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Origin of the Ammonitina (Ammonoidea) inferred from the internal shell features

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With 6 figures

Contents

Abstract

Based on well preserved ammonoid-specimens from the Triassic/Jurassic boundary of New York Canyon, Gabbs Valley Rang (Nevada), the internal shell features of species from the genera *Placites*, *Arcestes*, *Choristoceras* and *Rhacophyllites* (Upper Triassic, latest Norian), and one species of *Psiloceras pacificum* (earliest Jurassic, basal Hettangian) are investigated and compared. The early ontogeny of the chamber shape, the position of the siphuncle, and the septal neck morphology are more or less identical in *Rhacophyllites* sp. and *Psiloceras pacificum*, which strongly support the hypothesis that the Ammonitina evolved from the Phylloceratina.

Zusammenfassung

Auf der Basis von außergewöhnlich gut erhaltenem Ammonoideen aus dem Trias/Jura Grenzbereich von New York Canyon, Gabbs Valley (Nevada) werden die Embryonal-Gehäuse von vier

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Arten der Gattungen *Placites*, *Arcestes*, *Choristoceras* und *Rhacophyllites* (Ober-Trias, höchtes Nor) und von *Psiloceras pacificum* (Unter Jura, tiefstes Hettangium) untersucht und verglichen. Die Form des Protoconchs, die früontogenetischen Lage des Siphos und die Morphologie der Siphonaldüten sind bei *Rhacophyllites* und *Psiloceras pazificum* nahezu identisch, womit die Hypothese einer Abstammung der Ammonitina von den Phylloceratina bestärkt wird.

I. Introduction

The Ammonitina, which comprise the majority of Jurassic and Cretaceous ammonoid species, ranged from latest Triassic to the end of Cretaceous time (Hewitt et al., 1993; Page, 1996). The first Ammonitina was conventionally considered as belonging to the genus *Psiloceras*, which has been thought to evolve from a member of the Pinacoceratoidea in the Ceratitida (Tozer, 1981) or the Phylloceratina in the Ammonitida (Guex, 1982, 1995), based on the close similarities in the external suture lines and the conch morphology among these taxa. However, no detailed observations of various shell characters have been done as a basis for discussion of the ancestor of the *Psiloceras*.

Since Branco (1879, 1880), many works have been carried out to describe the internal shell features of various ammonoid taxa by means of optical and scanning electron microscopy. These previous works have demonstrated that the states of many qualitative characters appear to be stable at higher taxonomic levels (Druschits & Khiami, 1970; Druschits & Doguzhaeva, 1974, 1981; Tanabe et al., 1979, 2003; Tanabe & Ohtsuka, 1985; Ohtsuka, 1986; Landman et al., 1996). This fact suggests that the internal shell features are strongly constrained phylogenetically, and therefore, it is possible to investigate the higher-level systematics and evolution of the Ammonoidea on the basis of these character state changes (Shigeta, 1989; Shigeta et al., 2001; Tanabe et al., 2003).

We studied the internal shell features of some latest Triassic and earliest Jurassic ammonoids by means of scanning electron microscopy. In this paper, we describe some of our observations and discuss the results with special reference to the origin of the Ammonitina.

II. Material and methods

Four species of latest Triassic (late Norian) ammonoids and one species of earliest Jurassic (earliest Hettangian) *Psiloceras* have been examined. Specimens of these ammonoids were collected from the uppermost Triassic and lowest Jurassic strata of the New York Canyon, Gabbs Valley Rang, Nevada. Higher categories of these genera and species were determined following the classification of Hewitt et al. (1993) and Page (1993).

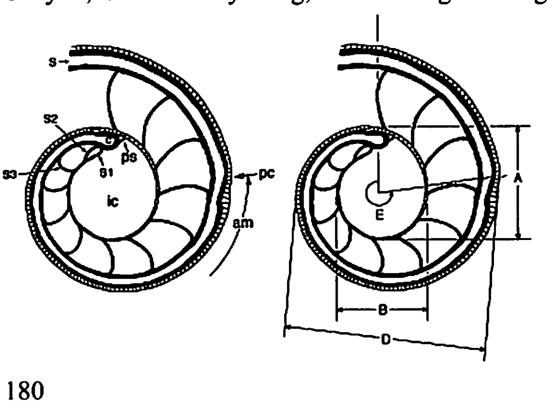


Fig. 1: Diagrams of the ammonoid early internal shell structure (left) and measurements (right) in median section. The terminology is from Branco (1879, 1880), Granjiean (1910) and Drushchits & Khiami (1970). Abbreviations: am: ammonitella; c: caecum; ic: initial chamber; pc: primary constriction; ps prosiphon; s siphuncle tube; A: maximum initial chamber size; B: minimum initial chamber size; D: ammo-nitella size; E: ammonitella angle.

