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A contribution to the theory of the cameral mantle in some Silurian Nautiloidea (Mollusca, Cephalopoda)

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Abstract. *Plagiostomoceras vestigium* sp. n., a new species of orthoconic cephalopods from the Silurian (Ludlow, Ludfordian, Kopanina Formation) of Central Bohemia, is described. Based on the proved original presence of the cameral mantle in gas chambers, the described species has been assigned to the family Leurocycloceratidae, order Pallioceratida Marek, 1998. Three morphological types of the cameral mantle have been distinguished in six species of *Protobactrites, Plagiostomoceras, Nucleoceras* and *Murchisoniceras,* in which this tissue has been proved. Characteristic cross-sections of their gas chambers are figured.

Abstrakt. V kopaninském souvrství (Ludlow, Ludfordian) siluru středních Čech byl zjištěn nový druh ortokonního hlavonožce, *Plagiostomoceras vestigium* sp. n. Na základě prokázané přítomnosti kamerálního pláště v plynových komorách byl tento druh zařazen do čeledi Leurocycloceratidae Sweet, 1964 (řád Pallioceratida Marek, 1998). U šesti druhů rodů *Protobactrites, Plagiostomoceras, Nucleoceras* a *Murchisoniceras*, u nichž byl kamerální plášť dosud prokázán, byly rozpoznány tři morfologické typy této tkáně. Vyobrazeny jsou charakteristické příčné řezy plynových komor těchto druhů.

Key words: Cephalopoda, Silurian, Ludlovian, Czech Republic, cameral mantle, functional morphology, taxonomy, new taxa

Introduction

The order Pallioceratida Marek, 1998 has been established in response to the increasing evidence on tissue that was present in gas chambers of some Palaeozoic orthoconic Nautiloidea. The purpose of this tissue was to secrete cameral deposits necessary for keeping the shell in the horizontal position with venter down and, presumably, also to take part in the buoyancy regulation. The organic origin of the cameral deposits was recognized already by Barrande (1859). Substantial articles on this topic were written by Teichert (1933) and especially by Flower (e.g. 1939, 1941) who introduced the term "cameral mantle" for this intracameral tissue. The present article brings additional information on this special group of Palaeozoic cephalopods.

Three morphological types of cameral mantle

Six orthoconic species of the "pallioceratid" character, all from the Silurian (Ludlow) of the Barrandian area, have been found by the author. Internal structures of five of them were already studied and documented (Kolebaba 1999a, 1999b). Cross-sections of their gas chambers revealed characteristic figures presented here in schematic drawings (Fig. 1). A cross-sectioned gas chamber of the sixth one – *Murchisoniceras murchisoni* (Barr.) – is shown here in Fig. 2. Three morphological types were discerned among them:

1. The cameral mantle of a pouch-like form. Only the ventral part of the connecting ring (connecting trough) is developed. It has been found in *Protobactrites styloideum* (Barr.) and *Murchisoniceras murchisoni* (Barr.), (Fig. 1/1a, b).

   A suspicion arose that all specimens of *P. styloideum* (an invalid synonym of which is *Mariaceras pragense* Kolebaba, 1974) were, in fact, "juvenile shell fragments attributable to *Murchisoniceras*" (Dzik 1984, p. 135). Although juvenile shells of *Murchisoniceras* are unknown yet, the specific identity seems to be improbable regarding the fact that all specimens of these species, which have been collected, come from different localities and also from different stratigraphic levels (*M. murchisoni* comes from younger horizons). Their relationship, on the other hand, is evident assuming that the internal shell morphology is more significant systematically than the external features like the sculpture and than the relative height of gas chambers, which tends to change during the ontogeny.
2. The cameral mantle of a pouch-like form. The connecting ring or connecting trough is absent. The dorsal side of the mantle bears a characteristic longitudinal groove. Two species of *Plagiostomoceras* have this feature: *P. pleurotomum* (Barr.) and *P. vestigium* sp. n. (Fig. 1/2a, b).

   The assumption that *Plagiostomoceras* and *Protobactrites* are "closely related if not identical forms" (Dzik 1984, p. 100) is hardly acceptable due to their different internal structures.
3. The cameral mantle possesses conspicuous lamellar projections. This feature has been found in *Nucleoceras obelus* (Barr.) and *N. hollandi* Kolebaba (Fig. 1/3a, b).

