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On the microscopic shell structure in some Jurassic ammonoids

By

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With plate 14 and 4 text-figures

Introduction

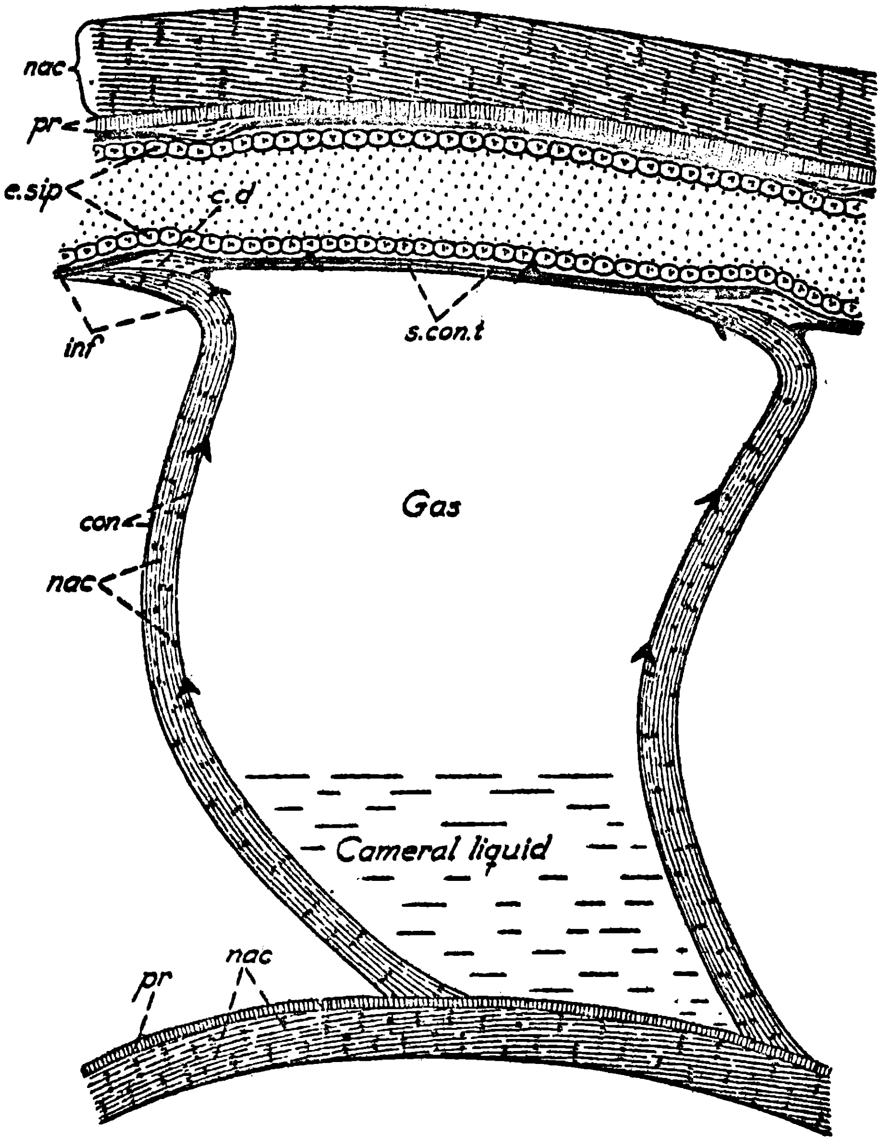
As those of other recent and fossil cephalopods, ammonoid shells are originally composed chiefly of aragonite which during fossilization usually recrystallizes into calcite. Due to recrystallization the original shell structure is considerably altered, or is destroyed altogether. Exceptionally favourable preservation, however, allows large parts of the shell to retain their aragonitic composition and in these cases the original microscopic shell structure can be studied in detail and compared with that in the recent *Nautilus*. Such excellent preservation occurred in the material of *Promicroceras planicosta* (Sow.), fam. Eoderoceratidae, kindly supplied by Dr. E. Currie and Dr. W. D. I. Rolfe, The Hunterian Museum, Glasgow. This material was collected from Lower Lias, Yeovil, Somerset, England. The present paper deals with the microscopic shell structure, ontogenetic growth of the siphonal tube and problems connected with control of buoyancy in *P. planicosta*. In addition, numerous thin sections of *Quenstedtoceras* spp. from Callovian, Luckow, Polen (cf. Makowski, 1962), and of other Jurassic ammonoids were prepared for comparison.

