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Early conch morphology of a gigantic Cretaceous ammonoid, *Pachydesmoceras*

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Gigantic ammonoids, with conch diameters exceeding 1 m, remain one of the most enigmatic groups of extinct organisms. Their paleoecology has been the subject of ongoing debate, with some uncertainties arising from preservation biases, especially of an early conch. This study focuses on an exceptionally preserved early conch of the giant Cretaceous ammonoid *Pachydesmoceras denisonianum* from southern India. Conch morphology and the ontogenetic trajectories of constrictions and septal spacings were examined. The results indicate that constrictions were frequently present in the early conch; based on the shell layers observed in the cross-section, these constrictions likely resulted from periods of halted or slowed growth. The common occurrence of constrictions during early ontogeny suggests that *Pachydesmoceras* lifespan may have been longer than previously assumed. Additionally, the ontogenetic patterns of septal spacing do not appear to reflect these growth halts or slowdowns.

Early conch morphology of a gigantic Cretaceous ammonoid, *Pachydesmoceras*

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ABSTRACT

Gigantic ammonoids, with conch diameters exceeding 1 m, remain one of the most enigmatic groups of extinct organisms. Their paleoecology has been the subject of ongoing debate, with some uncertainties arising from preservation biases, especially of an early conch. This study focuses on an exceptionally preserved early conch of the giant Cretaceous ammonoid *Pachydesmoceras denisonianum* from southern India. Conch morphology and the ontogenetic trajectories of constrictions and septal spacings were examined. The results indicate that constrictions were frequently present in the early conch; based on the shell layers observed in the cross-section, these constrictions likely resulted from periods of halted or slowed growth. The common occurrence of constrictions during early ontogeny suggests that *Pachydesmoceras*

lifespan may have been longer than previously assumed. Additionally, the ontogenetic patterns of septal spacing do not appear to reflect these growth halts or slowdowns.

INTRODUCTION

Gigantic marine invertebrates evolved across several groups during and after the Cambrian explosion (*Klug et al.*, *2015b*). Ammonoids flourished from the Devonian to the end of the Cretaceous period and are a prime example of this trend. During this period, some ammonoid species grew to enormous sizes, with conch diameters exceeding 1 m, and these species are known worldwide (*Klug et al., 2015b*; *Tajika*, *Nützel & Klug*, *2018*). One of the most notable examples is the Late Cretaceous *Parapuzosia seppenradensis* (Puzosiinae, Desmoceratidae, Perisphincitina; for higher taxonomy, see *Bessenova & Mikhailova*, *1991*, and *Yacobucci*, *2015*), which is currently recognized as the largest ammonoid species (*Ifrim et al.*, *2021*). Another prominent gigantic ammonoid is *Pachydesmoceras* (Puzosiinae, Desmoceratidae, Perisphincitina; *Tajika*, *Nützel & Klug*, *2018*), which occurred from the upper Albian to upper Turonian in regions across Europe, Africa, Madagascar, India, Japan, and New Zealand (*Wright*, *1996*). The type species of this genus is *Pachydesmoceras denisonianum*, with the lectotype (designated by *Matsumoto*, *1987*) originating from the northeast of Odiyam village in the Ariyalur region of southern India.

The inner whorls of gigantic ammonoids are often preserved poorly, primarily because the earliest whorls tend to be dissolved during diagenesis (*Maeda*, *1987*; *Maeda & Seilacher*, *1996*; *Maeda et al.*, *2010*; *Wani & Gupta*, *2015*). *Ifrim et al. (2021)* investigated the ontogeny of the largest ammonoid, *Parapuzosia seppenradensis*, including the early conch morphology (approximately 110 mm in conch diameter). In contrast, the internal conch morphology of *Pachydesmoceras* has rarely been documented, with *P. pachydiscoide* and *P. kossmati* being the exceptions (*Matsumoto*, *1988*; *Kennedy & Klinger*, *2014*).

During our fieldwork in the Ariyalur area of southern India, an exceptionally preserved early conch of *Pachydesmoceras denisonianum* (the type species of *Pachydesmoceras*) was collected from a horizon nearly identical to that of its lectotype, close to the type locality. In this study, the outer and internal morphology of this specimen were examined to identify the early conch morphology of a gigantic ammonoid that has rarely been recognized in previous studies.

