Swiss J Palaeontol (2016) 135:109–124
DOI 10.1007/s13358-015-0095-9

The internal structure of varices and constrictions in Jurassic and Cretaceous ammonoid shells

Gregor Radtke[1] **· Helmut Keupp**[1]

Received: 25 February 2015 / Accepted: 8 July 2015 / Published online: 29 September 2015

Abstract The structure of pristine preserved shells of Jurassic and Cretaceous ammonoids was examined to identify whether the character states of varices and constrictions are homologous or homoplasic traits. The internal structure of varices and constrictions of phylloceratids, lytoceratids, perisphinctids and desmoceratids shows no interruptions in shell growth which implies that varices and constrictions were formed by continuous secretion. Their internal thickenings are formed by the nacre layer, while the inner prismatic layer thins to compensate the internal relief. The corresponding surface relief, e.g. furrows or ridges, is formed by undulation of a continuous outer prismatic layer, similar to the way common ribs are formed. The absence of an interruption in shell secretion is different from the well-examined nepionic constriction of the ammonitella. However, a delayed secretion of inner nacreous portions which are responsible for the actual thickening of varices and constrictions is characterized by "internal interruptions"; only the most inner nacreous portions seem to continue shell growth. The nacreous thickening is secreted subsequent to the formation of a distinct peristome, e.g. furrows, ridges or flares, i.e. not at the same time the peristome is formed. The thickening of varices and constrictions does not narrow an (interimistic) aperture and does not represent a halt in growth. However, certain areas of the shell (e.g. furrows, ridges, flares) are reinforced by this process. Morphological transition from smooth shelled varices to ridged and constricted habitus within phylloceratids and desmoceratids prove to be a homology. Owing to the general structural conformity of varices and constrictions in shells of Jurassic and Cretaceous taxa, we support the theory that they are homologous traits.

Keywords Ammonoid · Shell structure · Constrictions · Varices · Nepionic constriction

Introduction

Varices and constrictions are conspicuous and more or less radial, internal thickenings (Fig. 1a, b) and flexures (Fig. 1a, c) of the shell wall occurring in a great number of ammonoid groups. Also, ridges and flares are accompanied by varix-like thickenings. Number, orientation (e.g. rectiradiate, prorsiradiate), outline (e.g. linear, concave, sigmoid) and periodicity (e.g. regular, irregular, terminal) of varices and constrictions vary greatly. Varices and constrictions are found in nearly all orders of ammonoids (Clymeniina, Anarcestina, Tornoceratina, Goniatitina, Ceratitina, Phylloceratina, Ammonitina including Lytoceratoidea) at different taxonomic levels with a variety of habitus in each taxon (see Arkell et al. 1957; Radtke 2012). For example, within order Clymeniina, superfamily Desmoceratoidea, family Desmoceratidae, Phylloceratidae or the genus *Prinoceras* varices as well as constrictions can be possible. Owing to the general appearance, the question is whether these structures are homologous or homoplasic traits at levels of different orders (e.g. Clymeniina × Phylloceratina), superfamilies (e.g. Desmoceratoidea × Perisphinctoidea), families (e.g. Desmoceratidae × Silestidae) or genera (e.g. *Calliphylloceras* × *Holcophylloceras*). A

✉ Gregor Radtke
gradtke@zedat.fu-berlin.de

[1] Department of Earth Sciences, Institute of Geological Sciences, Branch Palaeontology, Freie Universität Berlin, Malteteserstraße, 74-100, Building D, 12249 Berlin, Germany

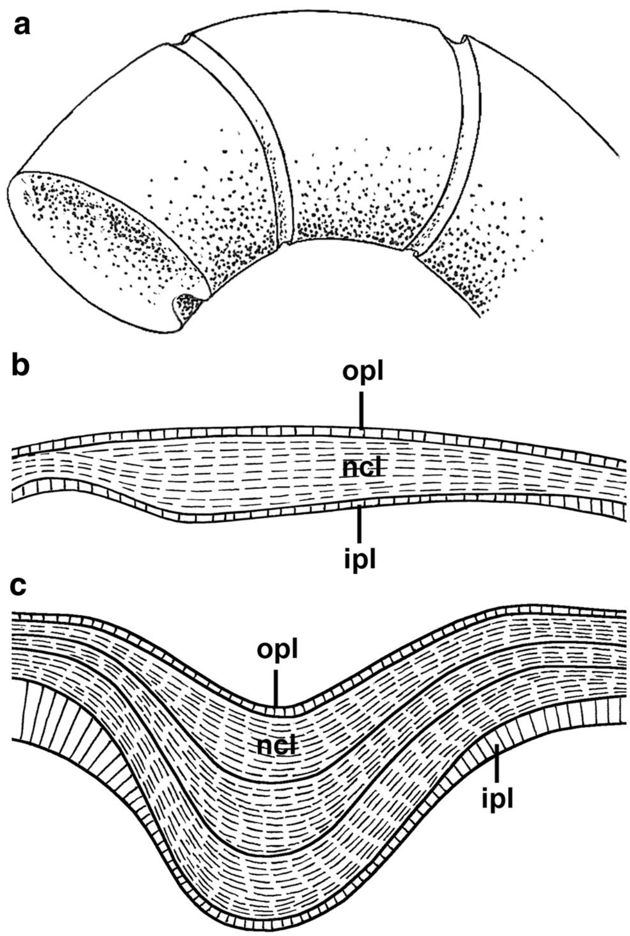


Fig. 1 General appearance of varices and constrictions (*growth direction left*). **a** Varices and constrictions leave furrow imprints on the internal mould. **b** Varices are formed by internal thickenings of the shell while shell surface remains smooth. **c** Constrictions are formed by flexures of the shell, often they are accompanied by an internal thickening. *ipl* inner prismatic layer, *ncl* nacre layer, *opl* outer prismatic layer

major problem is the isolated occurrence of varices and constrictions within ammonoid evolution, i.e. the single varix and constriction bearing taxa are not adequately connected by transitional forms. In some genera and species, the formation is even optional (*Archoceras, Cheiloceras, Lytoceras, Parandiceras*). Generally, there are more taxa without varices or constrictions than such taxa bearing these structures. Within Jurassic and Cretaceous ammonoids, varices and constrictions occur in Phylloceratoidea, Lytoceratoidea, Perisphinctoidea and Desmoceratoidea (Fig. 2). Whereas varices and constrictions are restricted to selected taxa, all ammonoids develop a nepionic constriction with a nacreous primary varix at the end of the ammonitella, associated with an interruption in shell secretion due to withdrawal of the shell secreting mantle edge (Birkelund 1967, 1980; Birkelund and Hansen 1968, 1974; Erben 1964, 1966; Erben et al. 1968, 1969; Howarth 1975; Kulicki 1974, 1979, 1996; Kennedy and Cobban 1976; Lehman 1976; Drushits and Doguzhaeva 1981; Doguzhaeva and Mikhailova 1982; Bandel 1986; Landman 1987; Kulicki and Doguzhaeva 1994; Keupp 2000; Sprey 2002; Tanabe et al. 2008; Doguzhaeva et al. 2010). Former observations mention a comparable thickening of the nacre layer within several phylloceratid, lytoceratid and desmoceratid varices and constrictions (Drushits and Khiami 1970; Drushits and Doguzhaeva 1974, 1981; Birkelund and Hansen 1974; Birkelund 1980; Bucher et al. 1996; Keupp 2008). This seems to apply to perisphinctid constrictions as well (Checa 1994). Furthermore, Checa (1994) assumes an interruption of shell growth subsequent to nacreous thickening in the area of the constrictions.

Within this study, we investigated the internal structure of varices (smooth, ridged, flared) and constrictions to identify a bauplan that may exist for Jurassic and Cretaceous taxa which would support a homologous origin of the previously mentioned shell structures. We investigated whether there are characteristics in the internal structure which are related to the habitus or taxon. For example, does the internal structure of constrictions indicate resorption, explaining the sculptural intersection often observed (see Arkell et al. 1957; Checa and Westermann 1989; Seilacher and Gunji 1993; Checa 1994; Bucher et al. 1996; Bucher 1997), or withdrawal of the mantle? Owing to the broad taxonomic distribution, the idea of the nepionic constriction and its primary varix as possible primary bauplan for every type of varix and/or constriction is discussed.