The terminology and orientation of the ammonoid shell here used are the same as proposed by the present writer for the cephalopod shell in his earlier papers (Mutvei, 1956, 1957, 1964a, b, c).

Microscopic structure of the shell wall

In addition to the uncalcified periostracum the shell wall of *Nautilus* consists of three calcareous layers: (1) the outer, spherulitic-prismatic layer, (2) the nacreous layer, and (3) the inner, prismatic layer (*sp.pr*, *nac*, *pr*, Text-fig. 2, respectively; see also Mutvei 1964a). In the shell wall of *Promicroceras*, and of the other ammonoids here investigated, only two of these three calcareous layers—the nacreous and prismatic layers (*nac*, *pr*, Text-fig. 1; Pl. 14, Fig. 1)—can be clearly distinguished, whereas the spherulitic-prismatic layer seems to be completely lost.

In microscopic structure the thick nacreous layer in *Promicroceras* is similar to that in *Nautilus*. Its tabular aragonite crystals are comparatively large and arranged in vertical (radial) columns separated from each other by columnar conchiolin-accumulations (*nac*, Pl. 14, Fig. 1). The thin, inner, prismatic layer differs from that in *Nautilus* in not forming supra-septal ridges (*s.sr*, Text-fig. 2), and being of rather uniform thickness (*pr*, Text-fig. 1; Pl. 14, Fig. 1). As in *Nautilus*, this layer in places is rich in conchiolin which has a granular appearance.



Text-fig. 1. *Promicroceras* sp. Diagrammatic dorso-ventral section of shell and siphonal cord showing microscopic shell structure; black arrows indicate osmotic drainage of cameral liquid from a shell chamber.

None of the specimens investigated has the periostracum preserved.

According to BÖGGILD (1930, p. 323, Pl. 14, Figs. 2—4) the shell wall of *Cadoceras* and *Harpoceras* also consists only of the nacreous and prismatic layers. On the other hand, BÖHMERS (1936) and HÖLDER (1952) described in the shell wall of *Daraelites* and *Parkinsonia*, respectively, the same three calcareous layers of *Nautilus*, although the microscopic structure of these layers could not be clearly seen.

Microscopic structure and ontogenetic development of the shell septa and siphonal tube

The shell septum and the inferior division of its siphonal funnel ("septal neck," "Siphonaldute") in *Promicroceras* have a somewhat simpler composition than those in the recent *Nautilus*.

In *Nautilus* these shell parts consist of three calcareous layers: a dorsal, spherulitic-prismatic layer, a nacreous layer, and a ventral, prismatic layer (*sp.pr, nac, pr,* Text-figs. 2; 3; cf. MUTVEI, 1964a). In addition, the dorsal and ventral faces of each septum and the inferior division of its siphonal funnel are coated by a thin conchiolin layer (*con,* Text-figs. 2; 3). The spherulitic-prismatic and prismatic layers are mostly very thin, but they increase considerably in thickness in the inferior division of the siphonal funnel (*inf,* Text-figs. 2; 3). Also, the spherulitic-prismatic layer is markedly thickened in the peripheral portion of the septum adjacent to the shell wall (Text-fig. 2). Conditions similar to those in *Nautilus* are met with also in the recent *Spirula* (MUTVEI, 1964a) and in several fossil nautiloids (MUTVEI, 1964c).

On the other hand, in *Promicroceras*, and in the other ammonoids here investigated, the shell septum and the prosiphonate (downwards directed) inferior division of its siphonal funnel consist of a single calcareous layer—the nacreous layer (*nac,* Text-figs. 1; 4; Pl. 14, Fig. 2; cf. BÖGGILD, 1930; BÖHMERS, 1936; VOORTHUYSEN, 1940; MILLER & UNKLESBAY, 1943)—coated on the dorsal and ventral faces by a thin conchiolin layer (*con,* Text-figs. 1; 4; Pl. 14, Fig. 2). The spherulitic-prismatic and prismatic layers of *Nautilus* here are either completely lacking or, if present, are extremely thin in their entire extension without increasing in thickness in the inferior division of the siphonal funnel and in the peripheral part of the septum (see above).

