Chapter 6
A Late Carboniferous Coleoid Cephalopod from the Mazon Creek *Lagerstätte* (USA), with a Radula, Arm Hooks, Mantle Tissues, and Ink

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1   Introduction

In the light of the current scanty knowledge of their origin and early evolutionary history, and our inadequate understanding of the higher-level phylogenetic relationships of the Coleoidea, any Carboniferous shell, which might have belonged to a coleoid cephalopod, is of exceptional interest. This report describes two relatively small (total shell and cephalic area is about 64 mm long in one specimen) cephalopod fossils from the Mazon Creek *Lagerstätte* (Middle Pennsylvanian – Desmoinesian) in Illinois, USA: specimen FMNH PE 32521 (Saunders and Richardson, 1979:

Fig. 9a, b, d) and specimen FMNH PE 20808; the latter as a gift to the Field Museum of Natural History by the collector David Young. Specimen PE 32521 originally was referred by Saunders and Richardson in 1979 to the only known Carboniferous non-rostrum-bearing coleoid *Jeletzkya douglassae* Johnson and Richardson, 1968. The diagnosis of the holotype of *J. douglassae* was based mainly on a moderately well-preserved crown of ten arms and a small, poorly preserved phragmocone. Johnson and Richardson (1968) interpreted this specimen as the earliest known teuthid. This assignment was questioned by Gordon (1971), who was convinced that the disposition of the arm hooks in pairs pointed to a belemnitid-phragmoteuthid affinity. In 1994, Doyle et al. in their "Phylogeny and Systematics of the Coleoidea," considered *Jeletzkya* as a taxon of undetermined status.

In contrast to the holotype of *J. douglassae*, the two specimens [PE 32521 and PE 20808 described by Saunders and Richardson (1979) from the Mazon Creek reexamined herein with SEM] each has a moderately well-preserved shell, but lacks clearly outlined tentacles. The lack of tentacles has been an insurmountable obstacle to the reconstruction of the arm crown and has hindered comparison of all other Mazon Creek and other coleoids recovered in the Upper Paleozoic with *J. douglassae*. Reexamination of these two specimens reveals new crucial data on the morphology of the coleoid shell and radula, presence of arm hooks, muscular mantle tissue, and traces of ink. These data, as well as those in the presently known diverse Carboniferous phragmocone-bearing coleoids (see Doguzhaeva, 2002c; Doguzhaeva et al., 2003 for summary) favor a reevaluation of the systematic placement of the specimens under discussion. These specimens are redescribed as *Saundersites illinoisiensis,* g. and sp. n., and the new genus is placed in the family Donovaniconidae (Doguzhaeva et al., 2003). This is the only coleoid family known to combine a moderately breviconic shell, a long body chamber, a short phragmocone, a short proostracum-like structure, and a substantial ink sac. This family is placed in the new order Donovaniconida, ord. n.

With the erection of *Saundersites illinoisiensis,* g. and sp. n., additional information is made available to evaluate the morphological plasticity and evolutionary trends of Carboniferous coleoids.

2   Studied Material, State of Preservation, and Methods

We have been able to borrow three specimens (FMNH PE 32521, PE 20808, and PE 28955) of the six specimens assigned to *Jeletzkya* by Saunders and Richardson (1979). One of the specimens (?*Jeletzkya douglassae* Saunders and Richardson, 1979: Fig. 10, PE 28955) appears to have been assigned to the Cephalopoda erroneously. Specimen PE 32521 (Saunders and Richardson, 1979: Fig. 9 a, b, d) preserves the arm hooks and an unusual radula structure. In addition, this specimen shows remnants of muscular mantle and probable ink that were not observed previously. The specimen PE 20808 shows a well-preserved adoral projection. In

both specimens the shell has a similar gross morphology and size. However, in neither fossil is the shell material preserved.

Specimen PE 32521 (Fig. 6.1A, B) shows its ventral side on split halves of a medium-sized, flat, brownish ironstone concretion. The shell is weakly compressed because of compaction. It has a triangular shape, with a pointed adapical end and almost straight sides. It consists of a proostracum-like structure, a body chamber, phragmocone, and an irregularly calcified rostrum. A radula is situated approximately in the middle of the length of the proostracum-like structure (Figs. 6.2–4). More than 20 arm hooks are preserved in front of the shell aperture, and most are more-or-less randomly dispersed (Figs. 6.5, 6), except in two cases where they occur in pairs. It is not possible to reconstruct the arm crown from the arm-hook distribution. Most of the hooks are exposed in cross, or longitudinal sections, but some show their sides and provide details of their gross morphology. The outer surface of the body chamber bears a dispersed black substance that SEM study suggests is probably ink (Fig. 6.7C, E). SEM analysis of the material bordering the body chamber and excavated from the middle of its length revealed numerous soft-tissue debris (Fig. 6.7A), some of which presumably belonged to the muscular mantle (Figs. 6.8–10). Specimen PE 20808 is also exposed on its ventral side and shows a nearly complete proostracum-like structure.

Initially, both specimens were examined under a dissecting microscope (x7 to x35 magnification) under alcohol. In specimen PE 32521, the structure of the radula, arm hooks, presumed ink, and muscular-mantle tissues were examined with SEM. To prevent destruction while making the SEM preparation, the specimen was trimmed from the concretion as part of a slab about 10 mm thick. The length of the slab (about 80 mm) was much longer than typical SEM preparations (usually 10–20 mm). To diminish charging that could occur under high voltage in the SEM, the opposite side of the slab was coated with colloidal silver.

The occurrence of fossilized ink in specimen PE 32521 was revealed by SEM examination of the black material on the surface of the specimen and by comparison with the previously studied ink and other kinds of organic substance in present-day and extinct cephalopods (Doguzhaeva et al., 2002b, c, 2003, 2004a, b, c; Doguzhaeva and Mutvei, 2003, 2005). The characteristic structure of the ink was compared with the structure of the sediment in the concretion around the specimen. In order to detect fossilized ink substance in specimen PE32521, pieces of dark material were sampled from the shell surface. In order to display presumed mantle remnants, tiny pieces (less than 5 mm in size) were removed from the groove between the shell and the sediment. For their SEM analyses, the selected fragments of the specimen were coated with gold. The same pieces also were used for EDAX analysis to determine the chemical composition and diagenesis of the presumed muscular mantle debris and ink during fossilization. For EDAX analysis seven spectra were taken, four from the remnants of soft tissue and ink and three from the sediment.

SEM and EDAX analyses were carried out with Hitachi S-4300 at the Swedish Museum of Natural History, Stockholm.

