



Stepwise growth changes in early post-embryonic stages among Cretaceous tetragonitid ammonoids

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Received: 3 June 2022 / Accepted: 2 February 2023 / Published online: 30 March 2023
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Abstract

In this study, we analyzed the ontogenetic trajectories of shell morphology in some Cretaceous tetragonitid ammonoid specimens (Tetragonitidae) collected from the Tomamae, Mikasa, and Hamanaka areas of Hokkaido, Japan. In all examined species, the ontogenetic trajectories of septal spacing between successive chambers had similar characteristics during their early ontogeny: two cycles, each comprising an increase and subsequent decrease in septal spacing until ~30th septum. The trends of whorl expansion rate changed at 5–7 or ~10 mm in the Gaudryceratinae and ~3 mm shell diameter in the Tetragonitinae. Based on these observations, we propose that the planktic phases of Gaudryceratinae and Tetragonitinae ended at those shell diameters. These different shell diameters at the end of the planktic phase suggest slightly differing strategies within the family Tetragonitidae.

Keywords Septal spacing · Cretaceous · Ontogenetic trajectory · Ammonoid ontogeny · Tetragonitid

Introduction

Marine mollusks have many modes of life through ontogeny. Some gastropods, such as heteropods, stay planktic throughout their lives (Beesley et al. 1998). However, some cephalopods (e.g., many octobranchians) are benthic (non-planktic), even during post-embryonic stages (Wani 2011; De Baets et al. 2015). The planktic phase in marine mollusks, such as the larval phase in gastropods and bivalves, plays an important role in their geographical dispersal and thus diversification (Jackson 1974; Scheltema 1977; Hansen 1980; Jablonski and Lutz 1983; Levin 2006; Nützel 2014; Fukumori and Kano 2014). This is because the geographic distribution of marine organism expands as they are transported by currents during their planktic phase. Even in modern squids with excellent swimming abilities, the planktic phase during the embryonic (i.e., floating egg masses) and/or post-embryonic

stages is a major factor influencing their geographical distribution (Boyle and Boletzky 1996; Villanueva et al. 2016; Roura et al. 2019). Understanding the planktic phase is thus highly relevant for studying the diversification and speciation of ammonoids because they likely had poorer swimming abilities than modern squids (Naglik et al. 2015b; Peterman et al. 2019, 2020a; Peterman and Ritterbush 2022).

It appears like most if not all ammonoid hatchlings were planktic (Kulicki 1974, 1979, 1996; Drushchits et al. 1977; Tanabe et al. 1980, 2001, 2003; Landman 1985; Tanabe and Ohtsuka 1985; Shigeta 1993; Landman et al. 1996; Westermann 1996; Rouget and Neige 2001; Mapes and Nützel 2009; Tajika and Wani 2011; De Baets et al. 2012, 2013, 2015; Ritterbush et al. 2014; Lemanis et al. 2015). However, several Jurassic and Cretaceous ammonoids have been interpreted as having been demersal during their post-embryonic or adult stages based on oxygen isotopic examinations (Moriya et al. 2003; Lécuyer and Bucher 2006; Lukeneder et al. 2010; Moriya 2015a, b; Sessa et al. 2015; Linzmeier et al. 2018; Hoffmann et al. 2019; Machalski et al. 2021). Among those lineages, we focused on the family Tetragonitidae (Lytocerozoidea) for this study. The family Tetragonitidae, which comprises two subfamilies (Gaudryceratinae and Tetragonitinae), evolved from Lytoceratidae during the Barremian and persisted until the Maastrichtian (Wright 1996; Maeda et al. 2005; Hoffmann 2010, 2015; Landman

Handling Editor: Christian Klug.

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et al. 2015). Many studies have reported the evolutionary and morphological stability of *Lytocerotina* relative to other ammonoid suborders (Arkell et al. 1957; Ward and Signor 1983; Page 1996; Hoffmann 2010, 2015; Neige et al. 2013; Yacobucci 2015), which is likely linked with their environmentally more stable open ocean habitats (House 1989; Tanabe et al. 2013). We examined the ontogenetic trajectories of shell morphology (septal spacing and outer shell shape) to assess their ecological characteristics.

The ontogenetic trajectories of septal spacing enable us to understand details of chamber formation throughout the development of these cephalopods. These trajectories (Kulicki 1974; Lehmann 1976; Bucher and Guex 1990; Bucher 1997; Dommergues 1988; Landman and Waage 1993; Mignot 1993; Bucher et al. 1996; Polizzotto et al. 2007; Kraft et al. 2008; Paul 2011; Arai and Wani 2012; Zell and Stinnesbeck 2016; Iwasaki et al. 2020; Beck et al. 2021; Kawakami et al. 2022; Takai et al. 2022) have mostly been analyzed using two-dimensional measurements (rotational angles or linear distance between two successive septa) (Naglik et al. 2015a; Tajika et al. 2020). The ontogenetic trajectories of septal spacing change at the transitions between ontogenetic stages (embryonic, neanic, juvenile, and mature stages) (e.g., Westermann 1958; Bucher et al. 1996; Klug 2001; Kraft et al. 2008). Shell morphology changes covariably at such transitions (e.g., whorl expansion rate; WER) (Linzmeier et al. 2018; Kawakami et al. 2022).

Therefore, in this study, we examined the ontogenetic trajectories of shell morphology (septal spacing and WER). Based on these examinations, we aimed (1) to elucidate whether the ontogenetic trajectories of septal spacing and shell morphology had similar characteristics in *Gaudryceratinae* and *Tetragonitinae* and (2) to discuss implications for the paleoecology and evolutionary trends of tetragonitid ammonoids.

Material

All specimens used in this study were collected from calcareous concretions found in the Tomamae (subdivided into Haboro and Kotanbetsu), Mikasa, and Hamanaka areas of Hokkaido, Japan (Fig. 1). None of the specimens exhibited irregular shell growth (e.g., injuries) and they are all preserved without diagenetic shell deformations (Fig. 2). We analyzed 40 specimens of *Gaudryceratinae* and *Tetragonitinae* (see Hoffmann 2015 for the definition of higher taxonomy). Seven specimens belonged to two species of Late Cretaceous *Gaudryceratinae*: (1) *Gaudryceras denseplicatum* (four specimens; two specimens each were collected from calcareous concretions embedded in outcrops of Cretaceous strata in the Mikasa and Tomamae areas) and (2) *Gaudryceras hamanakense* (three specimens were collected as

float from an outcrop of Cretaceous strata in the Hamanaka area). The other 33 specimens belonged to three species of Late Cretaceous *Tetragonitinae*: (1) *Tetragonites glabrus* [20 specimens; 18 specimens from the Tomamae area (15 were collected from calcareous concretions embedded in the outcrops of Cretaceous strata, and three were collected as float) and two specimens from the Mikasa area (all were collected calcareous concretions embedded in the outcrops of Cretaceous strata)], (2) *Tetragonites popetensis* [eight specimens from the Tomamae area (seven were collected from calcareous concretions embedded in outcrops of Cretaceous strata, and one was collected as float)], and (3) *Tetragonites minimus* (five specimens were collected from calcareous concretions embedded in outcrops of Cretaceous strata in the Tomamae area).