The most striking differences between *Promicroceras* and the other ammonoids here investigated, on the one hand, and *Nautilus, Spirula* and fossil nautiloids, on the other, occur in the microscopic structure and onto-

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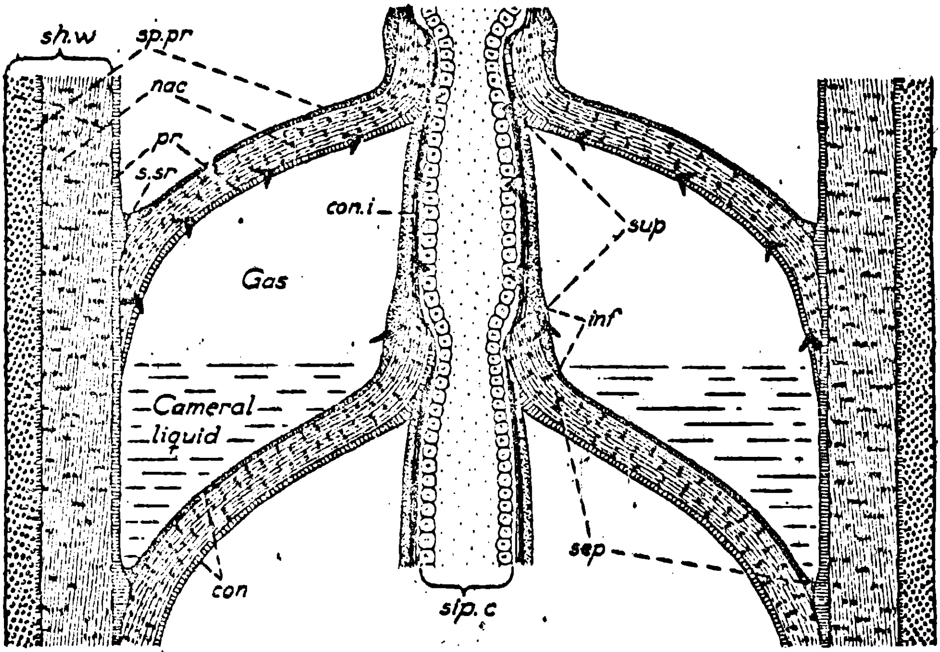
c.d, annular calcareous deposit; *con,* conchiolin layers on septal faces; *e.sip,* epithelium of siphonal cord; *inf,* inferior division of siphonal funnel; *nac,* nacreous layer; *pr,* prismatic layer; *s.con.t,* secondary conchiolin tube.



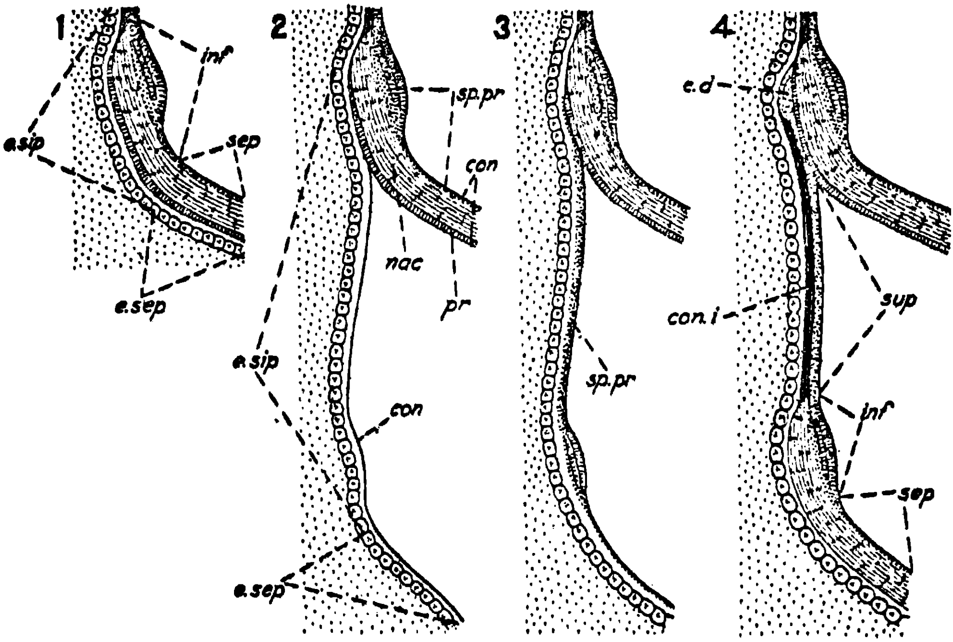
Text-fig. 2. *Nautilus* sp. Diagrammatic dorso-ventral section of shell and siphonal cord showing microscopic shell structure; black arrows indicate osmotic drainage of cameral liquid from a shell chamber.