Each 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 coated with gold using an ioncoater. The internal features 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 were measured on the etched surface using a digital micrometer (accuracy ±0.001 mm) attached to a Nikon model V16D profile projector.

The terminology of the morphologic features of the early shell (fig. 1) and septal neck is based on BRANCO (1879, 1880), GRANDJEAN (1910), DRUSHCHITS & KHIAMI (1970), TANABE et al. (1993), and TANABE & LANDMAN (1996). The specimens observed are reposited at the National Science Museum, Tokyo (NSM).

III. Observations

***Placites* sp. (Ceratitina, Pinacocerataceae):** One specimen (NSM PM16812) from the Upper Norian was studied.

The initial chamber is elliptical in median section, and the maximum and minimum initial chamber sizes are 0.360 mm and 0.287 mm (fig. 2A). The ammonitella is defined as the shell up to the end of the primary constriction, and the diameter in the median section is 0.637 mm. The ammonitella angle (= spiral length of ammonitella in degrees) is 268°.

The bulb-like beginning of the siphuncle, called caecum, is located in the initial chamber (fig. 2B). The shape of the caecum in median section is elliptical and the diameter is 0.059 mm. The caecum is attached to the inside surface of the initial chamber by means of the prosiphon, which was originally organic. The prosiphon length is 0.065 mm and gently curved ventrally.

The siphuncle is located in the ventral position throughout ontogeny. The first septum on the dorsal side is long and slightly convex adapically in the median section. The second septum is gently concave adapically with retrochoanitic septal neck and the septal neck is attached to the first septum. The retrochoanitic septal necks occur only the first whorl and are replaced by prochoanitic septal necks in the second whorl (fig. 2C).

***Arcestes* sp. (Ceratitina, Arcestaceae):** Three specimens (NSM PM16813-16815) from the Upper Norian were studied.

The initial chamber is nearly circular in median section. The maximum and minimum initial chamber sizes, ammonitella size and ammonitella angle are respectively 0.475 mm, 0.468 mm, 0.818 mm and 355° in NSM PM16813 (fig. 3A), 0.534 mm, 0.517 mm, 0.887 mm and 353° in NSM PM16814 and 0.515 mm, 0.465 mm, 0.915 mm and 350° in NSM PM16815.

The caecum and prosiphon of every specimen were not preserved. The siphuncle is initially located in the subcentral position and gradually shifts its position to the venter in the second whorl. The first septum on the dorsal side is slightly convex adapically in the median section. The second septum is close to the first septum on the dorsal side, but the two septa are distinctly separated on the venter (fig. 3B). The retrochoanitic septal necks occur only the first whorl and are replaced by prochoanitic septal necks in the second whorl (fig. 3C).

***Choristoceras* sp. (Ceratitina, Choristoceratidae):** Two specimens (NSM PM16816, PM16817) from the Upper Norian were studied.

The initial chamber is elliptical in median section. The maximum and minimum initial chamber sizes, ammonitella size and ammonitella angle are respectively 0.384 mm, 0.320 mm, 0.625 mm and 278° in NSM PM16816 (fig. 4A) and 0.420 mm, 0.375 mm, 0.685 mm and 295° in NSM PM16817 (fig. 4B).

The caecum, prosiphon and siphuncle tube of both specimens were not preserved. Shape of the first and the second septum and initial siphuncle position are indistinct because of bad preservation. The siphuncle is located in the dorsal position in the second whorl and shifts its position to the center in the third whorl. The retrochoanitic septal necks occur only the first whorl and are replaced by prochoanitic septal necks after the second whorl (fig. 4 C).

***Rhacophyllites* sp. (Phylloceratina, Phyllocerataceae):** Two specimens (NSM PM16818, PM16819) from the Upper Norian were studied.

The initial chamber is elliptical in median section. The maximum and minimum initial chamber sizes, ammonitella size and ammonitella angle are respectively 0.400 mm, 0.320 mm, 0.695 mm and 285° in NSM PM16818 (fig. 5a and 0.453 mm, 0.370 mm, 0.775 mm and 286° in NSM PM16819.

