Chapter 11
The Preservation of Body Tissues, Shell, and Mandibles in the Ceratitid Ammonoid *Austrotrachyceras* (Late Triassic), Austria

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1 Introduction

For many years, the discovery of mandibles associated with the shells of ammonoids was considered important to paleobiology, and these occurrences were reported to the paleontological community. Such an association was reported by Trauth (1935b), who described and illustrated mandibles associated with the Late Triassic ceratitid ammonoid *Austrotrachyceras*. The specimens were discovered from the Carnian beds in the northern Calcareous Alps near Lunz (Lower Austria). Observation of his described and illustrated specimens and especially a detailed analysis of previously unstudied specimens from this locality has provided new insight into the preservation of ammonoids.

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For convenience in the past, organs within the body of a fossil cephalopod including the mantle, stomach, ink sac, mandibles, and even arm hooks have been placed within the concept of "soft tissues" for ease of describing the fossil remains (Stenzel, 1964). In other cases the mandibles and the associated parts of jaws have been considered as "organic remains" (Teichert et al., 1964). Recognizing that different organs may have different ultrastructures, chemical compositions, and preservation potential, we believe that separation of these organs into categories is desirable for a better understanding of the paleobiology of fossil cephalopods.

We recognize three different categories: these are the "soft tissues," the "hard parts," and the "skeleton." We define "soft tissues" as the musculature of the buccal mass and mantle, the crop, stomach and gut, intestines, siphuncular cord, gills, ink sac, and other organs and tissue attachments that are generally within the head and body region of the animal. We separate from the "soft tissues" the category of "hard parts" that includes those structures that are all or partly chitin and some of which may be partly mineralized with calcium carbonate. These structures include the mandibles, the radula, and arm hooks. The "skeleton" includes such structures as the shell, rostrum, the guard, pro-ostracum, and gladius. We and many others have observed that some "hard parts" like the mandibles, have a much greater potential for fossilization than the "soft tissues" such as the internal organs and the tentacles, and that the "skeleton" material has the best fossilization potential of all.

2 Previous Work on Soft Tissues and Hard Parts

2.1 Fossil Mandible and Radula Overview

There is a voluminous literature on cephalopod hard parts, especially the mandibles, which we will not attempt to completely survey here. As a brief overview, Biguet described the first fossil mandible as a rhyncholite in 1819. From that time till the 1960s it was common for paleontologists to describe these parts of cephalopods as new genera and species (see, e.g., Trauth, 1927, 1935a, b) and in the Treatise of Invertebrate Paleontology, Volume K, Teichert et al. (1964) discussed these body parts extensively and provided a comprehensive compilation of the then known genera. More recent reports by Closs and Gordon (1966), Lehman (1987, 1990), Mapes (1987), Dagys et al. (1989), Doguzhaeva et al. (1997) and many others have not followed this naming trend and have generally used simpler terminology with the goal of investigating the modes of preservation, function – especially the operculum versus mandible problem (see Dagys and Dagys, 1975; Morton, 1981; Lehmann, 1970, 1972 a, b, 1987, 1990, and others), and paleobiology of both isolated and in situ occurrences (Closs and Gordon, 1966; Mapes, 1987; Tanabe and Mapes, 1997, and numerous other reports). To our knowledge, this report is the first study of the ultrastructure of fossil mandibles and their chemical makeup where the mandibles have not been mineralogically replaced (for phosphate and other mineral replacements and alteration examples, see Mapes, 1987;

Dagys and Weitschat, 1988). Indeed, as far as we are aware, the only report of the chemical makeup of the mandibles of an externally shelled cephalopod is that of modern *Nautilus* by Lowenstam et al. (1984).

Reports of fossil cephalopod radula are much fewer in number, and most occurrences are in association with mandibles (for examples, see Closs and Gordon, 1966; Lehmann, 1979; Tanabe and Mapes, 1995; Tanabe and Fukuda, 1983; Doguzhaeva and Mutvei, 1992). Many reported radula occurrences are in situ within the body chambers of fossil cephalopods, but some are not (for examples of both, see Saunders and Richardson, 1979). Most radula reports are descriptive, and the research focus has usually been to determine the morphological changes that reflect the evolutionary changes of this important structure.

2.2 Soft Body Tissues Overview

Coleoid soft body tissues, including ink-filled ink sacs and mantle tissue, and hard parts, including mandibles and arm hooks, have been known and reported for over 150 years (Buckland, 1829, in Huxley, 1864). These kinds of descriptive reports have been the research focus over the past decades (see, e.g., Naef, 1922); however, in the last decade new discoveries and interpretations have been made possible by using new technologies on older reposited material when the SEM was employed to elucidate the soft tissues, hard parts, and skeleton structures of different coleoids (see, e.g., Kear et al., 1995, and the numerous works of Doguzhaeva and her colleagues over the last decade).

Soft body tissues in ammonoids have only been reported in a few instances for the Ammonoidea. Lehman (1964) reported the presence of an ink sac with ink in a Jurassic ammonite from Germany; however, he retracted the report in Lehmann (1981). Additionally, he reported the preservation of a stomach and its contents in an ammonite from the same unit. In 2004b, Doguzhaeva and her colleagues described the remains of muscular mantle tissue and possible ink in specimens of the Late Triassic ceratitid *Austrotrachyceras* from the Lower Carnian-Austriacum Zone of Lunz (Schindelberg locality), Lower Austria. Additional material from this locality is now available including specimens with the mandibles near the aperture of the shell, and by using both standard and newer technology, new details are presented herein, as well as information on the ammonoid mandibles and shell material from the two collecting sites.

3 Locality and Material

The specimens studied are shells of the Late Triassic ceratitid *Austrotrachyceras* from the Lower Carnian–Austriacum Zone at Lunz (Schindelberg locality), Lower Austria. More than 100 years ago, the specimens were excavated with the

permission of Mr. Haberfelner, the director of the coal mine at Lunz, for the Geological Survey of Austria in 1885 and the Museum of Natural History in Vienna in 1905. Both sites are now inaccessible for collecting (Doguzhaeva et al., 2004b).

Fifteen relatively complete (30–75 mm in diameter) shells in a medium gray shale were available for study. All the ammonoid shells are crushed by compaction with the left and right body chamber walls in more-or-less contact with each other. Shiny, black, asphaltic-like material is located between the body chamber shell walls in places. Despite the fact that the shell of the animals is crushed, the pieces of the shell remain together in a fractured mosaic pattern. Five mandibles are associated with the ammonoid specimens. Three are located in front of or partly within the aperture; a similar condition was described by Krystyn (1991). The body chamber length (bcl) varies depending on the stage of maturity; on specimen 5 the bcl is interpreted to be about 230° at a crushed diameter of 32 mm, and on specimen 6 the bcl is about 270° at a crushed diameter of 48 mm.

