Chapter 14
The Body Chamber Length Variations and Muscle and Mantle Attachments in Ammonoids

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14.1 Introduction

The body chamber with the preserved mantle and muscle attachment marks provide some insight into the poorly known soft body organization and locomotion of extinct cephalopods (Trueman 1941; Mutvei 1957, 1964, 2013; Ivanov 1975; Kennedy and Cobban 1976; Chamberlain 1980, 1993; Saunders and Shapiro 1986; Zaborski 1986; Hewitt et al. 1991; Jacobs and Chamberlain 1996; Landman et al. 1996; Westermann 1996; Westermann and Tsujita 1999; Doguzhaeva et al. 2002, 2003a, b, 2010; Richter 2002; Richter and Fischer 2002; Mutvei and Dunca 2007; Klug 2004; Klug et al. 2007, 2008; Korn and Klug 2007). One of the ways to achieve a better understanding of these paleobiological questions is to continue recollecting localities famous for preservation of non-mineralized parts to recover ammonoid shells with unbroken body chambers and shell apertures, weakly recrystallized original shell material, traces of mantle and muscle attachments in the body chamber, and fossilized mantle tissue. Using this approach, previously unknown "unusual" large ventrolateral marks of the muscle and body chamber attachment structures were discovered in complete body chambers showing shell apertures and also containing buccal apparatuses (Doguzhaeva and Kabanov 1988; Doguzhaeva and Mutvei 1990, 1991, 1992, 1993a, b; Doguzhaeva 2014). In several specimens, the additional small spot near the foremost part of the large mark is separated (Doguzhaeva and Mutvei 1991, pl. 2, fig. 4; pl. 4, fig. 1, pl. 6, fig. 2). This suggests, by comparison with the squids (Wells 1988), that in some ammonoids, the cephalic retractor and funnel retractor muscles might have been well-developed and permitted

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jet-powered swimming (Doguzhaeva and Mutvei 1991, 1996; Doguzhaeva 2014). The two side by side ventrolateral marks support the assumption of higher-energy coleoid-like mode of locomotion in some ammonoids (Wells and O'Dor 1991; Jacobs and Chamberlain 1996), but conflicts with the widely spread opinion (based on small attachment marks) of a weakly developed muscular system and insufficient capacity of the ammonoids for jet-powered swimming (see Mutvei and Reyment 1973; Jacobs and Chamberlain 1996; Monks and Young 1998). In *Nautilus,* the funnel retractor muscles are part of branches of the cephalic retractor muscles, which originate from the inside part of the head and funnel and are inserted on the shell laterally. The cephalic retractor muscles drive lower speed jet-powered swimming (see Griffin 1900; Mutvei 1957, 1964; Mutvei et al. 1993; O'Dor et al 1990; Sasaki et al. 2010).

The mantle, so far known in the Late Triassic ceratitid *Austrotrachyceras*, was also found due to investigation of cephalopod remains from the paleoenvironment providing non-biomineralized structures (Doguzhaeva et al. 2004, 2007a, b; Doguzhaeva and Summesberger 2012). Fine lamination of the fossilized mantle is thought to have resulted from the original lamination of the muscular tissue. In coleoids, the mantle is thickened with layers of muscles and connective tissue but it is thin in *Nautilus* (Kier 1988; Kier and Thompson 2003; Sasaki et al. 2010).

Herein, the ontogenetic and evolutionary variations of the body chamber length and traces of mantle and body chamber attachment in Paleozoic and Mesozoic ammonoids (Appendices 1, 2) are analyzed. The mantle and the body chamber attachment marks of the Early Cretaceous heteromorph ammonoid *Audouliceras* from Ulyanovsk, Russia, are worth to be herein demonstrated in detail. They were observed in two large mature shells with aragonitic preservation and nearly complete body chambers (Doguzhaeva 2014). The possibilities of jet-powered swimming in some ammonoids together with the fossilization of the mantle and the mantle and body chamber attachment marks are discussed.

The illustrated heteromorphs (Figs. 14.1–14.4) are from the private collection of G. K. Kabanov (Moscow) donated to the first author. Prefix DPC preceding specimen numbers denote repository: Doguzhaeva's private collection.

14.2   Previous Studies

Münster (1839) and Suess (1865) were apparently the first researchers who demonstrated that the body and body chamber attachment marks and the variability of the body chamber length are potentially important aspects of the paleobiological study of ammonoids. After them, Crick (1898) described small scars in 13 genera of Paleozoic and Mesozoic ammonoids, suggesting that they served for shell and soft tissue attachment. Following Suess's idea (1865) on the taxonomic value of the body chamber length, Haug (1898) subdivided the Devonian ammonoids into two groups: Brevidoma, including the Agoniatitidae, characterized by a short body chamber ranging from half a whorl to a complete whorl, and Longidoma, comprising

the Anarcestidae, in which the body chamber length ranges from a complete whorl to 1.75 of a whorl. Arthaber (1911) accepted the erection of two groups in ammonoids based on the body chamber length and suggested the new names Microdoma and Macrodoma for them. Diener (1916a) established the intermediate group Metridoma for the ammonoids with body chamber lengths from 0.75 to one whorl. The essential variations of the body chamber length in taxa that were considered at that time to be closely related, were documented by Diener (1916a); he rejected the taxonomic value of the body chamber length (Diener 1916b). Trueman (1941) measured the body chamber length in about 80 ammonoid species and revealed two frequency peaks corresponding to 260 and 380 degrees. Ruzhencev (1962) suggested that a long ammonoid body chamber provided protection of the phragmocone; this conclusion was based on his observation of body chamber lengths that exceeded one whorl on specimens with complete apertures from the Late Paleozoic from southern Urals. Ruzhencev (1962) found also that the body chambers are usually shorter in prolecanitids than in goniatitids. Because of this, he confirmed a potential taxonomic value for body chamber length. Jones (1961) reported small umbilical and mid-ventral scars in a heteromorph ammonite. Jordan (1968) recorded the attachment scars in 22 Mesozoic genera, and in addition to small mid-dorsal scars, reported large lateral U-shaped marks interpreted as pallial line. In the end of the 20th and at the beginning of 21st century, the mid-dorsal and mid-ventral scars were revealed on the internal moulds of the phragmocones in a large number of Mesozoic genera of different systematic positions (Bandel 1982; Landman and Bandel 1985; Weitschat 1986; Weitschat and Bandel 1991; Sharikadze et al 1990; Richter 2002; Richter and Fischer 2002). Large ventrolateral marks extending from the last septum to about the midpoint of about 180 degrees long body chambers were documented in two Early Cretaceous genera (Doguzhaeva and Kabanov 1988). These unusually large and robust muscle scars co-occurred with the small mid-ventral, mid-dorsal and umbilical scars. The excellent preservation allowed the reconstruction of the mantle and muscle configuration inside the body chamber of *Aconeceras* (Doguzhaeva and Mutvei 1990, 1991, 1993a, b). Doguzhaeva and Mikhailova (1991) described the muscle scars in the Early Cretaceous heteromorph ammonite *Ancyloceras*. Sharikadze et al. (1990) documented mid-dorsal, mid-ventral and the large ventrolateral scars in a large number of ammonites from the Late Jurassic Volga Region and from Early Cretaceous sediments collected in the Adygeya Republic, north-west Caucasus, Russia. Doguzhaeva and Mutvei (1991) suggested principal anatomical differences between ammonoids and *Nautilus* in the muscular systems, shape of head-funnel region and its relationship to the shell aperture, and certain similarities between ammonoids and recent coleoids in the possible development of strong funnel retractors. Kyuma and Nishida (1987) recorded that the longest body chamber belonged to the Late Carboniferous goniatite *Akiyoshiceras* from Japan. While none of the specimens available to them had a complete body chamber with an aperture, the incomplete body chamber lengths of some of the Japanese specimens exceeded two complete whorls. A specimen of this genus from Oklahoma has a body chamber length of approximately two and a half whorls (RHM, personal observation) with a mature modification of the aperture giving a

body chamber length for the genus of approximately 900º. Kyuma and Nishida (1987) also noted that there were paired raised ridges and depressions about midway on the body chambers on some Japanese specimens. These ridges and depressions are almost certainly related to muscle attachments that possibly allowed extension and retraction of the body mass of the animal. However, anatomical details have not been studied at this time. Saunders and Work (1997) carried out experimental study on shell buoyancy and calculated the body chamber lengths of some Paleozoic ammonoids. They came to the conclusion that the two stocks Goniatitida and Prolecanitida differ in body chamber length. Their experimental data were supported by their observations on the body chamber lengths in three prolecanitid genera. Thus, the hypothesis of Ruzhencev (1962) on the body chamber length as an additional trait distinguishing prolecanitids, which gave rise to the Mesozoic ammonoids, was supported. In the Middle Carboniferous *Goniatites,* Tanabe et al. (1998) recorded mid-ventral marks and traces of pseudosutures. Dagys and Keupp (1998) described a pair of ventral internal keels in the two Middle Triassic ceratitids *Czekanowskites* and *Arctohungarites* from Arctic Siberia. The keels extend in the body chamber for 80° from the last septum. The authors suggested that the ventral internal keels might be the attachment structures of the funnel retractors. Monks and Young (1998) suggested that to maintain hydrodynamic stability, the heteromorph ammonoids might have changed their centers of gravity by the forward-backward shifting of a comparatively short body within the long body chamber. Kröger (2002) used this model for the explanation of the healing of an extensive damage seen on the monomorph shells of Jurassic ammonoids with a long body chamber; this damage extends over about two thirds of the body chamber length. He also concluded that a withdrawal of more than 35 degrees into the body chamber was only a strategy of emergency, and that longidome ammonoids were able to withdraw deeper into the body chamber. He suggested that the dactyliocatids characterized by a long body chamber possibly had a normal variability of soft body position between the aperture and 35° behind it. Kröger (2002) published new data on the body chamber length in five Jurassic genera and came to the conclusion that long (more than one whorl) body chamber lengths protected the phragmocone against lifetime damage, an idea previously presented by Ruzhencev (1962). Richter (2002) as well as Richter and Fischer (2002) reported small mid-ventral, mid-dorsal, umbilical and large ventrolateral marks in a number of Paleozoic and Mesozoic ammonoids. Klug (2004) recorded the shortest known body chamber (about 120 degrees long) on the Middle Triassic genus *Ceratites*. Later, Klug et al. (2007) observed on a Middle Triassic specimen of *Ceratites* a set of structures on the internal mould of the body chamber and phragmocone that were interpreted by them as the attachment marks of the cephalic retractors, the mantle myoadhesive band, the paired dorsal muscles, the unpaired ventral muscle, and the black layer. In the Early Carboniferous goniatite (?*Rhadinites* or ?*Anthracoceras*)*,* Landman et al. (2010) documented "*a spiral red band that extends from midway in the body chamber to the apical end of the jaw (Figs 3A, B, F). The position of this feature matches that of the cephalic retractor muscle illustrated in the reconstruction of Cretaceous ammonoids by Doguzhaeva and Mutvei* (1996*, Fig. 7*)". In the same specimens,

Landman et al. (2010) revealed the mid-dorsal band extending for about 200 degrees in the long body chamber, with the estimated length of more than one whorl.

14.3   Terminology and Abbreviations

The following terms are used in the present paper for characterizing the body chamber lengths and the body and body chamber attachment marks. Depending on their position in the body chamber, the marks are arranged in six categories: dorsal, umbilical, dorsolateral, lateral, ventrolateral and ventral.

Annular elevation (ae)—dorsolateral posterior structure in body chamber; formed by a swollen inner prismatic layer of shell wall;

Dorsal band (db)—dorsal dark color band-like attachment structure along the median plane of body chamber and phragmocone;

Dorsal ridge (dr)—dorsal thread-like ridge-shaped attachment structure along the median plane of body chamber and phragmocone; known in clymeniids;

Dorsal discrete mark (d)—dorsal small discrete attachment scars along the median plane of the body chamber and phragmocone;

Lateral mantle V-shaped sinus (lms)—this is a delicate mantle structure here recorded for the first time; it is evidenced by repetition of fine uneven lateral V-shaped lines on the body chamber in *Audouliceras* (Fig. 14.3). This structure is clearly different from the sinus-like attachment mark (Figs. 14.3, 14.5);

Lateral sinus (ls)—sinus-like attachment mark on sides of body chamber;

Long body chamber—length range is about 370º–900º;

Medium–long body chamber—length range is about 270º–370º;

Myoadhasive elevation (mae)—the elevation in front of the last septum;

Myoadhasive gutter (mg)—thin ridge surrounding the annular elevation;

Ventral band (vb)—ventral band-like structure along the median plane of body chamber and phragmocone visible due to its colour surface, lack a relief on the shell wall or on the internal mould of the body chamber;

Short body chamber—length range is about or shorter than 270 degrees;

Ventral discrete mark (v)—ventral small rounded or oval discrete marks along the median plane of body chamber and phragmocone;

Ventral ridge (vr)—ventral thread-like ridge along the median plane of body chamber and phragmocone;

Ventrolateral elevations (ve)—(= internal ventral keels by Dagys and Keupp 1998) two spiral elevations on the inner surface of the body chamber extending for about 80 degrees from the last septum;

Ventrolateral lobe-like marks (vl)—ventrolateral large lobe-like attachment marks; extend from the last septum approximately to the midpoint of the body chamber;

Umbilical small discrete mark (us)—discrete small, less than the interval between two neighbouring septa of the phragmocone, marks located at the umbilical corners of body chamber;

Umbilical tongue-like marks (ut)—elongated attachment marks in the umbilical corners of the body chamber; comparatively broad posteriorly and narrowing anteriorly, extend from the last septum for about 1/5-1/3 of the body chamber length.