Materials and methods

Material

The present study is based on 41 well-preserved ammonite shells of different Phylloceratoidea, Lytoceratoidea, Hildoceratoidea, Perisphinctoidea and Desmoceratoidea from four localities in Germany, Madagascar and Japan (Table 1). The material was provided by H. Keupp (FU Berlin), G. Schweigert (SMN Stuttgart) and Y. Hikida (NMNH Nakagawa) and is housed in the Bavarian State Collection Munich (coll. H. Keupp). Specimens originate from Heiningen, (Baden-Württemberg, SW–Germany, Lower Aalenian, Jurassic), the Sakaraha area (Morondava Basin, SW–Madagascar, Upper Oxfordian, Jurassic), the Ambatolafia area (Mahajanga Basin, Central Madagascar, Lower Albian, Cretaceous) and the Teshionakagawa area (Hokkaido, Japan, Lower Campanian, Cretaceous). According to Cochran et al. (2010), the examined shell material has a predominantly aragonitic preservation of a good (PI = 3) to fair (PI = 2) state. In most specimens, only the chambered shell portions (phragmocone) are

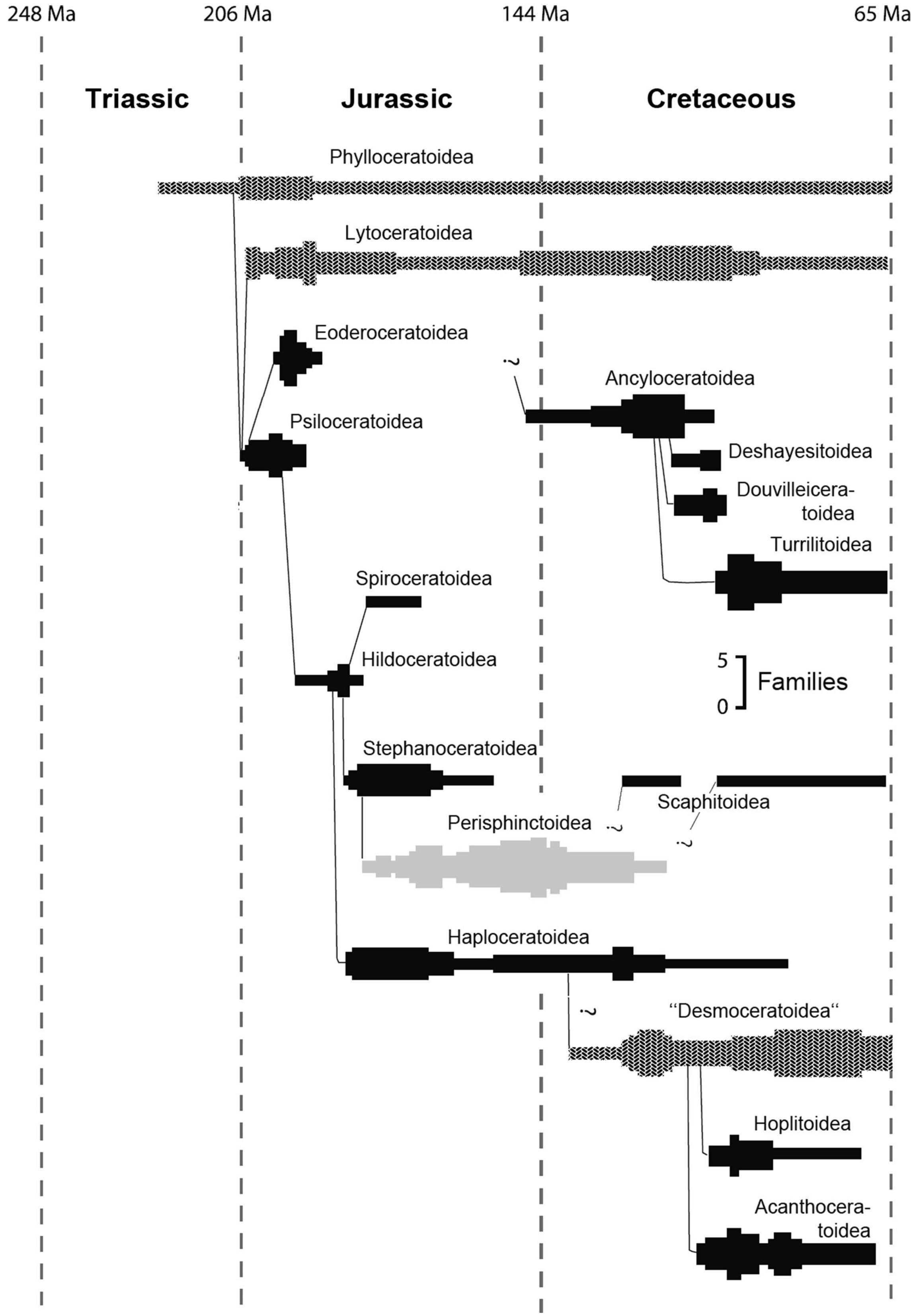


Fig. 2 Occurrence of pre-adult varices and constrictions in ammonoids in the Jurassic and Cretaceous (modified from Rouget et al. 2004). *Grey* superfamilies with constrictions. *Black-and-white pattern* superfamilies with varices and constrictions

Table 1 Taxa of the studied ammonites

Taxon	Collection no.	Locality	Age	Diameter (mm)	Type of observed structure	No. of observed structures
Phylloceratoidea						
Ptychophylloceras cf. *dacquei*	MAn-4514	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	40	V → RV	10
Ptychophylloceras cf. *dacquei*	MAn-4515	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	40	V → RV	15
Ptychophylloceras cf. *dacquei*	MAn-4516	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	40	V → RV	19
Calliphylloceras sp.	MAn-4511	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	21	V	12
Calliphylloceras sp.	MAn-4511	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	52	V	20
Holcophylloceras sp.	MAn-4510	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	41	V → C	16
Euphylloceras cf. *velledae*	MAo-1770	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	28	V	5
Euphylloceras sp.	MAo-1769	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	30	V	23
Phyllopachyceras sp.	MAo-1771	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	22	NC, V	12
Lytoceratoidea						
Eotetragonites umbilicostriatus	MAo-1773	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	36	V, DV	24
Eotetragonites umbilicostriatus	MAo-1774	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	39	V	18
Eotetragonites umbilicostriatus	MAo-1775	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	22	NC, V	17
Eotetragonites umbilicostriatus	MAo-1776	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	30	NC, V, FV	24
Tetragonites popentensis	MAo-1798	Teshionakagawa area, Hokkaido	Lower Campanian, Cretaceous	25	NC, V	5
Hildoceratoidea						
Leioceras opalinum	MAn-4518	Heiningen, SW–Germany	Lower Aalenian, Jurassic	27	NC	–
Perisphinctoidea						
Perisphinctidae indet	MAn-4501	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	19	C	5
Kranaosphinctes sp.	MAn-4500	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	26	NC, C	4
Divisosphinctes besairiei	PA-10151b	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	94	C	8
Divisosphinctes sp.	MAn-4498	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	23	C	6
Divisosphinctes sp.	MAn-4499	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	73	C	8
Epaspidoceras jeanneti	MAn-4505	Sakaraha area, SW–Madagascar	Upper Oxfordian, Jurassic	31	NC	–
Desmoceratoidea						
Desmoceras latidorsatum	MAo-1781	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	35	RV	6
Desmoceras latidorsatum	MAo-1782	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	33	RV	7

Table 1 continued

Taxon	Collection no.	Locality	Age	Diameter (mm)	Type of observed structure	No. of observed structures
Desmoceras latidorsatum	MAo-1783	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	34	RV	6
Desmoceras latidorsatum	MAo-1784	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	34	RV	6
Desmoceras latidorsatum	MAo-1785	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	35	NC, RV	17
Desmoceras latidorsatum	MAo-1786	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	35	RV	14
Desmoceras latidorsatum	MAo-1787	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	18	NC, RV	16
Desmoceras latidorsatum	MAo-1788	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	38	NC, RV	23
Puzosia saintoursi	MAo-1792	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	38	C	15
Puzosia saintoursi	MAo-1793	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	18	C	8
Puzosia saintoursi	MAo-1794	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	87	RV	12
Puzosia saintoursi	MAo-1795	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	35	C	4
Puzosia saintoursi	MAo-1796	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	–	C	8
Puzosia saintoursi	MAo-1797	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	52	C	20
Umsinenoceras linguatuberculatum	MAo-1791	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	18	C	3
Neosilesites ambatolafrensis	MAo-1780	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	23	C	10
Neosilesites sp.	MAo-1777	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	–	C	3
Neosilesites sp.	MAo-1778	Ambatolafia area, Central Madagascar	Lower Albian, Cretaceous	18	RV, C	7
Canadoceras kossmati	MAo-1799	Teshionakagawa area, Hokkaido	Lower Campanian, Cretaceous	49	V → C	19
Menuites sp.	MAo-1800	Teshionakagawa area, Hokkaido	Lower Campanian, Cretaceous	40	V → C	8

C constriction, *DV* discontinuous varix, *FV* flared varix, *NE* nepionic constriction, *RV* ridged varix, *V* varix

preserved, some specimens preserve parts of the living chamber. The last shell chambers are filled with fine or coarse, compact sediment; the remaining chambers are partial or completely filled by drusy calcite.

