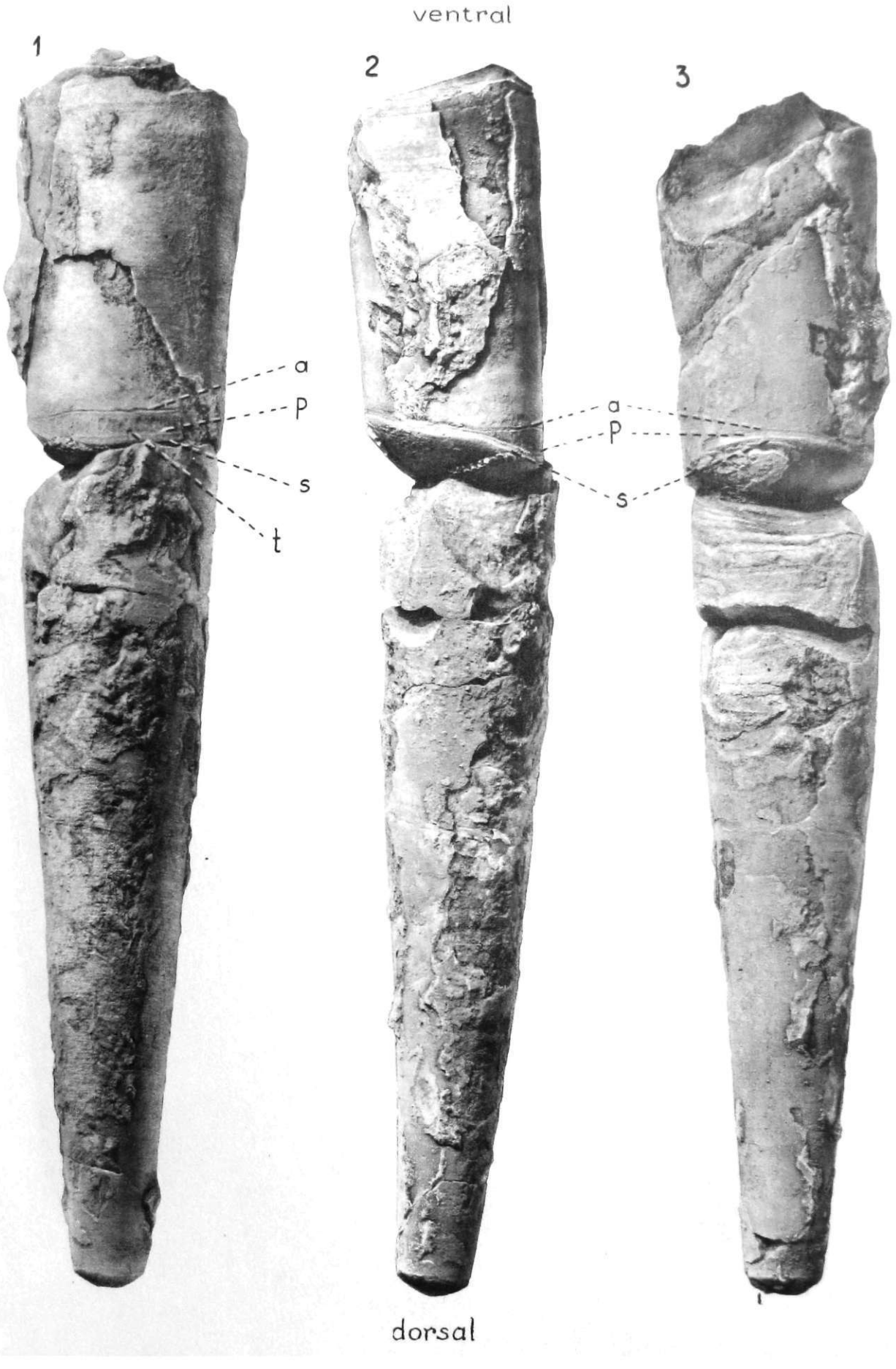

ventral
1
2
3
a
P
s
t
a
P
s
dorsal

Plate 11

Lyecoceras longistriatum n. sp.

Figs. 1, 2, 3. Shell in anterior, lateral, and posterior views, respectively, nat. size; specimen RM, No. Mo 149992 (holotype); Tänglings hällar, Etelhem, Isle of Gotland; Hemse-Group, Silurian.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part.

ventral

dorsal

Plate 12

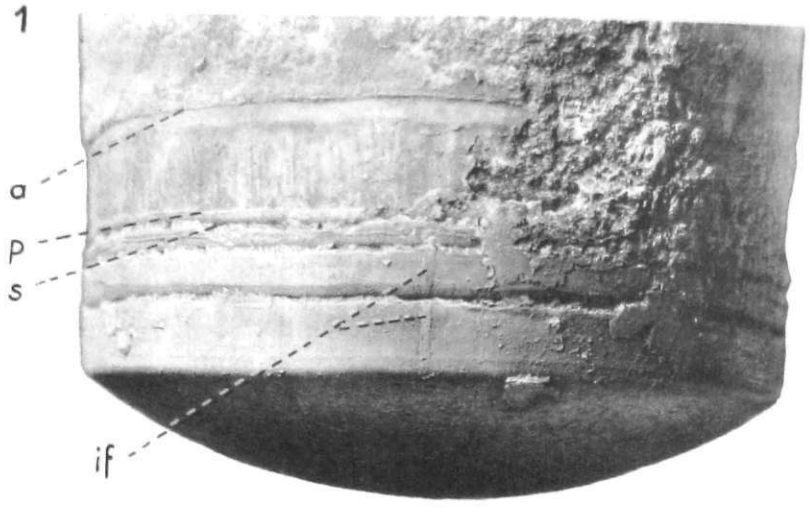
Lyecoceras (?) sp.

