

SIPHO-CAMERAL STRUCTURES IN SOME SILURIAN CEPHALOPODS FROM THE BARRANDIAN AREA (BOHEMIA)

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Abstract. New information on the cameral mantle contained in the gas chambers of orthoconic cephalopods from the Silurian (Ludlow, Gorstian) of Central Bohemia is presented. The pre-supposition about the direct connection of the cameral mantle and siphonal tissue has been proved. Special attachment structures which most probably fixed the tissue inside gas chambers have been found in *Protobactrites styloideum* (BARR., 1866) and *Plagiostomoceras pleurotomum* (BARR., 1866). This information also contributes to the understanding of the function of the dorsal and ventral furrows. Lamellar structures, till now known only in the Devonian Family Lamellorthoceratidae TEICHERT, 1961, have been found in *Nucleoceras* gen. n. The discussed taxa have been attributed to the recently established order Pallioceratida MAREK, 1998.

■ Mollusca, Cephalopoda, Pallioceratida, functional morphology, new cameral structures, connecting trough, open connecting rings, sipho-cameral tissue, attachment system, lamellar structures, new taxa, Silurian, Barrandian Area, Bohemia.

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Introduction

Numerous longiconic orthocones of Palaeozoic cephalopods assigned to the Nautiloidea are externally rather uniform but study of their internal structures brings sometimes surprising information. Some of them concern the way in which these animals faced the problem of buoyancy regulation and of keeping the shell in a horizontal position with the venter down. As regards the latter problem, a large group of predominantly orthoconic genera used calcite deposits placed in the adapical part of the phragmocone.

The idea of a tissue that was present in the gas chambers of some Palaeozoic cephalopods and served to secrete the deposits, was first expressed by Teichert (1933). Flower (1939, 1941, 1955, 1964, 1975) developed and demonstrated it in detail, above all in *Leurocycloceras* cf. *niagarensis* (HALL, 1868) and later also in a lituitid genus *Ancistroceras* BOLL, 1857. Flower also proposed the term "cameral mantle" for this tissue. Holland (1965) and Collins (1969) studied other species of *Leurocycloceras* Foerste, 1928 and confirmed Flower's conclusions. Collins (1969) reported that in *L. superplenum* COLLINS, 1969 "no trace of the connecting ring can be seen... The cameral deposits in some specimens are remarkable in that they bulge into the siphuncle and encase the septal necks... In one small specimen branching vein-like structures can be seen... between the episepal deposits and the septum" (p. 40, 41). Kolebaba (1974) described a similar morphology in the new species *Mariaceras pragense*, [=a junior synonym of *Protobactrites styloideum* (BARR., 1866).] Sweet (1958) demonstrated a clear opening in the wall of the connecting ring in a lituitid *Rhynchorthoceras helgoyense* SWEET, 1958 and ex-

plained it as being as a result of the resorption "after the entire structure had been formed, giving the siphuncular tissues access to the camerae" (p. 122).

Zhuravleva (in Shimanskiy and Zhuravleva 1961), describing the connecting rings of a new lamellorthoceratid *Gorgonoceras visendum*, reported that they "evidently were poorly calcified, as they are fully absent in the dorsal side and hardly visible in the ventral one, even though they are protected against destruction by the siphonal deposits". She reviewed all published data and presented a series of arguments to support the hypothesis on the organic origin of cameral deposits as well as the correlative idea on the cameral mantle. She also admitted that, in some nautiloid cephalopods, connecting rings possibly did not exist at all (p. 63).

Bandel and Stanley (1989) thoroughly studied the lamellorthoceratids and discovered the elaborate structures in the gas chambers; these structures had been originally "organic sheets, secreted by the cephalopod visceral mass during chamber formation" (p. 391). The authors described remarkable attachment sheets, probably analogous to those described here in two species of the very different Family Leurocycloceratidae. They claimed that the connecting rings probably were closed and communication had taken place through their porous walls (p. 404). The published photographs, according to our copy, nevertheless enable another explanation: the connecting rings were perhaps closed only on the ventral side but on the dorsal side they may had been open.

If well preserved, internal moulds can faithfully reproduce

the internal surface of the cameral deposits and can, therefore, be held for the replicas of a cameral tissue.

The organic origin of the cameral and siphonal deposits was recognized already by Barrande (1855, 1859) and also by others, e.g. Schröder (1888). These deposits differ from the secondary intracameral structures (originated after the death of the animal) in several features. They never are in contact with the whole surface of the connecting ring; their configuration is often very complicated and always bilaterally symmetrical; they have a symmetrical surface sculpture. The morphology of cameral deposits regularly repeats in the succeeding gas chambers; these deposits begin to originate in the apical chambers and gradually proceed adaperturally; there remains a certain number of empty chambers between the living chamber and those gas chambers which contain cameral deposits; cameral deposits are always more massive on the ventral side of the shell. In some well preserved specimens of *Pseudorthoceras* found in asphalt the cameral deposits consist of aragonite – like the shell wall – and contain thin dark membranes of organic matter (Teichert in Moore, 1964, p. K34). Remarkably, K. Histon (1993), having studied a sample of orthoconic nautiloids from the Lower Carboniferous of Ireland, successfully applied the technique of cathodoluminescence in distinguishing primary deposits from the secondary calcite.

Teichert in Fischer and Teichert (1969) concluded his polemic with the contradictory opinion of Fischer as follows: "All things considered, it seems to me that most of the facts which we have cited and discussed as proof of the organic nature of cameral deposits at the same time tend to support their origin from body tissues present in the camerae. How this tissue was connected with the siphuncle from which it must have been supplied with blood, is at present unknown" (p. 28).

All the evidence leads to the same conclusion but, in spite of it, the idea of the cameral mantle has not generally been accepted to date. Mutvei (1956, p. 188), Crick (1988, p. 16) and Dzik (1984, p. 18), for example, refused it. There are probably two main reasons for the surviving doubts. The idea of a phragmocone, the gas chambers of which contain a tissue that forms one unseparated anatomical unit with the siphonal tissue, differs strongly from the deep-rooted scheme based on the recent *Nautilus*. The second probable cause was expressed by Dzik (1984), noting that, up to then, "The absence of connecting rings has not been demonstrated in any nautiloid..." (p. 17). Crick (1982, p. 117) claimed, that his species under study (seven species of *Dolorthoceras* and *Mitorthoceras*) evidently did not have any cameral mantle, because they "do not have openings through which tissue would have passed into the chamber from the siphuncular cord". He also noted that such a mantle "would have had a mass that would have had occupied an ever decreasing volume", and "Decay of this tissue would have left a void near the center of the chamber" (ibidem).

In this statement Crick incidentally expressed two of the features which -if present- may confirm the presence of a cameral mantle: open connecting rings and empty space even in the chambers containing maximally developed cameral deposits.

Both of these conditions have been proved in our material as well as additional two: traces of vessels and the attachment system which most probably fixed the cameral mantle in the gas chambers.

The present study was based mainly on the specimens of *Protobactrites styloideum*, *Plagiostomoceras pleurotomum*

and "*Orthoceras*" *obelus* (the type species of *Nucleoceras* gen. n.) all of which originally were described by Barrande (1866, 1870).

The study material is deposited in the collections of the Department of Palaeontology, National Museum, Prague.

Locality and Material

All studied specimens come from the classical Barrande's locality "Butowitz". Barrande described more than a hundred cephalopod species from here but only a part of them come from the place now named "Na Břekvici", from which our material is derived. It is located in the southwestern part of Prague, at the SW border of the district Butovice and lies in close proximity to one of the Silurian volcanic centres. Stratigraphically, the locality belongs to the basal Ludlovian strata (Gorstian), biozone with *Colonograptus colonus*. It was re-investigated by Horný and Kříž (Kříž, 1961).

Most of the cephalopods come from concretions of dark grey, bituminous, micritic limestone embedded in tuffaceous shales and tuffs. The best preserved specimens were found in the weathered crusts of the concretions. The majority of internal moulds of the gas chambers are preserved in limonite which originated from pyrite during the quaternary weathering processes.

The following species predominate in this rich fossil taphocoenosis: Cephalopoda: *Dawsonoceras barrandei* HORNÝ, *Kionoceras originale* (BARR.), "*Orthoceras*" *amoenum* BARR., "*O.*" *aperiens* BARR., "*O.*" *capillosum* BARR., *Ophioceras rudens* (BARR.), *O. simplex proximus* (BARR.), *Peisimoceras pulchrum* (BARR.), *Plagiostomoceras pleurotomum* (BARR.), *Phragmoceras imbricatum* BARR., *Protobactrites styloideum* (BARR.), *Rizoceras robustum* (BARR.), *Sphooceras truncatum* (BARR.).

Gastropoda: *Coelocyclus novaki* PERNER, *Loxonema* sp., *Oriostoma* sp., *Platyceras* sp., *Ruedemannia? crassior* (BARR. in PERNER), *Spirina tubicina* BARR. in PERNER, *Spirina patula* BARR. in PERNER, *Tragotoma extensa* (HEIDENHAIN), *Turbocheilus immaturus* BARR. in PERNER.

Bivalvia: *Butovicella migrans* (BARR.), *Cardiola contrastans* BARR., *Cardiola gibbosa* BARR., *Isiola ampliata* (BARR.), *Manulicula manulia* (BARR.), *Slava bohémica* BARR.

Graptolites: *Colonograptus colonus* (BARR.), *C. roemeri* (BARR.), *Pristiograptus dubius* (SUESS).

