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Bituminous soft body tissues in the body chamber of the Late Triassic ceratitid *Austrotrachyceras* from the Austrian Alps

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With 5 figures

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Abstract

Black bituminous substance from the body chamber in six shells of the Late Triassic ceratitid *Austrotrachyceras* was investigated with the scanning electron microscopy and energy dispersive spectrometry to elucidate whether it originated from the soft body tissues. The shells come from the Carnian beds in the Northern Calcareous Alps of Lunz (Lower Austria). The interpretation that the analysed black substance in the body chamber represents fossilized mantle, in places intercalated by dispersed, fossilized ink substance, is supported by ultrastructural comparison with (1) bituminous

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plant remnants from a shale slab with *Austrotrachyceras* shells, (2) black substance from an orthoconic cephalopod shell from the Ordovician in Sweden, (3) industrial asphalt, (4) dried ink from recent squid *Loligo*, (5) fossilized mantle, ink sac and ink in Jurassic "fossil squid" *Loligosepia* and ink substance in *Teudopsis*, (6) fossilized mantle in belemnoids *Belemnoteuthis* and *Megateuthis* , (7) ink from fossilized ink sacs of Aptian and Late Carboniferous coleoids.

In the mantle of *Austrotrachyceras* the fibres show a granular replacement, and the C content is approximately 65 per cents of the total weight (EDAX data). This indicates that the soft body tissues probably have been reworked by carbon-accumulating bacteria. Bacteria and fungi are abundantly preserved on the surface of the black substance.The external mantle surface shows a regular honey-comb pattern with the diameter of the cells about 3-4 μm. Their size and shape are similar to those of the nacreous tablets of the nacreous layer on the inner surface of the body chamber. The mantle has a fine lamellar ultrastructure and a fibrous ultrastructure of each lamella. It lacks alternating circular and radial muscular bundles, and a criss-cross pattern of the mantle tunic typical for living and fossil coleoids. This is interpreted as an evidence of a "primitive" structure of a less muscular mantle in *Austrotrachyceras* and in ammonoids in general.

The idea that the ammonoids secreted an ink substance (LEHMANN, 1967; MAZUR, 1971) is supported by new observation.

Zusammenfassung

Schwarze bituminöse Substanzen in Wohnkammern von sechs Exemplaren der Gattung *Austrotrachyceras* (Ceratitina, Trachyceratacеae) aus dem Karn der nördlichen Kalkalpen von Lunz (Niederösterreich) wurden mit dem REM und EDAX untersucht, um festzustellen ob es sich dabei um Gewe-bereste des Ammoniten-Weichkörpers handelt.

Die Interpretation, dass es sich bei der untersuchten Substanz um fossiles Mantelmaterial des Ammonitenweichkörpers, teilweise vermischt mit fossiler Tinte handeln könnte, wird gestützt durch Vergleiche mit der Ultrastruktur von (1) fossilen Pflanzenresten, die gemeinsam mit den Ammonoideen vorkommen, (2) schwarzen Substanzen von orthoconen Cephalopoden aus dem Ordovizium von Schweden, (3) Industrie Asphalt, (4) getrockneter Tinte des rezenten Tintenfische *Loligo,* (5) fossiler Mantelsubstanz, Tintenbeutel und Tintensubstanz der ju-rassischen Tintenfische *Loligosepia* und Tintensubstanz bei *Teudopsis,* (6) fossiler Mantelstruktur bei den Belemniten *Belemnoteuthis* und *Megateuthis,* (7) Tintensubstanz fossiler Tintenbeutel von Coleoiden aus der Unterkreide (Aptium) und dem Oberkarbon.

Im dem hier untersuchten Mantel von *Austrotrachyceras* sind die Fasern in Granulen umgewandelt und der Kohlenstoff-Anteil macht etwa 65% des Totalgewichtes aus, was eine Umwandlung des Weichkörpergewebes durch Kohlenstoff-akkumulierende Bakterien wahrscheilich macht. Die externe Manteloberfläche zeigt ein regelmäßiges Wabenmuster mit einem Zellendurchmesser von 3-4 μm. In Form und Größe ähneln diese den Plättchen der Perlmutterchicht der inneren Ober-fläche der Wohnkammer. Der Mantel hat eine feinlamellare Ultrastruktur und die einzelnen Lamellen sind faserig. Es fehlen die typischen alternierenden und radialen Muskelbündel und das Kreuzmuster der Mantelhülle rezenter und fossiler Coleoiden. Dies könnte als Zeichen einer "primitiven" Struktur eines weniger muskulären Mantels bei *Austrotrachyceras* und bei Ammonoideen generell gedeutet werden. Die Untersuchungen stützen die Idee, dass auch Ammonoideen ein Tinten-ähnliche Substanzen abgeschieden haben könnten (LEHMANN, 1997; MAZUR, 1971).

I. Introduction

The present paper deals with scanning electron microscopic (SEM) and energy dispersive spectrometric (EDAX) analysis of uniquely preserved Triassic ceratitid *Austrotrachyceras* from the Austrian Alps. The body chambers in these ammonites contain a shiny,

black, anthracite-like substance that can be easily mistaken for fossilized ink. Our study shows that it is a bituminous remnant of a mantle that in places includes dispersed ink substance.

