Paleontological Research, vol. 5, no. 3, pp. 201-213, September 28, 2001

Origin of the Ceratitida (Ammonoidea) inferred from the early internal shell features

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Received 1 May 2001; Revised manuscript accepted 25 June 2001

Abstract. The early internal shell features in 40 species of the Goniatitida, Prolecanitida and Ceratitida are described on the basis of well-preserved specimens from the Carboniferous and the Permian of North America, England, Siberia and Urals. Seven morphotypes were recognized in the species examined by differences of the caecum shape (bottle-shaped, gourd-shaped, subelliptical, or elliptical), the proseptum length on the dorsal side (long or short), position of the second septum (close to proseptum or not) and initial position of the siphuncle (ventral, subcentral, or central). *Paraceltites elegans*, the oldest known representative of the Ceratitida, has a long proseptum on the dorsal side, a relatively small ammonitella angle, the second septum does not appear in close vicinity to proseptum, and the siphuncle is ventral. These features are essentially the same as those of the prolecanitid *Daraelites elegans*. This fact supports the hypothesis that the Ceratitida evolved from the Prolecanitida, probably *Daraelites*.

Key words: Ceratitida, early internal shell features, Goniatitida, phylogeny, Prolecanitida

Introduction

The Ceratitida, which is the dominant ammonoid order of the early Mesozoic and one of the major orders of Ammonoidea, ranged from early Permian to the end of Triassic times, and has an almost worldwide distribution (Hewitt *et al.*, 1993; Page, 1996). The origin of this order has been thought to be from a member of the Prolecantitida, because previous authors believed that both taxa shared a common lobe development (i.e., VU type of Ruzhencev, 1960, 1962 or U type of Schindewolf, 1934, 1953; see Smith, 1932; Spath, 1934; Spinosa *et al.*, 1975; Shevyrev and Ermakova, 1979; Saunders and Work, 1997). Zakharov (1983, 1984, 1988), however, showed that the Prolecanitida (Medlicottida in Zakharov, 1983) and the Permian Ceratitida (Paraceltitina in Zakharov, 1984) do indeed share the same lobe developmental type, (i.e., VLU type of Ruzhencev, 1960, 1962 or A type of Schindewolf, 1934, 1953), but one identical to that of the Goniatitida. He also pointed out the difficulty in determining the ancestor of the Ceratitida based on the lobe development patterns, because all early to middle Permian ammonoids have the same lobe development pattern (Zakharov, 1984). After his works, no detailed observations of various shell characters have been done as a basis for discussion of the ancestor of the Ceratitida.

Since Branco (1879, 1880), the ammonoid early internal shell features have been studied by many authors, and it has been determined that there are a number of common characters in the early shells of all ammonoids. States of these characters appear to be stable at suborder or superfamily levels (Druschits and Khiami, 1970; Druschits and Doguzhaeva, 1974, 1981; Tanabe *et al.*, 1979; Tanabe and Ohtsuka, 1985; Ohtsuka, 1986; Landman *et al.*, 1996). This fact suggests that the early internal shell features are strongly constrained phylogenetically, and therefore, it is possible to investigate the higher phylogenetic relationships within the Ammonoidea by analyzing these character state changes (Shigeta, 1989).

As compared with Jurassic and Cretaceous ammonoids, Carboniferous and Permian ammonoids have been little studied for their early internal shell features. Most previous studies (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959; Zakharov,

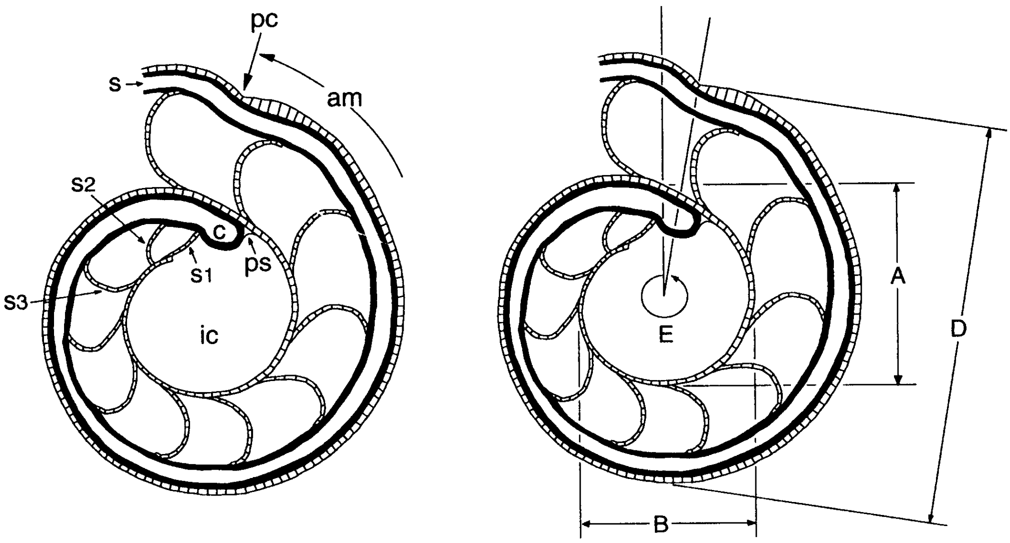


Figure 1. Diagrams of the internal shell structure (left) and measurements (right) of the early ammonoid shell in median section. The terminology is from Branco (1879, 1880), Grandjean (1910), and Drushchits and Khiami (1970). Abbreviations: am: ammonitella; c: caecum; ic: initial chamber; pc: primary constriction; ps: prosiphon; s: siphunclar tube; s1: proseptum (first septum); s2: primary septum (second septum); s3: third septum; A: maximum initial chamber size; B: minimum initial chamber size; D: ammonitella size; E: ammonitella angle.

1978) excluding Tanabe *et al.* (1994) and Landman *et al.* (1999) are based on optical microscopic observations. Detailed microstructural relationships of the morphologic features have received little examination.

We have studied the early internal shell features of some Carboniferous and Permian ammonoids belonging to the Goniatitida, Prolecanitida and Ceratitida, by means of scanning electron microscopy. In this paper, we describe some of our observations and discuss the results of our analysis with special reference to the origin of the Ceratitida.

