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# Analysis of septal spacing and septal crowding in Devonian and Carboniferous ammonoids

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## Abstract

Septal crowding is widely known as a sign of maturity in conchs of ammonoids and nautiloids. However, reduced septal spacing may also occur as a consequence of adverse ecological conditions. Here, we address the question how septal spacing varied through ontogeny in representatives of some of the major clades of Devonian and Carboniferous ammonoids. We found that the degree of ontogenetic variation is similar between clades and that variation is only weakly linked with conch form. The results show that septal crowding alone is insufficient to identify adulthood in ammonoids; intermediate septal crowding is a common phenomenon and occurs in various growth stages. Changes in septal distances during ontogeny were, in addition to adulthood of the individuals, a passive reaction likely caused by fluctuating environmental conditions.

**Keywords:** Ammonoidea, Devonian, Carboniferous, Septal distances, Ontogeny

## Introduction

Septal crowding is a long-known phenomenon in ectocochleate cephalopods (cephalopods with external shell) and has frequently been used as an indicator of the end of conch growth in nautiloids (e.g. Ward, 1987; Ward et al., 1981; Willey, 1902) and ammonoids (e.g. Klug, 2001, 2004; Klug et al., 2015b; von Buch, 1849; Westermann, 1971). It was widely accepted to be the most important conch character to recognise the fully adult state of nautiloid and ammonoid specimens (Fig. 1). It is also widely known that ammonoids had a considerably greater variation in the spacing of their septa than the living *Nautilus* (Tajika et al., 2015, 2020).

Although septal crowding has indeed proven to be one of the cardinal features for detecting maturity in cephalopods in many cases, there is evidence that maturity can

no longer be considered the sole cause (Hoffmann et al., 2018a, 2018b; Klug, 2001). In an experimental study of *Nautilus*, Keupp and Riedel (1995) found that septal crowding is more likely to occur in individuals kept in aquaria in response to unfavourable conditions. More precisely, these authors demonstrated a sharp drop in septal spacing associated with anomalous growth of the aperture of a captive specimen, ending with low septal spacing associated with thickening of the septa, shortening of the body chamber and eventual death of the specimen (see also Keupp, 2012).

Kraft et al. (2008) exemplified why approximation cannot be explained by adulthood alone; many of the specimens from Oued Temertasset (Central Sahara, Algeria) display 'terminal' but also intermediate phases of septal crowding (septal crowding at any growth interval before the terminal stage) and none of the species studied shows any other adult modification characteristic of terminal growth. In turn, septal crowding cannot be used as single character for maturity in ectocochleate cephalopods (Klug et al., 2015b), i.e. additional conch modifications

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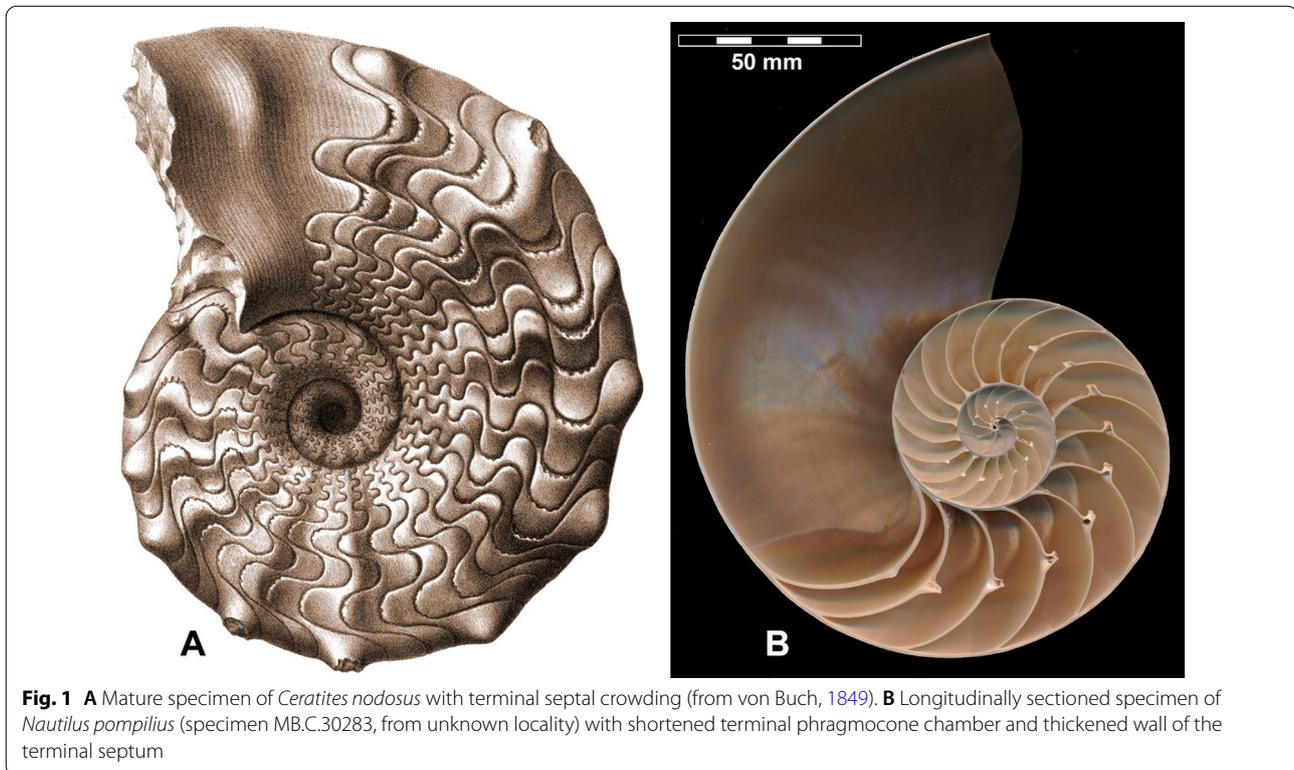
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have to be identified to be certain about the presence or absence of the terminal growth stage.

In general, not much is known in ammonoids about variations in chamber length during longer ontogenetic intervals, variations in septal spacing and specific patterns of septal approximation immediately before death of the individuals. While terminal septal crowding has been quite well documented, intermediate septal spacing, e.g. possibly caused by unfavourable ecological circumstances, pathologies or injuries, has rarely been studied (Bayer, 1977; Kraft et al., 2008; Lehmann, 1975). However, recent studies show that intermediate septal crowding is far from being a special case, but can be observed almost regularly in ammonoids (Arai & Wani, 2012; Bucher et al., 1996; Iwasaki et al., 2020; Kraft et al., 2008; Tajika et al., 2015, 2020; Zell & Stinnesbeck, 2016).

The phenomenon of varying septal distances in ammonoids has already been explained by a number of hypotheses. These hypotheses include both internal factors (changes in conch shape and ornament, changes in lifestyle) and external factors (change in the environment, injuries resulting from failed predation or parasitic infestation) or a combination of both.

Here we present the results from an analysis of the septal distances of more than 620 ammonoid specimens of the late Givetian (Middle Devonian) to the latest Viséan (Early Carboniferous). We studied septal spacing (and

thus the length of the phragmocone chambers) in angular degrees to gain data on fluctuations during the ontogenetic development of individuals, within species and larger taxonomic units, and throughout the evolutionary history of the Palaeozoic ammonoids.

### Septal spacing in nautiloids

For the understanding of conch ontogeny and the formation of septa in ammonoids, the comparison with recent nautiloids (Fig. 1B) is of utmost importance, even though there is only a rather distant phylogenetic relationship (Klug et al., 2015c; Kröger et al., 2011). However, due to the fact that both groups have an external shell with the same basic physical properties, similar conditions in the secretion of shell and septa can be inferred. The growth of the conch of *Nautilus* had already intensively been studied in the 1960s to 1980s (Denton & Gilpin-Brown, 1966; Kahn & Pompea, 1978; Saunders, 1984; Stenzel, 1964; Ward, 1985, 1987; Ward & Chamberlain, 1983).

The process of septal formation was studied directly in *Nautilus*. Denton and Gilpin-Brown (1966) and Kahn and Pompea (1978) reported a constant time interval between septal secretion of 14 and 30 days, respectively. Subsequent studies have shown that the period of chamber formation is not constant in *Nautilus*. In specimens kept in aquaria, the time between two chamber formation events was between 85 and 132 days in *N. pompilius*

(Ward, 1985; Ward & Chamberlain, 1983). The periods in specimens living in nature are similar: 60–90 days in immature specimens of *N. pompilius* (Cochran et al., 1981; Landman & Cochran, 1987) and 120–230 days in immature specimens of *N. belauensis* (Cochran & Landman, 1984; Saunders, 1983).

According to Landman (1987), the period of septum formation in *Nautilus* is not determined by an external source, but instead depends on internal buoyancy requirements and the rate of aperture growth. *Nautilus* adds shell to the aperture, thereby initiating the formation of new chambers to maintain neutral buoyancy. This process of septal secretion and shell growth at the aperture has to be coordinated to maintain neutral buoyancy (Ward et al., 1980).

Landman (1987) discussed the different patterns of septal spacing in *Nautilus* and ammonites; while in *Nautilus* the septa tend to be evenly spaced with an average angular spacing of about 25°, septal spacing in ammonoids is often highly variable. A reduction in chamber length (defined by the septal distance, measured by angular degrees) could reflect a deceleration of growth at the aperture, but the time interval between adjacent septa may vary. Injuries to the shell margin can lead to an interruption of the normal cycle of septum formation (Ward, 1985). According to Westermann (1973), variations in septal spacing may also represent indirect responses to morphometric changes during ontogeny. Several parameters influence the septal spacing, including the thickness of the shell wall and the shape of the whorl profile.

Chirat et al. (2008) emphasised that a relationship between septal spacing and relative growth seems obvious, but that the relationship with absolute growth rate is less clear. Ward (1987) already pointed out that although the apertural growth rate in *Nautilus* decreases with maturity, this largely occurs after the last septum has been secreted. For this reason, Chirat et al. (2008) considered that septal spacing is not a reliable indicator of absolute growth rate. Even in the case that several individuals show a similar pattern of septal spacing, this does not mean that they have grown at the same absolute rate.

## Septal spacing in ammonoids

### Reasons for changes in septal distances

Ammonoid species are known to vary for a series of reasons (e.g. De Baets et al., 2015b and references therein). The reasons for variations in septal distances of externally shelled cephalopods are manifold and range from intrinsic factors (conch geometry and its growth, function of the conch and its hydrodynamic properties, changes in life habits, adulthood) to extrinsic factors (environment, predation, parasitism); these reasons and causes can also

occur in combination and complement each other. In the following, we give a brief overview of the most important causes of variations in the distances between septa.