4 Purpose of this Study

The purpose of this research is to study the unusual shiny, black, asphaltic-like material that occurs within the body chambers of the shells of *Austrotrachyceras* and the material of the mandibles to determine the composition and ultrastructure. In addition, the black material is compared to the mandibles to determine similarities and differences. The shell ultrastructure is evaluated to determine the overall quality of preservation. To accomplish these goals, (1) energy dispersive spectrometry (EDS), (2) scanning electron microscopy (SEM), and (3) light microscopy were used.

5 Ultrastructure and Preservation of the Soft Tissue, Hard Parts, and Skeleton in *Austrotrachyceras*

5.1 The Black Bituminous Substance in the Body Chamber

The black, bituminous substance in the body chamber (Fig. 11.1A, C–E) looks like shiny pitch that has solidified after being squeezed between the crushed shell walls of the body chamber. The black substance (1) is missing in the chambers of the phragmocone, (2) is only present orad of the last septum, (3) has a somewhat variable thickness and extent, and (4) is restricted to the body chamber and is not present in the surrounding sediment. The black substance is best exposed where the wall of the body chamber is removed when the enclosing shale is split. The black material separates easily from the underlying shell wall and is lighter than the shell material.

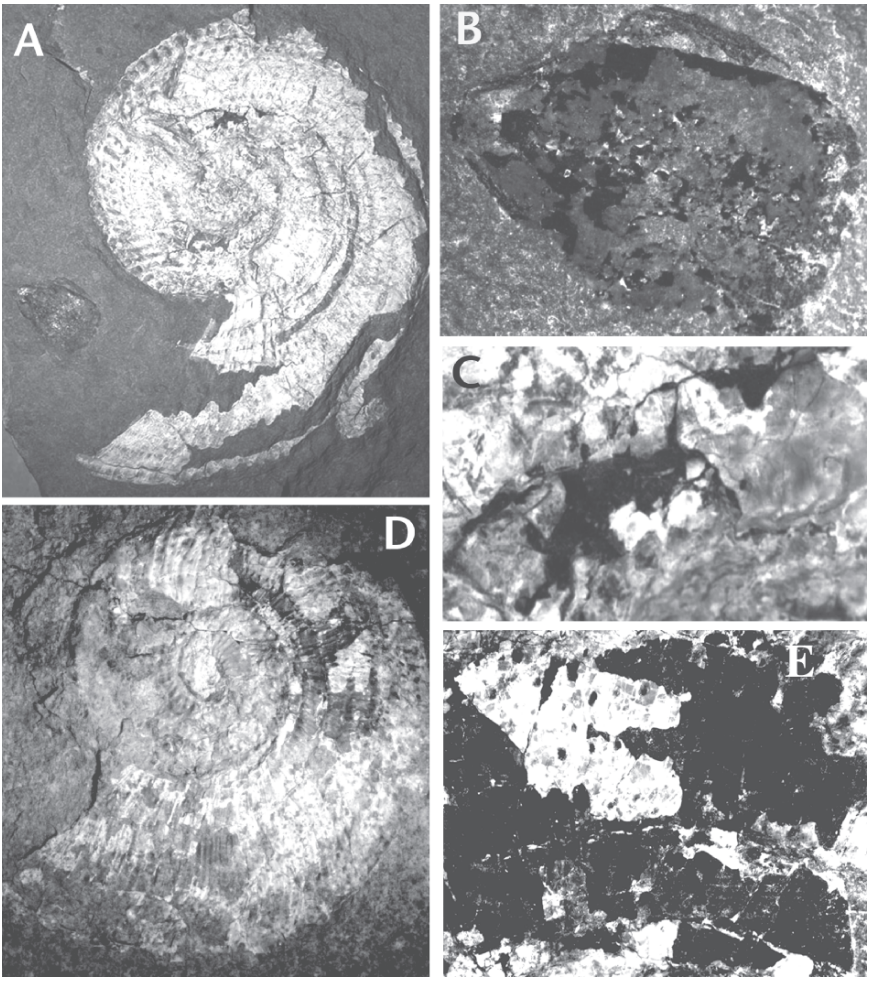

Fig. 11.1A–E Austrotrachyceras *sp. A–C. NHMW 2005z/0006/0006. D,E. NHMW 2005z/0006/0001. A. Shell and mandibles near the aperture. Black material in the shell is exposed where the body chamber shell wall has been removed. x 1.5. B. Enlarged view of the upper and lower mandibles; the lower mandible is poorly exposed around the periphery of the upper mandible. x 5.5 C. Enlarged view of a fragment of the black material in the body chamber. x 5.2, D, E. Lateral view of the compressed shell with black material squeezed in the body chamber and exposed in its middle part where the shell wall is removed. x 1.0. E. Enlarged view of the black material showing its pitch-like appearance. x 3.5.*

The SEM study shows that the black substance forms two sheets that are indistinctly separated by an uneven interspace (Fig. 11.4A, B). These sheets are laminated (Figs. 11.2A, C, 4C), and the laminae are often broken into irregular plates and patches (Figs. 11.4E, F, 6C). Due to differences in preservation, the sheets have a varying ultrastructure: a granular porous ultrastructure (Fig. 11.3B, C), a globular

ultrastructure consisting either of irregularly sized globules (Fig. 11.6A) or regularly sized globules (Fig. 11.5C), or an irregular rodlike interconnected ultrastructure (Fig. 11.5D–F). In places, the laminae show a fibrous ultrastructure with the fibers consisting of numerous globules (Figs. 11.2C, 3A) or granules (Figs. 11.4E, F, 6C; see also Doguzhaeva et al., 2004b: Fig. 11.2A). The interspace between the two sheets contain debris that was probably originally organic material and organ pieces, which has been plastically deformed and sometimes folded (Fig. 11.4D). The outer surface of the sheets facing the wall of the body chamber shows a regular honeycomb-like pattern (Doguzhaeva et al., 2004b: Fig. 11.3A–C) with cells the size of which corresponds to that of nacreous tablets of the shell wall (ca. 0.3 μm). The microlamination of the two sheets of black substance, and the fibrous structure of each lamina (Fig. 11.3A), indicate that the sheets were originally a muscular tissue.