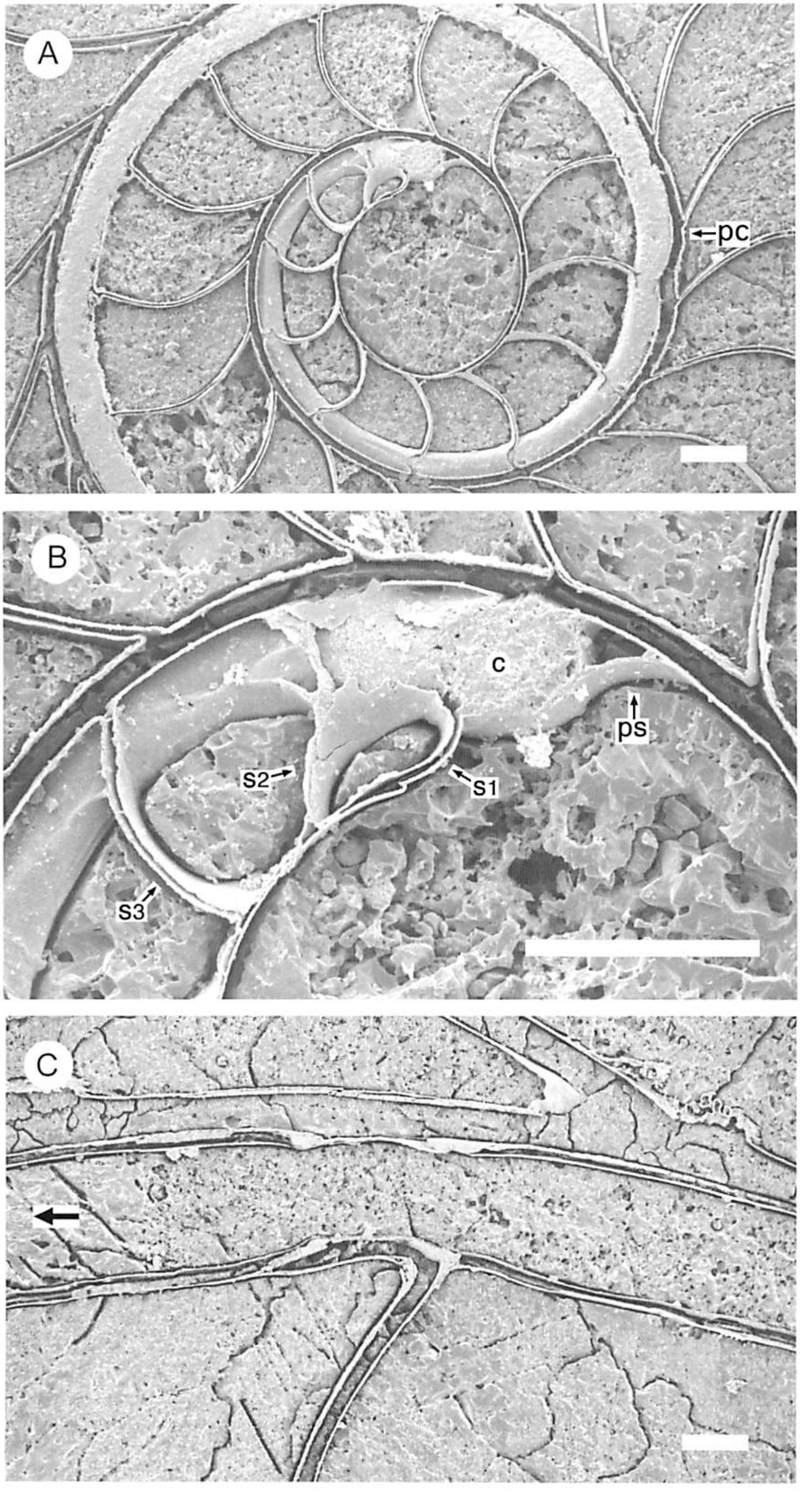
The caecum and prosiphon of both specimens were not preserved. The siphuncle is initially located in the subcentral position and shifts its position to the venter in the second whorl. The first septum is long and slightly convex adapically on the dorsal side in the median section. The second septum is gently concave adapically with retrochoanitic septal neck and the septal neck is attached to the first septum (fig. 5B. The retrochoanitic septal necks occur only in the first whorl and are replaced by type A modified retrochoanitic septal necks in the second and later whorls (fig. 5C).