### Function of the conch

A common opinion is that variations in septal spacing are related to hydrostatic properties and serve to regulate buoyancy (Hammer & Bucher, 2006; Klug et al., 2008; Pérez-Claros, 2005). Differences in septal spacing were explained by different conch forms; compressed forms had smaller septal spacing than depressed forms (Hammer & Bucher, 2006). However, these differences only reflect variation within species or higher taxonomic units; rapid ontogenetic changes in septal distances cannot be explained by different conch shapes. Changes in the mode of growth caused by changes in habitat during ontogeny or by possible daily vertical migrations (Westermann, 1990) would also affect the distances between the septa (Bucher et al., 1996).

### Changes in life habits

Several scientists suggested that ammonoids have undergone an ontogenetic change from a planktonic to a more active nektonic lifestyle (e.g. Arai & Wani, 2012; De Baets et al., 2012, 2015a; Klug, 2001; Landman et al., 2013; Tajika et al., 2020; Westermann, 1996; Zell & Stinnesbeck, 2016). This can explain why septal crowding occurs more frequently in macroconchs, as their life span might have been longer and included a period long enough for migration and egg deposition (Zell & Stinnesbeck, 2016). Given this assumption, however, it remains questionable why megaconchs usually do not show any crowding (Hoffmann & Keupp, 2015). Ivanov (1975) introduced the term megaconch to refer to single very large specimens of otherwise growth-restricted species. The phenomenon has commonly been interpreted to indicate pathological gigantism and the shells of these megaconchs generally show no sign of growth limitation, such as terminal septal crowding or deterministic differentiation of the aperture (Hoffmann & Keupp, 2015). Manger et al. (1999) reported rare individuals (perhaps megaconchs) of several Late Palaeozoic ammonoid and nautiloid species which were two to four times the size of their normal counterparts in the same beds and interpreted as pathological gigantism related to trematode infestation. However, as argued before (De Baets et al., 2015c; Klug et al., 2015a), no additional support for parasitic infestations was found and these observations could just indicate that large specimens reaching old ages are comparatively rare and once reaching a certain size might have a reduced number of natural enemies. In addition, such observations together with the lack of evidence for adult modifications in most Palaeozoic ammonoids (with some rare exceptions like *Prolobites*) might suggest determinate growth and terminal

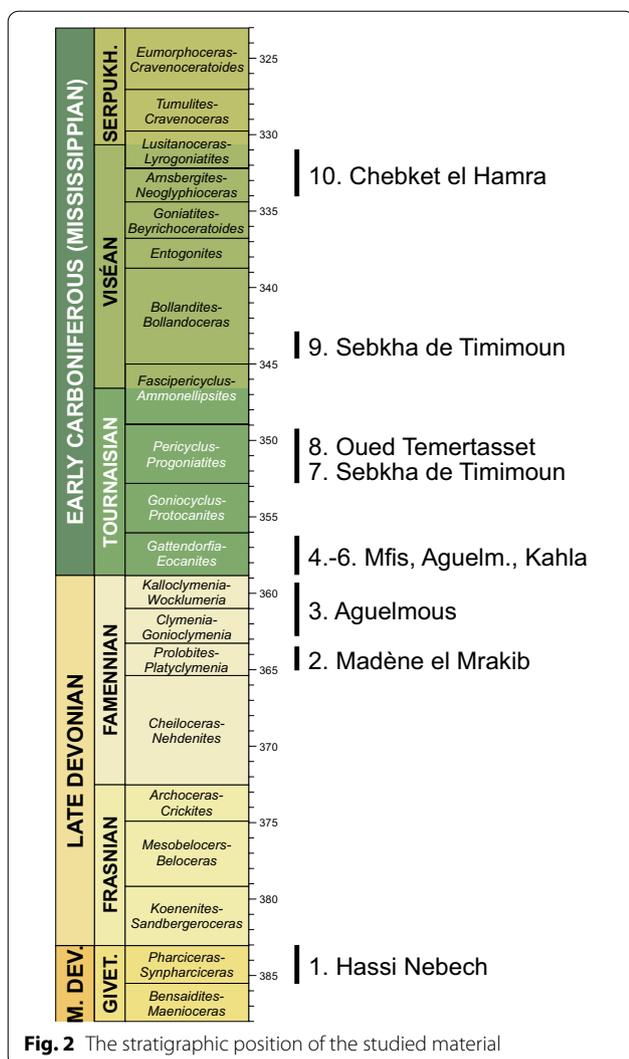


Fig. 2 The stratigraphic position of the studied material

septal crowding is rare to begin with and would also not be picked up if the specimens died before actually showing it.

**Changes in the environment**

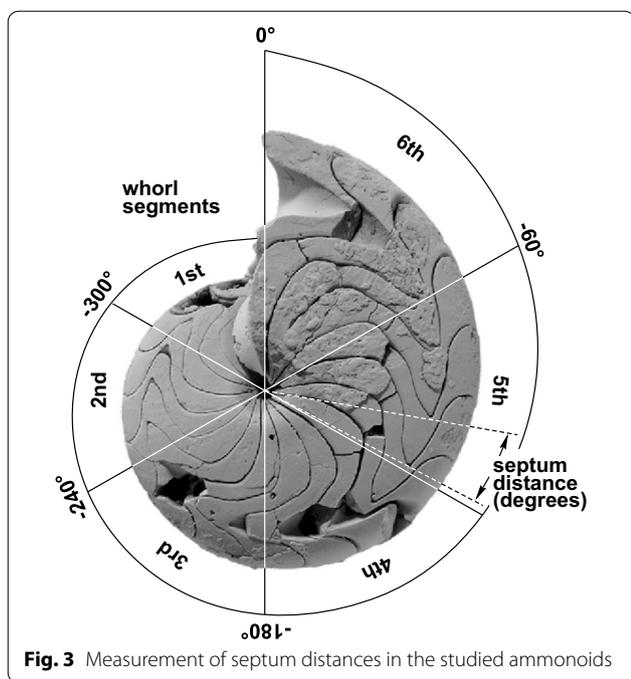
Unpropitious conditions caused a periodic loss of oxygen in the water leading to a lack of food; presumably, septal crowding occurs because the conditions became poor or lethal (Bucher et al., 1996; Kraft et al., 2008). Decrease in septal spacing without obvious injuries or pathologies has also been attributed to environmental perturbations (water temperature, pH, salinity, lack of food) in modern *Spirula spirula* (Hoffmann et al., 2018a, 2018b).

**Injuries and pathologies**

Septal approximation was found to be associated with severe shell injuries (e.g. Keupp, 2012, p. 124). Bucher

et al. (1996) gave three reasons for septal crowding; the cessation of forward movement of the soft body due to an injury, the interruption of the normal cycle of chamber formation and the need for additional weight to counteract the effect of positive buoyancy resulting from the loss of shell material. However, as Chirat et al. (2008) pointed out, the last reason is not convincing, since *Nautilus*, after a serious injury at the aperture edge, can delay the formation of new chambers by two months until the lost shell material is completely replaced (Ward, 1985; Ward & Chamberlain, 1983) but likely not longer (compare Keupp & Riedel, 1995). Klug et al. (2004) showed how ceratitid ammonoids reacted to excess weight due to bivalve epizoans by slowing down apertural growth and thus shortening the body chamber. Thus, the alignment of the septa occurs long after the sudden decrease in density. Furthermore, epizoans, such as bivalves, branching colonial organisms and tube worms growing on the external shell, might have affected the buoyancy of the ammonite (Checa et al., 2002; Ramming et al., 2018; Stalkerich et al., 2017; Tajika et al., 2015).

In addition, at least some papers indicate that ammonoids (De Baets et al., 2013b) as well as some extinct groups of nautiloids (Mironenko, 2018; Turek & Manda, 2016) and the modern coleoid *Spirula spirula* (Hoffmann et al., 2018a, 2018b) show changes in septal distance and/or shape associated with injuries and pathologies attributed parasitic infestations (reviewed in De Baets et al., 2021). De Baets et al., (2013b, 2015a, 2015b, 2015c) did not find a general correlation between septal spacing and spacing of structures interpreted to reflect repeated parasitic infestations in a specimen of the Early Devonian ammonoid *Ivoites opitzi*. However, these authors could demonstrate that the parasitic pits were associated with an abnormal development of the aperture/body chamber as well as often coincided with a temporary drop in septal spacing. A temporary decrease in septal spacing following a chamber with a blister pearl interpreted to indicate parasitism was also reported in modern *Spirula* (Hoffmann et al., 2018a, 2018b). Parasitism might also lead to changes in the shape of the septa and the course of the suture line which further support the link between apertural growth and septal spacing (e.g. temporary crowding). This has been well documented for Palaeozoic nautiloids (Mironenko, 2018; Turek & Manda, 2016). The temporary drop in septal spacing is often restricted to 1 or a couple septa at maximum. For the rest of the manuscript, we will focus on changes in septal spacing which persist longer and are not associated with obvious injury or pathology.



with regard to their septal distances (Additional file 1). These specimens represent 178 species of all Palaeozoic ammonoid suborders (except the Ceratitina). Of these specimens, 469 were used for our analyses; the additional specimens (e.g. 36 specimens of the species *Pseudoproboloceras nebechense*) were used to study intraspecific variation.

For our study of a satisfactorily high number of specimens, we had to focus on material in internal mould preservation. All the material is likely to have been originally preserved as pyrite-filled internal moulds and was later transformed into limonite or haematite (Frey et al., 2019). The original host rock for these materials was always a dark shale, but not black shale in the strict sense. Nevertheless, it is quite possible that at the time and place where these sediments were deposited, there was a certain lack of oxygen in the lower part of the water column.

