Coleoid cephalopods through time (Warnke K., Keupp H., Boletzky S. v., eds)

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THE SHELL AND INK SAC MORPHOLOGY AND ULTRASTRUCTURE OF THE LATE PENNSYLVANIAN CEPHALOPOD *DONOVANICONUS* AND ITS PHYLOGENETIC SIGNIFICANCE

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ABSTRACT

Shell and ink sac morphology and ultrastructure of Late Pennsylvanian (Desmoinesian) *Donovaniconus oklahomensis* Doguzhaeva, Mapes and Mutvei from Oklahoma, USA, is described. This small, 30 - 40 mm long, breviconic form with a proportionally short phragmocone demonstrates a unique combination of morphological features including a long body chamber, a characteristic element of ectochochleates, and several coleoid attributes, namely: a pro-ostracum, an ink sac, and lamello-fibrillar nacre.

The pro-ostracum is evident due to the configuration of growth lines showing a dorsal projection and an irregular ultrastructure of the outermost portion of shell wall, the latter being interpreted as a result of diagenetic alteration of original, mostly organic and weakly calcified material of the pro-ostracum. The pro-ostracum surrounds the whole phragmocone and has a dorsal lobe-like anteriorly rounded projection beyond the aperture that extends approximately 1.5 - 2 camerae lengths. The ultrastructural data support the idea that the pro-ostracum represents an innovation of coleoid evolution (Doguzhaeva *et al.* 2002, Doguzhaeva 2002a) rather than a dorso-lateral remnant of the body chamber shell wall of their ectochochleate precursors as was suggested earlier (see Jeletzky 1966).

The lamello-fibrillar nacre was observed with scanning-electron-microscopy (SEM) in split shells of *D. oklahomensis.* It is formed by numerous lamellae each of which consists of parallel compactly packed fibres. This nacre, or nacre Type II (Mutvei 1970) has been previously observed only in septa of Jurassic-Cretaceous belemnites and spirulids.

The presence of ink in an ink sac in *D. oklahomensis* is confirmed by SEM observations of a globular ultrastructure of the black mass in the body chamber. This mass is interpreted to be an ink sac because of the SEM ultrastructural similarities of the globular ultrastructure of dried ink of Recent squids, cuttlefish and octopus. As in Recent coleoids, in *D. oklahomensis* the ink sac is relatively large, approximately 0.3 - 0.5 of the body chamber length, and is subdivided into compartments.

Donovaniconus oklahomensis belongs within the Coleoidea, and because of its unique characteristics, is assigned to the monotypic family *Donovaniconidae* Doguzhaeva, Mapes and Mutvei, 2002 that is placed within the Order Phragmoteuthida.

The fossil record of the Carboniferous phragmocone-bearing coleoids is discussed.

Keywords: Cephalopoda, Coleoidea, evolution, systematics, shell ultrastructure, fossil coleoid ink, Carboniferous, Pennsylvanian, Desmoinesian

INTRODUCTION

This study is based in part on scanning-electron-microscopy (SEM) examinations of uniquely preserved shells, one containing an ink sac, of the Late Pennsylvanian coleoid *Donovaniconus oklahomensis* Doguzhaeva, Mapes and Mutvei. The studied material was collected by Royal Mapes in the 1980s from Oklahoma, USA. The SEM studies of the material were carried out in the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm, Sweden.

Based on shell gross morphology alone (Figs 1, 2, 4), *D. oklahomensis* could easily have been mistaken for an unknown parabactritid or even an orthocerid. The presence of a large black mass within the body chamber of one of the best preserved shells, which could be intrepreted as an ink sac, suggested the possibility of a coleoid origin for the shell. The marginal position of the small diameter siphuncle eliminated the possibility that the form belonged to orthocerids. However, breviconic shells with short camerae with a small diameter, marginal siphuncle and long mural parts of septa, like those exhibited by *D. oklahomensis*, are observed in both parabactritids and coleoids, presenting the dilemma that either *Donovaniconus* is a parabactritid and belongs in the bactritoid lineage, or that it is an undescribed coleoid with a long body chamber and an ink sac. With the discovery that the growth lines curve orad in a typical pro-ostracum pattern in *D. oklahomensis* (Fig. 2), the probability that this genus is an undescribed coleoid became higher. It is known that there are some bactritoids with a short dorsal projection, such as the late Devonian *Lobobactrites ellipticus* (Babin & Clausen 1967, Pl. I, Figs 1 - 4); however, these projections are not like a belemnite pro-ostracum.

In *D. oklahomensis* the annular body/shell attachment scar located in the posterior portion of the body chamber (Fig. 1) differs from those known in ectochochleates. This observation sheds light on the differences in the process of phragmocone formation in *D. oklahomensis* relative to bactritoids and other ectochochleates. Phragmocone formation is important for the separation of *D. oklahomensis* and bactritoids and the identification of the former's systematic position. In addition, the presence of a breviconic phragmocone and short camerae with long mural parts of the septa in *D. oklahomensis* is similar to that of the Late Carboniferous *Rhiphaeoteuthis margaritae* from the southern Urals which was also placed in the Order Phragmoteuthida (Doguzhaeva 2002b).

Well preserved ink sacs of fossil “teuthids” are well known from the Jurassic of Germany (Riegraf 1982), France (Guérin-Franiatte & Gouspy 1993) and England (Donovan 1983), and from Upper Jurassic and Lower Cretaceous of Central Russia (Hecker & Hecker 1955). As in Recent coleoids they have a flask-like shape. When fossil ink sacs do not retain their proper shape it becomes more uncertain whether the black mass within the body trunk of a fossil coleoid is an ink sac, stomach content or “a play of nature” (Allison 1987). The most ancient coleoid ink currently known and sufficiently documented with ultrastructural analysis belongs to the Late Carboniferous (Pennsylvanian, Missourian; =Kasimovian) undescribed coleoids from Nebraska, USA (Doguzhaeva, Mapes, Mutvei & Pabian 2002, a).

In modern coleoids, the ink sac is a pear-shaped organ sticking out of the rectum. The ink sac is subdivided into a reservoir and a duct, the latter opening into the rectum near an annulus. In a medium-sized (weight of approximately 400 g), modern *Sepia*, about 1 - 2 g of raw ink can be extracted from the ink sac. *Sepia* ink consists of small granules (0.2-0.3 μ) of melanin suspended in a colorless plasma; melanin provides the black color. According to Nicolaus (1968), this ink seems to lack any proteins, although melanins isolated from natural sources are usually conjugated with proteins. Melanin in cuttlefish ink, or so-called sepiomelanin, readily binds with Calcium and Magnesium ions in sea water because the melanin granules act as a cation-exchange resin (Nicolaus 1968). The chemistry of melanin remains uncertain, and “If the mechanism of melanogenesis *in vivo* is the same as that which occurs *in vitro*, then eumelanins are macromolecules, or rather, mixtures of macromolecules, formed by the copolymerization of the different precursors of which the most important one is 5, 6-indolequinone. The type of linkages which bind the units are unknown. It thus seems most probable that eumelanins are macromolecules built from heterogenous units with heterogenous bonds.” (Nicolaus 1968, p 68).