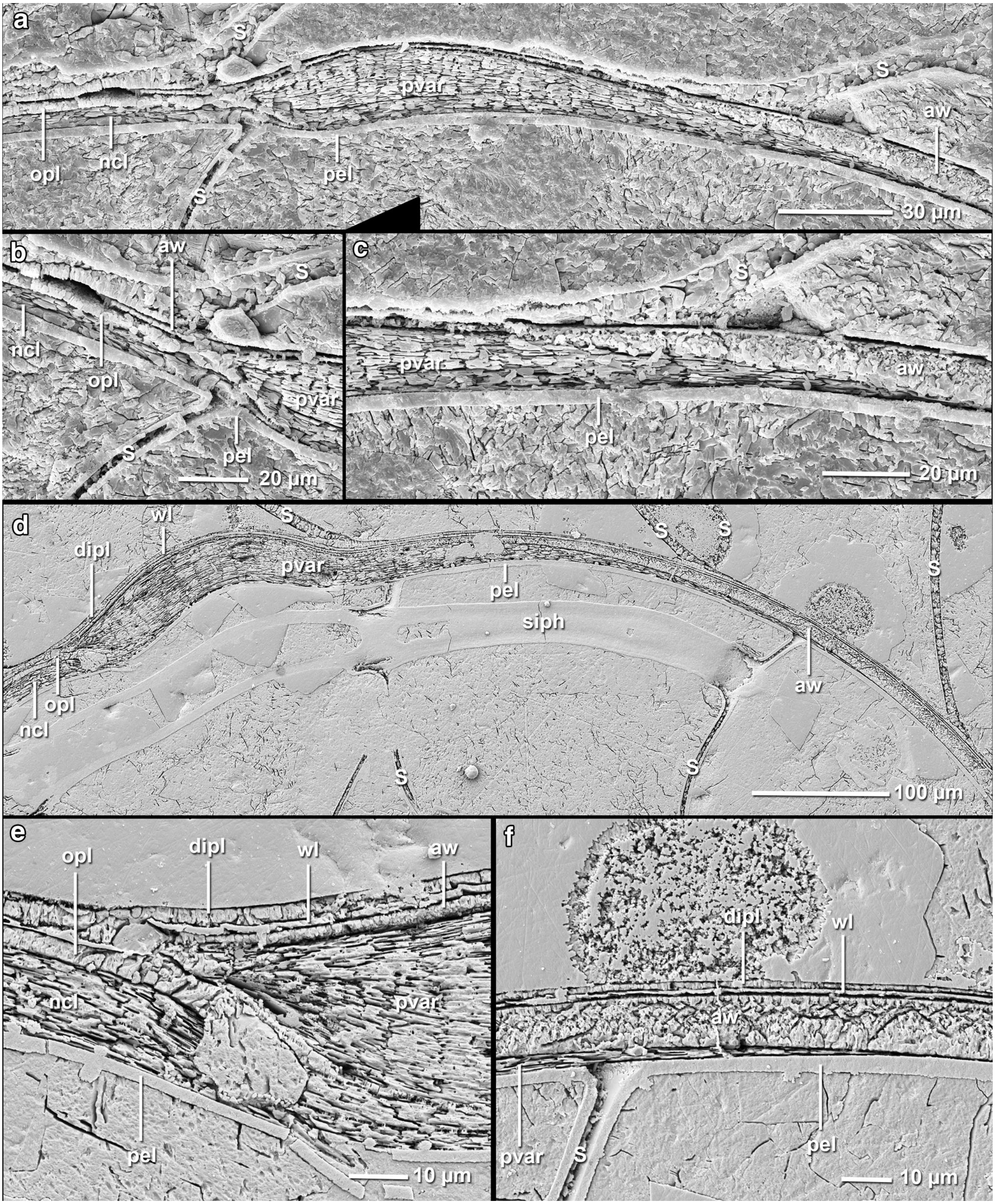
Methods

Fresh broken pieces and etched section were prepared for study. Etched sections were polished with aluminium oxide and afterward treated with 10 % formic acid for 5–10 s. All samples were fixed on aluminium stubs with conductive carbon glue and sputtered with gold. They were observed and photographed by means of the scanning electron microscope (Type: Zeiss SUPRA 40VP) of the paleontological section of the FU Berlin.

Observations

Shell wall structure

In all taxa, the ventral and lateral shell wall consists of three aragonitic shell layers: the outer prismatic layer (opl), the nacre layer (ncl) and the inner prismatic layer (ipl). Outer and inner layers are formed by parallel arranged prisms. The middle nacre layer is formed by stacks of hexagonal



aragonite plates. The thickness of these layers can vary greatly within individual taxa; in particular, the members of the Perisphinctoidea seem to reduce the prismatic layers in the outer whorls. The shell of the larval ammonitella is made of (sub-) prismatic material (aw) and forms nacre only at its end, the primary varix (pvar) of the nepionic constriction.

◀**Fig. 3** Internal structure of the nepionic constriction and its primary varix (*growth direction left*). **a–c** *Phyllopachyceras* sp. (MAo-1771), **a** nepionic constriction and its primary varix, the post-nepionic shell (opl and ncl) is attached to its adoral end; **b** close-up of **a**, discontinuity of the nepionic constriction; **c** close-up of **a**, first appearance of the nacreous material which forms the primary varix. **d–f** *Eotetragonites umbilicostriatus* COLLIGNON (MAo-1773), **d** untypical nepionic constriction, this specimen forms an unusual adoral rib, the post-nepionic shell (opl and ncl) is attached to its adoral end; **e** close-up of **d**, discontinuity of the nepionic constriction; **f** close-up of **d**, first appearance of the nacreous material which forms the primary varix. *aw* ammonitella wall, *dipl* dorsal inner prismatic layer, *ipl* inner prismatic layer, *ncl* nacre layer, *opl* outer prismatic layer, *pel* pelicula, *pvar* primary varix, *S* septum, *siph* siphon, *wl* wrinkle layer

Structure of the nepionic constriction and primary varix

The nepionic constriction and corresponding primary varix in Phylloceratoidea (*Phyllopachyceras*), Lytoceratoidea (*Eotetragonites*, *Tetragonites*), Hildoceratoidea (*Leioceras*), Perisphinctoidea (*Kranaosphinctes*, *Epaspidoceras*) and Desmoceratoidea (*Desmoceras*) represent a halt in shell secretion during transition from the ammonitella to the teleoconch (Fig. 3). Its internal structure is more or less identical in all taxa, with minor differences in detail. The constriction forms a weak furrow on the shell surface, an undulation of the (sub-) prismatic ammonitella wall (aw in Fig. 3a–c), strengthened by a lenticular or slightly asymmetric nacreous ridge-like thickening on its inner surface called the primary varix (pvar in Fig. 3a). The ammonitella wall vanishes and disappears at the adoral varix edge (aw in Fig. 3b, c, e, f). One specimen of *Eotetragonites* (MAo-1773) has a prominent rib at the end of the ammonitella instead of the usual slight furrow (Fig. 3d). The discontinuity of the nepionic constriction results from the attachment of the teleoconch shell from beneath: A new outer prismatic layer and nacre layer are attached to the inner surface of the nacreous varix, proceed to the outer shell surface and then form the subsequent teleoconch shell (opl and ncl in Fig. 3b, e). An inner prismatic layer is not formed but appears in older sections of the teleoconch.

Structure of teleoconch varices

Several Phylloceratoidea (*Calliyphylloceras*, *Euphylloceras*, *Phyllopachyceras*) form distinct internal ridges of more or less identical internal structure (Fig. 4a–d). *Calliyphylloceras* develops slightly asymmetrical ridges in transsection (Fig. 4c), whereas *Euphylloceras* and *Phyllopachyceras* form elongated asymmetrical thickenings (Figs. 1b, 4a). The prolonged adapical flank of these asymmetrical thickenings has a flat slope; the adoral flank ends in an abrupt reduction of the thickening with a steep slope (Fig. 4b). The actual body of the varices is formed by thickening of the nacre layer (ncl in Figs. 1b, 4a–d). The inner prismatic layer becomes thinner beneath the thickening (ipl in Figs. 1b, 4a–d). The outer prismatic layer is unaffected (opl in Figs. 1b, 4a–d), but some varices of *Calliphylloceras* develop a weak adoral furrow. No discontinuity in shell growth is formed. However, at several varices, the outer portions of the nacre layer seem to vanish in adoral direction, while the inner portions which form the thickening continue in adoral direction (ncl in Figs. 1b, 4a–d, 6b, c).