14.4   Ontogenetic and Evolutionary Variations of Body Chamber Length

The data on body chamber length of 120 genera from the orders Goniatitida, Prolecanitida, Clymeniida, Ceratitida, Phylloceratida, Lytoceratida and Ammonitida are represented in Appendix 1. The body chamber lengths of ammonitellae of 73 genera and of the adult shells of 42 genera is shown as well; 18 genera show the body chamber length, both in the ammonitellae and in adult shells. These data are summarized as follows:

1. The range of body chamber length varies between 223º–410º in ammonitellae and between 180º–900º in adults. This shows that in ammonitellae, the body chamber length varies in smaller range than in the adults.
2. The minimum length of the body chamber of the ammonitella is 300º in goniatitids (*Glaphyrites*), 290º in prolecanitids (*Hedenstroemia*), 230º in ceratitids (*Arctohungarites* and *Crumbergia*) and phylloceratids (*Holcophylloceras*), 260º in lytoceratids (*Eurystomiceras*), and 242º in ammonitids (*Subprionocyclus*) (Appendix 1). The ammonitellae possessing the longest body chamber (410º) are recorded in the order Goniatitida; the ammonitellae with the shortest body chamber (223º) are from the order Phylloceratida. Thus, the evolutionary development of the angular length of the body chamber shows a long-term decreasing trend of the ammonitella body chamber length in the goniatitids–prolecanitids–ceratitids–phylloceratids branch. This long-term trend supposedly indicates the common early ontogenetic evolutionary direction of the goniatitids, prolecanitids, ceratitids and phylloceratids. The reversal of this trend in the lytoceratids and ammonitids presumably indicates a different and innovative early ontogenetic strategy of these two groups in the Jurassic.
3. The ontogenetic decrease of the body chamber length is documented in the following genera (Appendix 1): Prolecanitida, *Metapronorites*—from 340º in ammonitella to 250º in the adult shell; *Neopronorites*—from 310º–340º in the ammonitella to 230º in the adult shell; Ceratitida, *Sakmarites*—from 340º in the ammonitella to 225º in the adult shell; Lytoceratida, *Eurystomiceras*—from 290º–300º in the ammonitella to 270º in the adult shell; Perisphinctida *Indosphinctes*—from ca. 330º in the ammonitella to ca. 180º–220º in the adult shell; Ammonitida *Deshayesites*—from 307º–330º in the ammonitella to 180º in the adult shell; ammonitid *Aconeceras*—from 270º–360º in the ammonitella to 180º at the 7th to 8th whorls. The ontogenetic increase of the angular body chamber length is documented in the goniatite *Neoglyphioceras* (from 360º in the ammonitella to >450º at 32 mm diameter adult shell) and in the ceratitids *Proarcestes* (from c. 360º in the ammonitella to >450º in the 8th whorl), *Phyllocladiscites* (from c. 330º in the ammonitella to 360º at the 9th whorl), and *Prosphingites*

(from 265º in the ammonitella to c. 360º in the adult shell). Thus, the ontogenetic development of angular length of the body chamber in these ammonoid groups shows either a decrease in body chamber length (Miller et al. 1957) or an increase in body chamber length (Doguzhaeva 1990). In no known case does the ammonitella body chamber length remain the same throughout ontogeny.

14.5   Muscle and Mantle Attachment Marks, and their Interpretation

The data on the mantle and body chamber attachment marks or scars in mature shells of 102 genera from the orders Goniatitida, Prolecanitida, Clymeniida, Ceratitida, Phylloceratida, Lytoceratida and Ammonitida are given in Appendix 2. The marks are interpreted as traces of the mantle and the body chamber attachment because of their regular arrangement in different ammonoid taxa in various lineages from the Devonian to the Cretaceous. The marks originated on the inside of the body chamber wall, but during ontogeny, the marks became part of the phragmocone wall where some marks remained visible and others are probably hidden under the shell of the dorsal wall. The muscle attachments are best observed in mature shells because deposition of shell material around the mark sites probably took a long time. The castings of these marks by internal moulds formed by Fe-containing minerals have yielded extensive information on the mantle and body chamber attachment. The marks are arranged in five categories depending on their position in the body chamber: dorsal, dorsolateral, lateral, ventrolateral and ventral; these are briefly characterized and discussed in the following interpretations.

14.5.1   Dorsal Marks

The dorsal discrete scars, dorsal band, and dorsal internal ridge are the marks arranged along the median plane on the dorsal side of the body chamber (Appendix 2). The dorsal marks produced earlier in the ontogeny are often visible between the septa in the phragmocone. These marks were, in all probability, the attachment areas of the dorsal muscles. To judge from the small size of the dorsal marks and their remoteness from the anterior of the body chamber, the dorsal muscles must have been comparatively weakly developed and restricted in extension to the posterior part of the mantle.

14.5.1.1   Dorsal Small Discrete Marks

Relatively small, rounded, oval or cruciform marks with a typically rugose texture in the dorsal position are located in the body chamber immediately in front of the last septum inside the internal (dorsal) lobe of the last suture. These discrete dorsal marks

are interpreted as evidence of the periodic interruption of the attachment of the body tissue during its periodic shifting forward with shell growth. The marks are often expressed on the interior of the body chamber shell surface by a positive relief rugose structure that is repeated at regular intervals in the juvenile portions of the phragmocone and at the posterior end of the mature body chamber. These marks seem to be a universal structure in the ammonoids or have higher potential for preservation as they are observed in the shells lacking any other attachment marks or in association with the other attachment marks (Appendix 2). Those produced earlier in ontogeny often visible between the septa in the phragmocone; every chamber has a solo mark.

14.5.1.2   Dorsal Band

The dorsal band is a brown or black stripe, which forms neither a relief, rugosity nor porous surface on the dorsal side of the body chamber (Figs. 14.1, 14.4). In long body chambers with lengths of more than one whorl, the middorsal band extends for about 200° (Landman et al. 2010). The intensive color difference between the middorsal band and the matrix apparently indicates the originally high content of non-biomineralized "soft" material in the body chamber wall along its middorsal side. During shell growth, the middorsal band remains visible in the chambers of the phragmocone. Contrary to the discrete dorsal marks, the dorsal band indicates continuous attachment of the body during its shifting within the growing shell.

14.5.1.3   Dorsal Internal Ridge

This is a thread-like elevation in the body chamber, which is located in the dorsal median plane. This dorsal internal ridge bears a weak transverse striation. The dorsal internal ridge extends for about one-third to one-fourth of the body chamber length. It is sometimes preserved on the external surface of the phragmocone and its length can indicate the length of a missing portion of the body chamber (B. I. Bogoslovky, personal communication, 1980's). To our knowledge, this feature is only known in clymeniids.

14.5.2   Umbilical Marks

These marks are situated in the shoulders of the body chamber (Appendix 2). There are two kinds of marks: umbilical small discrete rounded or transverse kidney-shaped marks and large tongue-like marks.

14.5.2.1   Umbilical Small Discrete Marks

These marks, which are shorter than the distance between two adjacent septa, are rounded imprints located in the umbilical region posterior to the terminal septum. A
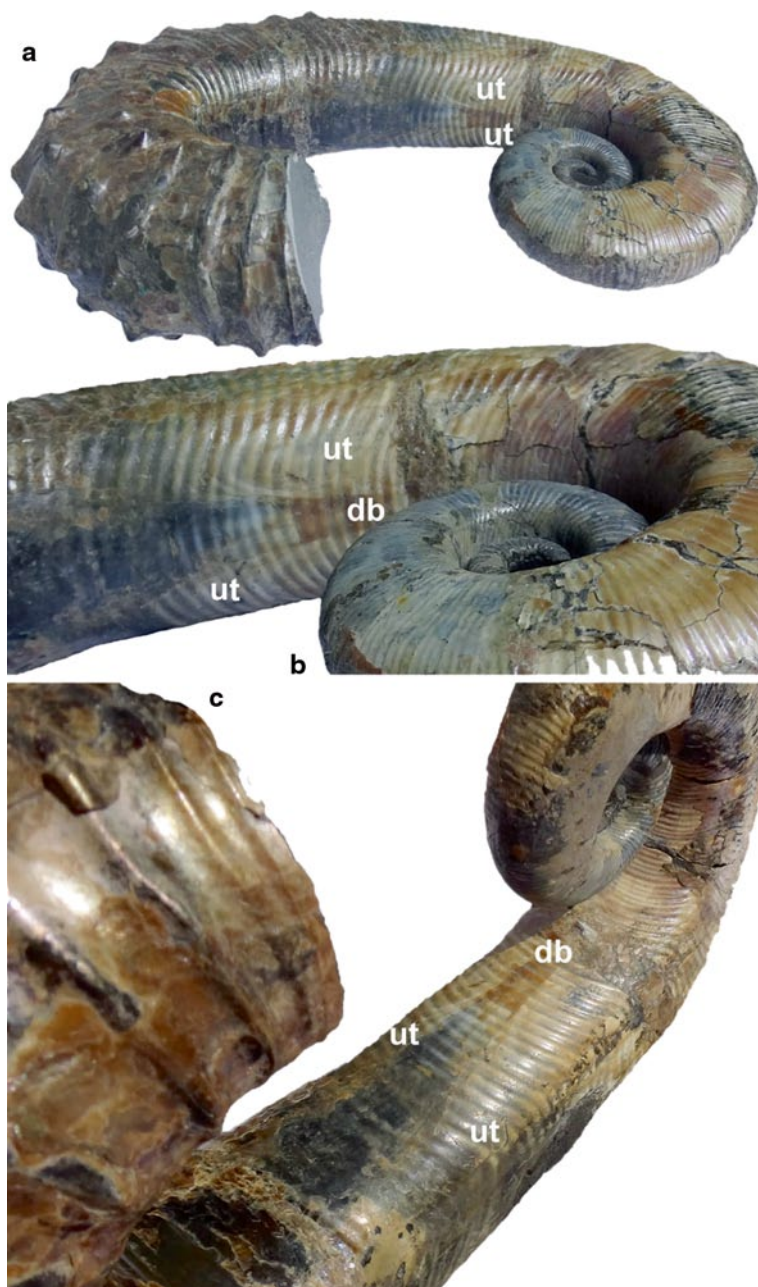
Fig. 14.1 *Audouliceras renauxianum* (d'Orb., 1841), DPC/1. Aptian, Lower Cretaceous; Uly-anovsk Region, Central Russia. Fully-grown shell showing umbilical tongue-like marks in the posterior portion of the body chamber; **a** × 0.5, **b** × 0.8, **c** × 0.6. *db* dorsal band, *ut* umbilical tongue-like mark

set of these marks remains visible on the phragmocone so that every chamber of the phragmocone has a single mark. The imprints of these marks are formed by minute raised tubercles, which are the hole fillings in the inner surface of the inner shell surface. The discrete character of these scars indicates the periodically interrupted attachment between the mantle and the body chamber during the forward movement of the body in the growing shell. These marks are observed in shells with a short, medium and long body chamber (Appendices 1, 2).

Based on the relatively small size and location in the posterior portion of the body chamber, these small umbilical marks must have been the attachment sites of the branches of the muscles in the posterior portion of the muscular mantle to the inner shell wall.

14.5.2.2 Umbilical Large Tongue-Like Marks

The tongue-like umbilical marks have only been observed in the terminal body chambers of Cretaceous heteromorphs including *Audouliceras* (Figs. 14.1, 14.2, 14.3, 14.4; Doguzhaeva 2014), *Ancyloceras* (Doguzhaeva and Mikhailova 1991), *Ptychoceras* (Doguzhaeva and Mutvei 2015), *Pseudocrioceratites* (DLA, personal observation), and possibly in *Baculites* (Kennedy et al. 2002, pl. 6, Figs. 1, 2). These marks are relatively broad posteriorly, narrow anteriorly, and extend for about 20–30% of the body chamber length along the umbilical corners (Figs. 14.1, 14.2, 14.3, 14.4). In *Pseudocrioceratites*, the mark is a tongue-like depression on the internal mould of an incomplete body chamber. In *Audouliceras, Ancyloceras* and *Ptychoceras*, the umbilical tongue-like marks are recognized by their nacreous incrustation retained on dark grey siderite internal moulds of body chambers. In these three genera, the tongue-like marks comprise small rounded brownish marks placed in the umbilical corners (Fig. 14.2). In *Audouliceras,* there are two equal sized marks situated close to each other located near the body chamber midpoint (Fig. 14.2). In *Ptychoceras*, the small rounded marks within the tongue-like umbilical marks are arranged in two pairs, one of which is situated in front of the last septum, and the next pair is situated near the midpoint of the body chamber (Doguzhaeva and Mutvei 2015).

