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Primary structure of the connecting ring of ammonoids and its preservation

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The most distinctive and important element of the hydrostatic organ of ammonoids and nautiloids is the siphuncular tube. It consists of mineral and organic segments (so-called connecting rings). The connecting ring of ammonites never preserves its original organic matter in the mineralized state, usually having undergone diagenetic phosphatisation, more rarely, calcification, or even complete loss. Our knowledge about its original ultrastructure is based upon comparison with Recent *Nautilus* and phosphatised or calcified ammonite fossils. We show that depending on the taphonomic history, both calcium phosphate and calcite can participate in the diagenesis of the connecting ring wall. Under standard light microscopy, the phosphatised elements are indistinguishable from the calcified ones. Both are dark brown in colour, due to an excess of carbon. The structure of the phosphatised siphuncle does not closely replicate the structure of its organic elements. This casts doubts on conclusions of other authors who described a complex porous structure in ammonite siphuncles, which is completely dissimilar to the siphuncular structure of Recent *Nautilus* and suggests that this organ functioned differently in ammonites. SEM observations using a BSE detector on the calcified parts of the walls of connecting rings revealed a multilayered structure with perpendicular elements connecting particular layers, resembling the structure of a stacked nacreous layer.

Introduction

The siphuncular cord of nautiloids and ammonoids is encased in a tube. The tube consists of mineral and organic segments. The organic segments are called connecting rings. In the ammonoid prochoanitic condition, the mineralised segments are connected to the nacreous septal necks and consist of spherulitic-prismatic or prismatic elements and are called auxiliary deposits, and cuffs. In *Nautilus*, the connecting ring is a simple, non-mineralised extension of the retrochoanitic septal neck. Differences between retrochoanitic and prochoanitic conditions were described by Kulicki (1979, 1996). According to the generally accepted interpretation, the mineral and mineralised segments are impermeable to cameral liquid, while the organic segments are conductive to fluid. Such a siphuncular cord allows osmoregulation of the liquid content of the phragmocone chambers, thus regulating the buoyancy of a living animal.

The mineral segments fossilize comparatively well, preserving the shape and ultrastructural details during diagenesis and only the original metastable mineral, aragonite, changes into stable calcite in some cases. The connecting rings of ammonoids have usually been phosphatised with francolite (Andalib 1972; Hewitt and Westermann 1983; and the authors' own observations). The ontogenetically newest sections of the connecting rings are usually not preserved. Only in exceptionally well-preserved phylloceratids, a fully preserved siphuncular tube can be observed in the last phragmocone chamber and in the living chamber. In the case of a representative of the Ammonitida, *Damesites*, the part protruding into the body chamber is a very elongated prochoanitic septal neck (Tanabe et al. 2005). In case of other Phylloceratida (Tanabe et al. 2005), the elements protruding into the body chamber are precursory siphuncular membranes, equivalent to the outer component of the siphuncular tube of prochoanitic ammonoids of Kulicki (1979, 1994).

Tanabe et al. (2000) described a similarity in the anatomical features between exceptionally well-preserved soft tissue remains in the Permian ammonoid *Akmilleria* and the siphuncular cord of Recent *Nautilus*. Anatomical similarity of their siphuncular epithelia suggests also a functional similarity, as well as a similarity in the structure of secretory products, such as the siphuncular tube. Mutvei et al. (2004) described phosphatized connecting rings with perpendicular pores in fractured specimens of *Aconeceras* and *Grammoceras*. They interpreted the pores as pore canals with cytoplasmic extensions from the epithelial cells of the siphuncular cord. Such an interpretation is completely at odds with the relationships between the siphuncular cord and siphuncular wall in Recent *Nautilus*.

Institutional abbreviation.—ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and methods

Specimens used for study were cut, ground and polished along the median and transverse planes. They were treated with diluted, 2% HCl for 2–5 seconds. In case of acid etching of partly phosphatised and partly calcified connecting rings, the phosphatised elements remain almost intact, while the carbonate is removed. The etched specimens were platinum-coated for stud-