MATERIALS

A single gigantic ammonoid specimen was discovered in the Karai Formation (Uttatur Group), located approximately 4 km southwest of Odiyam village (11°13′01″N, 78°59′32″E) in the Ariyalur area (for detailed geological information, see *Sundaram & Rao*, *1986*; *Sundaram et al.*, *2001*). The ammonoid, with a conch diameter of approximately 0.7 m, was unfortunately fragmented into several pieces, preventing the collection of the complete specimen. Only the nearly intact innermost part of the conch was retrieved in the field. Based on the conch morphology of the broken fragments and the large conch diameter, this specimen was identified as *Pachydesmoceras denisonianum*. The geological age of the specimen was considered to be late Albian, based on associated species from nearby localities, including *Mariella bergeri*, *Puzosia compressa*, and *Mortoniceras* spp.

The preserved outermost whorl shows little to no outer shell layer, likely due to dissolution and/or peeling caused by the adjacent broken whorl. Consequently, the presence and prominence of ribs on the shell surface of the preserved outermost whorl could not be accurately assessed.

The specimen examined in this study are deposited in the Mikasa City Museum (MCM), Hokkaido, Japan.

METHODS

To observe the outer conch shape of the early conch, the specimen was first blackened using colloidal graphite and then whitened with ammonium chloride. Conch terminology follows that of *Klug et al. (2015a)*.

The examined specimen was subsequently polished along its median plane (plane of symmetry) using silicon carbide powder. Constrictions were observed on the median plane, and the spacing between successive constrictions was measured. These spacings are the rotational angle between two consecutive constrictions (i.e., M and M-1 constriction numbers) at the ventral positions. The center of rotation was defined as the center of the approximated logarithmic spiral. The measured constriction spacings were presented as graphs plotted against conch diameter throughout early ontogeny. Additionally, cross-sectional observations of the shell structure, particularly around the constrictions, were made.

The septal spacing between successive septa was also measured on the median plane. These spacings were defined as the rotational angle between two consecutive septa (i.e., N and N-1 septal numbers) at the positions where the septum intersects with the siphuncle. The measured septal spacings were presented as graphs plotted against the phragmocone diameter throughout early ontogeny.

EARLY CONCH MORPHOLOGY OF *PACHYDESMOCERAS DENISONIANUM*

Outer morphology of early conch

The early conch of the gigantic *Pachydesmoceras denisonianum* (109 mm in conch diameter) exhibits a discoidal shape (B/D = 0.38), is weakly compressed (B/H = 0.91), and has a moderate whorl expansion ratio (WER = 1.90) and a very wide and evolute umbilicus (U/H = 0.78) (Table

1; Fig. 1). The whorl is ovoid in cross-section, with a rounded venter, convex flanks, rounded umbilical shoulder, and steep umbilical wall.

Constrictions are frequently observed, with 10 distinct constrictions identifiable on the preserved outermost whorl (Fig. 1A; Table S1). All constrictions are concave, prosiradiate, and project forward on the venter, exhibiting nearly uniform widths and depths from the umbilical seams to the venters. Due to the dissolution or peeling of the outer shell layer caused by the adjacent broken whorl, the presence and intensity of other ornamentations, such as ribs, remain uncertain.

Internal morphology of early conch

The earliest whorl is dissolved, and only approximately 1.5 whorls are preserved, with the smallest preserved conch diameter measuring 32 mm (Fig. 2). Thus, the earliest conch morphology, such as the ammonitella and initial chamber, cannot be observed or evaluated. The early conch follows a logarithmic spiral, with a moderately embracing imprint zone rate (IZR = 0.29; Table 1).

Twenty constrictions, including the 10 that are discernible on the outer morphology, are recognized at the median plane (Figs. 1, 2; Table S1). The conch diameters corresponding to the first and second constrictions are not measurable due to the dissolution of the earliest whorl. The smallest measurable conch diameter with a constriction is 33 mm (corresponding to the third constriction; Fig. 2; Table S1). Due to the dissolution of the earliest whorl, it remains unclear whether constrictions exist before the preserved first constriction (Fig. 2). The rotational angles between successive constrictions of the 20 observed constrictions in the specimen ranged from 22° to 82° (average = 42.3°, standard deviation = 13.29°; Figs. 1–3; Table S1).