The tongue-like umbilical marks show that in the heteromorphs listed above, the mantle and the body chamber attachment sites moved forward to the middle part of the body chamber and are probably the attachment sites of the powerful umbilical retractor muscles. In heteromorph ammonoids with a planispiral irregularly coiled or hook-shaped body chamber, the development of these muscles might have speculatively occurred in order to change the mantle cavity volume to improve filter feeding on small planktonic organisms (Doguzhaeva 2014). This mode of feeding is supported by the three-dimensionally preserved jaw apparatus extracted from the body chamber of the Early Cretaceous heteromorph *Australiceras* (Doguzhaeva and Mikhailova 2002). The jaw apparatus lacks a rostrum and has a large cavity between the lower and upper jaws, which is formed by the deep and wide lower jaw with a solid flat ventral side, and the long wings of the upper
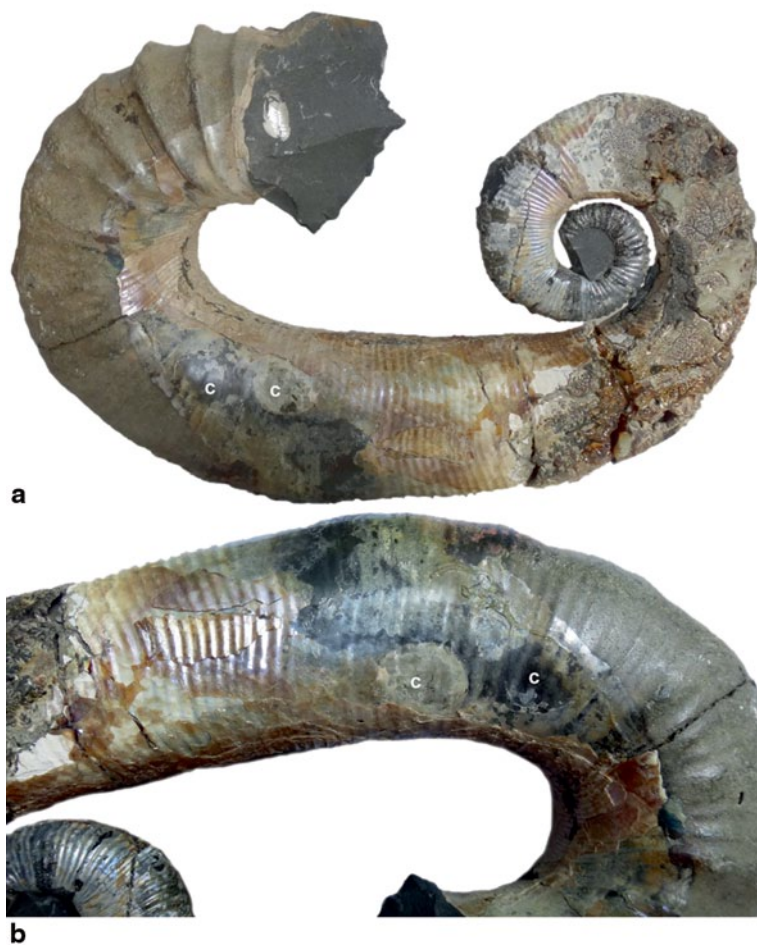
Fig. 14.2 *Audouliceras renauxianum*, DPC/2. Aptian, Lower Cretaceous; Ulyanovsk Region, Central Russia. Fully-grown shell showing rounded umbilical scars within the umbilical tongue-like marks in the middle part of the body chamber; **a** Lateral view, ×0.6. **b** Close-up of (a) to show two side by side rounded marks, ×0.7. *c* umbilical rounded scar within the umbilical tongue-like mark

jaw. The absence of the rostrum suggests that *Australiceras* did not hunt for large prey; hence, there was no need to hold and crush large prey. Large surfaces of the wings could serve as sites for the attachment of well-developed buccal muscles, suggesting that the large cavity between the lower and upper jaws could be used for sucking and filtering seawater, which suggests that these organisms fed on minute plankton or suspended organic particles. This hypothesis is supported by the heavily ribbed shell of *Australiceras*, which has the shape of irregular coiled
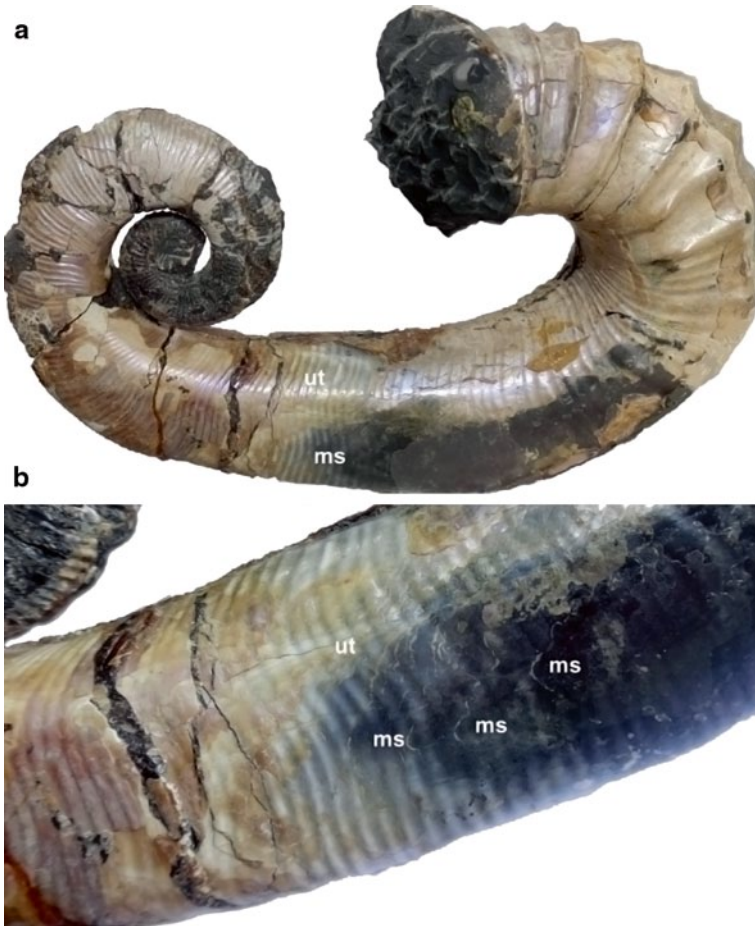
Fig. 14.3 *Audouliceras renauxianum* (d'Orbigny, 1841), DPC/2. Aptian, Lower Cretaceous; Ulyanovsk Region, Central Russia. **a** Lateral view of fully-grown shell showing lateral V-shaped sinus of the mantle, ×0.6. **b** Close-up of (**a**) to show the repetition of muscle scar traces in the lateral sinus that were apparently left during the movement of the mantle; ×1. *ms* muscle scar, *ut* tongue-like mark

spiral, i.e., the form best suited to floating and perhaps vertical (diurnal) migrations (Doguzhaeva and Mikhailova 2002).

14.5.3 Lateral Marks

14.5.3.1 Lateral Sinus-Like Attachment Marks

The lateral sinus-like marks are adaperturally open, relatively large in comparison with the body chamber length, with sinus- or bay-shaped outlines on the body

Fig. 14.4 *Audouliceras renauxianum* (d'Orbigny, 1841) : A, C, DPC/1; B, DPC/2. Aptian, Lower Cretaceous; Ulyanovsk Region, Central Russia. **a** Ventral view of the body chamber (aperture is down) showing a colour ventral band with a rounded ventral mark ending the ventral band and the ventral ridge in front of the ventral mark; ×1.2. **b** Dorsal view of the posterior portion of the body chamber to show a colour dorsal band between the paired umbilical marks; ×1.5. **c** Two umbilical rounded scars within the umbilical tongue-like marks; ×1.3. *db* dorsal band, *ut* umbilical tongue-like mark, *c* umbilical rounded scar within the umbilical tongue-like mark, *v* ventral rounded scar, *vb* ventral band, *vr* ventral ridge

chamber sides. The lateral sinusoidal marks extend from the posterior portion of the body chamber to about its midpoint. This mark is narrowly rounded behind and gets broader in the adapertural direction. It may co-occur with ventrolateral and other marks (Appendix 2). The morphology of the sinus-like attachment marks is here illustrated by those of *Deshayesites* (Figs. 14.5, 14.7b). Their function is unknown.

Fig. 14.5 Shape variations of ventrolateral attachment marks in the body chamber of three specimens of *Deshayesites deshayesi*; DPC/3, 4, 5. Aptian, Lower Cretaceous; Ulyanovsk Region, Central Russia. **a** ×3.5. **b** ×3.8. **c** ×3. *bc* body chamber; *vl* ventrolateral mark
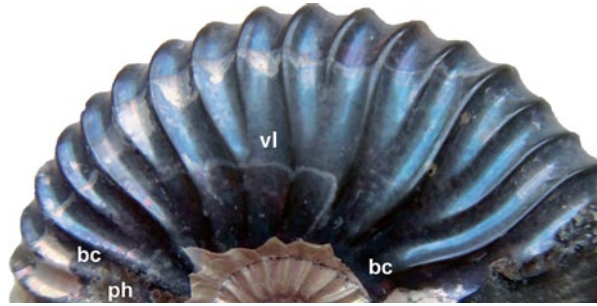
14.5.3.2 Lateral Mantle V-Shaped Marks

The lateral mantle V-shaped marks represent a delicate structure here illustrated for the first time; it is evidenced by repetition of fine uneven V-shaped lines on sides of the body chamber in *Audouliceras* (Fig. 14.3). This structure is clearly different from the sinus-like attachment mark by its extremely fine structure (compare Figs. 14.3, 14.5, 14.7b). It is highly likely that the lateral V-shaped lines reflect the similar pattern of the periphery of the mantle.

14.5.4 Ventrolateral Marks

These are marks situated ventrolaterally of the body chamber; there are lobe-like and sinus-like marks, which can have ridge-like elevations (Figs. 14.6, 14.7a, 14.8, 14.9, 14.10).

14.5.4.1 Ventrolateral Lobe-Like Marks

These are large, adaperturally closed, lobe-like marks on the ventrolateral portions of body chamber. The ventrolateral marks extend from the last septum for about the midpoint of the body chamber. Posteriorly, a pair of these marks is separated on the ventral side with a slit-like interspace, which gets broader towards the anterior portion of the marks (Figs. 14.6, 14.7a, 14.8, 14.9, 14.10). The outline of the ventrolateral marks is usually strengthened with a ridge-like elevation forming a thin rim. Within the marks, additional nacreous and prismatic layers thicken the shell wall.

This type of attachment marks has only been observed in the body chambers, which are shorter than a whorl (Appendices 1, 2). Their adapertural side shows two separated spots situated next to each other. They are considered as potential attachment sites for the cephalic retractor and funnel retractor muscles.
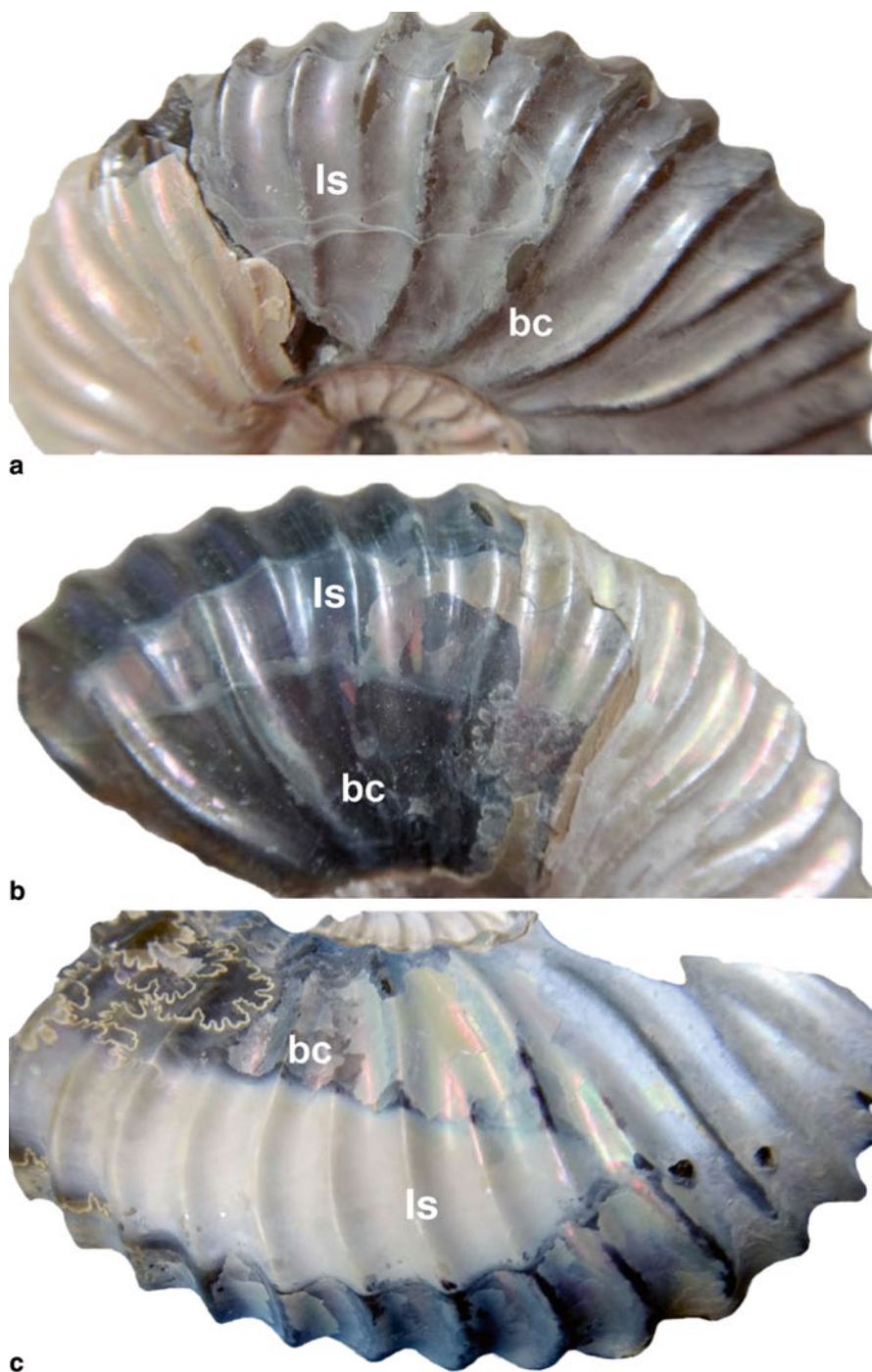
Fig. 14.6 Lateral sinus-like attachment mark in the posterior portion of body chamber in *Deshayesites deshayesi;* Doguzhaeva Private Collection DPC/6. Aptian, *Lower* Cretaceous; Ulyanovsk Region, Central Russia; ×2.6. *bc*, body chamber; *Is*, lateral sinus, *ph* phragmocone

