# Gradual opening of the siphonal tube in an orthoconic cephalopod from the Silurian of Central Bohemia (Czech Republic)

## Postupné otvírání sifonální trubice u ortokonního hlavonožce ze siluru středních Čech (Czech summary)

*(2 text-figs, 2 plates)*

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A specimen of an orthoconic cephalopod from the Silurian (Ludlow, Ludfordian), Kopanina Formation of Central Bohemia, described by Barrande (1870) as *Orthoceras obelus*, has been studied in detail. New information was obtained on the morphology of the sipho-cameral structures; the gradual opening of the siphonal tube, enabling the tissue to enter the gas chambers during the ontogeny, has been found out. The specimen was established the holotype of a new species *Nucleoceras hollandi* sp. n., and was, based on the proved presence of the cameral mantle, attributed to the Family Lamellorthoceratidae Teichert, 1961, Order Pallioceratida Marek, 1998 .

*Key words*: Mollusca, Cephalopoda, Pallioceratida, functional morphology, internal structures, new taxon, Silurian, Barrandian Area, Bohemia.

### Introduction

Joachim Barrande was the first who recognized the organic origin of the siphonal and cameral deposits (1855, 1859, 1877). In the last century, also some other palaeontologists, e.g. Schröder (1888) came to a similar conclusion. Later Teichert (1933) and Flower (1939, 1941, etc.) published the theory about a tissue (cameral mantle) originally present in the gas chambers of some orthocones. This has been supported by many authors – a detailed history of the development of opinions published e.g. Zhuravleva in Shimanskiy and Zhuravleva (1961) and, partly, Kolebaba (in print), who also demonstrated dorsally open connecting rings (troughs) enabling the immediate connection of the siphonal and cameral tissues in two Silurian orthoconic species.

The purpose of the cameral deposits – to ballance the shell into the horizontal position with venter down – seems now to be generally accepted. However, up to now, many questions remain, one of them being *in which way the animal controlled the precipitation of the deposits*. For a good effect, the animal had to place the deposits into the distal portion of its shell; while the gas chambers lying in the proximity of the living chamber served for the buoyancy changes and had, therefore, to be free of the deposits.

It has been observed for many times that there are e.g. twenty five gas chambers free of deposits behind the living chamber and, that in the next few chambers (traced adapically), the cameral deposits rapidly increase to their maximum thickness. The study of *Nucleoceras hollandi* enabled following explanation of this change of the gas chambers morphology and strikingly quick formation of the deposits.

### Material, methods and terms

One of Barrande's syntypes of *O. obelus* (Pl. 366, fig. 15), represented by the phragmocone with 32 gas chambers, was a subject of the study. Its adapical third was sectioned longitudinally as well as transversally (Fig. 1). Serial cross-sections (Fig. 2) and two thin sections have been made; the specimens were embedded into an epoxide resin before being ground. Internal structures in the adoral part (free of the deposits) showed a considerable recrystallization which almost entirely obliterated most of the septa. The number of gas chambers in this unsectioned part (Pl. I, fig. 1) was estimated at 18. Internal structures in the more adapical portion of the phragmocone are favourably preserved. The outer layer of the shell wall is, up to tiny remainders, unpreserved.

The term "connecting trough" is used herein for the dorsally open connecting ring (see also Kolebaba, in print).

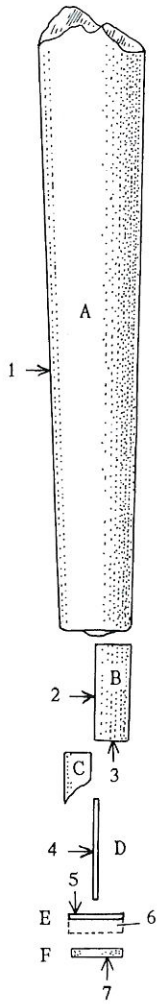


Fig. 1. Schematic drawing of the holotype showing the individual separated parts (A–F) and positions of the figures illustrated in Plates I, II: *1* – Pl. I, fig. 1; *2* – Pl. I, fig. 2; *3* – Pl. I, fig. 3; *4* – Pl. I, figs 4, 5; *5* – Pl. II, fig. 7; *6* – Pl. I, fig 7, Pl. II, figs 1–6; *7* – Pl. I, fig. 6, Pl. II, fig. 8.