con, conchiolin layers on septal faces; *con.i*, inner conchiolin layer of superior division of siphonal funnel; *inf*, inferior division of siphonal funnel; *pr*, prismatic layer; *sep*, shell septum; *sip.c*, siphonal cord; *sh.w*, shell wall; *sp.pr*, spherulitic-prismatic layer; *s.sr*, supra-septal ridge; *sup*, superior division of siphonal funnel.

genetic development of the superior divisions of the siphonal funnels ("connecting rings;" "Hüllen").

In *Nautilus* each of these divisions consists of two layers: (1) an outer, porous, spherulitic-prismatic layer which is a direct continuation of that layer in the septum, and (2) an inner, conchiolin layer which is a direct continuation of the nacreous layer in the septum (*sp.pr*, *con.i*, Text-figs. 2; 3; cf. Mutvei, 1964a). However, in *Spirula* and in fossil nautiloids hitherto investigated by the present writer this division seems to be made up solely of the spherulitic-prismatic layer (Mutvei, 1964a, c). The ontogenetic development of the septum and its siphonal funnel in *Nautilus* is shown in Text-fig. 3 (see also Mutvei, 1964a, Text-fig. 17).

In contrast, in *Promicroceras* and its allies this division of the siphonal funnel is replaced by a fairly thick conchiolin tube (*s.con.t*, Text-figs. 1; 4; Pl. 14, Fig. 2). Its thin outermost part seems to be continuous with the thin conchiolin layer on the ventral face of the septum, but its other parts are not continuous with the septal layers. The ventralmost portion of this conchiolin tube is calcified and rigidly attached to the inner face of the



Text-fig. 3. *Nautilus* sp. 1, 2, 3, 4, diagrammatic dorso-ventral sections of last septum, its siphonal funnel and shell-secreting epithelium at four different growth-stages.

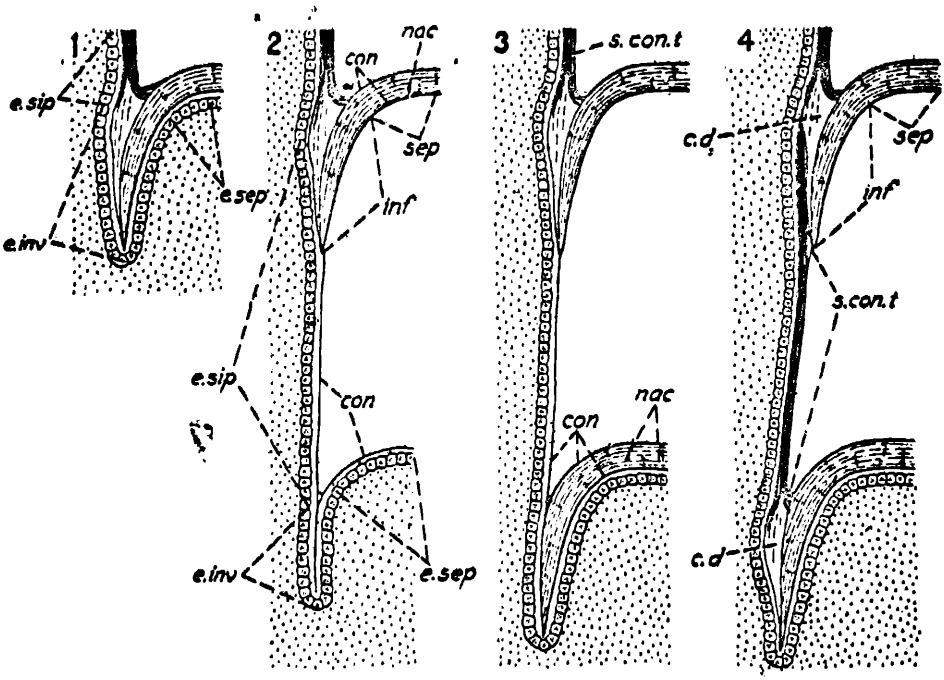
c.d, annular calcareous deposit; *con*, conchiolin layers on septal faces; *con.i*, inner conchiolin layer of superior division of siphonal funnel; *e.sep*, septal epithelium; *e.sip*, epithelium of siphonal cord; *inf*, inferior division of siphonal funnel; *nac*, nacreous layer; *pr*, prismatic layer; *sep*, shell septum; *sp.pr*, spherulitic-prismatic layer; *sup*, superior division of siphonal funnel.