Figs. 1, 2, 3. Cast of domiciliary cavity of shell in anterior, lateral, and posterior views, respectively (text-fig. 13), $\times \frac{6}{4}$; specimen RM, No. Mo 47702, Isle of Gotland, Silurian.

a, impression of ventral margin of annular elevation of shell; *if*, impressions of septal furrows; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part.

ventral

1



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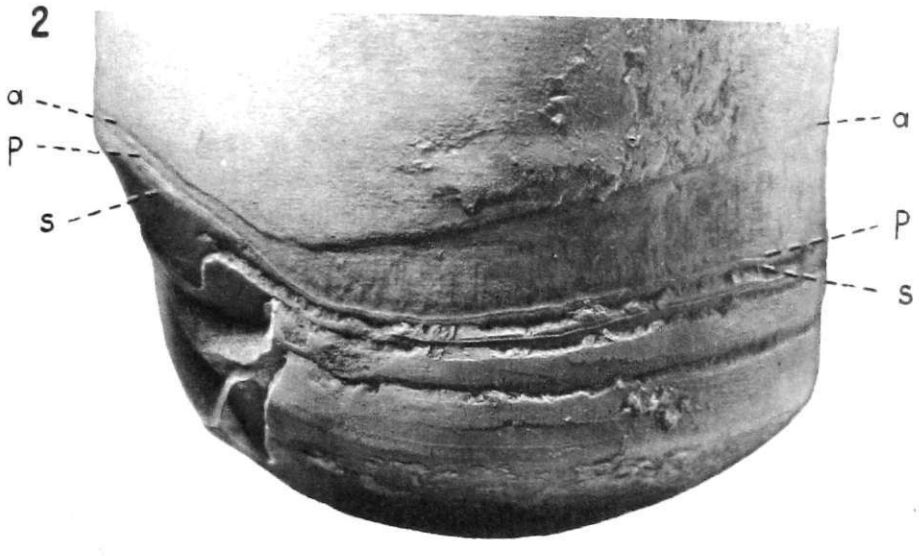


3

dorsal

Plate 13

"Geisonoceras" scabridum (ANGELIN).

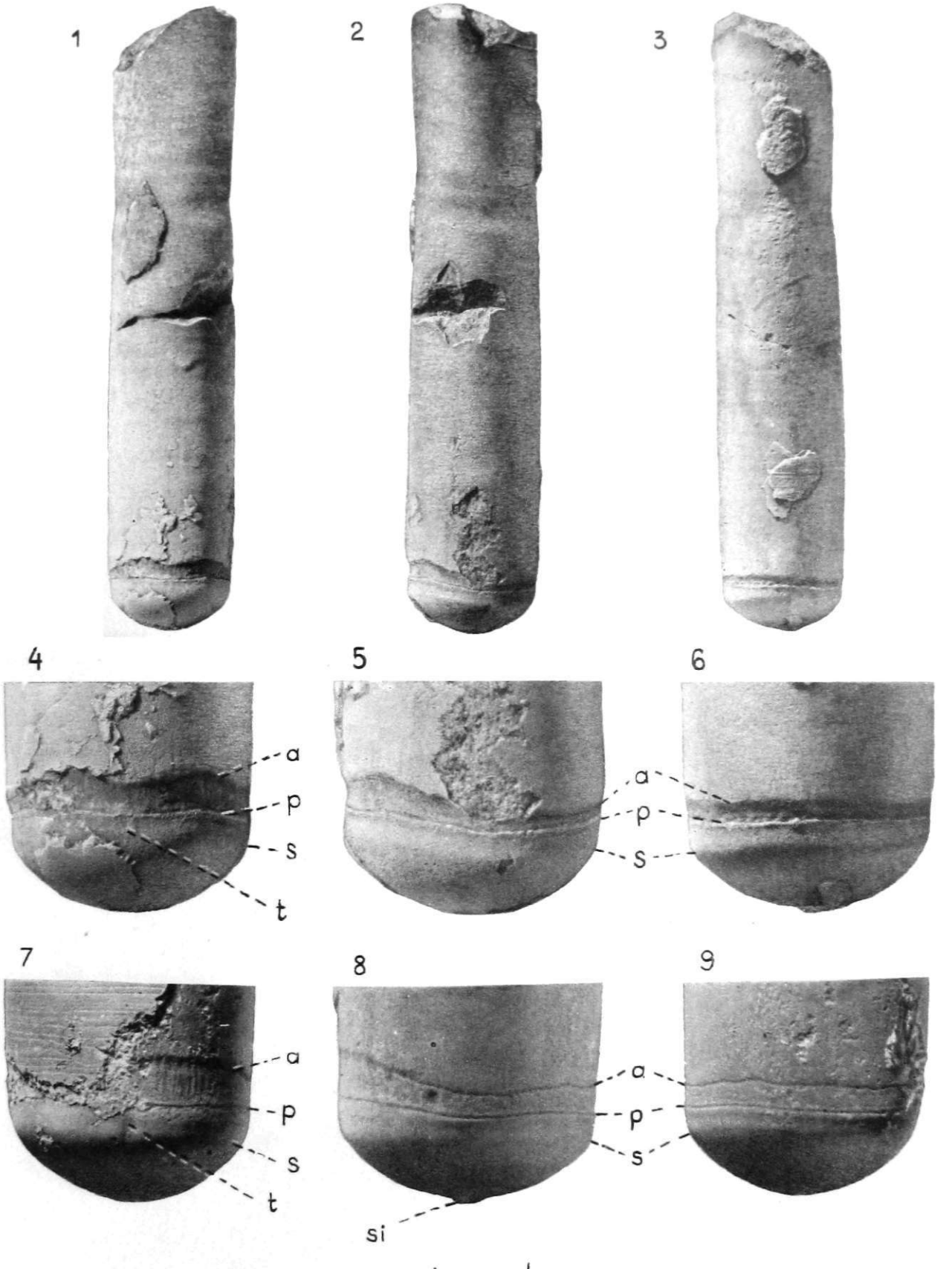
Figs. 1, 2, 3. Cast of domiciliary cavity of shell in anterior, lateral, and posterior views, respectively (text-fig. 15 A–D), nat. size; specimen RM, No. Mo 149986, Isle of Öland, Schroeteri limestone, Middle Ordovician.

Figs. 4, 5, 6. Details of same specimen, × 2.