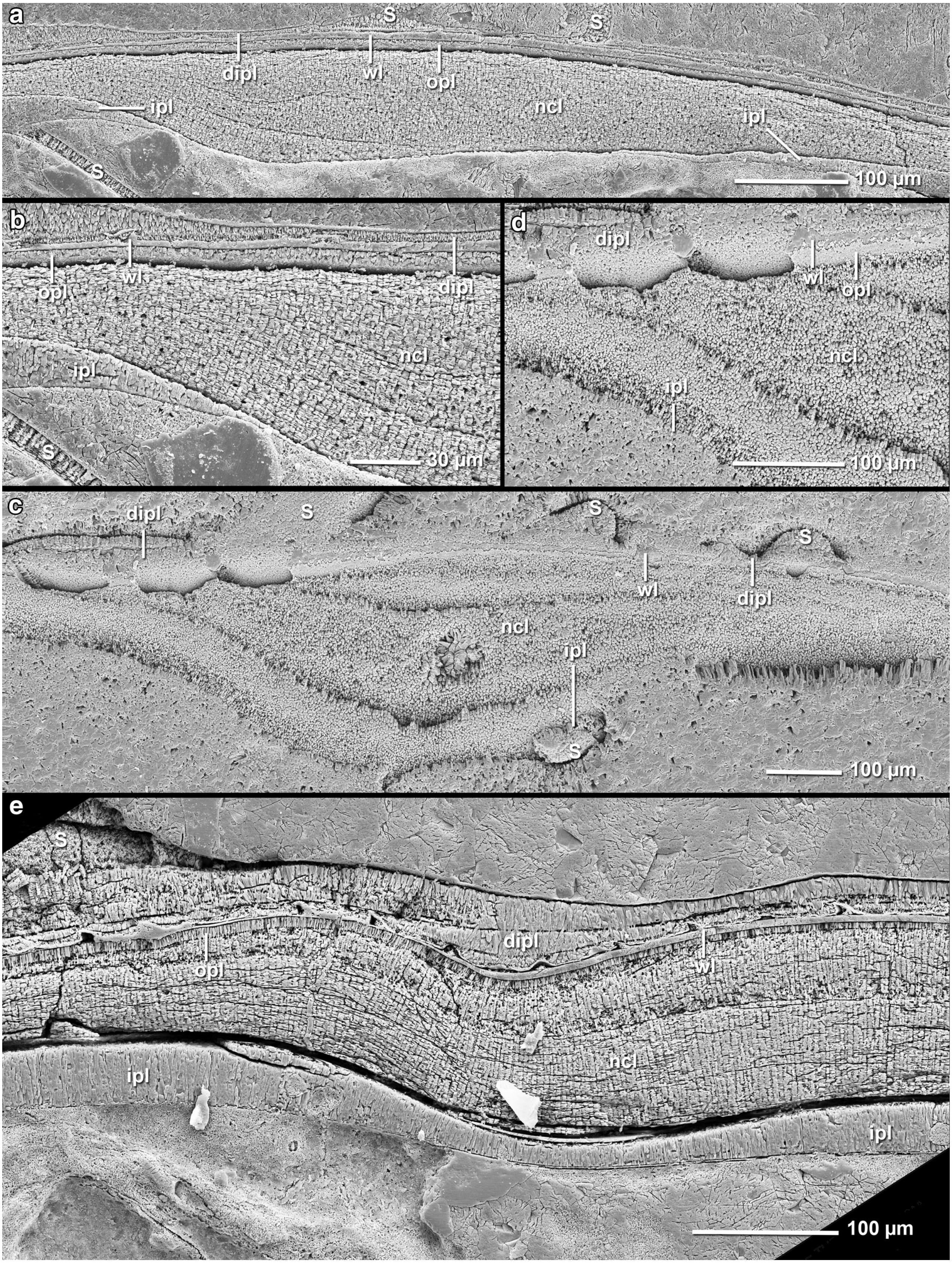
Structure of teleoconch ridged varices

Juvenile varices of *Ptychophylloceras* (Phylloceratoidea) resemble those of *Euphylloceras* and *Phyllopachyceras* (Fig. 5a). As ontogeny progresses (Diameter (D) = 1.2–1.7 cm), *Ptychophylloceras* develops symmetric ridges which display the nacreous varices at the ventral shell surface. The ridge of the outer shell surface is formed by an undulation of the outer prismatic layer. The nacre layer merely smoothes the ridge relief and forms the asymmetrical varix body (ncl in Fig. 5b). Sometimes the whole inner relief is completely smoothed out by the inner prismatic layer which forms adoral strong thickenings (ipl in Fig. 5b).

Desmoceras (Desmoceratoidea) develops similar ridges at the ventral shell surface (Fig. 5c). However, in contrast to *Ptychophylloceras*, the varices of *Desmoceras* are formed only at the flanks, i.e. the ventral shell portion has no internal thickening and the internal surface is smooth. Ridge and varix are separated. The nacre layer compensates the outer ridge relief almost completely (ncl in Fig. 5c); the remaining relief is smoothed out by the inner prismatic layer (ipl in 5c). The internal structure of the nearly symmetric varices (the adoral flank is usually a little shorter) is consistent with the above general observations. The outer surface seems to be smooth, but two specimens of *Desmoceras* (MAo-1782, MAo-1785) show a very weak corresponding furrow at the surface of some varices.

Structure of teleoconch constrictions

The internal structure of phylloceratid (*Holcophylloceras*) and desmoceratid (*Puzosia, Umsinenoceras, Neosilesites*, *Canadoceras, Menuites*) constrictions resembles that of varices with exception of an additional strong surface furrow which is formed by an undulation of the uninterrupted outer prismatic layer (opl in Figs. 1c, 4e, 6d). A slight thickening of the outer prismatic layer can occur (opl in Fig. 4e). All constrictions are reinforced by the nacre layer (ncl in Figs. 1c, 4e, 6d). Sometimes its outer lamellae seem to wedge out in adoral direction and are replaced by


a
s
s
dipl
wl
opl
ipl
ncl
ipl
s
100 µm
b
opl
wl
dipl
ncl
ipl
s
30 µm
d
dipl
wl
opl
ncl
ipl
100 µm
c
dipl
s
s
s
wl
dipl
ncl
ipl
s
100 µm
e
s
dipl
opl
wl
ncl
ipl
ipl
100 µm

◀**Fig. 4** Internal structure of varices and constrictions (*growth direction left*). The internal thickening is formed by the nacre layer, the inner prismatic layer becomes thinner in these areas. **a**, **b** *Euphylloceras* sp. (MAo-1769), **a** asymmetrical varix, **b** close-up of **a**, adoral end of varix, only the inner portions of the nacre layer seem to continue; **c**, **d** *Calliphylloceras* sp. (MAn-4511), **c** symmetrical varix, **d** close-up of **c**, adoral end of varix, only the inner portions of the nacre layer seem to continue; **e** *Puzosia saintoursi* COLLIGNON (MAo-1792), asymmetric constriction, the outer prismatic layer forms the outer relief which is compensated by the dorsal inner prismatic layer, only the inner lamellae of the nacre layer seem to continue. *dipl* dorsal inner prismatic layer, *ipl* inner prismatic layer, *ncl* nacre layer, *opl* outer prismatic layer, *S* septum, *wl* wrinkle layer

new ones which are added from the inside and form the thickening (Figs. 4e, 6d). Underneath the thickening, the inner prismatic layer becomes thinner (ipl in Figs. 4e, 6d) but in some cases it forms a strong thickening at the adoral edge of the constriction (e.g. *Holcophylloceras, Puzosia*). This smooths the angle between adoral shell wall and adoral flank of the constriction (ipl in Fig. 6d). Especially the desmoceratid constrictions are asymmetric in nacre distribution, the aboral flank is much thicker (ncl in Fig. 4e) and they resemble juvenile constrictions of *Holcophylloceras*. Often the general outline is modified: For