The studied material is reposited at the Field Museum of Natural History in Chicago, USA (FMNH PE 32521, PE 20808, and PE 28955).
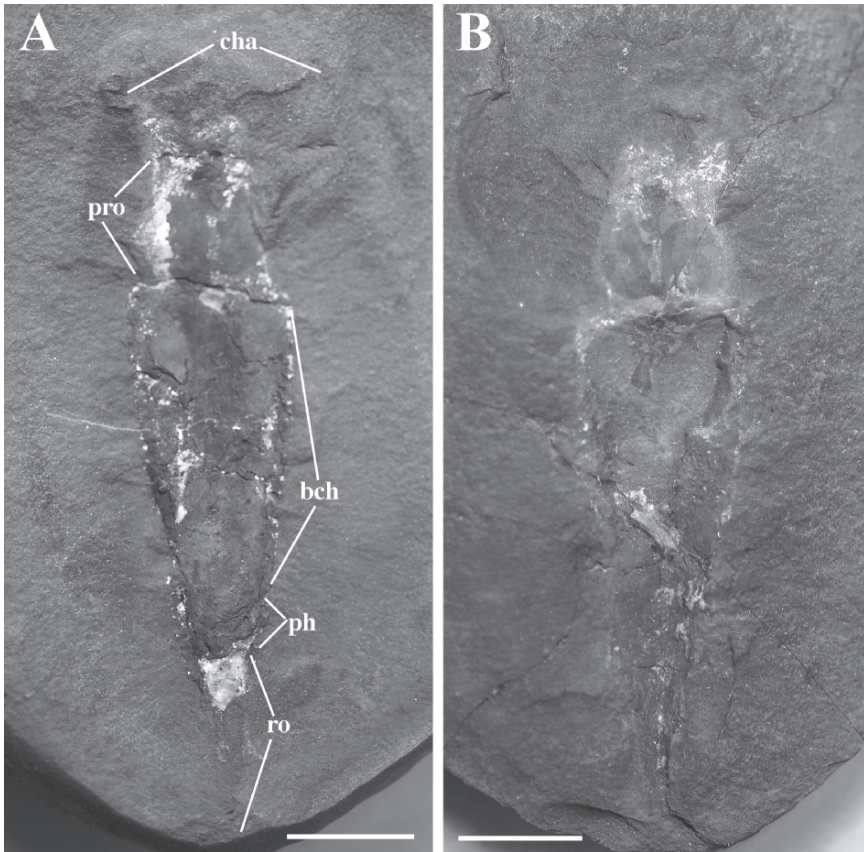
Fig. 6.1A, B. Saundersites illinoisiensis *g. and sp. n., PE 32521. General view (A – part and B – counterpart) shows the cephalic area (CHA), proostracum like structure (PRO), body chamber (BCH), probable phragmocone (PH), and probable rostrum (RO), Upper Carboniferous, Middle Pennsylvanian, Desmoinesian (Westfalian D), Francis Creek Shale, Mazon Creek, northwestern Illinois, USA. Scale bar is 1 cm.*
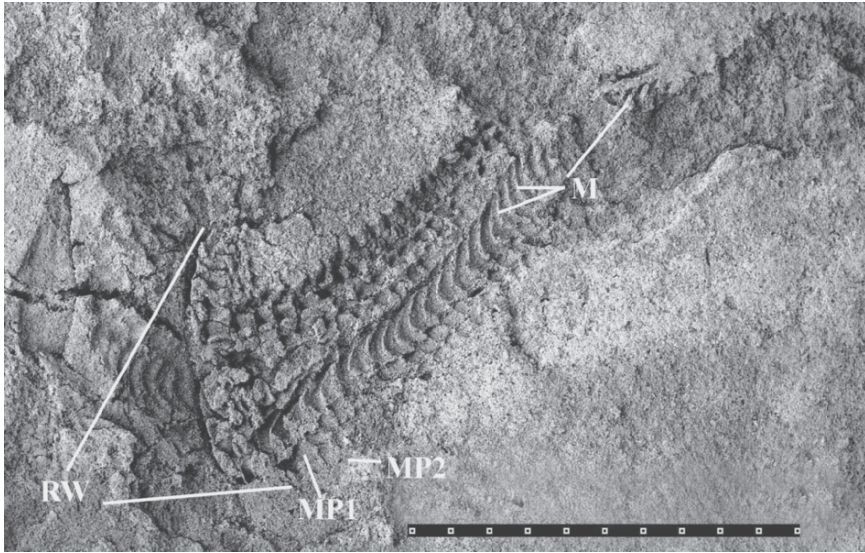
3   Comparative Morphology

3.1   Shell

3.1.1   Morphology

The shell length in specimens PE 32521 (Fig. 6.1A, B) and PE 20808 is 56 mm and 46 mm, respectively, and the maximum diameter is 12 mm and 14 mm, respectively. In both specimens the shell has a narrow triangular shape with an apical angle of approximately 12°–15°. The shells appear to be exposed from the ventral side.
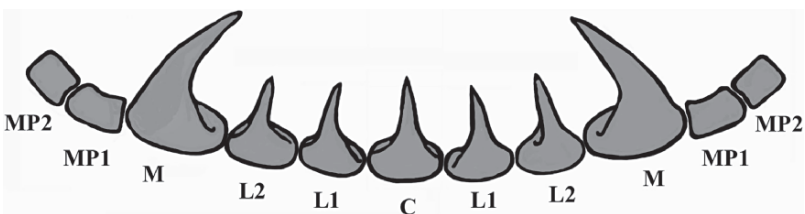
Fig. 6.2 Saundersites illinoisiensis *g. and sp. n., PE 32521. General view of a radula showing the approximate radula width (RW) and longitudinal rows of two marginal plates on each side (MP1, MP2) and marginal teeth (M). Scale bar is 1.25 mm.*