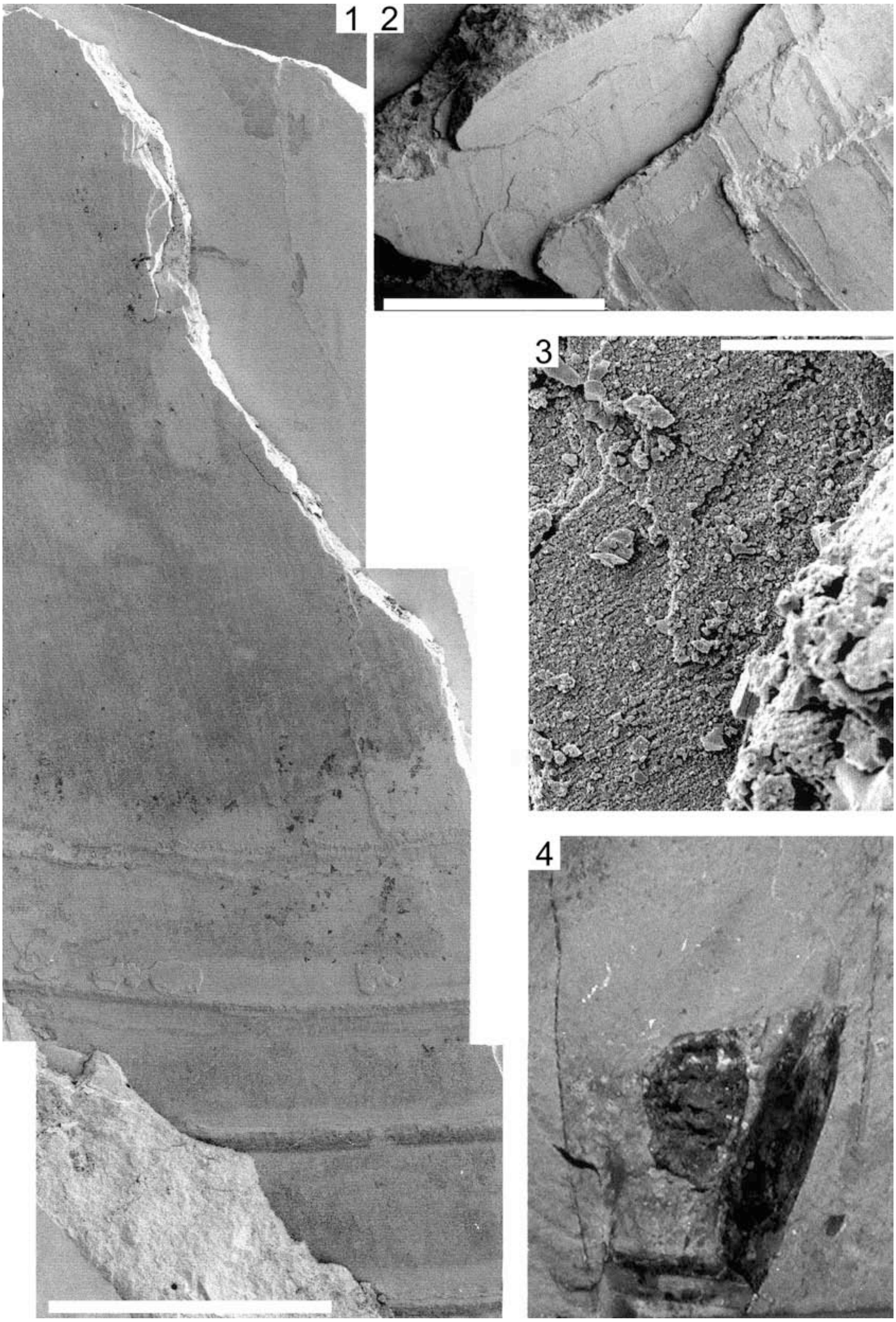


Figure captions. ***Donovaniconus*** *oklahomensis* Doguzhaeva, Mapes & Mutvei, 2002, Desmoinesian, Upper Pennsylvanian, Oklahoma, USA.

Fig. 1 Inner lateral side of living chamber and two camerae, showing annular attachment scar and fine, longitudinal, closely spaced ribs (paratype OUZC 4075), scale bar = 3 mm. **Fig. 2** Inner dorsal view of three camerae with mid-dorsal scars; imprint of pro-ostracum on the left shows adorally curved growth lines (paratype OUZC 4076), scale bar = 3 mm. **Fig. 3** Lamello-fibrillar nacre of septum (paratype OUZC 4075), scale bar = 15 µm. **Fig. 4** Lateral view on holotype (ventral side to the left) with partly preserved living chamber and last two camerae of phragmocone; ink sac medially fractured containing fossil ink (OUZC 4074), x 3.6

The unusual shell structure and presumed ink sac of the Late Pennsylvanian *D. oklahomensis* forced us to search for distinguishing ultrastructural features (Fig. 3) that can be used for comparison with the bactritoids and orthoconic phragmocone-bearing coleoids and allow a reasonable taxonomic assignment of the monotypic family Donovaniconidae Doguzhaeva, Mapes and Mutvei, 2002. With the description of this new genus and the other new Carboniferous coleoid discoveries described recently (Doguzhaeva *et al.* 1999a, b, Doguzhaeva *et al.* 2002a, b, Doguzhaeva 2002b) an overall discussion of the phragmocone-bearing Paleozoic Coleoidea is warranted.

GEOLOGICAL SETTING AND ENVIRONMENTAL CONDITIONS

The studied specimens come from lenticular carbonate concretions recovered from the Wewoka Formation, Upper Pennsylvanian, Desmoinesian, of Oklahoma, USA. The concretions are always longer than thick (maximum and minimum length about 150 and 450 mm, respectively by about 70 mm in thickness). Most concretions are roughly oval in shape, although some irregular shapes have been observed. The concretions commonly contain a diverse fauna of ammonoids at all stages of growth, numerous bactritellas of several genera (Mapes 1979, see locality P-6 for additional details), rare and diverse orthoconic and coiled nautiloids, rare cephalopod mandibles, the spat of bivalves and gastropods, and shark and fish debris. Larger cephalopod specimens in the concretions are moderately rare. The shells of *Donovaniconus* are always preserved on a single bedding plane within each lenticular concretion. Only one bedding plane in any concretion contains a specimen or fragments of a specimen of *Donovaniconus,* and only about 1 in 100 concretions will contain a *Donovaniconus* specimen.

The concretions are interpreted as having formed early (prior to massive compaction) in the depositional history of a mud that was deposited in a strongly dysoxic bottom environment, in a relatively deep-water, offshore, marine setting. The concretions are finely laminated and relatively few burrows interrupt the bedding. The water at the sediment/water interface and pore water condition in the mud probably became rapidly anoxic as aerobic bacteria depleted the limited oxygen available in the already dysoxic marine water. This oxygen depletion may have coincided with the change from the normal alkaline condition of marine water to a slightly acid or neutral water condition. This chemical change would have caused the melanin in the ink sac in the body of the coleoids to precipitate into a solid cohesive mass (Fox 1966). If alkaline bottom water conditions had been present, the melanin would have been dispersed colloidally, and the fossil coleoid ink would not have been preserved.

MATERIAL, STATUS OF PRESERVATION AND METHOD OF STUDY

The best preserved specimen of *D. oklahomensis* (holotype OUZ 4074) is 20 mm long, comprising part of a weakly compressed three-dimensionally preserved small breviconic shell (Fig. 4). The phragmocone shows 5 adoral camerae and a completely compressed and fractured apical portion of the phragmocone. During preparation, the shell was exposed along its left side; where the shell wall was partly removed, the internal structure of the phragmocone and a long body chamber containing a large black mass were exposed. The right part of the shell rests within the concretion. Although the presumed ink sac (the black mass) was partly exposed, its main body still rested within the fine-grained, brownish sediment filling the body chamber. The external surface of shell wall was exposed on the dorso-lateral side. On the ventral side the fractured shell wall was preserved within the concretion.

The shell has a brownish color. The presumed ink sac contents have a shiny black, anthracite-like appearance. The anterior portion of body chamber and the apical portion of the phragmocone are broken and missing. The shell wall and septa are fractured into separate pieces and are exposed on the same bedding plane. Rostrum, jaws, and arm hooks are missing in the concretion that yielded the shell.

Shell ultrastructure was studied with the aid of longitudinal and cross sections as well as fractured portions of the shell. The cross sections were made through the most apical and adoral broken ends of the shell. The adoral section went through the ink sac which was diagenetically compressed together with the body chamber. The longitudinal section was made through the ventral side and siphuncle. The obtained surfaces were polished, etched by 2 - 5% hydrochloric acid for 5 - 10 seconds, coated by gold and examined with SEM. The pieces of black substance from the potential ink sac were coated by gold and examined with SEM as well.

The remaining specimens differ in their preservation from the holotype. Approximately 10 concretions have masses of fragmented body chamber and phragmocone pieces scattered over the surface of a single bedding plane within each concretion. The pieces are small, about 20 mm long or less. It appears that in all the specimens the body chamber and phragmocone of the conchs were not filled with sediment prior to implosion and subsequent burial and concretion formation. Because of this, it is possible to observe the internal surfaces of the body chamber and camerae of the phragmocone. The shell on some layers shows a whitish color (as compared to the brownish color on the holotype), and iridescent plays of color from some of the surfaces suggest that these whitish parts of the shell are, in part, calcium phosphate. Due to this preservation, many fine morphological features such as the shell/body attachment scars, ornamentation of inner surface of body chamber and phragmocone, the shell wall and septa ultrastructure were observed and are described herein.

