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Devonian pearls and ammonoid-endoparasite co-evolution

KENNETH DE BAETS, CHRISTIAN KLUG, and DIETER KORN

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Raised shell projections on the inner shell walls that form pits on the internal moulds of Devonian ammonoids have been known for several decades. New specimens from Morocco reveal novel details of these structures; most, if not all, of which consist of a capsule of ammonoid shell that covers tiny tubes attached to the outer (= lateral or ventral) shell wall from the inside. In accordance with comparable Recent occurrences of similar structures in molluscs, we use the term "pearls" for these structures and the pits they form on the internal moulds. The nature of these encapsulated tubes is described and discussed. Because of the presence of these tubes inside the pearls, pearl arrangement, and their similarity to Recent mollusc occurrences, the tubes are interpreted as traces of parasitoses. The pearls and pits were grouped into five types based on differences in morphology, size, and arrangement. Then, having used these traits to perform a simple cladistic analysis, the resulting cladogram was compared to the phylogeny of ammonoids. Based on this comparison, it appears likely that the parasites underwent a co-evolution with the ammonoids, which lasted 10 to 15 Ma. Patterns of evolutionary events include co-speciation, "drowning on arrival" (end of parasite lineage near base of a new host clade), and "missing the boat" (parasite lineage does not adapt to a new host clade, thus not evolving a new parasite clade). Because of the lack of fossilised soft tissue, only speculations can be made about the systematic affiliation of the parasites, their life-cycle, infection strategy, and ecological framework. Some co-occurring bivalves also have pits reminiscent to structures caused by trematodes in Recent forms. Based on the available information, the tubes are interpreted as artefacts of trematode infestations, which, if correct, would extend the fossil record of parasitic trematodes into the Early Devonian.

Key words: Ammonoidea, Trematoda, parasite, pearl, co-evolution, Devonian, Morocco, Algeria, Germany.

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Introduction

Evolutionary lineages, which interact ecologically and adapt to evolutionary changes of an unrelated lineage while one or both undergoes evolutionary modifications "co-evolve" (see, e.g., Yip. et al. 2008). The co-evolution of pollinating plants and insects is probably the most famous example of co-evolution (e.g., Krassilov and Rasnitsyn 2008). Perhaps less poetic, but still as valid, is the co-evolution of parasites and their hosts. Identification of a Recent parasite can be hampered by various problems such as the heterogeneous distribution of parasites in the infected tissues. An anecdotic example for cephalopods is for example the original description of the hectocotylus or modified arm of the male cephalopods as a parasitic helminth (Chiaje 1825; Cuvier 1829, 1830). In palaeontology, identification of parasitoses and parasites is often hampered by the fact that parasites (at least in some stages) are commonly small (+/- microscopic), often lack hard parts and many parasites lived within the host for the largest part of their lifecycle. These three phenomena weigh against the preservation of the parasitoses, and as a consequence, the detection of parasitic biota is rare in the fossil record. Additionally, even when preserved and detected, the quality of preservation will hamper examination and identification of such fossil parasitoses. In many cases, only faint traces of the parasite or the damage caused by it can be seen and not much, if anything at all, is known about the parasite itself (e.g., MacKinnon and Biernat 1970; Welch 1976; Brett 1978; Conway Morris 1981, 1988, 1990; Keupp 1986; Ruiz and Lindberg 1989; Underwood 1993; Bates and Loydell 2000; Lukševics et al. 2009). In some other cases, fossil remains of invertebrate taxa are occasionally found that are commonly known to represent parasites today (e.g., Waloßek and Müller 1994; Waloßek et al. 1994, 2006; Maas and Waloßek 2001), but where the host is not preserved. In rare cases, both host and parasite are found together in their thanatocoenosis, reflecting their actual biocoenosis (e.g., Riek 1970; Ponomarenko 1976; Baumiller 1990; Rasnitsyn 1992; Baumiller and Gahn 2002; Zapalski 2007, 2009; Schemm-Gregory and Sutton 2010).

In this report, we discuss a parasitosis that was already tentatively suggested by House (1960). He was the first to

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describe the more or less regularly distributed pits in the internal moulds of early ammonoids from the Early and Middle Devonian (Davis and Mapes logically named these pits "Housean pits" in honour of him in 1999). Hengsbach (1991, 1996) included them with other similar structures (e.g., Keupp 1986) in a palaeopathology he dubbed "forma concreta". Some other authors published specimens showing these pits, but without discussing them in detail (Chlupáč and Turek 1981; Becker and House 1994; Klug 2002a, b, 2007; Bockwinkel et al. 2009; Ebbighausen et al. in press). House (1960) and others concluded these pits represent the moulds of pearls that must have formed during the ammonoid's life on the inside of the shell within the body chamber, i.e., the part of the shell that contained the soft parts and lacked chambers. The pits/pearls are commonly arranged spirally, radially or chaotically on the flanks and venter of these ammonoids and are oval to circular in outline, occurring in varying numbers. House (1960) lacked sufficient information to decide whether these pits represent traces of a parasite or particles that entered between mantle and shell, causing an irritation and the formation of a pearl-like structure. By contrast, Keupp (1986) found similar structures in dactylioceratids and suggested that these structures may have been caused by parasites. We here show new material and provide evidence for the parasite hypothesis of House (1960), which was thought to be the most likely explanation by Davis and Mapes (1999).

Ammonoids have repeatedly been the subject of evolutionary studies with various focuses (e.g., Schindewolf 1933; Haas 1942; Donovan 1987, 1994; Landman 1988; Dommergues et al. 1989, 2006; Dommergues 1990; Korn 1995, 2003; Saunders et al. 1999, 2008; Korn and Klug 2002, 2003; Gerber et al. 2008). Although numerous studies on ammonoids have been published, many aspects of their phylogeny are still unresolved, which is partially due to the fact that only little is known about their soft parts (e.g., Cloos 1967; Riegraf et al. 1984; Lehmann 1985; Tanabe et al. 2000; Doguzhaeva et al. 2004; Landman et al. 2010) and covariation traits (Claude Monnet, Christian Klug, and Kenneth De Baets, unpublished data). Soft tissue imprints on the inside of the ammonoid body chamber have yielded some insights into ammonoid anatomy and chamber formation cycle (Richter 2002; Richter and Fischer 2002; Klug et al. 2008a). This is crucial to understand the formation of the aforementioned pearls that had grown in the body chamber of some Devonian ammonoids. House (1960) noted that the course of pit rows does not coincide with that of suture lines or with former apertures (i.e., growth lines). He concluded that various ligaments or other soft tissues attached to the inside of the shell marked the lines where these structures were formed.

In this study, we demonstrate that (i) the "Housean pits" are blister pearls, which encapsulated parasites and that (ii) the ammonoid hosts, as well as their parasitic counterparts, underwent a more than 10 million year co-evolution before the parasites either became extinct or stopped causing the formation of "Housean pits".

Institutional abbreviations.—GPIT, Institut für Geowissenschaften of Tübingen University, Tübingen, Germany; H, Steinmann Institute, Division of Palaeontology, University of Bonn, Germany; HS, Deutsches Bergbau-Museum, Bochum, Germany (German specimens are parts of the collections of C. Bartels); NM-L, National Museum, Prague, Czech Republic; PIMUZ, Paläontologisches Institut und Museum of Zürich University; MNHN-R, Musée d'Histoire Natuelle, Paris, France (Algerian specimens); SMF-HF, Senckenberg Museum, Frankfurt, Germany.

Material and methods

The majority of the material is from Emsian to Givetian strata. Most of the Moroccan material was collected by ourselves. Additional data were obtained from the literature, mainly from House (1960) and from Chlupáč and Turek (1983).

In order to compare the evolution of both host and parasite clades, we carried out a cladistic analysis. For the analysis of the parasites (i.e., the pits), we used the following parameters (Fig. 1):

Host size: Maximum diameter of the chambered part of the shell (phragmocone) of the ammonoid specimen showing the pits. We measured only the phragmocone because the body chamber is not always completely preserved. Where

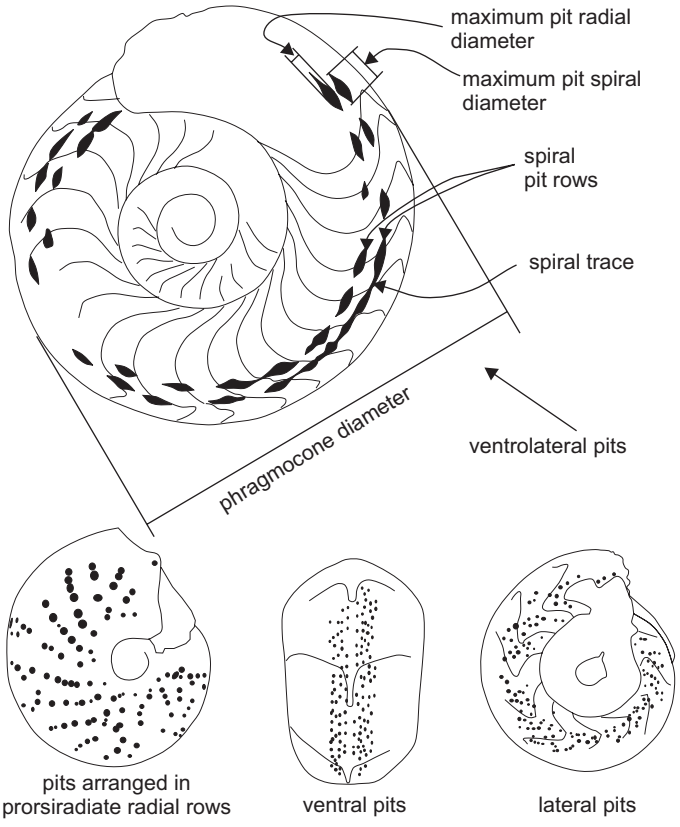


Fig. 1. Terminology and measurements. For more information on the specimens see Figs. 2 and 5.

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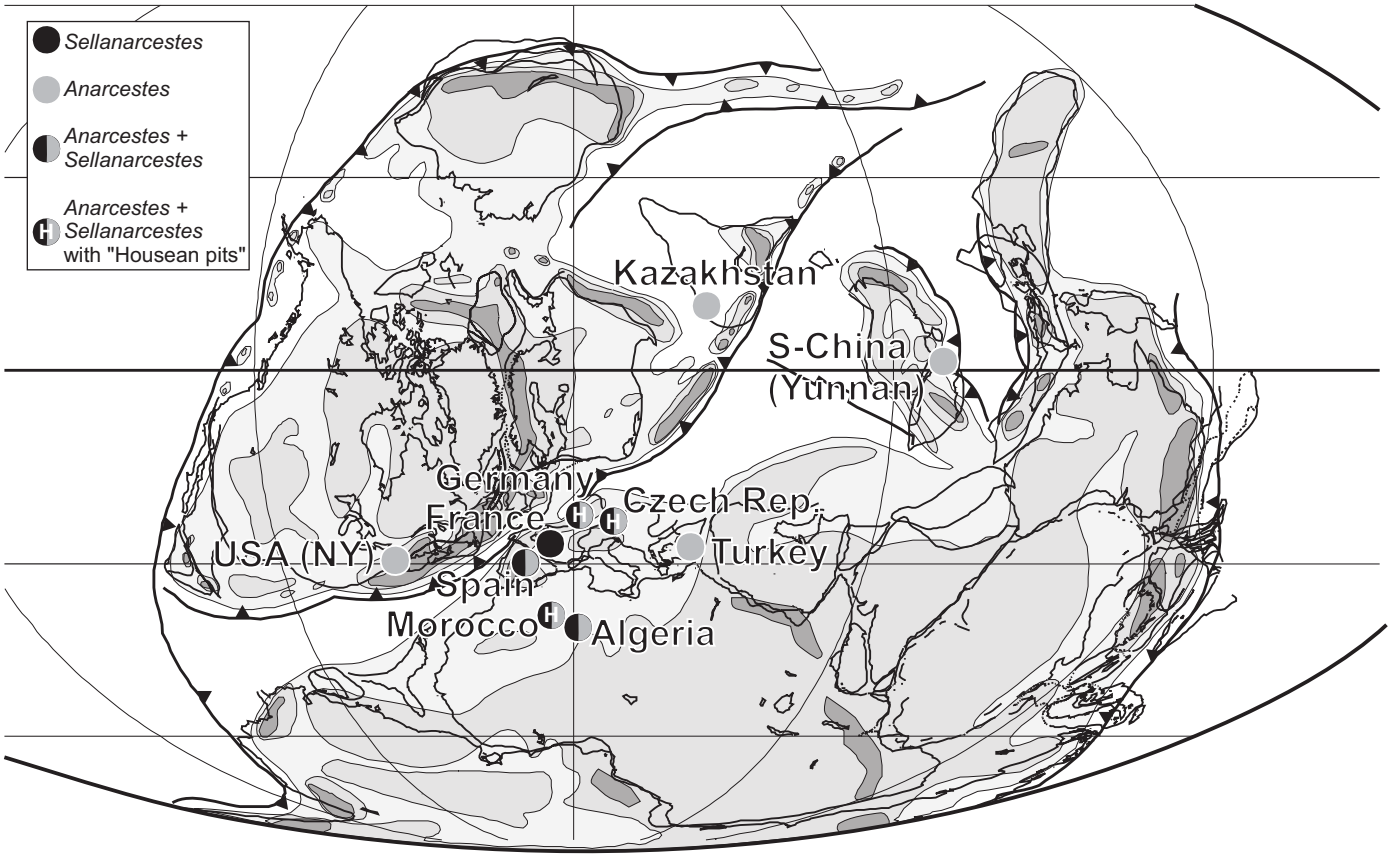


Fig. 2. Palaeogeographic map for the Emsian showing occurrences of the genera *Sellanarcestes* and *Anarcestes* with and without "Housean pits" of type 1. Modified from Scotese (2001).

several specimens were available, the size of the largest specimen was used because in all specimens, the traces of infestation continue more or less until the last septum. Alternatively, the ammonoid whorl height or apertural height may be used, but for this study, this does not make a significant difference.