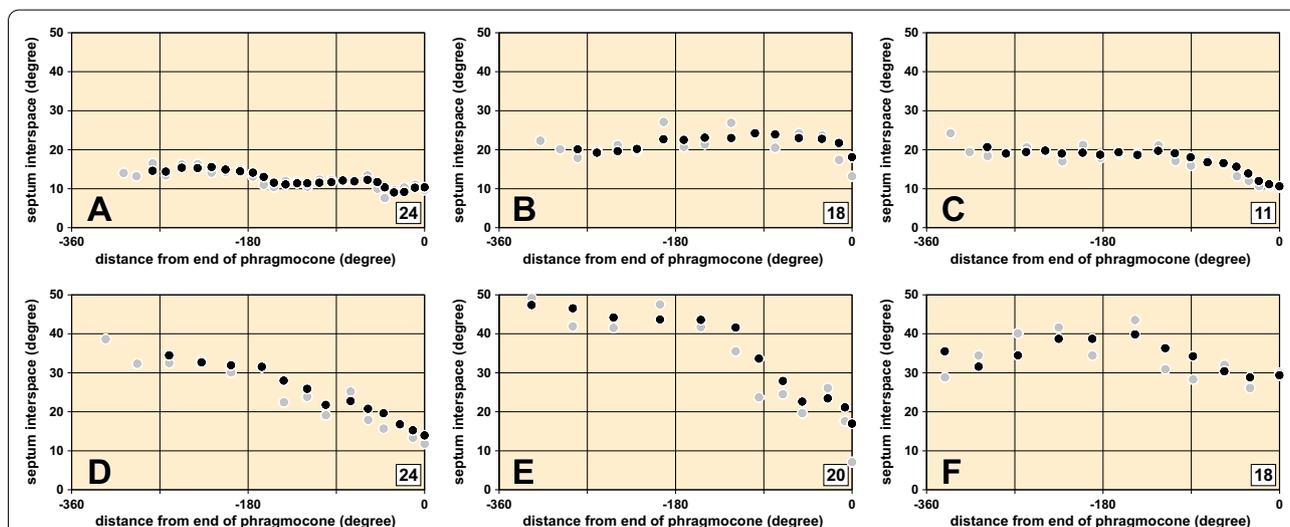
The material comes from several localities and the following stratigraphic units (in ascending order) (Fig. 2):

**Material and methods**

**Material**

We examined a total of more than 620 specimens of late Givetian to latest Viséan (Devonian and Carboniferous) ammonoids from localities in Morocco and Algeria

1. Hassi Nebech, 19 km east-northeast of Taouz (Anti-Atlas, Morocco); late Givetian *Pharciceras* assemblage: septal distances of 215 specimens representing the suborders Gephuroceratina, Pharcicratina and Tornoceratina (Bockwinkel et al., 2013) were measured. Of these, the conch parameters were also determined for 71 specimens.



**Fig. 4** Ontogenetic trajectories representative for the six distinguished groups with different modes of septal distance, shown in specimens of Late Tournaisian ammonoids from Oued Temertasset (Algeria). Phragmocone diameters in the lower right boxes. Grey dots = empirical data; black dots = three neighbouring data points averaged. **A** Group 1: *Jerania persimilis* Korn, Bockwinkel & Ebbighausen, 2010a; specimen MB.C.18940.1. **B** Group 2: *Muensteroceras multitudum* Korn, Bockwinkel & Ebbighausen, 2010a; specimen MB.C.18992.1. **C** Group 3: *Helicocyclus inornatus* Korn, Bockwinkel & Ebbighausen, 2010a; specimen MB.C.19035.1. **D** Group 4: *Pericyclus intercicus* Korn, Bockwinkel & Ebbighausen, 2010a; specimen MB.C.18862.2. **E** Group 5: *Pericyclus circulus* Korn, Bockwinkel & Ebbighausen, 2010a; specimen MB.C.18862.4. **F** Group 6: *Temertassetia temertassetensis* Korn, Bockwinkel & Ebbighausen, 2010a; specimen MB.C.18865.1

2. Madène el Mrakib, 27.5 km south-east of Fezzou (Anti-Atlas, Morocco); middle Famennian *Prionoceras* assemblage; 61 specimens in total, mainly prionoceratids, tornoceratids and platyclymeniids (Klein & Korn, 2014; Korn et al., 2014, 2015a, 2015b, 2016a, 2016b).
3. Aguelmous, 5 km north-east of Fezzou (Anti-Atlas, Morocco); late Famennian *Mimimitoceras* assemblage; 60 specimens in total, mainly prionoceratids, tornoceratids and cymaclymeniids (Klein & Korn, 2014; Korn et al., 2015a, 2015b, 2016a, 2016b).
4. Mfis, 16 km north-northeast of Taouz (Anti-Atlas, Morocco); Early Tournaisian *Gattendorfia* assemblage; 20 specimens in total, predominantly prionoceratids and a few early prolecanitids (Bockwinkel & Ebbighausen, 2006).
5. Aguelmous, 5 km north-east Fezzou (Anti-Atlas, Morocco); Early Tournaisian *Gattendorfia* assemblage; 28 specimens in total, predominantly prionoceratids and a few early prolecanitids (Ebbighausen & Bockwinkel, 2007).
6. Gara el Kahla, 35 km south-west of Timimoun (Gourara, Algeria); Early Tournaisian *Gattendorfia* assemblage; 15 specimens in total, predominantly prionoceratids and a few early prolecanitids (Ebbighausen et al., 2004).
7. Sebkha de Timimoun, 15 km west-southwest of Timimoun (Gourara, Algeria); Early Late Tournaisian *Pericyclus* assemblage; 13 specimens in total,

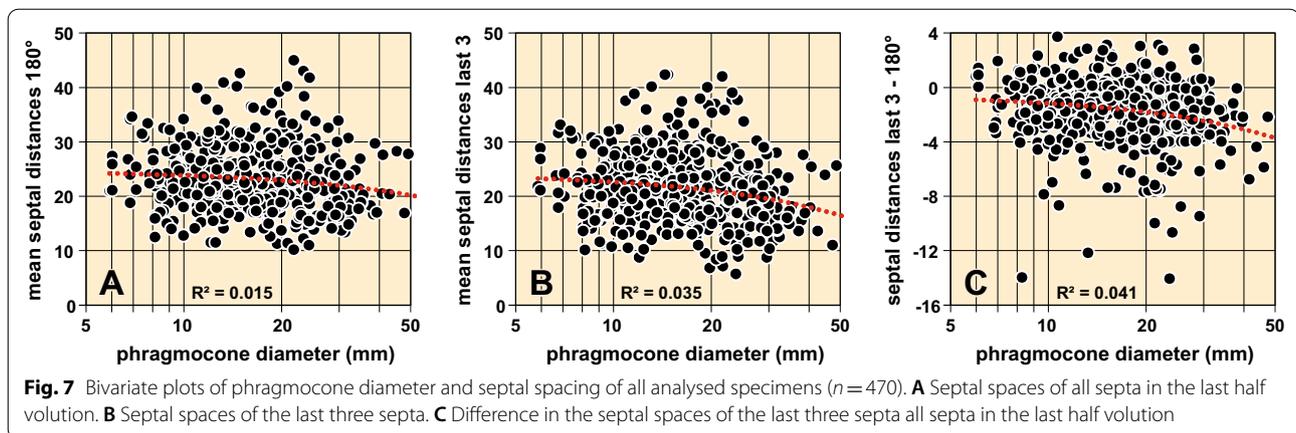
	n	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Clymeniina	24	8	13	42	21	4	13
Cyrtoclymeniina	23	13	0	26	13	17	30
Prolecanitina	22	23	14	36	9	5	14
Goniatitina	185	22	20	32	12	6	8
Tornoceratina	155	26	11	38	15	5	5
Pharciceratina	50	36	6	32	2	0	24
Gephuroceratina	10	30	20	30	0	10	10
<b>all</b>	<b>469</b>	<b>24</b>	<b>14</b>	<b>34</b>	<b>12</b>	<b>5</b>	<b>10</b>

**Fig. 6** Percentages of the six distinguished groups with different modes of septal distance in six Devonian and Carboniferous ammonoid suborders

- with prionoceratids, pericyclids, muensteroceratids and prolecanitids (Korn et al., 2010a, 2010b).
8. Oued Temertasset, 140 km east-southeast of In Salah (Mouydir, Algeria); Early Late Tournaisian *Pericyclus* assemblage; 125 specimens in total, with prionoceratids, pericyclids, muensteroceratids, goniatitids and prolecanitids (Korn et al., 2010a, 2010b).
  9. Sebkha de Timimoun, 10 km west-southwest of Timimoun (Gourara, Algeria); Early Viséan *Bollanodoceras* assemblage; 40 specimens in total, predominantly muensteroceratids (Bockwinkel et al., 2010).

		n	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Late Viséan	Chebket el Hamra	38	29	13	37	8	3	11
Early Viséan	Sebkha de Timimoun	40	25	25	37	0	5	8
Late Tournaisian	Oued Temertasset	125	21	18	30	17	6	6
	Sebkha de Timimoun	19	26	21	32	5	5	5
Early Tournaisian	Gara el Kahla	14	14	7	50	7	7	14
	Aguelmous	26	27	17	27	8	12	8
	Mfis	20	25	0	30	25	0	20
late Famennian	Aguelmous	56	23	13	38	25	5	0
middle Famennian	Madène el Mrakib	65	17	6	38	15	6	17
late Givetian	Hassi Nebech	71	34	10	31	4	3	18
	<b>all</b>	<b>469</b>	<b>24</b>	<b>14</b>	<b>32</b>	<b>12</b>	<b>5</b>	<b>10</b>

**Fig. 5** Numbers of percentages of the six distinguished groups with different modes of septal distance in the stratigraphically successive assemblages



10. Chebket el Hamra, 2 km west-northwest of Touissit (Jerada Basin, Morocco); Late Viséan *Arnsbergites* and *Lusitanoceras* assemblages; 39 specimens in total, predominantly represented by *Arnsbergites* and *Lusitanoceras* (Korn & Ebbighausen, 2008).

## Methods

We measured septum distances (which define the phragmocone chamber lengths) as angular degrees, starting with the last preserved septum, which is often also the last before the body chamber, and continuing towards the protoconch (Fig. 3). Using this method, size-independent values can be obtained for all specimens. Of course, it has to be taken into account that the length of the chambers in angular degrees has a certain dependence on the length of the body chamber and the total length of the coiled spiral; rapidly expanding conchs (as in *Nautilus*) should therefore have shorter body chambers (Klug, 2001; Saunders & Shapiro, 1986) and tend to have shorter chambers of the phragmocone. However, this does not play a role in explaining rapidly changing chamber lengths during the ontogeny of individuals.

The different ontogenetic trajectories of septal spacing can be classified (Kraft et al., 2008), although not all specimens can be unambiguously assigned in one of the groups owing to the fact that the boundaries between the groups that cannot be sharply delineated (Fig. 4).

Group 1: Steady growth—without reduction of septal distances and without distinct septal crowding in the last half volution (Fig. 4A).

Group 2: Minor changes—with rather steady septal distances with minor fluctuations in the first five segments of 60° length, followed by slight septal crowding in the last segment (Fig. 4B).