Psiloceras pacificum GUEX **(Ammonitina, Psilocerataceae)**: Two specimens (NSM PM-16820, PM16821) from the lowest Hettangian were studied.

The initial chamber is elliptical in median section. The maximum and minimum initial chamber sizes, ammonitella size and ammonitella angle are respectively 0.376 mm, 0.310 mm, 0.719 mm and 280° in NSM PM16820 (fig. 6A) and 0.370 mm, 0.293 mm, 0.758 mm and 285° in NSM PM16821.

The shape of the caecum in median section is elliptical and the diameter is 0.085 mm in NSM PM16820 and 0.076 mm in NSM PM16821. The prosiphon of both specimens was not preserved. The first septum is long and slightly convex adapically on the dorsal side in the median section. The second septum is gently concave adapically with a retrochoanitic septal neck and the septal neck is attached to the first septum (fig. 6B). The siphuncle is initially located in the subcentral position and shifts its position to the venter in the second whorl. The retrochoanitic septal necks occur only the first whorl and are replaced by type A modified retrochoanitic septal necks in the second whorls (fig. 6C).

Figs. 2 A-C: Median section of the *Placites* sp. (**Ceratitina, Pinacocerataceae**) from the uppermost Triassic (Upper Norian), New York Canyon, Gabbs Valley Rang, Nevada (NSM PM16812). Scale bars: 0.1 mm.
A: Overview of the early whorl showing the primary constriction (pc); **B:** Close-up of the prosiphon (ps), the caecum (c), the first septum (s1), the second septum (s2) and third septum (s3); **C:** Prochoanitic septal neck of the 52nd septum in the third whorl. The siphuncle is located in the ventral position. Arrow indicates the adoral direction.