Two well-preserved constrictions reveal that ribs are positioned adapical to the constrictions in the cross sections (Fig. 2). Additionally, the outer shell layer at the constrictions is distinctly oblique to the shell surface. This feature is especially noticeable in the adoral parts of the constrictions (Fig. 2B, C). In contrast, the inner shell layer remains continuous, even across the constrictions.

The preserved first septum was located at a conch diameter of 38 mm (phragmocone diameter without the body chamber), and 25 septa were recognized in this specimen (Fig. 2; Table S1). The rotational angles between successive septa ranged from 18° to 26° (average = 21.9°, standard deviation = 1.93°; Figs. 2, 3; Table S1).

DISCUSSION

Intraspecific and interspecific comparison of early conch morphology

Based on the measurements of *Pachydesmoceras denisonianum*, including the lectotype and specimen examined in this study (Table 1), intraspecific comparisons were made regarding the conch morphology at different conch diameters (Fig. 4). The graph between umbilicus width (U) and conch diameter (D) indicates that the U/D ratio tended to increase with growth, reflecting an enlarging umbilicus relative to the conch diameter (Fig. 4D). In contrast, the graphs of morphological ratios for whorl width (W/H and W/D; Fig. 4E, F) show greater variation in larger specimens, although the sample size is limited. These trends suggest that whorl width (W) exhibited more variation than other morphological parameters. This variability in whorl width may be attributed to the inflation of body chambers in *Pachydesmoceras* as it matured (*Matsumoto*, *1988*), or to diagenetic deformation in larger specimens.

A relatively smaller conch of *P. denisonianum* (166 mm in diameter; Table 1) was reported by *Collignon (1961, pl. 8)*, collected from the Cenomanian of Madagascar. This specimen displays crowded ribs of unequal length, with some of the longer ribs accompanied by indistinct constrictions (*Matsumoto*, *1988*). In the specimen examined in this study, ribs are not visible on the shell surface, likely due to the preservation of the outer shell layer. Given the relationship between constrictions and ribs observed in Collignon's specimen (1961), a similar relationship is likely present in the examined specimen.

At a later stage in *P. denisonianum*, *Matsumoto (1988)* noted that constrictions become less distinct and may only appear as shallow furrows along some of the longer ribs. Considering this observation alongside the early conch morphology identified in this study, it can be inferred that the frequency and prominence of constrictions would decrease with growth in *P. denisonianum*.

Early conch morphology has been recognized in *P. pachydiscoide* and *P. kossmati* (*Matsumoto*, 1988; *Kennedy & Klinger*, *2014*). According to *Matsumoto (1988)* and *Kennedy & Klinger (2014)*, early conchs of both species exhibit frequent constrictions associated with ribs, which later become more indistinct. In contrast, the ribs become more prominent, thicker, and coarser in the later stages. In the mature stage, the ribs gradually weaken, resulting in a nearly smooth conch (*Matsumoto*, *1988*). From the early to later stages, these ontogenetic trends in shell ornamentation are similar to those observed in *P. denisonianum*. Therefore, observing the early conch in the type species of the genus *Pachydesmoceras* is crucial for interpreting the taxonomy and phylogenetic relationships of this and related genera.

Implication for shell growth from constrictions and associated ribs

The observation of the cross section of the examined specimen revealed that ribs are located just adapical to the constrictions (Fig. 2). The nearly identical width and depth of each constriction (Fig. 1) suggests that the ribs at these positions extend along the constrictions, resulting in “long ribs.” Similarly, in the relatively smaller specimen from the Cenomanian of Madagascar

(*Collignon*, *1961*), some long ribs are accompanied by indistinct constrictions. *Matsumoto (1988)* noted that long ribs begin to appear at least by the middle stage in *Pachydesmoceras*. In later stages, these long ribs are spaced at gradually broadening intervals, with shorter ribs intercalated. However, based on the current observations, long ribs may appear as early as the initial stages, at least when the conch diameter reaches 33 mm.