Group 3: Terminal decrease—without or with gradual, slow reduction of septal distances throughout the last whorl ending in septal crowding (Fig. 4C).

Group 4: Continuous decrease—with conspicuous reduction of septal spaces over a growth period, such as one whorl (Fig. 4D).

Group 5: Escalating decrease—with slow (sometimes distinct) reduction of septal distances in the first three segments; slow continuous reduction in segments 4 and 5, followed by drastic septal crowding in the last segment of 60° length (Fig. 4E).

Group 6: Regular oscillation—with continuous change from increasing to decreasing distances at regular intervals (Fig. 4F).

## Results and discussion

### Modes of septal spacing

Most of the specimens from ten stratigraphic intervals could be assigned to one of the six categories defined above; only a few specimens could not be assigned. A quarter of the specimens belong to group 1, i.e. to the group without any significant reduction in septal distance; thus, reductions in chamber length are recognisable in nearly three quarters of the specimens. More than one third of the specimens belong to group 3, which show a continuous reduction on the last whorl of the phragmocone.

In the temporal succession of the assemblages studied, there is no trend in the frequency distribution of the groups (Fig. 5). This may mean that the most important taxonomic units (Gephuroceratina and Pharciceratina in the Givetian, Tornoceratina in the Famennian and Early Tournaisian, Goniatitina in the Late Tournaisian and Viséan) do not differ with respect to their characteristics in the length of the phragmocone chambers. This finding is supported by the proportions of the groups within

the large systematic units (Fig. 6). All suborders, with the exception of the *Cyrtoclymeniina*, show very similar proportions of the groups; no trend is discernible.

### Septal distances and maturity

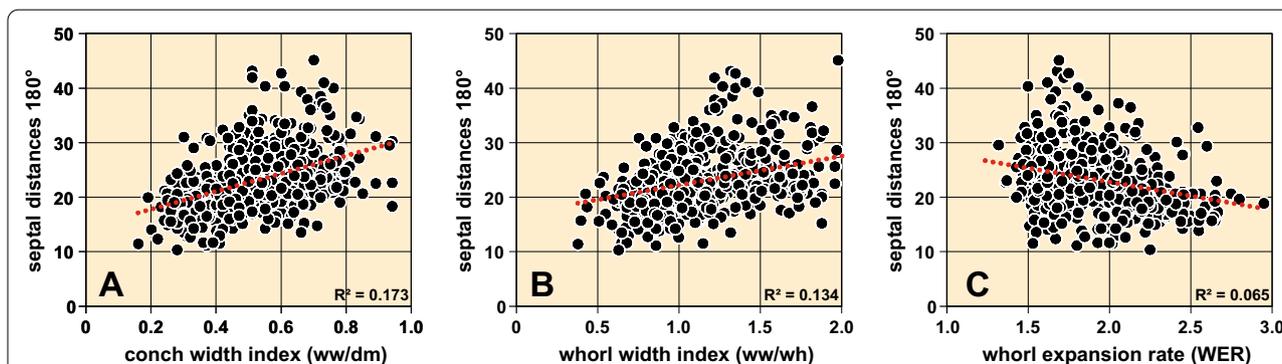
We analysed 469 specimens, in which septal distances of at least one half volution were measured and calculated a simple crowding index by subtracting the mean angular degrees of the last three septa from the mean angular degrees of the last half volution of the phragmocone. Negative values therefore indicate septal crowding. Of these 469 specimens, 62 (13%) show an increase in septal distances; 85 specimens (18%) show an insignificant variation between  $+0.5$  and  $-0.5$  and thus almost no change, while 322 specimens (69%) show a variation of at least  $-0.5$ . This means that, in our material, death was more than five times as frequent in a period of septal approximation. It can be assumed that most of the specimens died during an interval of adverse conditions before reaching their maximum size, which is well known to be larger than in the studied specimens. As will be shown below, there is no obvious relationship between conch size and septal density (Fig. 7), although an ontogenetic decrease in chamber length can be observed in the trajectories of numerous specimens.

Septal crowding at the end of conch growth in ammonoids is a phenomenon that has been known for a long time. Already von Buch (1849, p. 8) stated in his description of *Ceratites nodosus* (Fig. 1): ‘The number of chambers is very considerable; they are very close together,

and more so the closer they come to the end of the whorls, which is common to all ammonites.’ Particularly in the study of ceratitid ammonoids, the idea that the completion of growth is indicated by crowding of the last septa has become entrenched (e.g. Klug et al., 2005; Riedel, 1916; Urlichs, 2006). This does not only apply to Triassic species; already late Permian representatives of the order Ceratitida show septal crowding, together with simultaneous attenuation of sculpture, as a rather reliable mature modification (Korn et al., 2016c). Only the combination of several mature modifications permits to identify maturity in incomplete specimens and the calculation of the maximum conch size (Kiessling et al., 2018).

In Palaeozoic ammonoids, adult modifications are rarer and far less pronounced than in Mesozoic forms. A compilation was given by Davis (1972) and Klug et al. (2015a, 2015b, 2015c); it is striking that the majority of the Palaeozoic examples described have a Permian age. The modifications frequently affected the adult apertural margin of the conchs. However, little is known about the spacing of the septa in these examples.

In Devonian ammonoids, changes in the aperture margin have rarely been recognised. However, two examples (*Wocklumeria*, *Prolobites*) with very conspicuous modifications of the terminal apertural margin have been reported (Ebbighausen & Korn, 2007; Walton et al., 2010). Both are impressive examples of a morphogenetic countdown (Seilacher & Gunji, 1993); the septal crowding is obviously caused by a slowdown of growth at the apertural margin. However, even the earliest ammonoids,



**Fig. 8** Bivariate plots conch parameters and septal spacing (of the last half volution) of all analysed specimens. **A** Conch width index (ww/dm) and septal spaces. **B** Whorl width index (ww/wh) and septal spaces. **C** Whorl expansion rate (WER) and septal spaces

(See figure on next page.)

**Fig. 9** Bivariate plots of conch parameters and septal spacing (of the last half volution) in the Late Tournaisian assemblage of Oued Temertasset (grey background dots represent the entire sample). **A, D, G, J, M** Conch width index (ww/dm) and septal spaces. **B, E, H, K, N** Whorl width index (ww/wh) and septal spaces. **C, F, I, L, O** Whorl expansion rate (WER) and septal spaces. **A–C** Complete assemblage. **D–F** Family Prionoceratidae. **G–I** Family Pericyclidae. **J–L** Family Muensteroceratidae. **M–O** Family Goniatitidae