The shells of *Austrotrachyceras* were collected at the locality Schindelberg, Lunz, Niederösterreich, a hundred years ago from an excavation executed by Mr. HABERFELNER, the director of the coal mine at Lunz, for the Geological Survey of Austria in 1885 and for the Museum of Natural History in Vienna in 1905. Both tunnels are not accessible any more. *Austrotrachyceras* from this locality has the anaptychi often preserved close to the shell that indicates that the body was retained within the body chamber when the animal died and was deposited on the bottom (KRYSTYN, 1991).

Recent knowledge of the soft body in ammonoids is mainly deduced from the shape of the body chamber and size and position of attachment scars at the body chamber wall (see DOGUZHAEVA & MUTVEI, 1996). In extinct coleoids the fossilized soft tissues have been known since the middle of 19th century. R. OWEN seemed to be the first who distinguished the muscular mantle in *Belem-noteuthis* from the Callovian of England (1844). It has been later studied in more detail in squid-like coleoids (see ALLISON, 1988; MAEDA & SEILACHER, 1996; DOGUZHAEVA & MUTVEI, 2003) and in belemnoids (KEAR et al., 1995; DOGUZHAEVA et al., 2002). In living mobile squids (see KIER & THOMSON, 2003) and extinct squid-like coleoids and belemnoids the mantle is thick, highly muscular being composed of circular, radial and longitudinal bundles of muscular fibres, and has a rigid tunic on the surfaces.

In Recent *Nautilus* the mantle is comparatively thin and has no radial and circular bundles of muscular fibres. It has a tunic-like outer layer. Up-to-now the mantle or other soft body tissue remnants have not been found in ammonoids. The Late Triassic ceratitid *Austrotrachyceras* from Central Austria, studied herein, seems to be the first ammonoid that gives us information of the soft body tissues.

II. Material and status of preservation

The studied material comprises six shells of *Austrotrachyceras* with black, shiny, bituminous substance in their body chamber. These ammonoids come from the Reingraben shales (Lower Carnian, Austriacum Zone) of the locality Schindelberg near Lunz (Lower Austria).

The shells are comparatively large, 50-75 mm in diameter, and flattened by compaction. Due to compression the shell wall is in varying degree fractured into small pieces. Nevertheless, the fragments of the shell wall show well-preserved ornamentation of ribs and tubercles that allow to identify their generic and even species assignment.

The shell material is whitish-grey and shiny, and according to ultrastructural and EDAX analysis it was not phosphatized but retained its aragonitic preservation. The shell matter shows the following elements: O (65-80 %), C (25 %), Ca (8-16 %), Sb (2 %), Mo (2%), Mg, K (1 %), S, Si, Mn, Fe, K (less than 1%).

The body chambers are flattened by compaction in such a way that their left and right sides either meet each other or become separated only by an indistinct, narrow, uneven, crack-like inter-space filled either by sediment (grey-green shales) or black bituminous substance (figs. 1A, B, C). The black substance is exposed where the shell wall is broken. In all studied shells it has a somewhat varying extension but it occurs approximately in the middle and posterior portion of the body chamber but never near the aperture or outside the

body chamber. The black substance can be easily split from the underlying shell wall. It is lighter than the shell material and bears on its surfaces organic debris and numerous diverse and well-preserved micro-organisms such as fungi and colonies of bacteria (figs. 3A, 4A, B).

The black substance from the body chamber shows the following composition in per cents to the total weight: C (65%); O (30%); S (2-6 %); Si (1-2 %); Cd (0.5-1.8 %); Fe (1 %) and K, Al, Zn (each less than 1 %). The EDAX data confirms that the black substance inside the body chamber is organic. When it is oxidised by high concentration of hydrogene peroxide solution it looses the black colour and becomes reddish-brown. A similar chemical treatment of the fossilized ink in Jurassic coleoids (*Teudopsis*) that according to EDAX analysis was phosphatized, did not react with hydrogene peroxide.

The ultrastructure of the black, bituminous substance from the body chamber in *Austrotrachyceras* was compared with ink of the living *Loligo forbesi* STEENSTRUP (from the North Sea, Sweden), and with mantle and muscle tissues of *Nautilus belauensis* SAUNDERS (from the Honolulu Aquarium, Hawaii), the latter preserved about ten years in alcohol.

The studied Triassic *Austrotrachyceras* material is deposited at the Museum of Natural History in Vienna. All other material here studied is stored at the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm.

III. Depositional environment

The green-grey shales at the locality Schindelberg, Lunz, that yielded the studied shells of *Austrotrachyceras* lack bioturbation and infauna (KRYSTYN, 1991). The shales contain numerous, tiny, probably juvenile shells of bivalve *Halobia rugosa* (1-2 mm in length). They are often preserved in "butterfly" position having two open valves still joined, although many are disarticulated. It is uncertain whether this bivalve had a benthic, pseudo-planctic, pelagic or free swimming mode of life. According to GRIFFITH (1977) *Halobia* could have been a member of low oxygen benthic fauna.

In addition to the ceratitid *Austrotrachyceras* the nectic fauna from Schindelberg includes numerous fish remnants, rare phragmoteuthids and phyllocarid crustaceans. Decapod crustaceans are preserved with delicate legs. Two so far undescribed shells of benthic gastropods were found in a slab together with *Austrotrachyceras* (our unpublished data). Soft tissue preservation is known in the underlying Göstlinger Limestone (KRYSTIN, 1991).