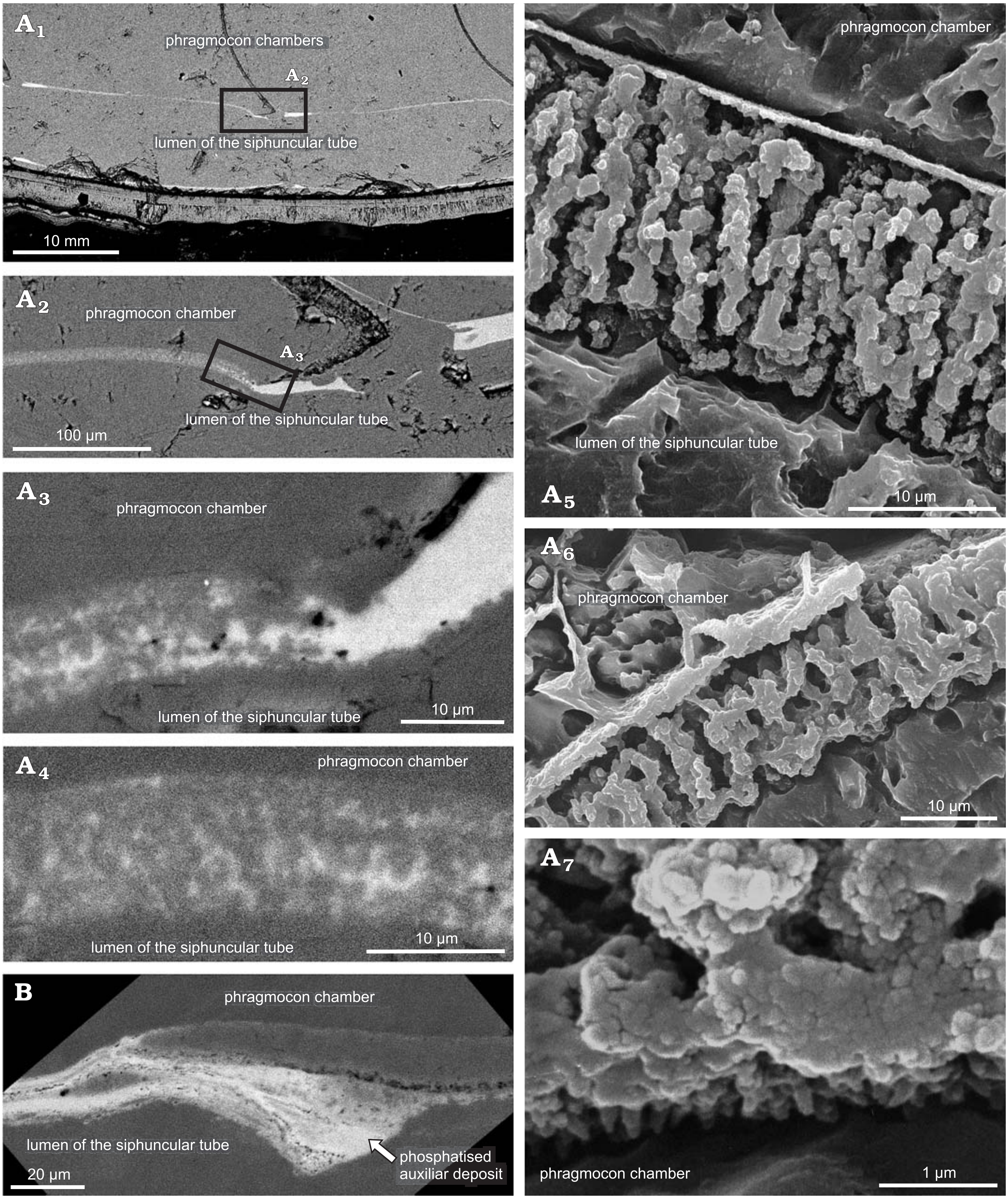

Fig. 1. Sections through the wall of the siphuncular tube. **A**. *Aconeceras traudscholdi* (Sinzow, 1870), ZPAL Am 21/1, Aptian, Volga River near Riazan, Russia. A_1–A_4. SEM micrographs (BSE detector): dark grey areas-calcium carbonate, light grey areas-calcium phosphate; A_1, A_2, overall view of longitudinal section of the siphuncular tube; A_3, enlargement of siphuncular wall close to the tip of the septal neck. The difference in the stage of phosphatisation is visible. The left portion of the tube wall is partly calcified and partly phosphatised, the right portion is fully phosphatised; A4, partly phosphatised and calcified portion of the siphuncular wall away from the septal neck. A_5–A_7. SEM micrographs (SE detector) of perpendicular sections through the connecting →