Pit cross-section: Length of the pit in spiral direction (i.e., coiling direction) divided by the length of the pit in radial direction (perpendicular to tangents to the venter).

Pit size/diameter ratio: Relation between the pit-length in spiral direction and the diameter of the ammonoid phragmocone.

Spiral rows: Number of pits per radial row or number of spiral rows of pits (fused or not), respectively.

Radial rows: Number of radial rows of pits per half whorl.

Direction of radial rows: The radial rows of pits may be arranged parallel to a radius, rectiradiately (i.e., sweeping posteriorly towards the venter) or rursiradiately (i.e., sweeping anteriorly towards the venter).

Position of the pits: The distribution of pits is not completely random. They can be located in a ventral, ventrolateral, or lateral position. Truly umbilical or internal positions have not been found so far.

Spiral trace: In some ammonoid taxa (e.g., *Sellanarcestes*, Tables 1, 2), the spiral rows of pits are linked by a shallow spiral furrow, leaving a spiral trace in the internal mould. This is probably caused by a continuing irritation of the shell-secreting mantle (cf. Keupp 1986).

These data were transposed into a character matrix (Table 2), which was used for a simple cladistic analysis. The analysis was carried out with PAST (Hammer et al. 2001), using a heuristic algorithm and Wagner optimisation. 8200 trees were evaluated with a shortest tree length of 53. A simplified majority rule consensus tree is shown in the section on co-evolution. Since the structures are simple and the number of characters is low, the resolution and quality of the resulting cladograms are equally low. Nevertheless, the cladogram did reveal insights into the similarity of pits in the different ammonoid clades as well as the generalised trend of parasite evolution.

Terminology

For largely economic reasons, pearls have unsurprisingly attracted the attention of numerous scientists. An overview of this literature is given in Lauckner (1983: 852) and in Landman et al. (2001), which is summarised and cited in this paragraph. Lauckner (1983) also listed some important types of pearls. The classical pearls used in jewellery are called "true

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Table 1. List of ammonoid taxa that show pits with measurements (in mm) and ratios of the pits. Abbreviations: irreg., irregular; prorsi., prorsiradiate; rursirad., rursiradiate; *P.*, *Polygnathus*; *S.*, *Schmidtognathus*; *T.*, *Tortodus*.

Taxon	Geographical occurrence	Conodont zone	Phragmocone diameter	Max. pit spiral diameter	Max. pit radial diameter	Spiral trace	Nr. of spiral rows	Nr. of radial rows/ 1/2 whorl	Direction of radial rows	Position	Reference
Ivoites sp. nov. A	Germany	*P. excavatus*				no	2		radial	lateral	K. De Baets, C. Klug, D. Korn, C. Bartels, and M. Poschmann, unpublished data; see Fig. 6A–C
Ivoites sp. nov. B	Germany	*P. excavatus*			1–2.5	?	2	4–8	radial	lateral	
Chebbites reisdorfi	Morocco	*P. gronbergi*	ca. 30	0.7	0.2	no	1	7–25	–	ventral	Klug 2001; Klug et al. 2008b
Chebbites undosus	Morocco	*P. gronbergi*	ca. 30	1.3	0.3	no	1	12–50	–	ventral	Klug 2001; Klug et al. 2008b
Gracilites maghribensis	Morocco	*P. gronbergi*	ca. 30	0.7	0.2	no	1	45–70	–	ventral	Klug 2001; Klug et al. 2008b
Sellanarcestes draensis	Morocco	*P. serotinus*	ca. 50	2.5	0.7	yes	2–3	10–12	irreg.	ventro-lateral	Ebbighausen et al. in press
Sellanarcestes ebbighauseni	Morocco	*P. serotinus*	63	4	1.2	yes	2–3	15–18	irreg.	ventro-lateral	Klug 2002
Sellanarcestes neglectus	Czech Republic	*P. serotinus*	?	2.5	0.8	yes	2	?	irreg.	ventro-lateral	Chlupáč and Turek 1983
Sellanarcestes neglectus	Morocco	*P. serotinus*	55	4	1.3	yes	2	13–14	rursirad.	ventro-lateral	Klug 2002
Sellanarcestes solus	Morocco	*P. serotinus*	50	2.5	1.1	yes	3	13–15	rursirad., radial	ventro-lateral	Klug 2002; Ebbighausen et al. in press
Sellanarcestes wenkenbachi	Germany	*P. serotinus*	35	2	1	yes	2–3	10–12	radial	ventro-lateral	House 1960; Ebbighausen et al. in press
Sellanarcestes wenkenbachi	Morocco	*P. serotinus*	65	4.4		yes	2	12–14	irreg.	ventro-lateral	Belka et al. 1999; Klug 2002
Anarcestes crassus	Morocco	*P. serotinus*/ *P. patulus*	36	1.2	1	yes	1–3	? 10	irreg.	ventral	Ebbighausen et al. in press
Anarcestes latissimus	Morocco	*P. serotinus*	54	2.8	2	yes	3–4	12–15	irreg.	ventral	Klug 2002
Anarcestes cf. *latissimus*	Czech Republic	*P. serotinus*/ *P. patulus*	20	0.3	0.2	no	3–5	25–30	rursirad.	ventral	Chlupáč and Turek 1983
Anarcestes sp.	Czech Republic	*P. serotinus*/ *P. patulus*	22	1.5	1	no	2–4	9–12	irreg.	lateral	Chlupáč and Turek 1983
Anarcestes sp.	Germany	*P. serotinus*/ *P. patulus*	ca. 50	0.5	0.5	no	1–5	15–25	irreg.	lateral	House 1960
Crispoceras tureki	Morocco	*P. costatus*	45	0.4	0.4	no	3–4	25–30	irreg.	lateral	Klug 2002
?*Werneroceras* sp.	Czech Republic	*P. partitus*/ *P. costatus*	ca. 35	1	0.9	no	3–5	15–20	irreg.	lateral	Chlupáč and Turek 1983
Subanarcestes marhoumensis	Algeria	*P. partitus*/ *P. costatus*	ca. 55	0.2–0.3	0.2–0.3	no	4–6	20–40	irreg.	lateral	Göddertz 1987
Subanarcestes cf. *marhoumensis*	Great Britain	*P. partitus*/ *P. costatus*	ca. 15	0.3	0.3	no	5–10	10–12	prorsi.	lateral	House 1960
Sobolewia nuciformis	Algeria	*P. varcus*/ *S. hermanni*	19	2	2	no	1	1–2	(radial)	lateral	Petter 1959; Korn and Klug 2002
Sobolewia nuciformis	Great Britain	middle *P. varcus*	14	0.5	0.5	no	2–5	5–7	rursirad., radial	lateral	House 1960
Holzapfeloceras sp. III	Czech Republic	*P. partitus*–*T. kockelianus*	?	0.3	0.3	no	2–3	?	radial	lateral	Chlupáč and Turek 1983
Afromaenioceras sulcatostriatum	Morocco	middle *P. varcus*	18	0.1–0.2	0.1–0.2	no	4–6	18–22	prorsi.	lateral	this study

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Table 2. Character matrix of the various pit types used in the parsimony analysis. The matrix is largely based on Table 1 (for the taxon abbreviations compare with Table 1). Bold: uncertain values.

Taxon	Host size	Pit cross section (pit width/pit length)	pit dm ratio (pit length/ phragm. diameter)	Spiral rows	Radial rows	Direction radial rows	Position
Ivoites schindewolfi	2	2	1	1	0	0	2
Ivoites opitzi	2	2	1	1	0	0	2
Chebbites reisdorfi	1	0	0	0	1	0	0
Chebbites undosus	1	0	1	0	2	0	0
Gracilites maghribensis	1	0	0	0	2	0	0
Sellanarcestes draensis	1	0	2	2	1	3	1
Sellanarcestes ebbighauseni	3	0	2	1	1	3	1
Sellanarcestes neglectus 1	**2**	0	**2**	1	**1**	3	1
Sellanarcestes neglectus 2	3	0	2	1	1	2	1
Sellanarcestes solus	2	0	1	2	1	2	1
Sellanarcestes wenkenbachi 1	**1**	0	2	2	1	0	1
Sellanarcestes wenkenbachi 2	3	**0**	2	1	1	3	1
Anarcestes crassus	1	1	1	1	1	3	0
Anarcestes latissimus	3	1	1	2	1	3	0
Anarcestes cf. *latissimus*	0	1	0	3	2	2	0
Anarcestes sp. 1	0	1	2	2	1	3	2
Anarcestes sp. 2	2	2	0	3	1	3	2
Crispoceras tureki	2	2	0	2	2	3	2
?*Werneroceras* sp.	1	1	1	3	1	3	2
Subanarcestes marhoumensis	3	2	0	3	2	3	2
Subanarcestes cf. *marhoumensis*	0	2	0	3	1	1	2
Sobolewia nuciformis Algeria	0	2	3	0	0	0	2
Sobolewia nuciformis UK	0	2	1	3	0	2	2
Holzapfeloceras sp. III	**0**	2	**0**	2	1	0	2
Afromaenioceras sulcatostriatum	0	2	0	3	1	1	2
Character coding:	0: < 30	0: < 0.5	0: < 0.03	0: 1 row	0: < 11	0: radial	0: ventral
	1: 31–40	1: 0.5 to 0.9	1: 0.03 to 0.05	1: 2 rows	1: 11 bis 20	1: prorsiradiate	1: ventrolat.
	2: 41–50	2: > 0.9	2: 0.06 bis 0.1	2: 3 rows	2: > 20	2: rursiradiate	2: lateral
	3: > 50		3: > 0.1	3: > 3 rows		3: irregular	

nacreous pearls" and consist of successively deposited layers of shell substance (i.e., conchiolin, in which the crystals of inorganic matter are deposited in the same manner as in shell), enclosing a central nucleus. By contrast, "blisters" are "nacreous protuberances on the inner surface" of the shell, which "result from the intrusion of foreign bodies between mantle and shell or from perforation of the valves by shell-burrowing organisms." "Non-nacreous pearls ('muscle pearls') may occur within connective tissues", but such pearls are highly unlikely to be fossilised. Therefore, the structures reported herein, belong to the "blister" pearl type. In the following text, we use the shorter term "pearl" for "blister pearl" and the terms "pits" or "Housean pits" are here used for the moulds left behind in the internal moulds by the dissolved blister pearls. These pits are not to be confused with pits inside the shell, which can also be caused by trematodes (Ruiz and Lindberg 1989; Ituarte et al. 2005).