Figs. 7, 8, 9. Cast of domiciliary cavity of shell in anterior, lateral, and posterior views, respectively, × 2; specimen RM, No. Mo 149987, Isle of Öland, Schroeteri limestone, Middle Ordovician.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *si*, siphonal tube; *t*, impression of tubercle of septal furrow of the youngest septum.

ventral



dorsal

Plate 14

Baltoceras burchardi (DEWITZ).

Figs. 1, 2, 3. Cast of domiciliary cavity of shell in anterior, lateral, and posterior views, respectively (text-fig. 16 D, E, F), nat. size; specimen RM, No. Mo 149999, Isle of Öland, Lower Ordovician.

Figs. 4, 5, 6. Details of same specimen, × 2.

"Geisonoceras" scabridum (ANGELIN).

Figs. 7, 8. Cast of domiciliary cavity of shell in anterior and lateral views, respectively (text-fig. 15 E), × 2; specimen RM, No. Mo 149988, Isle of Öland, Schroeteri limestone, Middle Ordovician.

Fig. 9. Cast of domiciliary cavity of shell in anterior view, × 2; specimen RM, No. Mo 149989, Isle of Öland, Schroeteri limestone, Middle Ordovician.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *t*, impression of tubercle of septal furrow of the youngest septum.

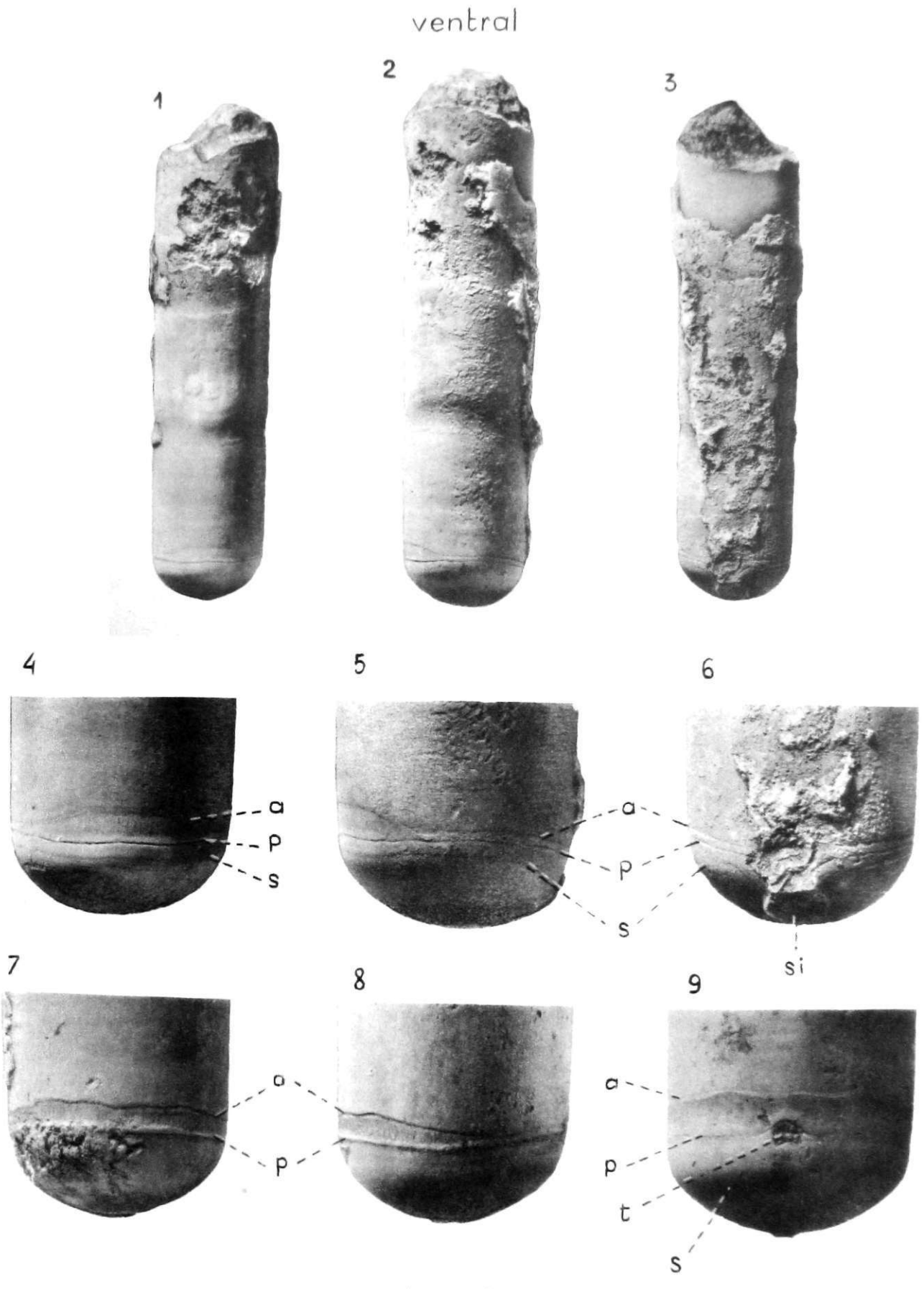

ventral
1
2
3
4
a
p
s
5
a
p
s
6
si
7
a
p
8
9
a
p
t
s
dorsal

Plate 15

"Orthoceras" angulatum WAHLENBERG.

Figs. 1, 2, 3. Cast of domiciliary cavity of shell in anterior, posterior, and lateral views, respectively (text-fig. 17), nat. size; specimen RM, No. Mo 149995, Isle of Gotland, Silurian.

Eutrephoceras bellerophon (LUNDGREN).

Figs. 4, 5, 6. Cast of domiciliary cavity of shell in posterior, anterior, and lateral views, respectively (text-fig. 18), nat. size; uncatalogued specimen, Paleontological Inst., Lund, Annetorp, Scania, Cretaceous.

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part; *si*, siphonal tube; *t*, impression of tubercle of septal furrow of the youngest septum.