Fig. 14.7 Soft-tissue attachment marks in the body chamber of *Deshayesites deshayesi*. DPC/7, 8. Aptian, Lower Cretaceous; Ulyanovsk Region, Central Russia; **a** ventrolateral muscle mark is getting narrower in adoral direction contrary to lateral sinus-like mark on **b** which is getting broader in this direction; ×2.5 and 2.7, respectively, *bc* body chamber; ls ventrolateral mark
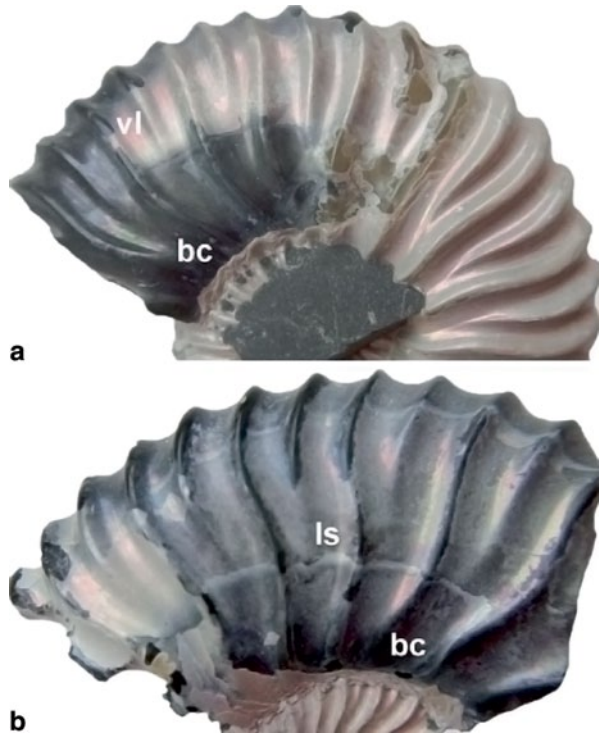

Fig. 14.8 Ventrolateral lobe-like attachment mark in the body chamber of *Aconeceras trautscholdi* (Sinzow, 1870) Doguzhaeva Private Collection DPC/9. Aptian, Lower Cretaceous; Ulyanovsk Region, Central Russia; ×3. *bc* body chamber, *vl* ventrolateral lobe-like mark

Fig. 14.9 Ventrolateral lobe-like attachment mark in the body chamber of *Aconeceras trautsholdi* (Sinzow, 1870); DPC/10. Aptian, Lower Cretaceous; Ulyanovsk Region, Central Russia; ×2.6. *bc* body chamber; *vl* ventrolateral mark

Fig. 14.10 Lateral attachment mark on the phragmocone surface of *Kashpurites* sp. DPC/11. Upper Jurassic, Moscow Region, Russia; x 1.8, *ph* phragmocone; *vl* ventrolateral mark
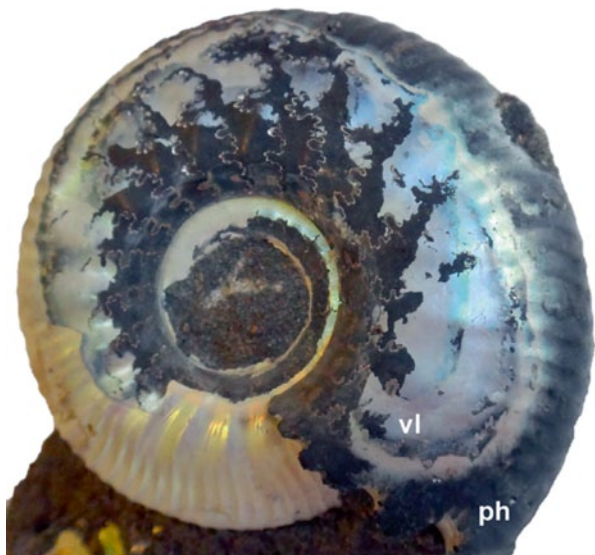
14.5.4.2   Ventrolateral Elevations

These are ridge-like paired structures described as internal ventral keels by Dagys and Keupp (1998). They represent two elevations on the inner surface of the body chamber along the ventral keel and extend from the last septum for about a quarter of the body chamber length.

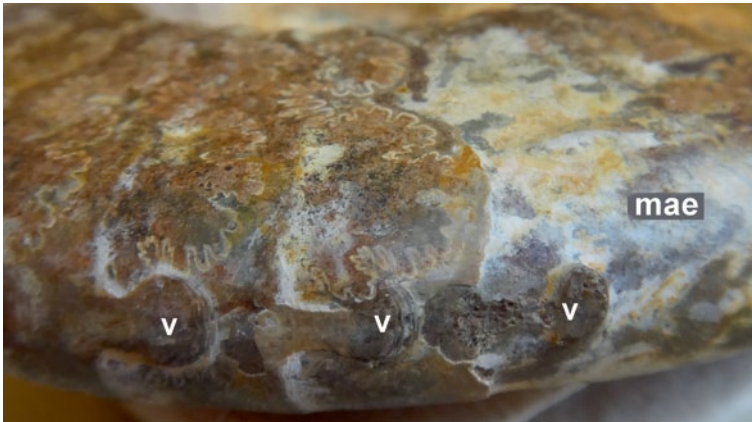**Fig. 14.11** The ventrolateral view on the last chambers of the phragmocone and posterior part of the body chamber of the gerontic shell of *Indosphinctes* sp. DPC/12; Upper Jurassic, Volga River, Central Russia; ×2. *mae* myoadhesive elevation; *v* ventral discrete scars

14.5.5   Ventral Marks

The ventral marks include the ventral small discrete scars, the ventral band, and the ventral ridge. During shell growth, the marks remained distinguishable in the chambers of the phragmocone and were also impressed into the internal mould. The midventral marks are observed in shells with short, moderately long, and long body chambers.

14.5.5.1   Ventral Discrete Marks

The rounded, oval or crescent-shaped mark is situated on the ventral side of the body chamber in front of the ventral lobe of the last suture at the maximum distance about one to three chamber lengths from the last septum, in rare cases in a greater distance (Figs. 14.4a, 14.11). This distance is shorter or equal to the length of the circumsiphonal invagination of the posterior portion of the body where the formation of the new segment of the siphonal tube began (Doguzhaeva 1988; Doguzhaeva and Mutvei 1996). Ventral marks produced earlier in the ontogeny are often visible between the septa in the phragmocone; every chamber has a solo mark (Fig. 14.11). In some shells (Jordan 1968), the ventral marks are partially black or brown; the color apparently originated from the pyritization of organic material within the attachment mark. The discrete ventral is considered evidence of the periodically interrupted attachment of the body during its shifting forward with shell growth. The marks can be observed in the shells lacking any other attachment marks or in association with the other marks. They are apparently a unifying morphologic element seen in the growth of all ammonoids (Appendix 2).
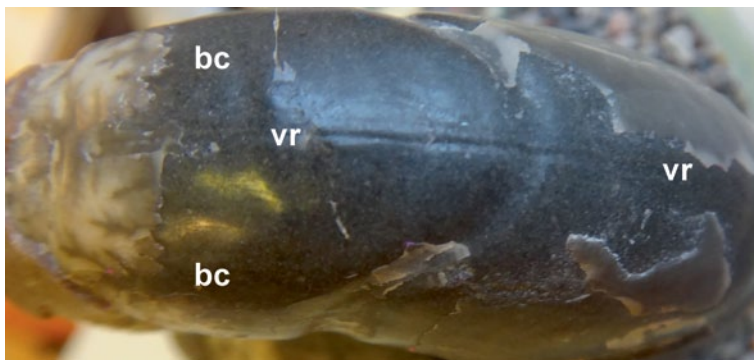
Fig. 14.12 Thin median incision on the internal mould of body chamber of *Damesites* that evidences a fine thread-like ventral ridge on the inner surface of body chamber. Aptian, Early Cretaceous, R. Hokodz, Adygeya Republic, NW Caucasus, Russia; DPC/13; x. *bc* body chamber, *vr* ventral ridge

14.5.5.2 Ventral Band

This is a brown or black band, not expressed as a feature with high relief, or a rugose or porous texture, which is located on the ventral side of the body chamber (Fig. 14.4a). The length of the midventral band in the body chamber is uncertain; the preserved portion that has been observed is usually short, equal to the length of the few last chambers of the phragmocone. The intensive color difference between the midventral band and the matrix apparently indicates the original structure had a higher concentration of non-biomineralized organic material in the body chamber wall along its ventral position. The ventral band is sometimes visible in the chambers of the phragmocone. Contrary to the discrete ventral marks, the ventral band indicates there was non-stop attachment of the body tissues during the forward movement of the growing shell. These marks have been observed in fewer genera than the discrete ventral marks (Appendix 2).

14.5.5.3 Ventral Ridge

The ventral ridge is present as a thin median incision in front of the ventral scar of the internal moulds of body chambers. This incision indicates that there was a fine thread-like ventral ridge on the inner surface of the body chamber. The ventral ridge is here illustrated in *Audouliceras* (Fig. 14.4a) and *Damesites* (Fig. 14.12). It extends to about half of the body chamber length in both of them. It was also observed in *Ptychoceras*. The ventral internal ridge is associated with a ventral discrete mark.

14.5.6   Pore Canals and Assumed Porous Apertural Band

Regularly spaced pore canals that penetrate the ventral keel and open from the outside have only been observed in *Aconeceras* so far. The canals are thought to have housed the mantle extensions and served for the body and body chamber attachment (Doguzhaeva and Mutvei 2015). In ammonoids, the mantle was probably attached along its apertural edge to the shell aperture in a manner similar to that of *Nautilus*. In the latter genus, the pore canals are developed on the inner surface of the body chamber wall along the apertural edge; they are arranged in a narrow apertural band that becomes hidden under the prismatic layers during shell growth Mutvei, Doguzhaeva 1997. By analogy with *Nautilus*, the apertural attachment of the mantle edge is suggested for the ammonoids. Coincident with this attachment at the aperture in *Nautilus* is a black layer (Stenzel 1964; Klug et al. 2004). A partial proof of this type of attachment in ammonoids is the presence of a black band at the shell aperture that was recently found in the mature shell of Triassic *Ceratites* and some other ammonoids (Klug 2004; Klug et al. 2004, 2007).

14.5.7   Myoadhesive Elevation

This is the elevation in front of the last septum, observed in association with enlarged ventral scars in gerontic shells (Fig. 14.11). The elevation is commonly formed by a thickening of the shell wall.

14.5.8   Septal Attachment

Henderson (1984) suggested that the muscles were attached to the periphery of the septum proper and the inner septum within the septal lobes in the Cretaceous lytoceratid *Pseudophyllites*. The septal lobe extends to the surface of the previous septum (Fig. 14.13); the successive septal recesses link one septum to the next, forming a septal tunnel. This is a unique pattern of muscle attachment in the posterior of this genus that is not present elsewhere in the ammonoid phylogeny but in lytoceratids (Hoffman 2010).

14.5.9   Cameral Membranes

Landman et al. (2006) suggested that in the Permian prolecanitid and goniatitid ammonoids, the cameral membranes which are continuations of septal organic layer strengthened the attachment of the siphuncle to the shell wall.
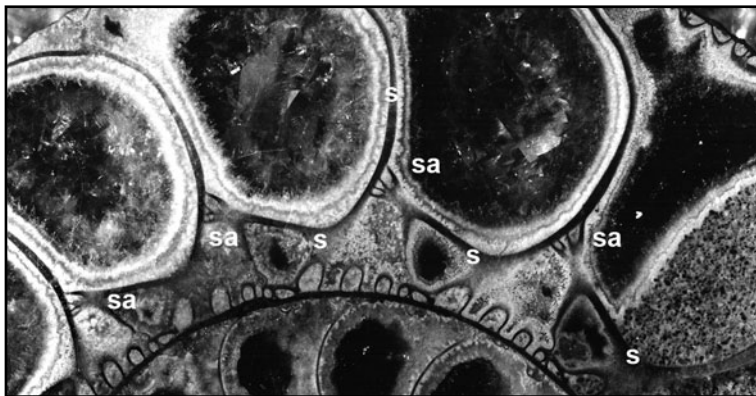
Fig. 14.13 The septal attachments in paramedial shell section of *Gaudryceras tenuiliratum.* Turonian-Campanian, Upper Cretaceous; island of Sakhalin; Russia; DPC/14.; ×3. *s* septum; *sa* septal attachment

14.6   Mantle Structure of the Late Triassic Ceratitid Austrotrachyceras

Remains of the fossilized mantle were detected in compacted body chambers of the Late Triassic ceratitid *Austrotrachyceras*, which co-occurs with the coleoids *Phragmoteuthis* and *Lunzoteuthis*. These coleoids show soft tissue preservation, which shows that the taphonomic conditions were suitable for soft tissue preservation of the co-occurring ammonoids as well (Doguzhaeva et al. 2004, 2006, 2007a, b; Doguzhaeva and Summesberger 2012). The mantle of *Austrotrachyceras* exhibits a thin laminate ultrastructure and in this respect, it is similar to the muscular mantle of the Jurassic coleoids *Belemnoteuthis* (Kar et al. 1995) and *Loligosepia* (Doguzhaeva et al. 2004). The mantle of *Austrotrachyceras* indicates that the external shell did not impede the development of a muscular mantle. Together with the cephalic retractor and funnel retractor muscles, this enabled ammonoids to jet-powered swimming.