"Housean pits": distribution and types

"Housean pits" occur quite commonly in several ammonoid genera of the Anarcestaceae and rarely in the Pharciceratataceae, but not in the time equivalent Mimagoniatitaceae and Agoniatitaceae. They have not been recorded from all genera of the two former superfamilies, but some of their genera, such as *Anarcestes* and *Sellanarcestes*, frequently show rather large, usually oval, spirally arranged pearls (see Table 1 for dimensions). Naturally, the outer shell needs to be missing because otherwise the pits are covered by the shell, and thus, are not visible. Quantification of the abundance of the pits is therefore hampered by these differences in preservation. Nevertheless, Chlupáč and Turek (1981: 122) estimated that about one third of representatives of the genus *Sellanarcestes* carry

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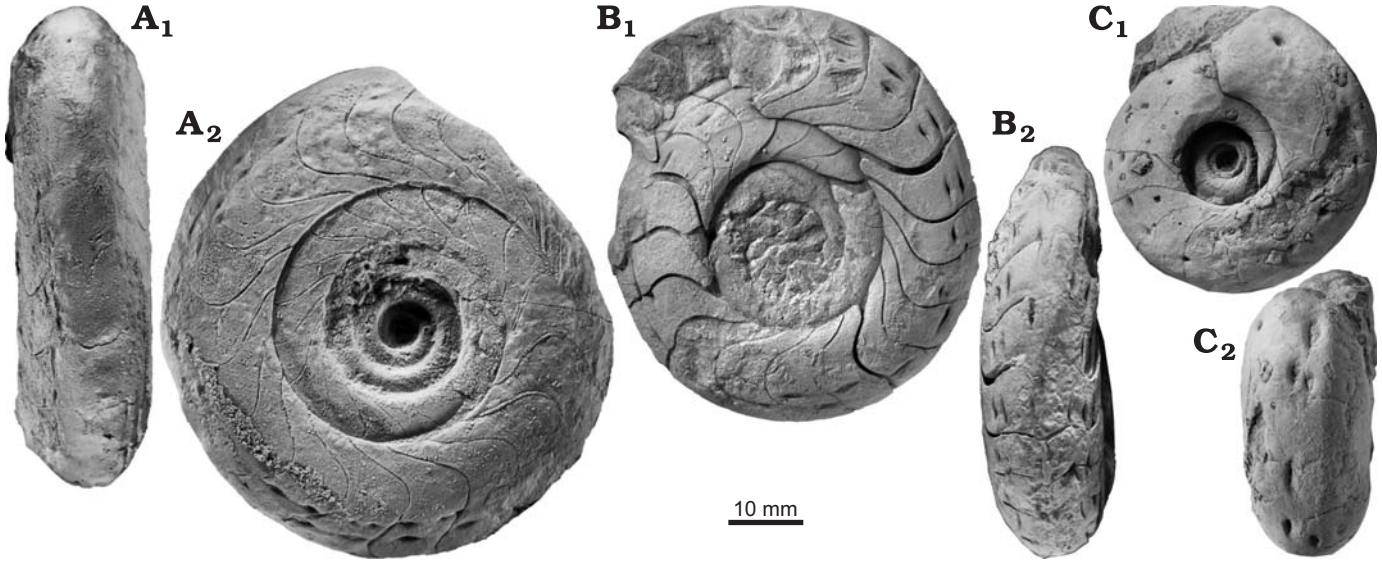


Fig. 3. "Housean pits" type 1. **A**. *Sellanarcestes ebbighauseni* Klug, 2002, GPIT 1871-171, *Sellanarcestes wenkenbachi* Zone, Emsian, northern Jebel Amessoui, Tafilalt, Morocco, from Klug (2002); in ventral (A_1) and lateral (A_2) views. **B**. *Sellanarcestes* cf. *ebbighauseni* Klug, 2002, PIMUZ 28582, *Sellanarcestes wenkenbachi* Zone, Emsian, Jebel Ouaoufilal, Tafilalt, Morocco; in lateral (B_1) and ventral (B_2) views. **C**. Large pits in *Anarcestes* sp., PIMUZ 28581, late Emsian, Jebel Mech Agrou, Tafilalt, Morocco; in lateral (C_1) and ventral (C_2) views. All specimens coated with NH_4Cl.

pits. Among our sectioned *Sellanarcestes* specimens from the late Emsian strata of Oufrane, more than 50% display pits. In a fauna of 18 specimens of *Anarcestes* spp. from Hamar Laghdad (Tafilalt, Morocco), we counted 13 specimens with pits (> 70%); the remaining specimens without pits are rather small (usually < 10 mm dm). In the Givetian *Afromaenioceras sulcatostriatum* from the vicinity of Taouz (Tafilalt, Morocco), only three specimens out of about 200 specimens show pits (ca. 1.5%). Remarkably, some genera such as *Crispoceras* and *Afromaenioceras* carry rather small pits (< 0.5 mm) at comparable shell sizes. The Devonian of Moroccan Anti-Atlas is more suited for an abundance study as it yields several intervals with abundant fossils (such as, e.g., ammonoids, bactritoids, bivalves, nautiloids) in internal mould preservation (Belka et al. 1999; Klug 2001, 2002a, b; Klug et al. 2008a, b; Kröger 2008; De Baets et al. 2010).

Geographic occurrences are so far limited to Great Britain, Germany, Czech Republic, Morocco, and Algeria (Table 1), i.e., the southern margin of the Rheic Ocean and the Palaeotethys or northern Gondwana, respectively (Fig. 2). Due to the scarcity of rich materials of Emsian and Eifelian age from outside the Rheic Ocean and the Palaeotethys, it is not clear whether this geographic range reflects the palaeogeographic limit of parasite distribution or whether the parasites were distributed globally and simply were not discovered elsewhere yet. As far as the distribution of pits of type 1 among the late Emsian genera *Sellanarcestes* and *Anarcestes* are concerned, it appears like the occurrences of this pit-type is limited to the centre of the distribution of the two genera while in marginal parts of their distribution, they do not display these pits (Fig. 2). Nevertheless, materials of these genera are less common in these marginal regions and this might thus be caused by a sampling bias or a preservational bias.

A peculiar occurrence is the sobolewiids from the Middle Devonian of Algeria (Petter 1959; Korn and Klug 2002). Unusually, these specimens retain shell remains, but not at the locations of the "Housean pits", where a tiny subcircular hole can be seen at the centre of the nearly circular spots without shell. The shell is just weathered away sooner above the pits (compare the specimens in Fig. 5B and C as opposed to the more heavily weathered specimen in Fig. 5A), which indicates that the shell was thinner at the position of the pits, which is true because part of the inner shell actually is detached from the shell wall, forming the pearl. In the sobolewiids, four to five pits occur in a single row on the flanks of these sobolewiids.

Common to all the above-mentioned pits is that they were found only on the phragmocone and the posterior quarter of the body chamber. Based on a morphological examination of the pits, and supported by the result of the cladistic analysis, three late Emsian to Givetian pit types can be differentiated (Fig. 2):

Pit type 1.—The most common type of pit can be found on representatives of *Anarcestes* and *Sellanarcestes*. The pits are rather large in relation to conch size (see Table 1), lengthened in spiral direction and are thus more or less oval. In most cases, the spiral pit rows are connected by a spiral trace, which represents a spiral shell thickening (Fig. 3).

Age: Late Emsian.

Pit type 2.—The second most common pit type was only found in Middle Devonian ammonoids of the genera *Anarcestes* (?), *Afromaenioceras*, *Crispoceras*, *Sobolewia*, and *Subanarcestes*. In this type, the pits are much smaller than in type 1, they occur in greater numbers, and they are either chaotically arranged or in more or less radial rows (for di-

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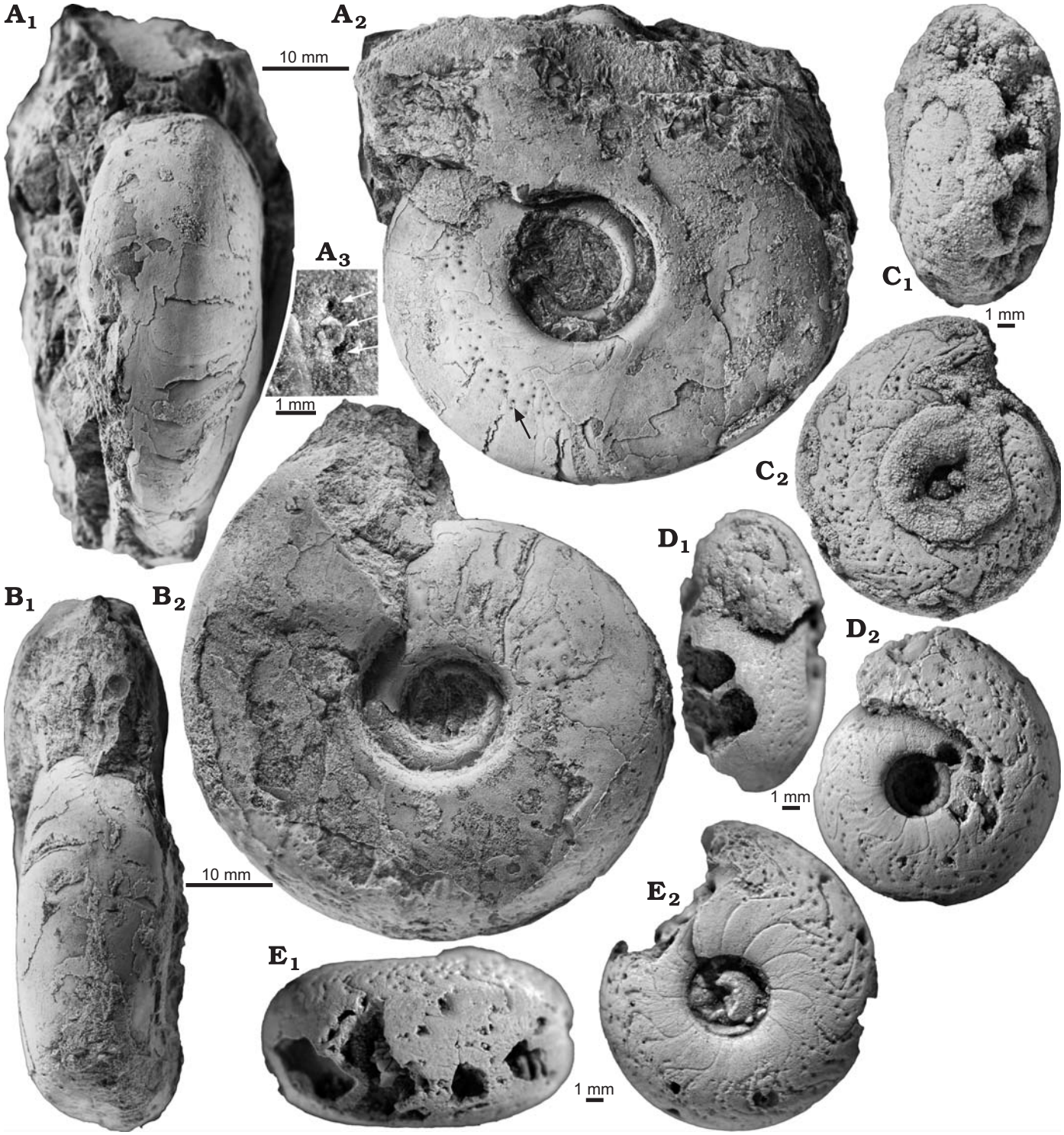


Fig. 4. "Housean pits" type 2. **A**. *Crispoceras tureki* Klug, 2002, PIMUZ 28591, *Pinacites jugleri* Zone, Eifelian, Jebel Ouaoufilal, Tafilalt, Morocco; in dorsal (A_1) and lateral (A_2) views; A_3, detail of A_2, whose position is pointed out by the black arrow in A_2, note the three pits (white arrows), the middle pit shows the pit filling and the base of the tube cross section. **B**. *Crispoceras tureki* Klug, 2002, PIMUZ 28590, *Pinacites jugleri* Zone, Eifelian, Jebel Ouaoufilal, Tafilalt, Morocco; in lateral (B_1) and (B_2) dorsal views, pits continue into the body chamber. **C**–**E**. *Afromaenioceras sulcatostriatum* Bensaïd, 1974, Givetian, Jebel Ouaoufilal, Tafilalt, Morocco; in ventral (C_1, D_1, E_1) and lateral (C_2, D_2, E_2) views. **C**. PIMUZ 28592. **D**. PIMUZ 28593. **E**. PIMUZ 28594. All specimens coated with NH_4Cl except in A_3.

mensions see Table 1). There are transitional forms between type 1 and type 2, where the pits have an intermediate size, and sometimes pits of type 1 are also more or less radially arranged. The internal tube was seen only rarely in type 2 pits, which may be due to their small size (Fig. 4, Table 1).

Age: Late Emsian to Givetian.

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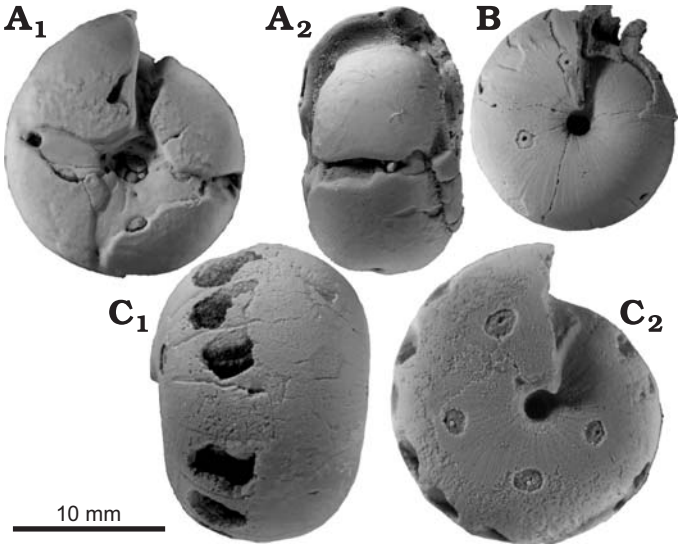


Fig. 5. "Housean pits" type 3. *Sobolewia nuciformis* (Whidborne, 1889), three specimens kept under the same number (MNHN-R.08459), Givetian, Redjel Iamrad, Algeria, Jacques Follot collection. **A**. A heavily weathered specimen in which the erosion was most intense around the pits; lateral (A_1) and (A_2) dorsal views, weathered specimen, where the shell broke at the pits and weathering intensified in those radii. **B**. Lateral view of a specimen showing only two pits, additional pits probably covered by shell. **C**. The best preserved specimen, previously published in Korn and Klug (2002: fig. 52B), in ventral (C_1) and lateral (C_2) views, well preserved specimen, where the shell broke off only at the four lateral pits, showing the tube cross section in the pits (the globular structures in the centre of the pit at the bottom and on the left are artefactsfrom the production of the cast). Images taken from epoxy casts. All specimens coated with NH_4Cl.