Longitudinal sections of these three morphological types are schematically drawn in the paper of Kolebaba (1999a, Fig. 5).

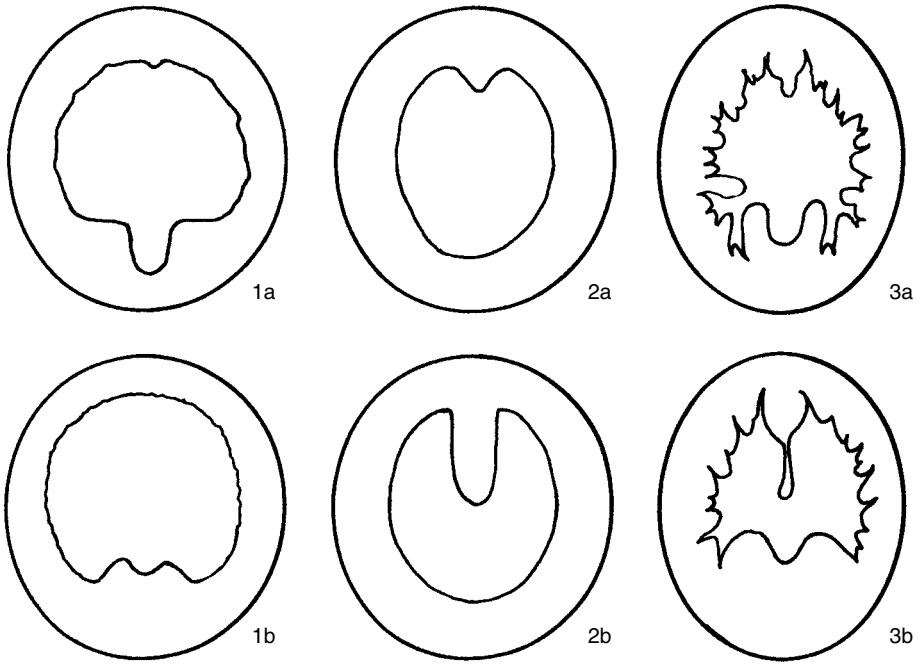

Fig.1. A schematic drawing showing three morphological types of cameral mantle (white central areas) as seen in the cross-sections. 1a – *Protobactrites styloideum* (Barr.), 1b – *Murchisoniceras murchisoni* (Barr.), 2a – *Plagiostomoceras pleurotomum* (Barr.), 2b – *P. vestigium* sp. n., 3a – *Nucleoceras obelus* (Barr.), 3b – *N. hollandi* Kolebaba. Lines of the cross-sectioned attachment system (see Kolebaba 1999a) are omitted. Ventral sides downwards.

Systematic part

Class Cephalopoda Cuvier, 1798
Order Pallioceratida Marek, 1998, emend.

Emended diagnosis: Orthoconic or moderately cyrtoconic shells originally with soft tissue in the gas chambers. Connecting rings, at least in the adapical part of the phragmocone, are not closed structures, but open with their internal space being joined with the cameral one. Cameral deposits in the adapical portion of the shell are well developed but never fill the entire space of the chambers.

Family: Leurocycloceratidae Sweet, 1964

Genus: *Plagiostomoceras* Teichert et Glenister, 1952, emend. Kolebaba 1999a
Plagiostomoceras vestigium sp. n.
Pl. 1, figs 1–9

Holotypus: Specimen NM L 36522a,b figured here on Pl. 1, figs 6, 7.

Paratypes: Specimens NM L 36518a,b; NM L 36519; NM L 36520a,b; NM L 36521 figured here on Pl. 1. (All specimens are deposited in the collections of the Department of Palaeontology of the National Museum, Prague.)

Stratum typicum: Silurian, Ludlow, Ludfordian, Kopanina Formation, horizon with *Ananaspis fecunda.*

Locus typicus: Praha-Radotín, "Lochkov" (northern slope of the Radotín valley, facing the Radotín cement works).

Derivatio nominis: *vestigium* (Lat., n.) = vestige, to express the resemblance of the characteristic cross-sections to the footprint of an unshod horse.

Material: Besides the types, three additional specimens.