14.7   Morphological Indications of Jet-Powered Swimming in Ammonoids

In adult shells of Paleozoic and Mesozoic ammonoids, the range of the body chamber length is about 180º–900º. From this range, the body chambers with lengths less than one whorl are associated with the large attachment marks located on the sides of body chambers extending to the midpoint of the body chamber. These situations can be seen in goniatitids (*Aulatornoceras, Cheiloceras*, *Linguatornoceras*,

Tornoceras) and ammonitids (*Aconeceras, Amaltheus, Amauroceras, Androgynoceras, Arieticeras, Armatites, Deshayesites*, *Hecticoceras, Kashpurites, Quenstedtoceras, Stolleyites*; see Appendices 1, 2). No large ventrolateral marks have been observed in the body chambers longer than one whorl, but this size-relationship still needs to be quantified in order to test its significance. Among the diverse sets of attachment marks that are seen on ammonoids, the large ventrolateral marks are the only ones that can be connected by a straight line with the rear of the cephalic region of the body. The remoteness of the dorsal, umbilical and ventral marks from the anterior ventrolateral part of the body chamber in planispiral shells makes it impossible to put a straight line between them and the cephalic area of the body. Therefore, the latter marks are here considered as less likely attachment sites for the cephalic retractor and funnel retractor muscles. Nevertheless, muscles in gastropods and other animals are known to bend around skeletal obstacles (shell, bone), so we cannot entirely exclude an insertion of such muscles at these remote posterior sites. By contrast, the large ventrolateral attachment marks are thought to be potential sites for the insertion of more or less strong retractor muscles. In several exceptionally well-preserved specimens of *Aconeceras*, the anterior part of the ventrolateral scar is subdivided into two minor lobes (Doguzhaeva and Mutvei 1991, pl. 2, Fig. 2, 4; pl. 3, Fig. 1; pl. 4, Fig. 1, 2). The functional interpretation of these marks arises from their comparison with the attachment of the cephalic retractor and funnel retractor muscles to the gladius in squids (Wells 1988; see Doguzhaeva and Mutvei 1996, Fig. 7a, b). The attachment sites of the powerful cephalic retractor and funnel retractor muscles in squids are located close to each other on the inside surface of the gladius (Wells 1988). In *Nautilus,* the attachment marks of the cephalic retractor muscles are relatively large, but those of the funnel retractor muscles are indistinctly separated branches of the cephalic retractor muscles (Mutvei et al. 1993). Doguzhaeva and Mutvei (1991), Fig. 8) postulated that the cephalic retractor muscles originated from the dorsal minor lobe and the hyponome retractors from the ventral minor lobe within the ventrolateral marks. This conclusion is applied to other genera showing large ventrolateral marks listed above.

In coleoids, the muscle contractions of the thick mantle due to contractions of the cephalic retractor muscle generate the water current into the pallial cavity and provide ventilation of the pallial cavity. In *Nautilus*, the ventilation of the pallial cavity is supported by undulating contractions of the funnel wings (Wells 1988; Wells and O'Dor 1991; Sasaki et al. 2010).

Thus, we assume that the preconditions for jet-powered swimming of ammonoids is a short body chamber with the appropriate location of the attachment of the cephalic and funnel retractor muscles, which should have been able to extend straight across to the head and funnel area (Doguzhaeva 2014). None of the small dorsal, umbilical and ventral marks are here considered to be the attachment sites of the cephalic and funnel retractor muscles. We suggest that the variations of the body chamber length (Appendix 1) in combination with the mantle and muscle

attachment marks (Appendix 2) indicate that the ventrolateral attachment marks occur exclusively in such body chambers, which are maximally one whorl long, where the ventrolateral marks extend from the last septum to the midpoint of the body chamber. In *Aconeceras* and similar genera (Appendix 2) the ventrolateral marks probably represented the attachment site of the cephalic retractor muscles that extended to the cephalic region and of the funnel retractor muscle that extended to the funnel.

Assuming that a muscular mantle was present in these brevidome to mesodome ammonoids like in the Late Triassic ceratitid *Austrotrachyceras*, we suggest that they may have had strong cephalic retractor and funnel retractor muscles and a well developed funnel and muscular mantle that was utilized for propulsion. Such a muscular system would have made these ammonoids suitable for a nektonic mode of life.

The soft body and the body chamber are traditionally assumed to be of approximately equal lengths in ammonoids. This presumption has been used for the experimental estimation of the orientation of the aperture in the shells of different geometry, ornamentation and body chamber lengths (Trueman 1941; Saunders and Work 1997; Saunders and Shapiro 1986; Jacob and Chamberlain 1996).

The hypothesis of the soft body size exceeding the body chamber volume arose from the additional external shell wall layers in some taxa, which caused or required a mantle extension over the external shell surface for the extra shell secretion; this was proposed by Drushchits et al. (1978) and supported by Doguzhaeva and Mutvei (1989, 1991, 1996, 2015). This hypothesis received further support from the discovery of the thin fragile apertural margin in *Ptychoceras* (Doguzhaeva and Mutvei 1993) and parabolic structures on the external surface of the body chamber in *Indosphinctes* (Doguzhaeva 2012).

A different hypothesis was proposed by Monks and Young (1998). They proposed that the body was much smaller than the analogy with *Nautilus* suggests, and the ammonites, especially heteromorphs, were more like a gastropod. Until now, this hypothesis has not yet been confirmed or rejected by direct observations or other indirect assumptions based on morphological data. Their hypothesis apparently arose from the so far poorly understood mode of life of heteromorph ammonoids. The previously mentioned thin fragile apertural margin of *Ptychoceras* and the large tongue-like umbilical marks in the heteromoph shells of *Ancyloceras, Audouliceras, Baculites*, and *Ptychoceras* question the hypothesis of Monks and Young (1998), because a small gastropod-like soft body in a big shell appears unlikely to require big muscles. For perisphinctids and *Dactylioceras*, it was also suggested that the body was significantly smaller than suggested by the body chamber volume (Kröger 2002). This assumption arose from the observation of over half a whorl deep sublethal injuries of the body chamber wall that supposedly would have required substantial withdrawing of the body into the body chamber (Kröger 2002).

14.8 Fossilization of Mantle and Muscle Attachment Marks

Ammonoid shells showing both mantle and body chamber attachment marks are very rare. There are several causes of post mortem loss of such shell features. First of all, there is the relatively likely destruction of body chambers because of the lack of septal support and because the aperture is prone to mechanical damage during transport. Secondly, recrystallization of the shell material can result in a fusion of the shell wall with the matrix, which makes the inner surface of the body chamber invisible. Thirdly, the attachment marks, which were expressed in a relief of the body chamber wall, might have been cast by the internal moulds but the other marks were not. Fourthly, the marks, which did not form a relief, might have been preserved due to higher concentration of organic (non-biomineralized) material, but in that case, a burial environment that allowed fossilization of such materials (e.g., melanin, chitin) would be required. Such environments are rare in the fossil record.

14.8.1 Mantle Fossilization

The soft tissue of the mantle in the body chamber was detected in seven comparatively large (diameter = 50–75 mm) specimens of Late Triassic ceratitid *Austrotrachyceras*. The conchs were compacted by lithostatic pressure, and their preserved shells retain their original aragonitic mineralogy with only little alteration (Doguzhaeva et al. 2004). One of the shells was associated with its mandibles (Doguzhaeva et al. 2007a). The mantle is a black glossy pitch-like mass restricted in distribution to the body chambers. Under SEM observation, the mantle revealed fine laminations and a fibrous ultrastructure. The fibers consisted of numerous micro-grains of microbial size. The fossilized mantle showed a high content of C but lacked Ca and P. The elemental composition is here given in weight percents: C (60–65 %); O (30 %); S (2–6 %); Si (1–2 %); Cd (0.5–1.8 %); Fe (1 %) and K, Al, Zn (each < 1 %) (Doguzhaeva et al. 2004). A similar chemical composition was detected in the mandibles: C (53–58 %), O (30 %), Si (1–5 %), Fe (1–2 %), and Ca (< 1 %) (Doguzhaeva et al. 2007a). The replacement of the muscular mantle tissues by carbon apparently resulted from the metabolism of anaerobic carbon-accumulating bacteria (Doguzhaeva et al. 2004, 2007a, b). Lack of phosphorus in the mantle matter and in the mandibles reveals that the preservation of the non-biomineralized soft tissue was not controlled by a phosphorus-rich medium. Contrary to the mantle and mandibles, the shell wall in *Austrotrachyceras* is calcareous; it is composed of O (65–80 %), C (25 %), Ca (8–16 %), Sb (2 %), Mo (2 %), Mg, K (each 1 %), and S, Si, Mn, Fe (each < 1 %) (Doguzhaeva et al. 2004, 2007b). The low oxygen depositional environment (Griffith 1977) responsible for carbonization of the mantle and the mandibles of *Austrotrachyceras* also favored the preservation of the muscular mantle, ink sacs and arm-hooks of the coleoid *Phragmoteuthis bisinuata* (Doguzhaeva et al. 2007b, Doguzhaeva and Summesberger 2012).

14.8.2   Fossilization of Mantle and Muscle Attachment Marks

Traces of the soft tissue attachment sites are often distinct on the inner surfaces of the body chamber wall in shells in aragonite preservation in such cases when the shell wall can be split from the internal mould (Doguzhaeva and Kabanov 1988; Doguzhaeva and Mutvei 1991). More commonly, these marks are preserved as imprints on pyritized internal moulds completely lacking shell wall (Kennedy et al. 2002; Richter 2002; Richter and Fischer 2002) or in aragonitic shells extracted from siderite concretions with a low content of Fe- minerals of the phragmocones and in posterior portions of body chambers. On internal moulds, the attachment marks can occur as small tubercles, shallow depressions or spots. These show often dark brownish or reddish colors due to pyrite or manganese hydroxides (Jordan 1968; Richter 2002; Richter and Fisher 2002; Doguzhaeva and Mutvei 2015). These differences corroborate that the inside of the body chamber wall originally carried attachment marks, which were either shallow pits, elevations or spots rich in organic material. The color differences probably resulted from the higher content of organic material in the attachment sites than in the rest of the shell wall. The surfaces of the attachment marks are often rough and bear pyritized micro-pits.

Currently, the best preservation of attachment marks is known from the body chambers of shells recovered from ankerite-siderite concretions in black clays (Doguzhaeva and Kabanov 1988; Doguzhaeva and Mutvei 1991, 1992, 1993; Doguzhaeva and Mikhailova 1991). For example, exceptionally well-preserved attachment marks were found in more than 50 shells from such concretions from the Lower Aptian of the Uljanovsk Region in Russia (Doguzhaeva and Kabanov 1988). These ammonoids display different ontogenetic growth stages. Multiple attachment marks were observed on phragmocone surfaces, interior surfaces of shells when the matrix was split from the ammonite, and especially on the internal mould of the body chambers of the conchs.

Attachment marks are typically observed in the shells or internal moulds from the environments favoring the genesis of rapidly deposited Fe-, S- or Mn-minerals. Additionally, the rapid post-mortem burial of the recently deceased ammonoid animal in the oxygen-deficient fine-grained sediments promoted the substitution of the organic-rich shell components with Fe- or Mn-minerals by anaerobic microbes. Attachment marks lacking relief but showing black, brownish or yellow coatings on the inside of the shell wall or on internal molds possibly appeared post mortem at the attachment sites; these can be distinguished from the rest of the shell wall by a higher organic content. The iridescent nacreous spots on the dark internal moulds of body chambers were formed due to secretion of additional portions of shell matter inside the weak impressions on the inside body chamber wall. The attachment marks forming low tubercles on the internal mould surfaces of the phragmocones, which rarely occur in body chambers, were formed by casting shallow pit-like attachment sites on the inside of the shell.

14.9   Conclusions

The data on variations of body chamber lengths (Appendix 1), traces of mantle and body chamber attachment (Appendix 2), muscular mantle preservation, and mode of preservation lead us to the following conclusions.

1. In the ontogeny of Paleozoic and Mesozoic ammonoids, the angular body chamber length may decrease (Miller et al. 1957) or increase (Doguzhaeva 1990); the first trend was documented in six and the second trend in seven genera from a total of 14 genera showing the body chamber length from the ammonitella to the adult stages; in one genus, the adequacy of measurements is insufficient (Appendix 1).

2. The gradual decrease of body chamber length at the ammonitella stage (Appendix 1) is an evolutionary trend characterizing the development of goniatitid–prolecanitid–ceratitid–phylloceratid lineage. It might indicate that the common early ontogenetic condition aimed at the achievement of a higher shell stability during early post-hatching stages; the replacement of this tendency with the contrary one in lytoceratids and ammonitids supposedly indicates an innovative early ontogenetic strategy of these two groups in the Jurassic.

3. A set of discrete dorsal, small umbilical and ventral marks along the phragmocone indicates that the mantle was regularly detached from the body chamber wall in each of these sites before it moved forward during growth to a new place of fixation. The discrete marks show a stepwise forward movement of the body within the growing body chamber and the band-shaped dorsal and ventral marks indicate continuing attachment and non-detached forward movement of the mantle. The overlap of discrete and band-shaped middorsal and midventral marks (Kennedy et al. 2002, pl. 5, Fig. 9; pl. 7, Fig. 5) possibly reflects the alternating weakening and reinforcement of the mantle and body chamber attachment along the middorsal and midventral areas of the body chamber wall. It is most likely that during the forward movement, the growing mantle was locally detached from the body chamber but remained attached in other sites. This partial detachment of the mantle presumably would produce differential extension of the mantle.

4. The dorsal internal ridge of clymeniids and the ventral internal ridge of all other ammonoids may have been the attachment structure between mantle and the siphuncular side of the body chamber wall.

5. In the ammonoids with a monomorph shell, there might have been forms combining a relatively short body (approximately equal to the body chamber length, or more) with well developed cephalic retractor and funnel retractor muscles. Those forms with a long body commonly had weakly developed cephalic retractor and funnel retractor muscles. With respect to higher- or lower-energy mode of locomotion (O'Dor et al 1990; Wells and O'Dor 1991), the former might have been more similar to the coleoids.

6. In the Early Cretaceous *Ancyloceras*, *Audouliceras*, *Pseudocrioceras*, *Ptychoceras,* and possibly also in the Late Cretaceous *Baculites,* in which the shell axis lies in the same plane throughout ontogeny*,* the body chamber bears enlarged tongue-like umbilical marks. In the first three genera*,* the terminal body chamber occupies a hook-like portion of shell with an estimated length of about 270º. The ventrolateral muscle scars are missing and the umbilical marks are the largest ones. The anterior end of these marks is located closer to the apertural portion of the body chamber. Therefore, the umbilical muscles were possibly the most powerful in these ammonoids and might have been designed for changing the mantle cavity volume to improve filter feeding on small plankton (Doguzhaeva 2014). This feeding mode is supported by the morphology of the buccal apparatus of the heteromorph ammonite *Australiceras*, which co-existed with *Audouliceras* and *Ancyloceras* (Doguzhaeva and Mikhailova 2002). In *Australiceras*, the jaw apparatus lacked a rostrum. Instead, it had a large cavity between the lower and upper jaws, which is formed by the deep and wide lower jaw with a solid flat ventral side, and the long wings of the upper jaw. Being the largest muscles, the umbilical muscles might have served for a regular water exchange of the mantle cavity that would be needed for respiration and filtering plankton. This suggests that these heteromorph ammonites perhaps fed on small plankton and were able to float as part of the plankton or performed vertical migrations.