Pit type 3.—This type was found in only one locality and only one species but in five specimens of *Sobolewia nuciformis* from Algeria. It is characterised by roughly circular pits, which show the circular end of the tube filling, preserved as a hole, in the centre (Fig. 5).

Age: Givetian.

Two additional pit types can be differentiated in ammonoids from the Early Emsian:

Pit type 4.—Solely in the genus *Ivoites* from the German Hunsrück Slate, several specimens with peculiar paired pits have been examined (Fig. 6A–C), which will be described in detail by Kenneth De Baets, Christian Klug, Dieter Korn, Christoph Bartels, and Markus Poschmann (unpublished data). These pits are peculiar because they are shallow, radially arranged, always paired, touch each other and they are linked to a pair of widely spaced ribs. In addition, they occur at the aperture, indicating that they were formed at this point. This type thus differs in the place of the initial formation of the pearls, which in pit types 1–3 form near the apical end of the body chamber. This apertural location might reflect an evolutionary change in site specificity of the parasite that formed pit types 1–3 or a difference in parasite type. Also if the mantle itself was the assumed tissue that was preferably infested by the parasite, the parasite might have changed its preference from the apertural mantle to the mantle near the cephalic retractor muscle attachment site, where the palliovisceral ligament or the mantle myoadhesive band was attached to the inside of the shell-tube (for nautiloid anatomy compare Mutvei 1957, 1964). One specimen of *Ivoites* also displays a structure that resembles the spiral trace seen in some *Sellanarcestes* specimens.

Age: Early Emsian.

Pit type 5.—Many specimens belonging to the early Emsian ammonoid genera *Chebbites*, *Gracilites*, and *Lenzites* (see Fig. 6D) display kidney-shaped to oval pits in the middle of the venter (Becker and House 1994; Klug 2001; Korn and Klug 2002; Klug et al. 2008b). These pits usually coincide with the most posterior points of the hyponomic sinus of their growth lines (Fig. 6D, E).

Age: Early Emsian.

Origin of the shell material that lined the pits

Since the initial description of the pits by House (1960), the cause for the formation of the "Housean pits" has remained somewhat unclear (discussions in Chlupáč and Turek 1981, Keupp 1986, as well as in Davis and Mapes 1999). As explanations for the pits, House (1960) listed the following possibilities: (i) they were a normal part of the shell and served a distinct function such as muscle attachment, (ii) they might have been "alien organic growths", although he did not have any material to demonstrate this, (iii) they might have been caused by borings (he also did not have evidence for this) or (iv) they might have represented "localised shell thickenings", which is a rather catch-all formulation in which House (1960) speculated that these structures were actually covered by the ammonoids' shell, secluding some organic or inorganic object. Notably, he did not favour any of these interpretations because he simply lacked evidence that would support any logical conclusion how to explain the formation of the pits.

Recently, we have produced sagittal (longitudinal) sections of several *Sellanarcestes* specimens from Oufrane (Figs. 7, 8), a locality in the Moroccan Dra-Valley (Ebbighausen et al. 2004). These sections were made through the plane of symmetry to measure certain morphologic features throughout ontogeny in order to quantify the embryonic shell and the septal spacing (see, e.g., Kraft et al. 2008). One of the polished sections shows detailed interior views of the "Housean pits". This view shows that the shell covers a foreign object, which thus is within the ammonoid shell. The only part of the shell affected is the inner part of the normal inner ammonoid shell layer. Consequently, these structures may indeed be termed pearls because the abnormal form of shell secretion has an external cause of a foreign object or organism. Inside many of the ammonoid pearls, however, tiny tubes were discovered that are attached to the shell wall and slightly inclined towards the ap-

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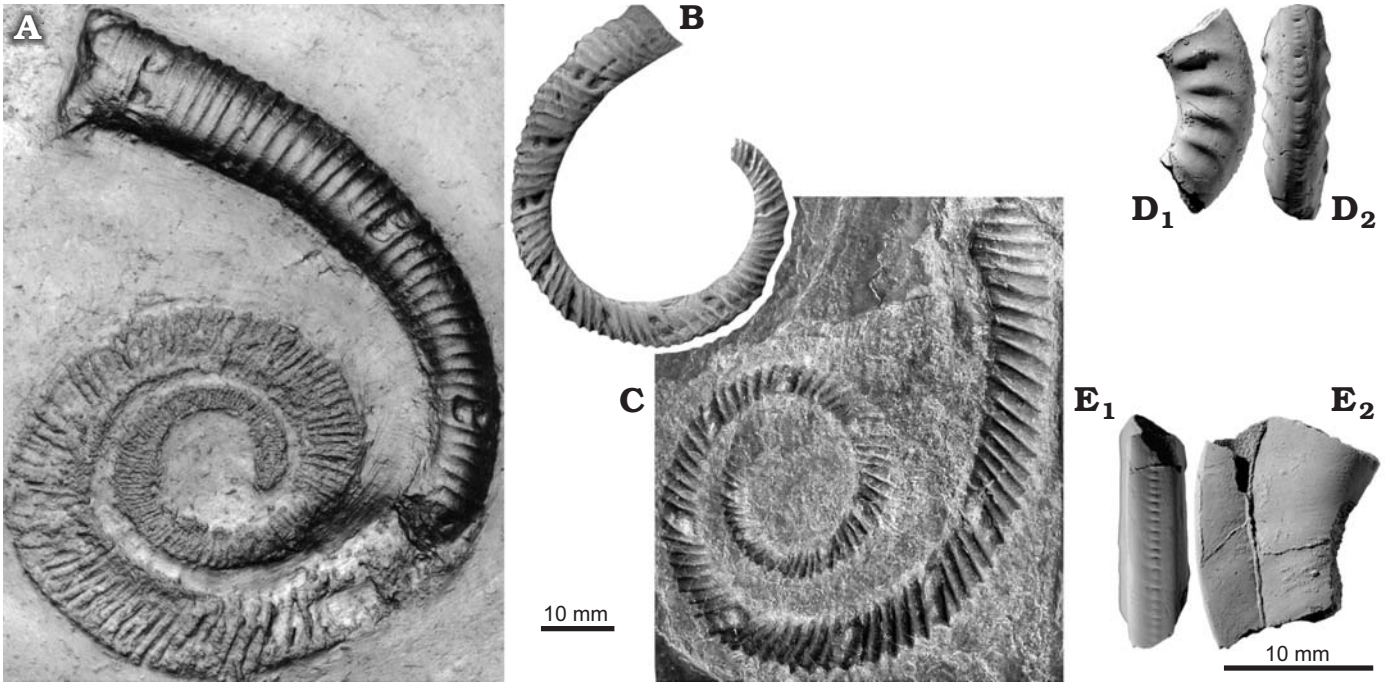


Fig. 6. **A**–**C**. "Housean pits" type 4, *Ivoites* sp. nov. B, early Emsian, middle Kaub Formation (Hunsrück Slate), W-Germany; the images were stretched in PhotoShop in order to reconstruct the original form. **A**. HS 371 (Bartels collection), Bundenbach (Eschenbach–Bocksberg quarry); note the flattened phragmocone. **B**. H 55a (Lehmann collection), Bundenbach (Eschenbach–Bocksberg quarry); note the spiral trace between the aperture and the first pit pair. **C**. SMF-HF 940 (Senckenberg collection), Herrenberg (Schielebach quarry). **D**, **E**. "Housean pits" type 5, early Emsian, Ouidane Chebbi, Tafilalt, Morocco, from Klug et al. (2008). **D**. *Chebbites reisdorfi* Klug, 2001, PIMUZ 7484; in lateral (D_1) and ventral (showing pits) (D_2) views. **E**. *Gracilites maghribensis* Klug, 2001, PIMUZ 7490; in ventral (showing pits) (E_1) and lateral (E_2) views. All specimens coated with NH_4Cl except in A and C.

erture (Figs. 5, 7, 8). These tubes are remains of a biological organism and falsify hypothesis 3 (see next chapter), which suggested that inorganic objects have caused the formation of the pearls and were overgrown by ammonoid shell.

Was the pearl formation caused by parasites?

For this discussion, the tentative interpretations by House (1960) and by Keupp (1986) are subsequently listed as the following hypotheses:

Hypothesis 1: The pits are a normal part of the shell (null-hypothesis).

Hypothesis 2: The pits are borings, repaired by the mantle producing a pearl.

Hypothesis 3: The pits were formed by inorganic particles (e.g., sand grains), overgrown by ammonoid shell (a classical pearl formation scenario)

Hypothesis 4: The pits are soft-tissue remains that were left behind during the forward movement of the ammonoids' soft parts and then overgrown by shell.

Hypothesis 5: The pits were formed by a parasite (dead or alive, partial or complete) overgrown by ammonoid shell.

Hypothesis 6: The pits were caused by a foreign organism, which lived on the ammonoid shell commensally.

Tests of the hypotheses

Test of hypothesis 1.—For this hypothesis to be correct, the pearls must occur in all specimens of at least one species if not in an entire clade. This is not the case. Additionally, the pits are almost never symmetrically arranged (Fig. $3C_2$). Therefore, hypothesis 1 is refuted for pit types 1 to 3. For type 5, this hypothesis appears likely because of their rather regular appearance and their good correlation with growth lines, and for type 4, evidence is lacking as commonly only one side is prepared. We did not find tubes inside pit type 4, and they are often linked to breaks in shell growth. Nevertheless, not all specimens of a particular species show pits and there is no clear correlation between the spacing of the pits and the septa, and one specimen shows a spiral trace, which documents the mantle irritation caused by the foreign organism or particle (cf. Keupp 1986; see Fig. 6B).

Test of hypothesis 2.—Although numerous ammonoid specimens with pits and shell remains have been sectioned through the pits, no trace of borings penetrating the outer shell have been found (Figs. 7, 8). Therefore, hypothesis 2 lacks any supporting evidence and it must be rejected at this time.

Test of hypothesis 3.— In all cases, where the content of the pits could be studied, a fine-grained matrix, a sparitic matrix, and/ or the aforementioned tubes were seen. There is no indi-

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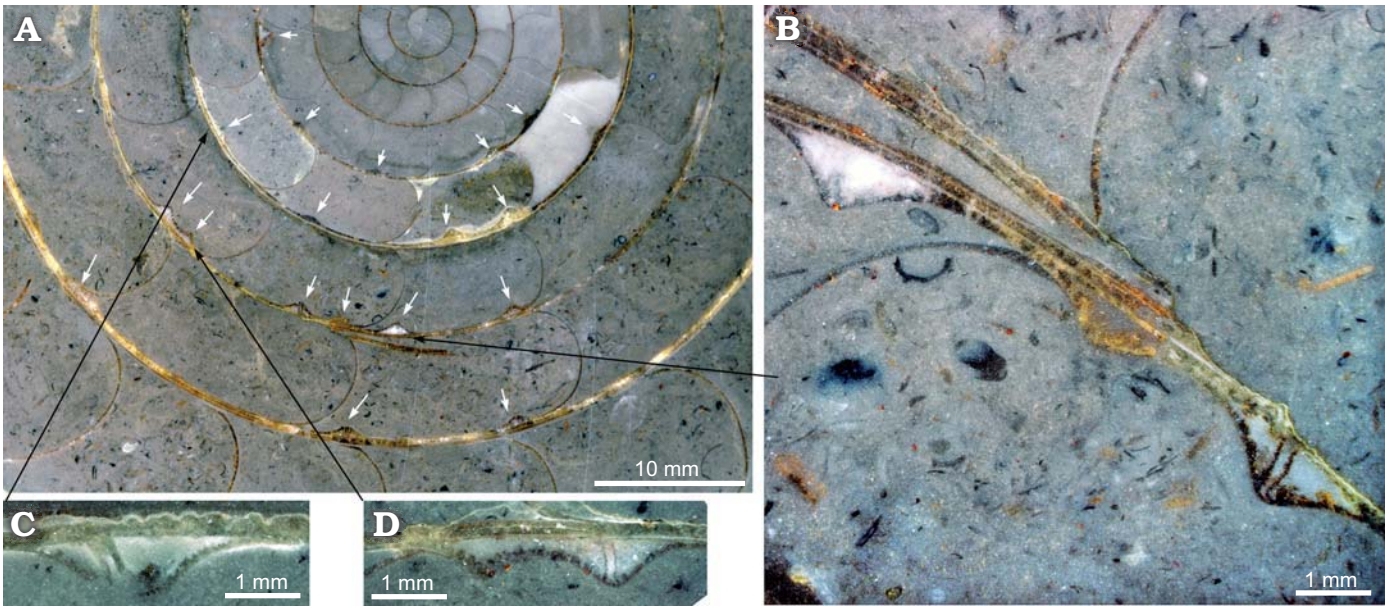


Fig. 7. Longitudinal section through the well preserved specimen PIMUZ 28583 of *Sellanarcestes* spp., *Sellanarcestes wenkenbachi* Zone, Emsian, Oufrane (S of Tata), Morocco. **A**. +/- median section displaying many "Housean pits", most with internal tube; overview. "Housean pits" are marked by white arrows. **B**. Three closely spaced pits, two displaying the internal tubes, the remaining void inside the pit is filled with a fine-grained sparitic matrix, note the continuous ammonoid shell layer covering the pits and the septum, which grew on the pit wall, note the distinguishable shell layers, which are recrystallised to varying degrees. **C**. A corroded pit with tube, note the continuation of the innermost ammonoid shell layer. **D**. Two adjacent fused pits, only the right pit shows the delicate internal tube, mural part of septum on the left.