The SEM observations on the dispersed material preserved within the interspace between the two sheets of black substance reveal agglomerations of tiny globules (diameter is ca. 0.1–0.4 μm) each of which consists of smaller particles (Fig. 11.6A, B). The globules lack laminations, fibrous patterns, or any other structure. This material with a globular ultrastructure between both sheets of the black substance is comparable to described occurrences of fossil and modern coleoid ink (Doguzhaeva et al., 2002, 2003, 2004a). This globular ultrastructure of the ink in cephalopods has been demonstrated in *Loligo* and in several other undetermined living squids, sepiids, and octopuses and in the fossil ink of Carboniferous, Jurassic, and Cretaceous coleoids (Doguzhaeva et al., 2002; Doguzhaeva and Mutvei, 2003; Doguzhaeva et al., 2003, 2004a). The solidified ink seems to be the result of rapid coagulation of the melanin particles (the main constituent of ink) during precipitation. The ink solidification requires an acid or neutral environment (Fox, 1966). Such a pH environment could be produced by either bacterial decomposition activity on the dead animal or by chemical alteration of the ocean water at the water/sediment interface by bacterial activity or both.

The ultrastructure of the black material in the body chamber was compared to the muscle tissue of the buccal mass in a specimen of the modern squid *Loligo*, which was air dried for one year, and in a specimen of *Nautilus* muscle mantle tissue, which was preserved in alcohol for 20 years. The muscle tissue in the buccal mass of the modern squid shows that a globular ultrastructure similar to the globular ultrastructure seen in the black material had formed. The longitudinal muscles have an almost smooth appearance with a fine granular surface, whereas the transverse muscles have a more robust globular size (Fig.11.7C–D). In *Nautilus*, the muscular mantle tissue is well preserved and has a globular ultrastructure (Fig. 11.7E, F).

The black substance that forms two sheets in the body chamber in *Austrotrachyceras* was compared by SEM with isolated blobs of black substances in the shale that surround the ammonoid shells. These blobs lack a fibrous, globular, or laminar ultrastructure, and thus, they are not related to the black material in the body chambers of the ammonoids.

EDS analysis on one specimen demonstrates that the black substance has the following chemical composition in percents of the total weight: C (60–65%); O (30%); S (2–6%); Si (1–2%); Cd (0.5–1.8%); Fe and K (1%), Al and Zn (each less than 1%) (Doguzhaeva et al., 2004b). The lack of significant amounts of iron

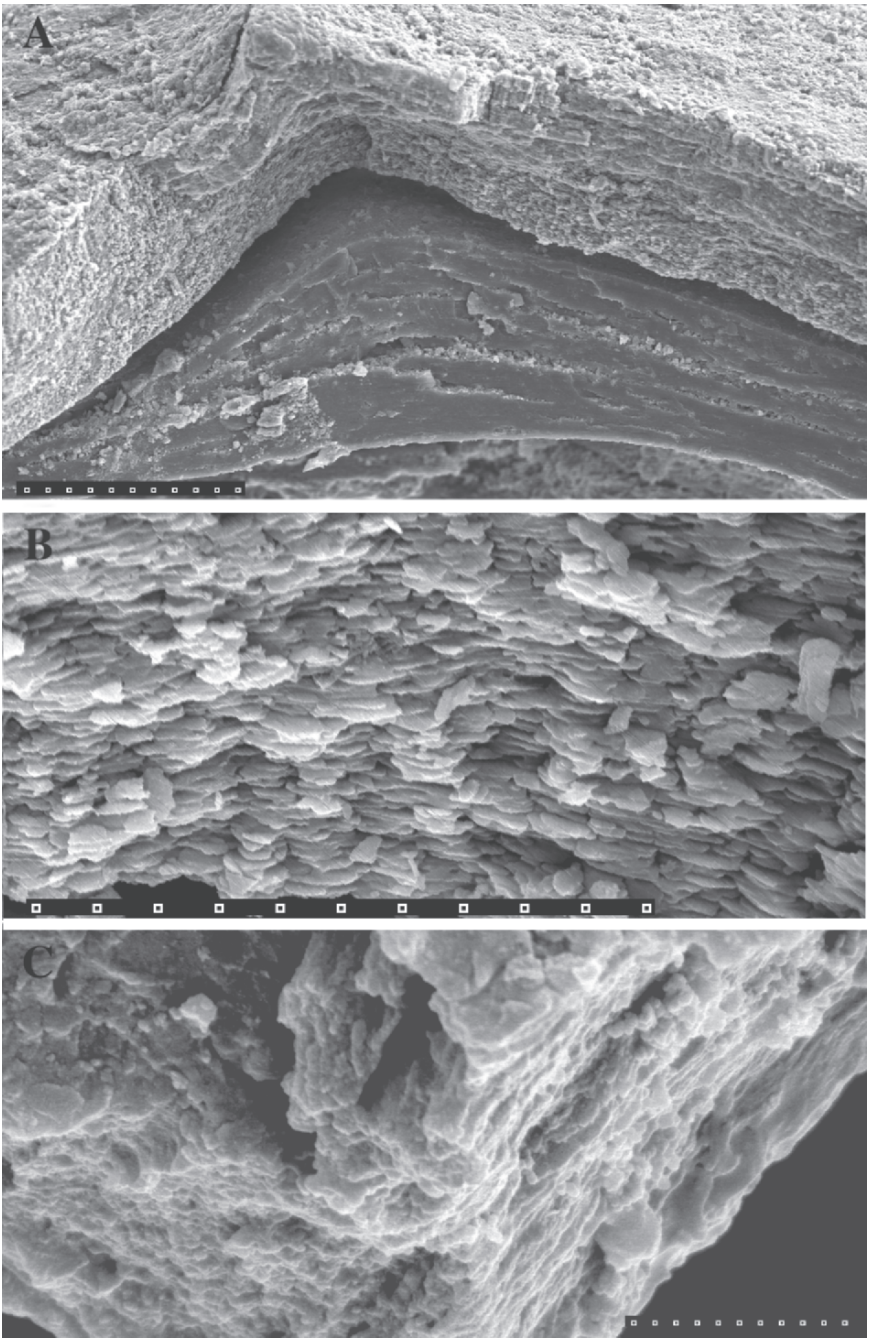

Fig. 11.2A–C Austrotrachyceras *sp. A, B. NHMW 2005z/0006/0002. C. NHMW 2005z/0006/0003. A. Fracture of the shell showing the squeezed black material (bottom) in compressed body chamber (top). The lamination in the middle of the black material is supposed to represent the contact between the left and right sides of the fossilized mantle preserved in the squeezed body chamber. Scale bar = 60µm. B. Enlargement of the body chamber shell wall composed mostly of the nacreous layer. Scale bar = 10µm; C. Enlarged view of A showing the microlaminations in the black material. Scale bar = 1.2µm.*