7. In *Ptychoceras,* the terminal body chamber occupies the third shaft and approximately equally long portion of the second shaft. The extremely thin apertural edge of the terminal body chamber must have been protected against destruction by the mantle fold. This shows that the soft body must have been longer than the body chamber (Doguzhaeva and Mutvei 1989, 1993a, b, 2015).

8. The mantle tissue of some ammonoids was probably elastic and muscular as it was shown by exceptionally preserved specimens of the Late Triassic ceratitid *Austrotrachyceras* (Doguzhaeva et al 2004). Also, some ammonoid genera possessed powerful cephalic retractor and funnel retractor muscles while others did not. The variety of different body chamber lengths and mantle and muscle attachment marks probably indicates highly diverse life modes among ammonoids (Doguzhaeva 2014). A similar pattern is expressed in the diverse life modes of Recent shell-bearing and shell-less coleoids.

Further search for cephalopod shells preserving body chambers with weakly recrystallized shell material showing details of soft tissue attachment marks is a way towards better understanding of the paleobiology of cephalopods, including ammonoids.

Appendix 1

Table A.1 The angular body chamber length of Paleozoic and Mesozoic ammonoid genera (abbreviations of ages: D-Devonian; C-Carboniferous; P-Permian; T-Triassic; J-Jurassic; K-Cretaceous; the subscript numbers 1 to 3 in combination with D, T and J mean early, middle and late; the subscript numbers 1 and 2 in combination with C, P and K mean early and late)

Genus	Age	Body chamber length (angle in degrees)		Reference
		Ammo-nitella	Adult	
Goniatitida				
Tornoceras	D_3	360°		Ruzhencev 1962
Aulatornoceras	D_3		< 360°	Richter and Fischer 2002
Linguatornoceras	D_3		< 360°	Richter and Fischer 2002
Cheiloceras	D_3		< 360°	Richter and Fischer 2002
Maeneceras	D_3		ca. 360°	Bockwinkel et al. 2002
Neoglyphioceras	C_1	360°	>450°	Zakharov 1974, 1978
Glaphyrites	C_1	300–405°		Landman et al. 1996, 1999a
?Rhadinites	C_1		360°	Landman et al. 2010
?Anthracoceras	C_1		360°	Landman et al. 2010
Gyrtioceras	C_2	400°		Landman et al. 1996
Cravenoceras	C_2	370–380°		Landman et al. 1996
Gatherites	C_2	385°		Landman et al. 1996
Pseudogastrioceras	C_2	370°		Landman et al. 1996
Paragastrioceras	C_2	360°		Landman et al. 1996
Goniatites	C_2	345–385°		Landman et al. 1996; Kulicki et al. 2002
Akiyoshiceras	C_2		900°	Kyuma and Nishida 1987
Agathiceras	C_2–P_1	360°	>370°	Shulga-Nesterenko 1925 Arthaber 1928; Miller et al. 1957; Ruzhencev 1962
Peritrochia	C_2–P_1	340–410°		Bogoslovskaya 1959; Landman et al. 1996
Thalassoceras	C_2–P_1	380°		Bogoslovskaya 1959
Hyattoceras	P		>450°	Miller et al. 1957
undet. juv. goniatite	C_2–P_1	360°		Doguzhaeva 2002
Uraloceras	P_1		ca. 360°	Ruzhencev 1956
Waagenina	P_1		?>360°	Ruzhencev 1956
Marathonites	P_1		ca. 360°	Ruzhencev 1956
Kargalites	P_1		?>360°	Ruzhencev 1956
Clymeniida				
Genuclymenia	D_3		275–280°	Bogoslovsky 1976
Cyrtoclymenia	D_3		275°–280°	Bogoslovsky 1976
Platyclymenia	D_3			Bogoslovsky 1976
Prolecanitida				

Table A.1 (continued)

Genus	Age	Body chamber length (angle in degrees)		Reference
		Ammo-nitella	Adult	
Neopronorites	C_2–P_1	310–340º	230º	Bogoslovskaya 1959; Saunders and Work 1997
Metapronorites	C_2–P_1	340º	250º	Ruzhencev 1962; Saunders and Work 1997
Pronorites	P	330º		Landman et al. 1996
Akmilleria	P_1		218º	Saunders and Work 1997
Medlicottia	P_2	326–340º		Bogoslovskaya 1959; Ruzhencev 1962
Sakmarites	P_1	340º	225º	Bogoslovskaya 1959; Saunders and Work 1997
Pseudosageceras	T_1	295º		Zakharov 1978
Hedenstroemia	T_1	287–296º		Zakharov 1978
Ceratitida				
Xenodiscus	T_1	280º		Zakharov 1978
Kingites	T_1	347º		Zakharov 1978
?*Paranorites*	T_1	280º		Zakharov 1978
Prosphingites	T_1	265º	>360º	Zakharov 1978
Paranannites	T_1	238º		Zakharov 1978
Owenites	T_1	270º		Zakharov 1978
Svalbardiceras	T_1	260º		Zakharov 1978
Nordophiceras	T_1	260º		Zakharov 1978
Boreomeekoceras	T_1	295º		Zakharov 1978
Arctomeekoceras	T_1	280–285º		Zakharov 1978
Columbites	T_1	240º		Zakharov 1978
Sucolumbites	T_1	240º		Zakharov 1978
Palaeokazachstanites	T_1	?265º		Zakharov 1978
Olenekites	T_1	300–315º		Zakharov 1978
Parasibirites	T_1	265º		Zakharov 1978
Sibirites	T_1	260º		Zakharov 1978
Keyserlingites	T_1	300º		Zakharov 1978
Arctohungarites	T_1	229–330º		Zakharov 1978
Crumbergia	T_1	229–330º		Zakharov 1978
Phyllocladiscites	T_1	265º		Zakharov 1978
Phyllocladiscites	T_2	330º	360º	Doguzhaeva 1990
Megaphyllites	T_2	270–280º		Drushchits and Doguzhaeva 1981
Ceratites	T_2		?120º	Klug 2004
Proarcestes	T_2	?350º	>450º	Doguzhaeva 1990

Table A.1 (continued)

Genus	Age	Body chamber length (angle in degrees)		Reference
		Ammo-nitella	Adult	
Placites	T_3	268º		Shigeta and Weitschat 2004
Choristoceras	T_3	295º		Shigeta and Weitschat 2004
Phylloceratida				
Rhacophyllites	T_3	286º		Shigeta and Weitschat 2004
Partschiceras	J_2	260–280º		Drushchits and Doguzhaeva 1981
Holcophylloceras	J_2	270º		Drushchits and Doguzhaeva 1981
Phyllopachyceras	K_1	234–300º	ca. 360º	Zakharov 1978; Drushchits and Doguzhaeva 1981
Holcophylloceras	J_2	223–270º		Zakharov 1978; Drushchits and Doguzhaeva 1981
Salfeldiella	K_1	280º		Drushchits and Doguzhaeva 1981
Hypophylloceras	K_2	280º		Drushchits and Doguzhaeva 1981
Lytoceratida				
Eurystomiceras	J_2	290–300º	270º	Drushchits and Doguzhaeva 1981; Doguzhaeva 1990
Tetragonites	K_1	300–330º		Zakharov 1978; Drushchits and Doguzhaeva 1981
Gabbioceras	K_1	280–300º		Drushchits and Doguzhaeva 1981
Eogaudryceras	K_1	330º		Doguzhaeva et al. 2010
Parajaubertella	K_2	270º		Drushchits and Doguzhaeva 1981
Gaudryceras	K_2	330º		Zakharov 1978
Zelandites	K_2	320º–336º		Zakharov 1978
Tanabeceras	K_2		300º	Shigeta and Izukuda 2013
Ammonitida				
Psiloceras	J_1	285º		Shigeta and Weitschat 2004
Peronoceras	J_1		>360º	Keupp 2000
Asteroceras	J_1		ca. 180º	Keupp 2000
Hecticoceras	J_1		ca. 270º	Keupp 2000
Cleviceras	J_1		ca. 270º	Keupp 2000
Hildoceras	J_1		260º	Kröger 2002
Kepplerites	J_2		180°	Mitta and Starodubceva 2000
Pseudoneuqueniceras	J_2		330º	Matsuoka et al. 2010
Pelekodites	J_3		ca. 270º	Keupp 2000

Table A.1 (continued)

Genus	Age	Body chamber length (angle in degrees)		Reference
		Ammo-nitella	Adult	
Perisphinctes	J_3		370°	Kröger 2002
Dactylioceras	J_3		390°	Kröger 2002
Harpoceras	J_3		260°	Kröger 2002
Pseudolioceras	J_3		220°	Kröger 2002
Indosphinctes	J_3	330°	?330°	Ruzhencev 1962; Dogu-zhaeva 2012
Valanginites	K_1		>360°	Keupp 2000
Speetoniceras	K_1	300°		Drushchits and Doguzhaeva 1981
Craspedodiscus	K_1	300–315°		Drushchits and Doguzhaeva 1981
Parahoplites	K_1	305–330°		Drushchits and Doguzhaeva 1981
Aconeceras	K_1	270–365°	180°	Drushchits and Doguzhaeva 1981; Kulicki and Dogu-zhaeva 1994
Deshayesites	K_1	300–330°	180°	DLA, personal observation
Desmophyllites	K_1	307–332°		Zakharov 1978
Melchiorites	K_1	270–290°		Drushchits and Doguzhaeva 1981
Zurcherella	K_1	270–285°		Drushchits and Doguzhaeva 1981
Beudanticeras	K_1	330°		Drushchits and Doguzhaeva 1981
Damesites	K_1	307–309°		Zakharov 1978
Ancyloceras	K_1		180–270°	Doguzhaeva and Mikhailova 1991
Audouliceras	K_1		180–270°	Figs 14.1–14.3
Subpriomocyclus	K_2	242–348°		Landman et al. 1996
Discoscaphites	K_2		180°	Landman et al. 2007

Apendix 2

Table A.2 Record of mantle and body chamber attachment marks Abbreviations of ages: D-Devonian; C-Carboniferous; P-Permian; T-Triassic; J-Jurassic; K-Cretaceous; the subscript numbers 1 to 3 in combination with D, T and J mean early, middle and late; the subscript numbers 1 and 2 in combination with C, P and K mean early and late (for further abbreviations see Terminology and abbreviations)

Genera	Age	Type of attachment marks	References
Goniatitida			
Tornoceras	D	vl	Richter and Fischer 2002
Aulatornoceras	D	vl	Richter and Fischer 2002
Linguatornoceras	D	vl	Richter and Fischer 2002
Cheiloceras	D	vl	Richter and Fischer 2002
?*Rhadinites*	C_1	db	Landman et al. 2010
?*Anthracoceras*	C_1	db	Landman et al. 2010
Goniatites	C	us	Crick 1898; Tanabe et al. 1998
Muensteroceras	C	us	Crick 1898; Jordan 1968
Clymeniida			
gen. indet.	D_3	dr	(B.I. Bogoslovsky, pers. comm.)
Ceratitida			
Anagymnotoceras	T_2	d	Weitschat 1986
Amphipopanoceras	T_2	d	Weitschat 1986; Weitschat and Bandel 1991; Keupp 2000
Czekanowskites	T_2	d, ve	Weitschat et Bandel 1991; Dagys and Keupp 1998; Keupp 2000
Indigirites	T_2	d	Weitschat et Bandel 1991
Nathorstites	T_2	d	Weitschat et Bandel 1991
Aristoptychites	T_2	d	Weitschat et Bandel 1991
Arctoptychites	T_2	d	Weitschat et Bandel 1991
Sphaerocladiscites	T_2	d	Weitschat et Bandel 1991
Stolleyites	T_2	d	Weitschat et Bandel 1991
Paracladiscites	T_2	d	Weitschat et Bandel 1991
Ceratites	T_2	ae, us, v	Klug 2004; Klug et al.2007
Arctohungarites	T_2	ve	Dagys and Keupp 1998
Phylloceratida			
Tragophylloceras	J_1	us	Jordan 1968
Holcophylloceras	J_2	v	DLA, personal observation
Phyllopachyceras	K_1	v	Sharikadze et al. 1990
Euphylloceras	K_1	v	Sharikadze et al. 1990
Salfeldiella	K_1	v	Sharikadze et al. 1990
Lytoceratida			
Lytoceras	J_{1-2}	us, ls	Crick 1898; Jordan 1968; Rakús 1978

Table A.2 (continued)