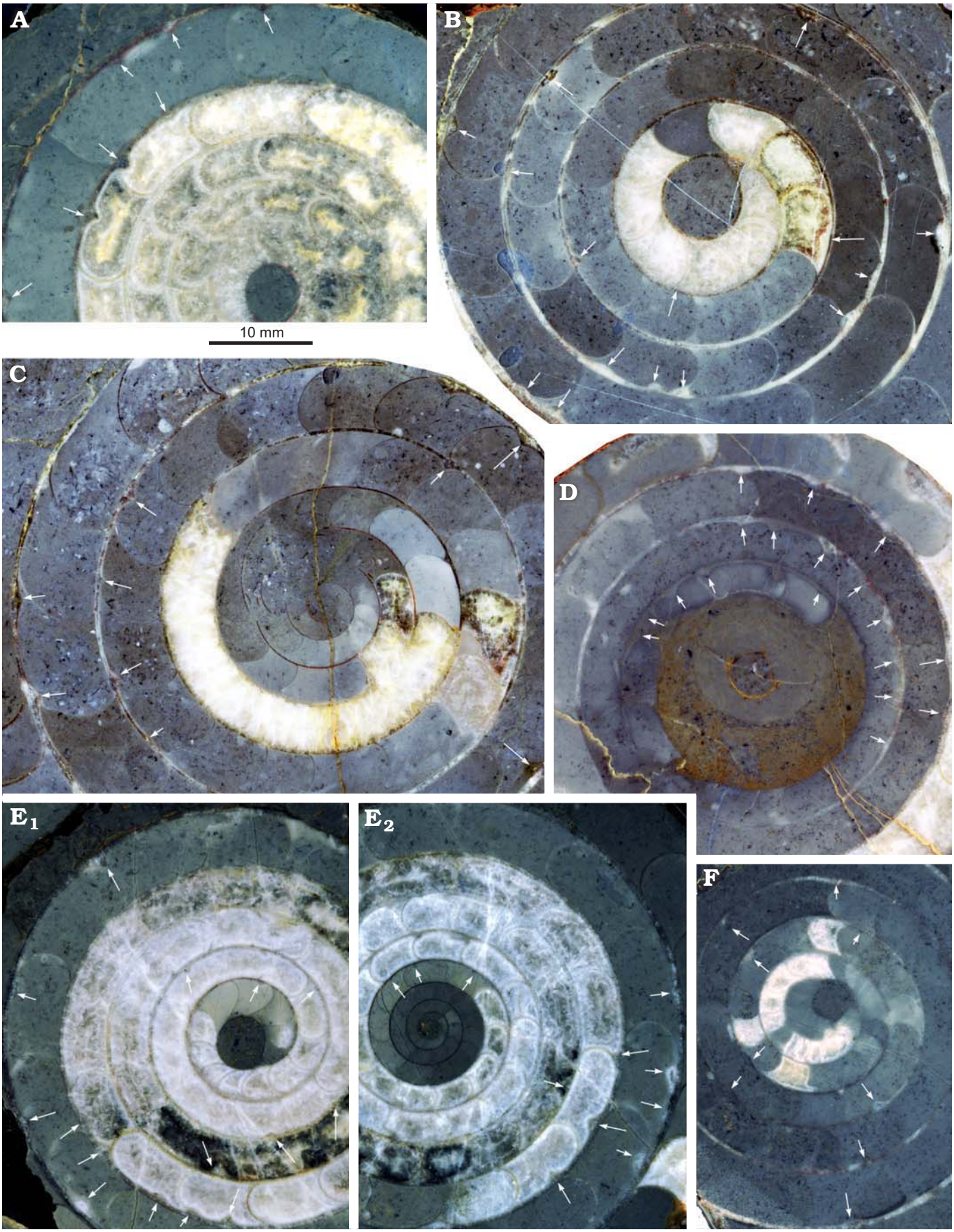
cation of any sand grains or other inorganic particles. The only distinguishable content of the pits are tiny calcareous tubes of biological origin. Thus, hypothesis 3 is highly unlikely in the cases involved in this study because there is no evidence to support the hypothesis.

Test of hypothesis 4.—This hypothesis is currently not testable because it requires soft-tissue preservation, which is rare in ammonoids and only occurs in exceptional preservational conditions (Cloos 1967; Riegraf et al. 1984; Lehmann 1985; Tanabe et al. 2000; Doguzhaeva et al. 2004; Landman et al. 2010). The presence of tubes in the pits somewhat contradicts this hypothesis because in so far as is known, the mantle musculature does not form strands of this size or form in Recent nautilids (see, e.g., Klug et al. 2008a), and blood vessels would not have a dead end (the tubes are ending at the inside of the ammonoid shell). Additionally, the pearls do not occur in juvenile specimens (for example, the smallest *Anarcestes* shows pits first at a diameter of ca. 10 mm). Hypothesis 4 is therefore not fully refuted, but it appears unlikely.

Test of hypothesis 5.—Since the hypothetic parasite is not preserved, how could a parasite infestation be evidenced in the present cases (compare Hengsbach 1990, 1991, 1996)? Several aspects of these pit-occurrences yield indications: If it was a part of the ammonoid animal, the pits would be arranged symmetrically, which is not the case. Additionally, the formation of pit rows has nothing in common with the formation of septa or the aperture because the course of the pit rows only rarely coincides with either of these structures, except in types 4 and 5, which are linked with the aperture. It can thus not be linked conveniently to the formation of some soft-tissue attachment structure like muscle attachment. Furthermore, only a varying percentage of specimens in different populations or species show pits. If the pits were a part of a normal shell, they would occur in all shells and also, small specimens (< 10 mm) never display the pearls. As a regular part of the shell like, e.g., some kind of soft-tissue attachment site, it should occur from the first whorl onward and in a regular pattern. Moreover, not all species of one clade have pits, even in such species inhabiting the same region at the same time and with sometimes similar shell shapes. This is hard to explain without the involvement of parasites because sometimes, several species of one clade co-occur in space and time and thus lived in the same habitat. Why should then one group suffer from this deformation while the other does not? There was apparently a distinct host-specificity, as in some modern parasites. The pits do not occur in strict regular rhythms or rhythms perfectly correlated with growth rhythms of the ammonoid specimen, and therefore, the pits are probably not related to the growth of the ammonoid (compare House 1960). Regional differences occur in the abundance and presence or absence of pits within the same

Fig. 8. Longitudinal sections through six specimens of *Sellanarcestes* spp., *Sellanarcestes wenkenbachi* Zone, Emsian, Oufrane (S of Tata), Morocco. They all display "Housean pits", marked by white arrows. **A**. PIMUZ 28584, subcentral section. **B**. PIMUZ 28585, subcentral section. **C**. PIMUZ 28586, median section. **D**. PIMUZ 28587, subcentral section. **E**. PIMUZ 28588; subcentral (E_1) and median (E_2) section. **F**. PIMUZ 28589, subcentral section. Note the absence of pits in the initial whorls of all specimens. →

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taxon (compare, e.g., Bockwinkel et al. 2009) at the same time interval. Another point in case is that pit-types 1 to 3 contain tiny calcareous tubes, which are closed toward the outer shell and toward the inside by the ammonoid shell overgrowing the tube. The irregular shape of the tubes, which are more or less inclined aperturally, toward the inside of the shell tube, indicate that the organism inhabiting the tube reacted to the forward movement of the soft body as the ammonoid grew (Fig. 7). Last, infestation occurred during the life of the ammonoid because it reacted by forming the pearl (Figs. 3–8). For type 5-pits, it was suggested by Royal H. Mapes (personal communication 2010) that these may have been formed by a parasite, which had infested the hyponome, thus explaining the midventral localisation of the pits. Therefore, we favour the explanation of pit types 1 to 3 and, with some reservation, also 4 and 5 as having been caused by a parasite.

Test of hypothesis 6.—Commensalism is highly unlikely, because no sea-water circulates in the rear body chamber between the mantle and shell and no holes or perforations were found in the external regions of the shell. Therefore, the organism had to cross the ammonoid soft-parts to reach the place where it was overgrown and possibly fed on the ammonoid host, because it had no direct contact to the ammonoid's environment.

Based on these characteristics, only the possibility of a parasite infestation can be used to explain the occurrences, arrangement, and shape of the pits.

Which parasite caused the formation of the tubes?

Answering this question is hampered by the absence of fossilised soft parts of the parasite. However, by comparison with modern parasites, an informed conclusion can be generated about the identity of the ammonoid parasite, with some reservation, however. The size, shape and oblique orientation of the tubes are similar to those of trematodes, which are encapsulated by invertebrates such as, for example, in the polychaete shown by Rangel and Santos (2009: fig. 5) where a metacercaria (intermediate stage) is encapsulated in a setal sac. Trematode infestations have been documented in various molluscs (digenetic trematodes in bivalves: Götting 1979; Keupp 1986; Ruiz and Lindberg 1989; Ituarte et al. 2001, 2005; Littlewood and Donovan 2003; Huntley 2007. Gastropods: Lebour 1918; Nikitina 1986; Ataev and Avanesyan 2000; Curtis 2002), including cephalopods (e.g., Overstreet and Hochberg 1975; Hochberg 1990; Shukhgalter and Nigmatullin 2001). Fossil platyhelminths are exceedingly rare and usually only indirectly preserved as traces or pearls in molluscs (Conway Morris 1981, 1988, 1990; Ruiz and Lindberg 1989; Knaust 2009). Nevertheless, Conway Morris (1981: 493) stated that "Pearls in recent molluscs arise from a variety of irritants, but in many instances the sources are trematode larvae". In Recent bivalves, trematode-induced pearls in the shell are typically formed by metacercariae of gymnophallids and have been documented for mytiloid, nuculoid, and veneroid bivalves (Götting 1979; Keupp 1986; Ituarte et al. 2001, 2005; Littlewood and Donovan 2003). These trematode-induced pearls/pits together with spionid-induced borings are highly characteristic and can be recognised in the fossil record (cf. Ruiz and Lindberg 1989; Huntley 2007). Bivalves can react very differently, which is thought to reflect the degree of adjustment reached in the host-parasite relationship (Ituarte et al. 2005): from minimal or no host reaction in the ideal case, to intermediate stages with a host reaction and survival of the parasite without apparent damage to the bivalve (shell pits, gelatinous coverings, igloo-shaped coverings or open blisters) or reactions leading to the parasite's death (pearls and closed blisters). The latter reflect a successful host strategy.

The trematod-venerid system described by Ruiz and Lindberg (1989: fig. 1D) shows some similarity to the Devonian ammonoid pits but also differences. For example, some pits in the bivalve shells have a central ovoid structure where the parasite was probably encapsulated. Additionally, the distribution, abundance, and shape of the pits resemble those of the ammonoids. The same holds true for the digenean-nuculoid/veneroid system studied by Ituarte et al. (2001, 2005). In this case, metacercarias formed tubes surrounded by bivalve pearls. An important difference to the ammonoid pits, however, is the presence of an opening in the pearl, which was not yet seen in the ammonoid blisters (except openings, which probably were caused by corrosion of the shell as seen in Fig. 7C). Perhaps there was an opening, which was overgrown at a stage where the parasite had already left its tube. The parasite also irritates the mantle tissue as evidenced by the spiral trace. The here described ammonoid pearls somewhat resemble those formed by mytilid bivalves as a reaction to a trematode reported by Götting (1979). This is remarkable, although in the mytilid case, the pearls were rather spherical and even free pearls occurred, enclosing metacercarias and eggs.