An examination of the well-preserved constrictions revealed that the outer shell layer at these constrictions is distinctly oblique to the shell surface, which is especially noticeable in the adoral parts of the constrictions (Fig. 2). The discontinuous shell layers across the constrictions and ribs suggest a transition in growth phases at these points, potentially indicating a growth halt or slowdown. Similar distinct shell layers have been reported by *Bucher et al. (1996)*, who studied the shell layers associated with conch ornamentation called megastria. This thick, continuous line extends around the flanks and venter of an ammonoid conch. Their study observed discontinuous outer shell layers and continuous inner shell layers at the megastria, concluding that such discontinuities represented growth halts. Based on these observations, constrictions have also been hypothesized to be associated with growth halts or slowdowns (*Arkell*, *Kummel & Wright*, *1957*; *Kulicki*, *1974*; *Kennedy & Cobban*, *1976*; *Obata et al.*, *1978*; *Westermann*, *1990*; *Bucher et al.*, *1996*; *Bucher*, *1997*; *Klug et al.*, *2015a*; *De Baets*, *Landman & Tanabe*, *2015*; *Urgy*, *2015*). The findings in this study align with this hypothesis. The repeated occurrence of constrictions in the early conch (at least 20 constrictions up to a conch diameter of 109 mm) suggests that the examined specimen experienced several growth halts or slowdowns during early ontogeny. As constrictions become less frequent in the later stages of *Pachydesmoceras*, growth halts, or slowdowns may decrease with growth. However, the frequency of constrictions could vary between specimens or species. Since only a single specimen was analyzed in this study, further investigation with additional specimens is necessary to determine whether the frequency of these growth halts or slowdowns are species-dependent, genus-dependent, or environmentally influenced (e.g., seawater temperature, chemical composition of seawater, nutritional condition, and oxygen condition).

Constrictions are commonly observed on the conchs of *Pachydesmoceras* and other ammonoids, in contrast to Cretaceous nautiloids from the same region, which does not exhibit constrictions except a nepionic constriction formed at hatching (*Blanford*, *1862*; *Stoliczka*, *1863–1866*; *Wani & Ayyasami*, *2009*; *Wani*, *Kurihara & Ayyasami*, *2011*). This difference may be attributed to growth halts or slowdowns in ammonoids, as opposed to nautiloids, which lack such features. The contrast between these two groups from similar environments and geological ages suggests that the occurrence of growth halts or slowdowns, and consequently the development of constrictions, is not likely influenced by environmental factors.

Given the repeated halts or slowdowns in shell growth during the early ontogeny and the large conch diameter of *P. denisonianum*, it is likely that their lifespan was longer than previously assumed. However, accurately estimating their life duration remains challenging at present.

Ontogenetic trajectory of septal spacing

The measured septal spacings of the early conch in *Pachydesmoceras denisonianum* reveal a nearly stable pattern with a slightly increasing trend (standard deviation = 1.93°) (Fig. 3B). The comparison of graphs for constriction and septal spacings (Fig. 3) indicates no clear relationship between the two, suggesting that constrictions and septal spacings are not directly linked in *Pachydesmoceras*. However, the precise correlation between the timing of apertural and septal formation remains unclear. This lack of connection implies that growth halts or slowdowns were not recorded in the ontogenetic trajectories of septal spacings, at least in *Pachydesmoceras*.

The ontogenetic trajectories of *Pachydesmoceras denisonianum* were compared with those of other ammonoids from the subfamilies Puzosiinae (e.g., *Puzosia* sp., from the Turonian of the Ariyalur area, southern India) and Desmoceratinae (e.g., *Desmoceras latidorsatum* var. *media*, from the Albian of the Mahajanga area, Madagascar), both within the family Desmoceratidae (*Takai et al., 2022*; *Nishino et al., 2024*; Fig. 5). Although the comparable conch diameters among the examined three taxa are limited, the observed ranges of septal spacings in

Pachydesmoceras fall within those of *Desmoceras* (especially those with phragmocone diameters >1 mm). The slope of the slightly increasing trend in *Pachydesmoceras* is almost parallel to that of *Puzosia*. These suggest that the septal spacings of *Pachydesmoceras* share characteristics with both taxa. These trends in the Puzosiinae and Desmoceratinae are similar to those observed in other Cretaceous Perisphinctina but differ from those seen in Phylloceratina and Lytoceratina from the Cretaceous period (*Arai & Wani, 2012*; *Iwasaki, Iwasaki & Wani, 2020*; *Kawakami, Uchida & Wani, 2022*; *Takai et al., 2022*; *Kawakami & Wani, 2023*; *Nishino et al., 2024*).