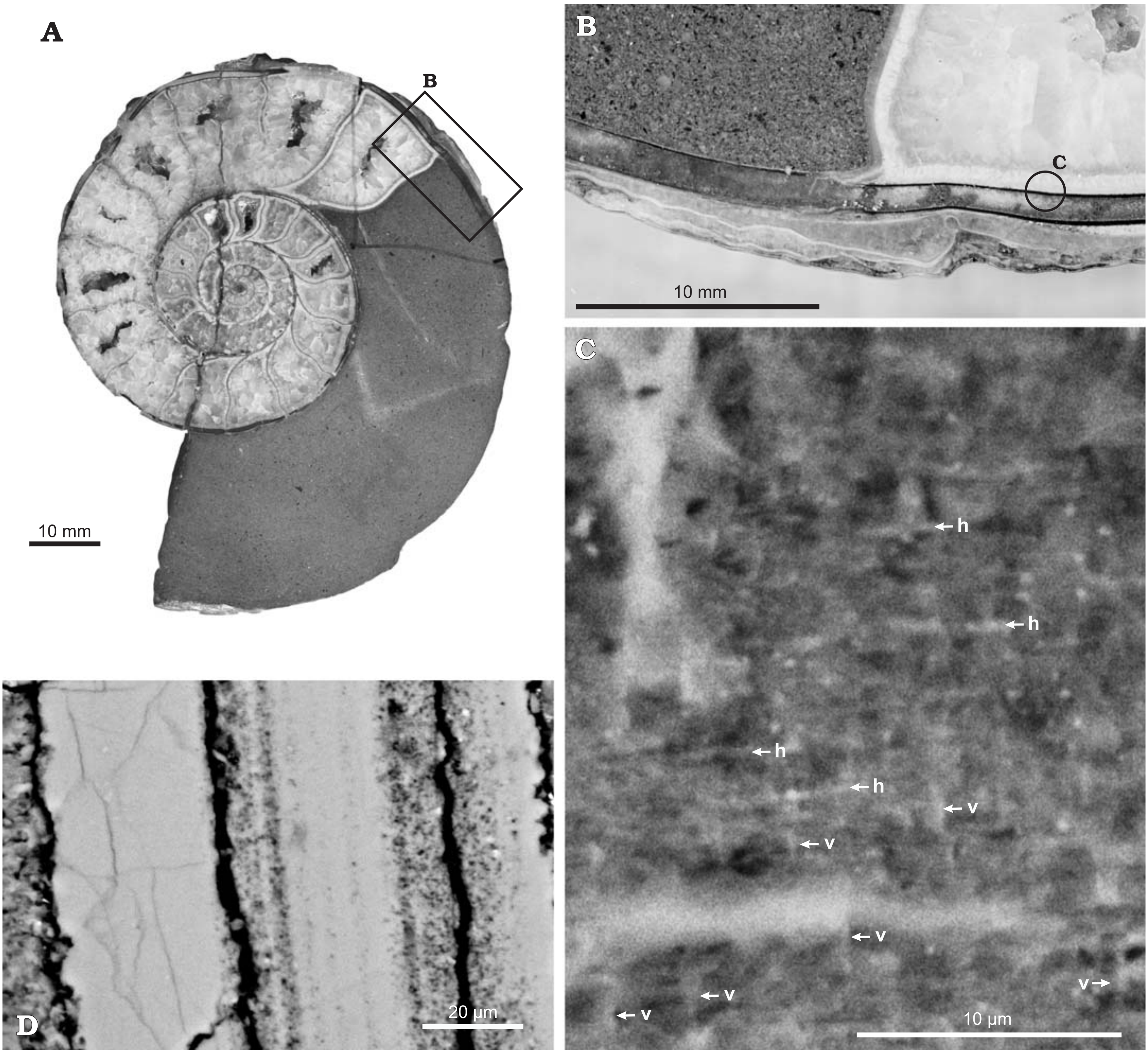

Fig. 2. Longitudinal median sections through the shell and the wall of the siphuncular tube of the Jurassic (Callovian) *Holcophylloceras zignodianum* (d'Orbigny, 1848), ZPAL (Am III/1), Satsiskvile River Valley, Ratcha region, Georgia. **A**. Median section of the whole specimen before cutting for SEM investigations. **B**. Enlargement showing siphuncular tube protruding into the living chamber. **C**. BSE picture showing structure of the dorsal wall of the calcified connecting ring. Dark areas are enriched in carbon. No phosphorus traces were detected in the connecting ring wall of the last phragmocone chambers. v, vertical calcium carbonate elements; h, horizontal nacreous-like lamellae elements. **D**. Phosphatised wall of the connecting ring between the 4th and 5th septum. Darker laminae are partly phosphatised and partly calcified.

ies with SE detector. The specimens used for the BSE detector and EDS analyses were polished and then carbon-coated.