Figures and other specimens examined in this study were deposited at the Mikasa City Museum, Hokkaido.

Geological setting

Tomamae area

Calcareous concretions, such as *G. denseplicatum*, *T. glabrus*, and *T. popetensis*, were collected from the Haborogawa Formation (Yezo Group) in the Migino-sawa, Katagiri-sawa, Pissiri-sawa, Nakafutamata, and Detofutamata Rivers in the Haboro area, and the Horotate-sawa and Kotanbetsu Rivers in the Kotanbetsu area (Fig. 1) (Toshimitsu 1985, 1988; Wani and Hirano 2000; Takashima et al. 2004; Ikeda and Wani 2012). The depositional environments reflect an outer shelf and a storm-dominated inner shelf–shoreface for the lower and upper parts of the Haborogawa Formation, respectively (Toshimitsu 1985, 1988; Wani 2003; Takashima et al. 2004). According to the co-occurring index inoceramids, the geological age of the examined specimens can be considered Santonian to earliest Campanian (Toshimitsu 1985, 1988; Wani and Hirano 2000; Okamoto et al. 2003; Wani 2003; Takashima et al. 2004; Ikeda and Wani 2012; Kawabe and Okamoto 2012).

Mikasa area

Calcareous concretions, including some specimens of *G. denseplicatum* and *T. glabrus*, were collected from the Kashima Formation (Yezo Group) located at Ashiyachi-sawa in the Mikasa area (Fig. 1) (Takashima et al. 2004; Futakami et al. 2008). The depositional environment of the Kashima Formation reflects an outer shelf–continental slope, and the geological age of the examined specimens from this area can be considered Santonian based on the co-occurring index inoceramids (Futakami et al. 2008).

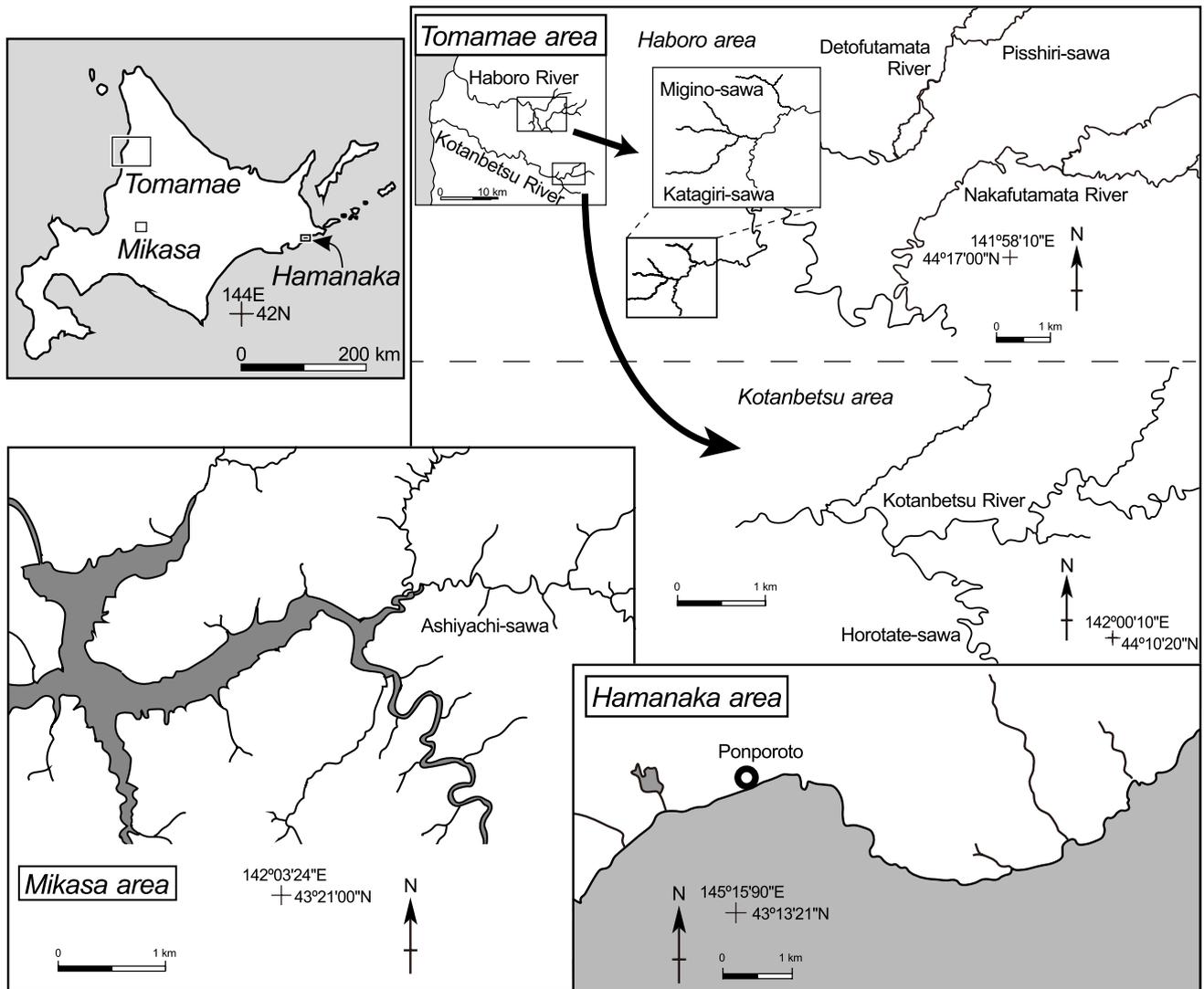


Fig. 1 Topographic maps of the Tomamae, Mikasa, and Hamanaka areas in Hokkaido, Japan. For geological information, see Toshimitsu (1985, 1988), Wani and Hirano (2000), Okamoto et al. (2003), Wani (2003), Takashima et al. (2004), Ikeda and Wani (2012), Kawabe and

Okamoto (2012) for the Tomamae area; Takashima et al. (2004) and Futakami et al. (2008) for the Mikasa area; and Naruse et al. (2000) and Naruse (2003) for the Hamanaka area

Hamanaka area

All the specimens of *G. hamanakense* were collected as float from the Akkeshi Formation (Nemuro Group) located at Ponporoto in the Hamanaka area (Fig. 1), which is the type locality of *G. hamanakense* (Matsumoto and Yoshida 1979; Naruse et al. 2000). The depositional environments of the Akkeshi Formation are channel-levee complexes at the foot of the slope environment (Naruse 2003). According to the index fossils, the geological age of the examined specimens can be considered Maastrichtian (Matsumoto and Yoshida 1979; Naruse et al. 2000).