Material and methods

Five species of the Prolecanitida, 34 species of the Goniatitida and one species of the Ceratitida have been examined (Appendix 1). Specimens of these ammonoids were collected from the Carboniferous and Permian strata of South Urals (Kazakhstan), Siberia (Russia), England and the U.S. mid-continent (Nevada and Texas). They include genera and species studied and figured by Tanabe *et al.* (1994). Higher categories of these genera and species were determined following the classification of Bogoslovskaya *et al.* (1999).

Every specimen was cut and polished along the median plane. The polished surface was etched with 5% acetic acid for a few minutes; the etched surface was washed with distilled water, dried in air, and then coated with gold or platinum using an ioncoater. The early internal features of each specimen were observed by means of a JEOL model JSM-5310 scanning electron microscope. Four characters: maximum initial chamber size, minimum initial chamber size, ammonitella size and ammonitella angle (= spiral length of ammonitella in degrees), were measured on the etched surface using a digital micrometer (accuracy $\pm$0.001 mm) attached to a Nikon model V16D profile projector.

Figure 1 illustrates the terms used to describe the morphologic features of the early shell in median section. The terminology is based on Branco (1879, 1880), Grandjean (1910), and Drushchits and Khiami (1970) (see Landman *et al.*, 1996, figure 1). The specimens observed are reposited at the University Museum, University of Tokyo (UMUT) for those described by Tanabe *et al.* (1994) and at the National Science Museum, Tokyo (NSM) for the remaining specimens.

Observations

Prolecanitida and Goniatitida

The early whorls of the Carboniferous and Permian Prolecanitida and Goniatitida consist of initial chamber (protoconch), caecum, prosiphon, proseptum (first septum), septa, siphuncle, septal neck and outer shell wall, as in other Paleozoic and Mesozoic Ammonoidea. The maximum initial chamber size in median section (A in Figure 1) ranges from 0.356 mm to 0.645 mm in the Prolecanitida and from 0.356 mm to 0.590 mm in the Goniatitida (Appendix 2). The ammonitella diameter (D in Figure 1) ranges from 0.702 mm to 1.250 mm in the Prolecanitida and from 0.660 mm to 1.048 mm in the Goniatitida (Appendix 1). The ammonitella angle (E in Figure 1) is generally small (328–355°) in the Prolecanitida and relatively large (352–385°) in the Goniatitida. The early internal shell features of the species examined can be classified into seven morphotypes; here named for the genera that best show each variation: *Epicanites*, *Neopronorites*, *Daraelites*, *Goniatites*, *Marathonites*, *Agathiceras* and *Thalassoceras* morphotypes (Figure

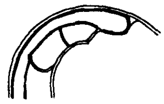
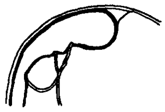
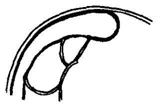
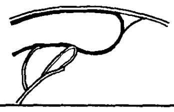
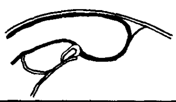
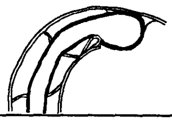
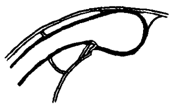
Morphotype	Shape of caecum in median section	Length of proseptum (dorsal side)	Proseptum & 2nd septum (dorsal side)	Initial position of siphuncle
Epicanites 	Bottle-shaped	Long	Separate (fairly)	Ventral
Neopronorites 	Gourd-shaped	Long	Separate (a little)	Ventral
Daraelites 	Bottle-shaped	Long	Separate (a little)	Ventral
Goniatites 	Subelliptical	Long	Close	Ventral
Marathonites 	Elliptical	Short	Close	Ventral
Agathiceras 	Elliptical	Short	Close	Central
Thalassoceras 	Elliptical	Short	Close	Subcentral

Figure 2. Comparison of the early internal shell features in seven morphotypes of the Carboniferous and Permian ammonoids. Each morphotype is named for the genera that best show each variation.

2). There is no intermediate form between a pair of these internal shell feature morphotypes in our data base. All of the morphotypes have a circular initial chamber in median section and a short prosiphon.

Epicanites morphotype.—In median section, caecum is elongate and subelliptical (bottle-shaped), without a conspicuous constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum resting on dorsal side of initial chamber wall is long and strongly convex adapically. Second septum is convex adorally in median section, with a retrochoanitic septal neck, and is located far from proseptum. Siphuncle keeps ventral position throughout ontogeny.

Akmilleria electaensis, *Artioceras rhipaeum* (Figure 3.5, 6) and *Epicanites loeblichi* (Figure 4.1, 2) possess the early internal shell morphology of this morphotype. Early internal shell features of this morphotype have been reported in other Medlicottioidea (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959).

Neopronorites morphotype.—Caecum is gourd-shaped, with a slightly constricted base at the proseptum, bulging part between proseptum and second septum, and gradual contracting part after second septum. Prosiphon is short, tube-like and straight. Proseptum resting on dorsal side of initial chamber wall is relatively long and slightly convex adorally in median section. Second septum is slightly concave adorally in median section, with a retrochoanitic septal neck, and is located relatively far from proseptum. Siphuncle is ventral throughout ontogeny.

Neopronorites skvorzovi (Figure 3.3, 4) possesses the early internal shell morphology of this morphotype, as described by Zakharov (1986). A similar shaped caecum was described in *Parapronorites* cf. *biformis* by Shul'ga-Nestere nko (1926), hence she named it as a double caecum. Böhmers (1936), Miller and Unklesbay (1943) and Bogoslovskaya (1959) reported similar early internal shell features in other Pronoritoidea.