Diagnosis: A species of the genus *Plagiostomoceras* Teichert et Glenister, 1952 with the height of gas chambers at least by 25 per cent greater than the corresponding dorso-ventral shell diameter. The dorsal groove, characteristic for the cameral mantle of this genus, is more deeply incised in the new species and extends as far as to the shell axis when cameral deposits are fully developed.

Description: Tiny, slender longiconic orthocones; maximum diameter of the studied specimens is 9 mm. Apical angle varies from 2° (at the living chamber) to 3°. The cross-section is slightly compressed with the dorso-ventral diameter larger by 6 to 7 per cent than the lateral one. Oblique surface ridges are arranged at intervals of about 1 mm. Gas chambers are unusually high, their height being by 25 to 37 per cent greater than the corresponding maximum diameter; the height of the last two gas chambers (just behind the living chamber) being 2.5 times their width (Pl. 1, figs 6, 7). Septal foramens are centroventral, shifted ventrally by about 40 per cent of the distance between the centre and the ventral margin of the shell. The diameter of septal foramens is 15 to 18 per cent of the corresponding shell diameter. Septal necks are orthochoanitic and reach about 14 per cent of the height of the corresponding gas chamber.

Cameral deposits – hyposeptal and episeptal – are well developed in the phragmocones under study. The cameral mantle space (the free space surrounded with the cameral deposits) is characterised by a prominent dorsal groove the depth of which increases depending on the increase of the cameral deposits. Therefore a characteristic figure resembling a footprint of an unshod horse appears in the cross-sections (Pl. 1, figs 3, 4). The shape of a longitudinal section orientated perpendicular to the dorsoventral plane (Pl. 1, fig. 9) is also characteristic.

Stratigraphic distribution: The species has been found only in the type stratum.

Discussion – remarks and doubts

The main diagnostic feature of Pallioceratida is: "Connecting rings are not a closed structure, so that their internal space is joined with the cameral one" (Marek 1998,

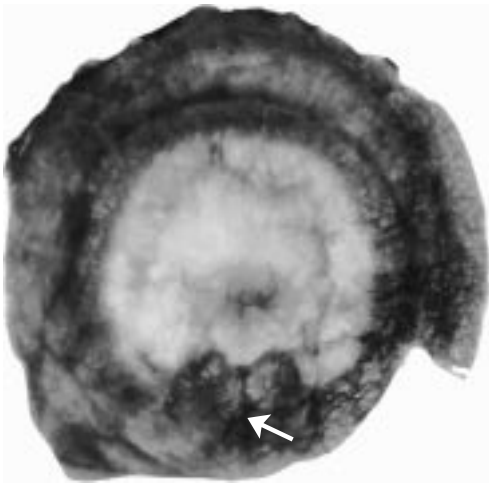

Fig. 2. A thin cross-section of two adjacent gas chambers of *Murchisoniceras murchisoni* (Barr.), NM L 36557, showing the shape of the cameral mantle (white central area). The ventral axial line (median membran) is indicated by an arrow. Kopanina Formation, Jarov near Beroun, coll. Barrande; × 4.3

page 181). This statement, in its strict form, seems to be disputable because of the gradual opening of the siphonal tube during the ontogeny found in *Nucleoceras hollandi* (see Kolebaba 1999b). Connecting rings of this species are closed, tubular in the adoral portion of the phragmocone but in more adapical chambers they gradually open on their dorsal side enabling the siphonal tissue to extend into the chambers and secrete the balance load – cameral deposits. An emendation of the diagnosis of the order is, therefore, necessary (see the Systematic part).

Some of the Silurian orthocones also suggest that they had been furnished with a sort of a tissue in their gas chambers although their connecting rings were well developed. Barrande figured several orthocones in a view *into* the gas chamber with the septum removed. Adapical surface of the internal mould of the gas chambers of "*Orthoceras" severum* Barr. (Pl. 229, figs 2–10, Pl. 443, figs 7, 8) is covered with a bilaterally symmetrical system of rounded projections with a massive rampart extending from the area of the septal foramen to the dorsum. Low, flat projections surrounding the septal foramen and also running dorsally are visible e.g. in *"O." cruciferum* Barr. (Pl. 413, figs 33, 34), *"O." billingsi* Barr. (Pl. 469, fig. 11), and *"O." palma* Barr. (Pl. 518, figs 2, 3). Other, radially arranged structures cover the adapical surfaces of the moulds of gas chambers of *"O."* indeterminé (Pl. 484, figs 3, 4, 5) and *"O." sarcinatum* Barr. (Pl. 341, figs 19, 20). An explanation of these special structures is the matter of further investigation. If the presence of tissue in gas chambers of these species is proved, it can be expected that the order Pallioceratida Marek, 1998 should be re-evaluated.