Four portions can be distinguished in each shell. The most adoral portion forms a plate on the apparent dorsal side of the shell. The length of this plate is about one-fifth of the total shell length. In PE 32521, the anterior and lateral margins of this plate are fractured, and the surface of the plate is uneven due to compression. In PE 20808, the adoral plate is well preserved and shows a slightly forward curved, broadly rounded anterior margin. Its surface shows growth lines parallel to the anterior margin. Because it is developed only on one side of the shell the anterior plate is here interpreted as a proostracum-like structure. The middle portion of the shell is here interpreted as the body chamber. In both specimens, it is three times longer than the proostracum-like structure. It has a rounded cross section that is slightly compressed in PE 32521. As in all other cephalopod shells from the Mazon Creek area (Richardson and Johnson, 1971; Saunders and Richardson, 1979), the shell material is not preserved. The third portion, immediately apical of the body chamber, can be clearly distinguished from the rest of the shell, because, in PE 32521, it is completely filled and, in PE 20808, partially filled with white calcite and has a sharp boundary toward the middle portion (the body chamber) of the shell. The length of this portion is about one-sixth of the total shell length. It is here interpreted as a phragmocone, although septa cannot be clearly distinguished. Because the phragmocone is short (one-sixth of the shell length only), it could have been truncated during the lifetime of the animal. The most apical portion of the shell is a narrow, short structure that in each specimen shows irregularly shaped longitudinal ridges. This portion is here interpreted as a partly calcified, partly organic rostrum. It is interesting to note that, in
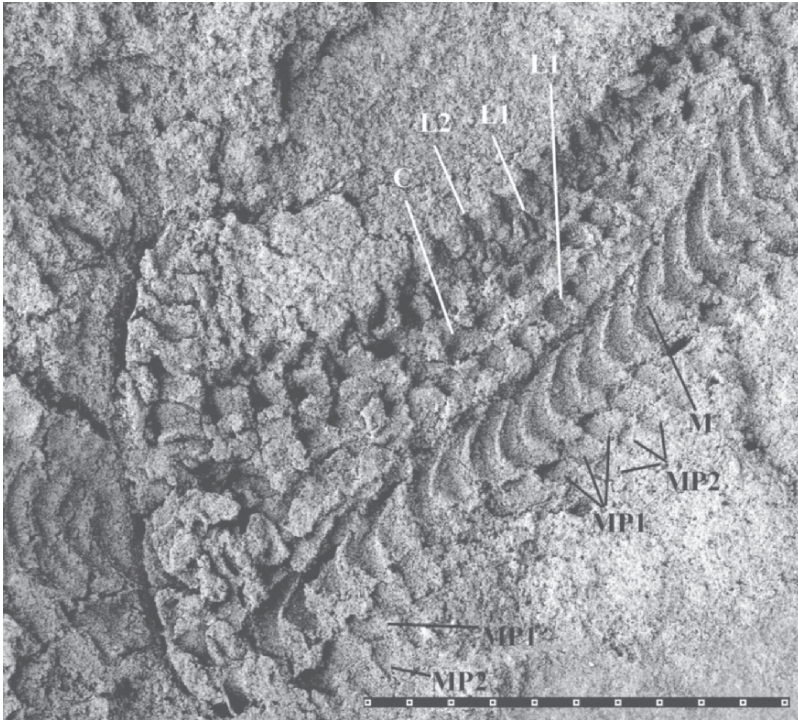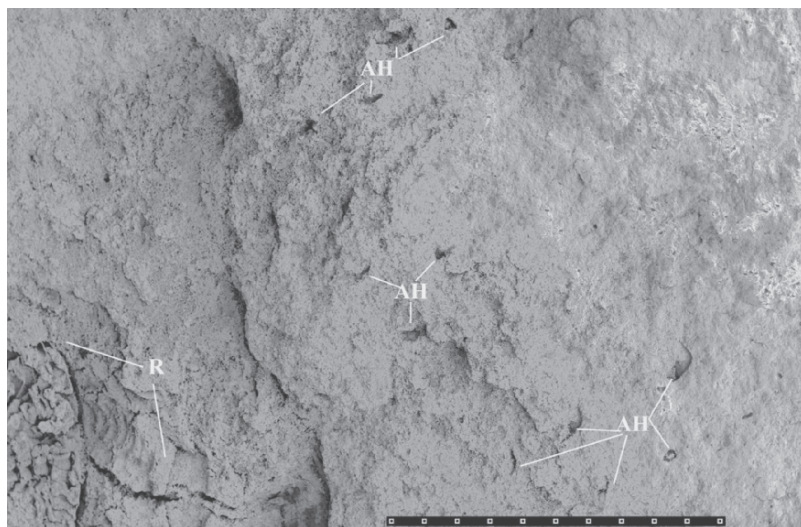
Fig. 6.3 Saundersites illinoisiensis *g. and sp. n., PE 32521. Enlarged detail of Fig. 2. The anterior portion of the radula shows two rows of marginal plates (MP1, MP2), a row of well exposed marginal teeth (M) that have a broad basal part, two rows of lateral teeth (L1, L2), which are partly preserved, and a row of central teeth (C) of which only the tips are exposed. Scale bar is 1.25 mm.*

Fig. 6.4 Saundersites illinoisiensis *g. and sp. n., PE 32521. Model of a radula with 11 elements in each transverse row: on each side of the central tooth (C) there are two lateral teeth (L1, L2), a marginal tooth (M), and two marginal plates (MP1, MP2).*

these two Mazon Creek specimens, the apical portion of the phragmocone and rostrum shows certain similarities to those in the Early Carboniferous coleoid *Hematites* Flower and Gordon, 1959 (Doguzhaeva et al., 2002a: Fig. 6.4; pl. 7, Figs. 1, 2). In specimens of this genus, the apical portion of the phragmocone that is totally

Fig. 6.5 Saundersites illinoisiensis *g. and sp. n., PE 32521. Arm hooks (AH) preserved in front of the radula (R, left bottom corner). Two hooks with tips turned to the left show their general shape (right bottom corner). Other hooks, exposed in cross section, demonstrate that they are hollow and have a thin, originally organic wall. The hooks are arranged in pairs and in longitudinal rows. Each division of the scale bar is 0.5 mm.*

surrounded by the rostrum is almost always truncated, and the internal ultrastructure of the rostrum suggests that it was constructed of both organic and calcified material. In addition, the surface of the rostrum of specimens of this genus has longitudinal ridges that vary in size and spacing.

3.1.2 Comparison

From the Desmoinesian deposits of the Mazon Creek *Lagerstätte*, Saunders and Richardson (1979: Fig. 1d) illustrated an orthoconic shell and identified it as *Bactrites* sp. (specimen PE 25584). This shell is 52 mm long and ca 20 mm in diameter at the aperture. It has a long body chamber, seven short camerae in the phragmocone, a ventral marginal siphuncle, straight sutures, and an apical angle of about 20°. With the exception of this specimen, bactritoids have not been found in the Mazon Creek fauna. Assignment of this shell to *Bactrites* sp. is questioned herein, and its relationship to the studied specimen PE 32521 is left open. However, the overall lack of distinct morphological characteristics and the poor preservation of PE 32521 makes its taxonomic assignment to either the coleoids or bactritoids difficult, if not impossible.

Another comparable specimen of Desmoinesian age is the shell of the coleoid *Donovaniconus oklahomensis* Doguzhaeva et al., which also has a proportionally long, moderately breviconic body chamber, comparatively short phragmocone, and a short proostracum-like structure (Doguzhaeva et al., 2002b, 2003).
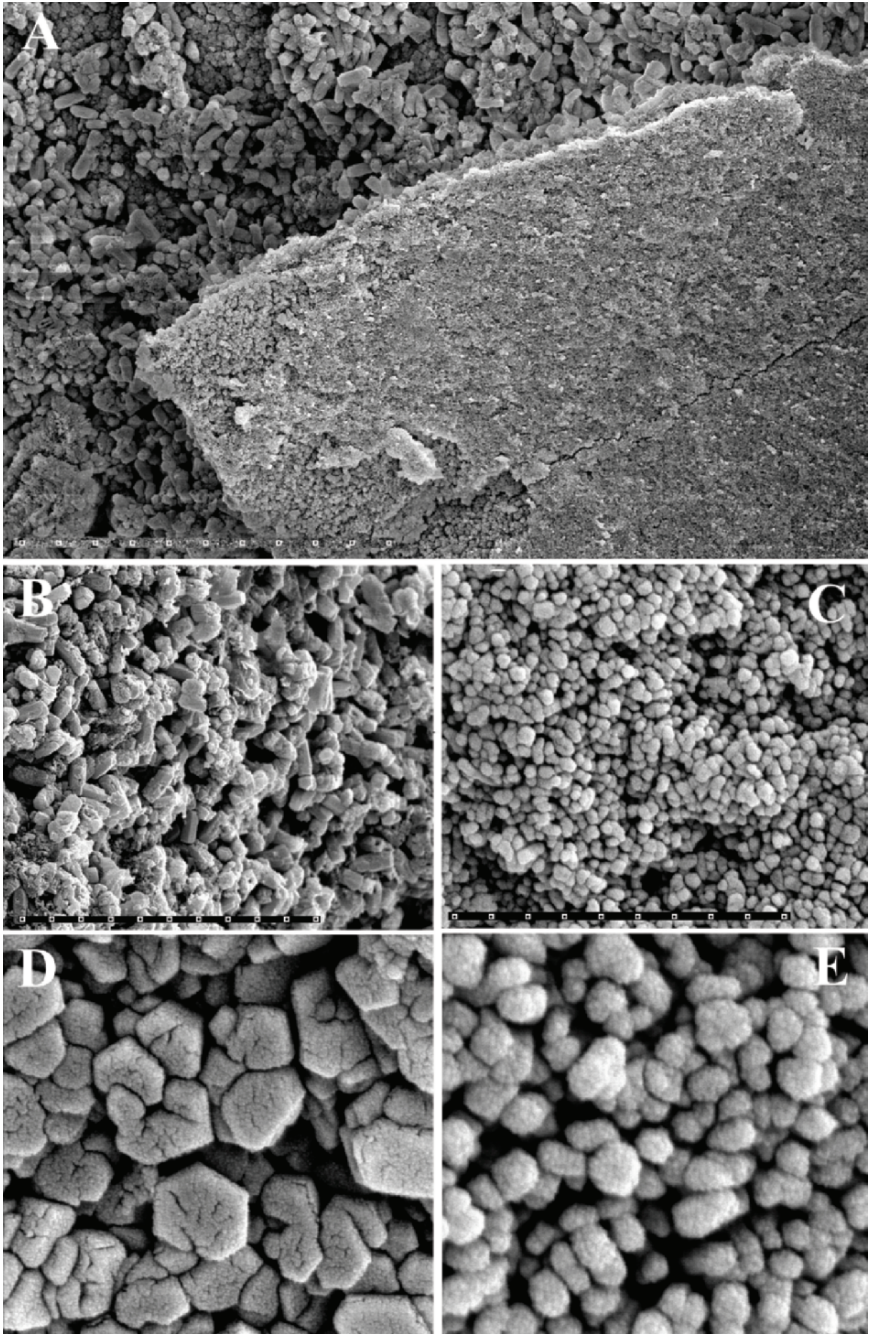
Fig. 6.6 Saundersites illinoisiensis *g. and sp. n., PE 32521. Enlarged detail of Fig. 5 (right bottom corner). Five arm-hooks (AH) are arranged in rows. Scale bar is 0.2 mm.*