Growth halts in ammonoids, which may be accompanied by constrictions, likely result from the covariance between isometric or allometric growth of the aperture and ornamentation (*Bucher, 1997*) and/or the balance between conch and soft part growth. The results of this work indicate that when the growth balance between the conch and soft parts in *Pachydesmoceras* was disrupted, this imbalance may have been compensated not by changes in septal spacing, but by modifications in the apertural shape, leading to the formation of constrictions. Whether this phenomenon was common across ammonoids remains uncertain, and therefore, the relationship between the ontogenetic trajectories of constrictions and septa in various taxa across different geological ages warrants further investigation in future studies. This would provide a deeper understanding of how growth patterns and environmental factors influenced the morphological evolution of ammonoids over time.

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Figure and table captions

Figure 1. Photographs of the examined specimen, MCM-W2145, late Albian, Ariyalur area, southern India. (A) Left lateral view; (B, C) ventral views; (D) right lateral view. Stars are only shown in the left-side photograph, indicating the ventral positions of constrictions that can be recognized in the preserved outer whorl. Scale bar is 10 mm.

Figure 2. Cross section of the examined specimen. (A) Photograph of the median section of the examined specimen; (B, C) enlarged photographs of constrictions and ribs shown in black

squares and its schematic drawings. The exterior is toward the top of the photos. Black arrow, the preserved smallest conch; white arrows, the ventral position of constrictions; star, the smallest position of constriction that can be recognized in the preserved outer whorl.

Figure 3. Ontogenetic trajectories of constriction and septal spacing. (A) Graph of constriction spacing through early ontogeny; (B) graph of septal spacing through early ontogeny.

Figure 4. Measurements of *Pachydesmoceras denisonianum*. (A) Conch diameter/umbilicus width relationship; (B) conch diameter/whorl height relationship; (C) conch diameter/whorl width relationship; (D) umbilicus width/conch diameter ratio (U/D); (E) whorl width/whorl height ratio (W/H); (F) whorl width/conch diameter ratio (W/D). Solid circle, measurements of lectotype.

Figure 5. Comparison of ontogenetic trajectories of septal spacings in the subfamilies Puzosiinae and Desmoceratinae. *Puzosia* and *Desmoceras* data are from *Nishino et al. (2024)* and *Takai et al. (2022)*, respectively.

Table 1. Morphological data of *Pachydesmoceras denisonianum*. Measurements except the examined specimen are from *Matsumoto (1988)*. D, conch diameter; d, conch diameter at 180° adapically from D; U, umbilical width; H, whorl height; h, whorl height at 180° adapically from H; W, whorl width; ah, aperture height.

Table S1. Raw data of *Pachydesmoceras denisonianum* conch morphology.

Figure 1

Figure 1. Photographs of the examined specimen , MCM-W2145, late Albian, Ariyalur area, southern India.

(A) Left lateral view; (B, C) ventral views; (D) right lateral view. Stars are only shown in the left-side photograph, indicating the ventral positions of constrictions that can be recognized in the preserved outer whorl. Scale bar is 10 mm.


A
B
C
D
10 mm

Figure 2

Figure 2. Cross section of the examined specimen.

(A) Photograph of the median section of the examined specimen; (B, C) enlarged photographs of constrictions and ribs shown in black squares and its schematic drawings. The exterior is toward the top of the photos. Black arrow, the preserved smallest conch; white arrows, the ventral position of constrictions; star, the smallest position of constriction that can be recognized in the preserved outer whorl.