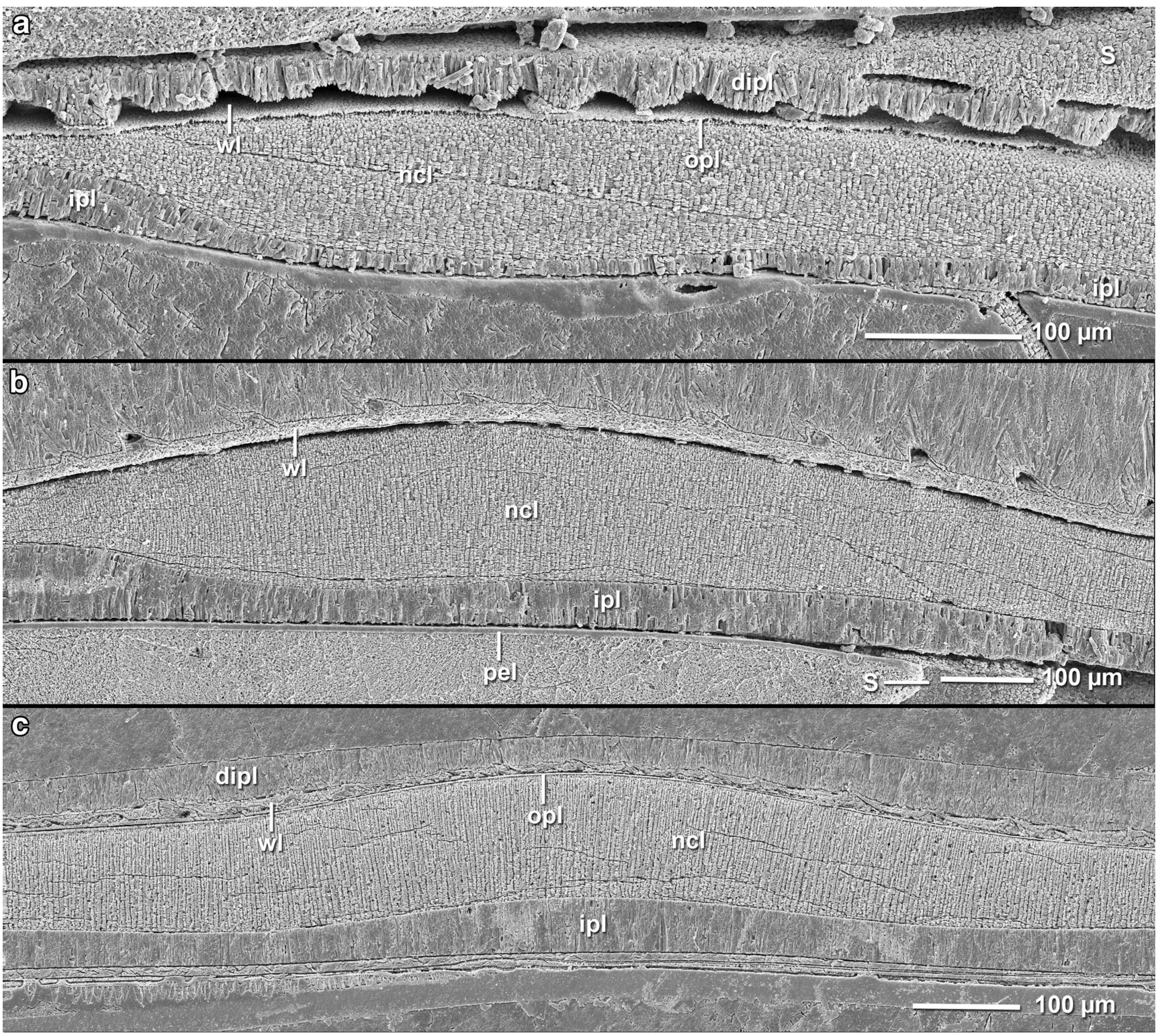
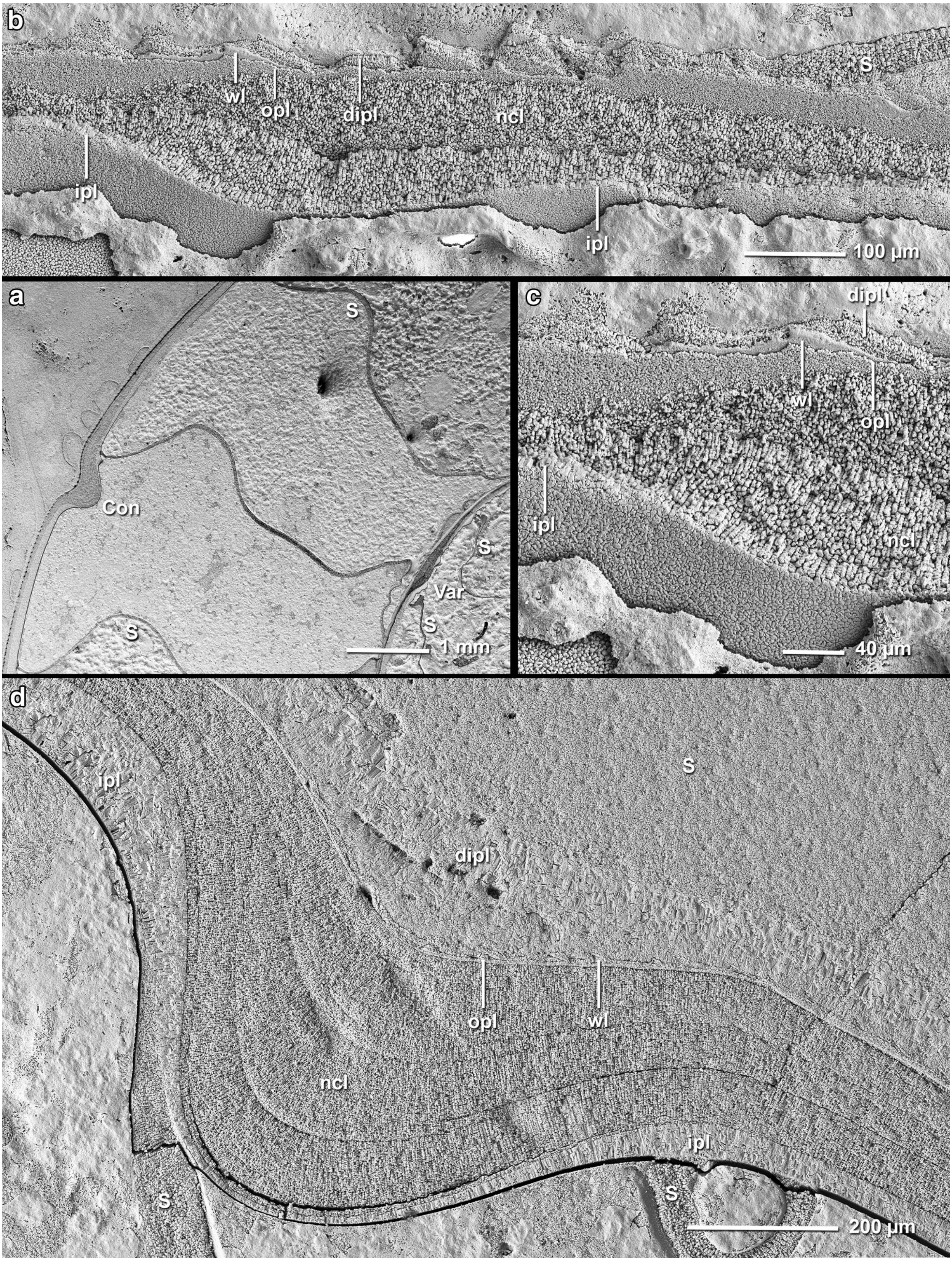


Fig. 5 Internal structure of ridges (*growth direction left*). **a**, **b** *Ptychophylloceras* cf. *dacquei* JOLY (MAn-4515), **a** young varices are characterized by smooth surface, **b** older varices are accompanied by a ventral ridge, the outer relief is formed by the outer prismatic layer; **c** *Desmoceras latidorsatum* MICHELIN (MAo-1788), in ventral position only ridges are formed; the outer prismatic layer forms the relief which is compensated by the nacre layer and the inner prismatic layer. *dipl* dorsal inner prismatic layer, *ipl* inner prismatic layer, *ncl* nacre layer, *opl* outer prismatic layer, *S* septum, *pel* pelicula, *wl* wrinkle layer


b
wl
opl
dipl
ncl
S
ipl
ipl
100 µm
a
S
Con
S
Var
S
S
1 mm
c
dipl
wl
opl
ipl
ncl
40 µm
d
S
ipl
dipl
opl
wl
ncl
ipl
S
S
200 µm

◀**Fig. 6** Parallel occurrence of varices and constrictions (*growth direction left*). The internal thickening is formed by the nacre layer; the inner prismatic layer becomes thinner in these areas. **a**–**d** *Holcophylloceras* sp. (MAn-4510), **a** in course of ontogeny, the varices are replaced by constrictions, **b** asymmetrical varix, **c** close-up of **b**, adoral end of varix, only the inner portions of the nacre layer seem to continue, **d** symmetric constriction, the outer prismatic layer forms the outer relief which is compensated by the dorsal inner prismatic layer. *con* constriction, *dipl* dorsal inner prismatic layer, *ipl* inner prismatic layer, *ncl* nacre layer, *opl* outer prismatic layer, *S* septum, *var* varix, *wl* wrinkle layer

example, *Puzosia* has an adoral and an apical rib which enclose the constriction. One bigger specimen of *Puzosia* ($D = 8.7$ cm, MAo-1795) forms weak ridges at the shell surface instead of the typical furrows. The genus *Neosilesites* sometimes develops an adoral enhanced rib next to the normal ribbing. The early whorls of one *Neosilesites* specimen (MAo-1778) have ventral ridges like *Desmoceras*.