Nevertheless, the question remains whether the pits could have been formed by other parasites besides trematodes. Boring groups like clionid sponges can be excluded since no holes penetrating the outer shell of the ammonoid have been discovered in the many sections of the ammonoid blister pearls we have produced and examined. A phoronid settling inside an atrypid brachiopod has been reported by MacKinnon and Biernat (1970), but this was strongly criticised by Emig (2010). The structure that had formed around the phoronid is much larger, has a shape differing from the ammonoid pits, and displays two distinct openings at the free end, thus differing from the ammonoid pits. The only possible parasites known from recent *Nautilus* are copepods (Hochberg 1990). They are well-known from Recent coleoids (Hochberg 1990), too, but mainly reside in the gills and live mostly commensally. Furthermore, copepods accidently trapped between

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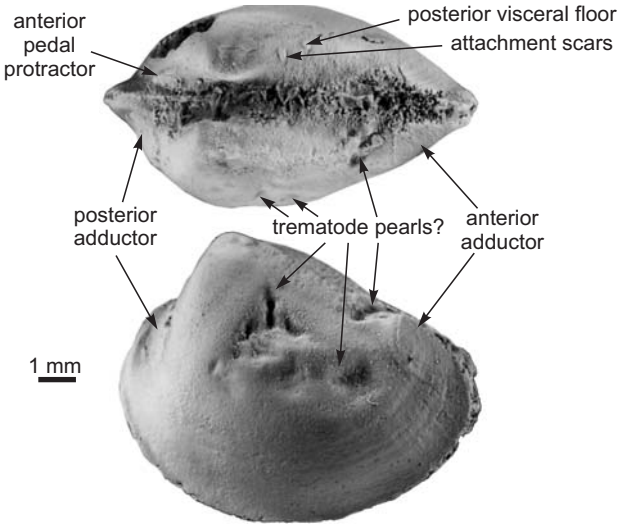


Fig. 9. Trematode (?) pits in the internal mould of an Early Devonian palaeotaxodont bivalve (modified after Klug et al. 2008b: pl. 3). *Nuculoidea grandaeva* (Goldfuss 1837), PIMUZ 7338, Faunule 2, *Polygnathus gronbergi* (*Polygnathus excavatus*) Zone, early Emsian, Ouidane Chebbi (Tafilalt, Morocco) in dorsal (**A**) and lateral (**B**) views.

mantle and shell would result in isolated blister pearls instead of regularly arranged pearls.

In modern molluscs, trematode parasitoses (including cephalopods; Overstreet and Hochberg 1975; Hochberg 1990) are common, making it likely that trematode infestations have been common before, although they rarely left distinguishable traces in the fossil record. Additionally, the fact that the parasite infestation can be survived by the host over a long time, even if the infestation is intense, points at an early origin of the digenetic trematode-mollusc system (Dönges 1988: 150). Apparently, the ammonoids under consideration survived intense infestations over long periods of time, as ammonoid specimens displaying many large pits (up to 4 mm long) reached their normal adult size with pits (sometimes several mm long) being formed continuously until the presumed anterior end of the annular elevation (Fig. 4A, B). It has been suggested by John Huntley (personal communication 2010) to test whether infected specimens differ in size from the healthy specimens of the same species. This is, however, nearly impossible to test because (i) determining maturity is not always possible and (ii) proving the absence of infestations is hardly possible (incomplete preservation, corrosion, etc.). Therefore, we abandoned this direction of research. Nevertheless, future collections of rich, partially infected ammonoid associations might yield the opportunity to examine the effect of the infections on growth. For the time being, it appears like the effect of the infestations on ammonoid growth was at least not extreme.

Remarkably, we also found pits in early Emsian palaeotaxodont bivalves of the species *Nuculoidea grandaeva* (Fig. 9), *Nuculites* (*Gonionuculites*) *celticus*, and *Cucullella* (*Cucullella*) *triquetra*. Bivalve pearls are known already in the Silurian (compare Kříž 1979; Liljedahl 1994). Specimens with pits have already been figured on plate 3 in Klug et al. (2008b), but these pits were not discussed in detail. When comparing those fossil palaeotaxodont pearls to pearls caused by intermediate stages of gymnophallid trematodes in Recent bivalves (including palaeotaxodont, venerid, and mytilid bivalves: Lauckner 1983; Ituarte et al. 2005) and their relative position on the shell, the similarity between the fossil and the Recent occurrences is striking. This again supports the interpretation that trematodes had already evolved a well-developed use of molluscs as hosts in the Early Devonian, although it appears more likely that gymnophallids had infested the bivalves rather than the ammonoids. Because of the size and shape of the tubes, the similarity to bivalve pits made by trematodes (at least since the Early Devonian: Fig. 9), the long-lasting non-lethal nature of this parasitic infection, the reaction of the host (the formation of a pearl) and the high probability of an Early Palaeozoic origin of the trematode-mollusc system, we suggest that the calcareous tubes inside the "Housean pits" were caused by trematodes (probably belonging to the subclass Digenea and perhaps to the family Gymnophallidae). This would extend the parasitic trematode fossil record from the Cainozoic (Ruiz and Lindberg 1989) via the Late Devonian (Upeniece 2001; Littlewood and Donovan 2003; Lukševics et al. 2009) to the Early Devonian. As demonstrated by Littlewood (2006: 12–13), the obligate parasitism of Neodermata must date back at least to the Ordovician or Cambrian (see discussion in the next chapter).

Considerations on a parasite strategy

Trematodes penetrate the host in various ways. Some are simply ingested with food (e.g., Dönges 1988; Ruiz and Lindberg 1989), some behave like prey organisms to attract the attention of predators, some enter at the mantle margin or in between mantle and shell (Lauckner 1983: 736), and some penetrate the skin or the anus of the host (e.g., Dönges 1988: 165). Digenetic trematodes have been reported from the caecum, intestines, stomach, mantle cavity and tissues around the arteries of Recent cephalopods (Overstreet and Hochberg 1975; Hochberg 1990). Some hints on evolutionary changes in the penetration strategy can be found in the localisation of the pearls. In the early Emsian *Ivoites*, type 4-pits were formed at the aperture (as documented by the altered rib spacing and occasional angular discontinuity between the ribs; Fig. 6A–C; Kenneth De Baets, Christian Klug, Dieter Korn, Christoph Bartels, and Markus Poschmann, unpublished data), thus making it likely that the parasites entered at the mantle margin, where the shell tube is secreted between the mantle folds or between mantle and shell. As suggested by Royal Mapes (personal communication 2010), infestation might speculatively have occurred at the hyponome in type 5.

For types 1 to 3 pits, only guesses can be made on how the trematodes (?) reached the anterior edge of the annular eleva-

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tion or the posterior end of the mantle cavity. The following methods are possible:

The parasites somehow entered the soft parts at one point (by ingestion or via other ways) and for some reason chose this particular part of the soft-tissues.

The parasites entered the mantle cavity (maybe attracted by faeces) either via the hyponome or the lateral or dorsal gap between mantle and head. Then they migrated as far posteriorly as possible and penetrated the soft tissues.

They entered between shell and mantle at the aperture and migrated backwards towards the mantle myoadhesive band/the attachment of the cephalic retractor muscle, where they perhaps could not proceed farther. This would cause a disturbance of the mantle at the aperture or anterior to the cephalic retractor insertion, thus leaving a trace in shell growth. Interestingly, some gymnophallid parasites are known to actively pierce the mantle border, ascend to the outer mantle epithelium to settle in the dorsal general extrapallial space just ahead the posterior adductor muscle in bivalves (Cremonte 2001; Cremonte and Ituarte 2003).

With our fossil material, this problem cannot be resolved conclusively. Recent cephalopods most commonly obtain trematodes by feeding on infected prey, typically without further development of the parasite and little or no damage to host tissues (Overstreet and Hochberg 1975; Hochberg 1990). Future studies might shed more light on the way that the Devonian trematodes (?) reached the position where they were encapsulated in the shell of the ammonoid body chambers.

Although the question of how the parasite entered the ammonoid body cannot be resolved in most cases, the closely related question of the localisation of the parasite remains. Did they live between shell and mantle or did they make their way from an internal organ to the shell wall, sticking into the soft parts? The latter hypothesis finds some support in the fact that the pits are not randomly distributed within the host ammonoids; within the collection, there is considerable variation. In some groups such as late Emsian anarcestids, there are always two lateral spiral rows, whereas in others there is only one. Some specimens have a lateral band with tiny pits, others have a ventral band with tiny pits and in some specimens, the pits are present at the aperture (all other pits were formed in the posterior quarter of the body chamber).

Again, there are two possible explanations for these patterns. Either the parasite lived in a certain organ (kidneys, gonads, digestive glands, coelomic cavity) and made its way to the mantle-shell interface or the parasite always lived there. Gonads are unlikely as there is so far no evidence for castration and the associated prolonged growth after maturity or gigantism as observed in some short-living, but not all gastropods (Miura et al. 2006; Genner et al. 2008 and references therein), however alterations in shell morphology might be more species-specific (Hay et al. 2005). In some long-living gastropods, trematodes even stunt growth (Miura et al. 2006), which is obviously not the case in ammonoids since the infestation continued over several whorls. Ammonoid gigantism has been discussed as perhaps being caused by parasitism (Manger et al. 1999) but not for the taxa showing pearls from the Devonian. Discussing gigantism for Early Devonian ammonoids (see Klug 2002b for a review) would not make sense here because the taxa under consideration did neither attain giant sizes nor significantly smaller sizes compared with the uninfested specimens (as far as testable with our materials).

Which tissues were infested by the parasite? The localisation of pits might reflect the position of organs where the parasites lived like, e.g., the kidneys; this would then point at the possible existence of four kidneys in ammonoids because of the paired spiral rows (Figs. 3, 6A–C). In cephalopods and several other molluscs, the number of gills correlates with the number of kidneys (Lindberg 2009) and thus would corroborate the interpretation of ammonoids as tetrabranchiate cephalopods like the Nautilida as opposed to all other living, more closely related cephalopods (Engeser 1996). Although some parasites, except trematodes, apparently like cephalopod kidneys (Hochberg 1982) and although the recurrence of double rows of pits on each side of the ammonoid is striking, this line of reasoning provides no evidence for ammonoids being tetrabranchiates. Nevertheless, when comparing the ammonoid pearls and especially their localisation in different parts of the body chamber, some similarities to occurrences of gymnophallids in Recent bivalves are apparent (Lauckner 1983: fig. 13-123). In the Recent bivalves, the metacercariae (resting or maturing stage within an intermediate host) enter between mantle and shell, causing parasite-induced mantle epithelial proliferations. It is well conceivable that such a process ultimately lead to the formation of blister pearls in the case of the Devonian ammonoids. No matter which organ(s) were actually infested, from the differences in localisation of the pits, a certain degree of microhabitat segregation appears likely (for examples of microhabitat segregation in Recent bivalves see Lauckner 1983: 734–750).

Often in Recent trematodes, molluscs represent intermediate hosts (Littlewood 2006), and the parasites reach their reproductive stage in a final vertebrate host. In Recent cephalopods, none act as first intermediary host, but many function as second intermediary, paratenic (through feeding without further development of the parasite) or, more rarely, even final hosts (Overstreet and Hochberg 1975; Hochberg 1990). Interestingly, Choisy et al. (2003) hypothesised that selection favours a complex life if intermediate hosts are more abundant than definitive hosts, while the selection advantage of complex life cycles increased with predation rates by definitive hosts on intermediate hosts. It might thus be no coincidence that the first appearance of this particular parasitosis in the Early Devonian is more or less synchronous with the first major radiation of gnathostomes (e.g., Janvier 1996; Klug et al. 2010). Recent cephalopods are not only preyed upon by fish, but often share similar prey (some even consider them similar in every aspect except their basic body plan; Packard 1972). Both might explain their infection with the same para-

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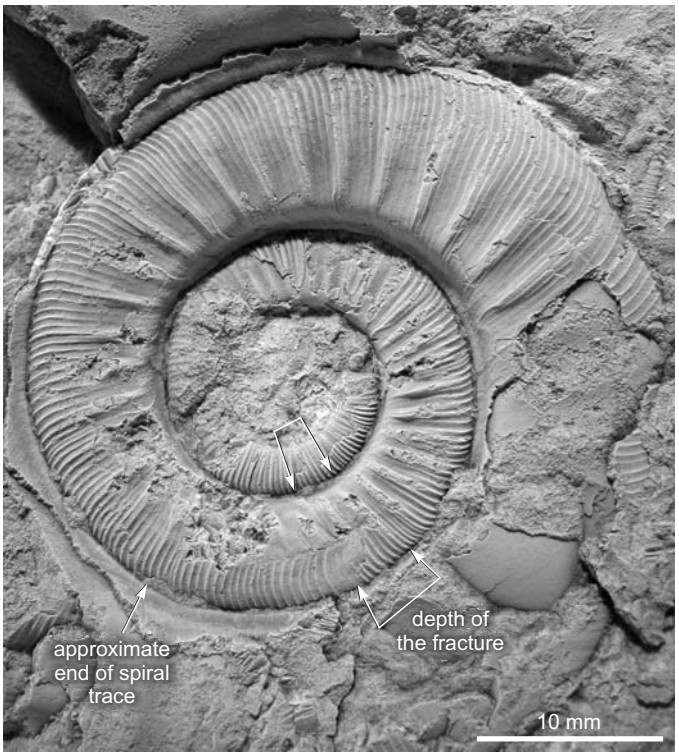


Fig. 10. *Mimosphinctes rudicostatus* Bogoslovsky, 1980, PIMUZ 28595, bed 48, *Polygnathus inversus* Zone, Dzhaus-beds, early Emsian, Khodzha-Kurgan Gorge, Zerashan Range, Uzbekistan. This individual had suffered from a deep fracture, which had caused an irritation of the mantle. This had the formation of a spiral trace as a consequence.