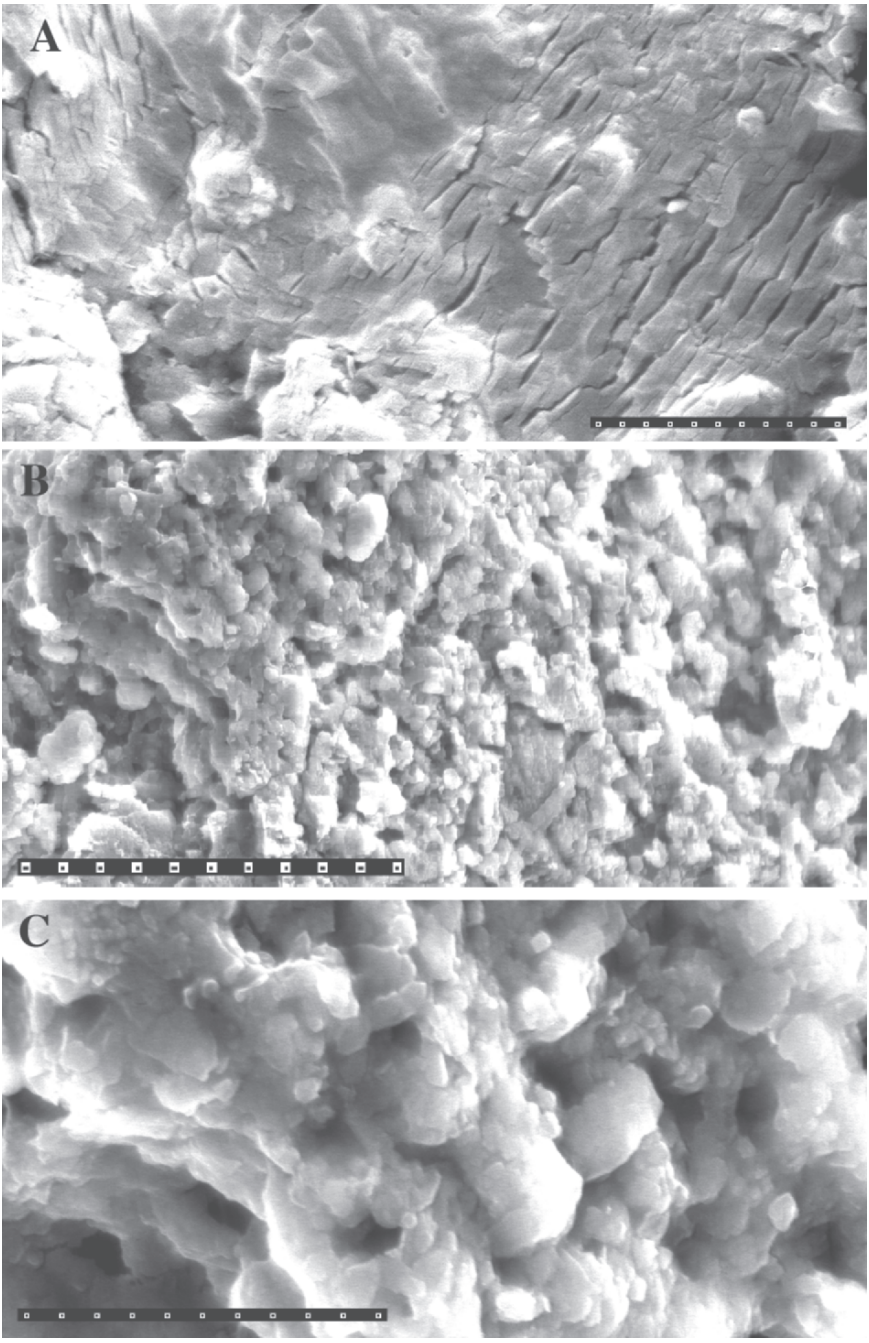

Fig. 11.3A–C Austrotrachyceras *sp., NHMW 2005z/0006/0004. A. Surface view of the black material (supposed fossilized mantle) showing microfractures possibly parallel to the muscle fibers. Scale bar = 3 μm. B. Piece of the mantle tissue showing porous surface. Scale bar = 12.0 μm. C. Enlarged view of B to show tubes perforated by pores. Scale bar = 3.0 μm.*