The constrictions of perisphinctids (*Kranaosphinctes, Divisosphinctes,* Perisphinctidae indet.) share the distinct surface furrow formed by the outer prismatic layer of phylloceratid and desmoceratid constrictions but lack the prominent ridge-like nacreous reinforcement. However, a thickening of the nacre layer can still be observed. Despite the missing internal ridge, the inner prismatic layer thins as well. Usually the constrictions are preceded and/or followed by stronger ribs. Within *Divisosphinctes*, the constriction may even include a middle ventral rib. The entire outer relief is formed by an undulated but continuous outer prismatic layer.

The early whorls of *Holcophylloceras* develop simple asymmetric varices which strongly resemble those of *Euphylloceras* or *Phyllopachyceras* (Fig. 6a, b). *Holcophylloceras,* from diameters of about 0.7 cm on, develops a continuous transition to prominent constrictions of older whorls (Fig. 6a, d). Early constrictions can be distinguished from varices by a weak adoral furrow which gradually becomes deeper in the course of ontogeny. *Canadoceras* and *Menuites* experience a similar development; in specimen, transition begins at diameters bigger than 1.1 cm and 1.3 cm, respectively.

Structure of *Eotetragonites*' varices

The general structural features of varices of *Eotetragonites* (Lytoceratoidea) are consistent with structural features of observed varices and constrictions. Its internal asymmetric ridge is formed by a thickening of the nacre layer (ncl in Fig. 7a) while the inner prismatic layer thins under the nacreous body (ipl in Fig. 7a). The adoral flank is steeper and much shorter than the apical flank. The shell surface has no distinct furrow. However, the outer prismatic layer which is bent slightly inwards forms a faint relief on the shell surface (opl in Fig. 7a). The outer prismatic layer is generally not interrupted but it becomes considerably thicker at the adoral edge. Basically, the structure of *Eotetragonites*' varices is identical with that of other lytoceratids like *Tetragonites* and that shown for *Saghalanites* by Birkelund and Hansen (1974).

The varices of *Eotetragonites* tend to develop interruptions in shell growth, 5 of 83 varices show a break in secretion. Some juvenile varices allow the observation of two distinct shell generations: At the adoral edge of two varices (MAo-1773), a new outer prismatic layer (opl 2 in Fig. 7c) is attached to the inner surface of the existing layer (opl 1 in Fig. 7c). The initially thin new outer prismatic layer thickens in adoral direction. As the new outer prismatic layer becomes thicker, the old layer becomes thinner and finally wedges out completely. No outer scarp or other mark remains. Presumably, the older shell generation represents a former apertural margin. The internal nacre thickening is part of the new shell generation (ncl 2 in Fig. 7c). A further varix develops a flare-like interruption (MAo-1776) which is reinforced by the internal nacre thickening (Fig. 7b). The first generation of shell, consisting of portions of the outer prismatic layer and nacre layer (opl 1 and ncl 1 in Fig. 7b), bends outward and is cut more or less horizontal to the shell surface. It represents the base of a resolved flared aperture (see Bucher et al. 1996; Doguzhaeva et al. 2010; Radtke et al. under revision). A new thin outer prismatic layer attaches immediately beneath the base and proceeds to the outer shell surface while it thickens (opl 2 in Fig. 7b). The new nacre layer (ncl 2 in Fig. 7b) develops as a typical varix (compare Drushits and Doguzhaeva 1981, fig. 31; Doguzhaeva et al. 2010, fig. 2). The inner prismatic layer is still missing; at the juvenile stage this flared varix appears.

Two rare pathological malformations of *Eotetragonites*' varices (MAo-1773) also allow the observation of the attachment of new shell material from the inside (Fig. 7d). These malformations are formed at the adoral edge of the varices. The existing outer prismatic layer and nacre layer are cut vertically (opl 1 and ncl 1 in Fig. 7d). A new outer prismatic layer which first runs parallel to the shell surface but then bends upwards vertically at the cutting edge is formed beneath the primary generation of nacre (opl 2 in Fig. 7b). The old shell becomes sealed at the cutting edge; no distinct surface relief is formed. New nacre material compensates the inner relief and forms the internal thickening (ncl 2 in Fig. 7b). These formations correspond to the regeneration of shell injuries, the so-called forma aegra substructa (Hölder 1973), but are distinguished by a reduction of the distinct relief.


a
s
s
s
ipl
opl
ncl
wl
dipl
pel
s
50 µm
b
pel
dipl
wl
ncl 1
opl 2
opl 1
ncl 2
pel
s
20 µm
c
dipl
wl
opl 1
ncl 1
opl 2
ncl 2
ipl
pel
20 µm
d
dipl
opl 1
ncl 1
wl
opl 2
ncl 2
40 µm

◀**Fig. 7** Discontinuities associated with varices (*growth direction left*). **a**, **b** *Eotetragonites umbilicostriatus* COLLIGNON (MAo-1776), **a** normal asymmetric varix, the internal thickening is formed by the nacre layer, the inner prismatic layer becomes thinner in that area, **b** young varix associated with a flare, the first shell generation is bent outward (opl 1 and ncl 1), the second shell generation forms the actual varix (opl 2 and ncl 2); **c**, **d** *E. umbilicostriatus* COLLIGNON (MAo-1773); **c** adoral end of a varix with slight discontinuity in the outer shell portions, a first generation of the outer prismatic layer and nacre layer (opl 1 and ncl 1) can be distinguished from a second one (opl 2 and ncl 2), the inner prismatic layer is not affected, **d** malformation associated with the adoral end of a varix, a first generation of the outer prismatic layer and nacre layer (opl 1 and ncl 1) can be distinguished from a second one (opl 2 and ncl 2), the first shell generation ends abruptly at a vertical edge, the inner prismatic layer is not affected. *dipl* dorsal inner prismatic layer, *ipl* inner prismatic layer, *ncl, ncl 1, ncl 2* nacre layer, *opl, opl 1, opl 2* outer prismatic layer, *S* septum, *pel* pelicula, *wl* wrinkle layer

Discussion

Formation of varices and constrictions

Independent of the taxonomic affiliation (Phylloceratoidea, Lytoceratoidea, Perisphinctoidea, Desmoceratoidea), varices and constrictions match in major characteristics: the outer prismatic layer is continuous and forms outer expressions such as furrows or ridges by way of undulation, if any. A smooth surface and associated sculpture represent different mouldings of a former peristome preformed by the periostracal groove at the mantle edge. Thus, it is frequently seen that growth increments and constrictions are arranged parallel. The nacre layer forms a prominent internal ridge in most species, indicating a major secretion effort which is in line with observations made earlier (see "Introduction"). Indeed, the observed Perisphinctoidea more or less lack a concurrent structure. However, a slight thickening nevertheless occurs, Checa (1994) has even shown in *Pavlovia* that these can become quite thick. The inner prismatic layer becomes thinner underneath the nacreous thickening and can form strong adoral thickenings. Since the inner prismatic layer is formed in the posterior parts of the living chamber, where it compensates the internal relief, the inner prismatic layer plays a more reactive role in the formation of varices and constrictions than the outer prismatic layer and nacre layer.

An interruption of the shell growth in the course of the formation of varices and constriction can be excluded for the vast number of observed structures. The continuous outer prismatic layer indicates a continuous secretion. Furthermore, resorption can be ruled out as explanation for sculptural inconsistencies associated with the formation of constrictions (see Arkell et al. 1957; Checa and Westermann 1989; Seilacher and Gunji 1993; Checa 1994; Bucher et al. 1996; Bucher 1997). In contrast to varices and constrictions, the nepionic constriction forms a prominent offset between ammonitella shell wall and teleoconch shell wall. This is classically explained by a halt in growth and subsequent withdrawal of the shell secreting mantle edge (e.g. Erben et al. 1968, 1969; Kulicki 1974, 1979; Kulicki and Doguzhaeva 1994; Tanabe et al. 2008). The teleoconch wall always begins beneath the nacreous primary varix which is part of the ammonitella aperture. At varices (and constrictions), withdrawal structures are rather rare and seem to represent exceptions which may indicate stress: In *Eotetragonites*, only 5 of 83 observed varices show a growth interruption associated with a withdrawal of the mantle edge. These interruptions differ in habitus; either they appear as a normal, wedge-like apertural margin (Fig. 7a), a (resolved) flared aperture (Fig. 7b) or a secondary broken edge (Fig. 7d), so that a general characteristic for varices can be excluded. The shell growth interruption of the flared aperture is typical for the formation of these structures (megastriae, Drushits and Doguzhaeva 1981; Bucher et al. 1996; Doguzhaeva et al. 2010; Radtke et al. under revision) and does not account for varix formation.