Paratype OUZC 4075 provides conclusive evidence of a long body chamber in *D. oklahomensis* (Fig. 1). It is a 17 mm long fragment of the lateral side of the shell that is exposed from the inside and shows the inner surface of an incomplete body chamber and two last camerae of the phragmocone. The preserved portion of body chamber is five times as long as the last camera. Posteriorly in the body chamber in front of the last septum there is an annular shell/body attachment scar located at a distance of the length of the last camera. It represents the attachment position of the body when the last septum was secreted. The inner surface of the phragmocone and body chamber is coated by a prismatic layer that shows numerous, closely spaced, distinct longitudinal ridges.

Paratype OUZC 4078 provides conclusive evidence of a pro-ostracum in *D. oklahomensis* (Fig. 2). This specimen is a 16 mm long portion of the phragmocone that exposes the inner surface of six camerae on the dorsal side and the imprint of the outer surface of the shell on the underlying concretion. As with paratype OUZC 4075 it has a distinct annular attachment scar behind each septum and unpaired mid-dorsal scars between septa.

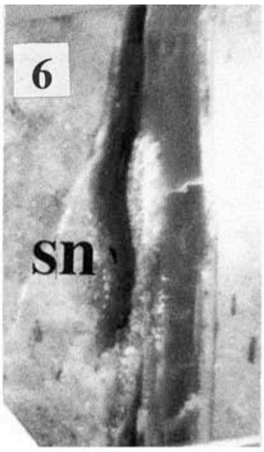
Two additional small specimens (OUZC 4076 and OUZC 4077) show mid-dorsal attachment scars in one or two camerae and imprints of curved growth lines like those in the paratype OUZC 4078. The adorally curved growth lines were observed only on the dorsal side; on the lateral sides they are straight and inclined towards the venter. In other concretions there are numerous smaller pieces of shell wall (most are in the 3 to 15 mm size range) that show either the inner surface of the phragmocone with its typical longitudinal ridges, or the outer surface with more or less curved ridges that are similar to those observed in larger fragments. Selected segments of these shell fragments were coated with gold and examined with SEM without etching. For comparison with the black anthracite-like material in the holotype, ink extracted from the ink sacs of Recent squid, cuttle-fish and octopus was dried, and together with the ink substance from the ink sac in the Late Jurassic *Loligosepia,* all the specimens were examined with SEM.

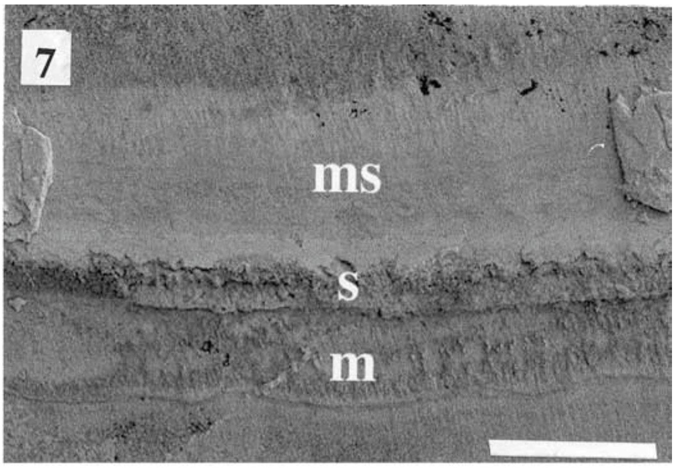
The material is stored in the Ohio University Zoological Collections (OUZC) in Athens, Ohio, USA.

SHELL MORPHOLOGY

In *D. oklahomensis* the shell represents a small brevicone (Fig. 4) with rounded to slightly oval cross section and thin shell wall ornamented by fine longitudinal and transverse ridges on its outer surface. Total length of the shell is estimated to be 30 - 40 mm, the apical angle of the phragmocone is 20 - 30°. The shell consists of a short phragmocone (its apical portion is so far unknown). A proportionally long body chamber and pro-ostracum surrounds the phragmocone along the whole circumference and has a dorsal lobe-like projection. The approximate length of the projection is estimated at 1.5 - 2 camera lengths.

The phragmocone is characterized by short camerae (Figs 1, 2, 4), long mural parts of the septa (Figs 5, 6) and a small marginal siphuncle. The phragmocone has an estimated length of 10 - 15 mm. The total number of camerae is estimated to be 15 - 20. The septa are nearly





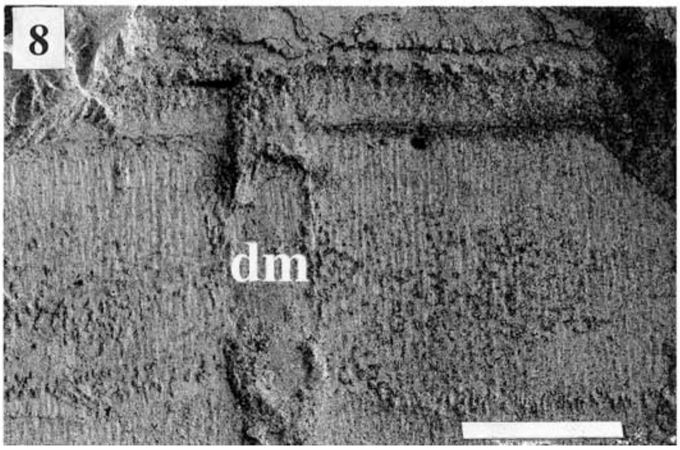


Figure captions. ***Donovaniconus** oklahomensis* Doguzhaeva, Mapes & Mutvei, 2002, Desmoinesian, Upper Pennsylvanian, Oklahoma, USA.

Fig. 5 Cross-section of a diagenetically compressed phragmocone; a fragment of a broken septum shows dorsal, cyrtochoanitic portion of a septal neck (sn) coated from the inside by an annular thickening; holotype OUZC 4074, x 25. **Fig. 6** Longitudinal section of a diagetically compressed phragmocone to show ventral portion of a septal neck (sn); note that this portion of the neck is longer than the dorsal portion; holotype OUZC 4074; x 25. **Fig 7** Inner lateral surface of a chamber close to the last septum to show annular muscular attachment scar (m) immediately behind the fractioned and comparatively long mural portion (ms) of a broken septum (s); paratype OUZC 4075; scale bar = 600 µm. **Fig. 8** Inner dorsal surface of the phragmocone to show a dorsal unpaired attachment scar (dm); note the ornamentation of this surface by closely spaced, longitudinal, narrow ribs; paratype OUZC 4078; scale bar = 0.3 mm

perpendicular to the phragmocone axis, and the sutures are almost straight. The dorsal side of the septal necks are short and strongly curved (Fig. 5); whereas, on the ventral side they are long (about a camera length), slightly curved, and touch the conotheca apically (Fig. 6).

The body chamber (Fig. 4) is broadly open. It has a thin shell wall. The body chamber length is estimated to be about twice as long as the phragmocone, or longer. The inner surface of the body chamber and the phragmocone (Figs 1, 8) bears numerous, closely spaced, fine, distinct longitudinal ridges. In the posterior portion of the body chamber, at a distance of approximately the length of the last camera from the last septum (Fig. 1), there is an annular band-shaped structure. Its width is about 1/4 - 1/5 of a camera length. Its anterior and posterior edges are wavy and bordered by low ridge-like elevations. The scar identifies the position of the posterior attachment of the shell to the body during the formation of the last secreted septum.