Methods

Each specimen was polished along its median plane (plane of symmetry) using silicon carbide powder. The septal spacing between successive septa was defined as the rotational angle between two successive septa (i.e., N and N-1 septal numbers) at the positions where the septum meets the siphuncle (Fig. 3) and was measured using a digital optical microscope (Keyence VHX-900; magnification $\times 25$ – $\times 175$; error $< 0.01^\circ$). The intraspecific variability of septal spacing and irregular septal spacing, especially in the early ontogenetic stage, was appropriately

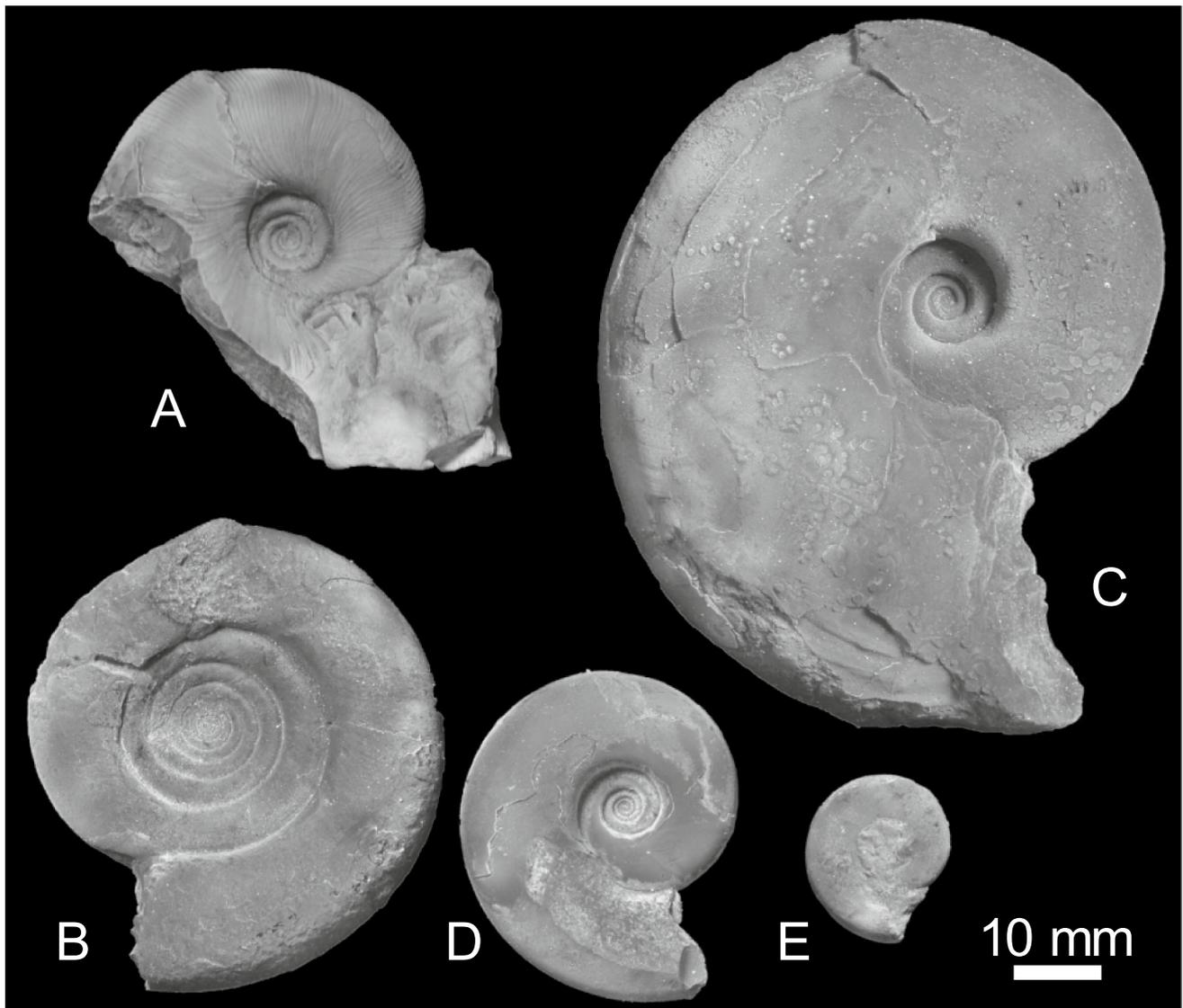


Fig. 2 Photographs of the examined species of Tetragonitidae; **A** *Gaudryceras denseplicatum*, MCM-W1983, Santonian, Kotanbetsu area; **B** *Gaudryceras hamanakense*, MCM-W1987, Maastrichtian, Hamanaka area; **C** *Tetragonites glabrus*, MCM-W1991, Santonian,

Nakafutamata River, Haboro area; **D** *Tetragonites popetensis*, MCM-W2010, Campanian, Katagiri-sawa Creek, Haboro area; **E** *Tetragonites minimus*, MCM-W2019, Santonian, Pisshiri-sawa Creek, Haboro area. Scale bar represents 10 mm

examined in this study. The center of rotation was defined as the center of the maximum diameter of the initial chamber through the base of the caecum (Fig. 3). The measured septal spacings are shown in the graphs of the septal spacing between two successive septa (N and N-1) against the septal number (N) and phragmocone diameter through ontogeny (Figs. 4 and 5).

The WER, which is one of the major parameters of ammonoid conchs was measured as a representative parameter of conch shape, following Klug et al. (2015a). In each specimen, the WER of every demi-whorl on the median plane was measured, and the ontogenetic trajectories of each WER were recorded.

Ammonitella diameters were measured using an optical microscope with a digital measurement tool (Keyence VHX-900; magnification $\times 25$ – $\times 175$; error < 0.01 mm). In this study, the ammonitella diameter was defined as the maximum diameter of the ammonitella from the primary constriction (Fig. 3).