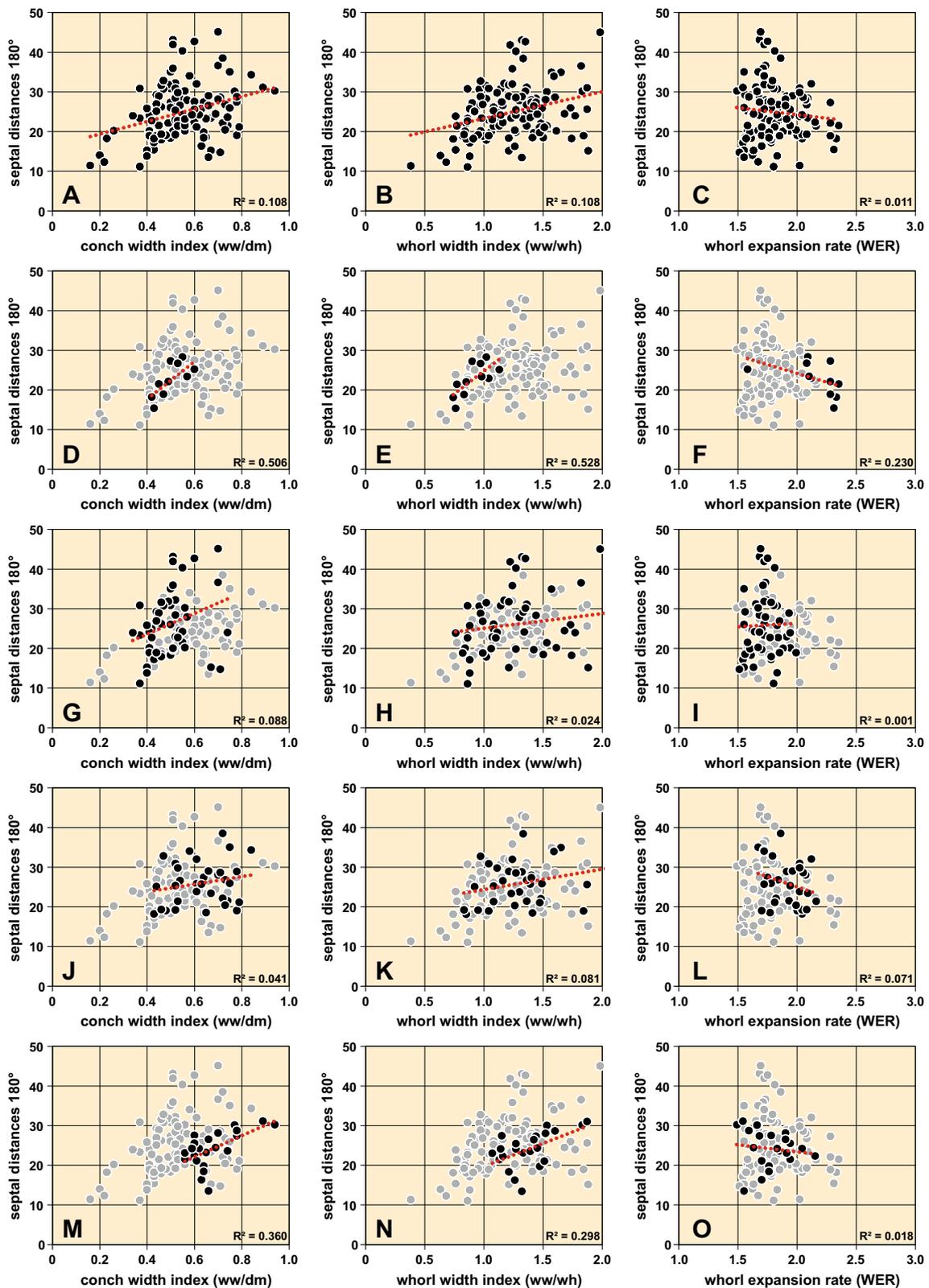
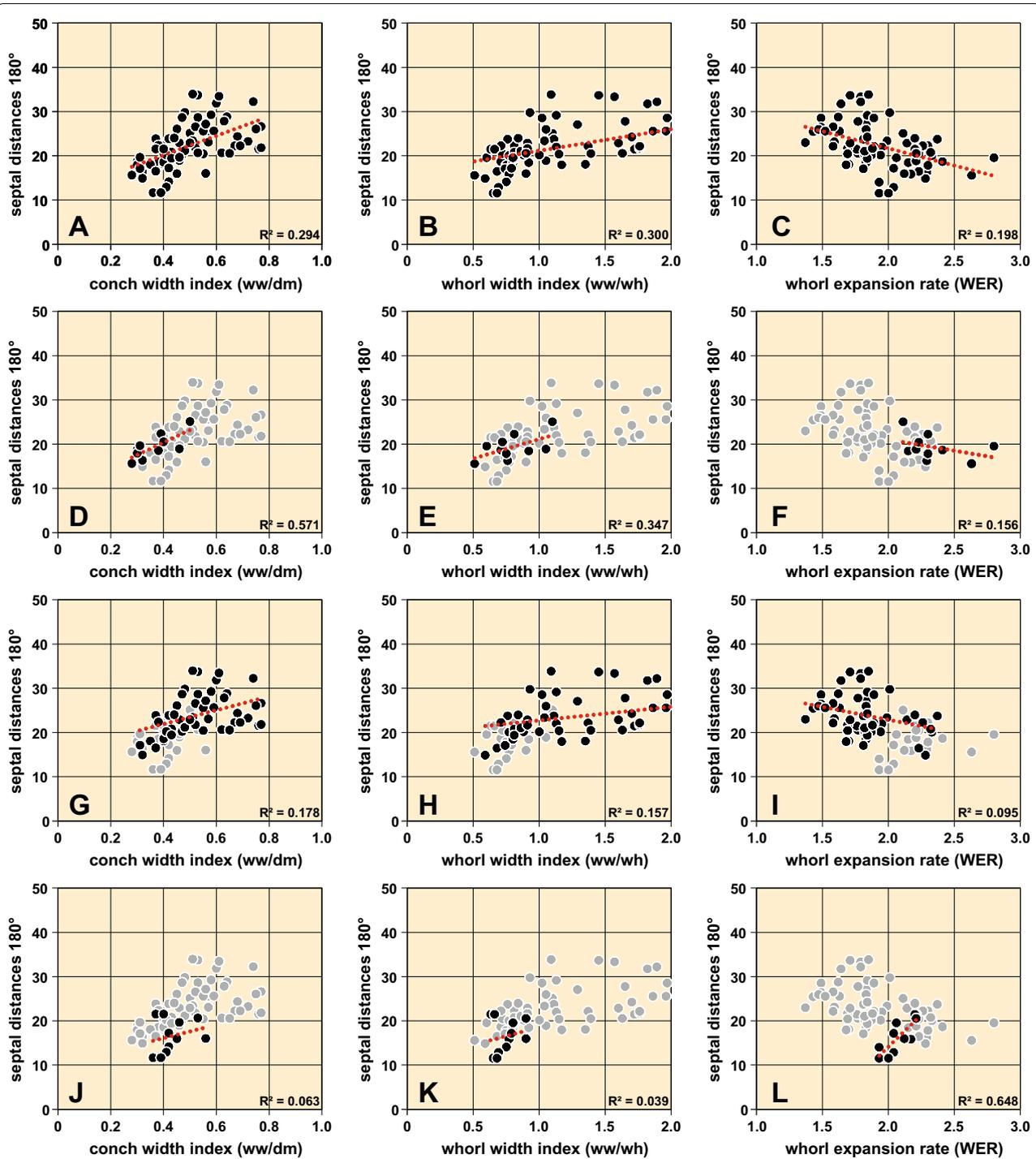
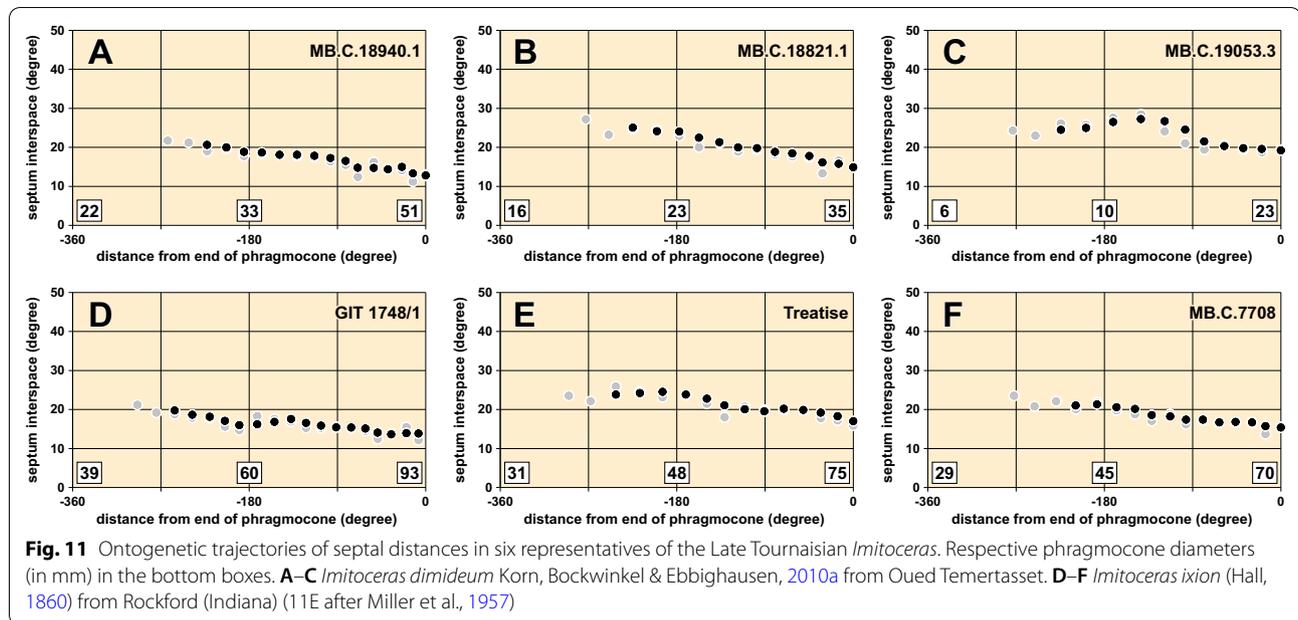


Fig. 9 (See legend on previous page.)



**Fig. 10** Bivariate plots of conch parameters and septal spacing (of the last half volution) in the Late Givetian assemblage of Hassi Nebech (grey background dots represent the entire sample). **A, D, G, J** Conch width index (ww/dm) and septal spaces. **B, E, H, K** Whorl width index (ww/wh) and septal spaces. **C, F, I, L** Whorl expansion rate (WER) and septal spaces. **A–C** Complete assemblage. **D–F** Suborder Gephuroceratina. **G–I** Suborder Gephuroceratina. **J–L** Suborder Tornoceratina



such as anetoceratids, show mature characters, such as loose coiling and umbilical egression (De Baets et al., 2013a, 2013b; Klug et al., 2015b) linked with a small decrease in septal spacing (De Baets et al., 2013b). Umbilical egression also occurs in agoniatitids, which sometimes form strong constrictions at the terminal aperture (Klug, 2001).

*Prolobites* is a pachyconic or globular representative of the middle Famennian prionoceratids. The conchs of the genus are characterised by two deep constrictions; the last has a position close to the terminal aperture and the first exactly one whorl before it and thus more or less below. Complete specimens of *Prolobites* were illustrated by Korn et al. (1984), showing that the ventral shell growth moves away from the whorl spiral after the second constriction. Bogoslovsky (1969) showed longitudinal sections with notable differences in the spacing of septa. While the last whorl of the phragmocone shows very wide spacing of the septa of nearly

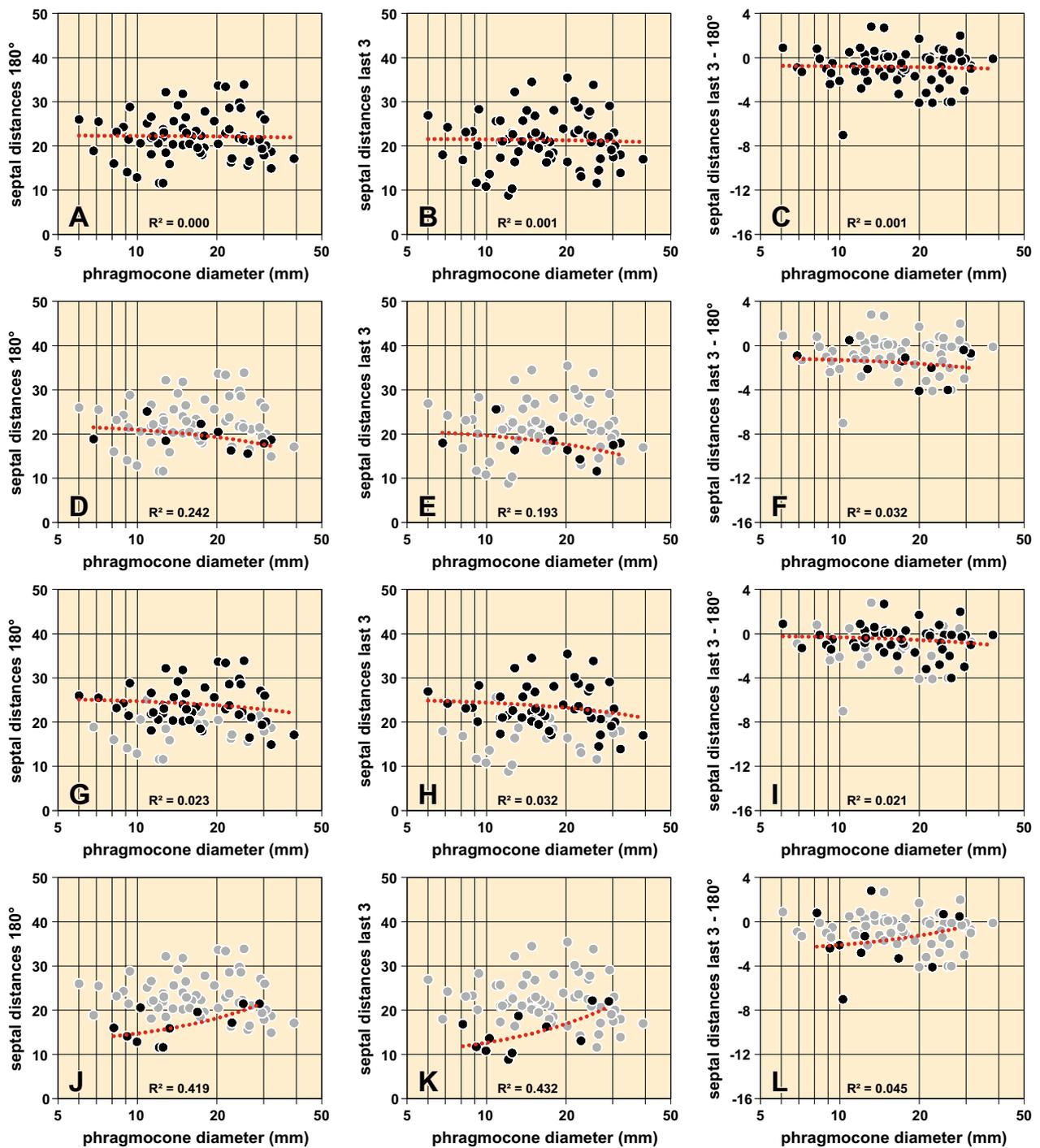
90 angular degrees (assuming that all septa are actually preserved), the septa spacing decreases rapidly to 28° just before the first constriction. The last five septa are finally in the area of the first constriction; they are very crowded with distances of about 7 angular degrees. Walton et al. (2010) discussed the possibility of terminal spawning behaviour of this genus, which might provide rare support for evidence for determinate growth and likely death after spawning (?semelparity) in at least some Palaeozoic ammonoids.