During the study of the Silurian pallioceratid orthocones *Protobactrites styloideum* (Barrande), *Plagiostomoceras pleurotomum* (Barrande), and *Plagiostomoceras vestigium* sp. n., additional special structures were found (Kolebaba 1999a). In both the cross and longitudinal sections they appear as dark straight lines which run from the

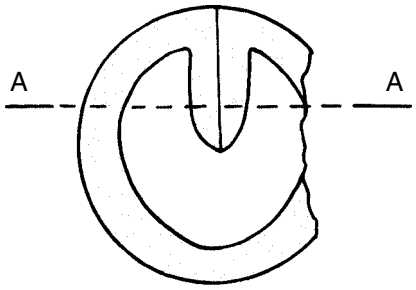

Fig. 3. A schematic drawing showing the position of the lateral section on Pl. 1, fig. 9 (line A-A).

periphery of the presumed cameral mantle across the cameral deposits and are connected to the internal wall of the shell. These lines – marked as DAM, DAL, VAM, VAL, together with the pseudoseptum (see drawing on page 7 and photographs on page 6 and Plates 2, 3), were interpreted as an attachment system of membranes which served for keeping the cameral mantle in a fixed position inside the gas chamber. In this interpretation, however, remains an uncertainty. The dark lines may simply represent contact planes of the fully developed episeptal and hyposeptal cameral deposits, but pyrite crystals, present in the lines, probably originated in connection with decayed cameral tissue. This, together with the regular shape of the lines, seems to support the first interpretation.

Short but distinct projections are arranged on the periphery of small irregular hollows on the surface of the internal moulds of *Protobactrites styloideum* (Kolebaba 1974, Pl. 2, 1999a, Pl. 1, figs 5, 6, 7). This indicates a possible affinity of the genus to the family Lamellorthoceratidae Teichert, 1961.

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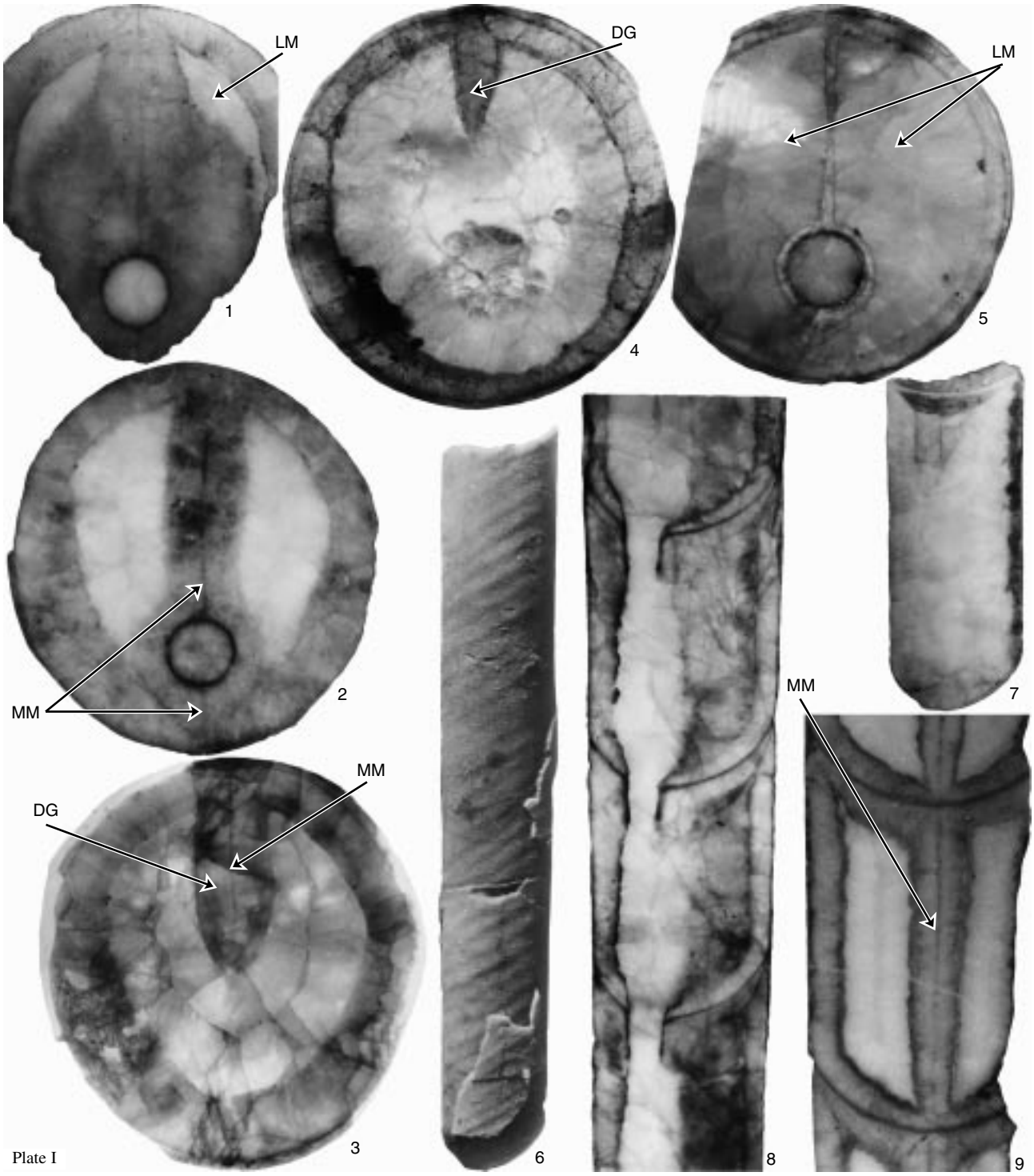