Genera	Age	Type of attachment marks	References
Derolytoceras	J$_1$	us	Rakús 1978
Pachylytoceras	J$_1$	us	Jordan 1968
Pleurolytoceras	J$_1$	us	Jordan 1968
Pictetia	K$_1$	d	Sharikadze et al. 1990
Tetragonites	K$_1$	v	Sharikadze et al. 1990
Hemitetragonites	K$_1$	us	Sharikadze et al. 1990
Ptychoceras	K$_1$	ut, d, vr	Sharikadze et al. 1990; Kakabadze and Sharikadze 1993; Doguzhaeva and Mutvei 2015
Hamites	K$_1$	us	Crick 1898; Jordan 1968; Doguzhaeva and Mutvei 1996
Diplomoceras	K$_2$	us	Crick 1898; Jordan 1968
Turillites	K$_2$	us	Crick 1898; Jordan 1968
Holcoscaphites	K$_2$	us	Landman and Waage 1993
Ammonitida			
Alsatites	J$_1$	us	Crick 1898; Jordan 1968
Arietites	J$_1$	us,?v,?ae	Crick 1898; Jordan 1968
Asteroceras	J$_1$	us	Jordan 1968
Paroxynoticeras	J$_1$	us	Rakús 1978
Eoderoceras	J$_1$	d	Rakús 1978
Amaltheus	J$_1$	us, d, v, ls, vl, ae	Crick 1898; Jordan 1968; Richter and Fischer 2002
Androgynoceras	J$_1$	us,?v	Crick 1898
Amauroceras	J$_1$	us, d, vl	Landman et al. 1990b; Richter and Fischer 2002
Armatites	J$_1$	vl	Münster 1839; Richter and Fischer 2002
Arieticeras	J$_1$	us, d, vl	Jordan 1968; Richter and Fischer 2002
Oedania	J$_1$	us, v	Richter and Fischer 2002
Polymorphites	J$_1$	us, v	Richter and Fischer 2002
Stolleyites	J$_1$	d, vl	Richter and Fischer 2002
Grammoceras	J$_1$	ls	Jordan 1968
Dorsetensia	J$_2$	us, v	Jordan 1968; Doguzhaeva and Mutvei 1996
Ludwigia	J$_2$	us	Jordan 1968
Sonninia	J$_2$	us, v	Crick 1898; Jordan 1968
Staufenia	J$_2$	us, ae	Jordan 1968
Leioceras	J$_2$	us	Jordan 1968
Distichoceras	J$_{2-3}$	ls	Crick 1898; Jordan 1968

Table A.2 (continued)

Genera	Age	Type of attachment marks	References
Paroecotraustes	J_2	d	Jordan 1968
Hecticoceras	J_2	us, ls, vl, mg, ve	Crick 1898; Jordan 1968; Dagys and Keupp 1998, 2000; Richter and Fischer 2002
Creniceras	J_3	us, ae	Keupp 2000; Crick 1898; Jordan 1968
Clydoniceras	J_2	us,?v, ae	Crick 1898; Jordan 1968
Bullatimorphites	J_2	v	Jordan 1968
Quenstedtoceras	J_2	d, v	Jordan 1968; Landman and Bandel 1985; Sharikadze et al. 1990; Doguzhaeva and Mutvei 1991, 1996; Tanabe et al. 1998
Cardioceras	J_3	us,?v, ae	Crick 1898; Jordan 1968
Grossouvria	J_1	v	Jordan 1968
Siemiradzkia	J_2	v	Jordan 1968
Peltoceras	J_2	us	Crick 1898; Jordan 1968
Aspidoceras	J_3	us	Crick 1898; Jordan 1968
Virgatites	J_3	v	Doguzhaeva and Mutvei 1996
Indosphinctes	J_2	us, v, vb	Sharikadze et al. 1990; Doguzhaeva 1986, 2012
Dorsoplanites	J_3	us, d	DLA, personal observation
Kashpurites	J_3	v, l	Fig. 14.10
Polyptychites	K_1	v	Vogel 1959
Olcostephanus	K_1	v	Doguzhaeva and Mutvei 1996
Beudanticeras	K_1	v	Doguzhaeva and Mutvei 1996
Melchiorites	K_1	vr, us, ls	Sharikadze et al. 1990
Zurcherella	K_1	ls	Sharikadze et al. 1990
Pseudosilesites	K_1	us, v	Sharikadze et al. 1990
Amoeboceras	K_1	us, ae	Crick 1898; Jordan 1968
Aconeceras	K_1	d, us, ls, vl, v	Figs 14.8, 9; Doguzhaeva and Kabanov 1988; Sharikadze et al. 1990; Landman et al. 1999c
Deshayesites	K_1	us, ls, vl, v	Figs 14.5-7; Doguzhaeva and Kabanov, 1988; Sharikadze et al. 1990; Doguzhaeva and Mutvei 1991
Ancyloceras	K_1	ut, v	Crick 1898; Jordan 1968; Doguzhaeva and Mikhailova 1991; Richter and Fischer 2002
Audouliceras	K_1	ut, db, v, vb, vr. lms	Fig. 14.1–4
Epicheloniceras	K_1	us	Sharikadze et al. 1990
Parahoplites	K_1	us, v	Landman and Bandel 1985

Table A.2 (continued)

Genera	Age	Type of attachment marks	References
Colombiceras	K_1	us, v	Sharikadze et al. 1990
Acanthohoplites	K_1	us, v	Sharikadze et al. 1990
Hypacanthoplites	K_1	d, v	Landman and Bandel 1985; Sharikadze et al. 1990
Diadochoceras	K_1	v	DLA, personal observation
Nodosohoplites	K_1	v	DLA, personal unpubl. observation
Euhoplites	K_1	d	Landman and Bandel 1985
Aegocrioceras	K_1	us	Crick 1898; Jordan 1968
Pseudocrioceratite	K_1	ut, d	Sharikadze et al. 1990; DLA, personal observation
Crioceratites	K_1	d	Richter and Fischer 2002
Bochianites	K_1	us, d	Richter and Fischer 2002
Hauericeras	K_2	d	Obata et al. 1978
Sciphoceras	K_2	ae	Henderson 1984
Tissotia	K_2	?d	Crick 1898; Jordan 1968
Scaphites	K_2	us, d	Landman and Waage 1993
Baculites	K_2	ae, d, us, ut, vb	Crick 1898; Kennedy et al. 2002

References

Arthaber GV (1911) Die Trias von Albanian. Beitr Paläont Geol Öster-Ungarns und des Orients 24:169–277

Arthaber GV (1928) Ammonoidea Leiostraca aus der oberen Trias von Timor. 2. Nederl Timor Expeditie 1916 onder Leiding von Dr. H. A. Brouwer. Jarb Mijnw Nederl Oost-Indiës 55(2):1–174

Bandel K (1982) Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. Facies 7:1–198

Bockwinkel J, Becker RT, Ebbighausen V (2002) Morphometry and taxonomy of lower Famennian Sporadoceratidae (Goniatitida). Abh Geol BA 57:279–297

Bogoslovskaya MF (1959) Internal shell structure of some Artinskian ammonoids. Paleontol Zh 1:49–57

Bogoslovsky BI (1976) Early ontogeny and origin of clymeniids. Palaeont Zh 2:41–51

Chamberlain JA (1980) The role of body extension in cephalopod locomotion. Palaeontology 23:445–461

Chamberlain JA (1993) Locomotion in ancient seas: constraint and opportunity in cephalopod adaptive design. Geobios Mem Spéc 15:49–61

Crick GC (1898) On the muscular attachment of the animal to its shell in some Cephalopoda (Ammonoidea). Trans Linn Soc London (2) Zool 7:71–113

Dagys AS, Keupp H (1998) Internal ventral keels in Triassic ceratid ammonoids: description and functional interpretation as muscle scars. [Interne Ventralleisten bei ceratitischen Ammonoiden der Trias: Beschreibung und funktionale Interpretation als Muskelansätze.]. Z Dt Geol Ges 149:81–89

Diener C (1916a) Einiges über Terminologie und Entwicklung der Lobenelemente in der Ammonitensutur. Centralbl Min Geol Paläont 23(8):553–568; 24:578–592

Diener C (1916b) Bemerkungen über die Inzisionen der Suturlinie als Grundlage einer natürlichen Klassifikation der Ammoniten. Centralbl Min Geol Paläont 15:374–381

Doguzhaeva LA (1981) The wrinkle layer in the shell of ammonoids. Paleont Zh 1:38-48 [In Russian]

Doguzhaeva LA (1986) How long did ammonites live? Science USSR 3:113–117

Doguzhaeva LA (1988) Siphuncular tube and septal necks in ammonoid evolution. In: Wiedmann J, Kullmann J (eds) Cephalopods—present and past. Schweizerbart, Stuttgart

Doguzhaeva LA (1990) Analysis of shell growth of ammonoids. Trudy Paleont. Inst. USSR 243:15-28 [In Russian]

Doguzhaeva LA (2002) Adolescent bactritoid, orthoceroid, ammonoid and coleoid shells from the upper Carboniferous and lower Permian of South Urals. Abh Geol B-A 57:9–55

Doguzhaeva LA (2012) Functional significance of parabolae, interpreted on the basis of shell morphology, ultrastructure and chemical analyses of the Callovian ammonite *Indosphinctes* (Ammonoidea: Perisphinctidae), Central Russia. Rev Paléobiol, Genéve, spec vol 11:89–101.

Doguzhaeva LA (2014) Muscle and mantle attachment marks as well as body chamber lengths indicative of diverse life styles of coexisted Aptian ammonites of the Russian Platform. In: Klug C, Fuchs D (eds) Intern Symp Cephalopods present and past in combination with the 5th Intern Symp Coleoid cephalopods through time Abstracts and program. Univ Zurich

Doguzhaeva LA, Kabanov GK (1988) Muscle scars in ammonoids. Dokl Akad Nauk USSR 301:210–212

Doguzhaeva LA, Mikhailova IA (1991) New data on muscle system of heteromorph ammonites. Dokl Akad Nauk USSR 318:981–984

Doguzhaeva LA, Mikhailova IA (2002) The jaw apparatus of the heteromorphic ammonite *Australiceras whitehouse*, 1926 (Mollusca: Cephalopoda) from the Aptian of the Volga Region. Dokl Akad Nauk USSR 382:38–40

Doguzhaeva LA, Mutvei H (1989) *Ptychoceras* - a heteromorphic lytoceratid with truncated shell and modified ultrastructure (Mollusca: Ammonoidea). Palaeontogr A 208:91–121

Doguzhaeva LA, Mutvei H (1990) Radula, aptychi and counter-aptychi in Cretaceous ammonite *Aconeceras*. Dokl Akad Nauk USSR 313:192–195

Doguzhaeva LA, Mutvei H (1991) Organization of the soft body in *Aconeceras* (Ammonitina), interpreted on the basis of shell morphology and muscle scars. Palaeontogr A 218:17–33

Doguzhaeva LA, Mutvei H (1992) Radula of Early Cretaceous ammonite *Aconeceras* (Mollusca: Cephalopoda). Palaeontogr A 223:167–177

Doguzhaeva LA, Mutvei H (1993a) Shell ultrastructure, muscle scars, and buccalapparatus in ammonoids. Geobios 15:111–119

Doguzhaeva LA, Mutvei H (1993b) Structural features in Cretaceous ammonoids indicative of semi-internal or internal shells. In: House MH (ed) The Ammonoidea Environment, Ecology, and Evolutionary Change. Syst Ass Special Vol 47: 99–114. Clarendon Press Oxford

Doguzhaeva LA, Mutvei H (1996) Attachment of the body to the shell in Ammonoids. In: Landman NH, Tanabe K, Davis RA (eds) Ammonoid Paleobiology, Topics in Geobiology 13:43–63. Plenum Press New York and London

Doguzhaeva LA, Mutvei H, Summesberger H & Dunca E (2004) Bituminous soft body tissues in Late Triassic ceratitid Austrotrachyceras Mitt Geol-Paläont Inst Univ Hamburg 88:37–50

Doguzhaeva LA, Mutvei H (2015) The additional external shell layers indicative of "endocochleate experiments" in some ammonoids. This volume

Doguzhaeva LA, Summesberger H (2012) Pro-ostraca of Triassic belemnoids (Cephalopoda) from Northern Calcareous Alps, with observations on their mode of preservation in an environment of northern Tethys which allowed for carbonization of non-biomineralized structures. N Jahrb Geol Paläont Abh 266:31–38

Doguzhaeva LA, Mapes RH, Mutvei H (2002) Early Carboniferous coleoid *Hematites* Flower & Gordon, 1959 (Hematitida ord. nov.) from Midcontinent (USA). Abh Geol B-A 57:299–320

Doguzhaeva LA, Mapes RH, Mutvei H (2003) The shell and ink sac morphology and ultrastructure of the Late Pennsylvanian cephalopod *Donovaniconus* and its phylogenetic significance. Berl Paläobiol Abh 3:61–78

Doguzhaeva LA, Mutvei H, Summesberger H, Dunca E (2004) Bituminous soft tissues in the body chamber of the Late Triassic ceratitid *Austrotrachyceras* from the Austrian Alps. Mitt Geol-Paläont Inst Univ Hamburg 88:37–50

Doguzhaeva LA, Summesberger H, Mutvei H (2006) An unique Upper Triassic coleoid from the Austrian Alps reveals pro-ostracum and mandible ultrastructure. Acta Univ Carolinae Geol 49:69–82

Doguzhaeva LA, Summesberger H, Mutvei H, Brandstaetter F (2007a) The mantle, ink sac, ink, arm hooks and soft body debris associated with the shells in Late Triassic coleoid cephalopod *Phragmoteuthis* from the Austrian Alps. Palaeoworld 16:272–284

Doguzhaeva LA, Mapes RH, Summesberger H, Mutvei H (2007b) The preservation of body tissues, shell, and mandibles in the ceratitid ammonoid *Austrotrachyceras* (Late Triassic), Austria. In: Landman NH, Davis RA, Mapes RH (eds) Cephalopods present and past new insights and fresh perspectives. Springer, Dordrecht

Doguzhaeva LA, Bengtson SM, Mutvei H (2010) Structural and morphological indicators of mode of life in the Aptian lytoceratid ammonoid *Eogaudryceras*. In: Tanabe K, Shigeta Y, Sasaki T, Hirano H (eds) Cephalopods—present and past. Tokai University Press, Tokyo

Drushchits VV, Doguzhaeva LA (1981) Ammonoids in electron microscope (internal shell structure and systematics of Mesozoic phylloceratids, lytoceratids and six families of the Early Cretaceous ammonitids). Moscow State University Press, Moscow

Drushchits VV, Doguzhaeva LA, Mikhailova IA (1978) Unusual coating layers in ammonoids. Paleont Zh 2:36–44 [In Russian]