As shown by EDAX analysis the shales with *Austrotrachyceras* contain the following elements (in per cent to the total weight): O (60 %), Si (20%), Ca (4.5-7%), Al (5-6 %), K (1.5-2.5 %), Fe (1-2 %), S (up to 2 %). They lack P and C.

The depositional environment of the Early Carnian in Austrian Alps was assumed to be similar to that of the Posidonia Shales at Holzmaden with the difference that the latter have a much greater thickness and contain aquatic reptiles and pieces of wood (SEILACHER, 1982,). Our EDAX analysis shows that the depositional environment in the early Carnian at Lunz was different from that in Holzmaden because of absence of phosphatization of the shell matter and soft tissues. For instance, *Loligosepia* from Holzmaden, preserved with gladius, muscular mantle, ink sac wall and ink substance, contains the P (EDAX analysis), while in *Austrotrachyceras* the shell material, the black substance from the body chamber, as well as the surrounding sediment, lack the P. The soft body tissues in the body chamber of *Austrotrachyceras* were probably preserved because the activity of carbon-accumulating

bacteria that replaced the organic fibres in the mantle by globular granules of the C at early post-mortem stages. The solidification of melanin in the ink can be explained as a chemical reaction of a slightly acid or neutral bottom water condition, which caused the melanin to precipitate into a solid. In alkaline environment the melanin is dispersed colloidally (Fox, 1966).

The black bituminous mantle and ink substance from the body chamber in *Austrotrachyceras* and the bituminous spots that occasionally occur in the shales (some of them could be a plant debris) were hospitable places for rich bacterial and fungi life. These micro-organisms were observed neither on calcitic *Halobia* shells, on aragonitic *Austrotrachyceras* shells, nor on the fractured surfaces of shales. The microorganisms probably played an important role in decay of the soft body tissues in *Austrotrachyceras*. To become black and bituminous the soft tissues probably first underwent aerobic and anaerobic decay. Aerobic decay resulted in reducing the volume significantly. Anaerobic decay continued to reduce the volume still further, and the acidity increased. When the pH reached to about 4.0 the acidity killed off the anaerobic bacteria. At this point the organic substances changed into a black material. The next was the thermal process that required a burial of the substance by at least two or three thousand feet of sediment depending on the geothermal gradient. Once the temperature reached 100° C the bituminization process began. Chemical reactions drive off water, oxygen and hydrogen that raised the percentage of carbon. When the C reaches 85 % the organic substances became sub-bituminous. The content of the C in the black substance in the body chamber in *Austrotrachyceras* is approximately 60-65% that is close to this value.

