3D-Analysis of a non-planispiral ammonoid from the Hunsrück Slate: natural or pathological variation? (#7994)

First submission

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Important notes

Editor and deadline

Graciela Piñeiro / 25 Jun 2016

Files	1 Other file(s) Please visit the overview page to **download and review** the files not included in this review pdf.
Declarations	No notable declarations are present

1) interesting, but your thesis remained unclear until the conclusion. This is highly problematic.

You need to a) establish a case for how much deviation from 'typical' the holotype is because of encrusters

b) describe & figure the difference in morphology caused by encrusters. You begin to do this well in "implications for taxonomy"

c) better establish both syn vivo argument and implications & the observed relationship to cause morphologic change

d) establish how rare non-planispiral coiling is in the taxon to add support for your desire to create a neotype

For assistance email peer.review@peerj.com

2) Some lesser concerns:

A) Your other arguments (e.g. earliest noted live-live btn hederellids & ammonoi

have as little support for them as your thesis. I don't disagree (but would like a better images of hederellids for confirmation) with them, but you haven't supported →

them w/sound arguments herein.

B) 'Pathological variation' and 'epicole' are terms I would avoid if you want others interested in fossil parasitism, commensalism, encrusters to take note. Maybe 'induced morphological variation' and encruster/sclerobiont

C) Your title & abstract don't lead the reader to think that I. opitzi should have a neotype replace the holotype. Rather, you lead me to believe the species was named wrongly for a plastically deformed specimen of another species.

D) Your photic zone argument has validity, but not as you wrote it. I don't know as much as I should about the depositional unit of the Hunsrück, but you won't find encrusters @ 250m. You almost never (<~.01%) in deep Cincinnati Arch environments (~100m at most), and similar #s exist in M. Dev. App Basin

3D-Analysis of a non-planispiral ammonoid from the Hunsrück Slate: natural or pathological variation?

Julia Stilkerich, Kenneth De Baets

(inst. time/unit)

We herein investigate the only known non-planispirally coiled early ammonoid specimen to test if its trochospiral coiling is the result of part of the natural variation within this species or if it is ~~rather~~ pathological, induced by encrustation with epicoles during its life-time. To test if runner-like sclerobionts infested the ~~historical~~ collected specimen ~~and~~ holotype of Ivoites opitzi during its life, we produced a three-dimensional model using microCT. Our results indicate that epizoans grew on both sides of the ammonoids, exactly at the location where the deviation from the planispiral was ~~could~~ be recognized. ~~This indicates that~~ At least some of the epicoles were present on overgrown the ammonoid in-vivo, making ~~that~~ this the oldest Ivoites opitzi records the oldest known ammonoid epizoa. ~~This suggests that~~ Non-planispiral coiling in this specimen is likely pathological and does not reflect ~~rather than~~ natural variation. ~~and that~~ a neotype has to be chosen to define this species. Despite obscured ~~these~~ anomalies in coiling and multiple generations of epizoa, the specimen reach adulthood, suggesting minimal effects on its mode of life. We herein identify these epizoa as hederelloids, a peculiar group of sclerobionts related with phoronids, which indicate the ammonoid lived in the euphotic zone and supports the latest interpretations of the Hunsrück Slate depositional environment. This is, to our knowledge, the first support for in-vivo encrustation of hederelloids on ammonoids.

doesn't need to do [illegible]

say what that is

*watch tense

if so, then maybe add a sentence describing how another could i.d. in vivo encrustation in the group.

3D-Analysis of a non-planispiral ammonoid from the Hunsrück-Slate: natural or pathological variation?

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Abstract:

We herein investigate the only known non-planispirally coiled early ammonoid specimen to test if its trochospiral coiling is part of the natural variation within this species or it is rather pathological – induced by encrustation with epicoles during its life-time. To test if runner-like sclerobionts infested the historical collected specimen and holotype of *Ivoites opitzi* during its life, we produced a three-dimensional model using microCT. Our results indicate that epizoans grew on both sides of the ammonoids, exactly at the location where the deviation from the planispiral could be recognized. This indicates that at least some of the epicoles overgrown the ammonoid in-vivo making that oldest known ammonoid epizoa. This suggests that non-planispiral coiling in this specimen is pathological rather than natural variation and that a neotype has to be chosen to define this species. Despite, these anomalies in coiling and multiple generations of epizoa, the specimen reach adulthood suggesting minimal effects on its mode of life. We herein identify these epizoa as hederelloids, a peculiar group of sclerobionts related with phoronids, which indicate the ammonoid lived in the euphotic zone supporting the latest interpretations of the Hunsrück Slate depositional environment. This is to our knowledge the first support for in-vivo encrustation of hederelloids on ammonoids.

Introduction

Ammonoids are a now extinct group of externally shelled cephalopods (Ritterbush et al. 2014), which are often used ~~for~~ in studies of biostratigraphy, diversity or evolutionary patterns. The ammonoid shell is typically coiled with touching or overlapping whorls, but some forms – so called heteromorphs – deviated from this shape as their shell is not entirely coiled and/or trochospirally coiled (Landman, Tanabe & Davis 1996). Such heteromorphs have convergently evolved in the Upper Triassic, Middle to Upper Jurassic and multiple times in the Cretaceous (Wiedmann 1969; Dietl 1978; Cecca 1997). Early ammonoids shells are ~~still~~ loosely coiled and can

→ and share affinities w/ early ammonoids from the Paleozoic.

therefore ~~also~~ be considered heteromorphs from a morphological perspective. However, early ammonoids differ in important ways from Mesozoic heteromorphs. ~~as~~ Paleozoic their embryonic shell ~~is~~ are also uncoiled (House 1996; De Baets et al. 2012), and not all types of coiling known from the Mesozoic have been reported from the Paleozoic (e.g., trochospiral coiling). A possible exception was a specimen of *Ivoites schindewolfi* from the Hunsrück Slate of Germany showing

phrasing

tense

Coiling in I[illegible] new

evidence for non-planispiral coiling (De Baets et al. 2013)~~, which was~~ originally interpreted to be part of the natural morphologic variation from gyroconic to trochospiral coiling~~, as it is also seen~~ in the Jurassic heteromorph *Spiroceras* (Dietl 1978).