Annular attachment scars are present in the camerae of the phragmocone in *D. oklahomensis* (Figs 1, 2, 7). Each scar lies just behind a septum so that the anterior edge of the scar fits with the posterior edge of the mural part of the corresponding septum (Fig. 1). This shows that the annular attachment scar is a marker for the placement of a new septum. This observation reveals that the formation of the phragmocone in *D. oklahomensis* must have differed from that in bactritoids and all other orthoconic ectochochleates. In contrast to *D. oklahomensis*, each annular attachment scar in ectochochleates lies immediately in front of the septum. This means that in *D. oklahomensis* each septum is fixed just in front of the preceding annular attachment scar, while during the period of septum secretion, the corresponding attachment was fixed at a distance of a camera length forward from this septum. In bactritoids and all other ectochochleates the secretion of a new septum started just behind the position of the body/shell attachment. This conclusion is deduced from the position of the muscular scar in ectochochleates that is located at a very short distance in front of the septum. In *D. oklahomensis*, as in belemnoids and spirulids, the shift of the shell/body attachment position forward provides a condition for a secretion of long mural parts of the septum. In ectochochleates the mural parts of the septum cannot be long because posteriorly the body is attached to the shell wall at a very short distance from the septum. Assuming that the longer mural parts of the septum (in ratio to a distance between the adjacent septa) would make the contact between the septum and the shell wall stronger, it may be that in *D. oklahomensis* the shift of the annular shell/body attachment forward provided the conditions for the secretion of septa with proportionally long mural parts and additionally for strengthening of the shell. The tendency of making the contact between the septum and the shell wall stronger follows the currently accepted course of spirulid evolution in that this strengthening would have allowed them to invade deep-water areas and withstand greater water pressures (Doguzhaeva 2000a). The exterior of the phragmocone in *D. oklahomensis* is similar to those in phragmocone-bearing coleoids, and therefore, the mechanisms of camerae formation must have been similar.

Like the belemnites and the many extinct ectochochleate cephalopods, *D. oklahomensis* has a small elongated unpaired mid-dorsal attachment scar (Figs 2, 8).

The pro-ostracum represents a brevicone surrounding the entire body chamber and phragmocone and protrudes in the shape of a comparatively broad lobe-like dorsal projection beyond the anterior edge of the body chamber. Length of the dorsal projection is approximately 1.5 - 2 camerae. Its outer and inner surfaces are ornamented by smooth transverse growth lines and longitudinal ridges. The transverse growth lines follow the shape of the apertural edge. They are strongly curved on the dorsal side. This dorsal side is defined by the unpaired mid-dorsal attachment scar (Figs 2, 8). On the lateral sides the growth lines are straight and inclined toward the venter. Lateral and ventro-lateral morphological elements of the pro-ostracum, asymptotes and hyperbolar zones, have not been observed.

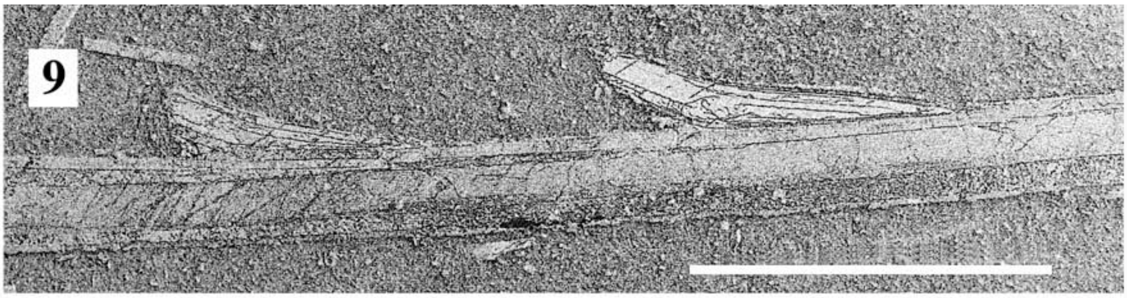
The presumed ink sac in *D. oklahomensis*is (Figs 4, 14) is proportionally large, approximately 15 mm long and 5 mm wide in maximum diameter. It is surrounded by a thin wall. The black substance (“fossil ink”) within the sac is compartmented into numerous cell-like units of different sizes.

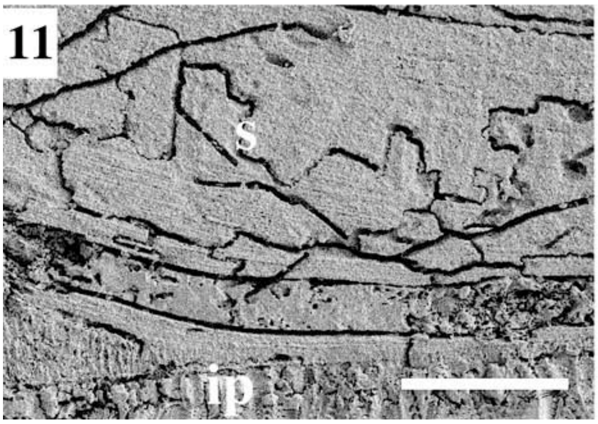
Evidence that a rostrum was present has not been detected. It was probably absent, or at most surrounded only the very apical portion of the phragmocone.

SHELL AND INK SAC ULTRASTRUCTURE

In *D. oklahomensis* the shell wall consists of three layers (Figs 9, 10). The inner layer is prismatic. It is thin, forming numerous, closely spaced, fine longitudinal ridges on the inner surface of body chamber and phragmocone (Figs 1, 8). Next layer is thick and nacreous. It seems to have a lamello-fibrillar ultrastructure formed by lamellae fabricated by closely packed longitudinal fibres (Fig. 13). The outer layer is irregularly mineralized and consists of two sub-layers (Figs 11, 12): a thick inner sub-layer having an irregularly granular structure with numerous empty spaces that probably indicate a high original content of organic matter, and a thin more compact prismatic outer sub-layer lacking regular size and shape of prismatic crystals. The irregularly mineralized and the nacreous layers are separated by a thin whitish (in SEM) lamina that was probably of organic origin. The outer surface of the irregularly mineralized layer bears growth lines.

The inner prismatic layer is absent in bactritoids (Doguzhaeva 1996b, c; 2002b) but present in belemnoids (compare: Doguzhaeva *et al.* 2003). The nacreous layer forms the main bulk of the shell in bactritoids and belemnoids as it does in *D. oklahomensis.* However, instead of the lamello-fibrillar ultrastructure observed in *D. oklahomensis,* it exhibits a columnar nacre characterized by stacks of tablet-like





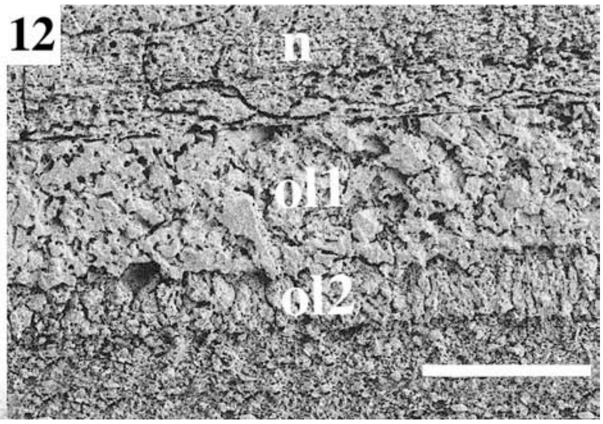
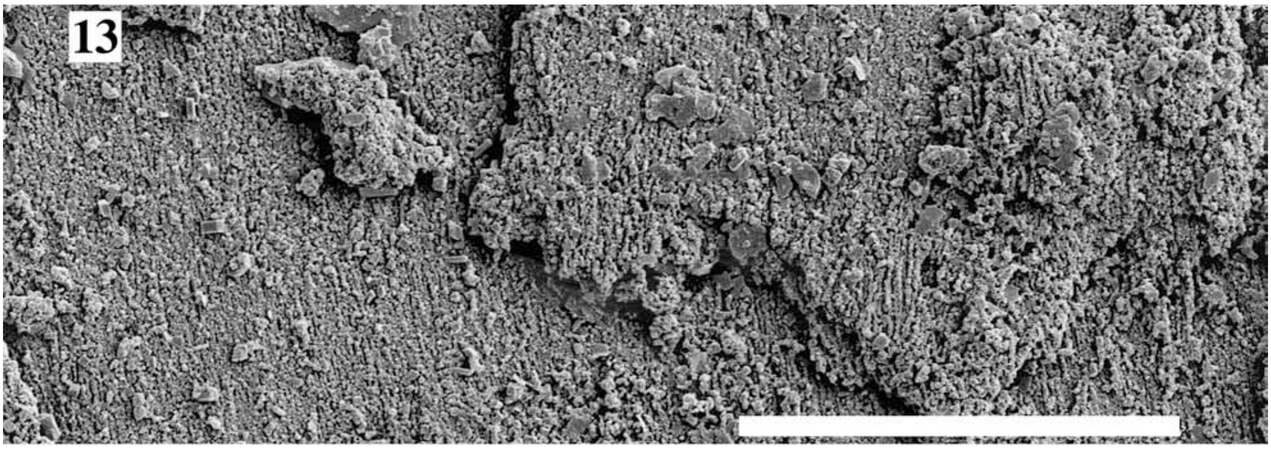
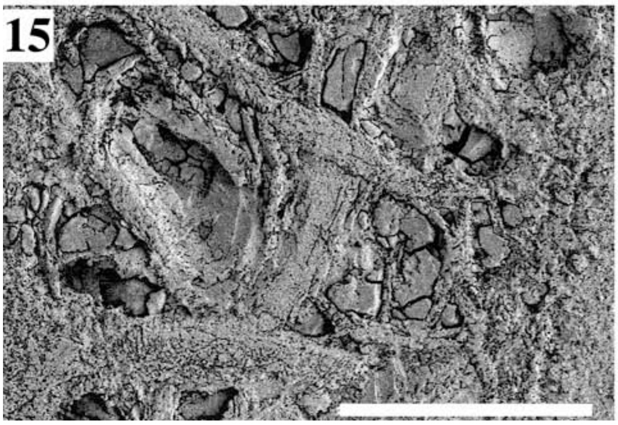