A
pc
B
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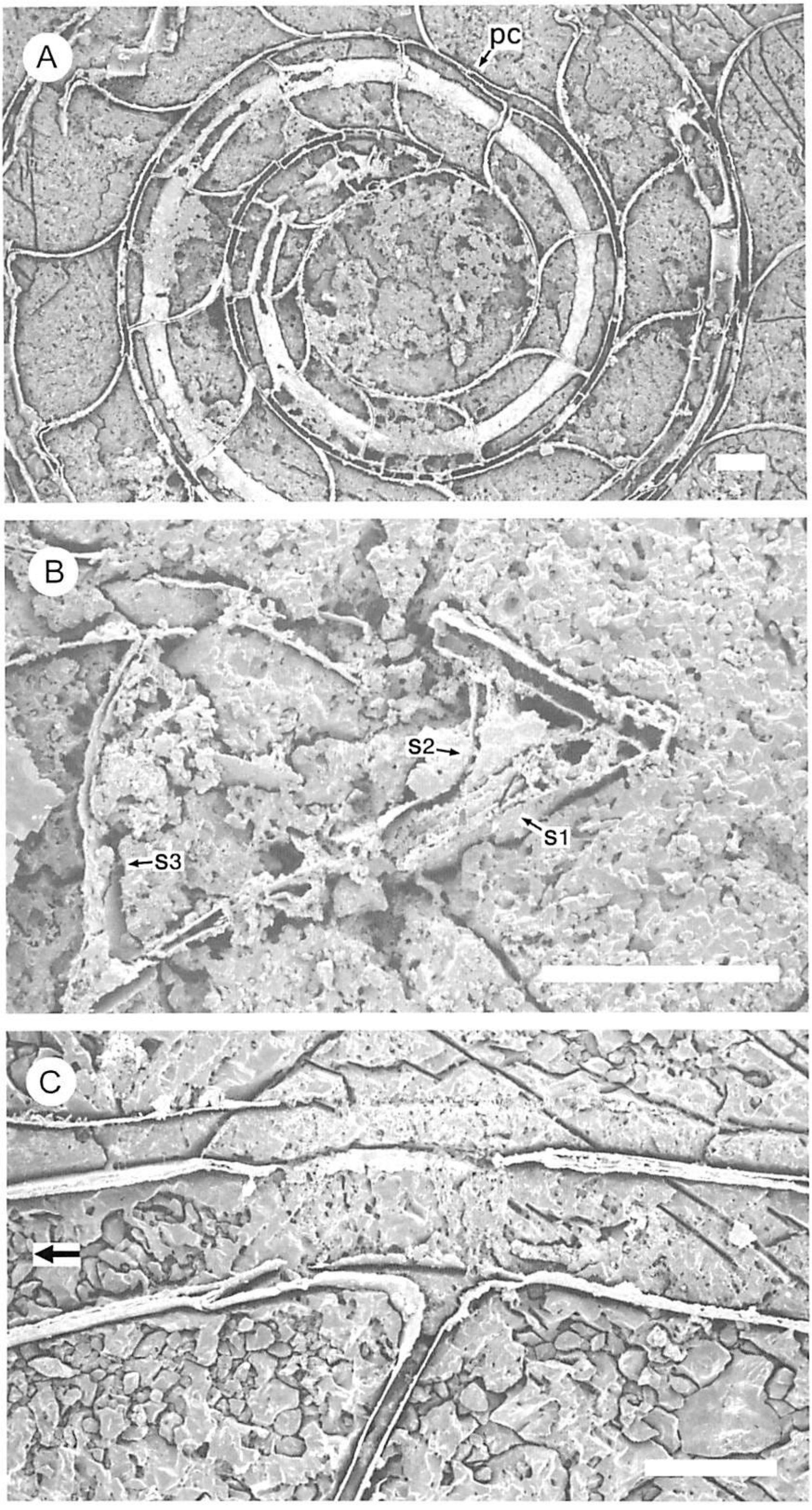
Figs. 3 A-C: Median sections of the *Arcestes* sp. (**Ceratitina, Arcestaceae**) uppermost Triassic (Upper Norian), New York Canyon, Gabbs Valley Rang, Nevada. Scale bars: 0.1 mm; **A:** Overview of the early whorl showing the primary constriction(pc), NSM PM 16813; **B:** Close-up of the first septum (s1), the second septum (s2) and third septum (s3), NSM PM16814; **C:** Prochoanitic septal neck of the 49th septum in the fourth whorl, NSM PM16813. The siphuncle is located in the ventral position. Arrow indicates the adoral direction.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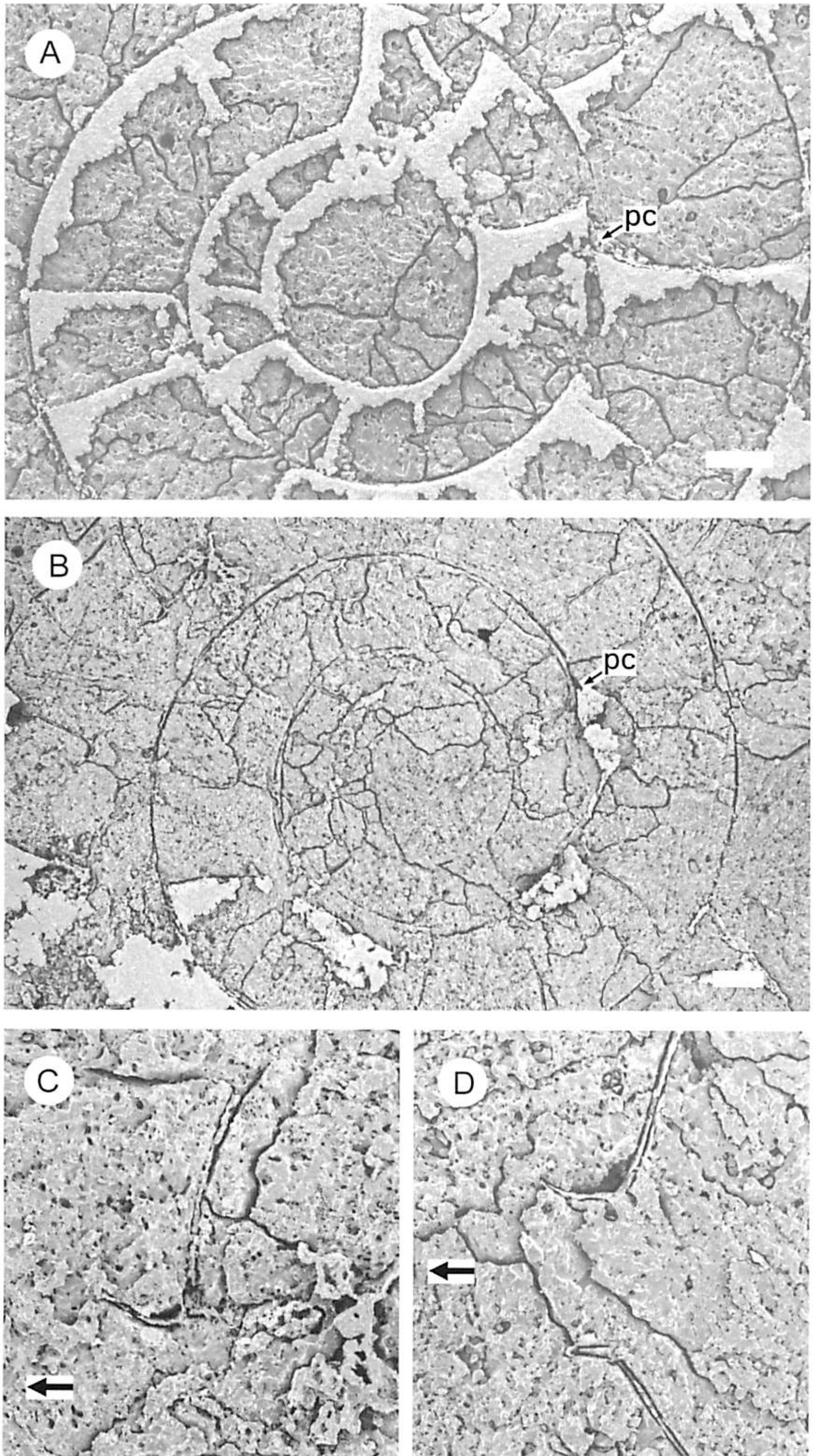
Figs. 4 A-D: Median sections of the *Choristoceras* sp. **(Ceratitina, Choristoceratidae)**, uppermost Triassic (Upper Norian) of the New York Canyon, Gabbs Valley Rang, Nevada. Scale bars: 0.1 mm; **A:** Overview of the early whorl showing the primary constriction (pc), NSM PM16816; **B:** Overview of the early whorl showing constriction (pc), NSM PM16817; **C:** Prochoanitic septal neck of the 25th septum in the third whorl, NSM PM16817. The siphuncle is located in the dorsal position. Arrow indicates the adoral direction; **D:** Prochoanitic septal neck of the 35th septum in the third whorl, NSM PM16817. The siphuncle is located in the central position. Arrow indicates the adoral direction.