similar to what is observed

However, this specimen is also encrusted by epicoles – any organism that spent its life attached to or otherwise inhabiting the exterior of any more or less hard object (Davis, Klofak & Landman 1999). If these epicoles settled or inhabit the host´s shell during its life ~~time~~, they would be called epizoa (Davis, Klofak & Landman 1999; Klug & Korn 2001) and ~~might~~ could potentially cause the observed deviations from ~~the~~ planispiral coiling (Merkt 1966; Keupp 1992; Checa, Okamoto & Keupp 2002) and various other pathologies (De Baets, Keupp & Klug 2015; Keupp & Hoffmann 2015). Distinguishing between in-vivo and post-mortem encrustations is always not straightforward, but can be achieved in particular cases using various lines of evidence (Seilacher 1960; Seilacher 1982; Baird, Brett & Frey 1989; Davis, Klofak & Landman 1999; Keupp 2012; De Baets, Keupp & Klug 2015). Although post-mortem encrustation~~s~~ ~~are~~ is common (Rakociński 2011), there are many ~~examples for different organisms settling on the shells~~ of living and fossil cephalopods including foraminifers, bivalves, sponges, corals and many others (Baird, Brett & Frey 1989; Davis, Klofak & Landman 1999; Keupp 2012; Wyse Jackson & Key Jr 2014). ~~They use the shell as solid substrate~~. But it necessarily a symbiosis ~~in every~~ case. Often the cephalopods are disadvantaged by encrustation, because ~~they are~~ encrusting organisms potentially limit~~ed~~ ~~in their~~ cephalopod movements by ~~an~~ increase~~d~~ drag and adding ~~an additional~~ weight load (Keupp 2012). In some cases ~~even~~ the encrusters ~~have a disadvantage themselves (Meischner 1968)~~ ~~as~~ if the host rotate~~s~~ ~~away~~ from their preferred position, and ~~might~~ may eventually be overgrown by the growth of the host ~~shell~~ in coiled ammonoids. However, the settlers sometimes profit in different ways. For sessile organisms that now have a pseudoplanktic method of locomotion, ~~it might have been~~ they may benefit from varied nutrition and increased mobility. Mobile organisms can potentially ~~be~~ use the shell as temporary pasture (Keupp, 2012), while epicoles can like use it as benthic island surrounded by soft and unconsolidated sediment (Seilacher 1982). For ~~pathological reactions in shell form and growth to occur~~ encrustation to impact ammonoid morphology, it is necessary that the epizoa settle~~d~~ on still growing, younger ~~animals~~ ammonoids. If the epizoans settle on the shell of adult animals which reached their final shell size it is only possible to prove that these are epizoans because of their preferential orientation with respect to water currents (Seilacher 1960; Seilacher 1982; Keupp, Röper & Seilacher 1999; Hauschke, Schöllmann & Keupp 2011). If the process of settling happens after the host's death the organisms can also colonize the inside of the shell. Shells which are lying on the seabottom are typically overgrown on one side (Keupp, 2012).

T2

Our main goal is to ~~test~~ discern if the epicoles settled on the ammonite during life~~time~~, which can tested by investigating if they are growing on both sides of the shell and if the beginning of non-planispiral coiling correlates with the settling of these epicoles. If these encrustations happened during lifetime and can be linked with (pathological) non-planispiral coiling, this might have important implications for taxonomy and indirectly for biostratigraphy (Spath 1945). An additional goal is to identify the identity of the epicoles, which have been preliminary determined ~~as~~ to be auloporid tabulate corals (De Baets et al. 2013), which have often been confused

species change btn abstract & intro, or is this another specimen? if so, make clear.

①

maybe negatively impacted by the movement of the cephalopod host.

③ important to distinguish btn live-live benefits & its of a general hard substrate (eg Seilacher)

→ like?

② + documented occurrences of live-live interactions btn cephalopods and sclerobionts, including

the encruster may shift away from their

① + new paragraph. distinguish btn identifying in vivo and deleterious effects of live-live interactions

this will be more clear when you set it up better in prev. paragraph

② Add descriptions of how to ascertain live-live & potential issues to better set up the argument. You make an attempt @ bottom of paragraph. Build on it and keep separate from impacts of live-live interactions with other sclerobionts with runner-like morphologies (Lescinsky 2001) like hederelloids and cyclostomate bryozoans (Fenton & Fenton 1937; Elias 1944; Bancroft 1986).

save this for discussion

It was important to use non-destructive → to investigate these questions

To test ~~these questions~~ we want to avoid using destructive analyses as ~~it~~ is an important historical specimen (Opitz 1932) and a holotype (De Baets et al. 2013) from the famous Hunsrück Lagerstätte. The Hunsrück Slate is facies typical so ~~for~~ the Lower Devonian (Emsium) ~~of~~ ~~the~~ Rhenish Massif which consists predominantly of dark Hunsrück Slate fine-grained argillites metamorphosed into slates (Bartels et al., 1998). In the Bundenbach area thes~~e~~ can contain fossils with remarkable preservation including articulated echinoderms and vertebrates as well as preserved soft tissues of arthropods and other groups without hard tissues (Bartels et al., 1998). ~~Although some fossils~~ Despite instances of reveal remarkable preservations, ~~they~~ fossils in the Hunsrück Slate are ~~al~~ typically flattened and it is difficult ~~to impossible~~ to prepare ~~such thin,~~ compressed ~~fossils~~ from both sides without destroying parts of it. This is ~~for example~~ illustrated by the only known specimen and holotype of *Palaeoscorpius devonicus*, the specimen where some parts of the ~~shale that~~ specimen are thinner than 1 mm are very fragile or missing altogether after preparation (Kühl et al. 2012). The~~se~~ ~~is~~ also ~~the case for~~ and preservational issue impacts ammonoids, which are important index fossils to date this deposit and are often extremely flattened hampering ~~also~~ ~~their~~ taxonomic assignment id (Bartels, Briggs & Brassel 1998; De Baets et al. 2013).