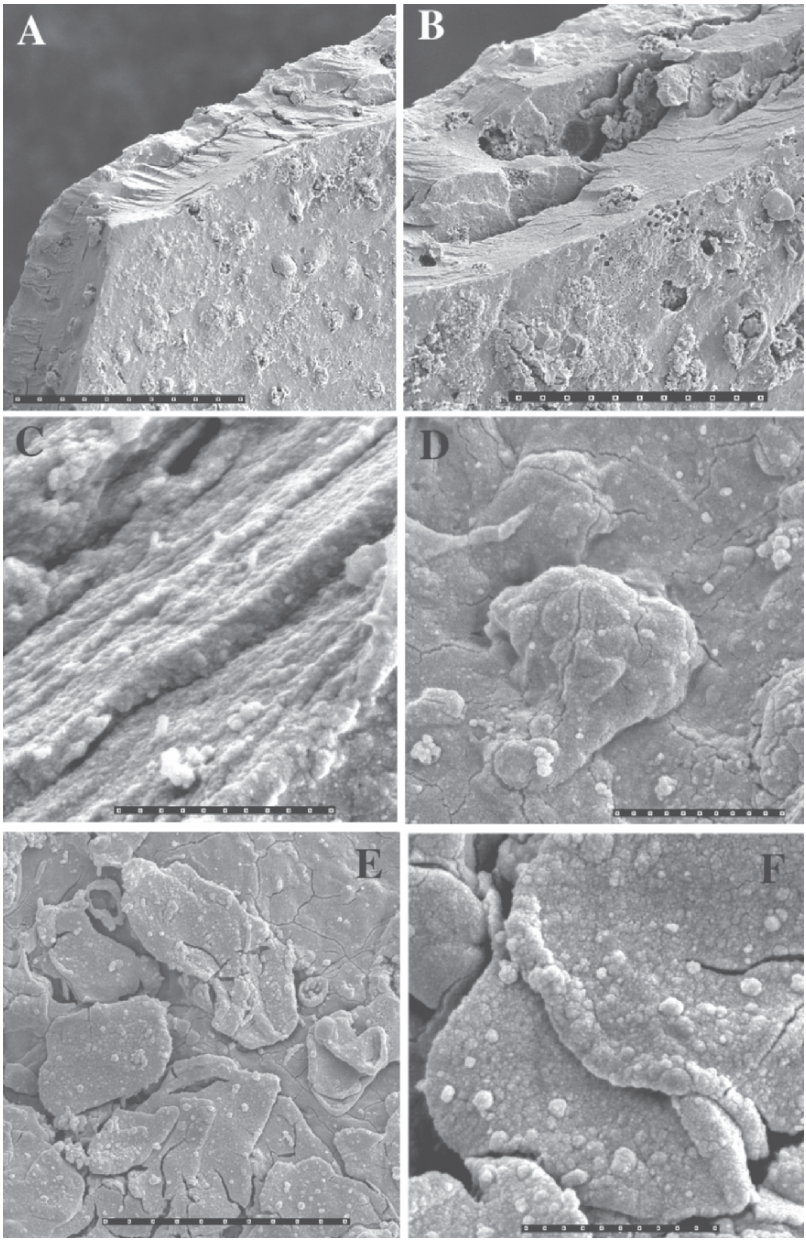

Fig. 11.4A–F Austrotrachyceras *sp., NHMW 2005z/0006/0001. A. Fragment of the black material from the body chamber showing its surface and fractures. Scale bar = 60.0 µm. B. Enlargement of A to show that the black material consists of the left and right portions separated by an interspace about midway between them. The interspace contains possible soft tissue debris. Scale bar = 30.0 µm. C. Fractured surface of the black material to show longitudinal microlamination. Scale bar = 1.2 µm. D. Irregularly shaped swollen structures on the surface of the black material supposed to be deformed soft tissue debris. Scale bar = 1.5 µm. E. Fragment of the black material (supposed fossilized mantle) to show that it was fractured into small broken pieces giving an impression of being originally composed of plastic organic material. Scale bar = 6.0 µm. F. Fractured and irregular plates as seen in E above. The plates have a granular surface. Scale bar = 1.2 µm.*

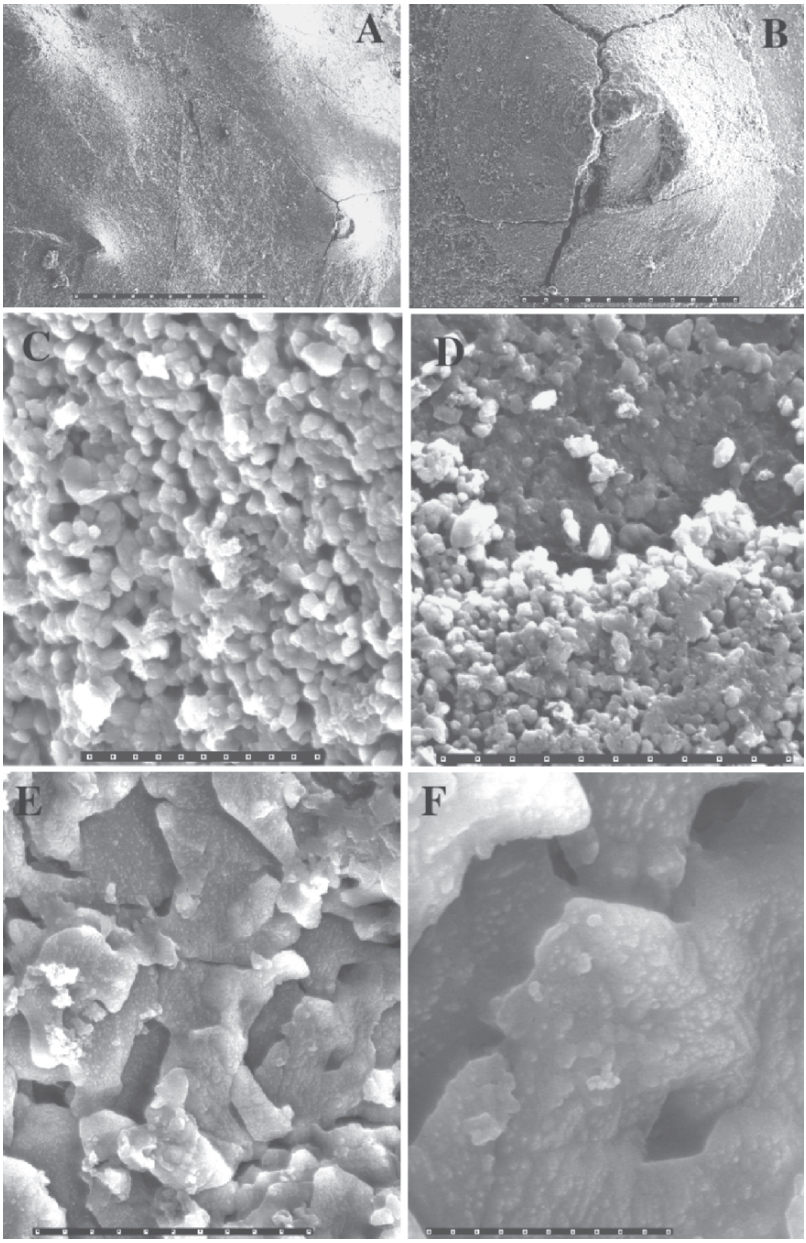

Fig. 11.5A–F Austrotrachyceras *sp., NHMW 2005z/0006/0009. A. Surface view on the exposed black material with the underlying shell wall of the body chamber bearing tubercles. Scale bar = 1.2 µm. B. Enlarged view of the black material coating the inner surface of the tubercle and forming the circular outline around its base. Scale bar = 0.3 mm. C. Porous globular ultrastructure of the black material on the conical surface of the tubercle. Scale bar = 6.0 µm. D. Enlargement of B to show the ultrastructural differences between the black material infilling the tubercle and lining the rest of the inner surface of the body chamber. The lighter material at the base of the photograph has a spherical ball-like globular structure while the upper darkened material has an irregular rodlike interconnected structure. Scale bar = 12.0 µm. E. Close up of the interconnected rodlike structures seen in D. Scale bar =6.0 µm. F. Detailed enlargement showing parts of the irregular rodlike structures and their granular ultrastructure. Scale bar = 1.5 µm.*