Specimens in figs 2, 3, 6, 7 come from the type locality (Praha-Radotín, northern slope of the Radotín valley, facing the Radotín cement works). Specimens in figs 1, 4, 5, 8, 9 come from several abandoned quarries in the same valley but their exact locality is unknown; they were acquired from old decorative facing plates. All cross-sections are directed with the ventral side to the bottom of the page. Used symbols: DG – dorsal groove; MM – median membrane (dorsal and ventral axial lines in Kolebaba 1999a); LM – lobe of the cameral mantle. All photographs were taken by the author.

1–9. *Plagiostomoceras vestigium* sp. n. **1.** Specimen NM L 36518a. Thin cross-section cutting septal necks and adoral portion of the lobes of the cameral mantle (light areas). The dorsal and ventral axial lines are also visible; × 8; **2.** NM L 36519c. 13th sequential cross-section of the series of 20, situated more adapically compared to fig. 1. Lobes of the cameral mantle, dorsal and ventral axial lines, and ventral attachment membranes are shown; × 8; **3.** The same specimen – the final (20th) sequential thin cross-section situated approx. in the mid-height of the gas chamber. Cameral deposits are fully developed and the dorsal groove deeply incised up to the centre; × 8; **4.** NM L 36520a. Thin cross-section of the gas chamber with cameral deposits in the initial stage. The dorsal groove in the cameral mantle is narrow and shallow. The section is situated near the mid-height of the gas chamber; × 15.5; **5.** NM L 36520b. The same specimen, initial stage of development of cameral deposits. Thin section is situated in the adoral part of the chamber and cuts across the septal necks. The cameral mantle lobes are almost in mutual contact; a thin layer of cameral deposits separates them and surrounds the septal necks; × 14; **6.** NM L 36522a. The holotype; the living chamber and adjacent gas chamber – internal mould with a small patch of the shell wall. A very oblique light was used to make the surface distinctive; × 2.8; **7.** NM L 36522b. The same specimen, a longitudinal dorso-ventral section of the second gas chamber behind the living chamber to show its overall height and the length of the septal necks; × 3.8; **8.** NM L 36521a. A longitudinal dorso-ventral thin section of a series of gas chambers containing well-developed cameral deposits; × 6; **9.** NM L 36518b. Lateral thin section of one gas chamber, the right side is corroded; the axial line represents a sectioned attachment membrane; × 6.7.