The studied specimens come partly from Barrande's study material, a part of them were collected in the sixties by Radvan Horný (National Museum Prague) and about a half of all have been collected from 1970 to 1997 by the author of this report. The total number of studied specimens is more than 300. The specimens of *Protobactrites styloideum* were very abundant in the locality being found about four times more frequently than those of *Plagiostomoceras pleurotomum* or both the discussed species of *Nucleoceras* gen. n.

Methods

To obtain thin sections, the small phragmocones (the average diameter of which is about 4 mm) and their fragments were

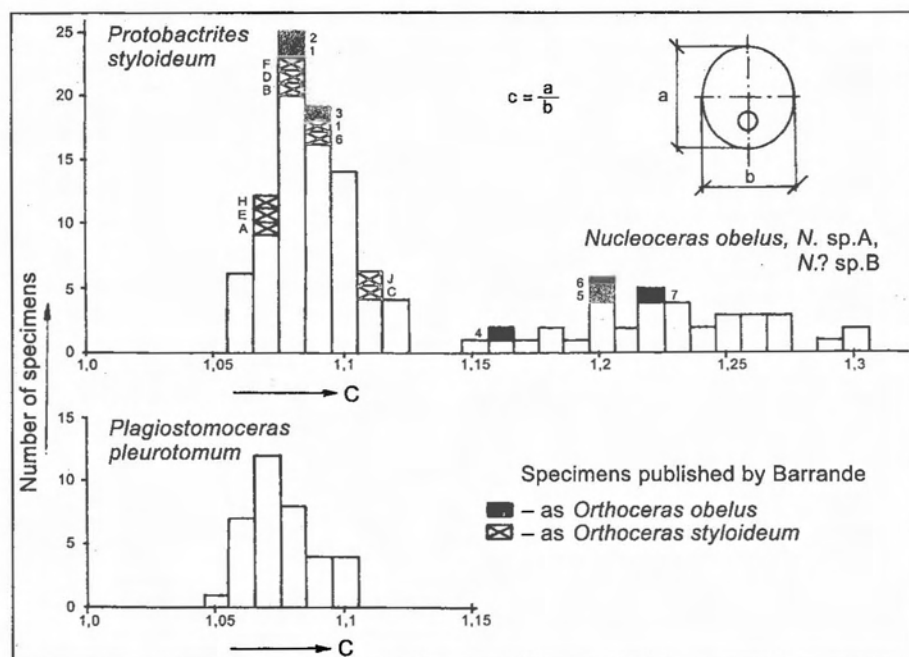


Fig. 1. Variability of the shell compression (c)

Symbols representing Barrande's specimens used in the diagrams: 1 - Pl. 365, fig. 9 (NM L 17980); 2 - Pl. 365, figs 16, 17 (NM L 17979); 3 - Pl. 366, figs 18, 19 (NM L 17993); 4 - Pl. 366, figs 16, 17 (NM L 17992); 5 - Pl. 366, fig. 20 (NM L 17995); 6 - Pl. 366, fig. 22 (NM L 17994); 7 - Pl. 366, fig. 24 (NM L 17996). A - Pl. 239, fig. 5 (NM L 6569); B - Pl. 239, fig. 6 (NM L 6570); C - Pl. 365, figs 1, 2 (NM L 6562); D - Pl. 365, fig. 3 (NM L 6563); E - Pl. 365, fig. 4 (NM L 6564); F - Pl. 365, fig. 6 (NM L 6566); G - Pl. 365, figs 7, 8 (NM L 6565); H - Pl. 365, figs 10, 11 (NM L 17981); I - Pl. 365, figs 14, 15 (NM L 6567); J - Pl. 365, figs 18, 19 (NM L 6568).

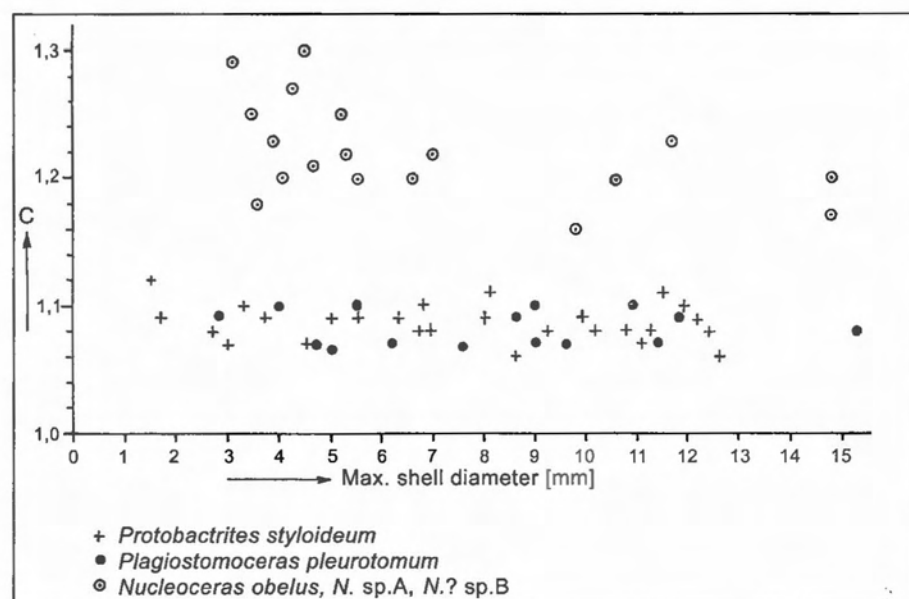


Fig. 2. The shell compression during ontogeny

embedded in an epoxide resin, cut and finely ground, then once again embedded in the resin and ground from the opposite side. Our thin sections are cca 0.2 mm thick. The pyritized/limonitized internal moulds of gas chambers have been obtained by etching calcite with weak organic acids; many of the moulds have been found already isolated naturally by weathering processes.

The majority of the collected phragmocones are fragmentary and lacking surface features of the shell. For the purpose of species determination the need therefore arose to verify the variability of two other features: the shell compression degree (Fig. 1) and the septal foramen position (Fig. 3). The ontogenetic changes of both features were also verified (Figs 2 and 4).

For the diagrams, shell compression (c) has been counted as the quotient of the dorso-ventral diameter (a) to the lateral diameter (b). The position of the septal foramen (s) is expressed as the distance (p) of its centre from the point of intersection of both diameters in per cent of the length of the half dorso-ventral diameter (a/2). Because it was impossible to identify the intersection point with acceptable accuracy, the dorso-ventral diameter and the distance between the centre of the septal foramen and ventral shell periphery (x) were measured. The calculation has been made according to the equation:

$$s[\%] = 100p : a/2 = 100(a-2x) : a$$

Changes of the relative height of gas chambers and the apical angle were the additional observed features but they proved to be hardly applicable for the purpose of identification. (The height/diameter ratio of gas chambers varied between 0.25-0.6 in the same specimen of *Protobactrites styloideum*.)

Results from the Diagrams

1. The dispersion fields of *Protobactrites styloideum* and *Plagiosiomoceras pleurotomum* are well delimited, narrow and approximately corresponding to the natural distribution curve. Both species mutually conform in the degree of their compression but clearly differ in the septal foramen position.

2. Specimens of *Nucleoceras* agree with *Protobactrites styloideum* in the septal foramen position but differ from both other species in its compression.

3. The dispersion fields of *Nucleoceras* occupy wide and flat areas; this fact indicates the presence of more than one species.

4. Three specimens considered by Barrande to be *Orthoceras obelus* are, in fact, *Protobactrites styloideum*. (Apical portion

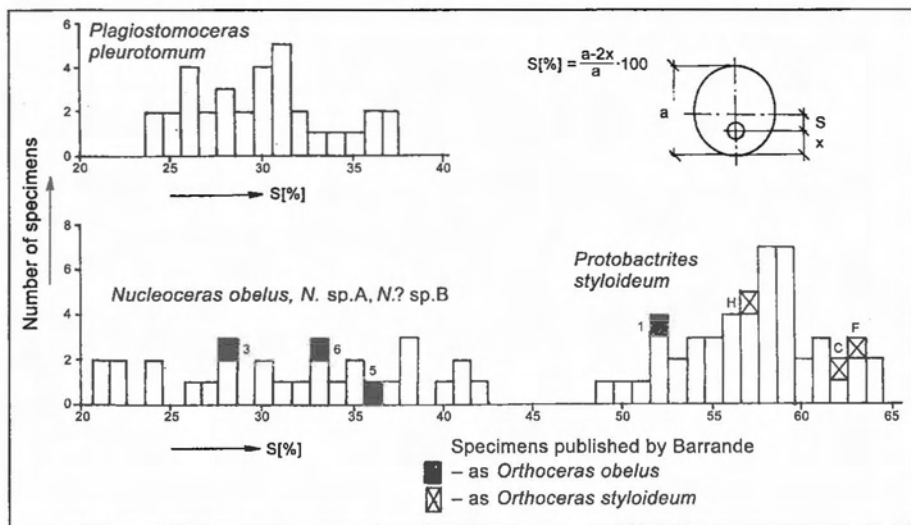


Fig. 3. Variability of the septal foramen excentricity (s)

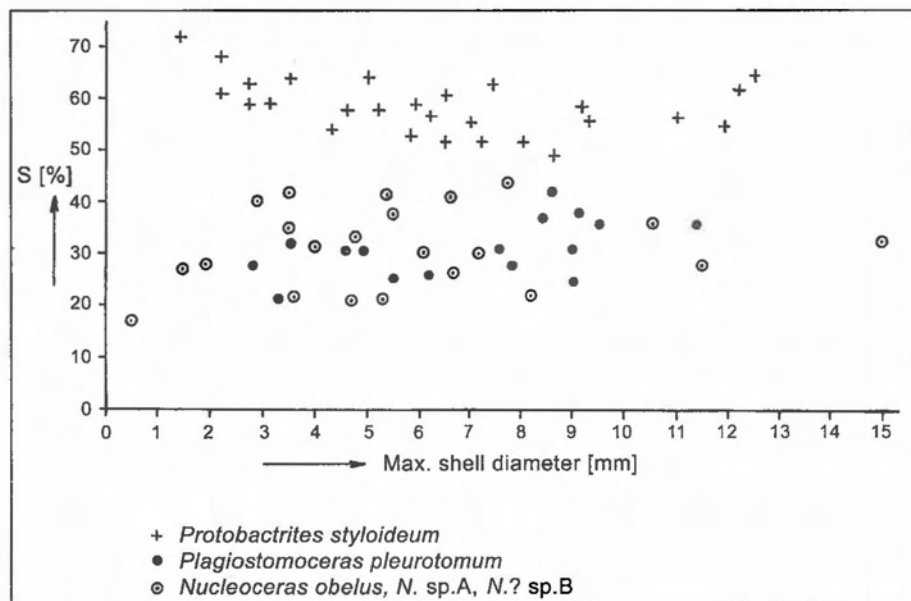


Fig. 4. The septal foramen position during ontogeny

of the specimen Pl. 365, fig. 9 was sectioned longitudinally and the disclosed internal structures proved this identification.)