→ the specimen under investigation

→ Emsian?

* is Bundenbach a familiar place to most? If not, add a description or remove. It comes out of nowhere here.

② This tool is appropriate

Micro-CT can be used to ①

Considering the size and the preservation of our specimen as well as the expected x-ray contrast between pyritic fossils and the slate matrix, we want to use micro-CT to ① create a three-dimensional model to ~~answer these questions~~ investigate x, y ②. This method is well suited for these purposes (Sutton, Rahman & Garwood 2014). Many CT-studies have focused on analyzing ontogeny or morphological traits for phylogenetic purposes (Monnet et al. 2009; Garwood & Dunlop 2014; Naglik et al. 2015), but they can be used to test ecological or paleobiological aspects (Kühl et al. 2012; Hoffmann et al. 2014) such as the interpretation of pathologies (Anné et al. 2015) and bioerosion (Beuck et al. 2008; Rahman et al. 2015). Tomographic studies in ammonoids have focused on functional morphology and empirical buoyancy calculations of the chambered shell (Hoffmann et al. 2014; Tajika et al. 2014; Lemanis et al. 2015; Naglik, Rikhtegar & Klug 2016).

describe tool, then explain why you're using it on specimen

Material

see prev comment

collected

The studied fossil specimen is the holotype of *Ivoites opitzi*, which ~~derives~~ from the Hunsrück Slate s.s., now ~~known as~~ the middle Kaub Formation (Schindler et al. 2002), at the Schieleberg-quarry near Herrstein, Germany (De Baets et al. 2013; see Fig.1 for a map and stratigraphic provenance of this specimen). It is deposited in the Karl-Geib-Museum in Bad Kreuznach: KGM 1983/147. The middle Kaub Formation contains some of most completely preserved early ammonoids (De Baets et al. 2013) and belong the oldest known ammonoids (Becker & House 1994) together with similar aged faunas from China (Ruan, 1996) and Morocco (De Baets et al., 2010). Th~~e~~ exact statigraphic provenance of our specimen is not known. However, *Ivoites* is ~~certainly~~ restricted to Early Emsian, particularly in the Hunsrück Slate. This particular species (*I.*

phrasing

only?

which they?

opitzi) has been found associated with dacryoconarid Nowakia pr~~a~~ecursor, but they have also been found in layers (Wingertshell member sensu Schindler et al. 2002), ~~which~~ that might ~~range~~ extend into the Barrandei Zone (De Baets et al. 2013). Other ammonoids (*I. schindewolfi, Erbenoceras solitarium*) reported from the Schieleberg quarry also ~~speak for~~ suggest/support an Lower Emsian (pr~~ae~~cursor to barrandei zone) age (De Baets et al. 2013).

capital consistency

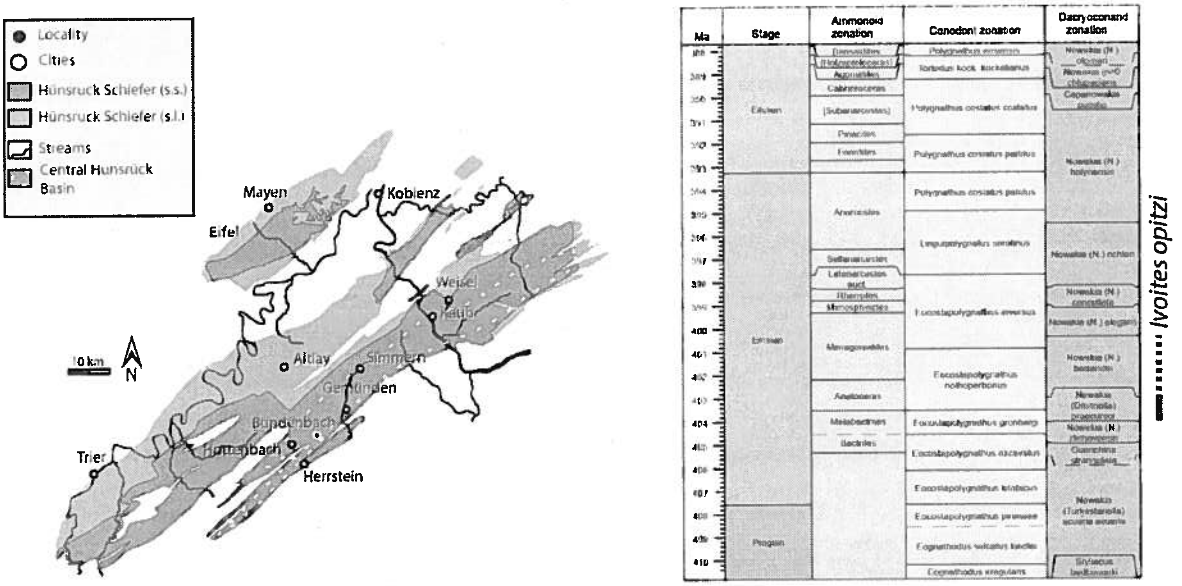


Fig.1: A map of the locality (modified from De Baets et al. 2013) and stratigraphic provenance of *Ivoites opitzi* (time-scale based on Becker, Gradstein & Hammer 2012; created with time-scale creator 6.4: http://engineering.purdue.edu/Stratigraphy/tscreator/)

who chose? cite

The specimen was chosen as the holotype as it is the most complete, three-dimensional and well-preserved specimen of the species. It has three complete whorls and a diameter of 105 mm (Fig. 2; De Baets et al., 2013). The specimen is mostly preserved as an internal, pyritic mould, as suture lines and other structures (e.g., opitzian pits) internal to the shell can be observed (taphonomic category IIB of De Baets et al., 2013). The infilling of the shell with pyrite in this taphonomic category is interpreted to have happened early in the diagenesis below the sediment-water interface before the dissolution, compaction and breakage of the shell supported by fracture patterns and similar preservation in Jurassic bioturbated shales (Hudson 1982). The whorls touch and overlap each other, but this is interpreted to be a consequence of compression and tectonic deformation as the inner whorl lies completely above the following whorl (De Baets et al. 2013).+ No clear evidence could be derived for an encrustation in vivo from the specimen, so the encrustation was interpreted to have happened post-mortem. Such post-mortem encrustations of externally shelled cephalopods and other invertebrates are common (~~Rakociński 2011~~), ~~also~~ in the Hunsrück Slate (Jahnke & Bartels 2000), and non-

break up argument for clarity

+ Attempt at description?

already said this in intro, you cannot have [illegible] make [illegible]

planispiral to planispiral coiling can form part of intraspecific variation of similarly coiled Jurassic heteromorphs (Dietl 1978). But only the left side was prepared in this historically collected material (Opitz, 1932, p. 121, Fig. 117). As this is a holotype, it could not be investigated destructively, but it well-suited to be studied with Micro-Computer-Tomography.