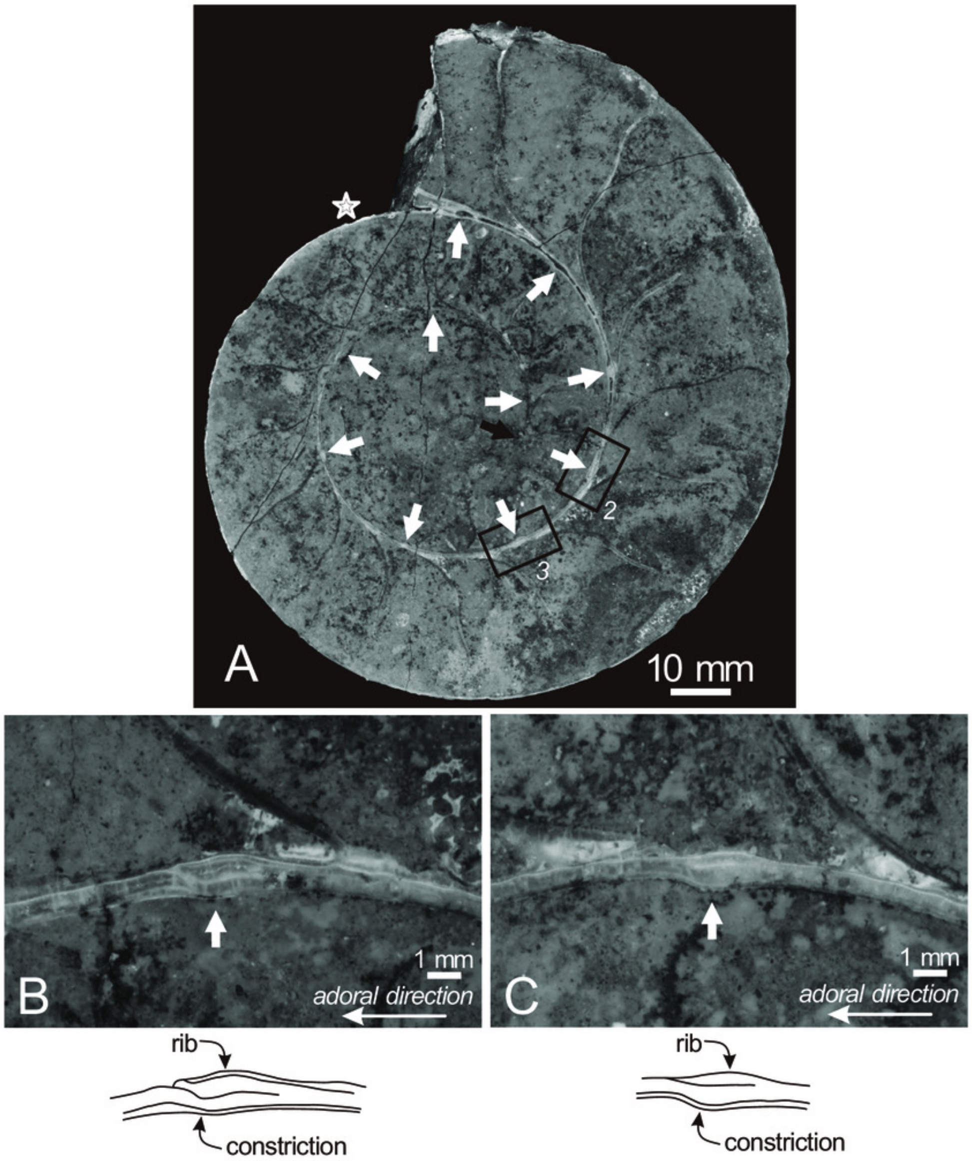
A
10 mm
2
3
B
1 mm
adoral direction
C
1 mm
adoral direction
rib
constriction
rib
constriction

Figure 3

Ontogenetic trajectories of constriction and septal spacing.

(A) Graph of constriction spacing through early ontogeny; (B) graph of septal spacing through early ontogeny.