5. Both observed features do not change significantly with shell size and can, therefore, be used for the identification of the studied species (see diagrams expressing the ontogenic changes in Figs 2 and 4).

Terminology

The morphological terminology of cephalopod shells (according to Teichert in Moore 1964) is used in this study, with two exceptions. The term *connecting ring* can be applied here only with doubt as the homological structure in those gas chambers of the discussed species which contain the cameral deposits has an open, not tubular or ring-like shape and should be rather named a *connecting trough*. The term *siphonal tube*

is, therefore, disputable for the discussed cephalopods; the term *siphonal channel* can be eventually used for this structure. The term *lamellae* is here used for the radial structure of the cameral mantle (compare with the *lamellae of cameral deposits*).

Morphology

Three models of the cameral mantle

Three different ways of arrangement of the internal shell structure have been distinguished providing information about three different morphological types of the cameral mantle. In Fig. 5 they are compared and the approximate positions of the cross-sections figured on the plates are indicated. All pieces of knowledge on the siphono-cameral structures, mentioned in this report, concern those parts of the shells which contain the cameral deposits.

Pouch-like cameral mantle with the connecting trough (Fig. 5a)

In *Protobactrites styloideum*, the cameral mantle of which had a pouch-like shape, cross-sections positioned in the gas chambers past the septal necks show an open, trough-like structure (TGH in Pl.2, figs 3, 8). Its ventral part is round, semi-circular, but the dorsal side is widely open. The line of the cross-sectioned connecting trough bends laterally to both sides and then backwards to the venter. It is sinuous,

bilaterally symmetrical and smooth. Several sections show an identical pattern which cannot be a consequence of the diagenesis. The massive, immediate communication between the siphonal and cameral internal moulds is well demonstrated e.g. in Pl. 1, fig. 5. In this species, the dorsoventral sections situated through septal foramens, have repeatedly shown clearly delimited openings (OP in Fig. 6).

Pouch-like cameral mantle completely free of connecting rings (Fig. 5b)

In *Plagiostomoceras pleurotomum* no connecting rings have been found. Their absence has proved to be a primary phenomenon, the main confirmation of which appears in longitudinal dorsoventral sections (Pl. 3, figs 5, 6, DC in fig. 7). The sharp curve delimiting hyoseptal deposits enters the chamber from inside of the septal foramen and smoothly, without any obstacles or irregularities, it runs not only dorsally (as in *Protobactrites*) but also ventrally and at both

sides passes into the pseudoseptum. No traces of connecting rings have been found, neither seen in cross-sections. A striking similarity of the elaborate cameral mantle attachment system of *Plagiostomoceras pleurotomum* (see the part "Cameral mantle attachment system" herein) to that of *Protobactrites styloideum* indicates also a similarly solid cameral mantle.

Lamellar type of cameral mantle with the connecting trough (Fig. 5c)

Cross sectioned apical shell parts of the two species of *Nucleoceras* described herein repeatedly show a broadly open connecting trough (TGH in Pl. 4, fig. 4; Pl. 5, figs 1, 2, 3; Pl. 6, figs 2, 4), strikingly similar to those of *Protobactrites styloideum*. This similarity is significant because both species have a very different morphology of the cameral mantle (that of *Nucleoceras* is characterized by the lamellar structure) and belong to different families. The connecting trough also opens with a continuous sinusoial curve that runs laterally to both sides and then bends backwards to the venter. Between these lines is located the ventral area where the cameral deposits first arise and form the thick pillar (lamella) of the cameral deposits. The internal surface of the connecting trough is ventrally covered with a continuous lining of the siphonal deposits (SD in Pls 4, 5, 6).

Empty central space in all gas Chambers

In the species discussed herein, the first traces of the cameral deposits are observable at approx. the 25th gas chamber behind the living chamber. Then the deposits grow quickly chamber by chamber in the adapical direction, stopping their development in a certain phase. Central spaces free of the cameral deposits therefore remain even in the most adapical portion of the phragmocone where the deposits are fully developed. These empty spaces most probably remained after the cameral mantle had decayed.

The central empty space in the gas chambers of *Nucleoceras* is smaller than those of *Protobactrites styloideum* and *Plagiostomoceras pleurotomum*. This is probably due to the lamellar structure of the cameral mantle (the lamellae themselves represent the empty spaces).

Traces of blood vessels

Tubular projections can be seen on the adoral and/or lateral surfaces of some larger, well preserved, originally pyritized internal moulds of *Protobactrites styloideum* (in very small moulds the surface features are suppressed by the crystals of pyrite). Some of them run radially from the siphonal area and are distally branching, the course of others is circular, concentric with respect to the septal foramen (BV in Pl. 1, figs 1, 2). Flower (1941) and Holland (1965) described much more complex but substantially identical structures on the internal moulds of two species of *Leurocyloceras*. Both authors concluded that these tubes must represent the blood vessels. It seems to be the only acceptable interpretation.

The cameral mantle attachment systems

Special morphological structures which most probably served to fix the mass of the cameral mantle inside the gas chambers were observed in numerous longitudinal and transversal sections of *Protobactrites styloideum* and *Plagiostomoceras pleurotomum*. Such a system supposedly enabled the cameral mantle to retain its position and shape during rapid movements and at buoyancy regulation. Its arrangement is best seen in Pl. 2, figs 6, 7 and 9 (*Protobactrites styloideum*), Pl. 3, figs 2, 3, Fig. 7a,b and in a schematic drawing in Fig. 8 (*Plagiostomoceras pleurotomum*).

The pseudoseptum, dorsal and ventral attachment membranes, apical spines and also lamellae of the lamellorthoceratids, are supposed parts of this remarkable system.

Pseudoseptum

The pseudoseptum is the most conspicuous part of the attachment system; it exists in all species discussed herein. This relatively thick pyritized trace of a membrane runs from the adoral rim of the cameral mantle adorally up to the place where the septum detaches from the shell wall (P in Figs 6, 8). There, the pseudoseptum is attached to the circumferential area of the free part of the septum (never to the shell wall), being thickened in the area of contact (T in Fig. 6).

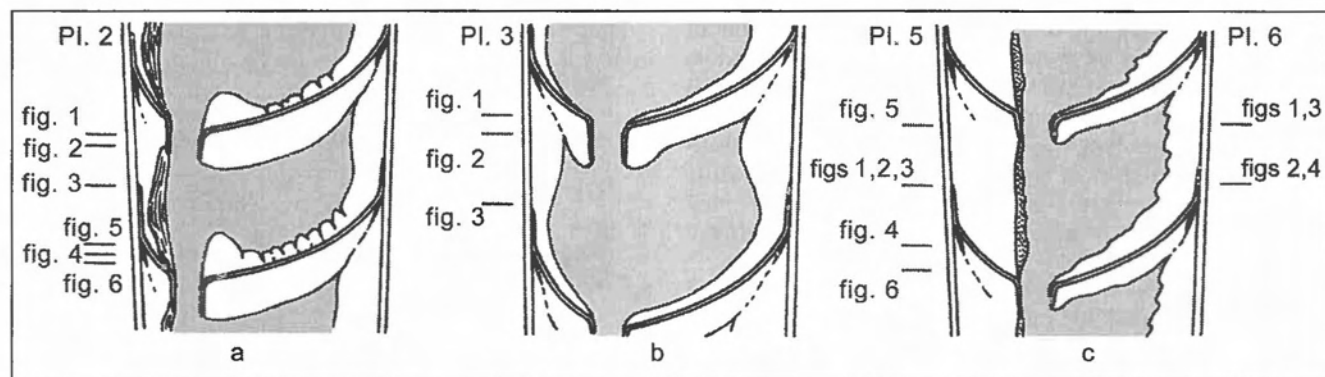


Fig. 5. Schematic drawings of three morphological types of the siphono-cameral space originally occupied by the tissue (dark grey area). Approximate location of the cross-sections figured on plates are indicated. a - *Protobactrites styloideum* (Pl. 2), b - *Plagiostomoceras pleurotomum* (Pl. 3), c - *Nucleoceras obelus* (Pl. 5), *N.?* sp. A, *N.?* sp. B (Pl. 6) Photos by R. Horný.