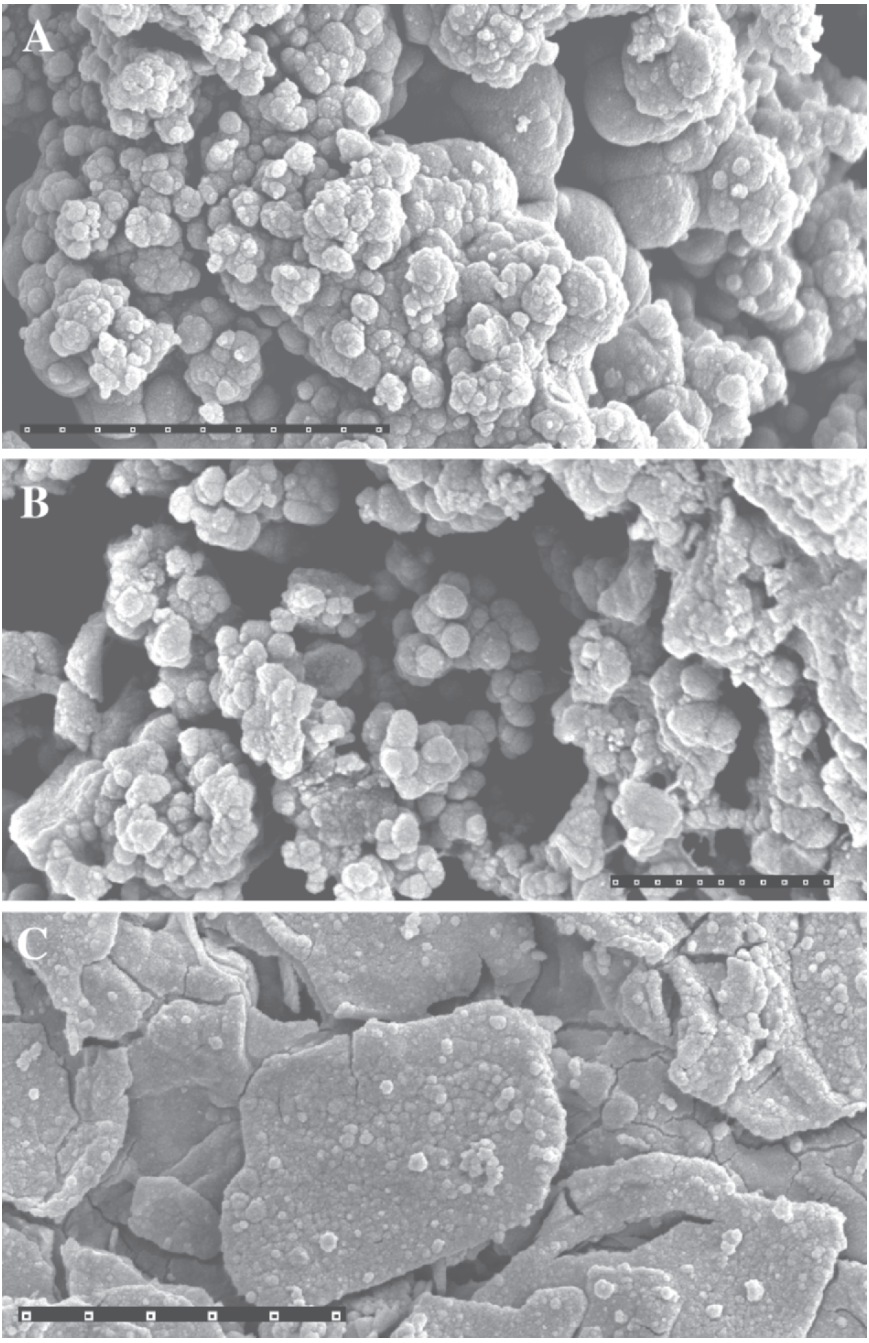

Fig. 11.6A–C Austrotrachyceras *sp. A. NHMW 2005z/0006/0002. View of the fractured black material in places where it consists of larger and smaller irregularly shaped and sized globular particles (supposed to be a mixture of organic debris preserved on the inner surface of the mantle). Scale bar = 3.0 µm. B. NHMW 2005z/0006/0001. View of the fractured black material in places where it consists of dispersed globules (central and left parts of the photo) that are similar in shape to described fossil and Recent ink of coleoids (also supposed to be an ink). Scale bar = 1.2 µm. C. Enlarged detail of Fig. 11.4E to show the granular ultrastructure of the fractured pieces of black material (supposed mantle). Scale bar = 3.0 µm.*