The observations were done, by means of the Philips XL20 scanning electron microscope, equipped with SE, BSE, EDS (dx4i) detectors by EDAX, in the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw. The SE detector was used to study micromorphology of the etched specimens. The BSE detector was used for polished and carbon-coated specimens, allowing us to discern the calcium phosphate (with higher molecular density) from the less dense calcium carbonate. The

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ring etched with 2% HCl. Calcified portions of the ring have been dissolved. **B**. *Tetragonites popetensis* Yabe, 1903, ZPAL Am 21/2, Campanian, Abeshinai River, Nakagawa, Hokkaido, Japan. SEM micrograph (BSE detector) showing auxiliary deposit and posterior section of the connecting ring. Both elements are partly phosphatised and partly calcified.

EDS detector with the dx4i system allowed us to study elemental content in the areas of interest.

Description

Quenstedtoceras.—Numerous specimens of this genus from the Callovian of Łuków, Poland were utilised. The material includes shells in different phases of ontogenetic development belonging to several species (Makowski 1952, 1962; Dzik 1990). As a rule, the connecting ring is strongly phosphatised; it is not preserved in the last chambers of the phragmocone. Phosphatisation is strong, and in etched specimens, or those observed with the BSE detector, it is homogeneous. The packs of laminae are observed to split only next to the tip of the septal neck, or back to the cuff (Kulicki and Mutvei 1982: pl. 4: 1, 2; pl. 5: 2).

Aconeceras.—Specimens of *Aconeceras trautscholdi* (Sinzow, 1870) were recovered from carbonate concretions of early Cretaceous (K_1 a) age at the bank of the Volga River, near Riazan in Russia. The wall of the connecting ring was treated with weak HCl (Fig. $1A_5$–A_7). The elements consisting of calcium carbonate were deeply etched while the calcium phosphate elements were barely changed. In *A. trautscholdi* the outer surface of the connecting ring, exposed to the phragmocone chambers, is coated with a comparatively thin, strongly phosphatised external membrane (Fig. $1A_5$, A_6). A layer of very small pillars is observed in many places on the surface of the outer membrane, approx. 0.15–0.25 micrometers across (Fig. $1A_7$). Below the outer membrane there are perpendicularly oriented irregular pillars, about 1.5–2 mm thick and spaced at about 5 mm. In some sections, the pillars are connected with phosphatic elements forming layers (Fig. $1A_6$). Specimens were polished and carbon-coated for observation with a BSE detector (Fig. $1A_1$–A_4, B). The chambers and the siphuncular lumen in both specimens are filled with calcite (medium grey tones in the images). The calcium phosphate details appear lighter coloured due to their higher mean atomic density. They show both the degree of phosphatisation and the structure of the phosphatised elements in cross-section. The *A. trautscholdi* specimen shown in Fig. $1A_1$–A_4 shows incomplete phosphatisation, like that shown in Fig. $1A_5$–A_7. Only fragments of the connecting rings directly connected with the cuff and auxiliary deposits are fully phosphatised (Fig. $1A_1$, A_3). In the remaining sections the connecting ring shows a structure comparable with the structure of etched specimens. Neither the auxiliary nor the angular deposits nor the cuff are phosphatised.

Tetragonites.—Specimens of *Tetragonites popetensis* Yabe, 1903 were recovered from carbonate concretions from the Lower Campanian, Abeshinai River, Nakagawa Town, north Hokkaido, Japan. Partly phosphatised and partly calcified siphuncular portions are preserved in the specimen of *T. popetensis* (Fig. 1B). In this instance, both the connecting ring and the cuff and auxiliary deposit are partly phosphatised, but differently than that in *A. trautscholdi*. Phosphatised whole packs of laminae are visible. There are no phosphatised elements perpendicular to the external surface of the siphuncle. This specimen clearly shows a light coloured, phosphorus-rich thin layer covering the adapertural surface of the septum and the septal neck extending into the connecting ring as its outermost layer. This is the inner lining, observed and described by Weitschat and Bandel (1991).