Figure captions. ***Donovaniconus*** *oklahomensis* Doguzhaeva, Mapes & Mutvei, 2002, Desmoinesian, Upper Pennsylvanian, Oklahoma, USA.

Fig. 9 Longitudinal section of the dorsal side of the shell wall with two broken septa; holotype OUZC 4074; scale bar = 1.2 mm. **Fig. 10** Detail of Fig. 9 (left side) in higher magnification to show four layers of the shell wall: inner prismatic layer (ip), nacreous layer (n) and two outer layers (ol); scale bar = 0.3 mm. **Fig. 11** Detail of Fig. 9 (right side) in higher magnification to show thin laminae and granular portions in the mural part of a septum (s); scale bar = 60µm. **Fig. 12** Detail of Fig. 10 with higher magnification to show the nacreous layer (n) of the shell wall and two outermost layers: a thick layer of irregular structure, probably originally rich in organic matter (ol1) and a thin layer of prismatic structure (ol2); scale bar = 60 µm





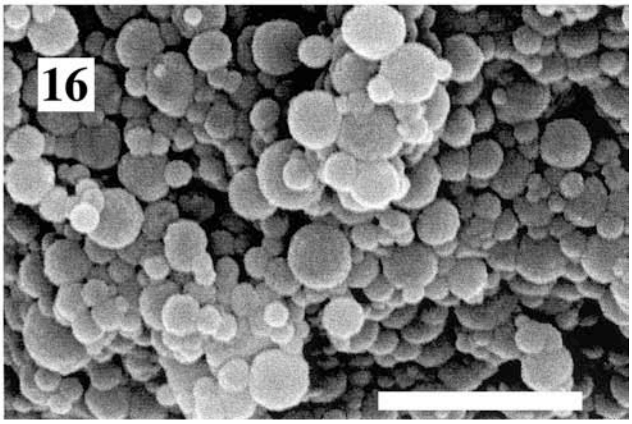


Figure captions. *Donovaniconus oklahomensis* Doguzhaeva, Mapes & Mutvei, 2002, Desmoinesian, Upper Pennsylvanian, Oklahoma, USA.

Fig. 13 Lamello-fibrillar nacre of mural part of septum; paratype OUZC 4075; scale bar = 15 µm. **Fig. 14** Cross section of the compartmentalized ink sac (is) surrounded by a thin wall. The shell wall of the body chamber is at the bottom and in the upper right corner; holotype OUZC 4074; scale bar = 1.2 mm. **Fig. 15** Detail of Fig. 14 showing higher magnification of compartments filled with ink, scale bar = 0.3 mm. **Fig. 16** Close up of the black substance (ink) showing its globular ultrastructure; scale bar = 1.2 µm crystals (nacre Type I) both in bactritoids and belemnoids. In bactritoids the irregularly mineralized layer is absent in the shell wall, and next to the nacreous layer, is the outer prismatic layer. However, the irregularly mineralized layer is present in the shell wall in belemnoids (compare: Doguzhaeva *et al.* 2003). In belemnoids this layer is subdivided into two sub-layers as well. This is a layer that forms a pro-ostracum (Doguzhaeva, Mutvei & Donovan 2002, Doguzhaeva *et al.* 2002b, and Doguzhaeva *et al.* 2003). On the base of this similarity the outer layer characterized by the irregular ultrastructure is interpreted as a layer of the pro-ostracum.

Septa (Figs 9 - 11) exhibit thin lamination and are built of lamello-fibrillar nacre. In bactritoids septa consist of a columnar nacre Type I and show stacks of tablet-like crystals (Doguzhaeva 2002b). However, in belemnoids, septa have lamello-fibrillar nacre as in *D. oklahomensis* (compare: Doguzhaeva *et al.* 2003).

The substance of the black mass within the body chamber in *D. oklahomensis* has a globular ultrastructure and is an agglomeration of spheres (Fig. 16). The spheres are 0.1 - 0.4 µm in diameter. Each sphere consists of smaller particles. All these features including the size of spheres are characteristic of the ink of Recent coleoids and the Late Jurassic *Loligosepia*. This evidence, the position of the black mass in the body chamber, and the fact that in the cephalopods only coleoids are known to have ink, support the conclusion that the black mass in *D. oklahomensis* is a real ink sac containing fossil ink.

SYSTEMATIC PALAEONTOLOGY

Subclass COLEOIDEA

Order PHRAGMOTEUTHIDA
Jeletzky in Sweet, 1964

Discussion. The shell wall/septum attachment in *D. oklahomensis* differs from that seen in bactritoids and all other ectochochleates but is most similar to that of phragmocone-bearing coleoids (compare: Doguzhaeva *et al.* 2003). As in coleoids, *D. oklahomensis* shows short camerae, long mural parts of septa, and a thin shell wall. *Donovaniconus oklahomensis* cannot be assigned to spirulids, because of the nacreous layer in the shell wall that is missing in this latter cephalopod group. Also, *D. oklahomensis* cannot be assigned to aulacocerids because of the breviconic phragmocone.

In summary, based on the short breviconic phragmocone, broad pro-ostracum and conotheca with a nacreous layer, the family, as presently understood, can only be placed in the Order Phragmoteuthida Jeletzky in Sweet, 1964. Mojsisovics (1882) erected the genus *Phragmoteuthis* and the family Phragmoteuthidae to clarify the concept, first introduced by Suess (1865), on the isolated taxonomic position of this genus that possesses the teuthid-like pro-ostracum and belemnoid-like phragmocone. We are aware that Jeletzky (1966) in his diagnosis of the order included the condition that the pro-ostracum should be three parted and that the members of the order should have arm hooks. Neither of the conditions were observed in the specimens of *Donovaniconus.* At this time we prefer to follow the more conservative course and place this new genus and species in the Order Phragmoteuthida with the possibility that we may be dealing with preservational problems rather than a true lack of these important morphological features. If these features are truly lacking, a revision of the diagnosis for the Phragmoteuthida will be required, or it may eventually prove to be necessary to establilsh a new order to accomdate taxa like *Donovaniconus*.

Family DONOVANICONIDAE
Doguzhaeva, Mapes and Mutvei, 2002

Type genus. *Donovaniconus* Doguzhaeva, Mapes and Mutvei, 2002

Diagnosis. Small, about 30 - 40 mm in length, breviconic phragmocone with an apical angle of 20° - 30°. Body chamber with pro-ostracum, longer than phragmocone; pro-ostracum covers entire shell; outer and inner surfaces ornamented by transverse and longitudinal smooth ridges; transverse ridges indicate a broad dorsal apertural projection beyond body chamber. Camerae short; mural parts of septa long, about 1/3 - 1/2 of camera length, sutures nearly straight. Siphuncle small, ventral marginal. Septal necks on ventral side about camera length, slightly curved, touching conotheca apically; on dorsal side short, strongly curved, in contact with septal adapical surface. Conotheca with thick outer nacreous and thin inner prismatic layers. Septa of lamello-fibrillar nacre.