Longitudinal membranes

Another, more complicated part of the attachment system, is fixed to the internal surface of the shell in mid-ventral and mid-dorsal regions and is connected with the pseudoseptum. In the cross-sections, near the shell wall, at somewhat advanced growth stages of the deposits, the continuous line of the pseudoseptum is broken and thin dark lines of pyrite run from the points of breakage, converge to each other and attach to the shell wall (VAM and DAM in Fig. 8). Between them, in the axis of their angle, another line runs towards the siphuncle (VAL and DAL in Fig. 8). These lines have been found in cross-sections taken in various levels of the chamber. In *Protobactrites styloideum* they are demonstrated on Pl. 2, figs 2, 4, 5, 6, 7 and 9; in *Plagiostomoceras pleurotomum* in Pl. 3, figs 2, 3 and in Figs 7a,b and 8.

It is assumed that these structures may represent traces of membranes which served to fix the cameral mantle longitudinally to the shell wall.

There exists a doubt regarding the explanation of the axial lines (VAL and DAL) running from the contact points of the attachment membranes towards the septal foramen but they are probably traces of another part of the attachment system.

Adapical spines

The internal moulds of *Protobactrites styloideum* are on their adapical surface covered with a number of tiny spines; similar projections protrude from the adapical septum to meet them or are connected with them (SP in Figs 6 and 9). This probably is a trace of another part of the attachment system. In the advanced stage of the cameral deposits formation the connection between the cameral mantle and the adapical septum most probably was broken but the adapical part of the cameral mantle remained anchored adapically in deposits with a number of spiky projections.

The origin of ventral and dorsal furrows

The unique specimen of *Protobactrites styloideum* (NM L 32821) yielded a remarkable information concerning the ventral (conchal) and dorsal (septal) furrows which are often found on the internal moulds of gas chambers. Fig. 10 (drawn after Pl. 2, fig. 10) shows the cross-sectioned mid-ventral area of the gas chamber in the initial stage of the cameral deposits formation. The limonitized trace of the cameral mantle (CM) lies in contact with the inside of the shell wall (SW) but its mid-ventral sub-oblong region (TR) is thickened and substitutes the internal part of the shell wall. If the shell wall is dissolved by diagenesis, the more resistant region TR may appear as a low, flat, longitudinal projection along the surface of the internal mould.

There is an area (WA) on each side of the region TR where the pyritized/limonitized plane is weakened by the cameral deposits (CD) which begin to grow between it and the shell wall. It can be supposed that from these weakened planes the membranes of the attachment system originated after the cameral mantle was gradually pushed towards the chamber centre by the growing cameral deposits. The adoral part of the cam-

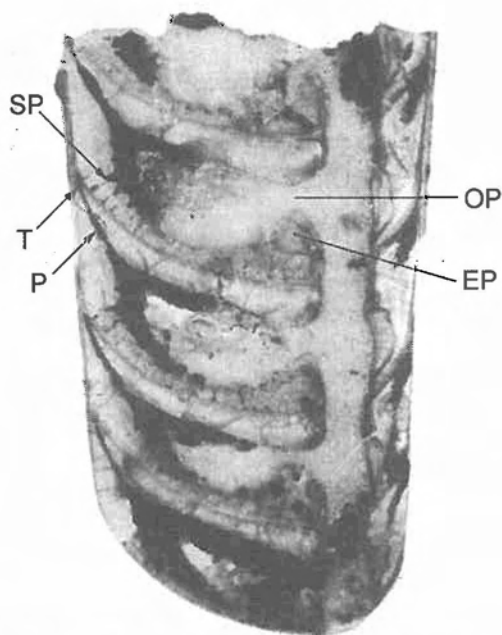


Fig. 6. *Protobactrites styloideum* (Barrande, 1866), specimen NM L 32878, dorsoventral thin section, x 10. EP – episeptal projection; OP – opening (connection between the siphonal and cameral spaces); SP – spines; P – pseudoseptum; T – thickened contact area of the pseudoseptum.

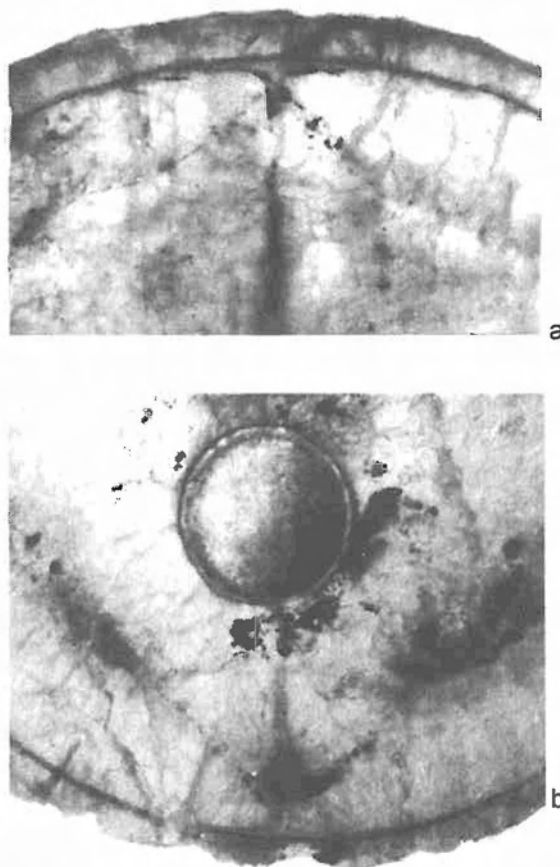


Fig. 7a,b. *Plagiostomoceras pleurotomum* (Barrande, 1866), thin cross-section – details of the specimen NM L 32823 figured in Pl. 3, fig. 2, x 32. a – dorsal area, x 38; b – ventral area; x 28. (For explanation of the symbols see Fig. 8.)

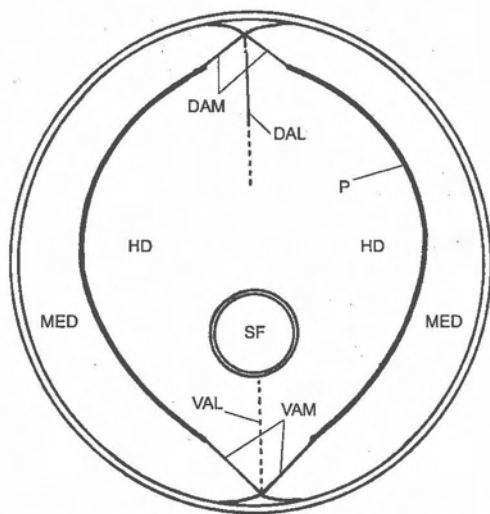


Fig. 8. Schematic drawing showing the arrangement of the attachment system of *Plagiostomoceras pleurotomum* (BARR., 1866). The cross-section cuts the septal necks. According to the specimen NM L 32823, pl. 3, figs 1, 2. DAL - dorsal axial line; DAM - dorsal attachment membranes; HD - hyposeptal deposits; MED - mural part of episepal deposits; VAL - ventral axial line; VAM - ventral attachment membranes; P - pseudoseptum; SF - septal foramen.

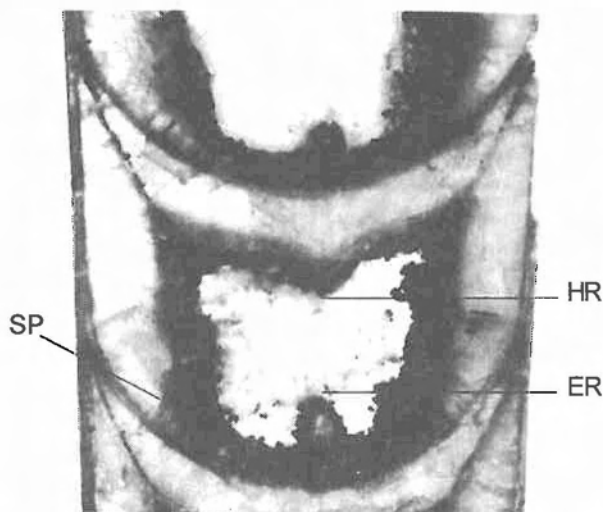


Fig. 9. *Protobactrites styloideum* (BARR., 1866), specimen NM L 32813, lateral thin section. Detail of Pl. 1, fig. 8. x 13. HR - ridge of the hyposeptal deposits; ER - ridge of the episepal deposits; SP - adapical spines.

eral mantle was, in this process, weakened and formed the pseudoseptum.

The ventral and dorsal attachment membranes (e.g. Fig. 8) are fixed to the shell wall exactly in the areas where both furrows occur. This fact indicates that, at least in *Protobactrites* and *Plagiostomoceras*, the ventral and dorsal furrows represent the areas where the attachment system of the cameral mantle was anchored to the shell wall. (The appearance of the dorsal furrow is shown in Fig. 11a,b.)

Note: In Moore 1964, K 29, Fig. 18, the dorsal furrow is wrongly indicated as the conchal (ventral) one.

Attachment system in *Nucleoceras* gen. n.

In the lamellar type of cameral mantle, the lamellae themselves probably played an important role in the tissue fixation. In *Nucleoceras* gen. n. a pseudoseptum has been proved (Pl. 6, fig. 8) but no concrete proof of other parts of the cameral mantle attachment system (as found in *Protobactrites* and *Plagiostomoceras*); neither dorsal, nor ventral furrows have been found in our material. Nevertheless, the cross-sections on Pl. 5, fig. 2 and Pl. 6, fig. 4 show the dark lines beginning at the tips of the ventral lobes (VL) of the cameral mantle; they run towards the venter and coalesce there. This may be an analogy of the "organic sheets... one of them formed an attachment membrane for the siphuncle" of Bandel and Stanley (1989, p. 397). The empty central space in the adapical chambers of *Nucleoceras* containing maximally developed cameral deposits is smaller than that of *Protobactrites styloideum* and *Plagiostomoceras pleurotomum*, but even the smallest found internal moulds (Pl. 4, figs 5, 6) keep the basic, elaborate morphological features of the cameral mantle.