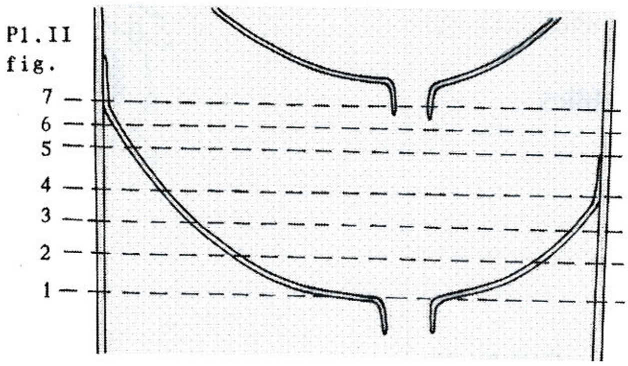


Fig. 2. Schematic drawing to show positions of the sequential cross-sections figured on Pl. II, figs 1–7.

## Morphology

In the chambers contaning the cameral deposits, the cross-sections revealed the contours of spaces in which the cameral mantle had been originally present (Pl. II, figs 1–8). The cameral mantle was of the lamellar type with the conspicuous gap (G) running dorsally from the central area and dividing the cameral mantle into two lateral lobes (L).

When traced adapically from the 19th chamber (Pl. I, fig. 2), siphonal structures show following development: The 19th to 21st chambers contain remainders of the connecting rings which was probably destructed by the crystals of the secondary calcite. The 22nd chamber contains almost complete tubular connecting ring. Going on, the first change can be observed: the structures homologous to the connecting ring are dorsally open in two consecutive chambers and form troughs. In the chamber No. 25 (the adoral one in Pl. I, fig. 4) we can again see a tubular, closed connecting ring. The second point of change occurs at the 26th chamber; there the connecting structure is again fully open on its dorsal side to form a trough. The same pattern is also in all remaining chambers (see also the sequential sections of the 31st chamber in Pl. II, figs 1–6 and polished sections of the 32nd chamber in Pl. II, figs 7, 8.)

The cross-sections figured on Pl. I, figs 6, 7 show walls of the connecting troughs; their ventral, rounded part consists of two parallel curves, the distance between them being about 0.02 mm (the arrow PM in Pl. I, fig. 7). They continue to the right, into the area of the dark cameral deposits. These originally parallel curves are here disjoined from one another (the arrow DM) and the outer of them is broken. Their length approximately equals to the missing part of the circular double curve which represents a cross sectioned wall of an originally closed, tubular connecting ring. The identical case can be seen in the polished section of the neighbouring gas chamber figured on Pl. I, fig. 6 where the missing part of the originally tubular connecting ring is indicated by a dotted curve.

In the dorsoventral thin section (Pl. I, fig. 5) similar double curves can be seen running from the septal foramen dorsally up and down, into the two neighbouring gas chambers.

## Interpretation

It appears proved that *Nucleoceras hollandi* sp. n. was able to control the cameral deposits formation in the dependence of the actual hydrostatic condition of its shell. It realized this by a gradual opening of the connecting rings and thus enabling the siphonal tissue to enter the chambers.