3.2 Cephalic Remains

3.2.1 Radula

Morphology

In specimen PE 32521, a long portion of the radula (Figs. 6.2–4) and several dispersed arm-hooks (Figs. 6.5, 6.6) are preserved. The radula is located on the proostracum-like structure close to its margin. A few irregular ridges can be distinguished in front of the proostracum-like structure (Fig. 6.1A, B). Several arm hooks occur close to these ridges (Figs. 6.5, 6.6). It is probable that the ridges are impressions of the arms. To judge from the distribution of the arm hooks in front of the proostracum-like structure, the arms probably were short. Short arms also occur in the holotype of *Jeletzkya douglassae* (Johnson and Richardson, 1968: Figs. 1, 2). The radula is about 3.5 mm in length and 1.5 mm in width (Fig. 6.2). In front of the radula, there are two poorly preserved carbonaceous, triangular elements oriented transverse to the radula axis (Fig. 6.2). They may be poorly preserved remains of the jaws. About 30 transverse rows of the radula are visible; one side of the radula is better preserved than the other side. SEM examination shows that the radula has two marginal plates on each side; both are situated outside the marginal teeth, in contact with each other (right side of Fig. 6.3). The two marginal plates and the

Fig. 6.7 Saundersites illinoisiensis *g. and sp. n., PE 32521. A. A fragment of the soft tissue remnant from the external surface of the shell showing traces of ink substance and from the shaly sediment around it. Each division of scale bar is 3 μm. B, D. Two types of crystals in the shaly sediment surrounding the soft tissue remnants, enlarged details of A. Each division of scale bar is 1.2 μm and 0.12 μm, respectively. C, E. Globular ultrastructure of the ink, enlarged detail of A. Each division of the scale bar is 0.3 μm and 60 nm, respectively.*
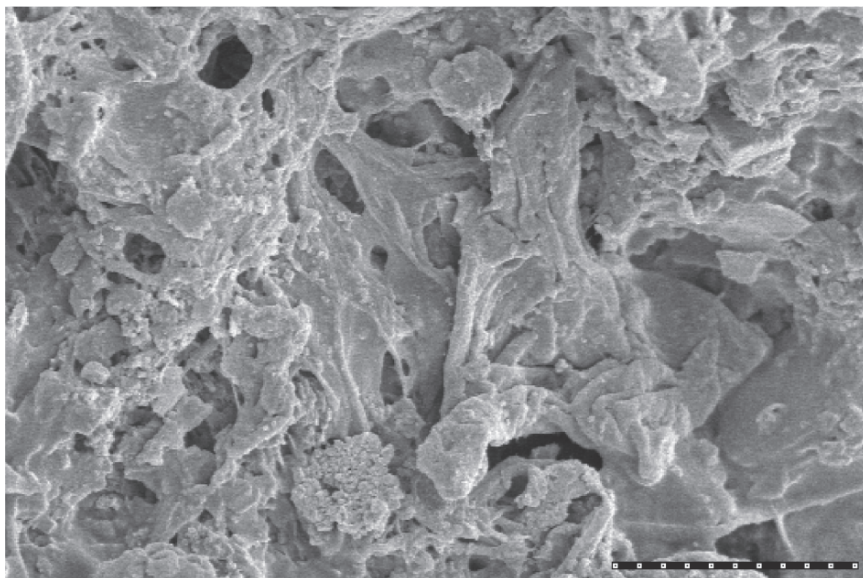
Fig. 6.8 Saundersites illinoisiensis *g. and sp. n., PE32521. General view of the fossilized soft tissue debris preserved on the shell surface. Each division of scale bar is 1–2 μm.*

large marginal tooth are distinct. The marginal tooth has a broad, semilunar shape in cross section; its basal portion, about one-third of the total height of the tooth, is massive; the rest of the tooth is pointed and curved backward; its sides form an angle of about 20°. The ratio between the height and maximum diameter of the tooth is ca 1:1. The central (or rachidian) and lateral teeth are poorly preserved and cannot be described in detail. This is particularly the case with the inner lateral tooth of which only indistinct remains can be seen. The radula formula is C L1 L2 M MP1 MP2 (11 elements in total) (Fig. 6.4).

Comparison

In present-day molluscs a radula of 11 elements in each transverse row is known in the class Monoplacophora (Starobogatov, 1990a). This class is considered a possible ancestor of the Cephalopoda (Yochelson et al., 1973). Two or more marginal plates along the periphery of the radula are known in the class Polyplacophora, and there are 17 elements in each transverse row (Ivanov and Sirenko, 1990; Starobogatov, 1990a, b).