inferior division of the siphonal funnel, where it forms an annular, ridge-like deposit ("auxiliary deposit;" *c.d*, Text-figs. 1; 4; Pl. 14, Fig. 2). A ridge-like, calcareous deposit of similar position and function also occurs in *Nautilus* (*c.d*, Text-fig. 3 : 4). The dorsalmost portion of the conchiolin tube is not calcified, but nevertheless is rigidly attached to the inner face of the inferior division of the siphonal funnel overlapping the annular, ridge-like, calcareous deposit (Text-figs. 1; 4 : 4). As in the septum, the spherulitic-prismatic layer is completely lacking in this portion of the siphonal tube.

Like those in *Nautilus*, each septum in *Promicroceras* was secreted by the septal epithelium, that covering the morphologically dorsal portion of the body proper (*e.sep*, Text-fig. 4). Because the inferior division of the siphonal funnel is directed downwards toward the domiciliary cavity (prosiphonate condition) the septal epithelium must have formed a rather deep and narrow, circular invagination around the ventralmost portion of the siphonal cord (*e.inv*, Text-fig. 4). The epithelium lining the outer (peripheral) face of this circular invagination secreted the inferior division of the siphonal funnel.

When secreting a new septum and an inferior division of its siphonal funnel the septal epithelium formed at first a thin conchiolin layer on its entire surface and then on the ventral face of this conchiolin layer secreted the nacreous layer. Secretion was terminated by the formation of another, thin, conchiolin layer.

After the formation of the new septum the soft body grew in size and simultaneously migrated downwards into the domiciliary cavity of the shell. During these processes the epithelium of the siphonal cord probably secreted a thin conchiolin layer around the siphonal cord (*con*, Text-fig. 4:2). This conchiolin layer seems to be directly continuous with the thin conchiolin layer on the ventral face of the last septum. Then the next new septum and inferior division of its siphonal funnel were secreted in the way outlined above (Text-fig. 4:3). After that growth stage or some time later (see below) the epithelium of the siphonal cord began to secrete concentric conchiolin membranes on the inner face of the primary conchiolin layer so that a comparatively thick, secondary, conchiolin tube was formed between the inferior divisions of two consecutive siphonal funnels (*s.con.t*, Text-fig. 4:4). Exactly when each secondary conchiolin tube was secreted is un-



Text-fig. 4. *Promicroceras* sp. 1, 2, 3, 4, diagrammatic dorso-ventral sections of last septum, its siphonal funnel and shell-secreting epithelium at four different growth-stages.

c.d, annular calcareous deposit; *con*, conchiolin layers on septal faces; *e.inv*, invagination of septal epithelium; *e.sep*, septal epithelium; *e.sip*, epithelium of siphonal cord; *inf*, inferior division of siphonal funnel; *nac*, nacreous layer; *s.con.t*, secondary conchiolin tube; *sep*, shell septum.

known. It is possible that the formation of the secondary conchiolin tubes proceeded slowly. If this was the case, the wall of the siphonal tube in one or several of the ontogenetically youngest shell chambers may have been so thin that it usually was destroyed during fossilization (cf. TRUEMAN, 1920).

From these considerations it follows that the secondary conchiolin tubes in the ammonoids under discussion cannot be strict homologues of the superior divisions of the siphonal funnels in *Nautilus* because (1) their main portions are not continuous with the septal layers, and (2) they were secreted after the formation of the adjacent septa and the inferior divisions of their siphonal funnels.