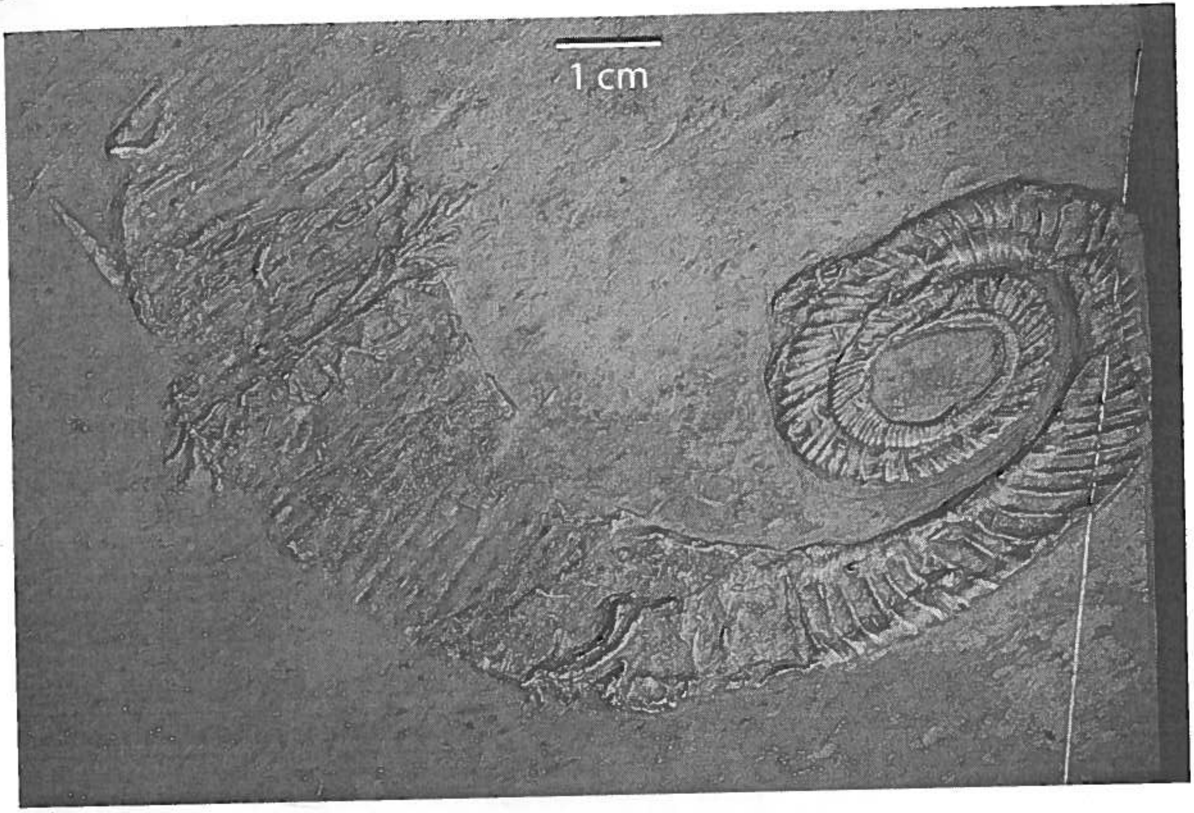


Fig. 2: Holotype of *Ivoites opitzi*. The growth of epicoles on the shell is well visible.

Methods

Markus Poschmann (Mainz) kindly ~~borrowed~~ brought the specimen ~~from the Karl-Geib-Museum and brought it~~ to the Steinmann Institute, where it could be investigated with the ~~aid of~~ X-ray micro-tomography; there a CT scan was conducted on a Phoenix v|tome|x s by Alexandra Bergmann (Steinmann Institute, Bonn), providing a voxel size of 118.1114µm with 0.400 s of exposure time. Two thousand two hundred unfiltered projections at 150 kV and 160 µA were used. Three-dimensional reconstructions and an animation were produced using the 107 tomograms in the x-z-plain by Julia Stilkerich using the free software SPIERS (Sutton et al. 2012; http://spiers-software.org). The fixed threshold value was chosen to maximally separate pyritic fossils from other materials; all tomograms were manually edited to ~~have the most~~ show a

define

does the CT tech impact interp? If not, put her in acknowl. & [illegible] name conservative interpretation of the position of the pyritic ammonoid vs. epicoles (Sutton, Rahman & Garwood 2014). Coloured masks were used to distinguish various features: ammonoid (yellow), runner-like epicoles (green), orthoconic nautiloid (red), brachiopod (blue) and dacryoconarids (yellow).

is pub colour?