Daraelites morphotype.—Caecum is elongate and subelliptical (bottle-shaped), without a conspicuous constricted base at proseptum and second septum. Proseptum resting on

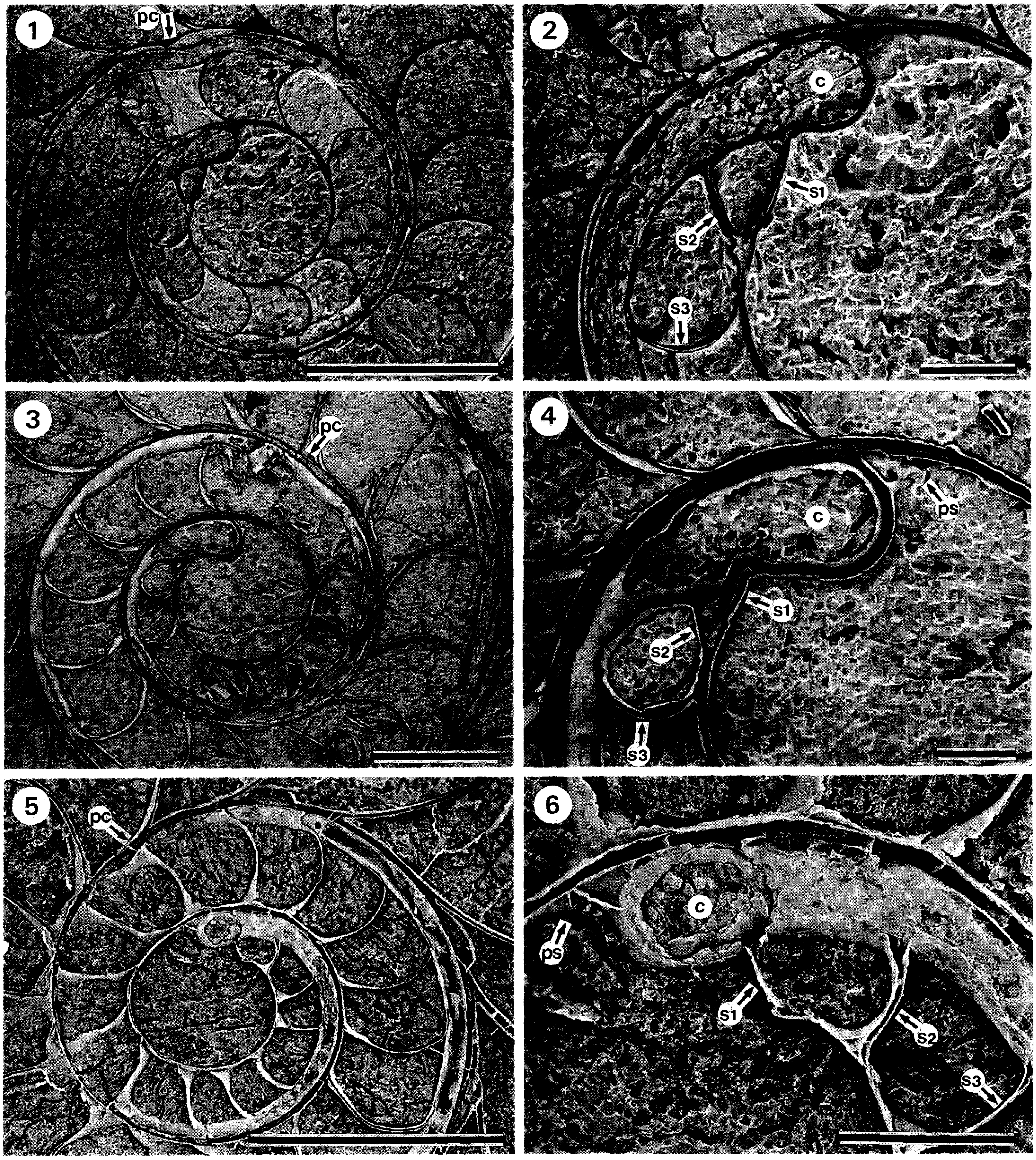


Figure 3. Median sections through the early whorls of the Permian prolecanitids. Over views of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2**. *Daraelites elegans* Tchernow (Prolecanitoidea), Artinskian, South Urals (NSM PM16189). **3, 4**. *Neopronorites skvorzovi* (Tchernow) (Pronoritoidea), Artinskian, South Urals (NSM PM16190). **5, 6**. *Artioceras rhipaeum* (Ruzhencev) (Medlicottioidea), Artinskian, South Urals (NSM PM16192).