*Wocklumeria* and *Parawocklumeria* belong to the clymeniids (ammonoids with dorsally situated siphuncle) of the late Famennian and also has pachyconic or globular conchs. The inner whorls appear trilobed due to conspicuous constrictions, while the adult whorl is normally coiled in *Wocklumeria*. In *Parawocklumeria* the outer whorl is also three-lobed due to constrictions. Ebbighausen and Korn (2007) showed that very conspicuous crowding of the last septa is visible in both genera, especially in *Wocklumeria*. Similar to *Prolobites*, the last five septa are extremely densely crowded; this occurs in parallel with a very clear simplification in the course of the suture line and a weak migration of the siphuncle towards the whorl centre.

Here we explicitly refrain from calling septal crowding at the end of conch growth ‘adult septal crowding’. This is mainly due to the fact that the specimens under study do not show any additional indicators of maturity, such as changes in the shape of the aperture or sculpture. As will be explained below, intermediate periods of septal crowding are common in the specimens we studied.

	c	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
<i>Discocl., Alpinites</i>	12	33	8	33	17	8	0
<i>Postt., Ebbighausen.</i>	8	38	0	38	25	0	0
<i>Gundolficeras</i>	15	20	13	47	13	7	0
<b>all</b>	<b>35</b>	<b>28</b>	<b>8</b>	<b>39</b>	<b>19</b>	<b>6</b>	<b>0</b>

**Fig. 12** Percentages of the six distinguished groups with different modes of septal distance in the morphologically successive Famennian tornoceratid representatives



**Fig. 13** Bivariate plots of phragmocone diameter and septal distance in the late Givetian assemblage of Hassi Nebech (grey background dots represent the entire sample). **A, D, G, J** Septal spaces of all septa in the last half evolution. **B, E, H, K** septal distances of the last three septa. **C, F, I, L** Difference in the septal spaces of the last three septa all septa in the last half evolution. **A–C** Complete assemblage. **D–F** Suborder Gephuroceratina. **G–I** Suborder Pharciceratina. **J–L** Suborder Tornoceratina

Therefore, it is quite possible that the death of the specimens occurred during any of these periods.

### Septal distances and morphology

Our data set with over 470 specimens measured with respect to septal distance and conch morphology shows a weak correlation ( $R^2=0.173$ ) between the conch width index (whorl width/conch diameter) and the distance of the septa (Fig. 8).

There are rather large differences in the correlation of conch geometry and septal distance between the subsamples. For example, the assemblage from Oued Temertasset shows an  $R^2$  value of 0.108 (Fig. 9) and that from Hassi Nebech even of 0.294 (Fig. 10). Smaller subsamples then give a mixed picture: in the assemblage from Oued Temertasset (Fig. 9), the prionoceratids show the strongest correlation ( $R^2=0.506$ ) and the muensteroceratids the weakest ( $R^2=0.041$ ). In the Hassi Nebech assemblage, the gephuoceratids show the highest correlation ( $R^2=0.571$ ), while the pharciceratids ( $R^2=0.179$ ) and the tornoceratids ( $R^2=0.063$ ) correlate less clearly (Fig. 10). In all cases there is a positive correlation of conch width index and septal distance.

An ontogenetic decrease in septal distances can be observed in the trajectories of numerous specimens. For example, almost all specimens of the Early Carboniferous genus *Imitoceras* (Prionoceratidae, Tornoceratina) show such a reduction in chamber length (Fig. 11).

The representatives of the Tornoceratina are suitable objects for investigating possible correlations between chamber length and the course of the suture line for the following reasons: many representatives of the suborder possess a very similar discoidal conch with a closed umbilicus. In the course of their evolutionary history, many forms retained the conservative conch morphology, while the suture line acquired greater complexity with increasing numbers of lobes and saddles (Korn et al., 2016a, 2016b, 2016c). However, there is no clear trend in the morphological evolution from tornoceratids with simple suture lines (*Gundolficeras*) to those with more complex suture lines (e.g. *Posttornoceras*, *Discoclymenia*); a pronounced covariation between chamber length and suture line complexity probably does not exist (Fig. 12).

Some studies have identified relationships between conch morphology and septal spacing. Such a dependence was suggested by Bucher et al. (1996); they saw the greater variability of ammonoid morphology, when

compared to *Nautilus*, as an indication of more variable septal spacing in ammonoids. A sudden increase in septal spacing was found in various ammonoids at the beginning of the neanoconch (Arai & Wani, 2012; Bucher et al., 1996; Kulicki, 1974), followed by a decrease at the end of the neanoconch. Matyja and Wierzbowski (2000) found a correlation of ornamentation and septal spacing, where tighter septal spacing correlates with irregular ornamentation. Saunders (1995) postulated that forms with thicker shells have fewer septa, while De Baets et al. (2015b) hypothesised that evolute forms have larger septal spacing than involute forms. This might partially depend on the method how septal spacing is measured.

Furthermore, several researchers associated crowded septal spacing with growth changes (Naglik et al., 2015). Growth spurts (Bucher et al., 1996), rhythmic slowing down of growth (Hoffmann & Keupp, 2015), rhythmically changing speed of secretion with growth interruptions (Kraft et al., 2008) and slower accretion at the aperture (Korn & Titus, 2006) were listed as causes of septal crowding.

### Septal distances and ontogeny

For the analysis of ontogenetic changes in septal density, we took three steps:

#### Analysis of the entire data set

The bivariate plot of phragmocone diameter and septal spacing (on the last half whorl) of all analysed specimens shows no evidence of a significant decrease in septal spacing with increasing size (Fig. 7), at least between 10 and 30 mm conch diameter, a size interval in which most of the examined specimens belong.

#### Analysis of smaller subsamples

A decrease of septal distances with larger size can also not be recognised when looking at smaller samples, e.g. the assemblages of Hassi Nebech (Fig. 13) and Oued Temertasset (Fig. 14). Even when smaller taxonomic units, such as subfamilies or genera, are considered individually, no universal pattern can be discerned that would indicate a reduction in septal distances during ontogeny, although an ontogenetic trend towards shorter septal distances occurs in several of the subsamples. The study of 40 specimens of *Pseudoproboloceras nebechense* from Hassi Nebech also showed that septal spacing remains constant between 10 and 30 mm conch diameter (Fig. 15).

(See figure on next page.)

**Fig. 14** Bivariate plots of phragmocone diameter and septal distance in the Late Tournaisian assemblage of Oued Temertasset (grey background dots represent the entire sample). **A, D, G, J, M** Septal spaces of all septa in the last half volution. **B, E, H, K, N** Septal spaces of the last three septa. **C, F, I, L, O** Difference in the septal distances of the last three septa all septa in the last half volution. **A–C** Complete assemblage. **D–F** Family Prionoceratidae. **G–I** Family Pericyclidae. **J–L** Family Muensteroceratidae. **M–O** Family Goniatitidae