Determination of the transition in modes of life

Isotopic analyses of pristine aragonitic shells provide interesting information on the modes of life of ammonoids (Moriya et al. 2003; Lécuyer and Bucher 2006; Moriya 2015a, b; Sessa et al. 2015; Linzmeier et al. 2018;

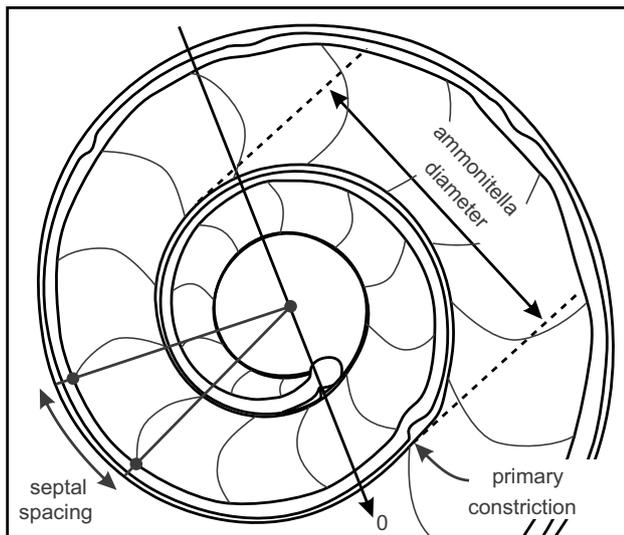


Fig. 3 Measurement of shell morphology exhibiting septal spacing, the base of measurement through prosepium (0), and ammonitella diameter (the maximum diameter through the primary constriction)

Hoffmann et al. 2019). Oxygen isotopes recording changes in water temperature should be examined. However, the shell materials of the specimens examined in this study were recrystallized into calcite; thus, the primary isotopic signal was lost.

Another decisive piece of information for determining the modes of life of ammonoids comes from the calculation of ammonoid buoyancy (Hoffmann et al. 2015). Shigeta (1993) examined and theoretically calculated the buoyancy of the same tetragonitid species that we used here. Therefore, we compared the calculated buoyancy of tetragonitid ammonoids in Shigeta (1993). However, there are some issues with these older buoyancy calculations (Hoffmann et al. 2015). If the ammonoid had negative buoyancy, they could actively swim to counteract their negative buoyancy (Lemanis et al. 2015). Furthermore, the density calculation depends on the values used for the soft part density and the amount of chamber liquid (Naglik et al. 2015a, b; Tajika et al. 2015; Peterman et al. 2019, 2020a). Moreover, buoyancy calculations are sensitive to differences in body chamber ratio (Naglik et al. 2015a, b; Tajika et al. 2015; Peterman et al. 2020b).

Therefore, we estimated the transition in modes of life from the covariation of ontogenetic changes in the septal spacing and outer shell shape. The changes in mode of life belonged to the major events in the ammonoid lifecycle. Therefore, both septal spacing and shell shape covariably change at these ontogenetic stages because the animal needed to maintain neutral buoyancy, at least to some degree. Similar covariations between the changes in shell shape and modes of life are thought to exist in other extinct mollusks (Tanabe 1973; Hayami and Hosoda 1988).

Results

Gaudryceratinae

Septal spacing

The ontogenetic trajectories of septal spacing followed a similar trend between the two examined Gaudryceratinae species (Fig. 4; Supplementary files 1–2). There were two cycles until the 27th–30th septum; each cycle comprised an increase and subsequent decrease in septal spacing. The ends of the first and second cycles were near the 12th–17th and 27th–30th septum, respectively (Table 1). The amplitudes of the first cycle were larger than those of the second cycle.

Different characteristics were found in the examined species. After the second cycle, no additional cycle was documented in *G. denseplicatum* (Fig. 4A–C). However, a distinct third cycle occurred after the second cycle in *G. hamanakense* (Fig. 4E–G). It was difficult to adequately recognize the end of the third cycle because it gradually transitioned into a flattening curve. We approximated the end of the third cycle in *G. hamanakense* as the point, at which the slope of the trajectories became gentler (the 45th septum).

The septal spacings of the three ontogenetic stages (during the first and second cycles, and afterwards) showed significant differences (ANOVA, $p < 0.01$), indicating that these cycles are not artifacts, but a biologically real phenomenon.

WER

The ontogenetic trajectories of the WER followed a similar trend between the two examined Gaudryceratinae species (Fig. 4; Supplementary files 1–2). The WER values first decreased and subsequently increased.

Different characteristics were documented in the positions transitioning from a decrease to an increase at around 5–7 and 10–15 mm shell diameters of *G. denseplicatum* and *G. hamanakense*, respectively. At these shell diameters, the WER values were ~1.8 in *G. denseplicatum* and ~1.5 in *G. hamanakense*.

Tetragonitinae

Septal spacing

The ontogenetic trajectories of septal spacing followed a similar trend among the three examined Tetragonitinae