Results

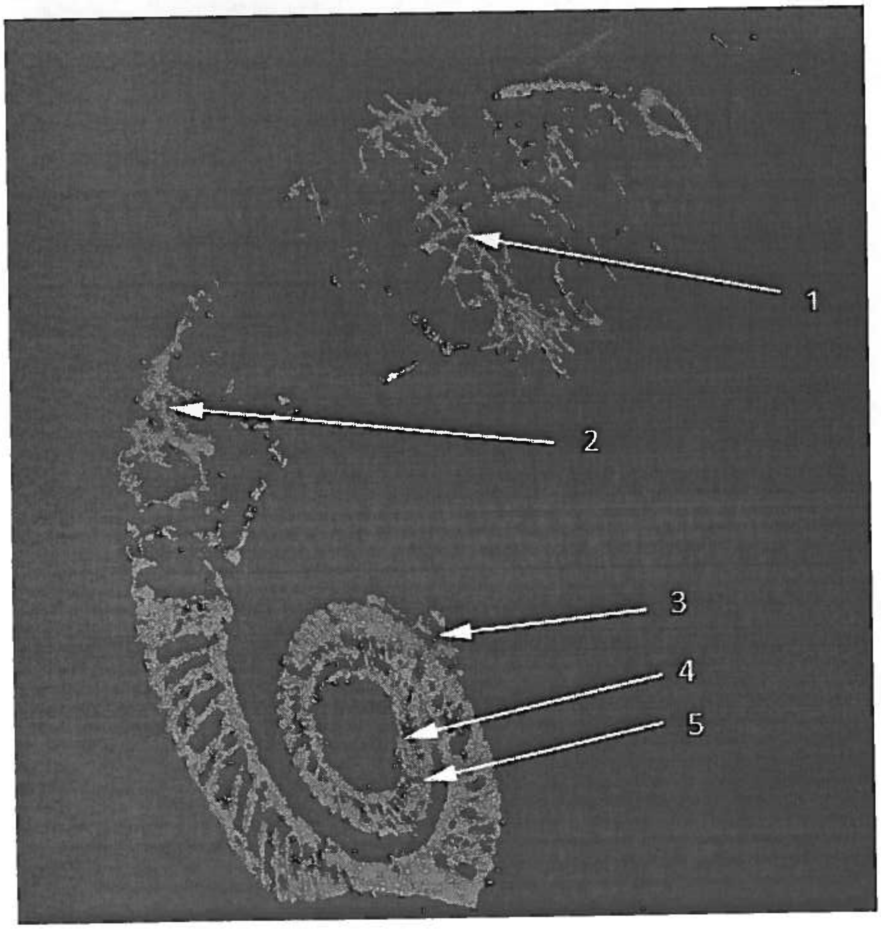
Position of the epicoles and its relationship with non-planispiral coiling

their

heading?

The 3D-model (see Figs. 3, 4) demonstrates the specimen is not entirely coiled planispirally as was previously suspected based on taphonomic arguments, e.g., the fact the innermost whorl lies entirely on top of the subsequent whorl (De Baets et al. 2013). Five clusters of epicoles can be recognized in the 3D-model (see Figs. 3, 4).

explain this, and relevance, again or cite



* Look on color diff btn 4 & 5?

Fig. 3: The ammonoid (brown), the epicoles (green) and the orthoconic nautiloid (red) in the 3D-model. The different clusters were numbered from 1-5.

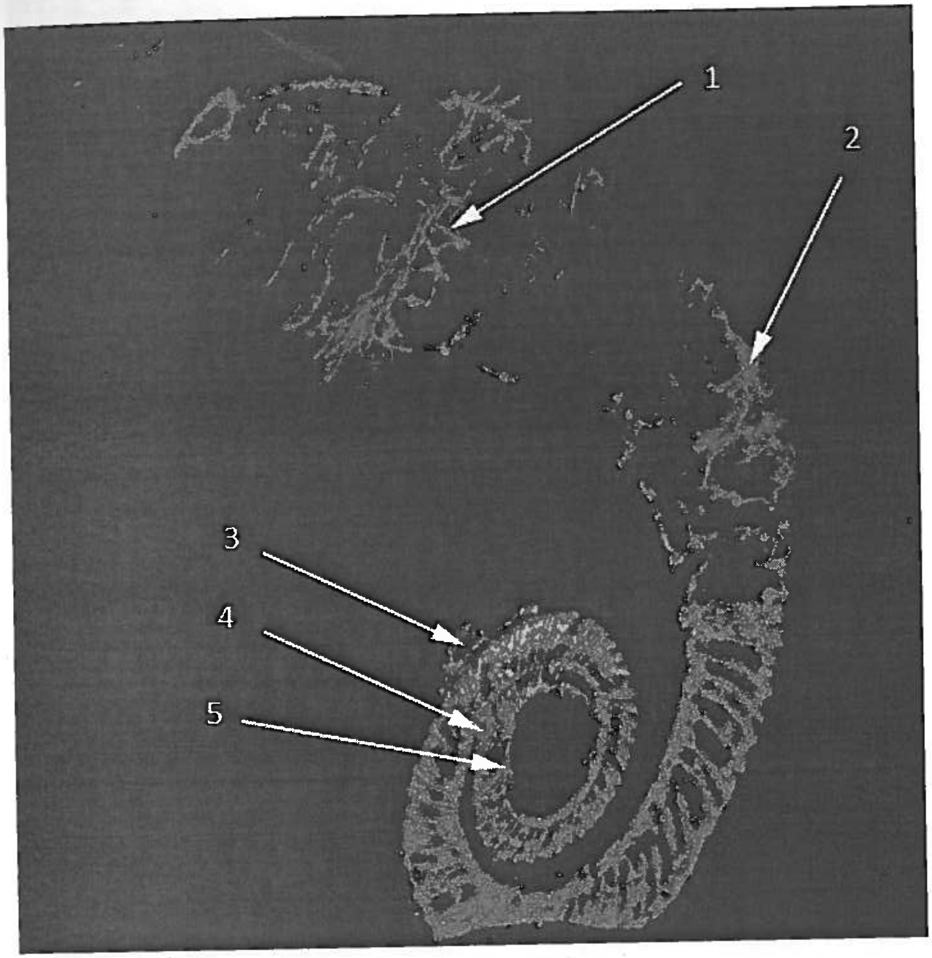


Fig. 4: The ammonoid (brown), the runner-like epicoles (green) and the orthoconic nautiloid (red) rotated 180°.