Ink sac big, approximately 1/5 of body chamber length.

Differences. The family *Donovaniconidae* is erected by monotypy. The body chamber is a characteristic feature of the family and distinguishes it from the younger (Orenburgian) Upper Carboniferous family Rhiphaeoteuthidae Doguzhaeva, 2002. The latter was assumed to have a body chamber at early post-hatching stages (Doguzhaeva 2002b, Pl. 15, Fig.1; Pl. 16, Figs 1, 6, 7). The pro-ostracum in *Donovaniconus* is distinguished by adorally curved growth lines which indicate that it projected a short (about 2 chambers), but significant distance beyond the edge of the body chamber. The layer forming the pro-ostracum can be traced around the entire shell. There is no evidence that this is a three part pro-ostracum.

The ultrastructural characters of the shell in *D. oklahomensis* are strong evidence that it could not be assigned to the bactritoid branch of the cephalopod phylogeny. In bactritoids the shell wall consists of two layers: a thin outer prismatic and a thick nacreous layer, the latter being formed of columnar nacre (Doguzhaeva 1996b, c, 1999, 2002b). The outer layer of the shell wall in *D. oklahomensis* differs remarkably from any layer in the bactritoid shell wall, but it is similar to the outer portion of the shell wall observed in belemnoids (Doguzhaeva, Mutvei & Donovan 2002, and Doguzhaeva *et al.* 2003) The outer layer seems to be responsible for the formation of a pro-ostracum.

Genus DONOVANICONUS
Doguzhaeva, Mapes and Mutvei, 2002

Type species. *Donovaniconus oklahomensis* Doguzhaeva, Mapes and Mutvei, 2002

Diagnosis. Same as for the family.

Differences. Differences of other genera in other families have already been stated. A comparison of *D. oklahomensis* with the holotype of *Jeletzkya* described by Johnson and Richardson (1968) is not possible since the latter taxon is preserved as the remains of 10 arms that were hook-bearing with only traces of a mineralized internal shell being present in the Mazon Creek concretion containing the holotype. The additional specimens assiged to *Jeletzkya* by Saunders and Richardson (1979) require additional analysis before a confident assignment to this genus can be made. *Donovaniconus oklahomensis* is established on the basis of the shell ultrastructure and morphology preserved on well mineralized phragmocone and body chambers on several specimens and the presence of preserved ink in the body chamber of one specimen; none of the *D. oklahomensis* specimens preserve the arms and no arm hooks have been observed in association with the shells of these fossils, so a useful comparison of these two genera cannot be made at this time and it seems reasonable that *Jeletzkya* should be placed in an uncertain order and family status.

Donovaniconus oklahomensis
Doguzhaeva, Mapes and Mutvei, 2002
Figs 1 - 16

***Holotype and paratypes*.** Holotype specimen no. OUZC 4074A, B, C, D, E; paratypes OUZC 4075, 4076, and specimens OUZC 4077 and 4078, Ohio University Zoological Collections, Ohio University, Department of Geological Sciences, Athens, OH 45701, USA.

***Type locality*.** Shale exposed at the base of a hill on the west side of the Deep Fork River bridge on Oklahoma Highway 56 approximtely 4.8 km west of the community of Okmulgee, Oklahoma (see Mapes 1979, locality P-6 for additional details).

***Type Horizon*.** Upper Carboniferous, Upper Pennsylvanian, Desmoinesian, Wewoka Shale.

***Emended Description*.** The holotype is a 20 mm long portion of a weakly breviconic shell with an apical angle of about 20° (Fig. 4). Body chamber, 15 mm long, is incomplete. Phragmocone is laterally compressed; cross section is slightly oval, short, estimated length of 10 - 15 mm but only a 4 mm long portion with two adoral camerae is preserved. Before sectioning the shell had 5 adoral camerae and a completely compressed and fractured apical portion of the phragmocone. Total number of camerae is estimated as 15 - 20. The pro-ostracum covers the entire shell, its thickness is about 1/2 - 2/5 of the conotheca thickness on the ventral side of the distal portion of the phragmocone. It is composed of a thin outer sublayer with a prismatic structure and a thick inner sublayer with an irregularly granular structure, containing numerous empty spaces, probably indicating a high original proportion of organic matter. The outer and inner surfaces of the pro-ostracum are ornamented by transverse and longitudinal, low, smooth ridges. Based on the course of the transverse ridges that are strongly curved adorally on the dorsal side, the pro-ostracum formed a short, broad, lobe-like dorsal projection at the shell aperture. The principal layer of the conotheca is a thick nacreous layer, separated from the pro-ostracum by a thin, distinct boundary. The inner surface of the conotheca is covered by a prismatic layer, about 1/4 of the thickness of the nacreous layer. Septa are nearly perpendicular to the phragmocone axis, and sutures are almost straight. The mural part of the septum is long, corresponding to 1/3 of the septal distance. The septal necks on the ventral margin are relatively long, about one camera in length, slightly curved, touching the conotheca apically (Fig. 6); on the dorsum they are short, strongly recurved, in contact with the septal adapical surface (Fig. 5). The body chamber contains an ink sac located in the apical one-third of the body chamber. In the broken longitudinal section of the body chamber, the ink sac is about 8 mm long and 5 mm in maximum diameter.

Paratype OUZC 4075 and OUZC 4076 are from the same concretion and are part of the same specimen. Paratype OUZC 4075 is 17 mm long, shows the inner surface of an incomplete body chamber 10 mm long, and a distal portion of phragmocone with two camerae on the lateral side (Fig. 1). The inner surface of phragmocone and living chamber is coated by a prismatic layer that shows numerous, closely spaced, distinct longitudinal striae. Preserved mural parts the septa are composed of lamello-fibrillar nacre (Fig. 3). Immediately behind each septum there is a distinct, narrow, annular, band-shaped, attachment scar visible on the inner surface of the phragmocone. In front of the last septum, at a distance of the length of the last camera, there is an annular muscular attachment scar without a new septum. The scar is anteriorly and posteriorly bordered by uneven ridges. This scar represents the attachment place of the body when the last septum was secreted. Paratype OUZC 4076 is a 16 mm long portion of the phragmocone with exposed inner surface of six camerae on the dorsal side (Fig. 2). As in the previous paratype there is a distinct annular attachment scar behind each septum. In each annular scar there is a distinct, mid-dorsal scar. In a place where the conotheca is broken, imprints of adorally curved growth lines from the outer surface of the pro-ostracum are visible on the underlying sediment. Two additional small shell fragments (OUZC 4077, 4078) show mid-dorsal scars and imprints of curved growth lines like those seen in paratype OUZC 4076. The adorally curved growth lines were observed only on the dorsal side. On the lateral side they are straight and inclined towards the venter.

Differences. See discussion under the family and the genus.

PHYLOGENETIC SIGNIFICANCE

Before the late fifties in the last century the existence of Carboniferous coleoids was considered doubtful, therefore the papers published by de Koninck (1843) and a century later by Flower (1945) were ignored. However, a large collection of specimens from the Upper Mississippian of USA, described by Flower and Gordon (1959), left no question that coleoids had appeared by the early Carboniferous. In the Early Carboniferous they were represented by *Hematites, Bactritimimus* and *Paleoconus*. Among these genera the Late Mississippian (Lower Eumorphoceras Zone; = Serpukhovian), *Hematites* is the sole genus with the shell ultrastructure studied (Doguzhaeva *et al.* 1999b, 2002a). These Late Mississippian genera were regarded by Flower and Gordon (1959) and Gordon (1964) as primitive forms that gave arise to Mesozoic belemnites. Shimansky (1960) did not support this idea, and assigned *Hematites and Bactritimimus* to the family Aulacoceridae instead of family Belemnitidae. This view was later accepted by Gordon (1966) and Jeletzky (1966), the latter erected the order Aulacocerida. Gustomesov (1976) erected a new family Hematitidae for *Hematites, Bactritimimus* and *Paleoconus.* Since then, *Hematites* has been assigned to the Order Aulacocerida by Reitner and Engeser (1982), Doyle *et al.* (1994) and Pignatti and Mariotti (1996, 1999).