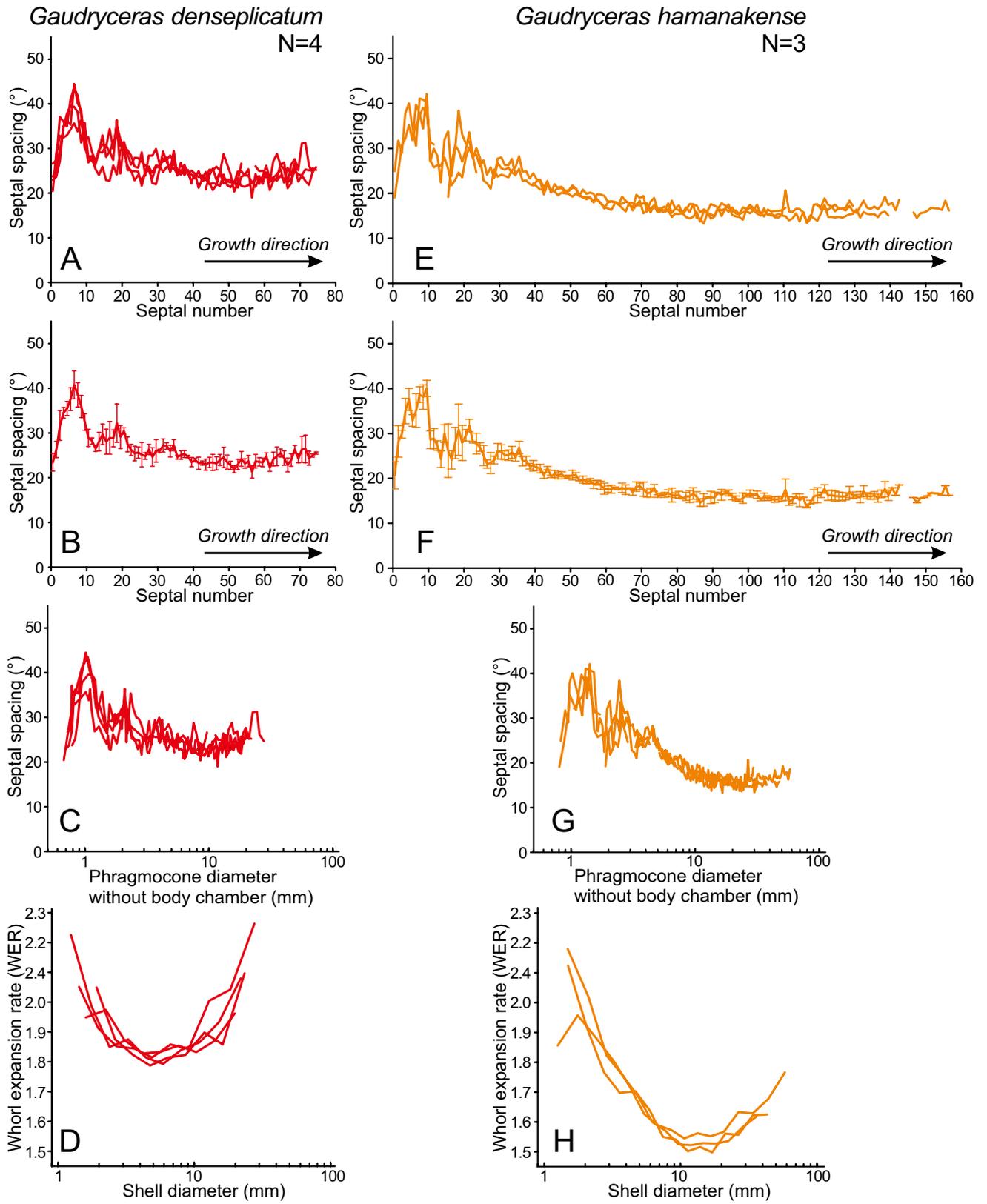


Fig. 4 Graphs of septal spacing (rotational angles) and whorl expansion rate (WER) through ontogeny; **A** all specimens of *Gaudryceras denseplicatum*; **B** average ontogenetic trajectories of septal spacing with error bars (standard deviations) in *G. denseplicatum*; **C** all specimens vs. phragmocone diameter of *G. denseplicatum*; **D** WER vs. shell diameter of *G. denseplicatum*; **E** all specimens of *Gaudryceras hamanakense*; **F** average ontogenetic trajectories of septal spacing with error bars (standard deviations) in *G. hamanakense*; **G** all specimens vs. phragmocone diameter of *G. hamanakense*; **H** WER vs. shell diameter of *G. hamanakense*

species (Fig. 5; Supplementary files 3–5). There were two cycles until 25th–35th septum. The ends of the first and second cycles were near the 12th–15th and 25th–35th septum, respectively (Table 1). The amplitudes of the first cycle were larger than those of the second cycle. The septal spacing after the second cycle was nearly constant, between 20 and 30 degrees.

Different characteristics were discovered only in *T. minimus*. After the 57th to 67th septum (phragmocone diameters of 8.7–12.2 mm), the septal spacings of the three specimens decreased sharply (Fig. 5I–K).

The septal spacings of the three ontogenetic stages (during the first and second cycles, and afterwards) showed significant differences (ANOVA, $p < 0.05$), indicating that these cycles are not artifacts, but a biologically real phenomenon.

WER

The ontogenetic trajectories of the WER followed a similar trend among the three examined Tetragonitinae species (Fig. 5; Supplementary files 3–5). The WER values first decreased and subsequently increased afterward, although this trend was unclear in the two species of *T. minimus*.

Different values were measured in the developmental positions transitioning from a decrease to an increase of 3–4 and ~2 mm in the shell diameters of *T. glabrus* and *T. popetensis*, and *T. minimus*. At these shell diameters, the WER values were 1.8–2.0 in *T. glabrus*, 1.7–1.9 in *T. popetensis*, and 1.8–1.9 in *minimus*.

Discussion

Stable ontogenetic trajectories of shell morphology during the earliest ontogeny within tetragonitids

Our results demonstrated that the ontogenetic trajectory patterns of septal spacing during the earliest ontogeny (until ~30th septum) had similar characteristics in the examined tetragonitid species. All examined species had at least two cycles of septal spacing during the earliest ontogeny (Figs. 4 and 5). This result is concordant with that of *G. tenuiliratum*, which is a common tetragonitid species found

in Hokkaido (Kawakami et al. 2022). The exception was *G. hamanakense*, which formed a distinct additional cycle (i.e., the third cycle) (Fig. 4E–G). Furthermore, the septal numbers at the ends of the first and second cycles were identical (~15th and ~30th septum) in all examined species and in *G. tenuiliratum* (Kawakami et al. 2022). The phragmocone diameters at the ends of the first and second cycles were measured at 1.2–2.2 and 2.6–5.9 mm, which were also identical in the examined tetragonitid species (Figs. 4 and 5; Table 1). These data suggest that the ontogenetic trajectory patterns of septal spacing during the earliest ontogeny (until ~30th septum) were stable in the Late Cretaceous tetragonitids, although we did not examine all species. At least two cycles during the earliest ontogeny in tetragonitids contrast with one cycle during the earliest ontogeny in modern and fossil nautiloids (Landman et al. 1983; Wani and Ayyasami 2009; Wani and Mapes 2010; Tajika et al. 2021, 2022) as well as Cretaceous desmoceratids (Takai et al. 2022).

Furthermore, considering the data from this study and those from Kawakami et al. (2022), the ontogenetic trajectories of the WER revealed similar characteristics within the family Tetragonitidae. In all examined species, the WER values first decreased and subsequently increased (Figs. 4 and 5). However, the ontogenetic stages transitioning from a decrease to an increase were different in Gaudryceratinae (5–7 or 10–15 mm shell diameters) and Tetragonitinae (~3 mm shell diameters) (Figs. 4 and 5).

The sharply decreasing trend of septal spacing in the later ontogenetic stages in some specimens of *T. minimus* (Fig. 5I–K) is different to those of the other examined species. These are thought to be terminal septal crowding (Klug et al. 2015b). The mature phragmocone diameter of *T. minimus* during the Santonian and Campanian is usually 10–19 mm (Shigeta 1989; Aiba 2022), which is consistent with our results.