At least three clusters (3-5) can be recognized on the phragmocone. Additional clusters (1, 2) can be found on the body chambers. In the inner whorls on the phragmocone, these are at least located dorsally on both sides of whorl cross section (see Figs. 3, 4). Their direction of growth and budding follows the spiral axis of the ammonoid shell. The earliest recognizable epicoles (cluster 5) coincide with the position where non-planispirality can be first recognized (Fig. 5).

the epicoles located geographically coincident w/ the youngest part of the ammonoid shell coincide w...

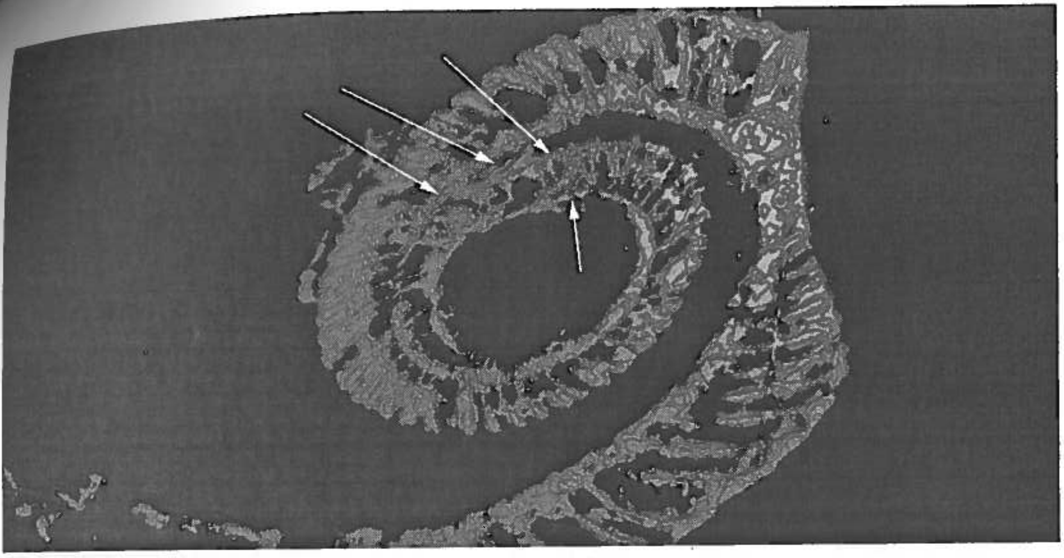


Fig. 5: The white arrows mark the position where non-planispiral coiling can be first recognized.

explain why this is important

3&5

~~More importantly,~~ ~~there is evidence that~~ Clusters (3-5) are growing on both sides of the ammonoid (Fig. 6, ~~cluster 5 exactly at the position where it starts uncoiling~~). For the other clusters on the body chamber this cannot be established with certainty as the phragmocone is not infilled with pyrite.

explain earlier, presumably this enhances contrast

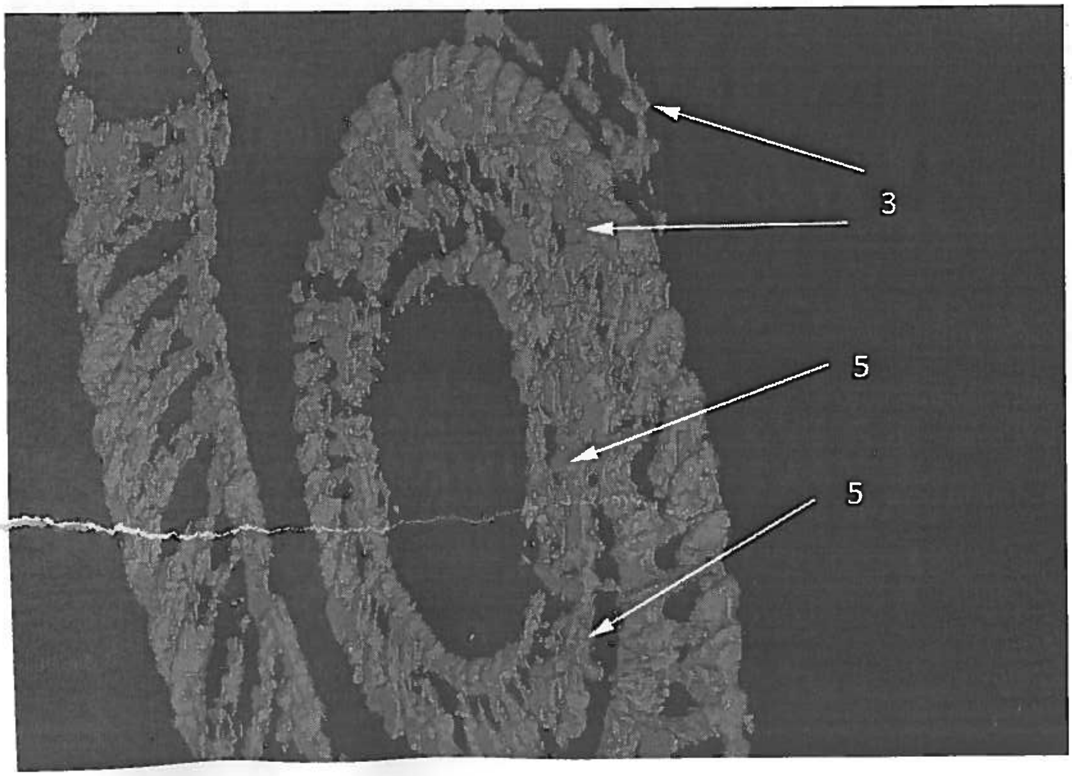


Fig. 6: Close-up of the 3D-model to show that the epicoles are settling on both sides of the shell.

preserved in the substrate associated with this specimen

[illegible]

Elongated components like the dacryoconarids (~~marked in yellow in Figure 7~~) are often orientated along the direction of the paleo-current (Hladil, Čejchan & Beroušek 1991). ~~Nor~~ the dacryoconarids nor the epicoles do not show a prefer~~ential~~ed orientation with respect to the substrate. The epicoles do show a preferential orientation with respect to the spiral axis of the ammonoids. The remainder of the components, which are small and bulky, probably are pryitic nodules in different sizes.