sites (cf. Overstreet and Hochberg 1975; Hochberg 1990). Gnathostomes originated much earlier (Donoghue et al. 2000), but only became abundant in the Devonian ("age of fishes"; cf. Janvier 1996; Klug et al. 2010). The nearly simultaneous Devonian gnathostome radiation occurrences of the mollusc parasites may be pure coincidence, but one could as well interpret this as an indication that this parasitosis is an early case of platyhelminth infestation, with ammonoids being used as intermediate hosts and jawed fishes acting as terminal hosts. Accordingly, one report of a probable trematode infestation of a Late Devonian acanthodian from Latvia, was published by Upeniece (2001) and refigured in Littlewood and Donovan (2003). Although this material is from a terrigenous deposit (Kuršs 1992a, b), it documents the presence of trematode infections in jawed fish. Damage and galls possibly caused by trematodes (or their larvae) have also been reported from Upper Devonian placoderms and sarcopterygians (see Lukševics et al. 2009). This indirectly corroborates the suggested Early Phanerozoic origin of the Neodermata–Gnathostomata system (cf. Littlewood 2006) with potential ammonoid intermediate hosts. Additional support for this hypothesis can only be achieved by the examination of exceptionally preserved Devonian fish like those described from Australia (e.g., Long 2006; Long et al. 2008) for trematodes. Traces of gnathostome predation on ammonoids, preferably infested specimens of the host species, would be an additional support for this hypothesis because this is the way the parasite migrates from the intermediate (mollusc) to final host (gnathostome). Although sublethal injuries are not uncommon, they are often hard to interpret with the taxonomic assignment of the predator (Klug 2007). Reports of sublethal injuries of Emsian and Eifelian ammonoids are, however, extremely rare. Even more problematic is the identification of the causer of such injuries. Evidence for the actual causer is highly exceptional (see, e.g., Richter 2009). One of the best preserved examples of a sublethal injury (forma verticata, cause unknown) from the early Emsian of Uzbekistan is shown in Fig. 10.

Despite the close phylogenetic connection between the Bactritoidea and primitive ammonoids, often occurring in the same stratigraphic horizons, pearls have not yet been described or discovered in any Devonian bactritoid nor have they been reported from fossil or Recent nautilids (Hochberg 1990), which also originated around this time (compare Bergmann et al. 2004; Kröger 2008). Note that rich material is available of both bactritoids (thousands of *Devonobactrites* specimens) and nautiloids in internal mould preservation from the early Emsian of Morocco (Klug et al. 2008 a, b; Kröger 2008). These fossils do show sublethal injuries (Klug 2007) but no "Housean pits". This suggests that the parasites are specialists in selecting their cephalopod hosts, and because of this, it is likely that this type of parasitism evolved before the Emsian and perhaps even before the Devonian, counting in the time required for the evolution of the parasite from being a generalist to a specialist in host selection.

Considerations on the pearl formation

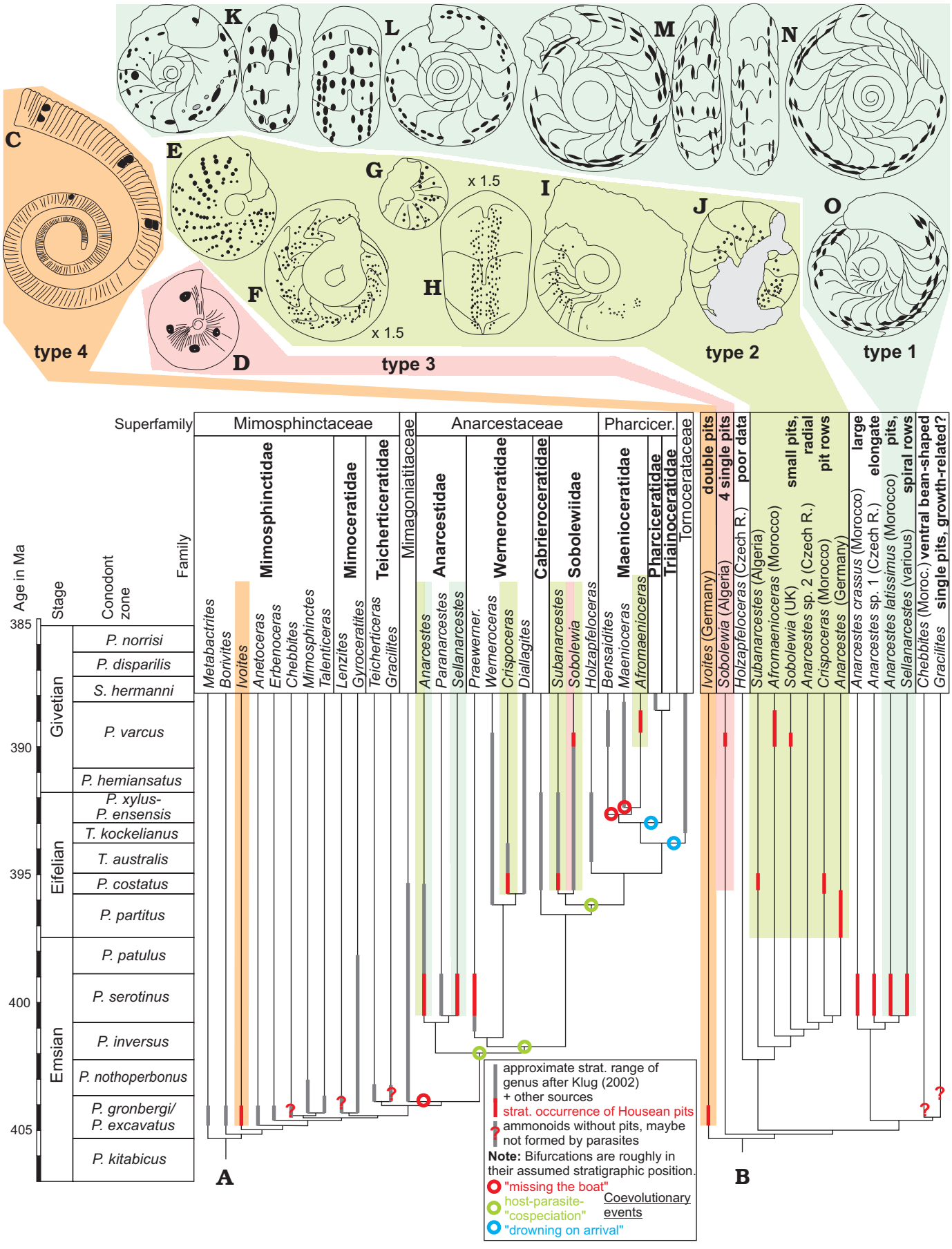
It is conceivable that at a certain stage a parasite would try to escape the body through a soft-body surface, being blocked by the shell and eventually dying. Perhaps it was the parasite carcasses, which were encapsulated by the ammonoid, thus forming the pearls (e.g., Lauckner 1983: 750). In this context, it has to be understood that the pearls under consideration were formed in two stages: At the beginning, there was only the tube, formed by either the ammonoid or the parasite. This tube was open until the tube was overgrown by shell. This implies the alternative possibilities that the parasite managed to escape the tube or that the parasite managed to release some further growth stages at one point prior to pearl-growth.

Another possibility is that the parasites entered through the hyponome into the mantle cavity, where they penetrated the soft body and wound up in the mantle directly anterior to the attachment of the cephalic retractor muscle. This hypothesis is corroborated by the fact that type 1 to 3 pits were formed anterior to the attachment site of this muscle (Fig. 4A, B).

Alternatively, the parasites may have simply entered between the shell and mantle at the aperture. This would par-

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tially explain why in some early Emsian ammonoids the pits were formed at the aperture (Fig. 6A–C) while more derived parasites managed to migrate to a more posterior position in the more derived late Emsian to Givetian ammonoids.

However, the only proved process is that, at least in types 1 to 3, a tube was formed, probably anterior to the insertion of the cephalic retractor. This tube (which might have been unmineralised in type 4) was then overgrown by shell, which was secreted either by the mantle myoadhesive band or by the slightly more posteriorly-located palliovisceral ligament. It appears less likely that the tubes were overgrown at the palliovisceral ligament because the most anterior pit of types 1 to 3 are actually well inside the body chamber and most likely anterior to the cephalic retractor insertion site. Additionally, the tube was apparently an obstacle for mantle growth, occasionally causing the formation of a spiral trace as a reaction of the mantle (cf. Keupp 1986).

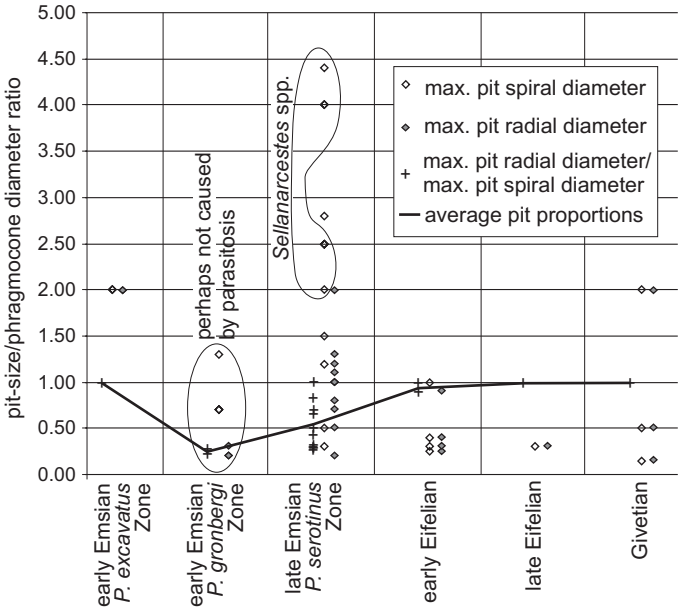


Fig. 12. Changes in pit-size and in the pit-size/phragmocone diameter ratio through time. Data from Table 1. *P*., *Polygnathus*.

Evolution of the parasite as reflected in the pits

As explained in the methods section, we made a simple cladistic analysis of the pit types (Fig. 11). Due to the low number of characters, the resulting trees must be interpreted with some reservation. Nevertheless, the resulting consensus tree (Fig. 11B) and the comparison with the host ammonoid phylogeny (Fig. 11A) as proposed by Korn (2001) and Korn and Klug (2002) revealed some remarkable possibilities. In order to understand all the details of both trees in Fig. 11, some basic biological and preservational considerations must be clarified. Briefly, there are problems with species assignments in general and specifically in the fossil record. In the majority of ammonoid fossils, only the internal mould (i.e., the sediment or cement filling of the commonly dissolved shell) is preserved. Additional problems like conch incompleteness or deformations due to diagenetic or tectonic processes hamper taxonomic assignments and, especially among morphologically similar taxa, taxonomic determination errors can and do occur. Despite these problems, the overall results of both phylogenetic analyses fit well and appear reasonably coherent. The five pit types group reasonably well in both trees and several evolutionary trends in the phylogenetic transformation of pit shape can be derived. One trend is the decrease in pit size from the early pit types to the derived type 2 pits (Pearson's r = 0.63 when all taxa are included and pit-size compared to phragmocone diameter, Pearson's r = 0.70 when type 2 and 5 are excluded and pit size is compared to whorl height; Figs. 12–14). An additional trend is the increase in pit number from early pit types to type 2 (except in *Sobolewia*; compare Table 1 and Fig. 14). The two trends are moderately strongly correlated (Figs. 12–14). This relationship is biologically reasonable because the larger the endoparasite(s), the less space is available for other individuals to inhabit the host.