Jeletzky (1966) characterized the order Aulacocerida by having a long tubular body chamber, an aperture with short dorsal and ventral crests, a conotheca with growth lines, a rostrum built predominantly of organic substance, prochoanitic adult septal necks, protoconch sealed completely by closing membrane, caecum and prosiphon apparently absent. In addition, aulacocerids have longer chambers, and a smaller apical angle than belemnitids, and as in many belemnites the conotheca consists of prismatic and nacreous layers.

Hematites lacks many characteristics of Aulacocerida such as a long tubular body chamber, ventral and dorsal crests, prochoanitic septal necks. The conotheca is multilayered, and structurally different from all known coleoids. It consists of five to six layers that are mainly prismatic or spherulitic-prismatic; one of the layers seems to have originally been rich in organic material; a nacreous layer is absent. The entire thickness of the rostrum is penetrated by numerous pore canals that are not known in any other coleoid rostra. The inner surface of the rostrum exhibits numerous pits, some with a pore opening. The terminal edge of the rostrum surrounds the terminal edge of the phragmocone, forming a peristome with a ventral broad and deep U-shaped sinus. *Hematites* regularly lacks the protoconch and the early chambers of the phragmocone which were truncated during its life-time, a feature that is not known in aulacocerids. The outer surface of rostrum shows no signs of damage near the place of phragmocone truncation, and this indicates that the truncation took place before the rostrum was formed. The truncation must have occured at the ontogenetic stage when soft tissues did not coat part of the posterior portion of the phragmocone. The post-alveolar part of the rostrum differs structurally from the alveolar region. It is composed of longitudinal calcareous rods which are loosely packed and were probably surrounded by an organic matrix. This central zone must have acted as a plug to the truncated apical end of the phragmocone. The final chamber is short, approximately equal to 1.5 to 2 times the length of the last chamber. Based on these significant differences, the order Hematitida Doguzhaeva, Mapes and Mutvei, 2002 was erected to comprise the family Hematitidae Gustomesov, 1976.

The genus *Bactritimimus* Flower and Gordon, 1959 is very similar to *Hematites* in rostrum morphology, although it differs by its more compressed phragmocone, strongly inclined septa and sutures with dorsal and ventral lobes. Therefore this genus is referred to the Hematitidae.

Following the idea that coleoids arose from the bactritoids, one can expect that there were Carboniferous orthoconic shells belonged to coleoids which looked more like *Bactrites* than *Hematites*. The idea that coleoids originated from bactritoids is based on the spherical protoconch and small ventral marginal siphuncle shared by bactritoids and phragmocone-bearing coleoids. If this phylogenetic assumption is correct, do we know how to differentiate these different orders, and are there any unique morphological characters in the rostrumless coleoid shells?

Based on shell wall ultrastructure, "*Bactrites*" *postremus* Miller, 1930 of the Missourian - Virginian (=Stephanian) age was redescribed as *Shimanskya postremus* and referred to the Order Spirulida (Doguzhaeva *et al.* 1996, 1999a). It has a longiconic phragmocone with narrow ventral marginal siphuncle and a long body chamber, but lacks a pro-ostracum and a rostrum. The morphological combination of the orthoconic shell and the small ventral marginal siphuncle was widely accepted as sufficient to classify any fossil shell exhibiting these features as a bactritoid (Mapes 1979). In the first description of "*B.*" *postremus,* Miller (1930) remarked that the general nature of the septa and sutures in "*B.*" *postremus* is rather similar to that of *Spirula.* Moreover, he noticed (1930) that, in "*B.*" *postremus*, the shell wall is thin. At that time it was already known that in *Spirula* the shell wall is formed by the outer and inner plates (*sensu* Appellof 1893). The wide-spread phylogenetic assumption that the origin of sepiids, including *Spirula,* was through the belemnites with the evolutionary elimination of their rostrum may have created a barrier on Miller's inspired and correct comparison of "*B.*" *postremus* and *Spirula*. SEM examination revealed that in "*B*." *postremus* the shell wall consisted of two porous prismatic layers. They differ from the prismatic layers of the shell wall in hitherto studied ectocochleates. The outer surface of the inner layer bears "wrinkles". Consequently the "wrinkle layer" lies within the shell wall between the inner and outer prismatic layers. The shell wall and septa are of about equal thickness. The mural parts of the septum on the venter extends slightly less than the entire camera length. Septal necks show the originally organic lamellae and granular-like matter between them and lack of a tabular nacre. In contrast, the shell wall of the Early Permian bactritoid *Hemibactrites* from the southern Urals consists of thin outer prismatic and thick nacreous layers (Doguzhaeva 1996b, c, 2002b). From the protoconch to the primary constriction, the shell wall is prismatic; the nacreous layer appears near the primary constriction, then becomes thicker and finally comprises the main bulk of the shell wall. Additionally, ammonoids and orthoceroids have an inner prismatic layer as an additional shell wall layer.

Thus, in "*B.*" *postremus* the shell wall is remarkably different from that in bactritoids. However, since the shell wall of "*B.*" *postremus* is composed of two prismatic plates without a nacreous layer, it is similar to the shell wall in *Spirula* and several extinct forms considered to be spirulids (Doguzhaeva 1996a). For instance, in the Aptian *Adygeya adygensis* the orthoconic or slightly cyrtoconic shell has a shell wall consisting of inner and outer plates, sharply separated by the intermediate layer. In this form there is no distinct boundary between the inner surface of the shell wall and the septa. This is because the lamellae in the septa and in the dendritic prisms of the shell wall are continuous, despite the ultrastructural differences. This indicates that contrary to ectocochleates, in *Adygeya* the secretional zones of the shell wall and septa were located close to each other, but were not separated by a long body chamber. These facts, namely, the absence of the nacreous layer in the shell wall, lack of a distinct boundary between the septa and the shell wall, and ultrastructural similarity with the shell wall of *Spirula* in addition to the gross morphology were used by Doguzhaeva (1996a) to demonstrate that *Adygeya* was not an ectocochleate cephalopod but falls within the Order Spirulida. In both genera, *Adygeya* and *Spirula*, the inner plate is represented by the inner acicular-prismatic layer with its dendritic structure. The outer plate is represented by the outer acicular-prismatic layer as well, with its simple prismatic structure, and the coating layer with its high content of organic matrix. The intermediate layer is predominantly organic, partly calcified, comprising alternate organic and calcified lamellae. It marks a strong interruption between the secretional zones of the inner and the outer plates. The inner plate seems to have been secreted within the final chamber, whereas the outer plate, on the outer side of the intermediate layer, was formed from the outside of the final chamber. The interruption was probably caused by "a thick, sharply defined layer of connective tissue which extends into the ventral wall of the anterior part of the shell sac", as observed in *Spirula* by Chun (1898-99). In the Aptian *Naefia kabanovi*, which is referred to spirulids, the shell wall is also prismatic and the nacreous layer is missing as well.

Cephalopods are known to have secreted two types of nacre (Mutvei 1970). In ectocochleates there is only one type of nacre known, in both shell wall and septa. It is called nacre Type I, or columnar or tabular nacre. This nacre is composed of mainly hexagonal tablets with the central cavity like those observed in the shell wall of the Jurassic belemnite *Megateuthis* (Doguzhaeva, Mutvei & Donovan 2002). However, in septa of the coleoids described herein, there is a modified nacre called nacre Type II, or lamello-fibrillar nacre (see Doguzhaeva *et al.* 2003). In section the fibers give an impression of a granular instead of a columnar exterior (compare Figs 3 and 5 in Doguzhaeva 1995). Like in the septum of the early Jurassic *Passaloteuthis* (see Doguzhaeva *et al.* 2003), each mineral lamella consists of numerous parallel aragonite rods with a different orientation in the consecutive lamellae. Also, the interlamellar organic membranes, which subdivide the septal nacre into thin mineral lamellae in the ectocochleates, are absent. In section the rods give an impression of a granular structure, in contrast to tabular nacre, which in section look like columns of tabulae. In addition to the belemnites, lamello-fibrillar nacre has only been observed in the septa of the following coleoids: *Groenlandibelus*, *Naefia*, *Adygeya* and *Donovaniconus.* Thus, the nacre Type II is a diagnostic feature of fossil coleoid shells and is missing in bactritoids and orthoceratids.