During the ontogeny, as the number of the gas chambers increased, the oldest deposit-free chambers had been receded from the living chamber and, consequently, their importance for the buoyancy regulation (by changes of the liquid/gas ratio) decreased. Simultaneously with the growing distance from the living chamber, these distant chambers – if weighted with the deposits – could more effectively help to ballance the shell into the horizontal position. The animal probably could reflect the tendency of the shell apex to lift up and, perhaps by the pressure inside the siphuncle, it had been able to open the connecting ring of the most distant but still deposit-free chamber. (The double curves, described in the paragraph Morphology, evidently represent sectioned membranes of the original siphonal wall.) After the wall of the connecting ring was open the tissue – cameral mantle – could enter the chamber and start to secrete the deposits. The large, folded surface of the cameral mantle contributed to the fast secretion of the deposits.

Another way of the connection of the siphonal and cameral spaces was described by Sweet (1958, p. 122). Based on the study of *Rhynchorthoceras helgoyense* Sweet he stated: “it appears likely that a portion of the connecting ring was resorbed after the entire structure had been formed, giving the siphuncular tissue access to the camerae”.

## Systematic part

Order P a l l i o c e r a t i d a Marek, 1998
(= Lituitina Dzik, 1984, partim)
Family L a m e l l o r t h o c e r a t i d a e Teichert, 1961
(emend. Kolebaba, in print)

### Genus *Nucleoceras* Kolebaba, in print

T y p e s p e c i e s : *Orthoceras obelus* Barr., 1870 (partim); Silurian, Barrandian Area, Czech republic.
S t r a t u m t y p i c u m : Silurian, Ludlow, Gorstian, Kopanina Formation, biozone with *Colonograptus colonus*.

### *Nucleoceras hollandi* sp. n.

Pls I, II

1870 *Orthoceras obelus* Barrande, Pl. 366, fig. 15.

H o l o t y p e : Specimen NM L 17991, figured by Barrande 1870, Pl. 366, fig. 15 as a syntype of *Orthoceras obelus.*

Stratum typicum: Silurian, Ludlow, Ludfordian, Kopanina Formation, horizon with *Encrinuraspis beaumonti*.
Locus typicus: Praha-Radotín, "Kosoř" (in the areal of the Radotín cement works).
Derivatio nominis: *hollandi* – in honour of professor Charles H. Holland, an excellent research worker in fossil cephalopods.
Material: The holotype only.

Description: Phragmocone with probably 32 gas chambers (sutures in adoral part are obscure), overall length 147 mm. Adapical portion of the phragmocone, 58 mm long, has been separated, divided into five parts and sectioned. The shell wall is poorly preserved; surface probably smooth. Shell is compressed with the dorsoventral diameter by 20 % greater than the lateral one. Apical angle is almost constant at 4.5°. Septal foramens are intracentroventral, shifted ventrally by 29 % of the distance between the centre and ventral margin. The average height of gas chambers is 36 % of the relevant dorsoventral diameter.
Discussion: *Nucleoceras hollandi* sp. n. differs from the type species, *N. obelus* (Barr.) in another shape of the cameral mantle (i.e. the space free of the cameral deposits in that part of the phragmocone containing the deposits). The large dorso-ventral gap dividing the mantle into two lateral lobes is the main identification feature.

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## Postupné otevírání sifonální trubice u ortokonního hlavonožce ze siluru středních Čech