No matter how the evolution of the traces left behind by parasites is interpreted, it is evident that evolutionary

← Fig. 11. Co-evolution of Devonian ammonoids and their parasites as reflected in the arrangement and shape of the pearls. **A**. Host phylogeny. **B**. Trematode (?) parasite phylogeny. Time scale created with Time Scale Creator (www.tscreator.com). Ages of stages standardised to Gradstein et al. (2004). The ammonoid phylogeny is based on majority consensus tree 11 most parsimonious trees original shortest tree length: 53 CI of shortest tree: 0.3673 (Korn 2001 and Korn and Klug 2002). The analysis made with PAST using the data from Table 2. **C**. *Ivoites* sp. nov. B, HS 371, early Emsian, middle Kaub Formation (Hunsrück Slate), Bundenbach (Eschenbach–Bocksberg Quarry), Germany. **D**. *Sobolewia nuciformis* (Whidborne, 1889), R.08459, Givetian, Redjel Iamrad, Algeria, Jacques Follot collection. **E**. *Subanarcestes* sp., *Pinacites jugleri* Zone, Eifelian, Erg El Djemel, Algeria (after House 1960). **F**. *Afromaenioceras sulcatostriatum* Bensaïd, 1974, PIMUZ 28592, Givetian, Jebel Ouaoufilal, Tafilalt, Morocco. **G**. *Sobolewia* aff. *nuciformis* (Whidborne, 1889), R.08459, *Maenioceras terebratum* Zone, Givetian, Pentonwarra Rd., Trevone, Cornwall, UK (after House 1960). **H**. *Anarcestes* sp., L19725, late Emsian, Koněprusy, Czech Republic (after Chlupáč and Turek 1981). **I**. *Crispoceras tureki* Klug, 2002, PIMUZ 28591, *Pinacites jugleri* Zone, Eifelian, Jebel Ouaoufilal, Tafilalt, Morocco. **J**. *Anarcestes* sp., Eifelian, Wissenbacher Schiefer, Germany (after House 1960). **K**. *Anarcestes* sp., PIMUZ 28581, late Emsian, Jebel Mech Agrou, Tafilalt, Morocco. **L**. *Anarcestes latissimus* Chlupáč and Turek, 1983, PIMUZ 1971-293, late Emsian, Hassi Moudaras, Tafilalt, Morocco, Jobst Wendt collection. **M**. *Sellanarcestes* cf. *ebbighauseni* Klug, 2002, PIMUZ 28582, *Sellanarcestes wenkenbachi* Zone, Emsian, Jebel Ouaoufilal, Tafilalt, Morocco. **N**. *Sellanarcestes ebbighauseni* Klug, 2002, GPIT 1871-171, *Sellanarcestes wenkenbachi* Zone, Emsian, northern Jebel Amessoui, Tafilalt, Morocco, from Klug (2002). **O**. *Sellanarcestes neglectus* Barrande, 1865, GPIT 1871-285, *Sellanarcestes wenkenbachi* Zone, Emsian, southern Jebel Mech Agrou, Tafilalt, Morocco (from Klug 2002). Sketches after images from Figs. 3–6 and the literature (House 1960; Chlupáč and Turek 1981). Where not indicated otherwise, the drawings are actual size. Abbreviations: *P.*, *Polygnathus*; Pharcicer., Parciceratacea; *S.*, *Schmidtognathus*; *T.*, *Tortodus*.

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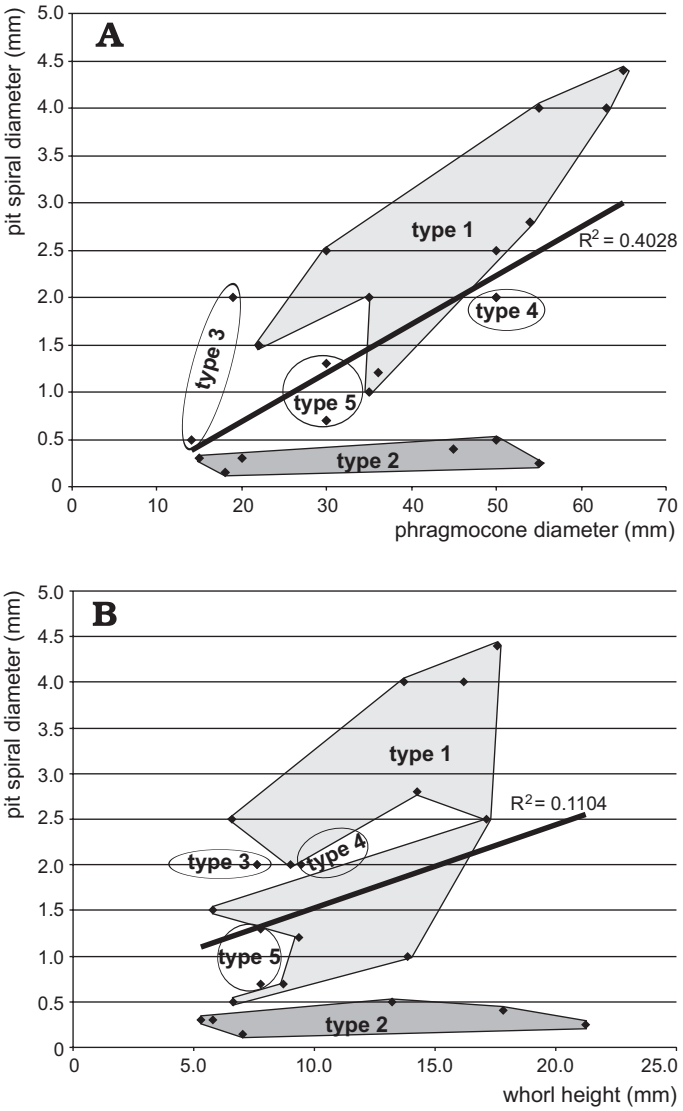


Fig. 13. Relation between phragmocone size and spiral pit diameter (**A**) and between whorl height and spiral pit diameter (**B**).

changes occurred in the 10 to 15 million years during which ammonoids produced "Housean pits". Ammonoids are valuable study objects because of their high evolutionary rates and, consequently, because those clades containing species, which occasionally display pits also evolved at high rates. This is particularly true for early Emsian ammonoid taxa, whose adaptive radiation was so rapid that extreme new morphologies evolved (Korn and Klug 2003; Claude Monnet, Christian Klug, and Kenneth De Baets, unpublished data). This caused the rapid occupation of much of the ammonoid morphospace within a short time span after the origination of ammonoids (Korn and Klug 2003). Although more details of the parasite-host relationship of these Devonian ammonoids and the pit-inhabitants will probably never be discovered, it is evident that both groups (hosts and parasites) underwent simultaneous evolutionary transformations. These transformations are most likely as reactions to evolutionary change in either of the host or of the parasite lineages, i.e., co-evolution.

Further aspects of parasite-host co-evolution are how the trees of the parasites and the host match or do not match. Branches of the parasite tree may get abandoned soon in the course of the evolution of a new host clade (termed "DOA" or "drowning on arrival" by Verneau et al. 2009). The parasite clade may fail to follow the evolution of a new host clade ("MTB" or "missing the boat", Verneau et al. 2009), or both hosts and parasites may develop new clades nearly simultaneously ("cospeciation", Verneau et al. 2009). It is also possible that a parasite clade switches from one to another host clade (here termed "swapping the boat"), or that a parasite clade fails to follow one of several host clades over a longer timespan. Naturally, a temporally precise cospeciation of host and parasite clades appears highly unlikely, but the timing of cladogenesis in both clades might be so close that the difference in evolutionary timing cannot be resolved by means of palaeontological methods (not even with high resolution quantitative biochronological methods such as Unitary Association: see Monnet et al. in press) or molecular clocks. Nature gets the closest to cospeciation in rapidly reproducing parasitic organisms such as viruses, bacteria, and protozoans (Verneau et al. 2009). In metazoans, such precise cospeciation will probably not occur and we use this term here in a sense allowing for a longer time span, which might be required by the parasite clade to follow evolutionary innovations of the host clade.

As far as the evolutionary patterns of the Devonian ammonoid hosts and their parasites are concerned, some of the aforementioned co-evolutionary phenomena occurred. "Missing the boat" is a common phenomenon in host-parasite co-evolution. The parasites living in the ammonoids apparently "missed the boat" at the origins of the Mimagoniatitaceae, Pharciceratidae, Triainoceratidae, and Tornocerataceae (red circles in Fig. 11A). "Drowning on arrival" probably occurred at the bifurcations to the Tornocerataceae and within the Pharciceratidae to the Pharciceratidae and Triainoceratidae-clade (blue circle in Fig. 11A). Apparently, "swapping the boat" did not occur among any of these early ammonoid parasites. "Cospeciation" in the broader sense, that it happened not immediately after the emergence of a new clade or taxon, might have occurred. When interpreted as more or less simultaneous cladogenesis in both host and parasite, then "cospeciation" might have occurred repeatedly, e.g., near the origin of the Wernerocerati dae, of the Sobolewiidae, and the Maenioceratidae (green circles in Fig. 11A).

The similarity between pearl shape and arrangement probably reflects some host specificity. *Sellanarcestes* always shows two to three rows of oval pits, *Afromaenioceras* always has many small chaotically arranged pits (< 0.3 mm in diameter) and in *Ivoites*, large paired pits (> 3 mm in diameter) are formed at the aperture (Figs. 3–6, 11). As far as the pit evolution is concerned, the database for the cladistic analysis was poor. Therefore, its results must be read and interpreted with caution. For instance, the large angular distance

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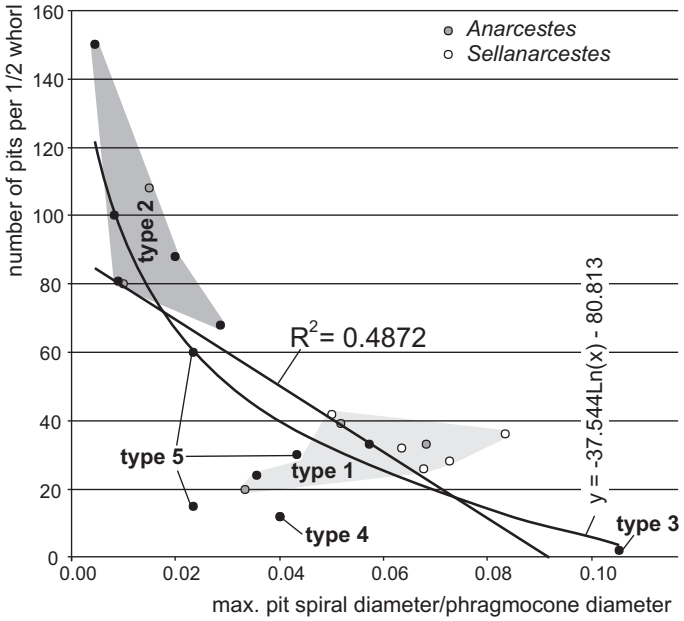


Fig. 14. Relation between the estimated amount of pits per half whorl and the ratio between pit size and phragmocone diameter.

between the pits in the Algerian sobolewiids (up to ca. 90°) and in the German *Ivoites* (up to ca. 50°) might indicate a closer relationship or might be a mere coincidence. The same is true for the low number of spiral rows of large pits in Algerian sobolewiids (pit diameter up to 2 mm) and in *Sellanarcestes* (pit diameter up to 4 mm). In spite of these poorly resolved evolutionary questions, it appears clear that the behaviour and size of the parasite has changed through time and evolution, most likely as reactions to evolutionary change in the hosts in, at least, some cases. It is thus appropriate to apply the term co-evolution.

Conclusions

Several species of early Emsian to early Givetian ammonoids sometimes display pits in their internal moulds, which are the moulds of pearls. In addition, pits in the internal moulds of bivalves resembling structures caused by gymnophallid trematodes in Recent bivalves in distribution and size were also discovered for the first time. Also for the first time, we describe and illustrate tiny tubes, which are located inside the ammonoid shell wall and where they are overgrown by the innermost layer of shell, thus forming the pearl (also called "Housean pits" by Davis and Mapes 1999). Based on pearl arrangement and size, we grouped the occurrences in 5 types (Figs. 3–6; for pearl dimensions see Table 1):

Type 1: two or three spiral rows of large oval pearls, small tube (max. ca. 0.6 mm long with max. 0.2 mm diameter and walls ca. 0.03 mm thick) inside pearl, formed in rear body chamber.

Type 2: many small pearls, chaotically or +/- radially arranged, small tube inside pearl, formed in rear body chamber.

Type 3: one row of pearls, four per whorl, small tube inside pearl (diameter ca. 0.5 mm), formed in rear body chamber.

Type 4: radially paired large pearls, altered rib-spacing, four to six pairs per whorl, formed at aperture.

Type 5: one ventral row of oval to bean-shaped pits, this is perhaps no parasitosis, formed at aperture (infested hyponome?).

We interpret these structures (perhaps except type 5) as being caused by parasites because of their irregular and asymmetric appearance, their absence in some specimens of the infected species, their absence in the earliest whorls, the fact that they do not correlate with septal growth and growth rhythms, the presence of calcified tubes in the pearls, the ammonoids' reaction to an alien organism, the consistent positioning of the pearls between mantle and shell, and the impossibility for the parasite to feed independently from the host (no commensalism).

By contrast, no definite conclusion can be drawn with regard to the identity of the parasite. We suggest that digenetic trematodes are responsible for the formation of the tubes and the pearls surrounding them because of the similarity to trematode-induced pearls in bivalves, the absence of borings in the ammonoid shell, the Recent abundance of trematode-mollusc parasitic systems, the probability that these parasites originated earlier than the Devonian as determined by the specialisation in host selection by the parasites, and the simultaneous adaptive radiation of jawed fish, which are common final hosts of Recent digenetic trematodes. The available data do not allow an unequivocal interpretation with respect to the life cycle of the parasites or the organs that were infested, except that in all cases the mantle was sufficiently impacted that localised shell was deposited on the infestation site.

In the 10 to 15 Ma interval of the occurrence of parasitic "Housean pits", both the ammonoid hosts and the parasites underwent evolutionary change as reflected in changing abundance, shape, and distribution patterns of the pits and the ammonoid shell morphology respectively. It is thus appropriate to suggest a co-evolution of the ammonoids and the parasites, although the evolutionary driving factors for either group cannot be identified in detail. Future research could focus on the search for material with better preserved shells in order to provide both ultrastructural details of the tubes inside the pits and morphological details of the tube in order to obtain more information about the parasite.

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