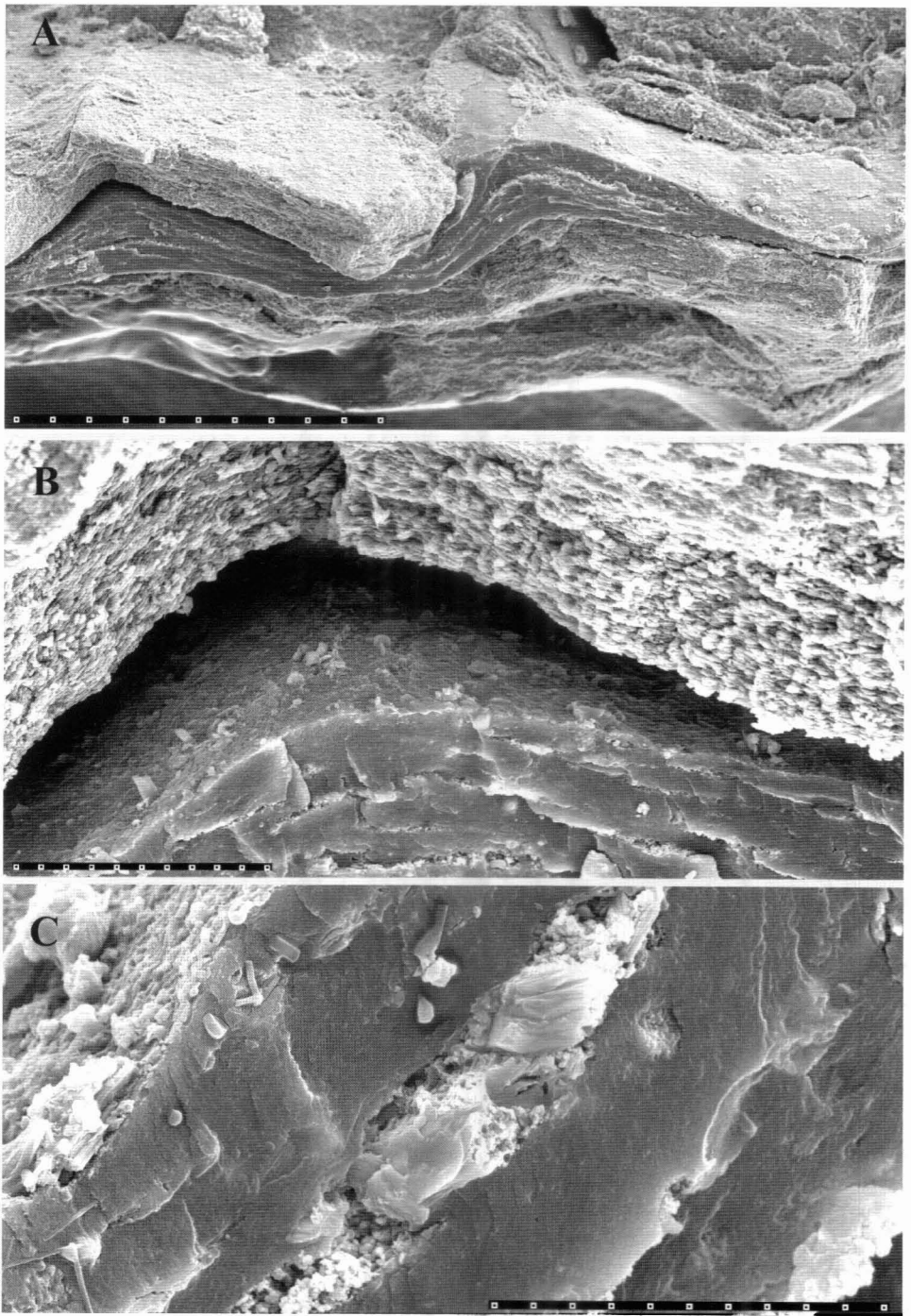
IV. Methods of study

The fossilized soft body tissues were revealed by an ultrastructural examination of the black bituminous substance in the body chamber of *Austrotrachyceras* and by a comparison with the previously studied fossilized organics of different kinds (mantle, ink sac wall, ink, gladius, connecting rings) of living and extinct cephalopods (see Doguzhaeva & Mutvei, 2003).

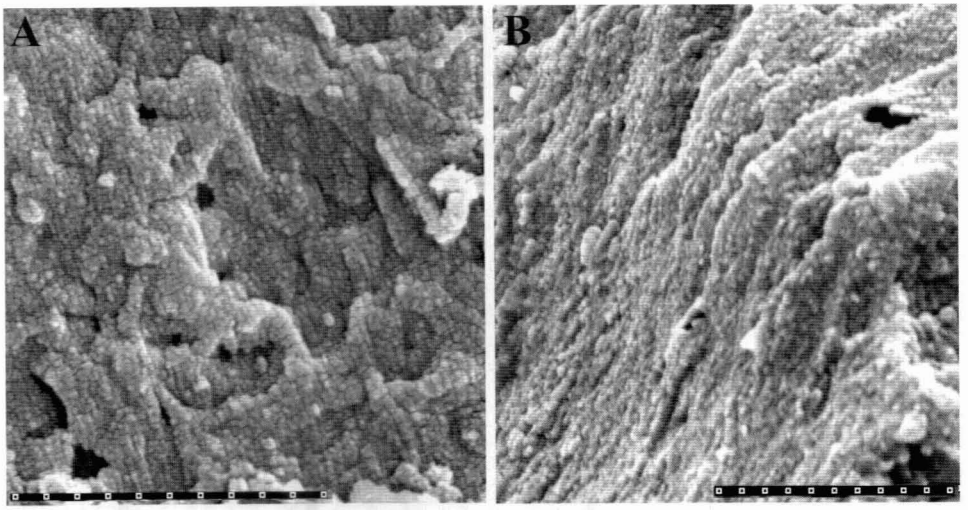
For SEM observations the specimens were glued to stabs, coated by gold and studied with Hitachi S-4300 at the Swedish Museum of Natural History, Stockholm. More than 200 images of *Austrotrachyceras* were taken, including surfaces and fracture planes of the shell wall, and surfaces and fracture planes of the bituminous soft body tissues. In addition, organic debris, bacteria and fungi on the tissue surfaces, *Halobia* shells, surrounding sediment, and occasional bituminous spots in the shale matrix, were examined with SEM.

The bituminous soft tissues from the body chamber were either studied without treatment or treated with circa 60 % H_2O_2 for three-four hours. They showed to be more resistant for oxidation than shell material. When oxidized the tissues changed from black to red-brown colour without being disintegrated while the shell material was nearly completely disintegrated.

For comparison, (1) ink material and ink sac tissues of living squid *Loligo* and (2) mantle and muscles in living *Nautilus* were examined with SEM after drying. To test the influence of environment on the ultrastructure of solidified ink, the ink extracted from *Loligo* was dried under the following different conditions: (1) within the ink sac at 20° C for several days, (2) dried at 20°C without ink sac for several days, (3) mixed with fresh water after washing the soft tissues coloured by ink and evaporated for several days at 20°



Figs. 1A-C: *Austrotrachyceras* sp.; **A:** Longitudinal fracture of a compressed shell and bituminous soft body tissues squeezed between the shell wall of the body chamber (top left side) and shell wall of the pre-vious whorl; each division of the scale bar 60 µm. **B:** Enlarged view of Fig. A to show nacreous shell wall and layers of soft body tissues with granular substance between the layers; each division of the scale bar 6 µm. **C:** Layers of soft body tissues and infillings in the interspaces in still higher magnification; each division of the scale bar 3 µm.



Figs. 2A-B:*Austrotrachyceras* sp.; **A:** Surface view of the fossilized mantle to show its fibrous ultrastructure; note that each fibre consists of a row of globular granules; each division of the scale bar 0.3 μm; **B:** Fracture of the fossilized mantle to show numerous consecutive lamellae each consisting of globular granules; each division of the scale bar 0.12 μm.