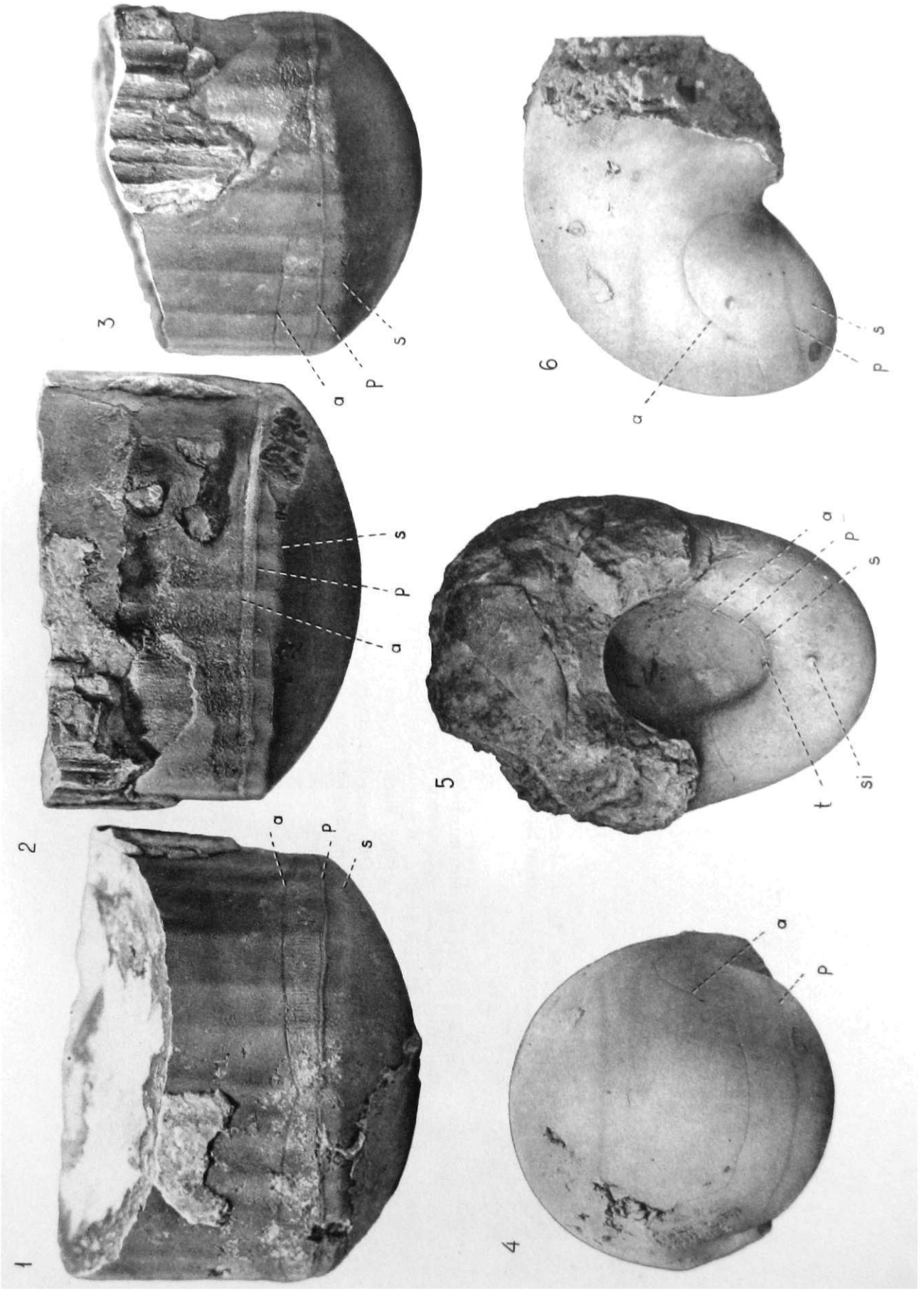

1
a
p
s
2
a
p
s
3
a
p
s
4
a
p
5
a
p
s
si
t
6
a
p
s

Plate 16

Apheleceras hibernicum (FOORD & CRICK).

Figs. 1, 2, 3. Cast of domiciliary cavity of shell in posterior, lateral and anterior views, respectively, nat. size; specimen No. C 7355, British Museum (Nat. Hist.), St. Doulaghs, Dublin, Ireland, Carbon.

Lyecoceras gotlandense n. sp.

Figs. 4, 6. Apical region of shell in posterior and lateral views, respectively, × 6; specimen RM, **No. Mo 149993, Isle of Gotland, Hemse-Group, Silurian.**

Fig. 5. Dorsal portion of septate division of shell in lateral view, nat. size; specimen RM, **No. Mo 53015, Tänglings hällar, Etelhem, Isle of Gotland, Hemse-Group, Silurian.**

a, impression of ventral margin of annular elevation of shell; *p*, impression of dorsal margin of annular elevation; *s*, impression of angle between the youngest septum proper and its mural part.