Bilateral symmetry

The bilateral symmetry of the internal structures according to the dorso-ventral plane is one of the common features in the studied species. In *Protobactrites styloideum*, a shallow but distinct depression runs along the adoral surface of the internal moulds from the siphonal area towards the dorsum (Pl. 1, fig. 3). Another, deeper depression, also running dorsally, occurs on the opposite - adapical - side of the internal moulds. In the longitudinal axis of the lateral sections (Pl. 1, fig. 8, Fig. 9) both these depressions are shown as mutually opposite hyposeptal and episepal ridges of the cameral deposits (HR and ER in Fig. 9), so that a "butterfly-like" picture arises. The adapical depression passes into a deep hollow located close to the siphonal area. It appears in dorsoventral sections (EP in Pl. 1, fig. 4 and Fig. 6), as an adorally directed round projection of episepal deposits.

In *Plagiostomoceras pleurotomum* the dorsal side of the internal moulds is cut out to form a V-shape groove the edges of which are connected with the shell wall by attachment membranes (Pl. 3, fig. 3). In the lateral sections, the bilateral symmetry is also shown as "butterfly-like" pictures (Pl. 3, fig. 8).

In *Nucleoceras* gen. n., the symmetrical ventro-lateral lobes of the internal moulds are a conspicuous feature (VL in Pls 4, 5, 6). A deep adapical depression on the internal mould, similar to that of *Protobactrites styloideum*, is seen in a specimen figured on Pl. 4, fig. 6, where the complex and elaborate morphology is apparent, even though the specimen is only 1.3 mm long.

Some remarkable deflections from the exact bilateral symmetry have been observed in *Protobactrites styloideum*. The cross-section of the specimen on Pl. 2, fig. 6 shows apparent mutual asymmetry of two succeeding chambers. The internal, darker, elliptic area belongs to a chamber sectioned near its base (adapically) and the outer annular plane is the adoral part of the preceding chamber (for the position of the section see Fig. 5a). In this chamber the cameral mantle attachment system is shifted to the right by an angle of approx. 15 degrees.

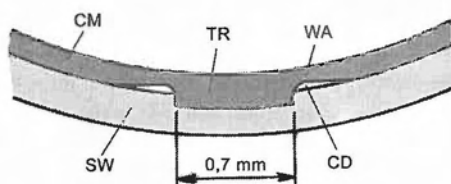


Fig. 10. *Protobactrites styloideum* (BARR., 1866), schematic drawing showing the penetration of the pseudoseptum into the shell wall, according to specimen NM L 32821, Pl. 2, fig. 10. CD - cameral deposits; CM - pyritized trace of cameral mantle; SW - shell wall; TR - thickened region; WA - weakened area.

Conclusions

1) Three morphological types of sipho-cameral tissue have been distinguished (Fig. 5): a. pouch-like cameral mantle and siphuncle with connecting troughs (a proposed term for connecting rings which are widely open on their dorsal side) [*Protobactrites styloideum* (BARR.)]; b. pouch-like cameral mantle and siphuncle without any connecting rings [*Plagiostomoceras pleurotomum* (BARR.)]; c. lamellar cameral mantle and widely open connecting trough [*Nucleoceras obelus* (BARR.), *N. sp. A*, *N.?* sp. B].

2) The immediate unity of the siphonal and cameral tissues in the gas chambers containing the cameral deposits has been proved and the existence of connecting troughs together with the morphology of internal moulds are the main arguments to support this conclusion.

3) The attachment system of a pouch-like cameral mantle has been found in *Protobactrites styloideum* (BARR.) and *Plagiostomoceras pleurotomum* (BARR.). Its parts include the membrane of the pseudoseptum that fixed the cameral mantle adorally to the convex surface of the septum, and ventral and dorsal longitudinal attachment membranes which served to fix the cameral mantle to the shell wall. Traces of ligaments (adapical spines) which supposedly fixed the cameral mantle to the surface of the adapical septum have been found in *Protobactrites styloideum*.

4) Ventral and dorsal furrows are interpreted as traces of the fixation of the longitudinal attachment membranes.

5) A lamellar type of the cameral mantle has been found in both species of *Nucleoceras* gen. n. - a Silurian ancestor of the Devonian lamellorthoceratids.

6) The pouch-like and lamellar types of cameral mantle have common features: immediate connection with the siphonal tissue, bilateral symmetry, elaborate structure, and a pseudoseptum as an attachment element.

7) The majority of Palaeozoic longiconic orthocones containing cameral deposits evidently possessed closed, tubular connecting rings. The cameral deposits of some of them, nevertheless, have a strikingly elaborate morphology; from this it follows that these cephalopods probably also had a cameral tissue connected with the siphonal tissue, perhaps by means of fine blood-vessels passing through the wall of the connecting rings.

Fig. 11a,b - *Protobactrites styloideum* (BARR., 1866), specimen NM L 32933. a - internal mould with the dorsal furrow and a unique holdfast of a bryozoan (?), x 20, b - the same specimen, detail of the dorsal furrow, x 40.

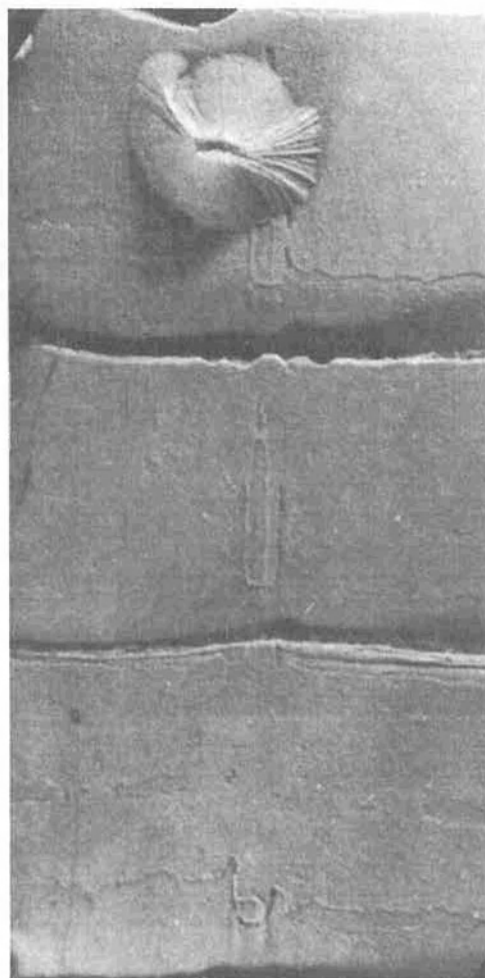


Fig. 11a

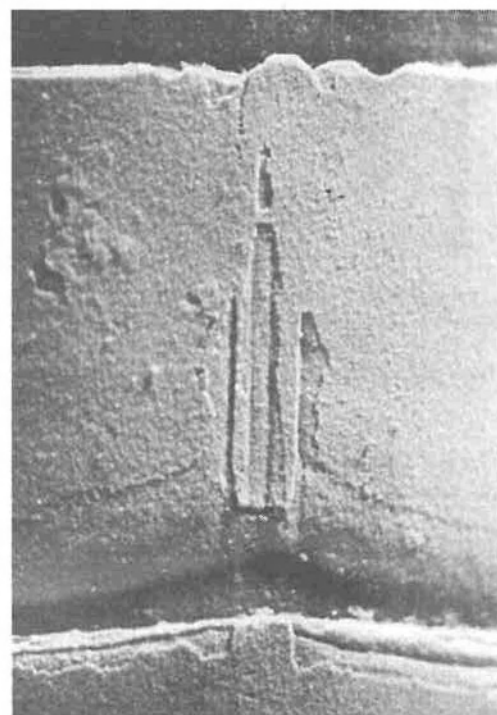


Fig. 11b

Systematic part

Class *Cephalopoda* CUVIER, 1798
Order *Pallioceratida* MAREK, 1998

Families: *Leurocycloceratidae* SWEET, 1964, *Lamel-lorthoceratidae* TEICHERT, 1961

Stratigraphic range: ? Lower Ordovician, Middle Ordovician, Lower Silurian - Lower Devonian, ? Lower Carboniferous.

Geographic distribution: Europe, N. America, N. Africa, W. Asia, ? China.

Note: Systematic units of this order are reliably recognizable only when internal features of the shell parts containing cameral deposits are known.

Family *Leurocycloceratidae* SWEET, 1964, emend.

(ex Subfam. *Leurocycloceratinae* SWEET in MOORE, 1964)
(= *Lituitina* DZIK, 1984, partim)

Emended diagnosis: Smooth or ornamented longicones of circular to compressed cross-section. Internal structures prove the original presence of a bilaterally symmetric, pouch-like but not lamellar cameral mantle. Connecting rings in the adapical chambers containing the cameral deposits are either dorsally open forming the connecting troughs or entirely absent.

Stratigraphic range: Middle Ordovician - Silurian - ? Devonian.

Geographic distribution: N. America, Europe, ? China

Genera: *Leurocycloceras* FOERSTE, 1928, *Murchisoniceras* BABIN, 1966, *Plagiostomoceras* TEICHERT et GLENISTER, 1952, *Protobactrites* HYATT in ZITTEL, 1900, *Rhynchorthoceras* REMELÉ, 1881, ? *Sinoceras* SHIMIZU and OBATA, 1935.

Genus *Protobactrites* HYATT in ZITTEL, 1900, emend.