C, (4) boiled in weak acid solution until complete evaporation of the water. These experiments showed that the coagulation of the melanin particles depends on the environment because the ink substance that was dried within the ink sac or outside it (experiments 1 and 2) formed uni-formly shaped and sized globules made up of smaller particles (fig. 5B). On the other hand, when the ink was mixed with fresh water or boiled in weak acid solution (experiments 3 and 4) the melanin mass shows a more irregular ultrastructure of coagulated particles. Thus, different environmental conditions may have produced the less regular globular ultrastructure of the ink in *Austrotrachyceras*.

V. Observations on the body chamber in *Austrotrachyceras*

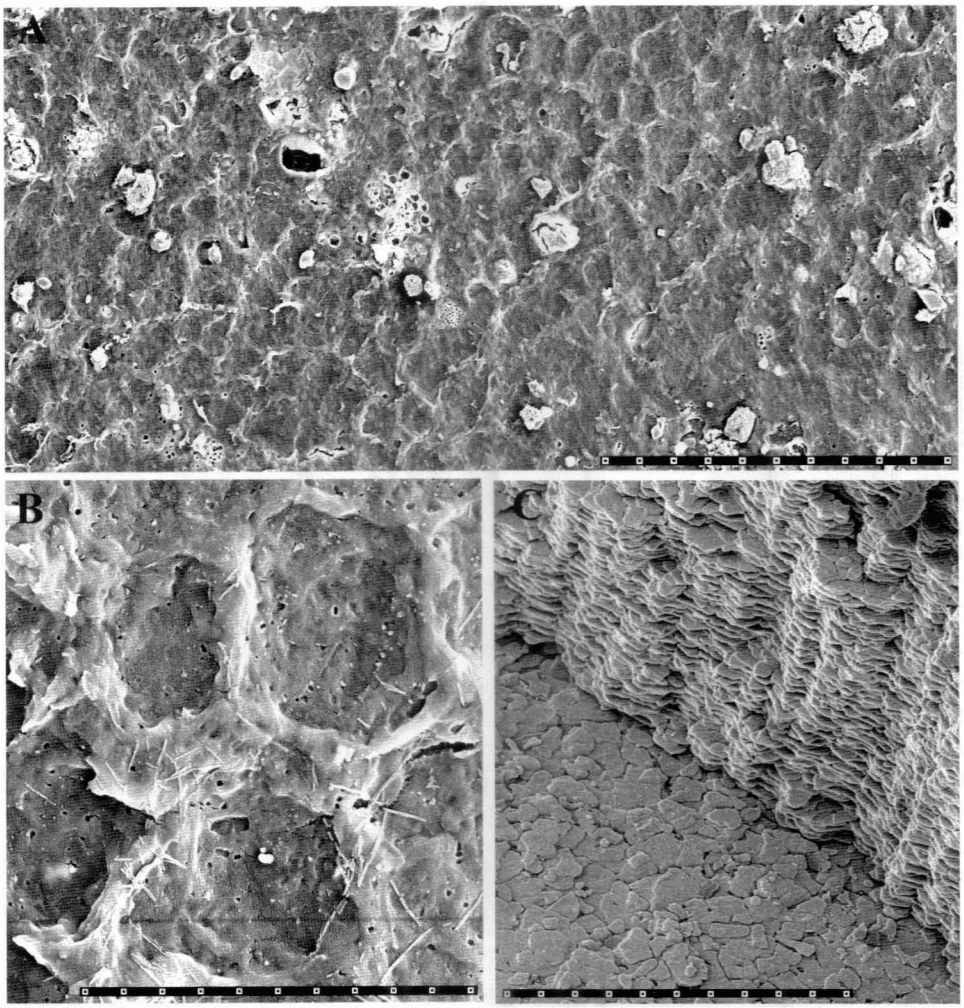
V.1. Shell wall ultrastructure (figs. 1A, B, 3B, C)

In ceratitids the shell wall is composed of three calcareous layers: comparatively thin outer and inner prismatic layers and a thick nacreous layer between them. In the body chamber the inner prismatic layer is restricted to the posterior portion. Therefore the nacreous layer is exposed on the inner surface of the anterior portion of the body chamber that corresponds to ca 2/3 of the body chamber length (DOGUZHAEVA & MUTVEI, 1986).

In *Austrotrachyceras* the main bulk of the body chamber wall is nacreous. The nacreous tablets are about 3 μm in diameter and arranged in columns (columnar nacre). The surface of nacreous layer shows a mozaic pattern. Because of diagenetic shell compression many of nacreous tablets were crushed and partially fused to each other having lost their regular hexagonal shape, although the columns of tablets are in places distinctly preserved (figs. 1B; 3C).