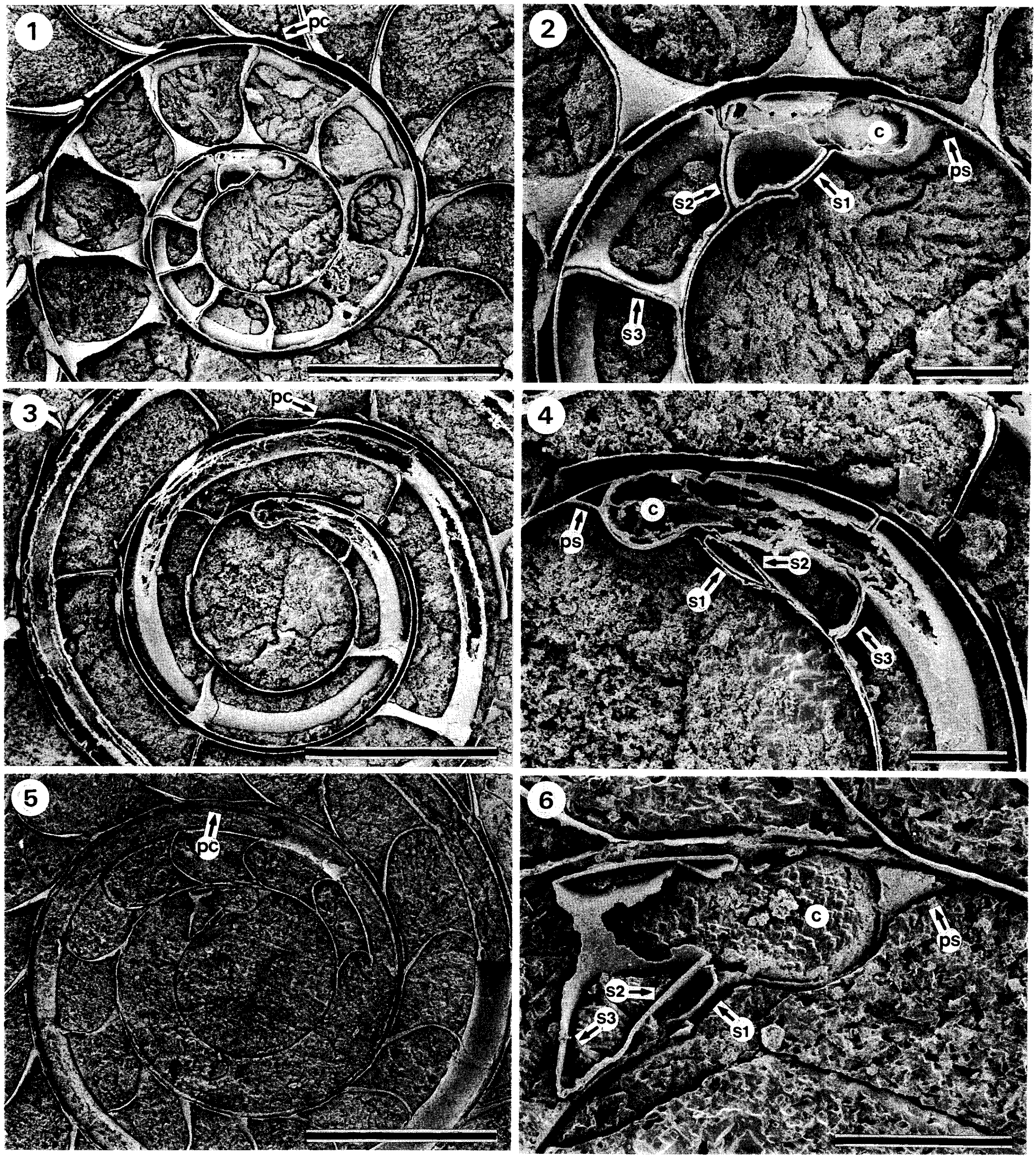


Figure 4. Median sections through the early whorls of the Carboniferous ammonoids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2**. *Epicanites loeblichi* Miller & Furnish (Prolecanitida: Prolecanitoidea), Chesterian, Oklahoma (NSM PM16188). **3, 4**. *Girtyoceras meslerianum* (Girty) (Goniatitida: Dimorphoceratoidea), Chesterian, Oklahoma (NSM PM16193). **5, 6**. *Cravenoceras incisum* (Hyatt) (Goniatitida, Neoglyphioceratoidea), Chesterian, Texas (NSM PM16198).

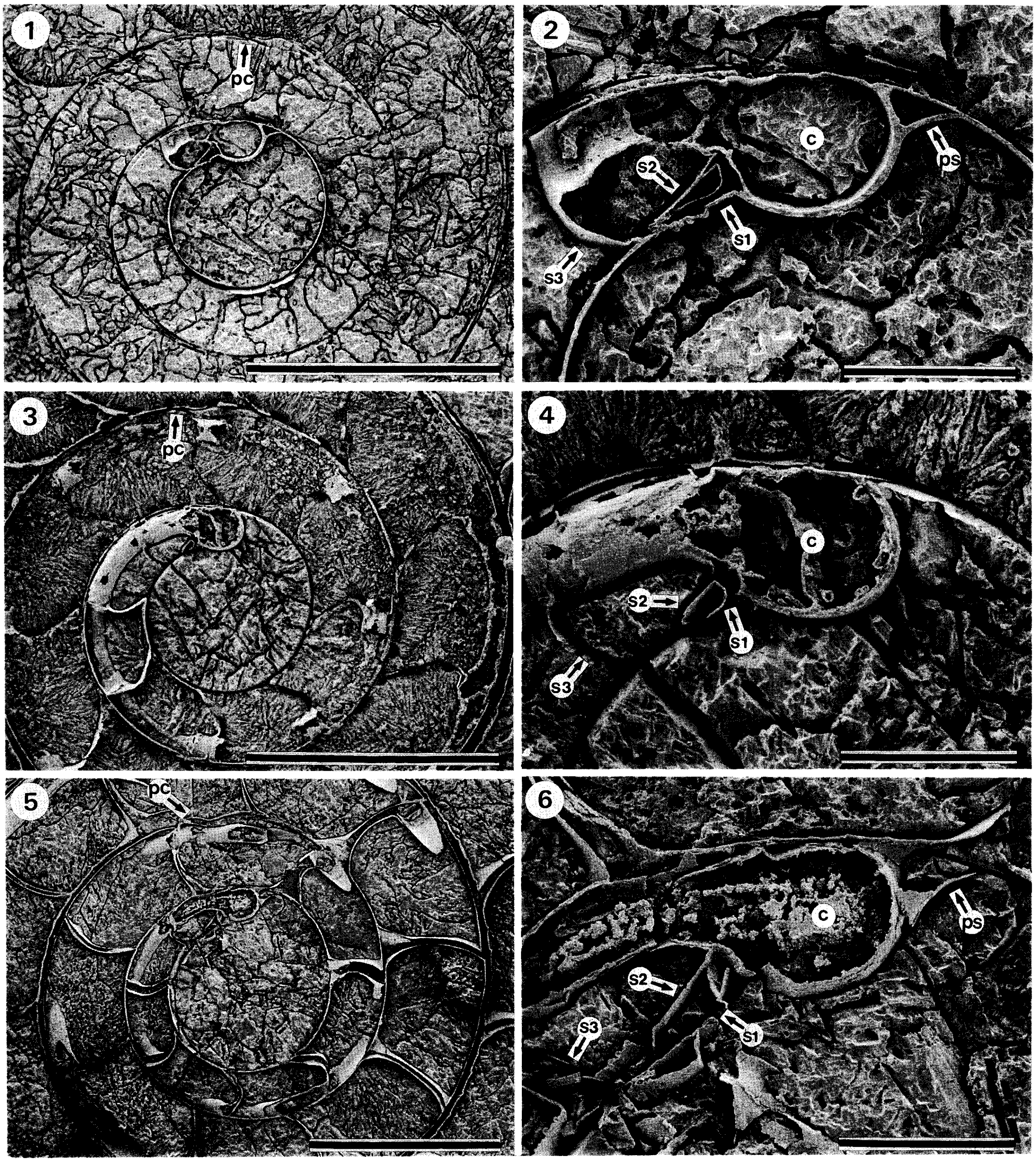


Figure 5. Median sections through the early whorls of the Permian goniatitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2**. *Popanoceras annae* Ruzhencev (Popanoceratoidea), Artinskian, South Urals (NSM PM16214). **3, 4**. *Marathonites invariabilis* (Ruzhencev) (Marathonitoidea), Artinskian, South Urals (NSM PM16207). **5, 6**. *Uraloceras* sp. (Neoicoceratoidea), Wolfcampian, Nevada (NSM PM16213).