Comparative ultrastructural studies of the Carboniferous bactritoid *Bactrites* sp. and "*B.*" *postremus* to Recent and fossil spirulids lead us to conclude that spirulids were present during Carboniferous time (Doguzhaeva *et al.* 1996, 1999a). The family Shimanskyidae was erected to accommodate *Shimanskya postremus*, the oldest so far known spirulid. Scanning electron microscopy reveals that Recent *Spirula* inherited the shell wall ultrastructure that is very similar to that of the Upper Carboniferous *Shimanskya postremus* and Cretaceous members of the order Spirulida (Doguzhaeva 2000b). Moreover, comparison of the shell wall structure in *Spirula* and extinct taxa that presumably belonged to spirulids suggests that in the lineage of Spirulida the shell possessed an outer plate instead of a rostrum. That means that taxa that had a rostrum can not be interpreted as precursors of *Spirula* (Doguzhaeva 1996a, 2000b). This gives additional support to the idea that the spirulids and true belemnites (Order Belemnitida) are distinct and well separated in their early evolutionary history. This conclusion contradicts the wide spread opinion introduced by Naef (1922) that evolution of the *Spirula* lineage was accompanied by the reduction and loss of a rostrum. That idea was criticized by Jeletzky (1966, p. 62) who supported the hypothesis that the hypothetical Mesozoic common ancestors of the Tertiary Sepiida and Groenlandibelidae were similar to *Groenlandibelus* and *Naefia* in having a slender orthoconic phragmocone with a thin covering of the internal shell.

Shimanskya (Virgilian = Stephanian) could have co-existed in time with the phragmocone-bearing coleoids (Missourian = Kasimovian) that, like *Donovaniconus,* are known to have had an ink sac (Doguzhaeva *et al.* 2002a). They are herein referred to as the ink-bearing Stark coleoids as they were found in the Stark Formation in Nebraska, USA (Doguzhaeva *et al.* 2002). These forms can be separated into several different taxa on the basis of the presence of a long versus short body chamber/pro-ostracum length, ink sac position in the body chamber, and the amount of shell mineralization. On some specimens the phragmocones have a thin shell wall showing a fibrous pattern on some surfaces, and on other specimens there are closely spaced septa and proportionally long mural parts of septa. None of the specimens shows a rostrum.

The systematic position of *Jeletzkya* remains uncertain in that the characteristics of its phragmocone and shell ultrastructure are unknown, and the presence of fossil ink has not been reported in this fossil. However, the presence of arm hooks on the ten-armed fossil suggests that this taxon could be placed in the Order Phragmoteuthida.

The Late Carboniferous phragmocone-bearing coleoid *Rhiphaeoteuthis margaritae* comes from the Orenburgian of southern Urals, Kazakhastan Republic and is placed in the family Rhiphaeoteuthidae (Doguzhaeva 2002b). The phragmocones of both *Rhiphaeoteuthis* and *Donovaniconus* are similar to the phragmocones seen in the true belemnites. They are orthoconic, with short camerae and a small, ventral marginal siphuncle, long mural parts of septa, short (cyrthochoanitic dorsally and long holochoanitic ventrally) septal necks. However, a significant difference in *Donovaniconus* is that it has a long body chamber, whereas the body chamber appears to be present in *R. margaritae* at adolescent stages and absent in the mature stages of ontogeny. Because of this difference, the family Donovaniconidae is erected to accommodate the genus *Donovaniconus oklahomensis*, and both families are referred to the Order Phragmoteuthida.

Mutveiconites mirandus co-existed with the coleoid *Rhiphaeoteuthis* from the southern Urals, Kazakhstan Republic (Doguzhaeva 2002b). *Mutveiconites* has a slender longiconic shell and could easily be mistaken for a juvenile bactritoid or orthocerid if it were not for the short rostrum. The shell exhibits a small marginal siphuncle, short septal necks; comparatively long camerae; a long body chamber; shell wall formed by thin inner prismatic and thick nacreous layers; no distinct primary constriction, and no primary varix. Its cone-like rostrum covers the oval protoconch and about the first ten camerae; the conical post-protoconch part is shorter than the protoconch length. The rostrum is similar to a primordial rostrum in belemnites (compare: Doguzhaeva *et al.* 2003). The family Mutveiconitidae was erected for this form on the basis of the following features: longiconic phragmocone with comparatively long camerae with small ventral marginal siphuncle; short rostrum coating the protoconch and about the first ten camerae, conical post-protoconch part shorter than protoconch length; body chamber present at least at early stages of growth; mature stages are unknown. It is so far unknown if *Mutveiconites* had a closing membrane like belemnoids or if it had a caecum like *Groenlandibelus* (Jeletzky 1966). In *Mutveiconites* the conotheca includes a nacreous layer that comprises the bulk of the shell wall thickness. The presence of a nacreous layer in *Mutveiconites* indicates that it cannot be a spirulid genus. Because of the longiconic shell with relatively long chambers, the shell wall with a nacreous layer, and the presence of a short, well-defined rostrum, the family is referred to the Order Aulacocerida.

LIST OF CARBONIFEROUS PHRAGMOCONE-BEARING COLEOIDEA

(Modified from Doyle *et al.* 1994)

Subclass COLEOIDEA Bather, 1888
  Superorder BELEMNOIDEA Hyatt, 1884
  (? Devonian; Carboniferous - Cretaceous)
    Order HEMATITIDA Doguzhaeva, Mapes and Mutvei, 2002 (Carboniferous)
      Family HEMATITIDAE Gustomesov, 1976

Hematites Flower and Gordon, 1959 - Upper Mississippian, Lower Eumorphoceras Zone (=Serpukhovan), Utah, Arkansas, USA.
Bactritimimus Flower and Gordon, 1959 Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovan), Arkansas, USA.
Paleoconus Flower and Gordon, 1959 - Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovan), Arkansas, USA.
Order PHRAGMOTEUTHIDA Jeletzky in Sweet, 1964 (Carboniferous - Jurassic)
Family DONOVANICONIDAE Doguzhaeva, Mapes and Mutvei, 2002 -
Donovaniconus Doguzhaeva, Mapes and Mutvei, 2002 - Upper Pennsylvanian, Desmoinesian, Oklahoma, USA.
Family RHIPHAEOTEUTHIDAE Doguzhaeva, 2002
Rhiphaeoteuthis Doguzhaeva, 2002 - Upper Carboniferous, Orenburgian, Southern Urals, Kazakhstan Republic (former USSR)
Order AULACOCERATIDA Stolley, 1919 (?Devonian; Carboniferous - Jurassic)
Family MUTVEICONITIDAE Doguzhaeva, 2002
Mutveiconites Doguzhaeva, 2002 - Upper Carboniferous, Orenburgian, Southern Urals, Kazakhstan Republic (former USSR).
Superorder DECABRACHIA Haeckel, 1866 (Carboniferous - Holocene)
Order SPIRULIDA Pompecky, 1912
Family SHIMANSKYIDAE Doguzhaeva, Mapes and Mutvei, 1999
Shimanskya Doguzhaeva, Mapes and Mutvei, 1999 - Upper Pennsylvanian, Virginian (= Stephanian); Texas, USA.
Order and/or Family Uncertain
?***Eobelemnites*** Flower, 1945 - Upper Mississippian, Chesterian, Alabama, USA
? Unnamed coleoid from Czech Republic (Kostak *et al.* 2002) - Early Carboniferous, Moravica Formation, Northern Moravia, Czech Republic
Undescribed Stark Formation coleoids (Doguzhaeva, Mapes, Mutvei & Pabian 2002) - Upper Pennsylvanian, Missourian (= Kasimovian), Nebraska, USA
Jeletzkya douglassae Johnson and Richardson, 1968 – Upper Carboniferous Desmoinesian, Mazon Creek, Illinois, USA

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