Implications for early life history

Although most ammonoid hatchlings are thought to have been planktic, adult tetragonitid ammonoids in Hokkaido have been reconstructed as demersal using oxygen isotopic examinations (Moriya et al. 2003; Moriya 2015a, b). However, Moriya et al. (2003) did not provide isotopic data of the embryonic and juvenile stages (Moriya 2015a). If the tetragonitid species examined in this study were planktic for a some time after hatching and later became demersal at a certain ontogenetic stage, then how large was the shell diameter at this stage? As the phragmocone diameters measured in this study did not include the body chamber, shell diameters, including body chambers, can only be estimated. However, it is difficult to accurately recognize the precise body chamber length at a certain

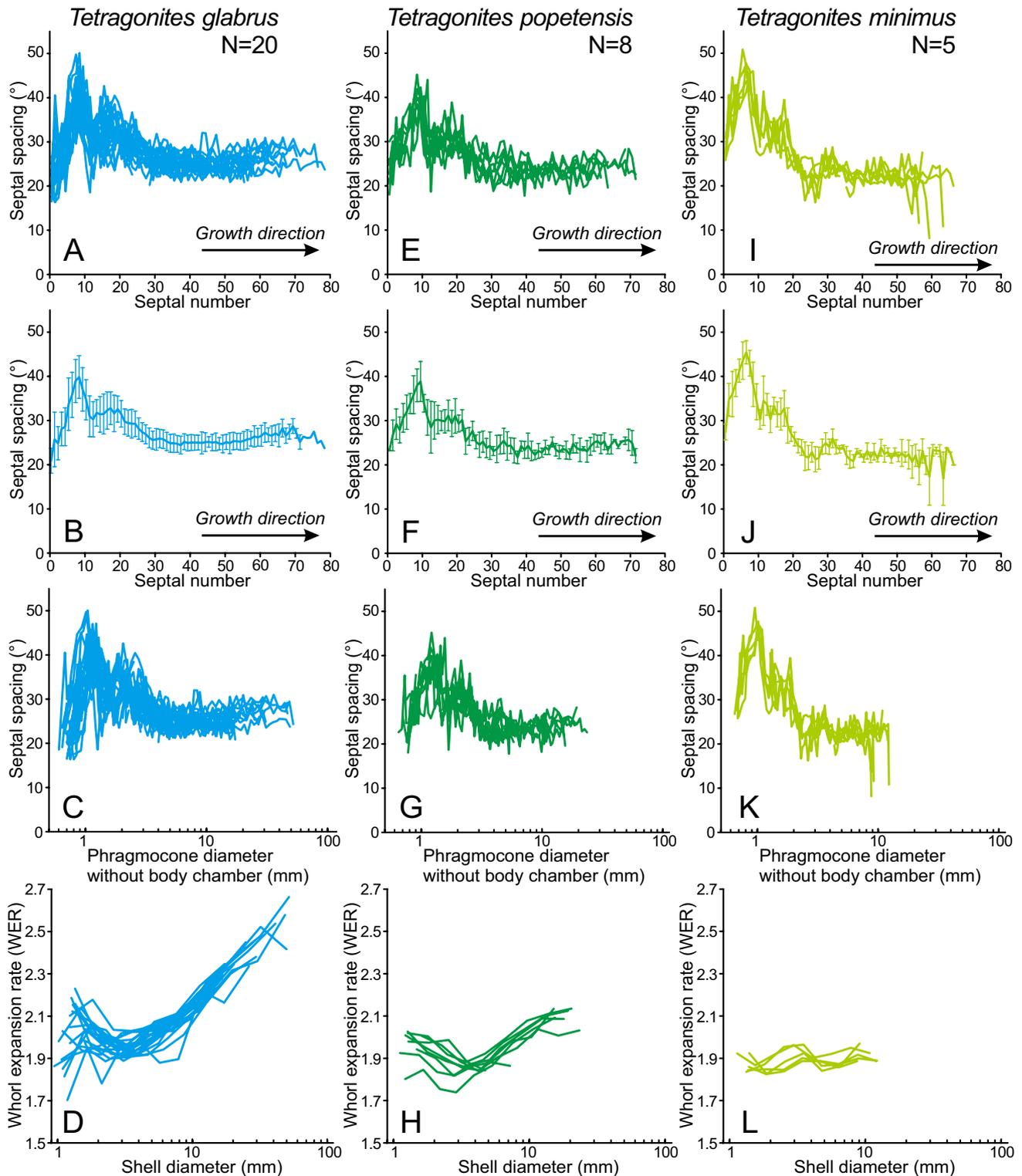


Fig. 5 Graphs of septal spacing (rotational angles) and whorl expansion rate (WER) through ontogeny; **A** all specimens of *Tetragonites glabrus*; **B** average ontogenetic trajectories of septal spacing with error bars (standard deviations) in *T. glabrus*; **C** all specimens vs. phragmocone diameter of *T. glabrus*; **D** WER vs. shell diameter of *T. glabrus*; **E** all specimens of *Tetragonites popetensis*; **F** average ontogenetic trajectories of septal spacing with error bars (standard

deviations) in *T. popetensis*; **G** all specimens vs. phragmocone diameter of *T. popetensis*; **H** WER vs. shell diameter of *T. popetensis*; **I** all specimens of *Tetragonites minimus*; **J** average ontogenetic trajectories of septal spacing with error bars (standard deviations) in *T. minimus*; **K** all specimens vs. phragmocone diameter of *T. minimus*; **L** WER vs. shell diameter of *T. minimus*

Table 1 Septal numbers and shell diameters at the end of the first, second, and third cycles of increasing to decreasing septal spacing

Species	Ammonitella diameter (mm)	Septal number at the end of first cycle	Phragmocone diameter at the end of first cycle (mm)	Reconstructed shell diameter at the end of first cycle (mm)	Septal number at the end of second cycle	Phragmocone diameter at the end of second cycle (mm)	Reconstructed shell diameter at the end of second cycle (mm)	Septal number at the end of third cycle	Phragmocone diameter at the end of third cycle (mm)	Reconstructed shell diameter at the end of third cycle (mm)
Tetratonoidea										
Gaudryceratidae										
<i>Gaudryceras denseplicatum</i>	1.16–1.36	13–17	1.5–1.7	2.7–2.9	27–30	2.9–3.4	4.8–5.7			
<i>Gaudryceras hamanakense</i>	1.41–1.50	14–17	1.9–2.1	3.2–3.6	28–29	3.4–3.8	5.4–6.0	45	5.7–6.1	8.4–10.0
<i>Gaudryceras tenuiliratum</i> *	1.18–1.38	11–17	1.3–1.9	2.4–3.1	25–33	2.6–3.6	4.4–5.8			
Tetragonitidae										
<i>Tetragonites glabrus</i>	1.07–1.51	12–16	1.4–2.2	2.4–3.9	25–36	2.7–5.9	5.0–12.0			
<i>Tetragonites popetensis</i>	1.14–1.43	12–16	1.4–2.0	2.5–3.3	23–31	2.7–3.7	5.0–6.5			
<i>Tetragonites minimus</i>	1.07–1.14	11–14	1.2–1.5	2.1–2.8	23–28	2.1–3.1	4.1–5.6			

*Data from Kawakami et al. (2022)

ontogenetic stage, except for the hatching (i.e., ammonitella) and mature stages. Arai and Wani (2012) estimated shell diameters by postulating that the body chamber length during the early post-embryonic stage was approximated to an ammonitella angle between the nepionic constriction and prosepium. We adopted this only moderately accurate method to estimate the shell diameters, including body chamber length. In Gaudryceratinae, the estimated shell diameters were 2.4–3.6, 4.4–6.0, and ~10 mm at the ends of the first, second, and third cycles (Table 1). In Tetragonitinae, the estimated shell diameters were 2.1–3.9 and 4.1–12.0 mm at the ends of the first and second cycles (Table 1). Desmoceratinae had a single cycle of septal spacing during the earliest ontogeny, at the end of which their mode of life changed, possibly from planktic to demersal (Takai et al. 2022). The examined tetragonitid specimens could have changed modes of life at the end of either the first, the second, or the third cycles.