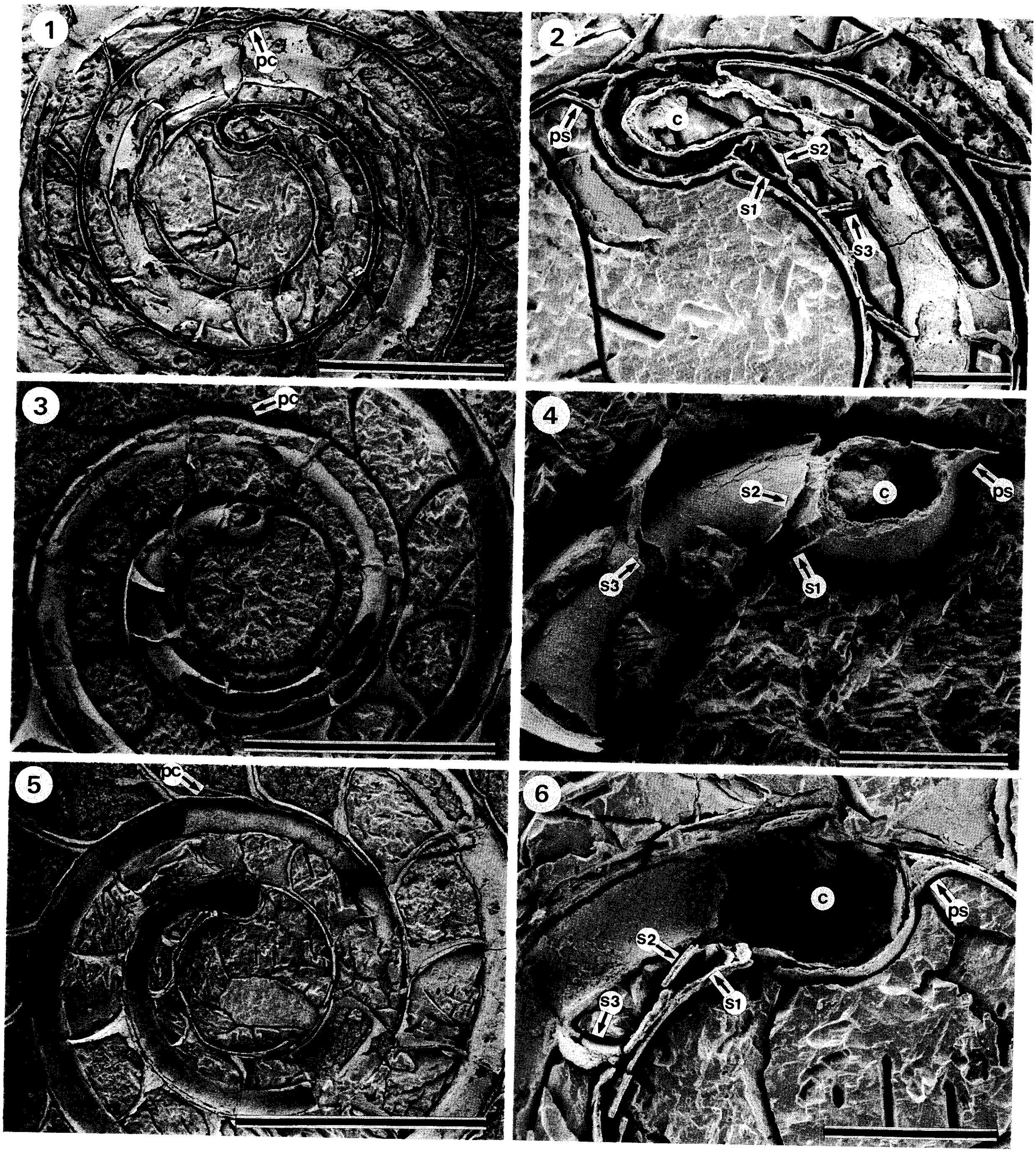


Figure 6. Median sections through the early whorls of the Permian goniatitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2**. *Agathiceras uralicum* (Karpinsky) (Goniatitoidea), Artinskian, South Urals (NSM PM16195). **3, 4**. *Thalassoceras gemmellaroi* Karpinsky (Thalassoceratoidea), Artinskian, South Urals (NSM PM16203). **5, 6**. *Crimites subkrotowi* Ruzhencev (Adrianitoidea), Artinskian, South Urals (NSM PM16204).