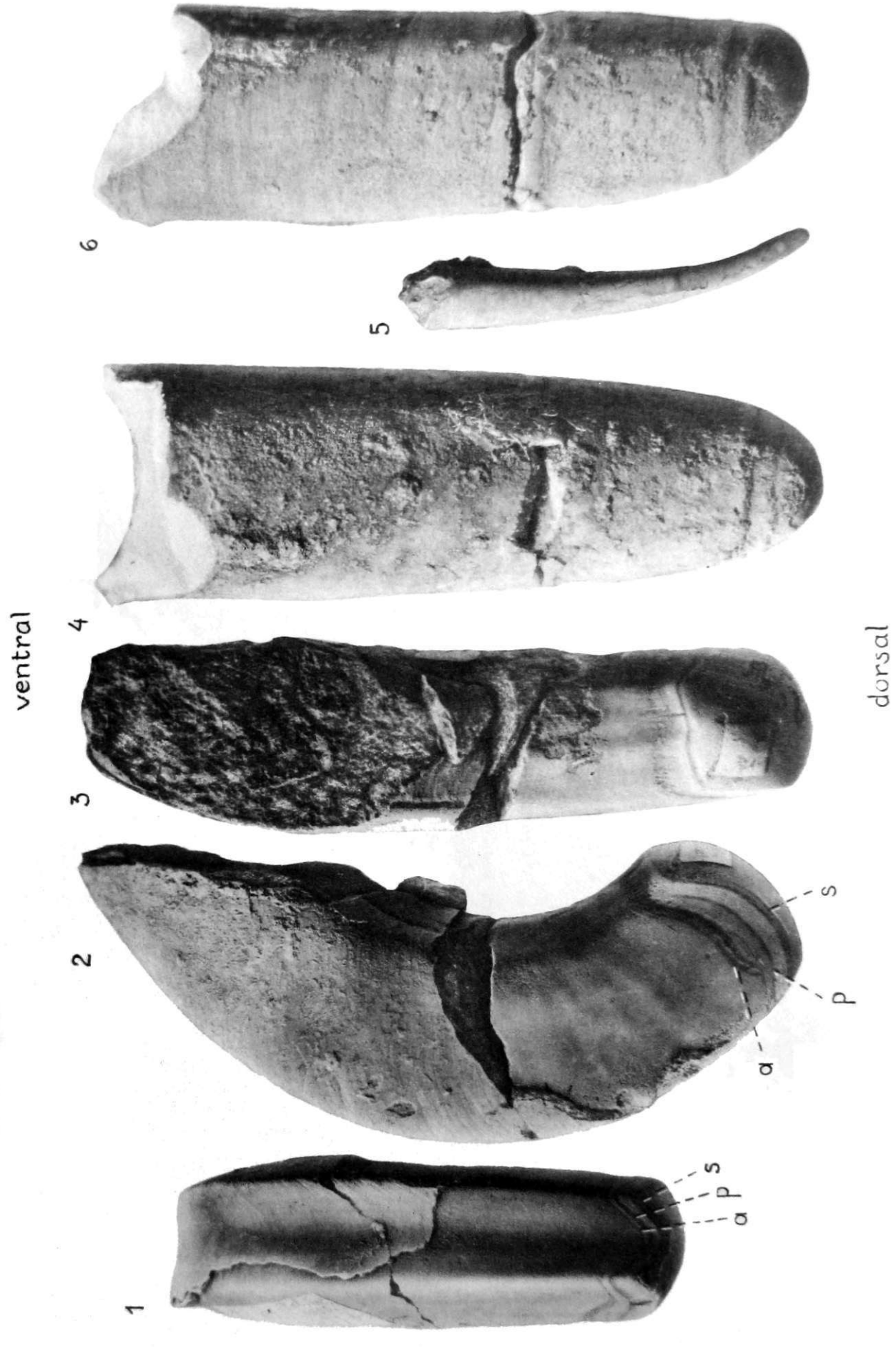

ventral
dorsal
1
2
3
4
5
6
a
p
s
a
p
s

Plate 17

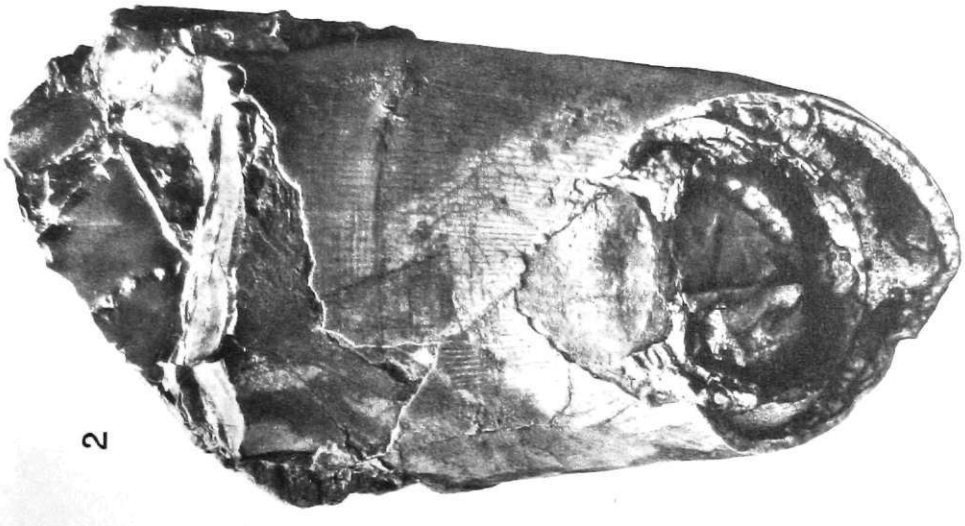
Uranoceras (?) *longitudinale* (ANGELIN).

Fig. 1. Median-sagittal section of ventral portion of septate division of shell, $\times\frac{1}{6}$; specimen UPI, No. D 433, Kallholn, Dalecarlia, Boda Limestone.

Figs. 2, 3. Lectotype in anterior and lateral views, respectively, nat. size; specimen RM, No. Mo 149998 (pl. 18:1), Osmundsberget, Dalecarlia, Boda Limestone.

dis, distal division of siphonal funnel; ***pro***, proximal division of siphonal funnel.