Nor do the epicoles attach to I [illegible]

on the ammonoid or in the substrate?

the [illegible]ple [illegible]tified in yellow in Fig 7)

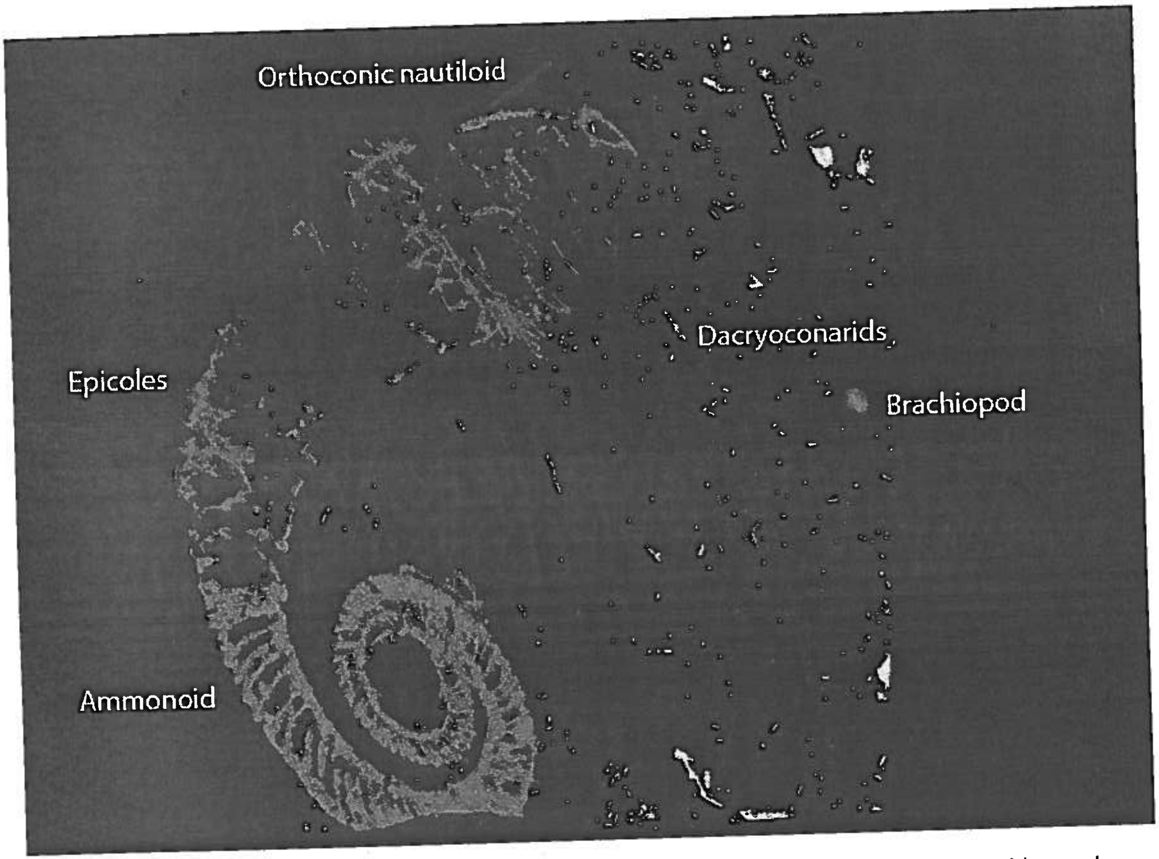


Fig. 7: The 3D-model showing all components. A brachiopod is coloured blue and dacryoconarids are shown in yellow. Runner-like epicoles are marked in green and orthoconic nautiloid in red.

Morphology of the runner-like epicoles

The pyritization and internal mould preservation does not ~~make it possible to look at~~ allow observations of fine details or microstructure, but it does ~~make it possible to look at~~ permit observation of the branching pattern in 3 dimensions. The initial zooids that produced the bush-like colonies cannot be distinguished, but

Which clusters, cite a figure to help us [illegible] it the shorter axes in each colony give rise to two to three long lateral branches, which are straight to slightly curved. The branching patterns ~~or growth forms are seemingly quite diverse~~ including uniserial rows with distal parts of tubes turned right and left; pluriserial rows made of subparallel tubes to irregularly bunched tubes. Part of the variation could have been amplified by differential compaction in shales (Ross 1978; Briggs & Williams 1981). Diameter of the more 3D-preserved tubes is about 1,5 mm, but this might have been artificially augmented by compaction (De Baets et al. 2013). The tubes expand distally and are slightly contracted at the apex, giving them a club-like appearance, which ~~is quite~~ are typical ~~for~~ of hederelloids (Elias 1944). The tubes are mostly entirely attached with the exception of the apex which can be diagonally upturned to upright.

to what?

of what

you describe the details so much, the reader has to wait. It might be of value to your study, but maybe better

Discussion

Synvivo vs. Post-Mortem encrustation

were watch those

3&5

The ~~fact that the clusters~~ 3-5 of runner-like epicoles are growing on both side of the ammonoid and that earliest cluster (5) coincides with the position where the deviations from planispiral coiling start speak for an encrustations of the ammonoid during its life-time. This is the oldest direct evidence for in-vivo encrustation of ammonoids. The previous record holders were *Paranarcestes*, *Latanarcestes* and *Sellanarcestes* from the Upper Emsian interpreted to be encrusted with auloporid corals during their lifetime (Klug & Korn 2001).