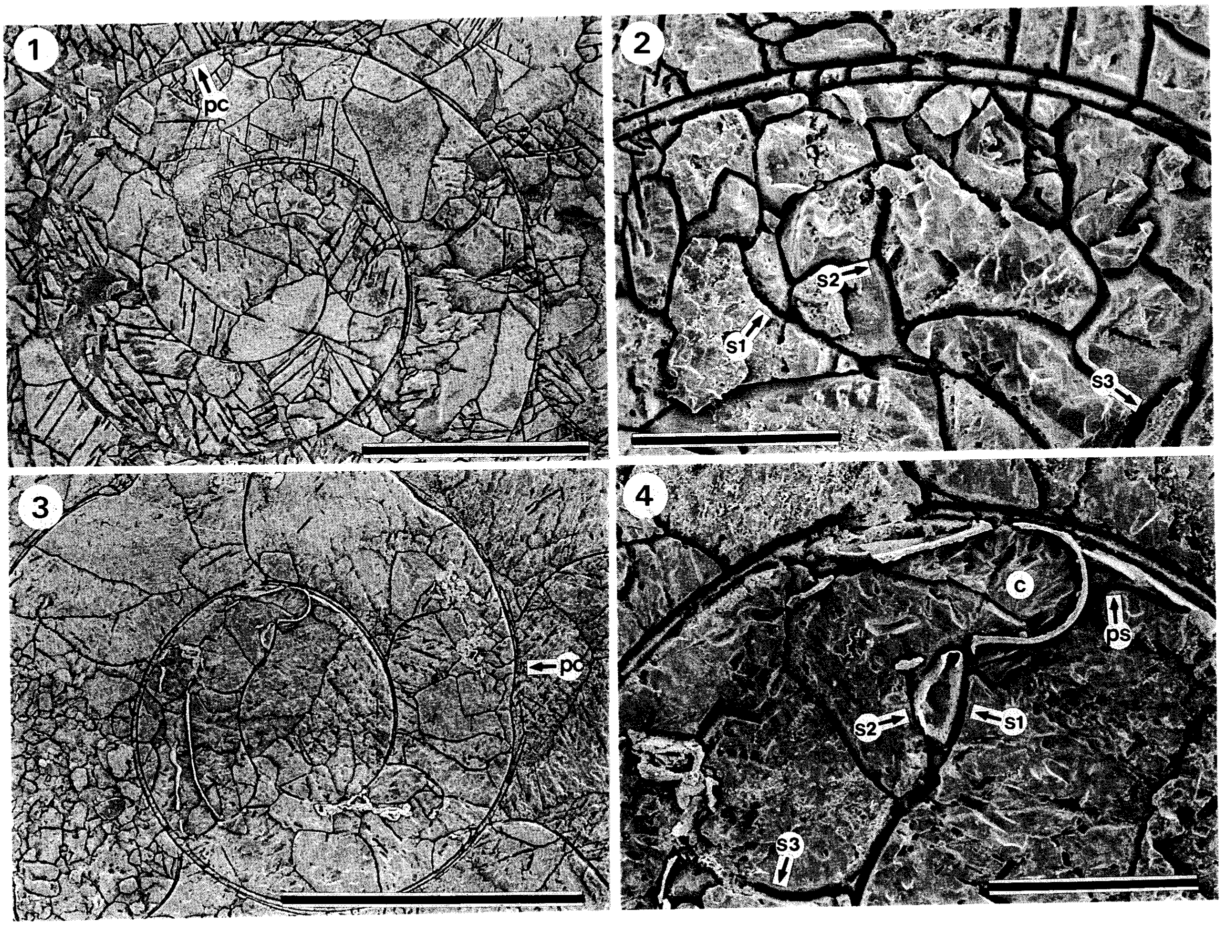


Figure 7. Median sections through the early whorls of the Permian and Triassic ceratitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4). Scale bars in 1 and 3: 0.5 mm. Scale bars in 2 and 4: 0.1 mm. **1, 2**. *Paraceltites elegans* Girty (Xenodiscoidea), Roadian, Texas (NSM PM16215). **3, 4**. *Nordophiceras jacksoni* (Hyatt & Smith) (Noritoidea), Spathian, Bear Lake area, Idaho (NSM PM16216).

dorsal side of initial chamber wall is long and slightly convex adapically in median section. Second septum is convex adorally in median section, with a retrochoanitic septal neck, and does not appear to be in close vicinity to proseptum. Siphuncle keeps a ventral position throughout ontogeny.

Daraelites elegans possesses the early internal shell morphology of this morphotype (Figure 3.1, 2). Early internal shell features of this morphotype have been found in other species of *Daraelites* (Böhmers, 1936; Miller and Unklesbay, 1943).

Goniatites morphotype.—In median section, caecum is subelliptical, without a conspicuous constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is long and slightly convex adapically. Second septum is attached to proseptum on the dorsal side, forming a necklike structure in median section. Siphuncle keeps a ventral position throughout ontogeny.

Genera in the major superfamilies of the Carboniferous Goniatitida, including those in the Dimorphoceratoidea, Goniatitoidea, Neoglyphioceratoidea, Somoholitoidea and Gastrioceratoidea listed in Appendix 1, possess the early internal shell morphology of this morphotype (Figure 4.3–6; Appendix 1). Our observations are consistent with the descriptions by previous authors (Böhmers, 1936; Miller and Unklesbay, 1943; Tanabe *et al.*, 1994).

Marathonites morphotype.—In median section, caecum is ellipsoid with a strongly constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is short and convex adapically. Second septum is attached to proseptum on dorsal side, forming a necklike structure in median section. Siphuncle keeps a ventral position throughout ontogeny.

Many superfamilies of the Permian Goniatitida, including the Adrianitoidea, Marathonitoidea, Neoicoceratoidea and Popanoceratoidea, possess the early internal shell morphology of this morphotype (Figures 5; 6.5, 6; Appendix 1). Additionally, our observations are consistent with the data of other authors (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959; Tanabe *et al.*, 1994).

Agathiceras morphotype.—In median section, caecum is ellipsoid with a strongly constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is short and slightly convex adapically. Second septum is convex adorally, with a retrochoanitic septal neck, and is close to proseptum on dorsal side, forming a necklike structure in median section. Siphuncle keeps a central position in first three whorls, and subsequently gradually shifts its position toward the venter. Migration of siphuncle to ventral marginal side is completed at end of fifth whorl.

Two species of *Agathiceras* examined possess the early internal shell morphology of this morphotype (Figure 6.1, 2; Appendix 1). Schindewolf (1934) and Böhmers (1936) reported similar early internal shell features in other Permian *Agathiceras.*

Thalassoceras morphotype.—In median section, caecum, which is preceded by short and curved prosiphon, is ellipsoid with a strongly constricted base at proseptum and second septum; proseptum on dorsal side is short, and second septum is close to proseptum on dorsal side. Siphuncle occupies a central to subcentral position in first whorl, and subsequently shifts its position gradually to the venter in the early part of second whorl.

Three taxa assigned to the Thalassoceratoidea, *Bisatoceras* sp., *Eothalassoceras inexpectans* and *Thalassoceras gemmellaroi*, possess the early internal shell morphology of this morphotype (Figure 6.3, 4; Appendix 1).