The internal structure of varices and constrictions negates a withdrawal during formation. However, in several cases, the nacre layer develops "internal interruption" which separates the thickening (Fig. 1b, c). We assume that this reoccurring pattern traces the original formation sequence and represents a delay in secretion. The internal thickening was added subsequent to the formation of the outer relief (furrows, ridges, flares or growth increments). The former aperture has to be regarded as more or less independent from formation of internal nacreous thickenings. Special habitus may only trigger the formation of a varix to subsequently reinforce certain shell sculptures. The concept of a subsequent secretion of the nacre thickening is supported by the withdrawal structures of *Eotetragonites*' varices. Their nacreous thickenings are always part of the second shell generation, the first generation represents unique mouldings of the aperture mentioned above. We assume that the thickening was secreted subsequent to formation of the apertural sculpture as shell growth progressed. This concept explains the often observed discordant arrangement of varices and growth increments. The thickening of varices and constrictions is not a narrowing of an (interimistic) aperture per se but can reinforce certain portions of the shell (e.g. furrows, ridges, flares). The model seems to clash with terminal constrictions/varices, as in *Dactilioceras* (e.g. Howarth 1975; Keupp 2000). However, such formations generally have short shell portions following the constriction. Hence, it is possible that the thickening was formed in course of the secretion of the appendage.

We suggest the following sequence for the formation of varices and constrictions:

1. Formation of periostracum with distinct aperture (smooth, furrow, ridge, etc.),
2. Start of mineralisation at the mouth border, outer prismatic layer and nacre layer are formed, the thickening does not exist,
3. Extension of the whorl tube proceeds, new shell is formed, extensive secretion of the nacreous epithel forms the thickening (subsequently), this may cause a slowing of the growth rate (e.g. Doguzhaeva 1990),
4. After a certain time span, apical parts of the soft body form the inner prismatic layer as shell growth proceeds and the soft body moves forward.

Phylogenetic considerations

The internal structure of the nepionic constriction and teleoconch varices and constrictions indicate that they are not closely related, the difference between discontinuous and continuous formation being the most notable indicator. Furthermore, the nacreous thickening (primary varix) and the (furrowed) aperture of the nepionic constriction seem to be apparent at the same time. However, we assume that nacreous thickenings of varices and constrictions are formed subsequent to the aperture.

In our opinion, the internal structure of varices and constrictions gives no indication for a multiple origin within the taxa subject to our analyses. Both structures are identical in their basic characteristics within each individual taxon (Fig. 1b, c) and seem to represent the same formation process; an alternative way of formation can be excluded (e.g. participation of other layers in the thickening process, discontinuities in growth). The morphological change of simple varices (smooth surface) to secondary constrictions and ridged varices, respectively, points to a homology of these structures which is at least proved in Phyllocertoidea (*Holcophylloceras, Ptychophylloceras*) and Desmoceratoidea (*Canadoceras, Menuites*). The three habitus (1. smooth surface, 2. furrow, 3. ridge) represent different expressions of the same structure with the simple varix (smooth surface) as primary state. We believe that the varices and constrictions within Jurassic and Cretaceous taxa must be of homologous origin based on Phyllocertoidea. The primary bauplan was altered in the different taxa. The formation of constrictions possibly follows a general pattern or develops several times. Varices/constrictions presumably persisted through time as a facultative feature which is reactivated at times. This would also explain the isolated occurrence in ammonoid evolution, including the occurrence on superfamily-level as well genus-level. However, owing to the sporadic occurrence of these features, a multiple origin cannot be completely excluded. A common bauplan of varices and constrictions suggests homology, but since no taxa or structures which form a link have been verified yet, a final conclusion is not possible. The internal structure alone does not provide sufficient evidence.

Functional implications

Function of the nepionic constriction

It is generally assumed that the interruption in shell formation serves an extensive reorganization of the mantle tissue, e.g. genesis of a nacre epithelium, incremental shell secretion (Birkelund 1967, 1980; Birkelund and Hansen 1968, 1974; Erben 1964, 1966; Erben et al. 1968, 1969; Howarth 1975; Kulicki 1974, 1979; Lehman 1976; Doguzhaeva and Mikhailova 1982; Bandel 1986; Landman 1987; Kulicki and Doguzhaeva 1994; Sprey 2002; Tanabe et al. 2008). It was assumed that the nepionic constriction and in particular the varix were formed as part of the metamorphosis process (Erben et al. 1969) or in course of an environmental adaption phase (Drushits and Khiami 1970). Functional morphological interpretations favour the idea of an additional weight for a distinct apertural position (Kulicki 1974, 1979). Owing to the spherical form and central first chamber of the ammonitella, the gravitational and buoyancy centre are too close together. The varix would increase the distance between gravitational and buoyancy centres, increasing stability. A different model suggests a strengthening of the aperture during hatching: Kulicki (1974, 1979) assumes an increased amount of stress between egg hull and aperture during hatching. Considering the reinforced rib at the end of a *Eotetragonites'* ammonitella, it can be assumed that this rib has the function of an architectural arc which relieves the stress during hatching.

Function of constrictions and varices

The theories concerning the function of constrictions and varices range from simple defensive structures (e.g. Keupp 2000) to a complex reorganization pattern of shell coiling, indicated by cut sculpture (Checa and Westermann 1989; Seilacher and Gunji 1993; Checa 1994; Bucher et al. 1996; Bucher 1997). Keupp (2000) believes that varices and constrictions help to prevent the intrusion of predators and parasites. However, the nacreous thickening seems to be added subsequently, i.e. as the shell grows; a verification of involvement in the formation of distinct apertures (e.g. furrows, ridges, flares) is not possible. The thickening still represents a shell reinforcement, serving as some kind of “inner ribs”. It has been shown that 75 % of (healed) injuries of upper Devonian cheiloceratids end at varices

(Keupp 2012). Furrows and ridges may evolve to enhance the effects of varices.

The internal thickenings might have served as additional weight for the reorientation of the aperture. However, it is not clear that the thickenings were part of the aperture, more likely they served as weight after aperture formation. Obata et al. (1978) consider the varices and constrictions as a structure which "*may have helped to secure the ammonite body against slipping from the chamber*". However, this theory only applies to the adoral soft body portion since the inner prismatic layer of *Ptychophylloceras*, which is formed by the apical mantle tissue, can smooth out the whole internal relief.

Especially for constrictions, a reorientation of the coiling due to constructional incompatibilities which produced an angular disconformity of the adoral and aboral sculpture was assumed (e.g. Perisphinctoidea, Desmoceratidae, compare Checa and Westermann 1989; Seilacher and Gunji 1993; Checa 1994; Bucher 1997). Examinations proved that this was not achieved by resorption of shell material and attachment of new shell material. The reorientation of the sculpture represents a former peristome formed by the mantle edge which deviates from the normal appearance. So, owing to a lack of shell growth interruption, the assumed episodic growth model for constricted ammonoids of Checa (1994) is rejected, instead a continuous secretion is generally assumed more likely.

Conclusion

In this study, we support the theory of a homologous origin of varices and constrictions in specimen of Jurassic and Cretaceous ammonoid taxa (Phylloceratoidea, Lytoceratoidea, Perisphinctoidea, Desmoceratoidea), although homoplasy cannot be definitely excluded. From our point of view, there are no evidences in the internal structure of varices and constrictions which indicate a multiple development of these features in ammonoid phylogeny. Varices and constrictions of Jurassic and Cretaceous taxa have several common features: (1) continuous outer prismatic layer, (2) nacreous thickening, (3) thinning of the inner prismatic layer. Transitional morphological change from (smooth shelled) varices to constrictions and to ridged varices, respectively, proves a homology for the three habitus, at least for Phyllocertoidea and Desmocertoidea. We assume that Phylloceratiodea—the stem group of Jurassic/Cretaceous ammonoids—is the group in which the varices of Ammonitina (including Lytoceratoidea) first occurred. Probably varices and constrictions are a facultative feature, explaining the scattered occurrence in ammonoid phylogeny.

The way varices and constrictions are formed is different from the way the nepionic constriction is formed. The formation of the nepionic constriction is accompanied by a withdrawal of the mantle, causing a distinct interruption of shell growth. Varices and constrictions are formed by continuous secretion. The accompanied surface relief, such as furrows or ridges, is formed by undulation of the outer prismatic layer. Generally, only flared varices mark an interruption in shell growth which is typical of flares and not of varices. Nacreous varix-like thickenings subsequently reinforce certain shell features (e.g. furrows, ridges, flares) as shell growth proceeds. We assume that slight discontinuities separating the nacreous thickening mark a delay in secretion. We recommend not to regard the internal nacreous thickenings as simultaneous formations of constriction furrows, ridges or flares.