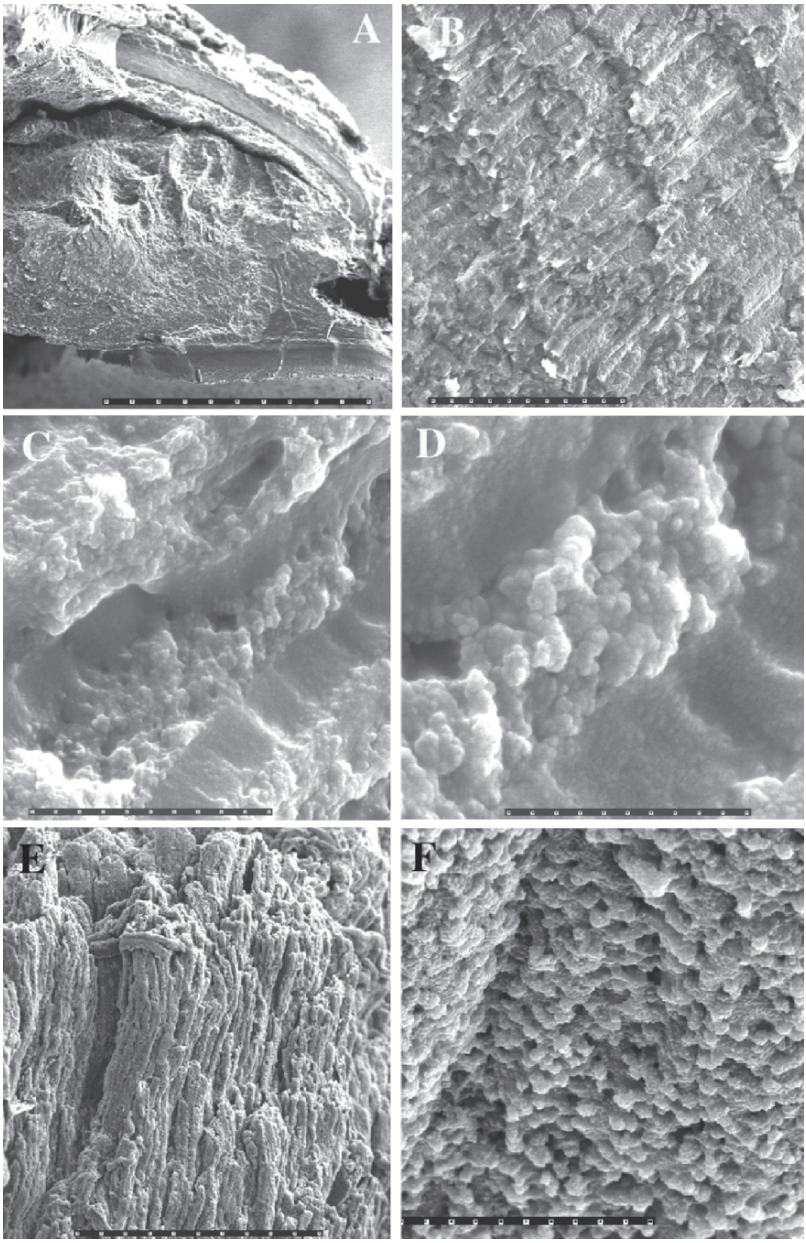

Fig. 11.7A–D *Modern squid* (Loligo) *after one year drying. A. Fracture of the buccal mass showing mandible and muscle preservation. Scale bar = 0.6 mm. B. Fibrous pattern of the buccal mass muscle seen in A, above. Scale bar = 30.0 μm. C. Enlarged view of B to show alternation of longitudinal and transverse muscle. Scale bar = 6.0 μm. D. Enlargement of C showing the transverse muscles with a globular surface bordered by longitudinal muscles with an almost smooth appearance consisting of smaller and less pronounced grains. Scale bar = 1.2 μm. E, F. Recent* Nautilus *after 20 years in 95% ethyl alcohol. Fibrous pattern of the muscular mantle. Scale bar = 120 μm. F. Enlarged view of the muscular mantle showing the interconnected globular ultrastructure with each globule having a granular surface. Scale bar = 12.0 μm.*

and calcium indicates that neither pyrite nor calcite is of importance as preservational elements in this substance. Even more significant is the lack of phosphorus. Many soft tissues in fossil coleoids are commonly replaced by phosphorus in the form of apatite. The lack of this element indicates that the preservation of the muscular mantle tissue and possible ink is not controlled by a phosphorus rich medium.

To summarize, the black substance (1) is restricted to the body chamber and is absent in the chambers of the phragmocone, (2) consists of the left and right sheets that are almost fused but separated by an indistinct interspace containing dispersed organic material, (3) exhibits in places both fine laminations, (4) a fibrous ultrastructure in each lamina, and (5) consists predominantly of carbon. The interspace between the two sheets of the black substance contains isolated agglomerations of tiny globules (ca. 0.1–0.4 μm in diameter); each globule consists of smaller particles. The globule agglomerations lack laminations, fibrous patterns, or any other discernable organized arrangement and are interpreted to be fossil ink. The fine laminations and fibrous ultrastructure of the black sheets, in combination with the high carbon content, are known to be the principal characters of fossilized muscular mantle material. The morphological, ultrastructural, and chemical features listed above allow the interpretation that the sheets of black substance are the bituminous remnants of the mantle squeezed within the compressed body chamber so that their left and right sides became nearly fused during compaction. Due to the fusion of the two portions of the mantle, the dispersed fragments of soft body tissues and organs seem to be partly preserved in the interspace between the sheets. It is likely that the ink sac was ruptured, and ink was dispersed throughout the body cavity and into the mantle tissues. This would explain the dispersed nature of the isolated agglomerations of tiny globules, which are typical of the ultrastructure of ink in other fossil and modern cephalopods. Our observations and conclusions are based on a limited number of specimens. The possible occurrence of ink in ammonoids is an important paleobiological discovery with many implications for the life mode and biology of this extinct group of animals. Previous suggestions that ammonoids had ink have been rejected as inconclusive. However, based on the ultrastructural evidence presented above, we suggest with reservations that it is possible that some ammonoids may have had ink and that it was used as a defensive mechanism. Thus, Lehmann's (1967) report of the occurrence of ink in some ammonoids should not be rejected, and additional specimens should be sought to confirm or reject this possibility in at least some ammonoids.

The replacement of the soft tissues in *Austrotrachyceras* by carbon is probably the result of the metabolism of carbon-accumulating anaerobic bacteria that replaced the organic fibers in the mantle by the globular granules of carbon during the slow fiber decay. The case for slow decay can be supported since the bottom environment in the sediment at and below the sediment/water interface at that time is assumed to be of low oxygen content (Griffith, 1977), and if this was the case, anaerobic bacteria would have been the dominant biological breakdown agent. Additionally, the removal of other chemical constituents other than carbon

was probably promoted by liquefying the body tissues and organs by bacterial action, hydrostatic and lithostatic pressures with pore fluid movement, and chemical reactions within the mud surrounding the ammonoid body and shell during diagenesis.

The depositional environment of the Lower Carnian Trachyceras Shale in the Lower Austrian Alps and that of the Posidonia Shale at Holzmaden (both have yielded numerous coleoids with preserved soft parts) was previously believed to have been similar (Seilacher, 1982). However, the EDS analysis of the soft tissues of the cephalopods from both localities does not completely support this depositional environmental interpretation (Doguzhaeva et al., 2004b). In contrast to the carbon-dominated preservation of the soft tissues in the ammonoid *Austrotrachyceras* from the Trachyceras Shale, the soft tissues in the coleoids preserved in the Holzmaden Shale are replaced by phosphorus in the form of phosphate minerals. The geochemical conditions that supported soft tissue preservation by carbon coating and/or carbon concentration by distillization versus phosphate replacement and/or coating have not been precisely determined. However, even though both environments are interpreted to have been a low oxygen environment, the pH of the sediment and pore water in which the dead cephalopods were encased was probably very different in the two shales.

5.2 The Mandible Ultrastructure

EDS analysis on one specimen demonstrates that the mandibles have the following chemical composition in percents of the total weight: C (58–53%); O (30%); S (2%); Si (1–5%); Fe (1–2%), and Ca (less than 1%). The lack of significant amounts of iron and calcium indicates that neither pyrite nor calcite is an important preservational element in these fossils. Even more significant is the lack of phosphorus. Many soft tissues in fossil coleoids and the chitinous mandibles of all fossil cephalopods are commonly replaced by phosphorus in the form of apatite (for examples, see Dagys and Dagys, 1975; Mapes, 1987). However, the EDS data indicate that replacement by apatite or any other phosphorus mineral has not taken place in *Austrotrachyceras*. Thus, the preservation of the mandibles in these ammonoids is by concentrated carbon. For the ultrastructural comparison, the mandibles of modern squid (*Loligo*) were studied with SEM (Fig. 11. 8E, F).