Podrobným studiem jednoho z Barrandových syntypů *Orthoceras obelus* (1870, Pl. 366, fig. 15) bylo zjištěno zvláštní uspořádání sifokamerálních struktur. V adorální části fragmokonu, kde se kamerální uloženiny nevyskytují, byly pozorovány spojovací prstence obvyklého trubicovitého tvaru. Naproti tomu v adapikálních plynových komorách, obsahujících kamerální uloženiny, je dorzální strana sifonální trubice široce rozevřená a její vnitřní prostor je bezprostředně propojen s prostorem plynové komory. V daném případě tato změna proběhla ve dvou fázích (při sledování adapikálním směrem); po prvých dvou plynových komorách s otevřeným prstencem následuje ještě jedna komora s normálně vyvinutým, trubkovitým spojovacím prstencem, dále adapikálně již všechny komory obsahují otevřené spojovací prstence. Složité a pravidelné uspořádání vnitřního prostoru těchto komor svědčí o přítomnosti kamerálního pláště. Morfologie vnitřních struktur studovaného hlavonožce poskytla pravděpodobné vysvětlení známé skutečnosti, že u mnoha nautiloidů s ortocerakonní schránkou následuje za sérií nejčastěji 23–25 plynových komor bez kamerálních uloženin tři až pět komor, v nichž se kamerální uloženiny poprvé objevují a nabývají maximální mohutnosti. Lze soudit, že sifonální trubice v adapikálních komorách byla hlavonožcem postupně otevírána jako reakce na potřebu zvýšit zatížení adapikální části schránky a zajistit tak její horizontální polohu. Po otevření spojovacího prstence plynové komory nejvíce vzdálené od obývací komory a dosud neobsahující kamerální uloženiny sifonální tkáň vstoupila do prostoru komory a začal intenzivní proces sekrece kamerálních uloženin.

Studovaný Barrandův syntyp byl stanoven jako holotyp nového druhu *Nucleoceras hollandi* sp. n. (Lamellorthoceratidae Teichert, 1961; Pallioceratida Marek, 1998).

#### Explanation of plates

Pl. I, II – *Nucleoceras hollandi* sp. n., HOLOTYPE NM L 17991, orig. Barr. 1870, Pl. 366, fig. 15.
The specimen comes from the Ludlow (Ludfordian), Kopanina Formation, horizon with *Encrinuraspis beaumonti*, locality Praha-Radotín, "Kosoř", and is deposited in the collections of the Department of Palaeontology, National Museum, Prague. All figures of the cross-sections are situated with venter to the bottom of the page. Chamber numbers indicated in the photographs relate to the text part Morphology.
If not otherwise denoted, the photographs were taken by the author.