Type species: *Orthoceras styloideum* BARR., 1866

Syn.: *Protobactolites* KOBAYASHI, 1934

Mariaceras KOLEBABA, 1974

Emended diagnosis: Longiconic orthocones of circular to moderately compressed cross-section. Surface smooth or with transversal or longitudinal striae. Aperture oblique, sloping adapically from the dorsal (antisiphonal) side. Septal foramens excentric, shifted ventrally but not marginal. Septal necks orthochoanitic to suborthochoanitic. Hyposeptal and episeptal deposits well developed in apical gas chambers; there are 23 or more chambers free of the cameral deposits adapically from the living chamber. Connecting rings in the chambers containing the cameral deposits are widely open on their dorsal side forming the connecting troughs.

Stratigraphic range: Middle Ordovician - Silurian.

Geographic distribution: Europe, ? N. America.

Protobactrites styloideum (BARR., 1866)

Syn.: *Mariaceras pragense* KOLEBABA, 1974

Lectotype: Specimen NM L 6570, Barrande 1866, Pl. 239, fig. 6, figured here in Fig. 12c.

Paralectotypes: Specimens NM L 6569, Barr. 1866, Pl. 239, fig. 5 and NM L 6571, Barr. 1866, Pl. 239, figs 7, 8.

Stratum typicum: Silurian, Ludlow, Gorstian; Kopanina Formation, biozone with *Colonograptus colonus*.

Locus typicus: Praha-Butovice, Na Břekvici.

Description: Surface smooth except for growth lines. Shell compressed with dorsoventral diameter by 6-13% greater than the lateral diameter. Apical angle decreases from about 6.5° to 2° during ontogeny. The height of gas chambers varies in the range 30-60% of their diameter, the last gas chamber (immediately preceding the living chamber) of the large specimens being the lowest - about 25% of its diameter. The height of the living chamber about six to seven times greater than the diameter of its base. Septa asymmetrically curved with the septal foramen located in their deepest point. Septal foramens centroventral to extracentroventral, shifted ventrally by 49-64% of the distance between the centre of the shell and its periphery. Septal necks orthochoanitic reaching 15-18% of the chamber height (measured in specimens with maximum diameter 6.5 mm). Between the gas chambers containing cameral deposits and the living chamber exist 23 to 25 chambers free of deposits. Cameral deposits pass between successive chambers slightly reducing the diameter of septal foramens. Internal moulds of those gas chambers containing cameral deposits bear on their apical surfaces tiny spines directed towards the adapical septum and/or slender pillars coalescing with its surface (Figs 6, 9). Interspaces between them form a honeycomb sculpture on the moulds.

Stratigraphic range: Silurian, Ludlow, Gorstian, Kopanina Formation, biozone with *Colonograptus colonus*.

Geographic distribution: Central Bohemia, Barrandian Area.

Material: 145 measured specimens.

Genus *Plagiostomoceras* TEICHERT et GLENISTER, 1952, emend.

Type species: *Orthoceras pleurotomum* BARR., 1866

Emended diagnosis: Longiconic orthocones of circular to slightly compressed cross-section. Surface with growth lines and weak ridges parallel to the aperture. Aperture strongly oblique sloping adapically from dorsal (antisiphonal) side. Septal foramens moderately excentric, shifted ventrally. Septal necks orthochoanitic. Connecting rings in the chambers containing cameral deposits are absent.

Stratigraphic range: Upper Ordovician - Lower Devonian.

Geographic distribution: Europe, Australia.

Plagiostomoceras pleurotomum (BARR., 1866)

Holotype: Specimen NM L 6613, Barr. 1866, Pl. 224, figs 12-14, figured here in Fig. 12d. (Not specimen NM L 6614 figured by Barrande later, in 1868, Pl. 296, figs 1-3, and incorrectly designated by Teichert and Glenister, 1952, p. 733 as the holotype.)

Stratum typicum: Silurian, Ludlow, Gorstian, Kopanina Formation, biozone with *Colonograptus colonus*.

Locus typicus: Praha-Butovice, Na Břekvici.

Description: Surface ridges arranged at intervals of 0.6-0.8 mm. Shell compressed with the dorsoventral diameter by 5-11% greater than the lateral diameter. Apical angle in speci-

mens of diameter 3.7–15 mm is almost constant at 2.5°. The height of gas chambers in younger specimens is approximately equal to their dorsoventral diameter, in later ontogenetic stages it decreases to a half. Septal foramens intracentroventral, shifted ventrally by 24–37% of the distance between the centre of the shell and its periphery. Septal necks orthochoanitic, reaching 15–18% of the chamber height. Hyposeptal deposits and the mural part of the episeptal deposits are well developed, the adapical area of episeptal deposits is weak (Pl. 3, fig. 6, Fig. 5b). Internal moulds (supposed replicas of the cameral mantle) of the gas chambers containing cameral deposits have a wrinkled surface (Pl. 3, fig. 4) and V-shaped dorsal groove (Pl. 3, fig. 3).

Stratigraphic range: Silurian, Ludlow, Gorstian; Kopanina Formation.

Material: 45 measured specimens.

Family **Lamellorthoceratidae** TEICHERT, 1961,
emend.
(= *Lituitina* DZIK, 1984, partim)

Emended diagnosis: Straight or slightly endogastric, smooth or crenulated longiconic shells, circular to compressed in cross-section. Internal structures prove the original presence of a cameral mantle which consisted of a system of radially arranged lamellae with respect to the axis of septal foramens. Septal foramens subcentral to moderately shifted ventrally, septal necks orthochoanitic or slightly bent outwards. Connecting rings in most of the genera unknown, supposedly open dorsally to form connecting troughs; the dorsal opening has been confirmed in *Nucleoceras*.

Stratigraphic range: Upper Silurian – Middle Devonian, ? Lower Carboniferous.

Geographic distribution: N. Africa, N. America, Europe, ? Asia.

Genera: *Arthrophyllum* BEYRICH, 1850, *Lamellorthoceras* TERMIER et TERMIER, 1950, *Gorgonoceras* ZHURAVLEVA, 1961, *Corallocceras* ZHURAVLEVA, 1962, *Esopoceras* STANLEY and TEICHERT, 1976, and *Nucleoceras* gen. n.

Genus ***Nucleoceras*** gen. n.

Type species: *Orthoceras obelus* BARR., 1870; Upper Silurian, Barrandian Area, Czech Republic.

Stratum typicum: Silurian, Ludlow, Gorstian, Kopanina Formation, biozone with *Colonograptus colonus*.

Locus typicus: Praha–Butovice, Na Břekvici.

Derivatio nominis: *Nucleoceras*, to emphasize the importance of internal shell structures of gas chambers for the understanding of the pallioceratid morphology; nucleus (Lat.), kernel.

Diagnosis: Genus of the family Lamellorthoceratidae, similar to *Gorgonoceras visendum* ZHURAVLEVA, 1961 but compressed in cross-section and with a smooth surface except for growth lines or lirae and striae. Connecting troughs well developed; their ventral part lined with intrasiphonal deposits.

Species included: *Nucleoceras obelus* (BARR., 1870), *Nucleoceras*? sp. A, *Nucleoceras*? sp. B.

Occurrence: Silurian, Barrandian Area, Czech Republic.

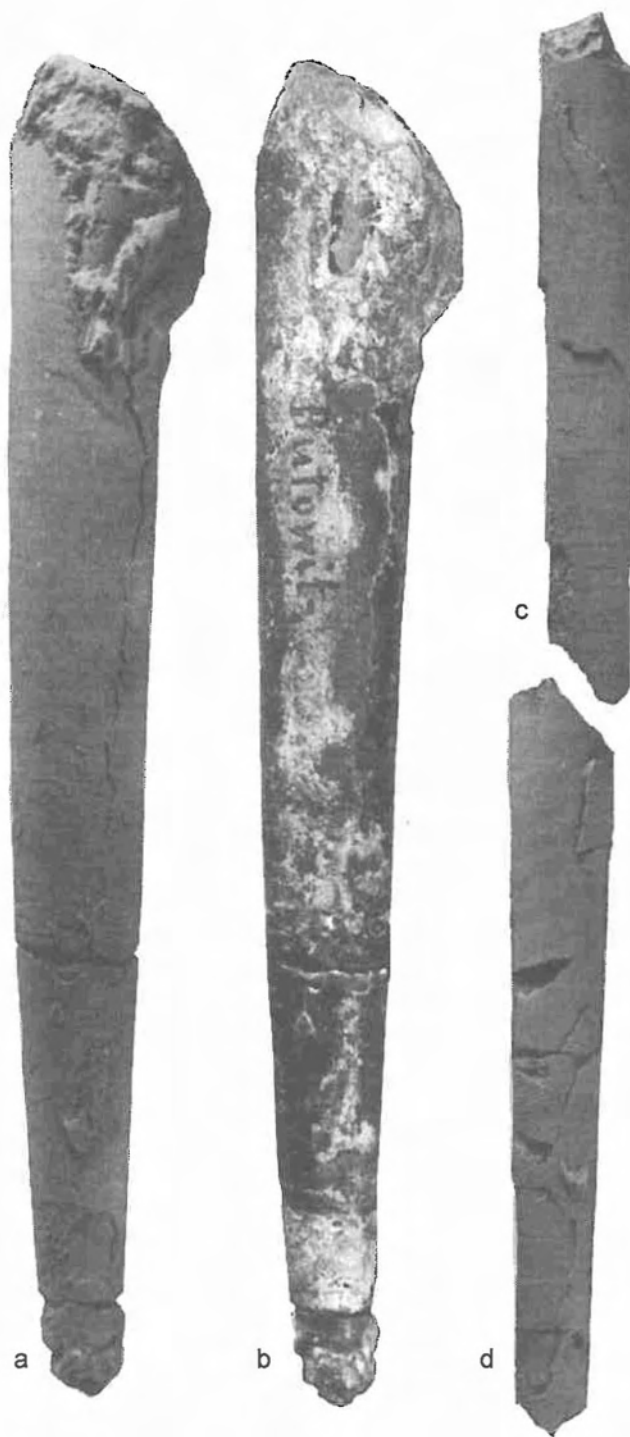


Fig. 12. Barrande's original specimens, a. *Nucleoceras obelus* (BARR., 1870), lectotype, Barrande (1870), Pl. 366, figs 16–17, NM L 17992. Internal mould, coated with ammonium chloride; b. the same specimen, uncoated to show original Barrande's indication of the locality; c. *Protobactrites styloideum* (BARR., 1866), lectotype, Barrande 1866, Pl. 239, fig. 6, NM L 6570. Specimen with a part of the shell preserved, lateral view, venter right; d. *Plagiostomoceras pleurotomum* (BARR., 1866), holotype, Barrande 1866, Pl. 244, figs 12–14, NM L 6613. A specimen with remainders of the shell wall preserved, lateral view, venter left. Photos by R. Horný. All figures x 1,25.