Most mandible studies have utilized standard light microscopy for the descriptive analysis. The only study we are aware of utilizing SEM analysis on

Fig. 11.8A–F (continued) *after one year drying. E. Broken surface of a longitudinal fracture showing the steplike conchoidal fracture surface; faint laminae are present. Scale bar = 60.0 μm. F. Enlargement of the fracture surface of the mandible showing a faint granular texture. Blob with fractures near the center is a SEM "burn" showing that the organic material is very sensitive to even short term exposure of the electron beam. Scale bar = 6.0 μm.*

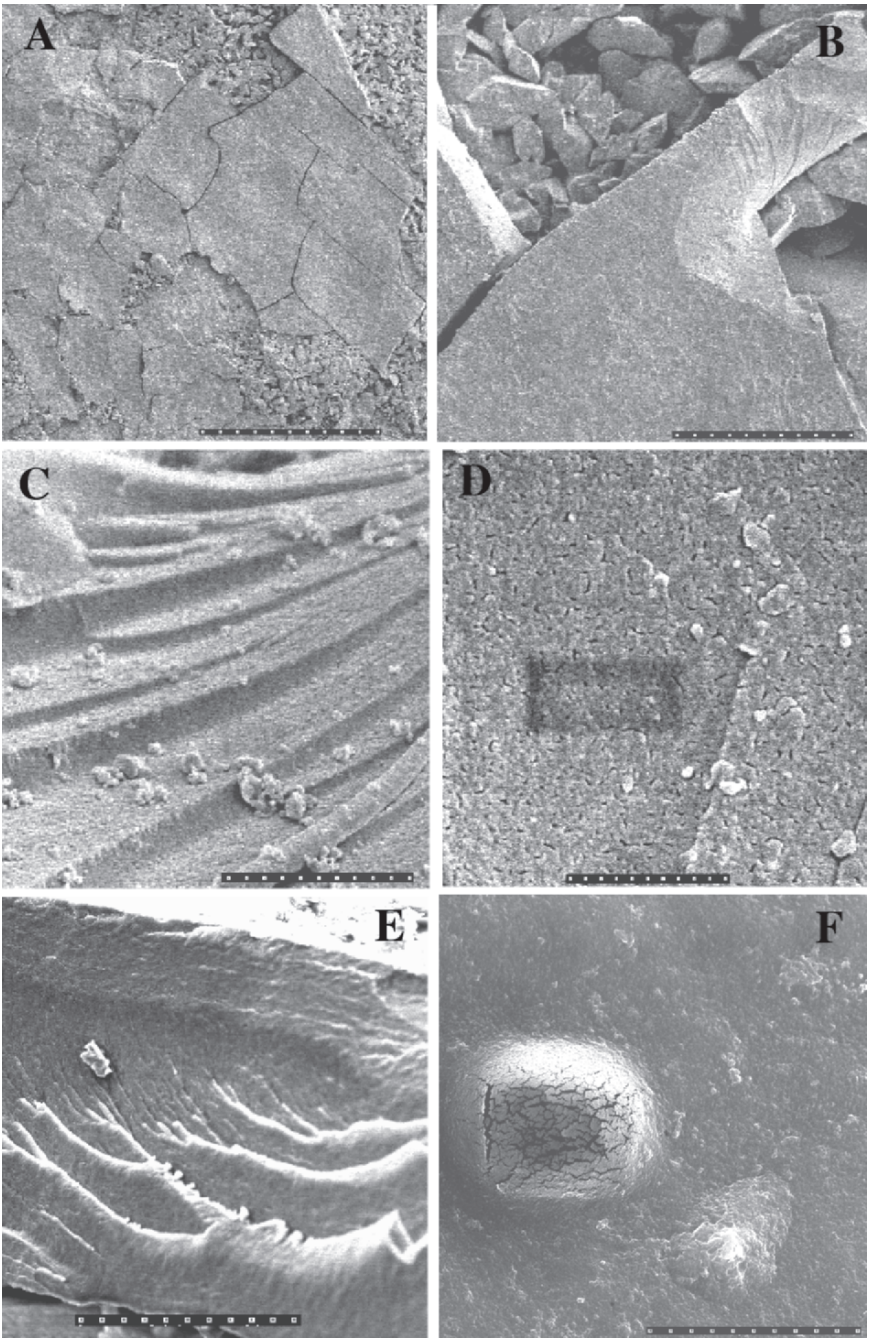

Fig. 11.8A–F *A–D.* Austrotrachyceras *sp. NHMW 2005z/0006/0014, mandibles. A. Mosaic fracture pattern of the mandible. Scale bar = 0.3 mm. B. Enlarged detail of A showing the conchoidal fracture surface. Scale bar = 30.0 µm. C. Enlargement of the fracture seen in B showing the stepped fracture surface. Scale bar = 3.0 µm. D. Fracture surface showing the ultrastructure of microporosity of small microslits. Scale bar = 1.5 µm. E, F. Modern squid* (Loligo) *mandibles*

ammonoid mandibles is the present report. It could be concluded that the original material was organic and that the carbonization had taken place to preserve the mandibles in situ.

5.3 The Shell Ultrastructure

The nacreous layer forms the main bulk of the shell wall in the body chamber of this genus of ammonoid and these layers give a bright iridescent luster to the shell. SEM analysis on one specimen demonstrates that the shell material is composed of nacreous plates and that the shell is well preserved and retains its original ultrastructure despite having been extensively crushed by diagenetic forces (Fig. 11.1 A, D).

EDS analysis demonstrates that the body chamber wall has the following chemical composition in percents of the total weight: C (6–8%); O (37–41%); and Ca (42–48%). In places, no trace elements were detected. This indicates that the shell is extremely pure calcium carbonate, which is most probably in the form of aragonite. In addition, the lack of trace elements indicates that the specimen has undergone virtually no replacement during fossilization. This then supports the conclusion that the entire animal, including the shell, mandibles, muscular mantle tissue, and the possible ink are not produced by chemical introduction from outside the specimen.

6 Conclusions

In summary, despite the diagenetic crushing of the shells, the preservational condition of the specimens is outstanding. The presence of the mandibles in life position indicates that the soft body was partly retained within the body chamber of some ammonoid specimens when the animal fell to the ocean bottom after death. Burial must have been rapid to preserve the body and jaws of the ammonoid within and in front of the shell, respectively. Preservation of the mantle, possible ink, and fragments of the internal organs between the two sides of the preserved muscular mantle began immediately after burial. Carbonization of the tissues by bacteria had already begun before the ammonoid shell was crushed. Crushing brought the mantle coatings on the left and right sides of the body chamber in contact. The fossilization process of carbonization continued to completion after crushing. Based on the pristine condition of the shell nacre in the body chamber and the EDS data, these ammonoid specimens with their preserved soft and hard tissues remained sealed from additional alteration by bacteria, pore water migration, weathering, and other geologic events until they were excavated more than 100 years ago. Given the preservation of the soft tissues in an externally shelled cephalopod and the rarity of such discoveries over the past 200 years of cephalopod fossil research, one must consider the preservation of

muscular mantle tissue, possible ink, and mandibles that are carbonized and not replaced, as a truly extraordinary occurrence.

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