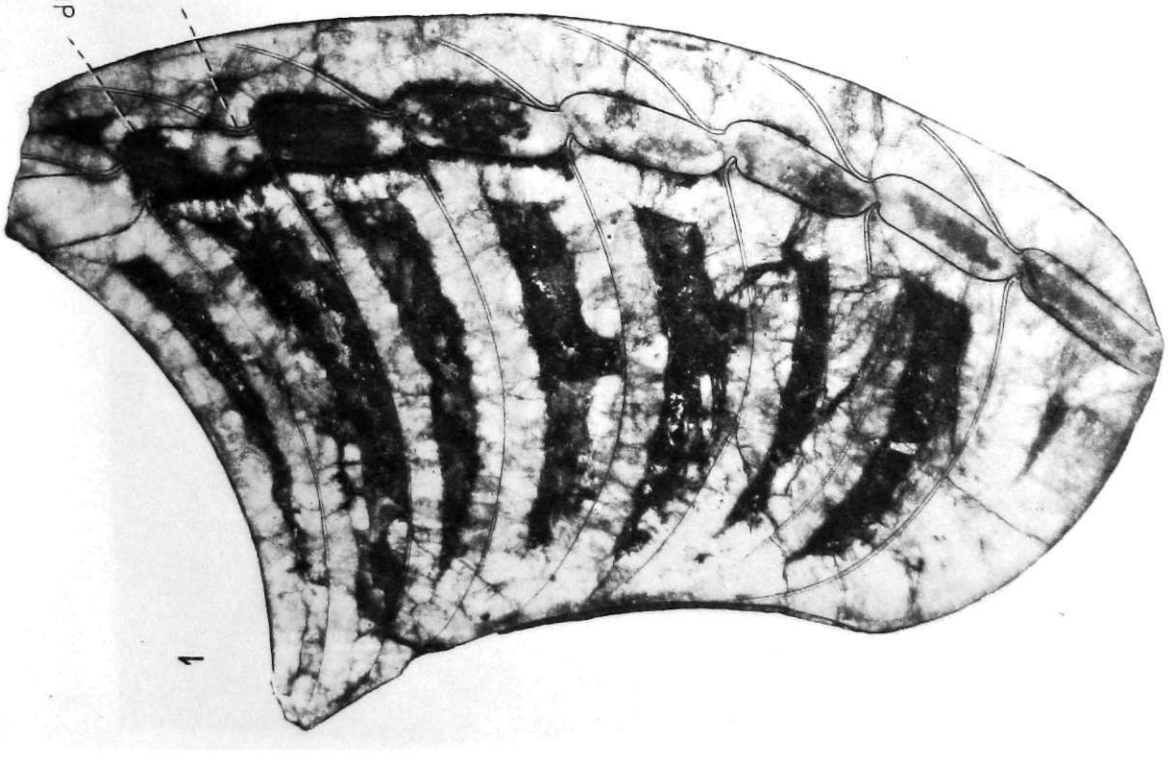
3



2

ventral

dorsal

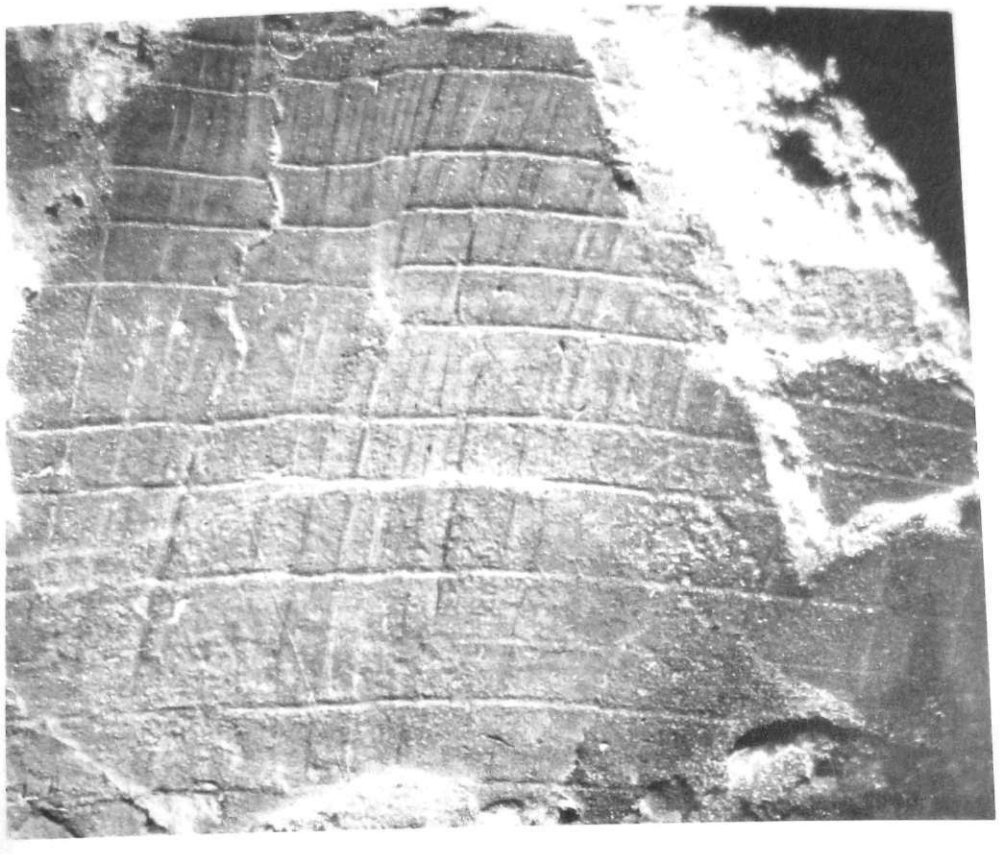


1

Plate 18

Uranoceras (?) *longitudinale* (ANGELIN).

Details of ornamentation of external shell surface, × 6.
Fig. 1. Same specimen as in pl. 17:2, 3.
Fig. 2. Same specimen as in pl. 6.