Nucleoceras obelus (BARR., 1870)

(Pl. 4, figs 1-4; Pl. 5, figs 1-8; Fig. 5c)

1870 *Orthoceras obelus* BARR., 1866 (partim)

Lectotype: Specimen NM L 17992, figured by Barrande, 1870. Pl. 366, figs 16, 17, here figured in Fig. 12a,b.

Paralectotypes: Specimens NM L 17994 and NM L 17995 figured by Barrande 1870, Pl. 366, figs 20 and 22, 23. (Not NM L 17980, NM L 17979 and NM L 17993, figured by Barrande on Pl. 365, figs 9 and 16, 17 and Pl. 366, figs 18, 19; these specimens are, in fact, *Protobactrites styloideum*. Also not specimen NM L 17991, Barrande 1870, Pl. 366, fig. 15, which comes from a younger stratigraphic level, from another locality (named by Barrande as "Kosoř") and contains different internal structures.

Stratum typicum: Silurian, Ludlow, Gorstian; Kopanina Formation, biozone with *Colonograptus colonus*.

Locus typicus: Praha-Butovice, Na Břekvici.

Description: Surface smooth except for growth lines. Shell compressed with the dorsoventral diameter by 15-30% greater than the lateral one. Apical angle in specimens of diameter 4-12 mm is rather constant and varies between 5-7°, then it decreases and in our largest specimens (living chambers of the diameter about 14-16 mm) it is only about 3°. Septal foramina shifted ventrally by 30-42% of the distance between the centre and ventral margin of the shell. Diameter of septal foramina varies in our material between 12-15% of the relevant dorsoventral shell diameter. Septal necks are orthochoanitic, ratio of their length to the chamber height changes during ontogeny; in specimens of max. diameter about 5 mm they reach approx. 18% of the relevant shell diameter, in the biggest specimen (Pl. 4, fig. 3) it reaches about 25%. Lamellae are at advanced development of the deposits in cross-section long (the length at least four times larger than their width), in the adapical region of the chamber distally bifurcating (Pl. 5, figs 2, 6, 8).

Material: 59 specimens.

Discussion: Observed in a cross-section, the lamellar system of the type species is similar to that of the Middle Devonian *Gorgonoceras visendum* ZHURAVLEVA in the general arrangement of lamellae, position of septal foramen and presence of the endosiphuncular lining on venter. It differs by its compressed, smooth shell and almost orthochoanitic septal necks.

Nucleoceras? sp. A

(Pl. 6, figs 1, 2, 3; Fig. 5c)

Stratum typicum: Silurian, Ludlow, Gorstian, Kopanina Formation, biozone with *Colonograptus colonus*.

Locus typicus: Praha-Butovice, Na Břekvici.

Description: Septal foramina shifted ventrally by 24-29% of the distance between the shell axis and ventral shell margin. Their diameter occupies approx. 18% of the dorsoventral shell diameter. Lamellae in cross-section short, resembling sub-triangular spines. Connecting troughs clearly open.

Discussion: Species A differs from the type species in its larger, closer to the shell axis positioned septal foramen and short, spine-like lamellae.

Material: 3 specimens.

Nucleoceras? sp. B

(Pl. 6, figs 4, 5, 6, 7; Fig. 5c)

Stratum typicum: Silurian, Ludlow, Gorstian, Kopanina Formation, biozone with *Colonograptus colonus*.

Locus typicus: Praha-Butovice, Na Břekvici.

Description: Septal foramina shifted ventrally by approx. 27% of the distance between the centre and ventral shell margin, their diameter occupies approx. 20% of the corresponding dorsoventral shell diameter. Connecting troughs well developed. Septal necks suborthochoanitic, short; in our specimens reaching 10% of the relevant gas chamber height. Lamellae insufficiently proved (that is the reason of the uncertainty regarding the systematic pertinence of the species).

Discussion: Species B differs from *Nucleoceras obelus* in the large, nearer to the longitudinal shell axis positioned septal foramen and very short septal necks. Lamellae unknown.

Material: 2 specimens.

Discussion

Functional interpretation

The cameral deposits in straight cephalopods enabled the animal to keep its shell in a horizontal position with the venter down, during the fully active period of ontogeny (compare Dzik 1984, p.132: cameral deposits "are to be regarded as a gerontic structure; an apex filled up with deposits could not function as an active hydrostatic organ").

As regards the cameral mantle, the question arises, as to how it functioned and which advantages it gave to the animal. A likely presumption is that the cephalopod was able to create the cameral deposits very promptly, much faster than in the process in which the liquid bearing calcite had to penetrate through the connecting rings.

Systematic position

Besides *Protobactrites*, *Plagiostomoceras* and *Nucleoceras* gen. n., discussed in this report, there are several other genera in which connecting rings are unknown or open to the gas chambers: *Ancistroceras* BOLL, 1857, *Leurocycloceras* FOERSTE, 1928, *Murchisoniceras* BABIN, 1966, *Rhynchorthoceras* REMELE, 1881, *Sphooceras* FLOWER, 1962, *Sinoceras* SHIMIZU and OBATA, 1935, and all lamellorthoceratids: *Arthrophyllum* BEY-RICH, 1850, *Lamellorthoceras* TERMIER et TERMIER, 1950, *Gorgonoceras* ZHURAVLEVA, 1961, *Coralloceras* ZHURAVLEVA, 1962 and *Esopoceras* STANLEY et TEICHERT, 1976.

Dzik (1984) suggested to place them, together with other genera (e.g. *Ophioceras* which has closed, tubular connecting rings) into the new Suborder Lituitina DZIK, 1984. Many of the taxa presented by Dzik as belonging to the Lituitina do not correspond with the suborder diagnosis: "Subcentral, cylindrical siphuncle with long septal necks. Exogastric coiling of the apical part of shell, extended in phylogeny over later ontogenic stages; funnel sinus narrow and deep, except in the most primitive forms" (1984, p. 131). For example: *Murchisoniceras murchisoni* (BARR.), *Sphooceras truncatum* (BARR.) and the five included lamellorthoceratids have short septal necks (reaching 1/6 - 1/5 of the relevant gas chamber height)

and show no tendency to coiling. In addition, the diagnosis of the suborder is based also on the shape of the shell aperture (funnel sinus) which can be only rarely observed in fossil material. The diagnosis does not allow *Protobactrites styloideum* to be associated with Lituitina because the siphuncle of this species is excentric.

The Family Sinoceratidae SHIMIZU and OBATA, 1935 (of Lituitina) contains, according to Dzik, genera with a lamellar type of cameral mantle (lamellorthoceratids) together with those similar (as for the internal structures) to *Protobactrites* and *Plagiostomoceras*, supposedly possessing the pouch-like cameral mantle. These two morphological types have, in my opinion, the systematic value of families.

Dzik accepts the biological origin of cameral deposits but not the idea of the cameral mantle: "To assume that phragmocone chambers were filled entirely with soft tissues is to deny their hydrostatic function" (p. 17), and is convinced of "functional implausibility" of the hypothetic cameral mantle. All our evidence proves that the open connecting rings (the connecting troughs) was a primary phenomenon and that the phragmocone had contained an integrated siphon-cameral tissue during the life of the cephalopod. Because of all the discrepancies mentioned above I cannot use Dzik's systematics. The internal morphology of *Protobactrites styloideum*, *Plagiostomoceras pleurotomum* and *Nucleoceras* gen. n., described herein, separates these taxa from the nautiloids, and the more natural and biologically substantiated order Pallioceratida Marek, 1998 seems to be suitable for them (and also probably for all the above named genera).

As regards the Lamellorthoceratidae TEICHERT, 1961, according to my information, study of this family presented no evidence of a closed siphonal tube as yet; the only exception is the statement of Bandel and Stanley (1989, p. 397): "Only in the material from the Hunsrück the actual organic siphuncular tube is preserved". Nevertheless, the figured cross-section (Pl. 7, fig. 44) shows only a semi-circular line, the dorso-ventral orientation of which is not given. Neither the figured radiographs (Pls 45a, 47, 48) give information about the aspect of the dorsal area. In a lateral view, two lines of the siphonal structure usually appear and can suggest the "tube" which, however, may be open on its dorsal side (compare Pl. 4, fig. 2 herein).

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Sifokamerální struktury u některých silurských hlavonožců z Barrandienu.