In addition to the present specimen, several radulae have been recovered from Paleozoic cephalopods: (1) in an unidentified Late Ordovician orthocone the radula has five teeth in each transverse row; the radula configuration is more similar to that of ammonoids and coleoids than to that of nautiloids (Gabbott, 1999); (2) in the

Silurian orthocerid *Michelinoceras* the radula is reported to have seven elements in each transverse row (Mehl, 1984), but this report has been questioned (Nixon, 1988: 113); (3) two separately preserved radulae with 13 elements in each transverse row have been found from the Late Carboniferous (Desmoinesian) Mazon Creek deposits; they are described as *Paleocadmus herdinae* (Solem and Richardson, 1975) and *Paleocadmus pohli* (Saunders and Richardson, 1979) and have the radula formula: C L1 L2 M1 MP1 M2 MP2; both *Paleocadmus* radulae have two marginal plates on each side, but they are separated by a second marginal tooth; the similarity of these two Carboniferous radulae with the 13-element radula in present-day *Nautilus* suggests that there is a strong evolutionary stability of the radula with 13 elements in each transverse row; (4) radulae with nine elements in each transverse row are reported in the following Carboniferous goniatites: *Glaphyrites* (Closs and Gordon, 1966), *Cravenoceras* (Tanabe and Mapes, 1995) and *Girtyoceras* (Doguzhaeva et al., 1997).

Present-day coleoids and fossil ammonoids have either seven or nine elements in each transverse radula row (see Nixon, 1988). Individuals of these taxa each have a single marginal plate on each side. The occurrence of radulae with two marginal plates that are located outside the marginal tooth makes the radula structure in the coleoid specimen under discussion unique in the class Cephalopoda.

Evolutionary Development of the Radula in Molluscs

In present-day molluscs, the number of elements in each transverse row in the radula is different in different classes: Polyplacophora – 17, Monoplacophora – 11, Scaphopoda – 5, Cephalopoda – 13, 9, 7, or none, Gastropoda – variable (Ivanov and Sirenko, 1990; Ivanov and Starobogatov, 1990; Rossolimo, 1990). Starobogatov (1990a, b) concluded that radulae in monoplacophorans evolved through oligomerization and that the number of teeth was about 80 in Paleozoic genera instead of 11 in present-day monoplacophorans. The evolutionary reduction of the number of elements in the radula of monoplacophorans was believed by Starobogatov to have been caused by migration of these molluscs from the littoral zone, characterized by coarse substrate, to abyssal zones with soft substrate.

At present, it is uncertain whether the evolutionary transformation of radula elements in cephalopods occurred by oligomerization. The possible scenario is as follows: at early stages of coleoid evolution, the radula with 11 elements (seven teeth and four plates) was derived from the nautiloid radula with 13 elements (Nixon, 1988: Fig. 6.2e) by the elimination of the second marginal tooth. That resulted in a changed position of the two marginal plates to side by side, which is the case with the present specimen (PE 32521). At the next evolutionary stage, the two marginal plates fused into one plate, and as a consequence, the radula had nine elements per transverse row. Finally, the marginal plates became entirely eliminated, and a radula with seven elements in each transverse row was formed.

One can also assume that the radula possessing 11 elements in each transverse row (like that in the studied specimen) was inherited from the monoplacophoran radula, and that the radula of the studied specimen is similar to the archaic radula of

early cephalopods. In this case, the nautiloid type of radula, with 13 elements in each row, might have arisen from a radula with 11 elements by adding an additional marginal tooth between the two marginal plates on each side. The radula in present-day coleoids could have been formed by oligomerization of the two marginal plates.

3.2.2   Arm Hooks

Morphology

The hooks (Figs. 6.5, 6.6) are small (about 0.2–0.3 mm in length), shiny, hollow structures composed of black horny material. The shaft is short and thick. The distal part, extending from the maximum curvature to the tip, is well developed and long. The angle between the shaft and the distal part is about 90°. The cross section through the basal part is triangular.

Comparison

The arm hooks of the present specimen and the separately preserved hooks from the Mazon Creek area, illustrated by Saunders and Richardson (1979: Fig. 9c), show significant morphological differences. The separate hooks appear to be similar to the hooks seen in the holotype of *Jeletzkya douglassae*. They are bigger than those seen in the specimen studied here (ca 1.0 mm versus 0.2–0.3 mm, respectively). In addition, the shaft in each of the hooks of the holotype of *J. douglassae* and the hooks illustrated by Saunders and Richardson (1979: Fig. 9c) are thicker and swollen on the internal side, and the distal part is relatively shorter than those in the studied specimen.

   The hooks of the present specimen show some similarity to the hooks of the Lower Jurassic "fossil teuthid" *Loligosepia aalensis* Zieten (Doguzhaeva and Mutvei, 2003: Fig. 1c, d, e). In both, the shafts are short and thick, and the distal parts are long. The approximately 90° angle between the shaft and distal part is also similar. Both the Carboniferous and the Jurassic hook-specimens have cross sections that are triangular, and the ratio of wall thickness to hook diameter is 1:3.

3.3   Fossilized Soft-Tissue Remnants

3.3.1   Chemical Composition

In spite of significant ultrastructural differences between the fossilized soft tissues and the sediment around the shell (Fig. 6.7A–E), the EDAX analysis did not reveal noticeable differences in their chemical composition with the exception of a

slightly higher content of Si in the former. Both contain O, Si, Fe, C, Mg, and Ca, but have no P.
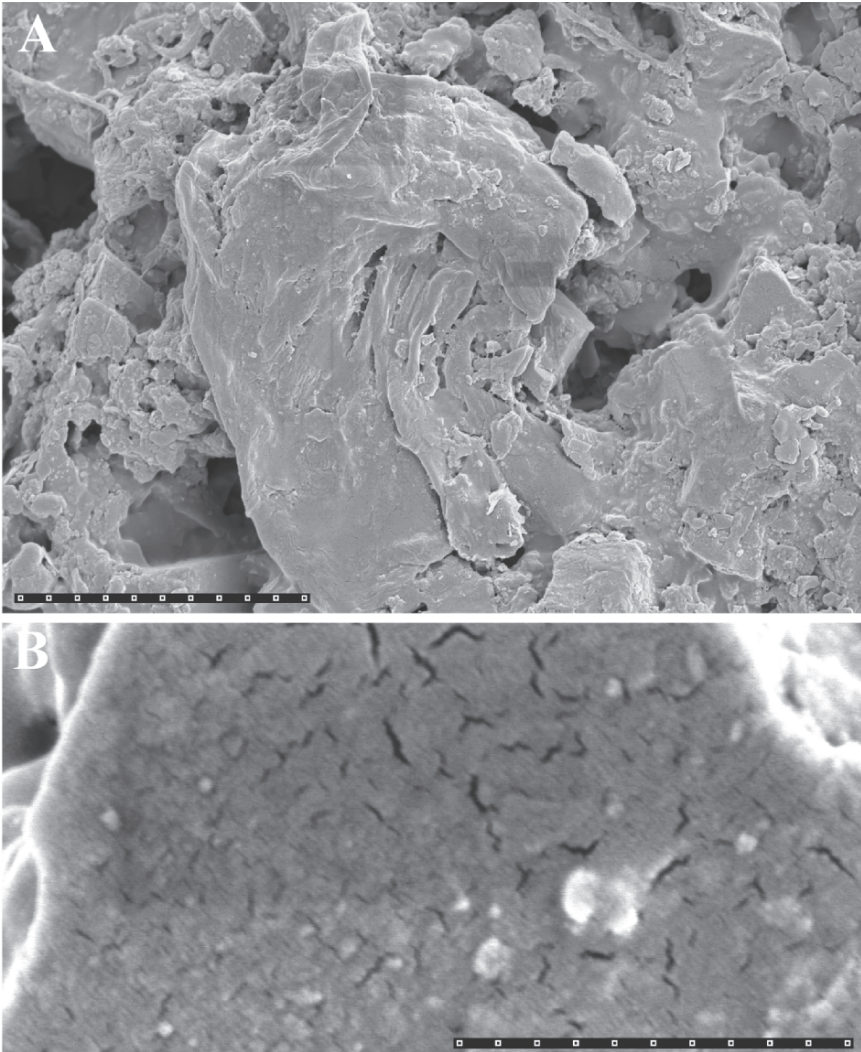
3.3.2 Muscular Mantle