Moreover, we examined the WER as a representative parameter of shell shape. The results demonstrated that the WER trends changed in Gaudryceratinae and Tetragonitinae when the shell was measured at 5–7 or 10–15 mm and ~3 mm diameter (Figs. 4D and H, 5D, H, and L). These shell diameters approximately fit the end of the second or third cycle in Gaudryceratinae and the first cycle in Tetragonitinae. Based on similar considerations, Kawakami et al. (2022) proposed that *G. tenuiliratum* changed its mode of life, possibly from planktic to demersal at 5–7 mm shell diameter (i.e., at the end of the second cycle). Lukeneder and Lukeneder (2014) distinguished embryonic, neanic, juvenile, and mature stages based on biometric analyses of the WER in Carnian (Late Triassic) ammonoids. Their analyses revealed that high WER values occurred in the embryonic to early juvenile stages; however, the WER values decreased drastically in older juveniles and increased markedly thereafter. Similar WER trends have been documented for some Devonian ammonoids (Klug 2001). This morphological change was hypothesized to mirror the ammonoid trend of change from planktic to nektic modes of life (Lukeneder and Lukeneder 2014; Lukeneder 2015), and the WER trajectory seen in Carnian (Late Triassic) ammonoids was comparable to that found in this study (Figs. 4D and H, 5D, H, and L).

Klug and Korn (2004) examined the shell morphology of several Paleozoic ammonoids and hypothesized that an increase in WER allowed an increase in maneuverability and maximum horizontal swimming speed. They reasoned that this happened because the horizontal alignment of the hyponome relative to the centers of gravity was achieved by increasing the WER, thereby improving swimming abilities. The ideal thrust angles between different planispiral conchs were demonstrated to be similar (Peterman and Ritterbush 2022). When this hypothesis is applied to Late Cretaceous ammonoids, the increase in WER after 5–7 or 10–15 mm

diameter in Gaudryceratinae and ~3 mm diameter in Tetragonitinae might also be reasonably related to adaptation to a nektic mode of life.

Furthermore, Shigeta (1993) theoretically calculated the buoyancy of living *Tetragonites glabrus* and suggested that their mode of life changed at shell diameters of 2.0–4.0 mm. When comparing this estimate with the ontogenetic trajectories of septal spacing in *T. glabrus* (Fig. 3D–F), we found that these shell diameters were comparable with the reconstructed shell diameters at the end of the first cycle (2.1–3.9 mm; Table 1).

Based on these considerations, we propose that (1) the planktic phase of *G. denseplicatum* ended at 5–7 mm shell diameter (i.e., at the end of the second cycle), (2) that of *G. hamanakense* ended at ~10 mm shell diameter (i.e., at the end of the third cycle), and (3) those of *T. glabrus*, *T. popetensis*, and possibly *T. minimus* ended at ~3 mm shell diameter (i.e., at the end of the first cycle) (Figs. 4 and 5; Table 1). These supposed shell diameters exhibit significant differences between the three groups (ANOVA, $p < 0.01$).

Linzmeier et al. (2018) analyzed oxygen isotopes of Late Cretaceous scaphitid specimens from the Fox Hills Formation in South Dakota, USA, and revealed that scaphitids lived in shallow water immediately after hatching and then transitioned to a more demersal mode of life after 270°–360° growth from the nepionic constriction. At this stage, scaphitid shell morphology covariably changed (Landman 1987; Linzmeier et al. 2018). Therefore, the covariation between changes in shell morphology and modes of life are concordant with the tetragonitid species examined in this study.

Different evolutionary trends in tetragonitid phylogeny

Although the ontogenetic trajectory patterns of septal spacing during the earliest ontogeny (until ~30th septum) in the examined tetragonitid species had similar characteristics, shell diameters at the end of the planktic phase were expected to be larger among Gaudryceratinae and smaller among Tetragonitinae. These differences have been discussed in greater detail from a phylogenetic perspective in the following paragraphs.

The subfamily Gaudryceratinae appeared in the Barremian and the subfamily Tetragonitinae was derived from *Eogaudryceras* (Gaudryceratinae) in the Aptian (Fig. 6A) (Murphy 1967; Kennedy and Klinger 1977; Hoffmann 2010, 2015). Although not all globally collected species of Gaudryceratinae and Tetragonitinae have been examined, the currently available data leads to two possible scenarios. The first scenario assumes that the timings at the end of the planktic phase in Gaudryceratinae did not change from the Aptian to the Santonian–Campanian (Fig. 6B). If the root species of

Fig. 6 **A** Timings at the end of the planktic phase in Tetragnostidae, together with their phylogenetic and stratigraphic contexts. Stratigraphic ranges and phylogenetic relationships were synthesized from Murphy (1967), Kennedy and Klinger (1977), Wright (1996), and Yacobucci (2015); **B** hypothesized scenario 1; **C** hypothesized scenario 2. Open circles in the graphs indicate the timings at which the planktic post-embryonic stage ended