Ivan Kolebaba

Článek předkládá nové poznatky o kamerálním plášti, který se nacházel v plynových komorách svrchnosilurských or-

tokonních hlavonožců (ludlow, Gorstian) středních Čech. Potvrdil se předpoklad o přímém propojení kamerálního pláště s tkání sifonální. U druhů *Protobactrites styloideum* (BARR., 1866) a *Plagiostomoceras pleurotomum* (BARR., 1866) byly zjištěny zvláštní struktury, které velmi pravděpodobně kamerální plášť v plynových komorách upevňovaly. Tento poznatek přispěl také k pochopení funkce dorzální a ventrální brázdy. U *Nucleoceras* gen. n. byly zjištěny lamelární struktury dosud známé pouze u devonské čeledi Lamellorthoceratidae TEICHERT, 1961. Všechny diskutované druhy byly přiřčeny k nedávno stanovenému řádu Pallioceratida MAREK, 1998.

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Explanation of the plates

All specimens figured come from the lower Ludlow (Gorstian), Kopanina Formation, *Colonograptus colonus* biozone, locality Praha-Butovice, Na Břekvici, and are deposited in the collections of the Department of Palaeontology, National Museum, Prague. If not otherwise denoted, the photographs were taken by the author. All figures of cross-sections are situated with venter to the bottom of the page.

Used symbols: BV – replicas of blood vessels; DAL – dorsal axial line; DAM – dorsal attachment membrane; DC – the curve delimiting hyposeptal deposits; EP – projection of the episeptal deposits; L – lamellae; TGH – connecting trough (a dorsally open connecting ring); VAL – ventral axial line; VAM – ventral attachment membrane; VL – ventral lobe of the cameral mantle; S – septum; SD – siphonal deposits.

PLATE 1

- 1-8. *Protobactrites styloideum* (BARR., 1866).
- 1 - specimen NM L 32806. Internal mould of a gas chamber showing replicas of the vascular system; adoral view, x 15.
- 2 - NM L 32807. Partly exposed internal mould of two gas chambers with the distally branching replicas of blood vessel. Lateral view, venter left, x 9.
- 3 - NM L 32808. Internal mould of the gas chamber exposed by etching; to show the axial depression, dorso-ventral symmetry and the compact connection of cameral and siphonal spaces. Adoral view, x 17.
- 4 - NM L 32809. Dorsoventral thin section of a part of the phragmocone, venter right, x 6.
- 5 - NM L 32810. Internal mould of a gas chamber showing the unity of the siphonal and cameral spaces. Lateral view, venter left, x 23.5.
- Scanning microscope, photograph by I. Čejková.
- 6 - NM L 32811. Internal mould of four gas chambers, lateral view, venter left, x 28.5.
- Scanning microscope, photograph by I. Čejková.
- 7 - NM L 32812. Internal mould of four gas chambers, ventral view, x 19.
- Scanning microscope, photograph by I. Čejková.
- 8 - NM L 32813. Lateral thin section situated in the centre of the phragmocone, to show the bilateral symmetry and regular features of the internal structures, x 8.8.

PLATE 2

- For the location of cross-sections see also Fig. 5a.
- 1-10. *Protobactrites styloideum* (BARR., 1866).
- 1 - NM L 32814. Thin cross-section cutting the septal necks and showing the bilateral symmetry of the cameral mantle; advanced stage of the cameral deposits, x 10.5.
- 2 - NM L 32815. Thin cross-section situated somewhat more adapically than that in fig. 1, x 12.
- 3 - NM L 32816. Thin cross-section situated approx. in the half height of the gas chamber and showing the dorsally open connecting ring, x 11.
- 4 - NM L 32817. Thin cross-section of two successive gas chambers showing the dorsally open connecting ring, x 8.8.
- 5 - NM L 32818. Thin cross-section of two successive gas chambers, x 12.
- 6 - NM L 32819. Thin cross-section of two successive gas chambers one of which shows a turning of the dorsoventral axis. The arrow indicates a septum – the boundary between chambers, x 9.5.
- 7 - the same thin section; detail of the dorsal area showing the dorsal part of the attachment system, x 23.
- 8 - the same thin section as in Fig. 4; detail of the ventral region showing the widely open connecting trough, x 20.
- 9 - NM L 32820. Thin cross-section, detail of the mid-dorsal area showing the dorsal axial line (? attachment membrane) running between two drop-like areas - sections of adoral lobes of the cameral mantle, x 33.
- 10 - NM L 32821. A polished cross-section, detail of the mid-ventral area showing a pyritized trace of the cameral mantle that occupies the internal layer of the shell wall, x 34.

PLATE 3

- For the positions of the cross-sections see also Fig. 5b.
- 1-8. *Plagiostomoceras pleurotomum* (BARR., 1866).
- 1 - NM L 32823. Thin cross-section of two successive gas chambers, one of them (central area) cut near its apical end, x 12.5.
- 2 - the same specimen. Thin cross-section through the septal necks showing ventral and dorsal parts of the attachment system, x 12.5.
- 3 - NM L 32824. Thin cross-section situated approx. in the half height of a gas chamber, the V-shaped dorsal groove and dorsal part of the attachment system are shown, x 13.8.
- 4 - NM L 32825. A part of the phragmocone with the internal moulds of three gas chambers; surface ridges are preserved in the adoral part. Approx. lateral view, venter right, x 14.5.
- 5 - NM L 32826. Dorsoventral polished section of the small phragmocone, venter left, x 6.4.
- 6 - NM L 32881. Dorsoventral thin section showing the pattern of cameral deposits, venter left, x 7.2.
- 7 - the same thin section. Detail of the septal foramen of the third chamber to show the sharp pyritized curve delimiting the hyposeptal deposits, x 47.
- 8 - NM L 32880. Lateral thin section situated in the central plane of the phragmocone, x 8.2.

PLATE 4

1-4. *Nucleoceras obelus* (BARR., 1870).

1 - NM L 32827. Dorsoventral thin section of four gas chambers, venter left, x 6.4.

2 - NM L 32828. Lateral thin section of two gas chamber situated in the axis of the septal foramen, showing an illusory siphonal tube, x 17.6.

3 - NM L 32829. Dorsoventral polished section of the phragmocone, advanced growth stage with shortened gas chambers, x 4.7.

4 - NM L 32834. Detail of the ventral part of fig. 3 in Pl. 5 to document the connecting trough, a lining of the siphonal deposits is shown in the ventral area of the trough, x 38.

5-6. *Nucleoceras* sp.

5 - NM L 32830. Internal mould of an adapical gas chamber, bilateral symmetry and ventral lobes of the cameral mantle are apparent. Adoral view, x 50.

Photograph by I. Čejková, scanning microscope.

6 - NM L 32831. The smallest found internal mould of the gas chamber close to the apex, showing a bilateral symmetry and elaborate morphology. Approx. adapical view, x 48.5.

Photograph by I. Čejková, scanning microscope.

PLATE 5

For the position of cross-sections see also Fig. 5c.

1-6. *Nucleoceras obelus* (BARR., 1870).

1 - NM L 32832. Thin cross-section showing the curve of the connecting trough, ventral lobes and the "ventral lamella" of the cameral deposits; cameral deposits are moderately developed, x 12.

2 - NM L 32833. Thin cross-section showing the open connecting trough and the lamellae; cameral deposits in the advanced stage, x 17.

3 - NM L 32834. Thin cross-section showing the open connecting trough and lamellae; cameral deposits in the advanced stage, x 13.

4 - NM L 32835. Thin cross-section of two successive gas chambers, one of them sectioned near its apical end (internal subcircular area) showing the lamellae, x 12.2.

5 - NM L 32836. Thin cross-section situated through the septal necks; cameral deposits in the initial stage, ventral lobes of the internal space (i.e. cameral mantle) are seen, x 13.3.

6 - NM L 32837. Thin cross-section of two successive gas chambers one of them sectioned at its apical end (internal subcircular area) showing the lamellae. x 11.

7 - NM L 32839. Polished cross-section showing the lamellar system in the adapical end of the gas chamber. x 14.

8-9. *Nucleoceras* sp.

8 - NM L 32838. Internal mould of a gas chamber; ventral lobes of the cameral mantle surround the subtriangular empty space which was, before etching, filled with the ventral lamella of the deposits. Adapical view, x 29.5.

9 - NM L 32840. Internal mould of three gas chambers, lateral view, venter right, x 11.5.

PLATE 6

For the positions of the cross-sections see Fig. 5c.

1-3. *Nucleoceras?* sp. A

1 - NM L 32842. Thin cross-section made across the tips of septal necks; short, in the section spiny lamellae are shown, x 12.3.

2 - NM L 32843. Thin cross-section situated near the centre of gas chamber; cameral deposits in advanced stage of development, x 14.

3 - NM L 32876. Polished cross-section through the septal necks, x 16.7.

4-7. *Nucleoceras?* sp. B

4 - NM L 32841. Thin cross-section situated approx. in the middle of the chamber height. Open connecting trough and the lateral lobes of the cameral mantle are shown, x 15.8.

5 - another part of the same specimen. Dorsoventral thin section of two gas chambers showing the internal structures (short septal necks, the septal foramen wider than that in the type species, endosiphuncular lining on the venter). Venter left. x 12.5.

6 - NM L 32877. Dorsoventral thin section of the phragmocone with 12 gas chambers, venter right, x 5.

7 - the same specimen, detail of the gas chamber showing the septal necks and endosiphuncular lining of the deposits, x 15.2.

8 - *Nucleoceras* sp. NM L 32822. Dorsoventral thin section of the adapical part of the phragmocone, the first gas chamber showing different (embryonic?) morphology. Venter right, x 12.3.