Several writers, e.g. BÖHMERS (1936), VOORTHUYSEN (1940), MILLER & UNKLESBAY (1943), have studied the microscopic structure of the wall of the siphonal tube in ammonoids. As far as can be judged from their publications, in all the cases where the inferior divisions of the siphonal funnels are directed ventrally (prosiphonate condition), the true superior divisions are lacking, being replaced by secondary conchiolin tubes, just as in the ammonoids studied here. In other cases where the inferior divisions of the siphonal funnels have retained their primary dorsal direction (retrosiphonate condition) it is unknown whether true superior divisions were present, or whether they also were replaced by secondary conchiolin tubes. There are certain indications that the siphonal funnels in the genus *Daraelites* may have true superior divisions (cf. BÖHMERS, 1936, p. 107, Text-fig. 11), but further investigations are needed to confirm this supposition.

Regulation of buoyancy in the ammonoids

DENTON & GILPIN-BROWN (1961) and DENTON (1961) demonstrated that the shell chambers in *Sepia* contain both gas and liquid. The buoyancy of the animal is regulated by changes in volume of this cameral liquid. Thus, during the day the cameral liquid is osmotically "pumped" from the siphonal cord into the shell chambers. Consequently, the animal becomes more dense and buries itself into the bottom sediment. During the night the cameral liquid is osmotically drawn out from the shell chambers into the siphonal cord. Consequently, the animal becomes less dense and swims near the surface of the sea. BIDDER (1962) and DENTON & GILPIN-BROWN (1963) reported that in *Nautilus* also the shell chambers contain liquid in addition to gas. These writers suggested that similar buoyancy regulation takes place in *Nautilus*.

Both in *Sepia* and *Nautilus* the cameral liquid is a solution of NaCl markedly hypotonic to sea water. The pressure of cameral gas is always less than 1 atm. irrespective of the depth at which the animal has been living. The vertical migrations of *Sepia* are 0—200 m. and those of *Nautilus* 0—700 m. (STENZEL, 1957). As pointed out by DENTON (1961), it is unknown how the osmotic "pump" mechanism functions at depths where the hydrostatic pressure is higher than the osmotic pressure.

Because the shell is coiled in *Nautilus* osmotic drainage of the liquid from the shell chambers is more difficult than in *Sepia*. Thus, in most chambers the liquid, when not filling the chambers entirely, does not contact the permeable wall of the siphonal tube (Text-fig. 2). DENTON & GILPIN-BROWN (1963) suggested that the shell chambers are drained of liquid according to the "blotting paper principle," i.e.: "inside walls of the chambers are lined with a thin membrane which makes these walls wettable, so helping to spread the liquid." These two writers also note that "the permeable parts of the siphuncular tube are like blotting paper, readily absorbing any water brought to them." Recent investigations (MUTVEI, 1964a) have shown that, in addition to the thin conchiolin layers, the dorsal and ventral faces of the septa are lined with thin, porous calcareous layers—the spherulitic-prismatic and prismatic layers—respectively; the spherulitic-prismatic layer continues onto the outer face of the siphonal funnel where it becomes considerably thickened (*sp.pr*, *pr*, Text-fig. 2). Thus, the conchiolin layers as well as the porous calcareous layers may function as blotting paper, leading the cameral liquid out of the shell chambers. The osmotic movements of the cameral liquid in these layers are indicated by black arrows on Text-fig. 2.

It may also be noted that, despite its permeability, the inner conchiolin layer of the superior divisions of the siphonal funnels in *Nautilus* has a structure highly resistant to damage from hydrostatic pressure, for it is made up of a great number of concentric layers of tightly packed, dorso-ventrally running, microfibrils (unpublished electron-microscopic investigations by the present writer).

As pointed out above, in *Promicroceras* and its allies the porous calcareous layers are completely lacking in the wall of the siphonal tube and probably also on the dorsal and ventral faces of the septa (Text-fig. 1; Pl. 14, Fig. 2). Both septal faces seem to be covered only by a thin conchiolin layer. Under these circumstances the osmotic drainage of the cameral liquid from the shell chambers should have been less effective than that in *Nautilus*. However, it was probably compensated by the folding of the septa which considerably increased the area of the septal faces and their wettable, thin conchiolin layers. It is therefore possible that the complicated morphology of the ammonoid septa, in addition to other functions, played an important role in the osmotic buoyancy regulation. A question which still cannot be fully answered is what functional advantages were achieved by recurving the inferior divisions of the siphonal funnels and by replacing the true superior divisions of these funnels by secondary conchiolin tubes? One of the effects must have been that the formation of these conchiolin tubes became independent from that of the shell septa and inferior divisions of the siphonal funnels. That being so, the secretion of the secondary conchiolin tubes may have been retarded. What effect this might have had upon the osmotic regulation of buoyancy is unknown.