Acknowledgments We would like to thank Dr. G. Schweigert and Dr. Y. Hikida for providing material for this study, M. Bulang-Lörcher for making the drawings and K. Hirsing and R. Lemanis for counterchecking the manuscript. This work was funded by the Berlin Universities' Elsa-Neumann-Stipend.

References

Arkell, W. J., Furnish, W. M., Kummel, B., Miller, A. K., Moore, R. C., Schindewolf, O. H., et al. (1957). *Treatise on Invertebrate Paleontology, Part L Mollusca 4, Cephalopoda, Ammonoidea* (p. 393). Lawrence: The Geological Society of America and The University of Kansas Press.

Bandel, K. (1986). The ammonitella: A model of formation with the aid of the embryonic shell of archaeogastropods. *Lethaia, 19*(2), 171–180.

Birkelund, T. (1967). Submicroscopic shell structures in early growth-stages of Maastrichtian ammonites (*Saghalinites* and *Scaphites*). *Meddelelser fra Dansk Geologisk Forening, 17*(1), 95–101.

Birkelund, T. (1980). Ammonoid shell structure. In M. R. House & J. R. Senior (Eds.), *The ammonoidea, systematics association special* (Vol. 18, pp. 177–214). London: Academic Press.

Birkelund, T., & Hansen, H. J. (1968). Early shell growth and structures of the septa and the siphuncular tube in some Maastrichtian ammonites. *Meddelelser fra Dansk Geologisk Forening, 18*(1), 95–101.

Birkelund, T., & Hansen, H. J. (1974). Shell ultrastructures of some Maastrichtian Ammonoidea and Coleoidea and their taxonomic implications. *Biologiske Skrifter: Danske Videnskabernes Selskab, 20*(6), 1–34.

Bucher, H. (1997). Caractères périodiques et mode de croissance des ammonites: Comparaison avec les gastéropodes. *Geobios Mémoire Spécial, 20*, 85–99.

Bucher, H., Landman, N. H., Klofar, S. M., & Guex, J. (1996). Mode and rate of growth in ammonoids. In N. H. Landman, K. Tanabe, & R. A. Davis (Eds.), *Ammonoid paleobiology. Topics in Geobiology* (Vol. 13, pp. 407–461). New York: Plenum Press.

Checa, A. (1994). A model for the morphogenesis of ribs in ammonites inferred from associated microsculptures. *Palaeontology, 37*, 863–888.

Checa, A., & Westermann, G. E. G. (1989). Segmental growth in planulate ammonites: Inferences on costal function. *Lethaia, 22*, 95–100.

Cochran, J. K., Kallenberg, K., Landman, N. H., Harries, P. J., Weinreb, D., Turekian, K. K., et al. (2010). Effect of diagenesis on the Sr, O, and C isotope composition of late Cretaceous mollusks from the Western Interior Seaway of North America. *American Journal of Science, 310*, 69–88.

Doguzhaeva, L. (1990). Analysis of shell growth in ammonoids. In A. A. Shevyrev & V. N. Shimansky (Eds.), *Fossil cephalopods Evolution and systematics of some groups* (Vol. 243, pp. 15–28). Moscow: Trody Paleontologicheskogo Instituta.

Doguzhaeva, L., Bengtson, S., & Mutvei, H. (2010). Structural and morphological indicators of mode of life in the Aptian lytoceratid ammonoid *Eogaudryceras*. In K. Tanabe, Y. Shigeta, T. Sasaki, & H. Hirano (Eds.), *Cephalopods: Present and Past* (pp. 123–130). Tokyo: Tokai University Press.

Doguzhaeva, L., & Mikhailova, J. (1982). The genus *Luppovia* and the phylogeny of Cretaceous heteromorphic ammonoids. *Lethaia, 15*(1), 55–65.

Drushits, V. V., & Doguzhaeva, L. (1974). Some morphogenetic characteristics of phylloceratids and lytoceratids (Ammonoidea). *Paleontological Journal, 8*, 42–53.

Drushits, V. V., & Doguzhaeva, L. (1981). *Ammonites in Electron Microscope* (p. 240). Moscow: Publishing House of Moscow State University.

Drushits, V. V., & Khiami, N. (1970). Structure of the septa, protoconch walls and initial whorls in early cretaceous ammonites. *Paleontological Journal, 4*(1), 26–38.

Erben, H. K. (1964). Die Evolution der ältesten Ammonoidea. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 120*, 107–212.

Erben, H. K. (1966). Über den Ursprung der Ammonoidea. *Biological Reviews, 41*(4), 641–658.

Erben, H. K., Flajs, G., & Siehl, A. (1968). Ammonoids: Early ontogeny of ultramicroscopial shell structure. *Nature, 219*, 396–398.

Erben, H. K., Flajs, G., & Siehl, A. (1969). Die frühontogenetische Entwicklung der Schalenstruktur ectocochleater Cephalopoden. *Palaeontographica A, 132*, 1–54.

Hölder, H. (1973). Miscelleana cephalopodica. *Münsterländer Forschungshefte Geologie Paläontologie, 29*, 39–76.

Howarth, M. K. (1975). The shell structure of the Liassic ammonite family Dactylioceratidae. *Bulletin of the British Museum (Natural History), 26*, 45–67.

Kennedy, W. J., & Cobban, W. A. (1976). Aspects of ammonite biology, biogeography, and biostratigraphy. *Special Papers in Palaeontology* (Vol. 17, p. 94). London: The Palaeontological Association.

Keupp, H. (2000). *Ammoniten: Paläobiologische Erfolgsspiralen* (p. 165). Stuttgart: Thorbecke Verlag.

Keupp, H. (2008). *Desmoceras* (*Pseudouhligella*) *intrapunctatum* n. sp. from the Lower Albian of NW-Madagascar with "Ritzstreifen". *Paläontologische Zeitschrift, 82*(4), 437–447.

Keupp, H. (2012). Atlas zur Paläopathologie der Cephalopoden. *Berliner paläobiologische Abhandlungen* (Vol. 12, p. 390). Berlin: Institut für Geologische Wissenschaften, Fachrichtung Paläontologie.

Kulicki, C. (1974). Remarks on the embryogeny and postembryonal development of ammonites. *Acta Palaeontologica Polonica, 19*, 201–224.

Kulicki, C. (1979). The ammonite shell: its structure, development and biological significance. *Palaeontologica Polonica, 39*, 97–142.

Kulicki, C. (1996). Ammonoid Shell Microstructure. In N. H. Landman, K. Tanabe, & R. A. Davis (Eds.), *Ammonoid paleobiology. Topics in Geobiology* (Vol. 13, pp. 65–101). New York: Plenum Press.

Kulicki, C., & Doguzhaeva, L. A. (1994). Development and calcification of the Ammonitella shell. *Acta Palaeontologica Polonica, 39*(1), 17–44.

Landman, N. H. (1987). Ontogeny of Upper Cretaceous (Turonian-Santonian) scaphitid ammonites from the Western Interior of North America: systematics, developmental patterns, and life history. *Bulletin of the American Museum of Natural History, 185*, 117–241.

Lehman, U. (1976). *Ammoniten. Ihr Leben und ihre Umwelt* (p. 171). Erlangen: Ferdinand Enke Verlag.

Obata, I., Futakami, M., Kawashita, Y., & Takahashi, T. (1978). Apertural features in some Cretaceous ammonites from Hokkaido. *Bulletin of the National Science Museum Series C (Geology & Paleontology), 4*(3), 139–155.

Radtke, G., (2012). Ultrastrukturelle Schalenuntersuchungen an einschnürungtragenden Ammoniten aus dem Mesozoikum. Unpublished Master-Thesis, FU Berlin, p. 261.

Radtke, G., Hoffmann, R. & Keupp, H. (under revision). Form and function of flares and parabolae based on new ultrastructural observations. *Acta Palaeontologica Polonica.*

Rouget, I., Neige, P., & Dommergues, J.-L. (2004). L'analyse phylogénétique chez les ammonites: état des lieux et perspectives. *Bulletin de la Société Géologique de France, 175*(5), 507–512.

Seilacher, A., & Gunji, P. Y. (1993). Morphogenetic countdowns in heteromorph shells. *Neues Jahrbuch für Geologie und Paläontologie, 190*, 237–265.

Sprey, A. M. (2002). Early Ontogeny of three Callovian Ammonite Genera (*Binatisphinctes, Kosmoceras (Spinikosmoceras)* and *Hecticoceras*) from Ryazan (Russia). *Abhandlungen der Geologischen Bundesanstalt in Wien, 57*, 225–255.

Tanabe, K., Kulicki, C., & Landman, N. H. (2008). Development of the embryonic shell structure of Mesozoic ammonoids. *American Museum Novitates, 3621*, 1–19.