A
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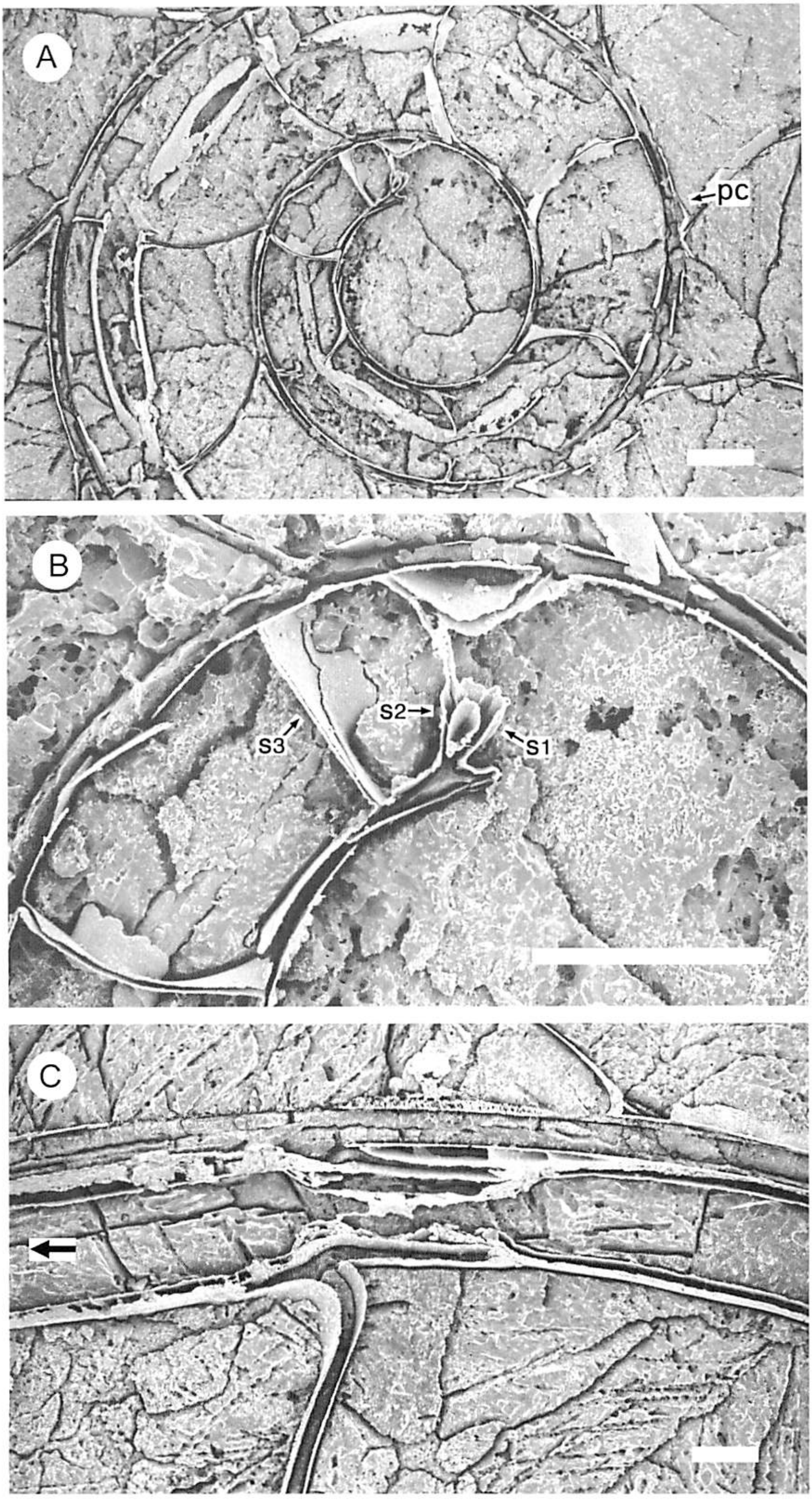
D