V.2. Mantle ultrastructure (figs. 1A, B, 2A, B, 3A, 4A, B)

The total thickness of the left and right sides of the squeezed mantle is about 15 μm. The mantle consists of numerous thin lamellae about 0.1 μm thick. The lamellae are composed of tiny (about 0. 02 μm) globular granules that have replaced the soft mantle tissues. The outer mantle surface shows a regular "honeycomb" pattern composed of

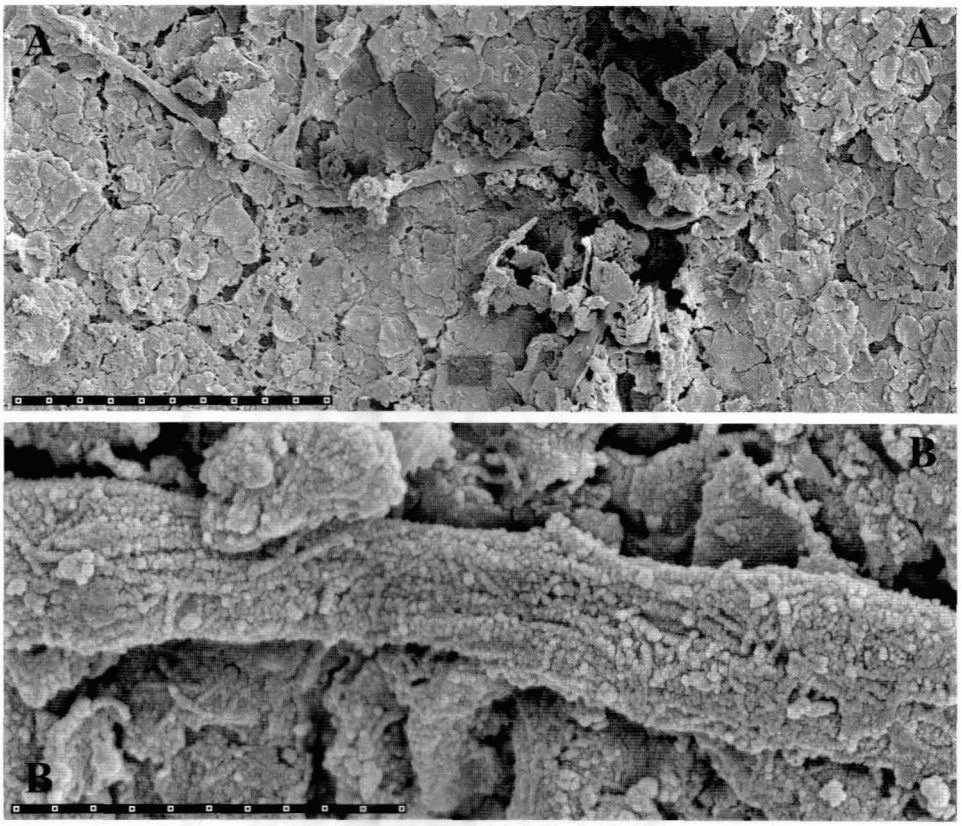


Figs. 3 A-C: *Austrotrachyceras* sp.; **A:** Surface view of the fossilized mantle to show the regular honey-comb pattern; each division of the scale bar 0.6 μm; **B:** Enlarged view of **A** to show angular depressions on the mantle surface; each division of the scale bar 0.2 μm; **C:** Fracture plane and surface view (top right) of the columnar nacreous layer of the shell wall; each division of the scale bar 3 μm.

somewhat angular depressions 3-4μm in diameter. The shape and size of these depressions correspond to those of the nacreous tablets.

The lamellar structure of the mantle is clearly shown in sections (fig. 2B). On surface views the mantle is often cracked (fig. 4A) and in several places the surfaces of the consecutive lamellae show fine, parallel striation (fig. 2A). This striation is much finer than the transverse striation of the muscular mantle surface in fossil coleoids where it is formed by strong circular and radial bundles of muscles (figs. 6A, B). The criss-cross striation of the mantle tunic in belemnites (DOGUZHAEVA et al., 2002), formed by impressions of helical collagen fibres and typical of coleoid muscular mantle, is also absent in *Austrotrachyceras*.

The mantle has a similar black colour as the fossilized ink probably because of breakage of the ink sac after the death of the animal and because of the bituminous consistence of the mantle. To test the presence of the main component of the ink, the melanin, the mantle containing scattered ink was treated with a concentrated solution of hydrogen peroxide. Due to



Figs. 4 A-B: *Austrotrachyceras* sp.; **A:** Surface view of the fossilized mantle to show fractured mantle lamellae and long, branching micro-organism ("fungi"); each division of the scale bar 3 µm. **B:** Enlarged view of fig. A to show fibrous-granular ultrastructure of a branch of the micro-organism; note the structural similarity with the fibres in the mantle in fig. 2A; each division of the scale bar 0.3 µm.

oxidation of the melanin the mantle changed its colour and became reddish -brown. This is an indirect indication of the melanin in fossilized ink and in the adjacent mantle.