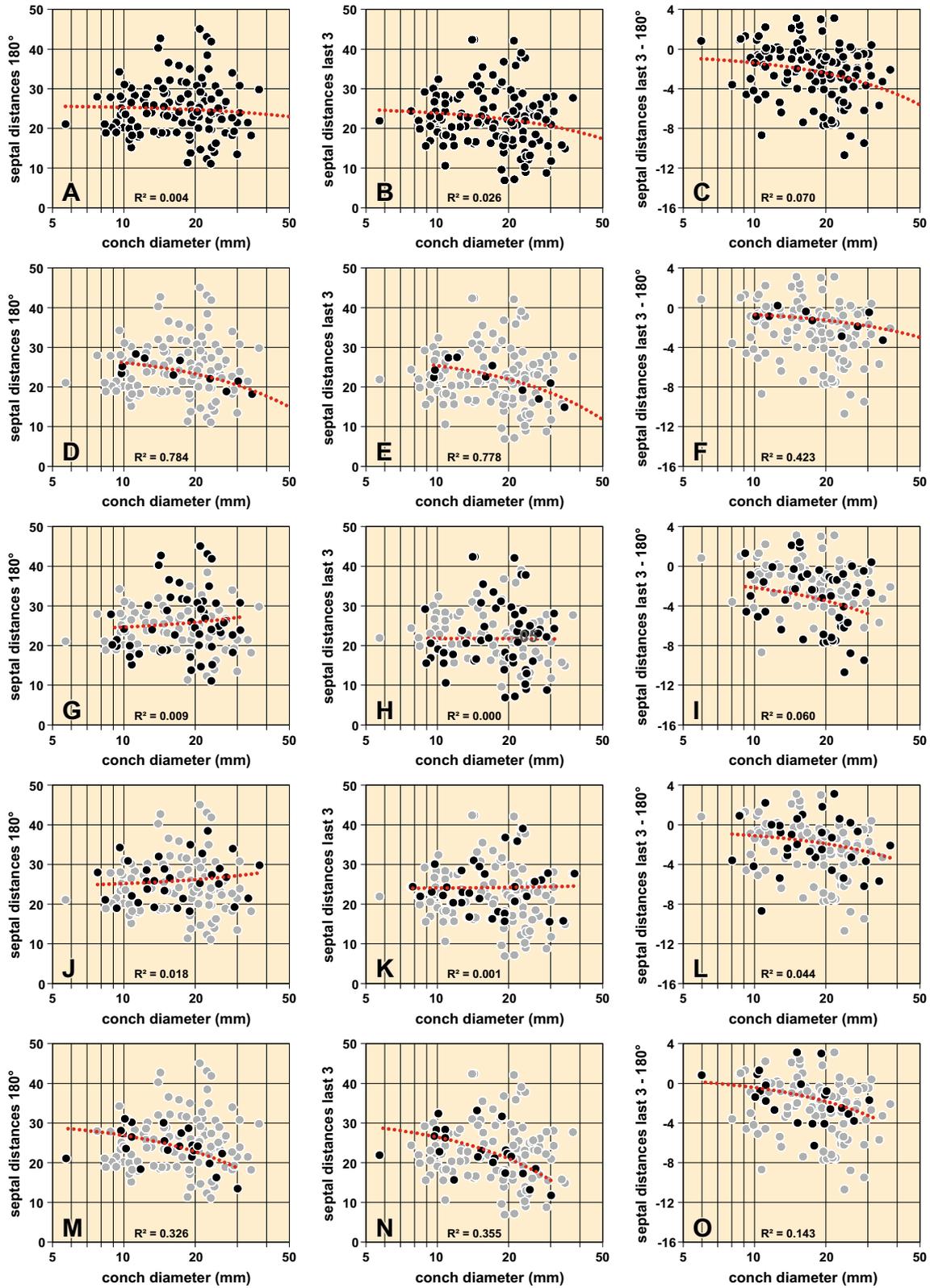
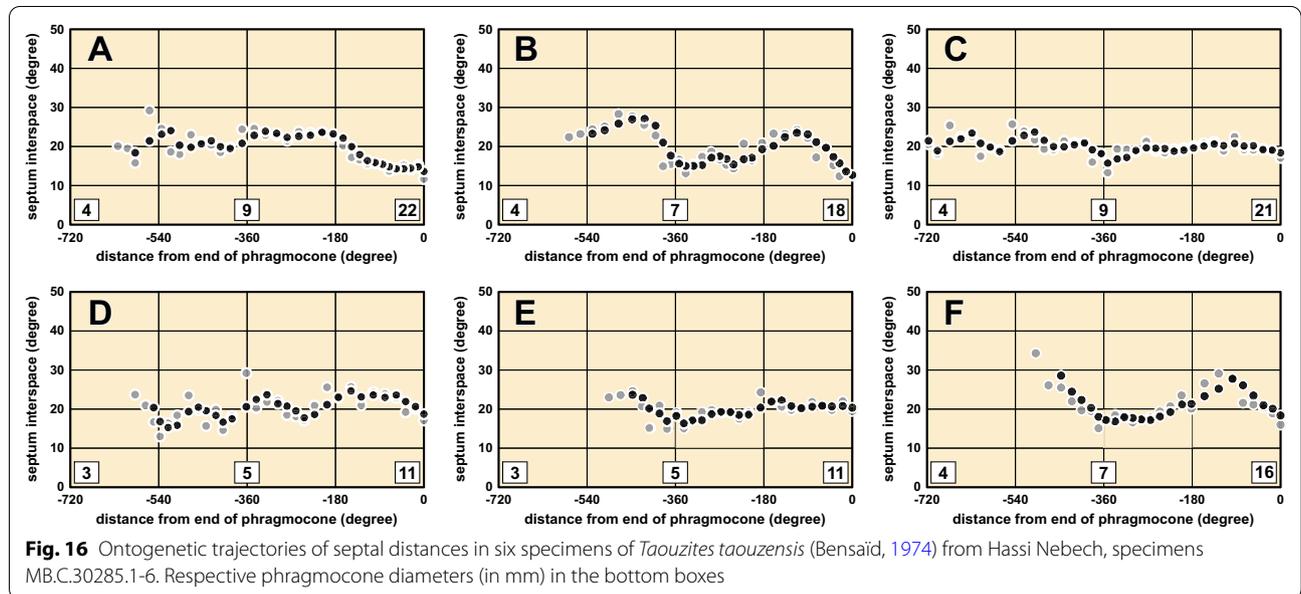
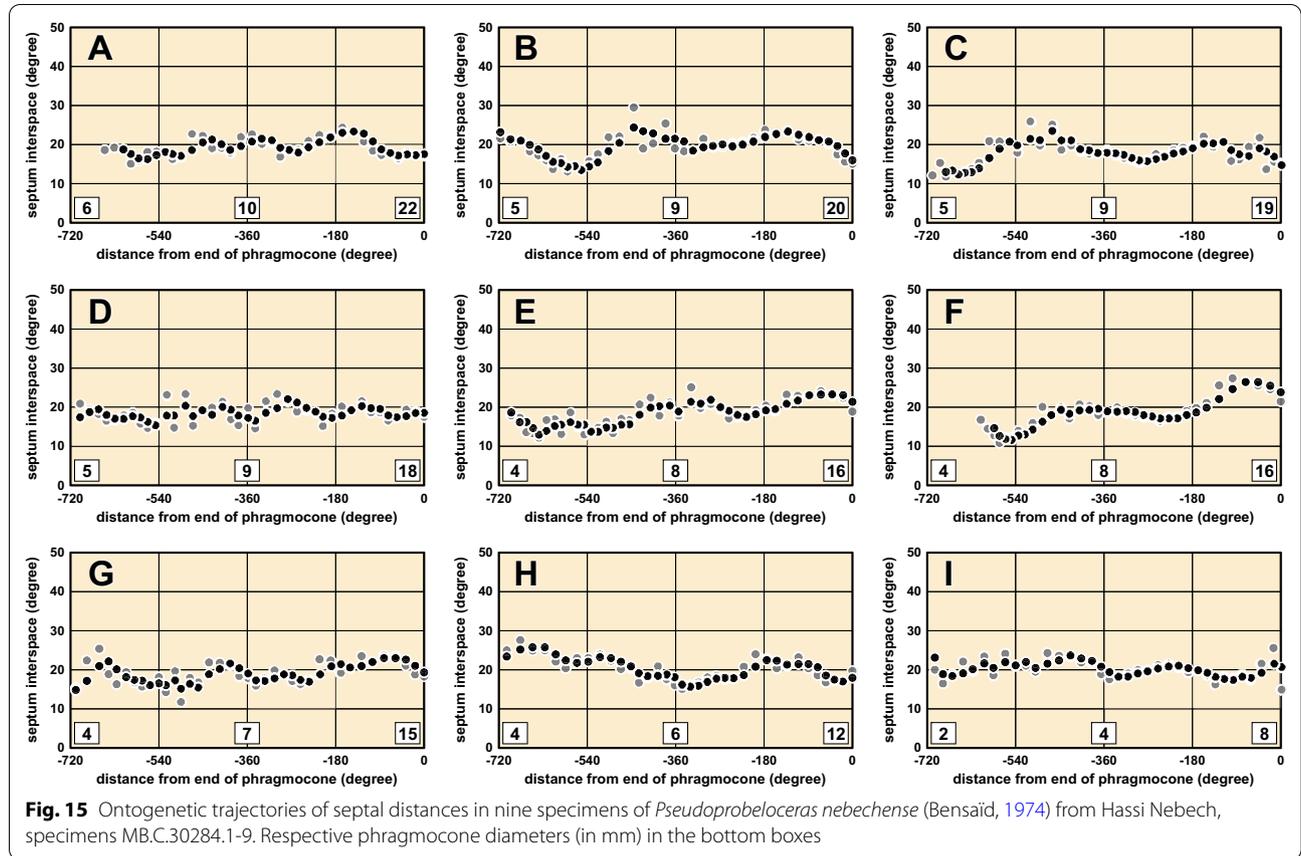


Fig. 14 (See legend on previous page.)



**Analysis on the specimen level**

A general decrease in septal distances is not evident in the individual ontogenetic trajectories of the septum

distances in *P. nebechense* (Fig. 15). Almost all of the examined specimens show conspicuously wavy trajectories but maintain stable values of septal distance. The

oscillation is in the range of about five angular degrees and the wavelength is often about  $180^\circ$  (Fig. 15). The undulating trajectories also indicate that the specimens in question experienced three to five intervals of septal displacement during the formation of two whorls, only the last of which was either fatal itself or paralleled possibly maturity and (subsequent) death of the animal.

Another species of Hassi Nebech, *Taouzites taouzensis*, shows overall similar trajectories, but differs from *P. nebechense* in the sometimes much stronger oscillation of up to about  $15^\circ$  (Fig. 16).

It has long been known that septal spacing in ammonoids changes during ontogeny. von Buch (1832, p. 153) already stated: 'The number of chambers increases with age in all ammonites.' Several studies (e.g. Arai & Wani, 2012; Bucher et al., 1996; Iwasaki et al., 2020; Kraft et al., 2008; Landman, 1987; Zell & Stinnesbeck, 2016) showed a distinct ontogenetic pattern in the septal distance in ammonoids. Apart from a partly significant decrease of the angular degree at the end of the neanic stage, all specimens show an oscillating pattern in the trajectories.

### Septal distances and phylogeny

The extensive material allowed to study possible differences in chamber length among the suborders Gephuroceratina, Pharciceratina, Tornoceratina, Goniatitina and Prolecanitina. This led to the result that these taxonomic units differ only slightly in the proportions of the distinguished modes of septal spacing; the percentage of group 1 (with rather stable septal distance) varies between 20 and 30 and the percentage of group 3 (with reduction of septal distances throughout the last whorl ending in septal crowding) between 30 and 40. Only the suborder Pharciceratina differs from the others in a higher percentage of group 6 with regular oscillations of septal distances (Fig. 6). The strongly deviating percentages of the clymeniids was possibly caused by sampling effects; due to the mostly fragmentary preservation of many species, particularly those with widely umbilicate conchs that have a lower preservation potential, the data set was therefore excluded from more detailed analyses.

To clarify possible within-clade variation, we have subdivided the long-lived subfamilies Prionoceratinae and Acutimitoceratinae into four temporal units, from bottom to top middle Famennian, late Famennian, early Tournaisian and late Tournaisian (Figs. 17, 18). All species of these subfamilies share a similar adult globular involute conch

shape with a closed umbilicus (compare Korn 2010); they differ in the width of the conchs and in the expansion of the whorls. Normally, these two characteristics display covariation: slender conchs tend to have higher apertures and thus higher coiling rates. The analysis shows an increase in correlation over evolutionary history: the dependence of septal distances on conch shape increases significantly in the Prionoceratinae between the middle Famennian and late Tournaisian, from  $R^2=0.035$  to  $R^2=0.506$ .