Ceratitida

The initial chamber of *Paraceltites elegans* is circular in median section (Figure 7.1, 2). Although the caecum, prosiphon and siphuncular tube are not preserved in specimen NSM PM16215, Spinosa *et al.* (1975, text-fig. 11) described an elongate and subelliptical caecum without a conspicuous constricted base at proseptum and one short prosiphon. The proseptum resting on the dorsal side of the initial chamber wall is long and slightly convex adapically in median section. The second septum does not appear in close vicinity to the proseptum, and the siphuncle maintains a ventral position throughout ontogeny. The maximum initial chamber size, ammonitella size and ammonitella angle in NSM PM16215 are 0.463 mm, 0.921 mm and 342° respectively (Appendix 1).

The early internal shell morphology of the early Triassic ceratitid *Nordophiceras jacksoni* (Figure 7.3, 4) is similar to those observed in *Paraceltites elegans* and *Daraelites elegans* except for the much smaller ammonitella angle (264°).

Discussion

Since the lobe development in the Prolecanitida has been thought to be identical with that in the Ceratitida, many authors have attributed the ancestor of the Ceratitida to the Prolecanitida (Spath, 1934; Schindewolf, 1953; Ruzhencev, 1960). The oldest representative of the Ceratitida is known from the lower Middle Permian (Roadian) and is referable to *Paraceltites*, which is characterized by a thinly discoidal, widely evolute conch, round venter, a prominent ventral salient in the growth lines, and unserrated lobes (Spinosa *et al.*, 1975). Compared to the other prolecanitid ammonoid genera, the genus shares more similar features of conch and suture morphology with *Daraelites,* so that previous authors considered that *Paraceltites* evolved from a daraelitid stock in the Prolecanitida, probably *Daraelites* (Ruzhencev, 1960, 1962).

Zakharov (1984, 1988), however, showed that the lobe development of the Prolecanitida is identical with that of the Goniatitida. He noted that the ammonoid family occurring in the Lower Permian, which shares common features of conch morphology, ornamentation and suture with *Paraceltites,* is the Eothinitidae in the Goniatitida. *Paraceltites* and Eothinitidae both display a widely evolute conch with marginal ribs rather than nodes, round venter, and simple adult suture line. Based on these facts Zakharov (1984, 1988) suggested that *Paraceltites* evolved from the Eothinitidae, probably *Epiglyphioceras* (Zakharov, 1984, 1988). However, except for the simple adult suture line, *Daraelites* also possesses these characters. Inference of a possible ancestor of *Paraceltites* on the basis of only conch morphology and ornamentation should be avoided if other features can be utilized to resolve this ancestor-descendant problem.

The Prolecanitida and Goniatitida each exhibit certain distinct features in their early internal shell features that can be brought to bear on this problem. Available data show that the Prolecanitida share a short and curved prosiphon, a bottle-shaped or gourd-shaped caecum without a conspicuous constricted base at proseptum in median section, long prosepta on dorsal side, a ventral siphuncle, and a relatively small ammonitella angle (328–350°). The second septum does not appear in close vicinity to the proseptum. Meanwhile, species of the Goniatitida share a short and curved prosiphon, a subelliptical or elliptical caecum with a strongly constricted base at proseptum, short prosepta on dorsal side, a ventral siphuncle, and a relatively large ammonitella angle (352–385°). The second septum is close to proseptum on the dorsal side, forming a necklike structure in median section.

Paraceltites elegans has a long proseptum on the dorsal side, and the second septum does not appear in close vicinity to proseptum. The ammonitella angle is 342° in the specimen examined. These features are characteristic of early internal shell features of the prolecanitid *Daraelites elegans* rather than the Goniatitida. These similarites of early ontogenetic shell features as well as the conch morphology of shell shape, ornamentation and sutural development strongly suggest a close phylogenetic relationship between *Daraelites* and *Paraceltites.* These observations strongly support the hypothesis of the daraelitid origin for the Ceratitida as proposed by Ruzhencev (1960, 1962).

Acknowledgments

We are very grateful to H. Maeda (Kyoto University) for his kind help and cooperation throughout the field survey, T. Sasaki (University of Tokyo) for arranging loans of specimens described by Tanabe *et al.* (1994), and K. Tanabe (University of Tokyo) for critical reading of the manuscript. This study was supported by the JSPS Fellowships for research in NIS countries and the Grant-in-Aid for Scientific Research from JSPS (nos. 12440141 and 13740302) to Y. Shigeta.

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Appendix 1. List of material, and measurement data and character states of the species exam- morphotype, G: *Goniatites* morphotype, E: *Epicanites* morphotype, M: *Marathonites* morphotype, N: Bogoslovskaya *et al.* (1999).