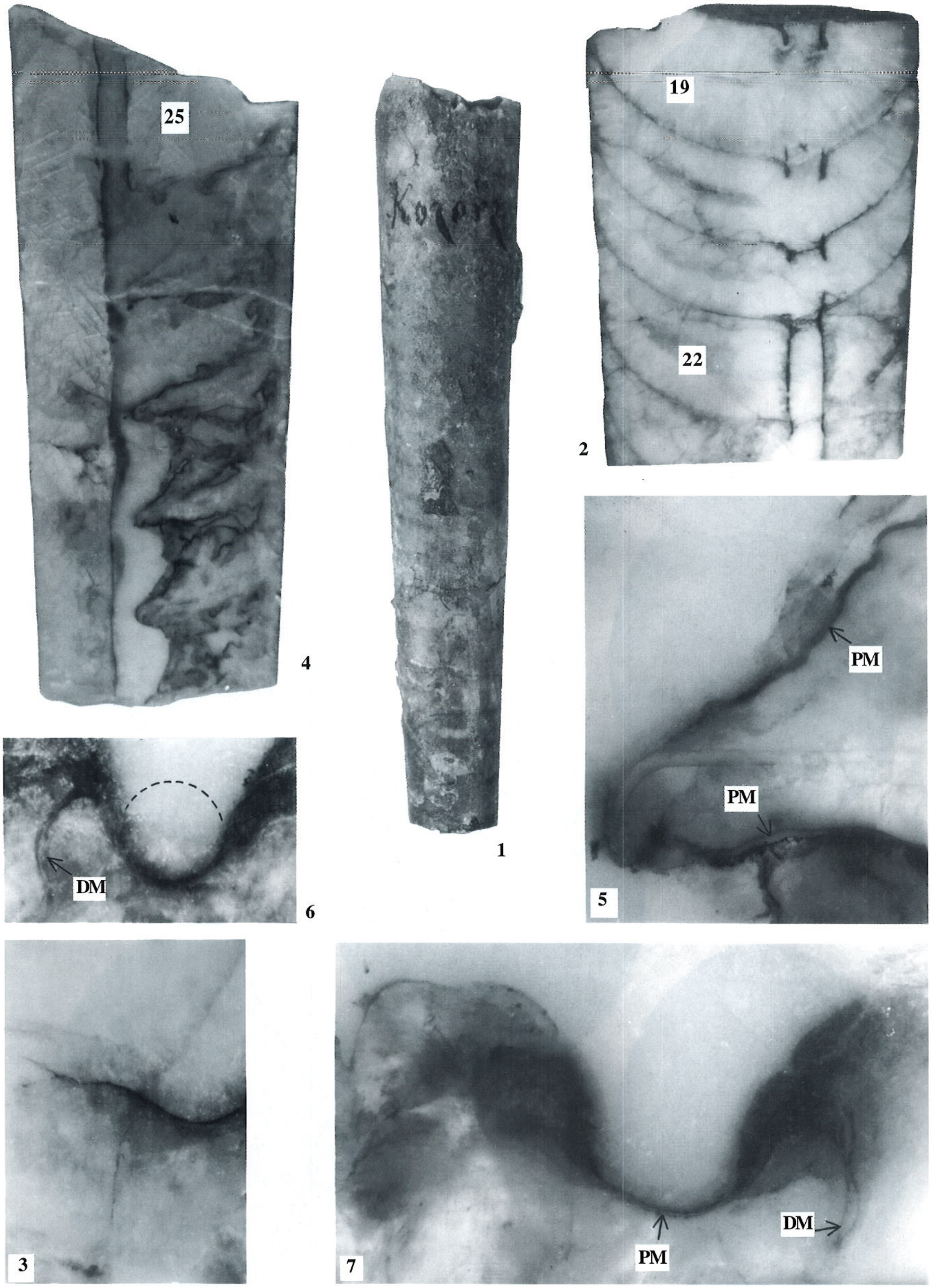
Plate I

1. Adoral part (A) of the holotype showing Barrande's original indication of the locality; lateral view, venter right; photograph by R. Horný; x1.5.
2. Dorsoventral polished section of the part B; a complete connecting ring is seen in the chamber No. 22, venter right; x5.6.
3. The same part B, a detail of the cross-section showing an open connecting ring = a connecting trough in the chamber No. 23; x36.
4. Dorsoventral thin section of the part D; the chamber No. 25 contains again a closed connecting ring, all consecutive chambers (adapically) have fully open connecting troughs and well developed deposits; venter left; x5.6.
5. Detail of the fig. 4; the parallel curves – sectioned membranes (PM) of the open walls of the connecting rings – are shown running from the septal neck dorsally into both neighbouring chambers. Venter left; x36.
6. Detail of the polished cross-section shown on Pl. II, fig. 8 (part F); the arrow DM indicates the disjoined membranes which originally formed the missing part of the circular (in cross-section) connecting ring (dotted curve); a view from the adapical side; x43.
7. Detail of the thin section on Pl. II, fig. 6 (Part E), the similar pattern as in fig. 6. Two cross-sectioned parallel membranes (PM) forming the unbroken wall of the connecting trough, and disjoined membranes (DM) originally closing the connecting ring are shown; a view from the adapical side; x50.

Plate II

1.–7. Sequential cross-sections of the adapical portion of the gas chamber (part E); for the positions of the sections see Text-fig. 2. 1.–6. – views from the adapical side, 7. – a view from the adoral side. 1.–5. Polished sections; x9. 6. Thin section; G – dorsoventral gap; L – lobes; x9. 7. Polished cross-section; x9.
8. Polished cross-section of the neighbouring chamber (part F), situated near the centre of its height, a view from the adapical side; x9.

I. K o l e b a b a: Gradual opening of the siphonal tube in an orthoconic cephalopod from the Silurian of Central Bohemia (Pl. I)




For explanation see p. 133

I. Kolebaba: Gradual opening of the siphonal tube in an orthoconic cephalopod from the Silurian of Central Bohemia (Pl. II)