Studies with SEM show that the material collected from the shell surface (Figs. 6.6, 6.7A) is porous and contains diverse microorganisms. It includes debris of plastically deformed (folded or rolled) material (Fig. 6.9). At higher magnifications (×10,000 to ×20,000), the material is seen to consist of numerous superimposed, sheets of irregular thickness. On the surface, these sheets are disrupted in numerous places and give the impression that they were exposed to strong tension during fossilization. The sheets exhibit distinct, parallel fibers about 0.1μm in diameter (Fig. 6.9B). The fibers have a fine granular ultrastructure, and they are arranged into bundles (Fig. 6.10A). The latter indicates that the sheets under examination represent a fossilized muscular mantle.

In some aspects, the mantle tissue of the Mazon Creek specimen is similar to the fossilized mantle in the Upper Triassic ceratitid *Austrotrachyceras* (Doguzhaeva et al., 2004c), but in other aspects it is also similar to the mantle in the Late Jurassic *Belemnoteuthis* (Owen, 1844) and the Early Jurassic squid-like coleoid *Loligosepia* (Kear et al., 1995; Doguzhaeva and Mutvei, 2003). The mantle in the ceratitid *Austrotrachyceras* (Fig. 6.11A) also has a sheet-like pattern (Doguzhaeva et al., 2004c: Fig. 6.4A) with a fine lamination and a fibrous ultrastructure (Doguzhaeva et al., 2004c: Fig. 6.2A, B), but it does not have the fibers arranged into bundles as in the squid-like *Loligosepia* (Doguzhaeva et al., 2004c: Fig. 6.6A, B). However the mantle in the Mazon Creek specimen has no distinct transverse striations formed by alternation of circular, longitudinal, and transverse muscle fibers. Therefore, the level of development of the mantle structure in the Mazon Creek specimen seems to have been somewhere between that in the less muscular mantle in ceratitid *Austrotrachyceras* and those seen with a more advanced mantle structure such as those in the squid-like coleoid *Loligosepia*.

In spite of a different chemical substitution during fossilization (phosphatized in soft-bodied squids from the Jurassic Oxford Clay, England (Allison, 1988), and *Loligosepia* from the Posidonian Schiefer, Holzmaden, Germany, bituminous in *Austrotrachyceras* from the Reihgraben Shales, Schindelberg locality, Lower Austria, and rich in Si in the specimen from the Mazon Creek area, Illinois, USA), the mantle in specimens of all taxa shows a granular ultrastructure. This was probably caused by different bacteria that caused the precipitation of different elements (in the Posidonian Schiefer by P-accumulating bacteria, in the Reihgraben Shales by C-accumulating bacteria, and in the Mazon Creek area by Si-accumulating bacteria).

3.3.3 Ink Substance

The substance that is interpreted to be dispersed ink (Fig. 6.7C) consists of a mass of tiny, globular granules, 0.1–0.4μm in diameter. Each granule is an agglomerate of

Fig. 6.9A, B. Saundersites illinoisiensis *g. and sp. n., PE32521. A. Fragment of fossilized muscular mantle among debris of soft tissues. B. Fibrous ultrastructure of the muscular mantle; the fibers form a criss-cross pattern, enlarged view of Fig. A. Each division of the scale bar in A is 1.2 μm and in B is 0.12 μm.*

smaller particles (Fig. 6.7E). These granules do not form layers or fibers as do the granules in fossilized soft-tissues, and they are ultrastructurally identical to the ink in present-day and fossil coleoids (Fig. 6.11B–D). The matrix of the concretion around the specimen has crystal-shaped grains (Fig. 6.7B, D) indicating its abiotic origin.
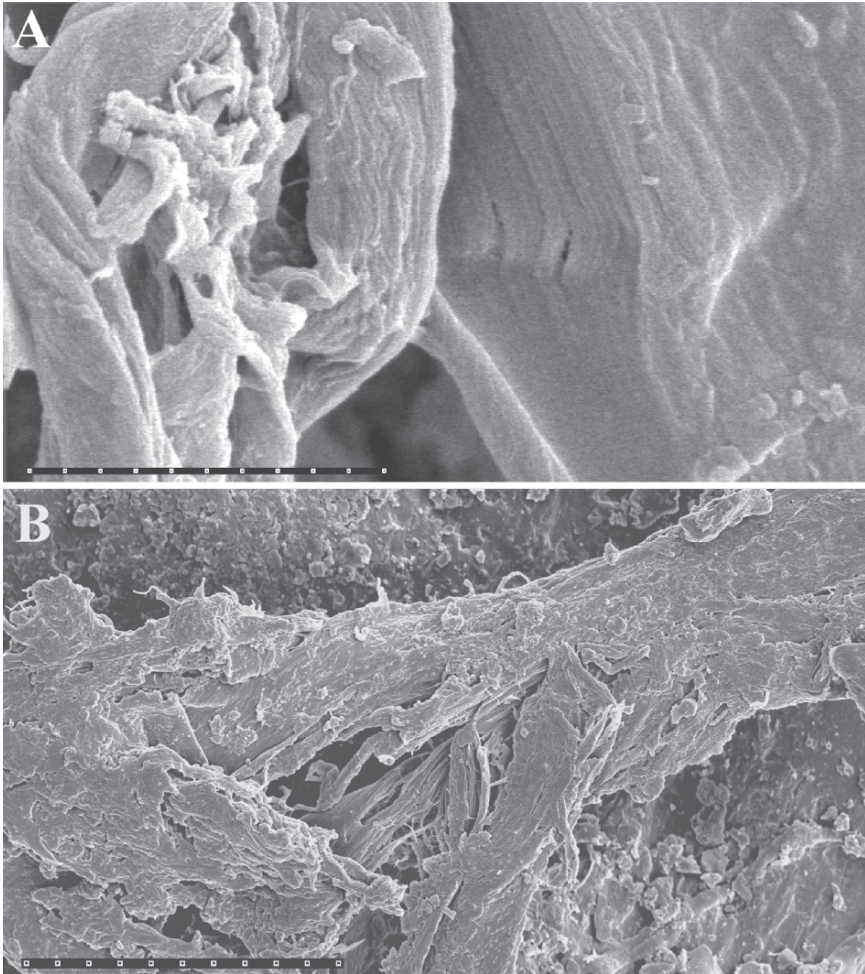
Fig. 6.10A Saundersites illinoisiensis *g. and sp. n., PE 32521. Fragment of fossilized muscular mantle. Each division of scale bar is 0.6 μm.* **B.** Austrotrachyceras sp., *NHMW 2005z/0006/0001, Upper Triassic, Lower Carnian, Lower Austria, locality Schindelberg near Lunz. Fragment of fossilized muscular mantle. Each division of the scale bar is 3 μm.*