Figs. 5 A-C: Median sections of the *Rhacophyllites* sp. (**Phylloceratina, Phyllocerataceae**) , uppermost Triassic (Upper Norian), New York Canyon, Gabbs Valley Rang, Nevad (NSM PM16818). Scale bars: 0.1 mm; **A**: Overview of the early whorl showing the primary constriction (pc); **B**: Close-up of the first septum (s1), the second septum (s2) and third septum (s3); **C**: type A modified retrochoanitic septal neck of the 28th septum in the third whorl. The siphuncle is located in ventral position. Arrow indicates the adoral direction.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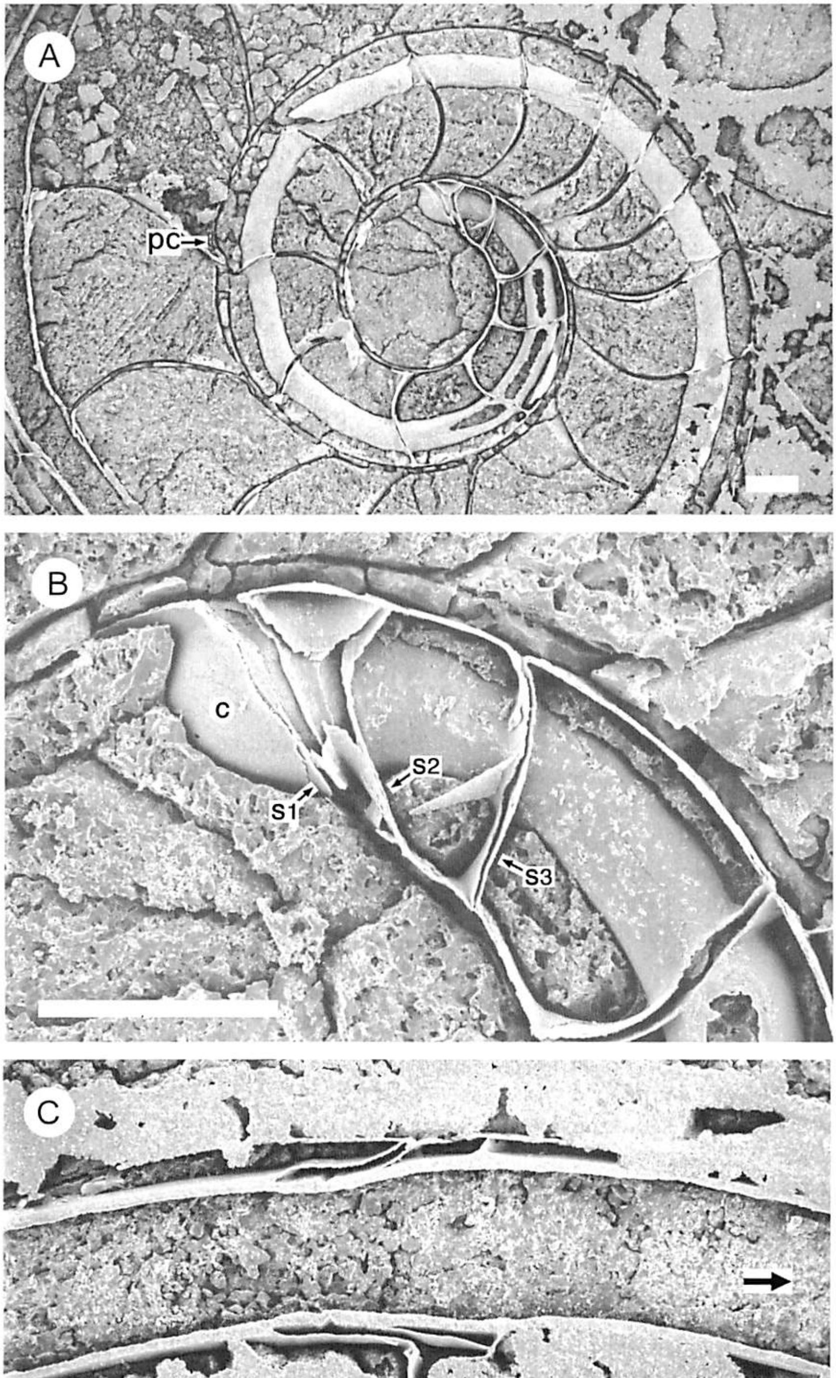
Figs. 6 A-C: Median sections of the *Psiloceras pacificum* (**Ammonitina, Psilocerataceae**), Lowest Jurassic (Lower Hettangian), New York Canyon, Gabbs Valley Rang, Nevad (NSM PM16820). Scale bars: 0.1 mm; **A:** Overview of the early whorl showing the primary constriction (pc); **B:** Close-up of the caecum (c), the first septum (s1), the second septum (s2) and third septum (s3); **C:** type A modified retrochoanitic septal neck of the 30th septum in the third whorl. The siphuncle is located in the ventral position. Arrow indicates the adoral direction.