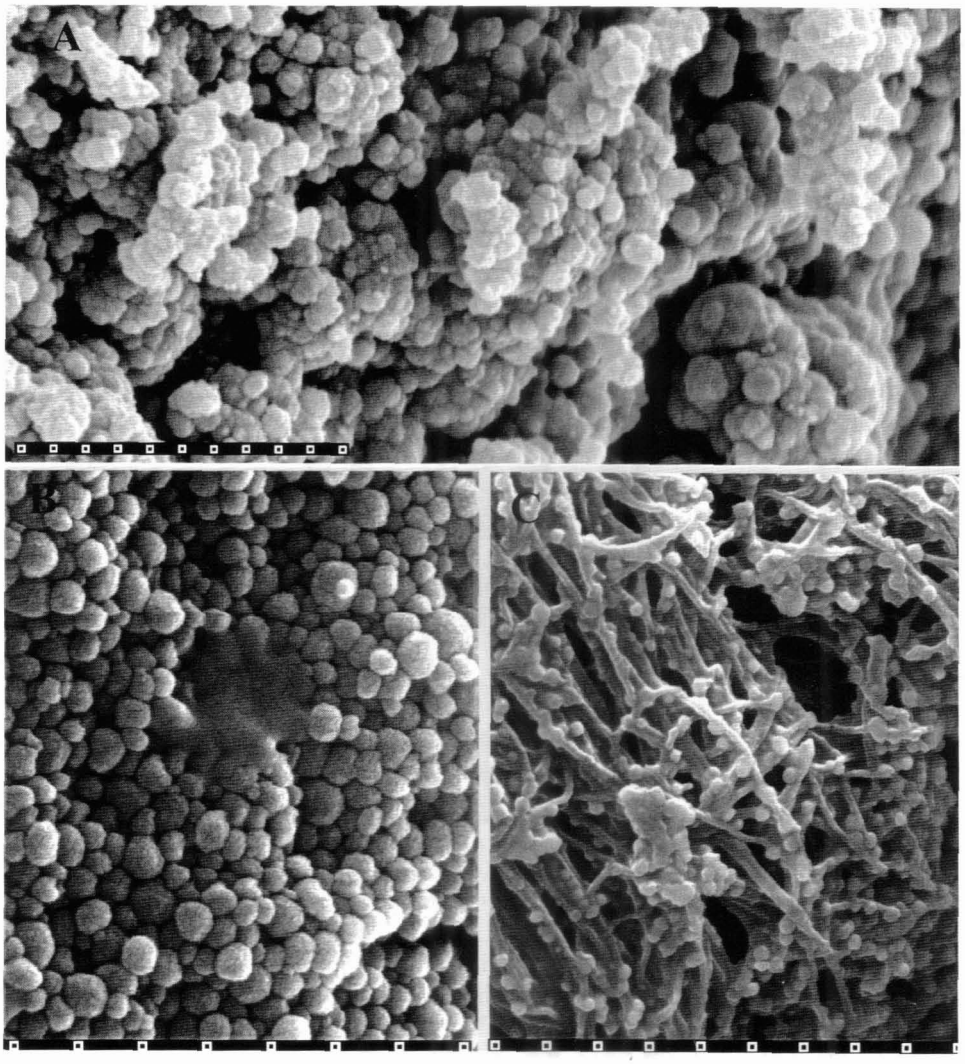
V.3. Ink ultrastructure (figs. 5A, B)

The occurrence of the ink substance in ammonoids and its ultrastructure has been for the first time described in *Austrotrachyceras* by DOGUZHAEVA et al. (2004 in print).

The ink sac is not preserved and the ink substance is dispersed in the inter-space between the right and left portions of the mantle, and in places between the mantle lamellae. The ink consists of a mass of tiny, globular granules, 0.1 – 0.4 µm in diameter (fig. 5A). Each granule is an agglomerate of smaller particles but dispersed individual particles may also occur between the globular granules. The ink in *Austotrachyceras* is ultrastructurally identical to that in recent and fossil coleoids (compare figs. 5A, B).

VI. Discussion

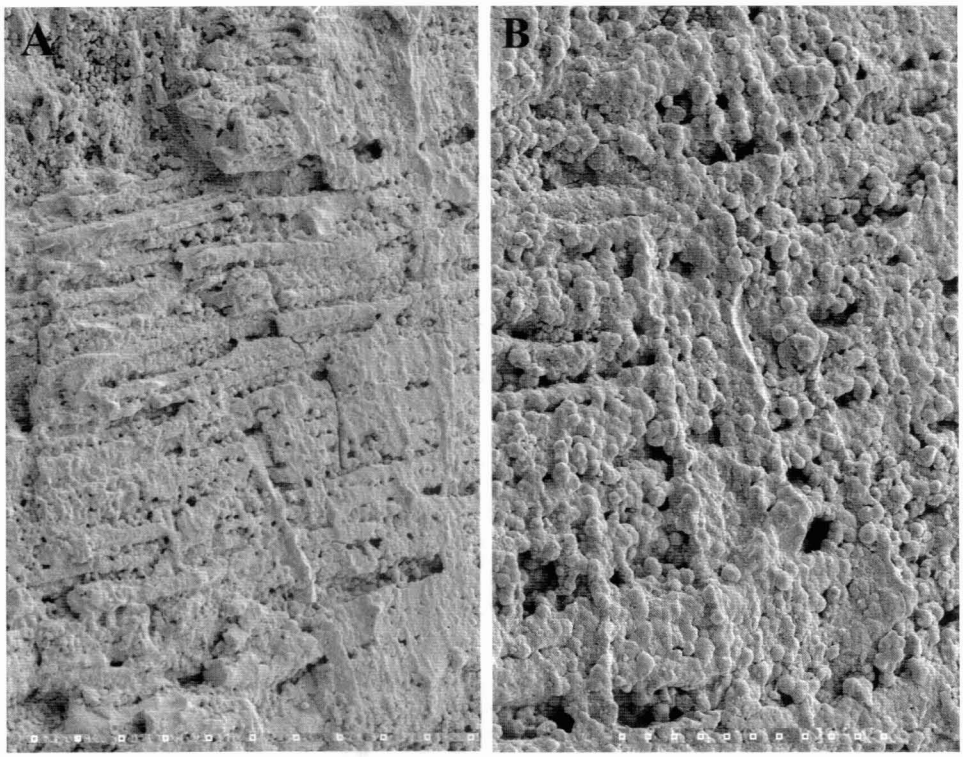
The formation of a muscular mantle was one of the most important evolutionary steps in coleoids. In living squids, the muscular mantle consists of alternating blocks of circular, radial and longitudinal muscles (KIER & THOMPSON, 2003). The inner and outer surfaces are