4 Systematic Paleontology

The following features of the morphology and preservation in the specimens under discussion were analyzed to elucidate their systematic assignment: (1) division of the shell into a proostracum-like structure, body chamber, phragmocone, and rostrum; (2) presence of fossilized soft-tissues covering the shell; (3) presence of the arm hooks, (4) presence of ink, and (5) a unique radula structure.
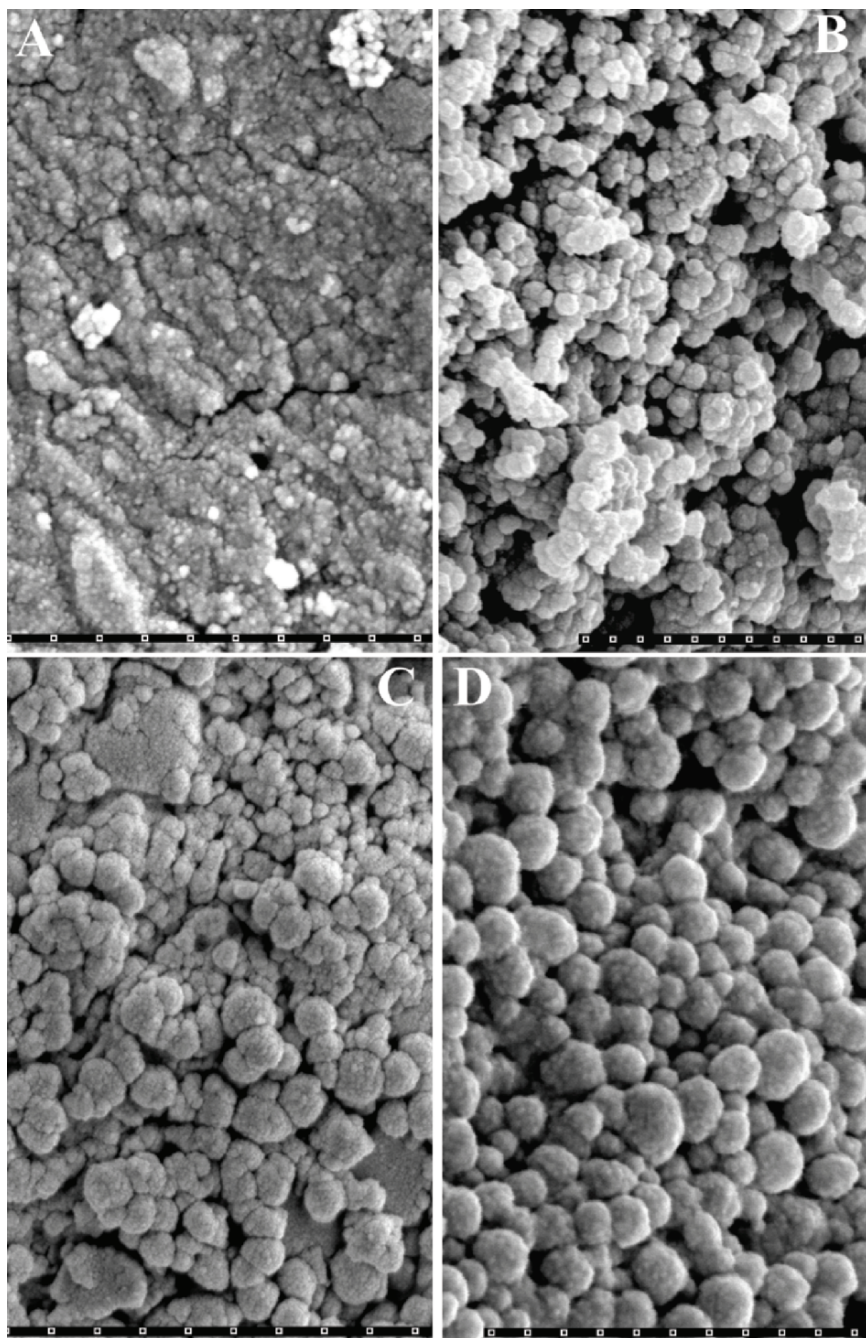
Fig. 6.11A, B Austrotrachyceras sp., *NHMW 2005z/0006/0001, Upper Triassic, Lower Carnian, Lower Austria, locality Schindelberg near Lunz. A. Fossilized mantle tissues preserved*

Subclass COLEOIDEA Bather, 1888
Superorder is unknown
Order DONOVANICONIDA, ord. n.

Diagnosis. Small to medium-sized, about 30–60 mm in length, phragmocone-bearing coleoids each with long body chamber, relatively short and broad proostracum-like structure at the aperture, ink sac, arm hooks, and small rostrum or sheath; siphuncle narrow, ventral; connecting rings thin, organic.

Comparison. The erection of a new order is required because no existing coleoid order can accommodate all of the characteristics of a new genus being described from the Lower Carboniferous Bear Gulch Formation in Montana (Mapes, personal communication, 2007, and submitted) and two described genera, one from the Upper Carboniferous Mazon Creek locality (Westphalian D), Francis Creek Shale, in Illinois (described herein), and the other from the Wewoka Formation in Oklahoma (Doguzhaeva et al., 2002b). This order better accommodates the family Donovaniconidae that was provisionally placed in the order Phragmoteuthida (Doguzhaeva et al., 2003). Members of the new order Donovaniconida have a relatively long body chamber, a relatively short rostrum, and a short broad proostracum-like structure.

Comparison of all the presently recognized Upper Paleozoic coleoid orders are in general as follows: Members belonging to the order Hematitida are readily distinguished from the Donovaniconida by having a very short body chamber and breviconic phragmocone, a massive, short rostrum that covers the entire phragmocone, and being without a proostracum-like structure. The order Aulacocerida has a longiconic phragmocone, a proostracum-like structure, and a relatively long, massive rostrum on more mature specimens and in the new order the phragmocone is very short and the rostrum is short and weakly developed. The order Spirulida in the Carboniferous can be separated from the new order by the presence of a longiconic phragmocone, and the lack of a proostracum-like structure. The order Phragmoteuthida differs from the new order by having an exceptionally long, broad tripartite proostracum, no enclosed body chamber, and a short phragmocone with closely spaced chambers. The new order can be separated from the order Octopoda because the latter lacks an internal shell.

Discussion. The geologic range of the new order is presently confined to the Carboniferous.

Fig. 6.11A, B (continued) *in the body chamber. **B.** Globular ultrastructure of possible ink dispersed in soft tissues from the body chamber. Each division of scale bar is: A – 0.12 μm; B – 0.15 μm. **C.** Unnamed phragmocone-bearing coleoid, Missourian, Middle Pennsylvanian, Nebraska, USA, University of Iowa Paleontology collections, SUI 62497. Globular ultrastructure of ink preserved within the ink sac. Each division of scale bar is 0.3 μm. **D.** Loligo forbesi Steenstrup, 1856, globular ultrastructure of dried Recent ink. Each division of the scale bar is 0.12 μm.*

Family DONOVANICONIDAE Doguzhaeva et al., 2003
Genus *SAUNDERSITES*, gen. n.

Derivation of name. In honor of W. Bruce Saunders for his valuable contributions to the study of fossil cephalopods and present-day *Nautilus*.

Type species. Saundersites illinoisiensis gen. and sp. n.