Griffith J (1977) The Upper Triassic fishes from Polzberg bei Lunz. Zool J Linnean Soc 60:1–93

Griffin LE (1900) The anatomy of *Nautilus pompilius*. Mem Nat Acad Sci 8:101–230

Haug E (1898) Études sur les goniatites. Mém Soc Geol France, Paléont 7(4). Mém 18:1–112

Henderson RA (1984) A muscular attachment proposal for septal function in Mesozoic ammonites. Palaeontology 27:461–486

Hewitt RA, Checa A, Westermann GEG, Zaborski PMP (1991) Chamber growth in ammonites inferred from colour markings and naturally etched surfaces of Cretaceous vascoceratids from Nigeria. Lethaia 24:271–284

Hoffmann R (2010) New insights on the phylogeny of the Lytoceratoidea (Ammonitina) from the septal lobe and its functional interpretation. Rev Paléobiol 29(1):1–156

Ivanov AN (1975) Late ontogeny in ammonoids, and its specific features in macro-, micro- and megaconchs. Scientific notes Yaroslavl Pedagogical Inst, Geol and Paleont 87:5–57 [In Russian]

Jacobs DK, Chamberlain JA Jr (1996) Buoyancy and hydrodynamics in ammonoids. In: Landman NH, Tanabe K, Davis RA (eds) Ammonoid Paleobiology, Topics in Geobiology 13:169–224

Jones DL (1961) Muscle attachment impressions in a Cretaceous ammonite. J Paleont 35:502–504

Jordan R (1968) Zur Anatomie mesozoischer Ammoniten nach den Strukturelementen der Gehäuse-Innenwand. Beih Geol Jahrb 77:1–64

Kakabadze MV, Sharikadze MZ (1993) On the mode of life of hetemmorph ammonites (heterocone, ancylocone, ptychocone). Geobios 15:209–215

Kar AJ, Briggs DEG, Donovan DT (1995) Decay and fossilization of non-mineralized tissue in coleoid cephalopods. Palaeontology 38:105–131

Kennedy WJ, Cobban WA (1976) Apects of ammonite biology, biogeography, and biostratigraphy. Spec Pap Palaeon 17:1–64

Kennedy WJ, Cobban WA, Klinger HC (2002) Muscle attachment and mantle-related features in Upper Cretaceous *Baculites* from the United States Western Interior. Abh Geol B-A 57:89–112

Keupp H (2000) Ammoniten. Paläobiologische Erfolgsspiralen. Thorbecke, Stuttgart

Kier WM (1988) The arrangement and function of molluscan muscle. In: Trueman ER, Clarke MR (eds) The Mollusca. vol 11. Form and Function. Academies Press, San Diego

Kier WM, Thompson JT (2003) Muscle arrangement, function and specialization in Recent coleoids. In: Warnke K, Keupp H, Boletzky S v (eds) Coleoid cephalopods through time. Berl Paläobiol Abh 3:141–162

Klug C (2004) Mature modifications, the black band, the black aperture, the black stripe, and the periostracum in cephalopods from the Upper Muschelkalk (Middle Triassic, Germany). Mitt Geol-Paläont Inst Univ Hamburg 88:63–78

Klug C, Korn D, Richter U, Urlichs M (2004) The black layer in cephalopods from the German Muschelkalk (Middle Triassic). Palaeontolology 47:1407–1425

Klug C, Montenari M, Schultz H, Ulrichs M (2007) Soft-tissue attachment of Middle Triassic Ceratitida from Germany. In: Landman NH, Davis RA, Mapes RH (eds) Cephalopods present and past. New Insights and fresh perspectives. 6th intern symp cephalopods—present and past. Springer, Dordrecht

Klug C, Meyer E, Richter U, Korn D (2008) Soft-tissue imprints in fossil and Recent cephalopod septa and septum formation. Lethaia 41:477–492

Korn D, Klug C (2007) Conch form analysis, variability, morphological disparity, and mode of life of the Frasnian (Late Devonian) ammonoid *Manticoceras* from Coumiac (Montagne Noire, France). In: Landman NH, Davis RA, Mapes RH (eds) Cephalopods—present and past. New insights and fresh perspectives. 6th International Symposium. Springer, Dordrecht

Kröger B (2002) On the ability of withdrawing of some Jurassic ammonoids. Abh Geol B-A 57:199–204

Kyuma Y, Nishida T (1987) *Akiyoshiceras*, a new neoicoceratid ammonoid genus from the Upper Carboniferous of Akiyoshi. Bull Akiyoshi-dai Mus Nat Hist 22:23–41

Kulicki C, Doguzhaeva LA (1994) Development and calcification of the ammonitella shell. Acta Palaeontol Pol 39:17–44

Kulicki C, Landman NH, HeaneyMJ, Mapes RH, Tanabe K (2002) Morphology of the early whorls of *Goniatites* from the Carboniferous Buckhorn Asphalt (Oklahoma) with aragonitic preservation. Abh Geol B-A 57:205–224

Landman NH, Bandel K (1985) Internal structures in the early whorls of Mesozoic ammonites. Am Mus Novit 2823:1–21

Landman NH, Waage KM (1993) Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills formaion in South Dakota and Wyoming. Bull Amer Mus Nat Hist 215:1–257

Landman NH, Tanabe K, Shigeta Y (1996) Ammonoid embryonic development. In: Landman NH, Tanabe K, Davis RA (eds) Ammonoid Paleobiology, Topics in Geobiology 13:343–405

Landman NH, Mapes RH, Tanabe K (1999a) Internal features of the embryonic shells of Late Carboniferous Goniatitina. In: Oloriz F, Rodriguez-Tovar FJ (eds) Advancing research on living and fossil cephalopods. Kluwer Academic Press, New York

Landman NH, Lane J, Cobban WA, Jorgensen SD, Kennedy WJ, Larson NL (1999b) Impressions of the attachment of the soft body to the shell in Late Cretaceous pachydiscid ammonites from the Western Interior of the United States. Amer Mus Nov 3273:1–31

Landman NH, Polizzotto K, Mapes RH, Tanabe K (2006) Camberal membranes in prolecanitid and goniatitid ammonoids from the Permian Arcturus Formation, Nevada, USA. Lethaia 39:365–379

Landman NH, Johnson RO, Garb MP, Edwards LE, Kyte FT (2007) Cephalopods from the Cretaceous/Tertiary boundary interval on the Atlantic coastal plain, with a description of the highest ammonite zones in North America. Part 3. Manasquan River Basin, Monmouth country, New Jersey. Bull Amer Mus Nat Hist 303:1–122

Landman NH, Mapes RH, Cruz C (2010) Jaws and soft tissues in ammonoids from the Lower Carboniferous (Upper Mississippian) Bear Gulch Beds, Montana, USA. In: Tanabe K, Shigeta Y, Sasaki T, Hirano H (eds) Cephalopods—present and past. Tokai University Press, Tokyo

Matsuoka A, Anso J, Nakada K, Terabe K, Sato T (2010) Biometrical analysis on primary rib number of the middle Jurassic ammonoids *Pseudoneuqueniceras yokoyamai* (Kobayashi & Fukuda) and its allied forms. In: Tanabe K, Shigeta Y, Sasaki T, Hirano H (eds) Cephalopods—present and past. Tokai University Press, Tokyo

Mitta VV, Starodubceva IA (2000) Stchirowsky and study of the Mesozoic in Alatyr-Kurmush area (Basin of the Middle Volga). VernadskyMus-Nov 5:1–20

Monks N, Young JR (1998) Body position and the functional morphology of Cretaceous heteromorph ammonites. Palaeontol Electronica 1.1.1A. http://palaeo-electronica.org/1998_1/monks/text.pdf

Münster GGz (1839) Beiträge zur Petrefaktenkunde mit XVIII nach der Natur gezeichneten Tafeln der Herren Hermann v. Meyer und Professor Rudolph Wagner. Buchner'sche Buchhandlung, Bayreuth

Mutvei H (1957) On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. Arkiv Mineral Geol 2:219–254

Mutvei H (1964) Remarks on the anatomy of Recent and fossil Cephalopoda. Stockholm Contr Geol 11:79–102

Mutvei H (2013) Characterization of nautiloid orders Ellesmerocerida, Oncocerida, Tarphycerida, Discosorida and Ascocerida: new superorder Multiceratoidea. GFF 135:171–183. doi: 10.1080/11035897.2013.801034

Mutvei H, Doguzhaeva LA (1997) Shell ultrastructure and ontogenetic growth in *Nautilus pompilius* L. (Mollusca: Cephalopoda). Palaeontogr A 246:33–52

Mutvei H, Dunca E (2007) Connecting ring ultrastructure in the Jurassic ammonoid *Quenstedtoceras* with discussion on mode of life of ammonoids. In: Landman NH, Davis RA, Mapes RH (eds) Cephalopods present and past. New insights and fresh perspectives. Springer, Dordrecht

Mutvei H, Reyment RA (1973) Buoyancy control and siphuncle function in ammonoids. Palaeontology 16:623–636

Mutvei H, Arnold JM, Landman NH (1993) Muscles and attachment of the body to the shell in embryos and adults of *Nautilus belauensis* (Cephalopoda). Amer Mus Nov 3059:1–15

Obata I, Futakami M, Kawashita Y, Takahashi T (1978) Apertural features in some Cretaceous ammonites from Hokkaido. Bull Nat Sci Mus C 4:139–155

O'Dor RK, Forsythe J, Webber DM, Wells J, Wells MJ (1990) Activity levels of *Nautilus* in the wild. Nature 362:626–627

Rakús M (1978) Sur l'existence de deux types distincts d'empreintes de muscles rétracteurs chez les ammonites. Bull Soc Vaudoise Sci Nat 354(74):139–145

Richter U (2002) Gewebeansatz-Strukturen auf Steinkernen von Ammonoideen. Geol Beitr Hannover 4:1–113

Richter U, Fischer R (2002) Soft tissue attachment structures on pyritized internal moulds of ammonoids. Abh Geol B-A 57:139–149

Ruzhencev VE (1956) Early Permian ammonoids from south Urals. II. The ammonoids of the Artinskya Stage. Trudy Paleont Inst USSR 60:1–275 [in Russian]

Ruzhencev VE (1962) General Part. In: Ruzencev VE (ed) Superorder Ammonoidea. Mollusca, Cephalopoda I. Osnovy Paleontologii. USSR Academy of Sciences, Moscow [In Russian]

Sasaki T, Shigeno S, Tanabe K (2010) Anatomy of living *Nautilus*: Reevaluation of primitiveness and comparison with Coleoidea. In: Tanabe K, Shigeta Y, Sasaki T, Hirano H (eds) Cephalopods—present and past. Tokai University Press, Tokyo

Saunders WB, Shapiro EA (1986) Calculation and simulation of ammonoid hydrostatics. Paleobiol 12:64–79

Saunders WB, Work DM (1997) Evolution of shell morphology and sutures complexity in Paleozoic prolecanitids, the rootstock of Mesozoic ammonoids. Paleobiol 23:301–325

Sharikadze MZ, Lominadze TA, Kvantaliani IV (1990) Systematische Bedeutung von Muskelabdrucken spätjurassischer Ammonoideae. Z geol Wiss 18:1031–1039

Shigeta Y, Weitschat W (2004) Origin of the Ammonitina (Ammonoidea) inferred from the internal shell structures. Mitt Geol-Paläontol Inst Univ Hamburg 88:179–194

Shigeta Y, Izukura M (2013) The earliest Cenomanian ammonoid *Tanabeceras yezoense* (Shigeta) from the Hobetsu area, Hokkaido. Bull Hobetsu Mus 28:1–6

Shulga-Nesterenko MI (1925) Internal shell structure of the Artinskian ammonites. Bull Moskovskogo obsh'estva ispytatelej prirody. Otd Geol 4(1–2):81–100

Stenzel HB (1964) Living *Nautilus*. In: Moore R (ed) Treatise on invertebrate paleontology, Mollusca 3: K59-K93. Geological Society and University of Kansas Press, Lawrence, KS

Suess E (1865) Über Ammoniten. Sitzungsber kaiserl Akad Wiss, Wien 52:3–19

Tanabe K, Landman NH, Mapes RH (1998) Muscle attachment scars in a Carboniferous goniatite. Paleont Res 2(2):130–136

Trueman AE (1941) The ammonite body-chamber, with special reference to the buoyancy and mode of life of the living ammonite. Q J Geol Soc 384:339–383

Vogel KP (1959) Zwergwuchs bei Polyptychiten (Ammonoidea). Geol Jb 76:469–540

Weitschat W (1986) Phosphatisierte Ammonoideen aus der Mittleren Trias von Central-Spitzbergen. Mitt Geol-Paläont Inst Univ Hamburg 61:249–279

Weitschat W, Bamdel K (1991) Organic components in phragmocones of Boreal Triassic ammonoids: implications for ammonoid biology. Paläontol Z 65:269–303

Wells MJ (1988) The mantle muscle and mantle cavity in cephalopods. In: Truman ER, Clarke MR (eds) The Mollusca, form and function 11. Academies Press, London

Wells MJ, O'Dor RK (1991) Jet propulsion and the evolution of cephalopods. Bull Mat Sci 49:419–432

Westermann GEG (1996) Ammonoid life and habitat. In: Landman NH, Tanabe K, Davis RA (eds) Ammonoid Paleobiology. Topics in Geobiology 13: 607–707. Springer US

Westermann GEG, Tsujita J (1999) Life habits of ammonoids. In: Savazzi E (ed) Morphology of invertebrate skeleton. Wiley, Chichester

Zaborski PMP (1986) Internal mould markings in a Cretaceous ammonite from Nigeria. Palaeontology 29:725–738

Zakharov JD (1974) New data on internal shell structures in Carboniferous, Triassic and Cretaceous ammonoids. Paleontol Zh 8(1):25–36

Zakharov JD (1978) Lower Triassic ammonoids of East USSR. Nauka, Moscow