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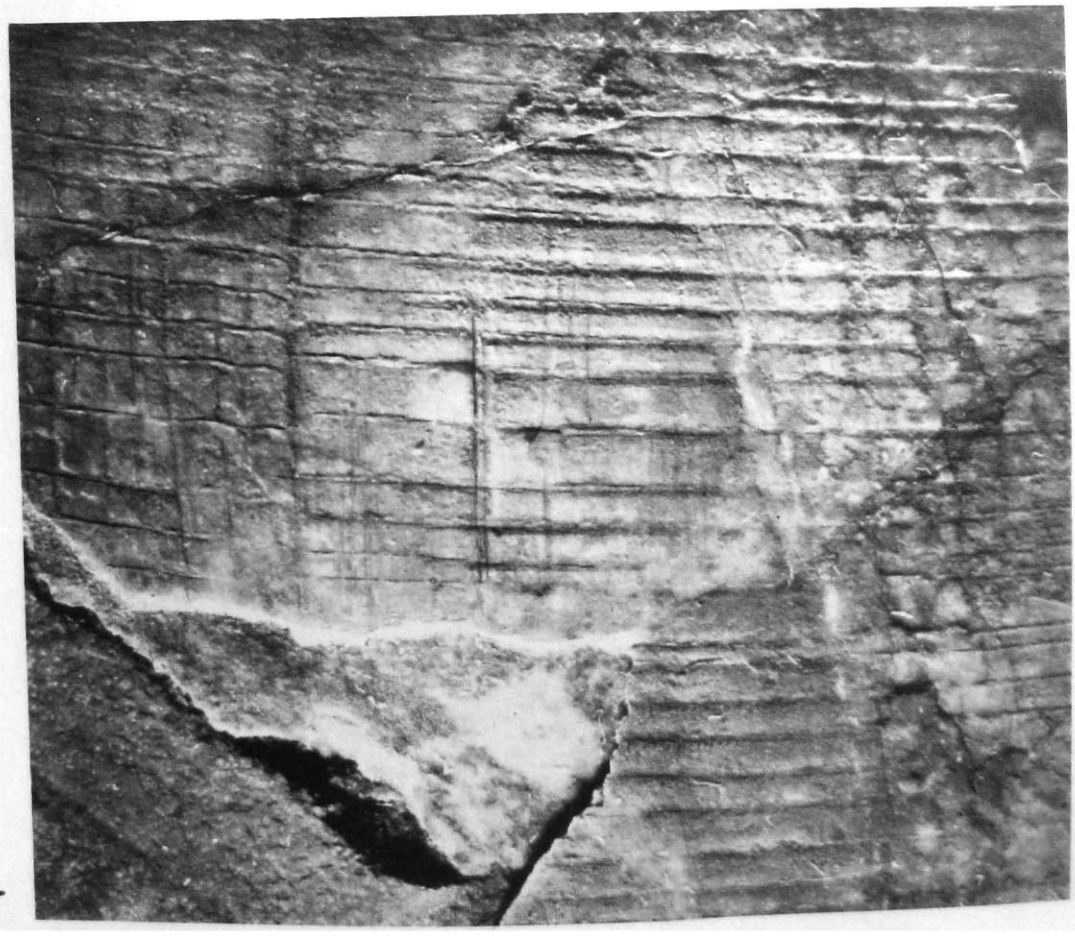


1

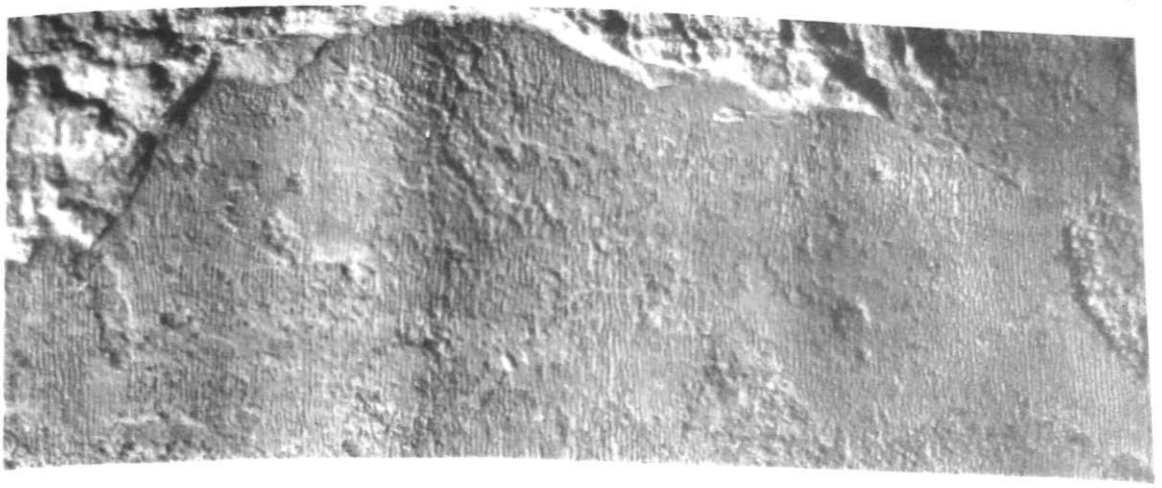
Plate 19

Lyecoceras longistriatum n. sp.

Figs. 1, 3. Details of ornamentation on external and internal surfaces of domiciliary division of shell, × 6; same specimen as in pl. 11.

Lyecoceras gotlandense n. sp.

Fig. 2. Details of ornamentation of external surface of shell, × 6; specimen RM, No. 51737, Sandarve kulle, Isle of Gotland, Hemse-Group, Silurian.