Figs. 5 A-C: *Austrotrachyceras* sp.; **A:** Fossilized ink substance consisting of irregularly arranged globular granules each of which composed of numerous small particles; each division of the scale bar is 0.15µm. **B:** *Loligo forbesi* STEENSTRUP, 1856; dried recent ink substance; note the ultrastructural similarity with the fossilized ink in fig. A; each division of the scale bar 0.3µm. **C:** *Nautilus belauensis* SAUNDERS, 1981;muscle fibres of the mantle, fixed and preserved in alcohol 10 years, afterwards dried 4 hours at 70 degrees C; note the numerous globules connected with fibres; each division of the scale bar 0.6 µm.

covered by tunics formed of 6-10 layers of crossed-helical collagen fibres, which serve to prevent distortion of the mantle during contraction (GOSLINE & SHADWICK, 1983).

The fossilized muscular mantle in coleoids has been known since OWEN (1844) described it in *Belemnoteuthis* (Callovian). More recently, the muscular mantle in *Belemnoteuthis* was studied by ALLISON (1988). He showed that the muscular fibres were pseudomorphed by bacteria into globular aggregates of apatite. The size of the globules ranks from 1.5 mm to 2.0 mm. He also analysed the environmental conditions of sedimentation in the lower part of the Oxford Clay where *Belemnoteuthis* was collected. The phosphate formation was probably promoted by high concentration of phosphate in the water near the anoxic-oxic boundary and by an alkaline micro-environment produced



Figs. 6A-B: *Loligosepia aalensis* (von ZIETEN, 1832), Lower Jurassic, Posidonien Schiefer, Holzmaden, sp. no. Mo. 160717, fossilized muscular mantle; **A:** Alteration of circular and longitudinal fibres; each division of the scale bar 50µm. **B:** Enlarged detail of fig.A to show granular replacement of fibres in muscular mantle; each division of the scale bar is 10µm.

by the decay of squid soft-tissues. Under these conditions bacterial activity may initiate phosphate precipitation.

Ultrastructure of the fossilized muscular mantle and ink sac wall was also studied in the Lower Jurassic coleoid *Loligosepia* (DOGUZHAEVA & MUTVEI, 2002). Both tissues show a multi-lamellar structure. In the mantle, each lamella consists of parallel bundles of muscle fibres alternating with stripes of dot-like pattern, probably representing circular and radial muscles, respectively (figs. 6A, B). The fibres show numerous globular granules up to 4 µm in diameter. The granules are composed of smaller particles. Similar granules were also found in the ink sac wall.

In the belemnites *Megateuthis* and *Passaloteuthis* the muscular mantle shows a pattern of impressions of alternate sets of fibres on the ventral surface of the pro-ostracum (DOGUZHAEVA et al., 2002: Pl.1, Figs. 1, 2). These impressions represent the fibres of the mantle tunic.

In order to test diagenetic changes in fossilized mantle, decay experiments on two living squids and a sepiolid were carried out by KEAR et al., (1995) over a period of one day to 50 weeks. SEM examination of the decaying soft tissues revealed that the collagen in the intermuscular connectives was covered with bacteria, comparable in size to phosphate globules in fossil material. The diameter of the globules was 0.3 mm - 0.6 mm.

Fossilized mantle in ammonoids is described herein for the first time in *Austrotrachyceras*. In contrast to the thick and muscular mantle in coleoids the mantle in ammonoids

was thin and considerably less muscular, having probably been similar to that in recent *Nautilus*. The mantle in *Austrotrachyceras* is not phosphatized contrary to that in many fossil coleoids. Despite of that, its ultrastructure is identical to that in coleoid phosphatized mantle. It consists of numerous, consecutive, thin lamellae, each composed of parallel fibres that have been replaced by globular granules. However, the fibres in *Austrotrachyceras*, inter-preted as muscle fibres, are much thinner than bundles of muscle fibres in radial, circular and longitudinal muscles of coleoids (compare figs. 2A, 6A, B). The mantle structure in *Austrotrachyceras* is also identical to the fibrous and globular structure in fungi-like organisms preserved on the mantle surface (figs. 4A, B).

It should be mentioned that SEM observations on dried mantle and muscular tissues in living *Nautilus*, preserved ten years in alcohol, show numerous granules what are intimately connected to the fibres and have the same diameter as the fibres (fig. 5C). Similar globules of the same size occur also in the mantle tissue. The origin of these granules is still unknown.

The black bituminous material preserved in the body chamber of *Austrotrachyceras* was also compared with occasional black substance in the shale sediment adjacent to the shells. In SEM the latter substance is homogeneous and consists of extremely small particles, visible at x 25.000 magnification. It lacks a laminar and fibrous ultrastructure. A similar structure was observed in bituminous black substance in shell chambers of Ordovician orthoconic nautiloid and in industrial asphalt.

The ink substance in recent and fossil coleoids, and in ammonoid *Austrotrachyceras*, also consists of globular granules but in contrast to the soft body tissues the ink granules lack spatial orientation and a fibrous and lamellar ultrastructure (fig. 5A).

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