A
pc
B
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S1
S2
S3
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IV. Discussion

The oldest representative of the Ammonitina is known from the uppermost Triassic (Rhaetian) and the lower Hettangian, and is referable to *Psiloceras*, which is characterized by a discoidal, evolute conch, round venter, smooth or with sporadic blunt rib, and phylloid saddles (Guex, 1995). The genus shares similar conch and suture morphologies with the Gyminitidae or Japonitidae in the Pinacoceratina or the Discophyllitidae in the Phylloceratina among late Norian ammonoids, so that previous authors considered that *Psiloceras* evolved from the Pinacoceratina in the Ceratitida (Tozer, 1981) or the Phylloceratina in the Ammonitida (Guex, 1982, 1995).

Only four ammonoid groups, the Pinacoceratina, Arcestina, Ceratitina and Phylloceratina occur in the Upper Norian (Tozer, 1981), and each group exhibits certain distinct features in their internal shell features. *Placites* sp. (Pinacoceratinae, Ceratitida) has an elliptical initial chamber, a ventral siphuncle throughout ontogeny and prochoanitic septal necks after the second whorl. Initial chamber of the *Arcestes* sp. (Arcestina, Ceratitida) is a nearly circular, and this species possesses a subcentral siphuncle in the first whorl and prochoanitic septal necks after the second whorl. *Choristoceras* sp. (Ceratitina, Ceratitida) has an elliptical initial chamber and prochoanitic septal necks after the second whorl. The siphuncle is initially located in the dorsal position and shifts its position to the center in the third whorl. *Rhacophyllites* sp. (Phylloceratina, Ammonitida) has an elliptical initial chamber, a subcentral siphuncle in the first whorls and type A modified retrochoanitic septal necks after the second whorl.

The initial chamber of *Psiloceras pacificum* (Ammonitina, Psilocerataceae) is nearly circular, and this species possesses a subcentral siphuncle in the first whorl and type A modified retrochoanitic septal necks after the second whorl. These features are essentially the same as those of the Phylloceratina. The similarities of internal shell features as well as the conch morphology and suture strongly suggest a close phylogenetic relationship between *Psiloceras* and the Phylloceratina. These observations strongly support the hypothesis of a phylloceratid origin for the Ammonitina as proposed by Guex (1982, 1995).

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