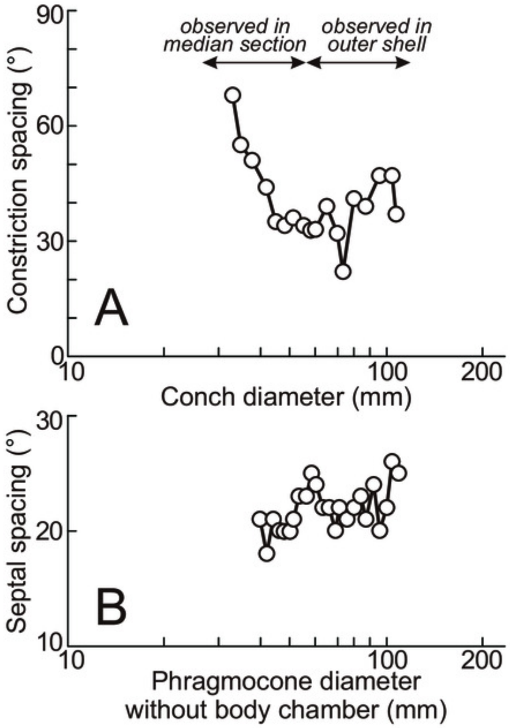
observed in median section
observed in outer shell
Constriction spacing (°)
90
60
30
0
A
10
100
200
Conch diameter (mm)
Septal spacing (°)
30
20
10
B
10
100
200
Phragmocone diameter without body chamber (mm)

Figure 4

Measurements of *Pachydesmoceras denisonianum* .

(A) Conch diameter/umbilicus width relationship; (B) conch diameter/whorl height relationship; (C) conch diameter/whorl width relationship; (D) umbilicus width/conch diameter ratio (U/D); (E) whorl width/whorl height ratio (W/H); (F) whorl width/conch diameter ratio (W/D). Solid circle, measurements of lectotype.

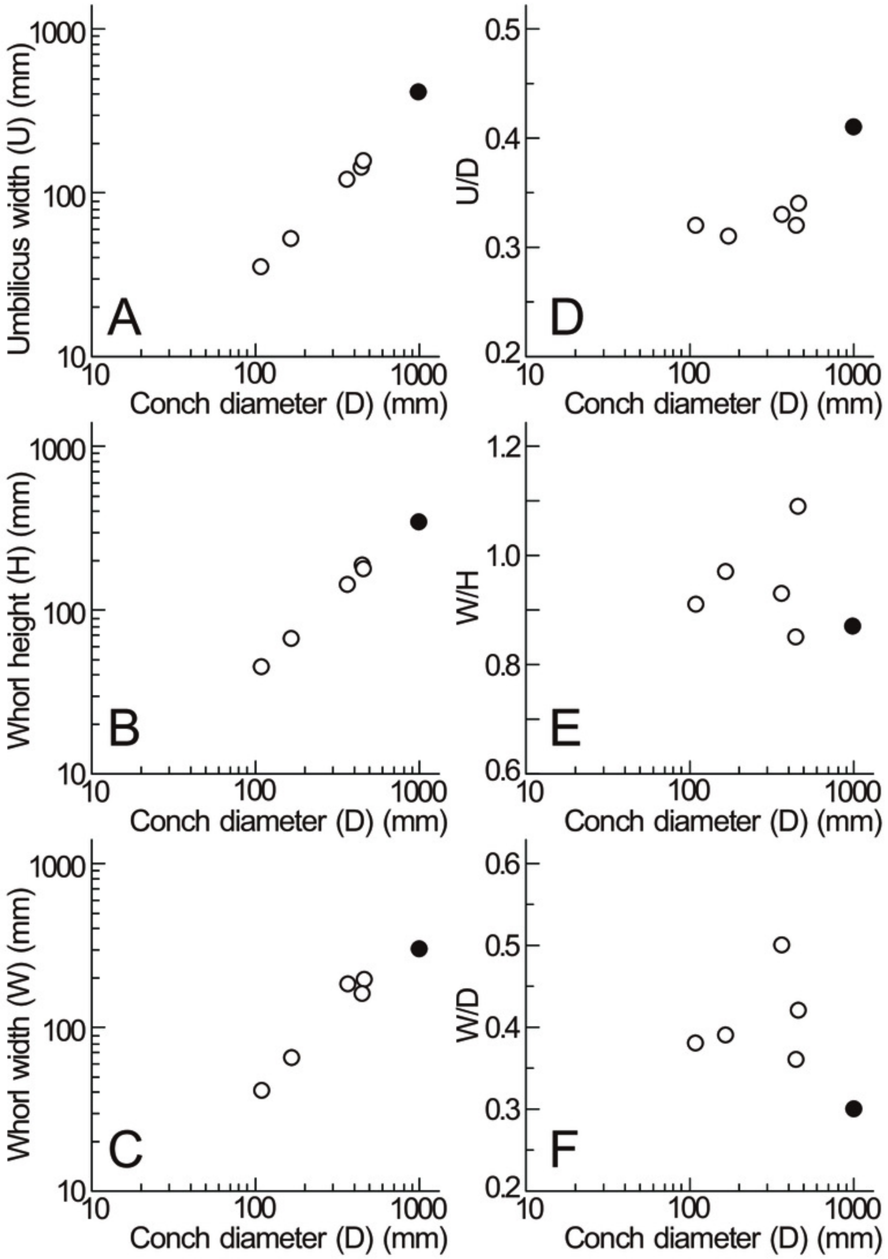
A
Umbilicus width (U) (mm)
1000
100
10
Conch diameter (D) (mm)
10
100
1000
D
U/D
0.5
0.4
0.3
0.2
B
Whorl height (H) (mm)
E
W/H
1.2
1.0
0.8
0.6
C
Whorl width (W) (mm)
F
W/D
0.6
0.5
0.4
0.3
0.2