The secondary conchiolin tubes in *Promicroceras* and its allies are approximately as thick as the inner conchiolin layers of the superior divisions of the siphonal funnels in *Nautilus*. As far as can be seen they have an identical microscopic structure (see above). This condition suggests that the wall of the siphonal tube in the ammonoids under discussion could stand as high hydrostatic pressure as that in *Nautilus*. On the other hand, if the secondary conchiolin tubes had a retarded ontogenetic development and were not well developed in the last, ontogenetically youngest shell chambers, and if the chambers were not entirely filled by cameral liquid, the tolerance of hydrostatic pressure in *Promicroceras* and other ammonoids must have been considerably smaller than that in *Nautilus*.

References

BIDDER, A. M., 1962: Use of the tentacles, swimming and buoyancy control in the Pearly *Nautilus*. — Nature, 196, No. 4853, London.

BÖGGILD, O. B., 1930: The shell structure of the mollusks. — Kongl. Danske Vidensk. Selsk. Skr., Natur.-Math. Afd., Raekke 9, 2, Copenhagen.

BÖHMERS, J. C. A., 1936: Bau und Struktur von Schale und Sipho bei permischen Ammonoidea. Apeldoorn.

DENTON, E. J., 1961: The buoyancy of fish and cephalopods. — Progr. Biophys., 11, Pergamon Press.

DENTON, E. J., & GILPIN-BROWN, J. B., 1961: The buoyancy of the cuttlefish, *Sepia officinalis* (L.). — J. Marine Biol. Assoc. U. K., 41.

— 1963: On the buoyancy of the pearly Nautilus. — J. Physiol., 168.

HÖLDER, H., 1952: Über Gehäusebau, insbesondere Hohlkiel jurassischer Ammoniten. — Palaeontographica, 102, A, Stuttgart.

MAKOWSKI, H., 1962: Problem of sexual dimorphism in Ammonites. — Palaeontologia Polonica, No. 12, Warszawa.

MILLER, A. K., & UNKLESBAY, A. G., 1943: The siphuncle of Paleozoic ammonoids. — J. Paleont., 17, Tulsa.

MUTVEI, H., 1956: A preliminary report on the structure of the siphonal tube and on the precipitation of lime in the shells of fossil nautiloids. — Ark. Miner. Geol., 2, No. 8, Stockholm.

— 1957: On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. — Ibid., 2, No. 10.

— 1964a: On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. — Ark. Zool., 16, No. 14, Stockholm.

— 1964b: On the secondary internal calcareous lining of the wall of the siphonal tube in certain fossil "nautiloid" cephalopods. — Ibid., 16, No. 21.

— 1964c: Remarks on the anatomy of recent and fossil Cephalopoda. — Stockholm Contrib. Geol., 11, No. 4, Ekenäs.

TRUEMAN, A. E., 1920: The ammonite siphuncle. — Geol. Mag., 57, London.

STENZEL, H. B., 1957: *Nautilus*. — Geol. Soc. Amer., Mem. 67, Treatise on marine ecology and paleoecology, 1, Ed. HEDGPETH, J. W., Baltimore.

VOORTHUYSEN, J. H., 1940: Beitrag zur Kenntnis des inneren Baus von Schale und Sipho bei triadischen Ammoniten. Assen.

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Explanation of Plate 14

Promicroceras planicosta (Sow.)

Fig. 1. Dorso-ventral thin section of shell wall; polarized light; ×450; specimen from Lower Lias, Yeovil, Somerset, England.

Fig. 2. Dorso-ventral thin section of wall of siphonal tube; polarized light; ×450; same specimen.

c.d, annular calcareous deposit; *con*, conchiolin layers on septal faces; *inf*, inferior division of siphonal funnel; *nac*, nacreous layer; *pr1*, *pr2*, prismatic layers of shell wall in two adjacent whorls; *s.con.t*, secondary conchiolin tube; *sep*, shell septum.