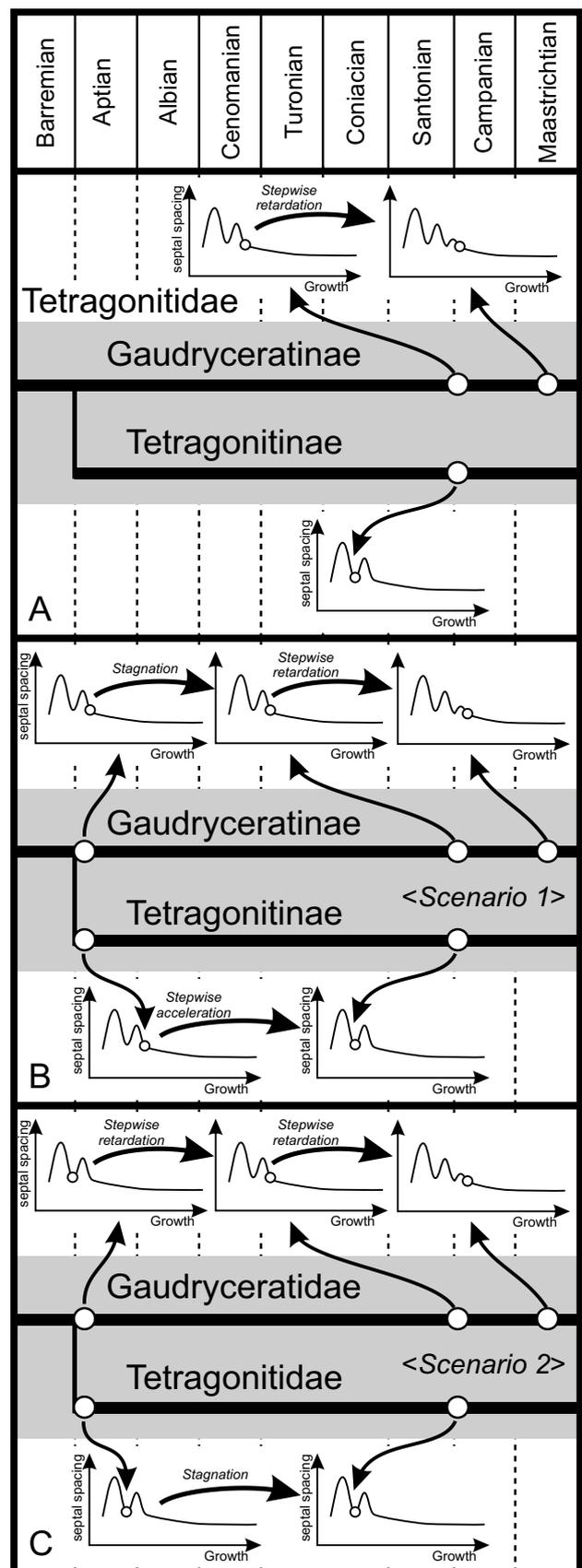
Tetragnostinae evolved from Gaudryceratinae, wherein the planktic phase ended at the end of the second cycle, the root species of Tetragnostinae possibly had a similar relationship between septal spacing and the ending time of the planktic phase. If these hypotheses are correct, the shell diameters at the end of the planktic phase of Tetragnostinae became smaller toward the Santonian–Campanian.

The second scenario assumes that the shell diameters at the end of the planktic phase in Gaudryceratinae increased in a stepwise fashion from the Aptian toward the Maastrichtian (Fig. 6C), which is based on the observation that the shell diameters at the end of the planktic phase for *G. hamanakense* in the Maastrichtian were larger than those of the other Gaudryceratinae species during the Santonian–Campanian. If *Eogaudryceras* ended their planktic phase at the end of the first cycle during the Aptian, the root species of Tetragnostinae might possibly have a similar relationship. Thus, the timings at the end of the planktic phase were constant within the Tetragnostinae lineage from the Aptian to the Maastrichtian. However, the timings at the end of the planktic phase in Gaudryceratinae were delayed in a stepwise fashion: from the end of the first cycle during the Aptian, through the end of the second cycle during the Santonian–Campanian, and toward the end of the third cycle during the Maastrichtian (Fig. 6C).

The evolutionary trends (for the definition, see McKinney 1990) of transitions at the end of the planktic phase differed between Gaudryceratinae and Tetragnostinae in each scenario. The timings at the end of the planktic phase exhibited a delay in the stepwise evolution of the Gaudryceratinae lineage in every scenario. In contrast, representatives of the Tetragnostinae lineage were accelerated (in the first scenario; Fig. 6B) or remained constant (in the second scenario; Fig. 6C). These different evolutionary trends highlight the slightly differing strategies within the family Tetragnostidae.

Comparison with other Cretaceous ammonoids

We examined ontogenetic trajectories of septal spacing of some Late Cretaceous Tetragnostidae (Lytocerozoidea). To date, this kind of ontogenetic trajectory pattern has not been found in other Cretaceous ammonoids (Arai and Wani 2012; Iwasaki et al. 2020; Takai et al. 2022), which likely is characteristic for this family.



The hatchling sizes (ammonitella diameters) of Tetragnonitidae tend to be larger than those of other Cretaceous ammonoids (Landman 1987; Landman et al. 1996; Tanabe et al. 2003; Tajika and Wani 2011; De Baets et al. 2015; Iwasaki et al. 2020; Kawakami et al. 2022; Takai et al. 2022). Furthermore, shell sizes at the end of the planktic phase in Desmoceratoidea were 1.1–2.4 mm and 2.0–2.5 mm in Phylloceratoidea (Shigeta 1993; Arai and Wani 2012; Takai et al. 2022). Correspondingly, the shell sizes at the end of the planktic phase were estimated to be ~3 in Tetragnonitinae and 5–7 or ~10 mm in Gaudryceratinae including body chamber length (Table 1). Our results confirm that Cretaceous Tetragnonitidae had larger hatchling sizes and shell diameters at the end of the planktic phase than compared with other Cretaceous ammonoids.

Identifying the absolute growth rate of ammonoids is challenging, thereby critically hampering comparisons between different taxa. However, assuming that the growth rates during the early growth stages of the Late Cretaceous ammonoids were comparable irrespective of taxonomy, the larger shell diameters of Tetragnonitidae species might indicate that they experienced a longer duration of planktic dispersal than other ammonoids (see Jablonski and Lutz 1983; Levin 2006; Fukumori and Kano 2014 for modern invertebrates). A longer duration of planktic dispersal would accordingly explain the wider geographic range of many tetragnonitid ammonoids (Wright 1996; Hoffmann 2010, 2015), which would have caused a greater genetic exchange within the geographical range and, therefore, a lower speciation rate. This might explain the comparatively slower evolutionary rate of Tetragnonitidae compared that of other ammonoids (Arkel et al. 1957; Ward and Signor 1983; Page 1996; Neige et al. 2013; Yacobucci 2015; Kawakami et al. 2022). However, phylloceratid and desmoceratid ammonoids had smaller shell diameters at the end of the planktic phase (Shigeta 1993; Arai and Wani 2012; Takai et al. 2022). Similar to Lytoceratoidea, the suborder Phylloceratina and superfamily Desmoceratoidea are known to show some evolutionary stability (Arkel et al. 1957; Ward and Signor 1983; Page 1996; Tanabe et al. 2003; Neige et al. 2013; Yacobucci 2015). Consequently, the supposed mode of life associated with the evolutionary and morphological stability of Lytoceratoidea (Page 1996; Yacobucci 2015) remains debatable.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12542-023-00650-0>.

Acknowledgements We are grateful to D. Aiba and T. Iwasaki for their cooperation during fieldwork and fossil sampling, and K. Komazaki and Y. Nishino for their cooperation with the morphological analyses. We sincerely thank R. Hoffmann, K. De Baets, and an anonymous reviewer as well as the editors (M. Rasser and C. Klug) for their valuable and thoughtful comments on an earlier draft of this manuscript.

This study was supported by the Sasakawa Scientific Research Grant from the Japan Science Society to YK and Grants-in-Aid for Scientific Research (no. 22K03794) and the Nakatsuji Foresight Foundation Research Grant to RW.

Funding Open access funding provided by Yokohama National University.

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