Figure 5

Comparison of ontogenetic trajectories of septal spacings in the subfamilies Puzosiinae and Desmoceratinae.

Puzosia and *Desmoceras* data are from *Nishino et al. (2024)* and *Takai et al. (2022)* , respectively.

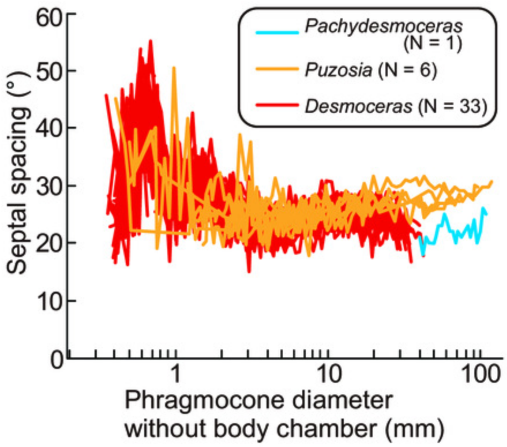
Septal spacing (°)
0
10
20
30
40
50
60
1
10
100
Phragmocone diameter without body chamber (mm)
Pachydesmoceras (N = 1)
Puzosia (N = 6)
Desmoceras (N = 33)

Table 1(on next page)

Table 1. Morphological data of *Pachydesmoceras denisonianum*.

Measurements except the examined specimen are from *Matsumoto (1988)*. D, conch diameter; d, conch diameter at 180° adapically from D; U, umbilical width; H, whorl height; h, whorl height at 180° adapically from H; W, whorl width; ah, aperture height.

specimen	D (mm)	d (mm)	U (mm)	H (mm)	h (mm)	W (mm)	ah (mm)	U/D	U/H	W/D	W/H	H/h	whorl expansion rate (WER; $(D/d)^2$)	imprint zone rate (IZR; (H-ah)/H)	reference
Lectotype, GSI. 208	995		410	345	208	300		0.41	1.19	0.30	0.87	1.44			Stoliczka (1865)
GSJ. F3469	460		156	179	136	195		0.34	0.87	0.42	1.09	1.43			Matsumoto (1988)
Yabe, 1914, pl. 12	446		142	188		160		0.32	0.76	0.36	0.85				Yabe (1914)
YKC. 610612	365		120	143	131	183		0.33	0.84	0.50	0.93	1.40			Matsumoto (1988)
MNHN. 3750	166		52	67	45	65		0.31	0.78	0.39	0.97	1.43			Collignon (1961)
MCM-W2145	109	79	35	45	31	41	32	0.32	0.78	0.38	0.91	1.45	1.90	0.29	this study