In parallel, the correlation of the coiling rate (whorl expansion rate) with the septal distances also increases (from  $R^2=0.001$  to  $R^2=0.528$ ). Here the correlation is negative; a higher coiling rate is correlated with lower septal distances. However, this pattern can be explained by the fact that, as in many ammonoids, there is a correlation between conch width and coiling rate; more slender forms tend to have higher apertures and thus higher coiling rates.

### Septal distances and environment

The vast majority of the studied specimens originate from shale formations and therefore represent a perhaps low-oxygenated area of the shelf seas. All specimens from North Africa are preserved as limonite or haematite internal moulds. Thanks to this preservation, it was possible to study such a large number of specimens without time-consuming preparation. However, a possible disadvantage of this material could therefore be that the animals have not been exposed to normal marine oxygen conditions during their lifetime and therefore show special patterns in the septal formation that deviate from the normal case (e.g. Clausen, 1969).

To test for such a possible divergence, we examined and compared morphologically similar time-equivalent species of the genus *Imitoceras* from the Argiles de Teguentour of Oued Temertasset and the Rockford Limestone of Indiana. The material from the two formations differs in the size of the specimens; while the diameters of the phragmocones of *I. ixion* from the Rockford Limestone range from 60 to 95 mm, the specimens of *I. dimideum* from the Argiles de Teguentour rarely reach 50 mm. However, these size differences are not reflected in the ontogenetic trajectories of septal distance; the majority of specimens show quite little variation during ontogeny. A common feature is the mostly almost continuous decrease in septal spacing and the weakly undulating course of the trajectories (Fig. 11).

(See figure on next page.)

**Fig. 17** Bivariate plots of conch parameters and septal spacing (of the last half volution) in the family Prionoceratidae (grey background dots represent the entire sample). **A, D, G, J, M** Conch width index (ww/dm) and septal spaces. **B, E, H, K, N** Whorl width index (ww/wh) and septal spaces. **C, F, I, L, O** Whorl expansion rate (WER) and septal spaces. **A–C** All representatives. **D–F** Late Tournaisian assemblage. **G–I** Early Tournaisian assemblage. **J–L** Late Famennian assemblage. **M–O** Middle Famennian assemblage

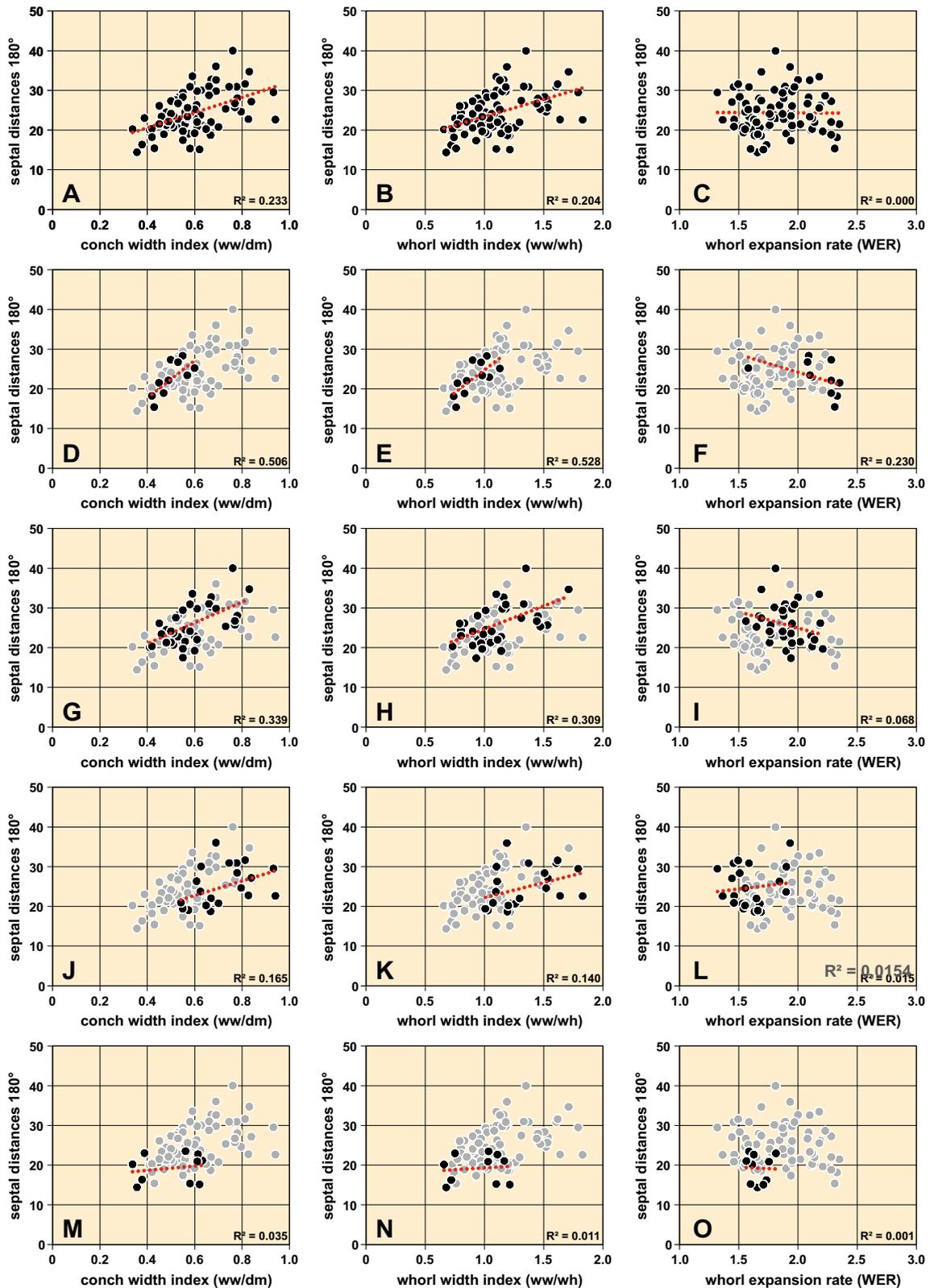


Fig. 17 (See legend on previous page.)

	c	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Late Tournaisian	14	36	7	50	7	0	0
Early Tournaisian	42	24	12	24	12	7	14
Late Famennian	22	27	14	32	18	0	0
Middle Famennian	11	9	9	73	9	0	0
<b>all</b>	<b>88</b>	<b>25</b>	<b>11</b>	<b>35</b>	<b>13</b>	<b>3</b>	<b>7</b>

**Fig. 18** Percentages of the six distinguished groups with different modes of septal distance in the stratigraphically successive assemblages containing the family Prionoceratidae

At least the comparison of these two samples does not indicate a dependence of the lithofacies of the embedded ammonoids and their chamber length; the ammonoids from the well-oxygenated Rockford Limestone do not differ from those from the possibly less-oxygenated Argiles de Teguentour. This could indicate that both lithofacies provided similar environmental conditions for the ammonoids, at least at times.

## Conclusions

The phenomenon of varying septal distances (i.e. varying length of phragmocone chambers measured in angular degrees) in ammonoids is known for a long time and has already been explained by a number of hypotheses. Both internal factors (changes in conch shape and ornament, changes in lifestyle, pathologies) and external factors (change in the environment, predation pressure) or a combination of both have been taken into account. We measured and analysed the septal distances of about 620 ammonoid specimens of the late Givetian (Middle Devonian) to the latest Viséan (Early Carboniferous) with respect to the various postulated reasons for the variation of septal distances.

Chamber length and conch morphology only show a weak correlation between the whorl width/ conch diameter ratio and the distance of the septa. Specimens with stouter conchs tend to have wider septal distances. The analysis of possible influences (differences in morphology, ontogeny and phylogenetic position) on chamber length in ammonoids showed only little correlation. Neither phylogenetic affiliation nor differences in conch shape and the course of the suture line can be held responsible for the striking ontogenetic changes in the length of the phragmocone chambers. It is therefore doubtful that morphological differences directly or indirectly controlled the distance between the septa.

Changes in spacing between septa are not considered here as direct active responses of the animal to changes in its conch geometry, disturbances in the availability of food

and oxygen, changes in life habit as well as injuries and pathologies. Rather, we present here the hypothesis that the formation of septa is a passive process subject to a temporal mode. According to this, new septa were secreted at more or less regular temporal intervals and not correlated with the pace of shell growth at the aperture. This means that any disturbance, slowing or interruption of shell growth at the aperture, whether caused by the formation of coarse ornamentation, injury, adverse environmental conditions or advanced age of the individual, will result in the crowding of septa. This means that septal spacing was influenced by environmental change, but only indirectly via growth change at the aperture and thus body chamber growth.

The fact that many specimens of ammonoids show crowded septa in front of the body chamber can only partly be interpreted as a mature character. Septal crowding is insufficient to identify maturity in the absence of other mature modifications. Mature growth is only documented when other features, like conch size, changes in the shape of the aperture, modifications of the sculpture, growth line strength and spacing, or umbilical width, are present in parallel. Our study showed that considerable fluctuations in septal spacing were evident in the majority of specimens (about 65%) and that intermediate septal crowding was very common. It is likely that individuals frequently recovered from these episodic disturbances and returned to normal septal spacing. However, many individuals may also have died during such periods, sometime before reaching the final size of the conch.

Consequently, the great abundance of irregularities in septal spacing documents fluctuations in apertural conch growth. Septal spacing had to follow to maintain neutral buoyancy. Irregular septal spacing indirectly reflects adverse conditions, which influenced the rate of shell formation at the aperture. Consequently, it is conceivable that the higher metabolism, which was proposed for ammonoids compared to nautiloids (Jacobs & Landman, 1993; Tajika et al., 2020), could indeed have altered shell secretion at the aperture with the consequent changes in septal spacing.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13358-021-00235-x>.

**Additional file 1:** Complete list of all specimens with their taxonomic classification and data on septal distances.

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**Authors' contributions**

SMB and DK designed the study and collected the data. All the authors contributed to interpretations and wrote parts of the text and proofread various versions of the text. All the authors read and approved the final manuscript.

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**Availability of data and materials**

A complete data sheet is added in Additional file 1.

**Declarations****Competing interests**

The authors have no competing interests.

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