Diagnosis. Orthocone about 60 mm in length and 12 mm in diameter, apical angle of about 12°–15°; length ratio of proostracum-like structure/body chamber/phragmocone together with rostrum is ca. 3:9:5; rostrum irregularly calcified; arms apparently short, with arm-hooks arranged in double rows; radula formula C:L1: L2:M:MP1:MP2.

Comparision. The closest coleoid taxon in the Upper Paleozoic to *Saundersites* is *Donovaniconus* from time equivalent beds located in the southern part of the American mid-continent in Oklahoma. These two taxa differ in the apical angle of the phragmocone; *Donovaniconus* has an apical angle of about 20° and *Saundersites* has an apical angle of about 15° degrees. Another difference is that the phragmocone of *Donovaniconus* makes up about one-third (33%) of the conch length, whereas *Saundersites* has a phragmocone that makes up about 40% of the conch length.

Discussion. Preservational differences of *Saundersites* and *Donovaniconus* prevent additional comparisons. In *Saundersites* the radula and arm hooks are preserved; ink is present as a dispersed material. With the exception of the dispersed ink, these structures are not preserved in *Donovaniconus*. However, *Donovaniconus* does preserve the shell ultrastructure, shell ornament, cameral spacing, ink in an ink sac, and siphuncular details. These features are not well preserved in either *Donovaniconus* or *Saundersites*. In both genera the proostracum-like structure is short and broad, and it can be determined that this feature is longer in *Saundersites* than in *Donovaniconus*. An ultrastructural comparison of this structure cannot be made because in *Saundersites* this structure is preserved as an impression, while on *Donovaniconus* the presence of this structure was identified by the shape of the growth lines on shell fragments and by the shape of a partly complete aperture.

Saundersites illinoisiensis, sp. n.

Holotype. Specimen PE 32521.

Paratype. Specimen PE 20808.

Type locality. Mazon Creek, northwestern Illinois, USA.

Type Horizon. Upper Carboniferous, Francis Creek Shale (Westphalian D), Middle Pennsylvanian, Desmoinesian.

Derivation of name. Named for the state of Illinois.

Description. The holotype is an orthocone 56 mm long and a short cephalic area 8 mm long. Apical angle of the shell is about 15°. Body chamber is long (ca. 30 mm in length and 12 mm in diameter). Proostracum-like structure is short (ca. 1/3 body chamber length) and broad (ca. 1/2 circumference length). Short phragmocone

(apparently truncated) and short rostrum are about 1/2 body chamber length together. Rostrum is irregularly mineralized. The radula has 11 elements and two marginal plates, on each side, located outside the marginal tooth (Figs. 6.2, 6.3). The arm hooks are arranged in double rows. The hooks are about 0.2–0.3 mm in length. They show a short and thick shaft. A distal part, extending from the maximum curvature to the tip, is long. The angle between the shaft and the distal part is about 90° (Fig. 6.4). The paratype shows a well-preserved proostracum-like structure at the aperture. The shell has a similar size and shape as that in the holotype.

5   Morphological Plasticity and Evolutionary Trends in Carboniferous Coleoids

The early appearance of coleoids in cephalopod evolution is no longer doubted as it was prior to the report of Flower and Gordon (1959), who discovered an extensive Early Carboniferous collection of rostrum-bearing coleoids they named *Hematites*. Recently, additional Carboniferous coleoids have been discovered from the mid-continent of North America (Johnson and Richardson, 1966, 1968; Gordon, 1964, 1971; Saunders and Richardson, 1979; Allison, 1987; Kluessendorf and Doyle, 2000; Doguzhaeva et al., 1996, 2002a, c, 2003), southern Urals in Russia (Doguzhaeva, 2002c), and northern Moravia, Czech Republic (Kostak et al., 2002). The currently known diversity of Carboniferous coleoid cephalopods is limited to fewer than ten described genera; almost all of these genera are monospecific.

Doguzhaeva (2002a) recognized the remarkable morphological plasticity in Carboniferous coleoids. Her conclusions were based on recently obtained morphological and ultrastructural data, and she demonstrated that different coleoids had the capability to combine different morphological elements into the same shell. This kind of recombination has not been observed in Mesozoic coleoids. The morphological elements are present either in the external shell, such as a long body chamber, or in the internal shell, such as the rostrum, proostracum-like structure, and lamello-fibrillar nacre in the septa. From the classical point of view (Naef, 1922; Jeletzky, 1966), the rearrangement of the morphological elements within the early coleoid shells was not considered to be possible. However, the recombination of these elements indicates a great morphological plasticity within Carboniferous coleoids, and it had a great impact on the early diversification within this cephalopod lineage.

The evolutionary plasticity of Carboniferous coleoids confirms the empirical rule in evolutionary theory according to which morphological plasticity is higher at early evolutionary stages, but it tends to become less variable at later evolutionary stages, when stabilization control created more stable morphotypes (Mamkaev, 1968).

The following early evolutionary trends can be distinguished in the subclass Coleoidea:

The order Hematitida (for example, *Hematites*, Flower and Gordon, 1959), in which the longiconic phragmocone was not completely covered by the mantle (and rostrum) during early ontogeny, but became covered in later stages of growth; the body chamber was already eliminated, and the terminal chamber was about 1. 5 camerae

long; the rostrum is prominent with numerous longitudinal ridges separated by deep grooves, its anterior portion has a short dorsal protrusion, the conotheca is multilayered, and it lacks a nacreous layer (Doguzhaeva et al., 2002a);

The order Spirulida (for example, *Shimanskya*, Doguzhaeva et al., 1999), in which the body chamber and phragmocone are long and tubular, the shell wall lacks a nacreous layer and is covered by the outer plate instead of a rostrum; a proostracum-like structure is not developed (Doguzhaeva et al., 1996, 1999);

The order Aulacocerida (*Mutveiconites*, Doguzhaeva, 2002c), in which the rostrum is a small, cone-like structure surrounding the protoconch and the initial portion of the longiconic phragmocone; the conotheca has a nacreous layer; the body chamber is long and tubular, at least in early ontogenetic stages (Doguzhaeva, 2002a, c; Doguzhaeva et al., 2006).

The order Donovaniconida, ord. n. (*Rhiphaeoteuthis*, Doguzhaeva, 2002c; *Donovaniconus*, Doguzhaeva et al., 2003, *Saundersites*, gen. n.) in which the moderately breviconic body chamber is present either through the whole ontogeny (*Donovaniconus, Saundersites*), or during early ontogeny only (*Rhiphaeoteuthis*); the proostracum-like structure is comparatively short with a broadly rounded anterior edge with growth lines *(Donovaniconus, Saundersites)*; a substantial ink-sac is present *(Donovaniconus)*; the breviconic phragmocone is about the same length as the body chamber or shorter; the rostrum is weakly calcified (*Saundersites*), or sheet-like, or missing (*Rhiphaeoteuthis*); the conotheca has a principal nacreous layer; mural parts of septa are long, up to 1/2 camera length, they are embedded into a shell wall and seem to be organic-rich; sutures are nearly straight or weakly undulated; septa consist of lamello-fibrillar nacre *(Donovaniconus)* (Doguzhaeva, 2002a; Doguzhaeva et al., 2002c, 2003); arm hooks are in double rows (*Saundersites*).

Acknowledgments

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