Holcophylloceras.—The studied specimen of Callovian *Holcophylloceras* sp. was recovered from the Callovian, Satsiskvile River Valley, Ratcha region, Georgia. It has connecting rings preserved in the last chambers of the phragmocone, as well as the siphuncular tube protruding into the body chamber (Fig. 2A). This specimen was already described and illustrated due to the presence of the siphuncle in the body chamber (Kulicki 1979), but no observations of mineral composition of the siphuncular tube were made at that time. Both macro and microscopically, the siphuncular tube of this specimen looks identical along the whole length, suggesting homogeneity of its mineral composition. However, this is not the case. In the inner whorls, the wall of the connecting ring is uniformly strongly phosphatised, without any special structural features. Between the fourth and the fifth septum, the wall of the connecting ring shows not only phosphatisation, but also partial calcification (Fig. 2D), with darker laminae. In the next chambers of the phragmocone towards the living chamber, the amount of phosphatisation of the connecting ring wall decreases while calcification increases. In the last chamber, the wall of the connecting ring is already completely calcified (and consists of calcite), like that of the living chamber, and shows no trace of phosphorous. A comparatively well preserved fragment of the connecting ring wall of the last phragmocone chamber is illustrated with the BSE detector image (contrast of atomic number) in Fig. 2C. In this instance, the lighter places represent the purer calcite, while the darker ones indicate the calcite considerably enriched in carbon. Distinct tiny lamination are visible, parallel to the outer surface of the connecting ring. The thickness of the laminae averages 0.36 mm, being similar to that in the nacreous layer. Lighter-coloured vertical elements are visible and are set apart by about 2.5 to 3.1 mm (*v* in Fig. 2C).

Discussion and interpretation

The common belief that the siphuncle of ammonites is either phosphatised, or does not fossilize at all, is here questioned. Both cryptocrystalline calcium phosphate and calcite participate in siphuncular fossilization. The siphuncle itself, if preserved, may be phosphatised to a different degree, calcified, or both minerals can participate in its mosaic permineralisation, as in the above described connecting ring of *Aconeceras trautscholdi*.

The earliest *post mortem* fossilization process of the ammonite phragmocone is the phosphatisation of its organic, internal elements, such as the siphuncular walls, siphuncular membranes and cameral linings (Weitschat and Bandel 1991). Organic components of the nacreous and prismatic layers (the elements not exposed to the lumen of phragmocone chambers) did not undergo phosphatisation. *Post mortem* calcification is a later process, as shown by the sequence of the occurrence of these minerals in the siphuncular and shell walls. The elements of the originally organic siphuncular tube that were calcified during the lifetime of the animal are represented by the basal lamella, auxiliary deposit and cuff (Kulicki and Mutvei 1982). Most of the specimens examined reveal strongly phosphatised organic elements, such as connecting rings and linings of the phragmocone chambers in the inner whorls, distant from the living chamber, and thus also from the external environment. In the studied specimen of *Holcophylloceras* sp., we noted an increasing gradient of phosphorus content towards the inner whorls, attaining the full value, characteristic for francolite, approximately: whorl adapical of the living chamber. At first, the external layer of the connecting ring, contacting the lumen of the phragmocone chambers was subject to stronger phosphatisation. In the studied specimens of *Aconeceras trautscholdi*, the thickened portions of the connecting ring adjacent to the septal neck, or covered by the tip of the septal neck are strongly phosphatised (Fig. $1A_1$, A_3). These portions were most likely less penetrable to cameral liquid and sea water. The calcified portions of the connecting ring (Fig. 2C) have a structure similar to the stacked nacreous layer typical of ammonite shells. This confirms the multilayered structure of the connecting ring, while the perpendicular elements can be compared to the central axes of the stacks. This corresponds with the idea by Mutvei (1972) that the connecting ring is built of organic components of the uncalcified nacreous layer. Besides the multilayered structure, the organic content of the connecting ring should preserve some preferentially phosphatised perpendicular structural elements, leading to results as shown in Fig. $1A_5$–A_7. The phosphatised walls of the connecting ring with hollow pores illustrated by Mutvei et al. (2004) can be interpreted as a result of selective phosphatisation leading eventually to formation of closed pores, thus blocking the PO_4 ion transport and consequently producing the porous structure.

After the animal's death, a gradient of physicochemical conditions appeared in its phragmocone. The conditions were most favourable towards phosphatisation of the organic matter that occurred in the first chambers of the phragmocone. On the contrary, in the last chambers having more contact with the external environment, the organic content of the siphuncle decayed completely, or in exceptional circumstances underwent calcification. Phosphatisation can result in compact layers, without distinct structure, or granular layers (Kulicki 1994: pl. 4), or layers with distinct vertical elements, as described here in *A. trautscholdi*. The formation of particular structures is influenced by chemical conditions and saturation in PO_4 ions.

In summary, the pore-like structures documented by Mutvei et al. (2004) in the connecting rings of *Aconeceras* are simply artifacts of preservation. They do not reflect the original structure of the connecting ring. As a result, the implication that the connecting ring in ammonites was structurally different from that of *Nautilus* and permitted a more rapid exchange of cameral fluid is not supported.

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