Species	Horizon	Locality	Sample
Order Prolecanitida			
Prolecanitoidea			
Epicanites loeblichi Miller & Furnish	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16188
Daraelites elegans Tchernow	Artinskian	Aktasty R., South Urals	NSM PM16189
Pronoritoidea			
Neopronorites skvorzovi (Tchernow)	Artinskian	Aktasty R., South Urals	NSM PM16190
Medlicottioidea			
Akmilleria electraensis (Plummer & Scott)	Wolfcampian	Buck Mountain, Nevada	NSM PM16191
Artioceras rhipaeum (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16192
Order Goniatitida			
Dimorphoceratoidea			
Girtyoceras meslerianum (Girty)	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16193
Eumorphoceras plummeri Miller & Youngquist	Chesterian	San Saba, Texas	UMUT PM19030
Gatherites morrowensis (Miller & Moore)	Morrowan	Gather Mt., Arkansas	UMUT PM19032
Goniatitoidea			
Goniatites multiliratus Gordon	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16194
Goniatites aff. *crenistria* Phillip	Chesterian	Ahloso, Oklahoma	UMUT PM19019-2
Goniatites choctawensis Shumard	Meramecian	Clarita, Oklahoma	UMUT PM19020-2
Agathiceras uralicum (Karpinsky)	Artinskian	Aktasty R., South Urals	NSM PM16195
Agathiceras applini Plummer & Scott	L. Permian	Coleman, Texas	NSM PM16196
Neoglyphioceratoidea			
Neoglyphioceras abramovi Popow	Namurian	Menkyule R., Verkhoyansk	NSM PM16197
Cravenoceras incisum (Hyatt)	Chesterian	San Saba, Texas	NSM PM16198
Cravenoceras lineolatum Gordon	Chesterian	Lick Mountain, Arkansas	NSM PM16199
Cravenoceras richardsonianum (Girty)	Chesterian	Wapanucka, Oklahoma	UMUT PM19021
Somoholitoidea			
Glaphyrites hyattianus (Girty)	Desmoinesian	Okmulgee, Oklahoma	NSM PM16200
Glaphyrites warei (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	NSM PM16201
Glaphyrites jonesi (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	UMUT PM19027
Glaphyrites clinei (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	UMUT PM19028
Gastrioceratoidea			
Homoceras subglobosum (Bisat)	L. Namurian	Stonehead Beck, Yorkshire	NSM PM16202
Arkanites relictus (Quinn, McCaleb & Webb)	Morrowan	Bradshaw Mt., Arkansas	UMUT PM19029
Thalassoceratoidea			
Bisatoceras sp.	Desmoinesian	Okmulgee, Oklahoma	UMUT PM19033-1
Eothalassoceras inexpectans (Miller & Owen)	Desmoinesian	Okmulgee, Oklahoma	UMUT PM19036-1
Thalassoceras gemmellaroi Karpinsky	Artinskian	Aktasty R., South Urals	NSM PM16203
Adrianitoidea			
Crimites subkrotowi Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16204
Crimites elkuensis Miller, Furnish & Clark	Wolfcampian	Buck Mountain, Nevada	NSM PM16205
Texoceras sp.	Roadian	El Capitan, Texas	UMUT PM19037-1
Marathonitoidea			
Kargalites typicus (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16206
Marathonites invariabilis (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16207
Neoicoceratoidea			
Metalegoceras sp.	Wolfcampian	Buck Mountain, Nevada	NSM PM16208
Metalegoceras baylorense White	Wolfcampian	Buck Mountain, Nevada	UMUT PM19035
Eothinites kargalensis Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16209
Paragastrioceras kirghizorum Voinova	Artinskian	Aktasty R., South Urals	NSM PM16210
Paragastrioceras artolobatum Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16211
Uraloceras complanatum (Voinova)	Artinskian	Aktasty R., South Urals	NSM PM16212
Uraloceras sp.	Wolfcampian	Buck Mountain, Nevada	NSM PM16213
Popanoceratoidea			
Popanoceras annae Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16214
Order Ceratitida			
Xenodiscoidea			
Paraceltites elegans Girty	Roadian	Guadalupe Mts., Texas	NSM PM16215

ined. Data source: 1. Spinosa *et al.* (1975). Abbreviations: A: *Agathiceras* morphotype, D: *Daraelites*
Neopronorites morphotype, T: *Thalassoceras* morphotype. Major taxonomic positions from

Initial chamber size (mm)		Ammonitella		Length of pro-siphon	Shape of caecum in median section	Length of prpseptum (dorsal side)	Proseptum & 2nd septum (dorsal side)	Initial position of sipuncle	Morpho-type
Max.	Min.	size (mm)	angle (deg.)						
0.426	0.393	0.870	355	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.466	0.405	0.913	350	?	Bottle-shaped	Long	Separate (a little)	Ventral	D
0.645	0.578	1.147	328	Short	Gourd-shaped	Long	Separate (a little)	Ventral	N
0.633	0.550	1.250	338	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.356	0.311	0.702	334	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.543	0.462	0.906	368	Short	Subelliptical	Long	Close	Ventral	G
—	—	1.032	—	?	?	?	?	Ventral	?
0.416	0.370	0.833	385	?	?	Long	Close	Ventral	G
0.545	0.470	0.978	360	Short	Subelliptical	Long	Close	Ventral	G
0.566	0.533	0.995	380	?	Subelliptical	Long	Close	Ventral	G
0.541	0.483	0.996	383	Short	Subelliptical	Long	Close	Ventral	G
0.513	0.451	0.949	369	Short	Elliptical	Short	Close	Central	A
0.520	0.466	1.010	365	?	Elliptical	Short	Close	Central	A
0.522	0.476	0.927	370	Short	Subelliptical	Long	Close	Ventral	G
0.490	0.446	0.910	360	Short	Subelliptical	Long	Close	Ventral	G
0.484	0.403	0.815	368	Short	Subelliptical	Long	Close	Ventral	G
0.486	0.446	0.813	367	?	?	Long	Close	Ventral	G
0.590	0.498	1.048	370	Short	Subelliptical	Long	Close	Ventral	G
0.527	0.458	0.916	369	Short	Subelliptical	Long	Close	Ventral	G
0.535	0.470	0.920	372	?	?	Long	Close	Ventral	G
0.413	0.373	0.720	379	?	?	Long	Close	Ventral	G
0.496	0.458	0.933	367	Short	Subelliptical	Long	Close	Ventral	G
—	—	0.800?	—	?	?	?	?	?	?
0.360	0.335	0.620	358	Short	Elliptical	Short	Close	Subcentral	T
0.386	0.360	0.680	365	Short	?	Short	Close	Subcentral	T
0.365	0.338	0.694	356	Short	Elliptical	Short	Close	Subcentral	T
0.376	0.332	0.681	365	Short	Elliptical	Short	Close	Ventral	M
0.384	0.350	0.725	365	Short	Elliptical	Short	Close	Ventral	M
—	—	0.958	—	?	?	?	?	?	?
0.468	0.419	0.909	360	Short	Elliptical	Short	Close	Ventral	M
0.382	0.356	0.767	366	Short	Elliptical	Short	Close	Ventral	M
0.472	0.411	0.833	365	?	?	Short	Close	Ventral	M
0.480	0.410	0.866	365	Short	Elliptical	Short	Close	Ventral	M
0.381	0.349	0.672	372	?	?	Short	Close	Ventral	M
0.396	0.366	0.689	365	?	?	Short	Close	Ventral	M
0.413	0.377	0.736	365	?	?	Short	Close	Ventral	M
0.408	0.370	0.735	362	?	Elliptical	Short	Close	Ventral	M
0.517	0.463	0.850	371	Short	Elliptical	Short	Close	Ventral	M
0.356	0.321	0.660	352	Short	Elliptical	Short	Close	Ventral	M
0.463	0.400	0.921	342	Short[1]	Bottle-shaped[1]	Long	Separate (a little)	Ventral	D