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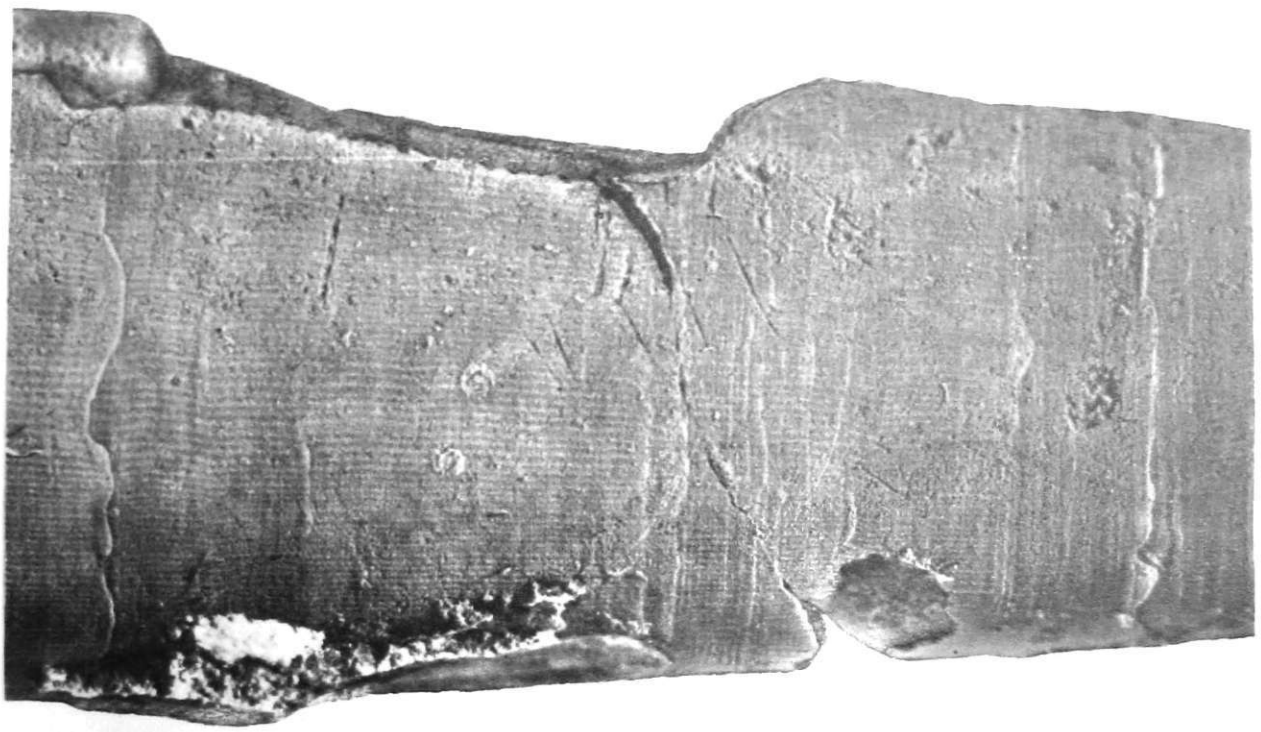

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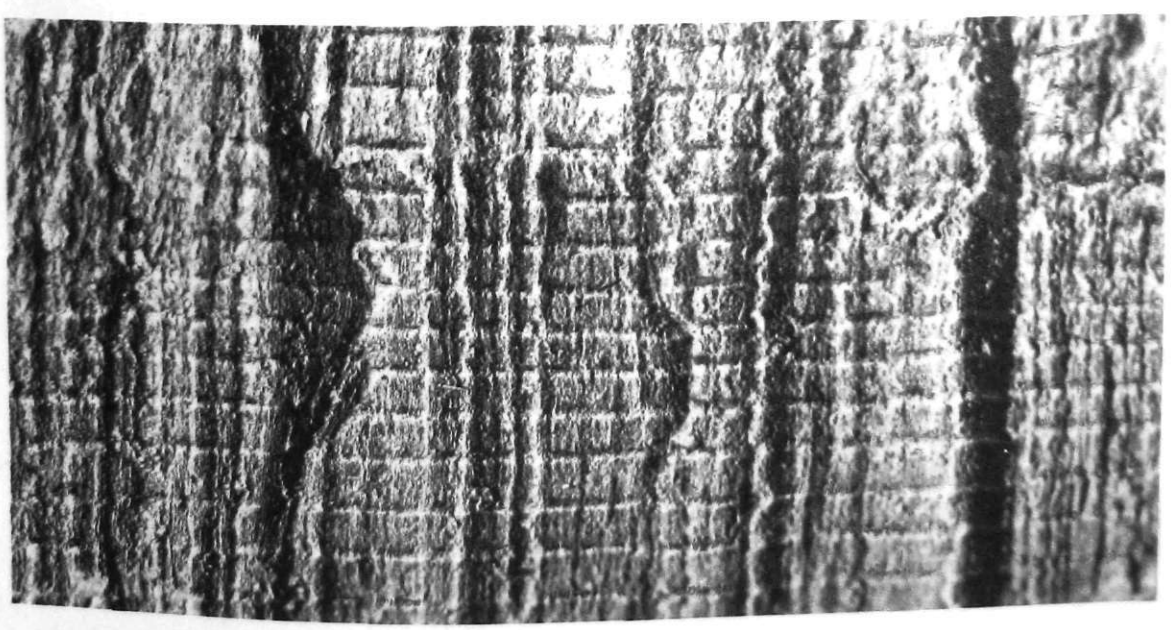


1

Plate 20

Lyecoceras gotlandense n. sp.

Median-sagittal section of septate division of shell.

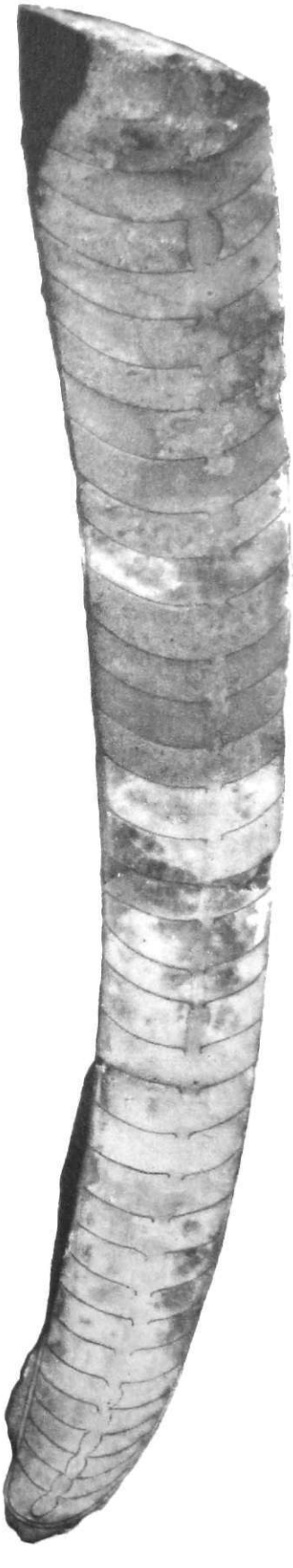
Fig. 1. Specimen RM, No. Mo 149994, × 2, Tänglings hällar, Etelhem, Isle of Gotland.

Fig. 2. Specimen RM, No. Mo 51535, × 5, Sandarve kulle, Isle of Gotland; both specimens are from Hemse-Group, Silurian.

ventral

1

2



dorsal