phrasing

— explain the 3 separate clusters & their importance here

please give us more support for deviation in planispiral and synvivo. The argument needs support

in each case — was the evidence used

Identity of the encrusters

Stick w/ one term, encruster is common

The runner-like encrusters were initially thought to be auloporid corals (De Baets et al. 2013), which are known to encrust brachiopods (Zapalski 2005; Mistiaen et al. 2012) and ammonoids (Klug & Korn 2001) during their life-time. Auloporids are, however, often confused with hederelloids (Fenton & Fenton 1937; Elias 1944). Hederelloids are a problematic group of runner-like sclerobionts, which occurred in the fossil record from the Silurian ~~until~~ through the Permian and ~~reach their highest~~ were most diverse in the Devonian (Solle 1952; Solle 1968; Taylor & Wilson 2007). Hederelloids ~~themselves have~~ were traditionally ~~been~~ treated as cyclostome bryozoans (Bassler 1939; Elias 1944; Solle 1952; Solle 1968; Dzik 1981), but ~~they are clearly not based~~ more recent assessments based on branching patterns, skeletal microstructure, lack of an astogenetic gradient, and wide range in tube diameters support an unknown affinity (Bancroft 1986; Wilson & Taylor 2001; Taylor & Wilson 2007). They are currently mostly interpreted to be closely related to phoronids (Taylor & Wilson 2007; Taylor, Vinn & Wilson 2010; Frey et al. 2014). Both auloporid corals and hederelloids would be quite rare in the middle Kaub Formation as they need a solid substrate like shells to settle within the clayey environments of the Hunsrück Slate (Bartels, Briggs & Brassel 1998).

Maybe when you finish it will h[illegible]

omit, what point is this to your argument

these refs from before 1950, it's not known how common this, but your preservation makes it hard to distinguish

The nature of the pyritic preservation does not make it possible to look at the microstructure or fine details, but the general morphology, branching patterns and tube diameters speak for their

you said this earlier, rephrase

Preservation is said so you named [illegible] there are strong morphologic features that make it hard to distinguish b/n the two if poorly preserved identification as hederelloids rather than auloporids or bryozoans (Elias 1944; Bancroft 1986; Taylor & Wilson 2007). Hederelloids have been reported to encrust externally shelled cephalopods before (Thayer 1974; Brassel 1977; Bartels, Briggs & Brassel 1998; Frey et al. 2014), but these are, to our knowledge, the first reported to encrust an ammonoid in vivo. The nature of the preservation does not allow for a clear diagnosis, but it might belong to the yet unnamed species of *Hederella* previously reported from the Hunsrück Slate (Brassel 1977; Bartels, Briggs & Brassel 1998). Sclerobionts can provide also important information on paleoecology, sedimentary environments and taphonomy, both when they encrust shells in vivo or after death of their host (Baird, Brett & Frey 1989; Kacha & Šaric 2009; Rakociński 2011; Brett et al. 2012; Wilson & Taylor 2013; Luci & Cichowolski 2014; Wyse Jackson, Key & Coakley 2014; Luci, Cichowolski & Aguirre-Urreta 2016). Hederelloids are typical for the photic zone (Brett et al. 2012), which could indicate that the ammonoid lived primarily within the photic zone. This would be in line with the latest interpretations of the Hunsrück Slate with maximum depths of about 200 m (Bartels, Briggs & Brassel 1998; Sutcliffe, Tibbs & Briggs 2002). Additional studies on epicoles on ammonoid shells from the Hunsrück Slate would be necessary to further test this hypothesis. So far, bivalves, brachiopods, bryozoans, crinoids and tabulate corals have been reported to encrust conchs of ammonoids or other externally shelled cephalopods from the Hunsrück Slate s.s. or middle Kaub Formation (Bartels, Briggs & Brassel 1998; De Baets et al. 2013), but these have mostly thought to have happened post-mortem (Bartels, Briggs & Brassel 1998; Jahnke & Bartels 2000; De Baets et al. 2013).

What does this add.

add to intro

This argument is off. The deepest photic zone in modern clear H₂O is ~200m. No way it would be euphotic @ that depth. BUT supports your syn vivo argument; had to live in the H₂O column.

Implication for mode of life

Loosely coiled early ammonoids are ~~mostly treated~~ considered ~~as~~ poor swimmers based on their little lack of streamline~~d~~ ~~with~~ and high drag (Westermann 1996; Klug & Korn 2004; Klug et al. 2015) so that additional limitations imposed by epizoa on streamlining and shell orientation might be ~~(even)~~ less important in these forms than in normally coiled ammonoids interpreted to ~~better~~ swimmers. The fact that our specimen survived ~~at~~ least 3 encrustations and growth deformations associated with them (e.g., alterations in the mode of coiling) until adulthood further corroborates this idea, although further investigation~~s~~ is needed ~~on additional specimens would be necessary to confirm this hypothesis~~. The hederelloids generally grow along the spiral direction and do not cross from one whorl to the next, which could speak they already encrusted the ammonoid during its lifetime too. We cannot entirely rule out a post-mortem encrustation of clusters 1-2. Their apertures are preferentially orientated away from the aperture of the ammonoid conch as opposed to those of the inner whorls (cluster 3-5) which are preferentially orientated towards it. Associated dacryoconarids do not show a preferential orientation with respect to the substrate or the epizoa. This does not necessarily speak against their encrustation during the life-time of the ammonoid as the terminal uncoiling is interpreted to have influenced the life orientation from an upturned aperture in the inner whorls to a downturned aperture during the terminal uncoiling at the end of the ontogeny (Klug & Korn

stickout terms

you missed a good set up for this

in the syn vivo section

Explain how we know which those are

syn vivo argument

but depth of 200 m suggests it is unlikely

2004; De Baets et al. 2013; Klug et al. 2015). We know the ammonoid specimen reached adulthood because it terminally uncoils, which is interpreted as a sign of adulthood (De Baets et al. 2013). *Hederella* is known to encrust other ammonoids from the Hunsrück Slate, but ~~this~~ known instances probably happened post-mortem (Brassel 1977; Bartels, Briggs & Brassel 1998). There is ~~least~~ no evidence that these happened in-vivo as these are located on incompletely preserved body chambers, and some have been interpreted to encrust the inside of the shell – but this should be further test with μCT. Additional studies would be necessary to confirm if our specimen is an isolated case of in vivo encrustation or part of a more common phenomenon.

tense

Implications for taxonomy

Defining pathological specimens as species can also have important taxonomic implications (Spath 1945). Some even claim assigning a pathological specimen might undermine the status of the species which are based on a pathological specimen and that a new type should be selected (Haas 1946). This has recently been more intensively discussed for the holotype of *Homo floriensis* (Kaifu et al. 2009; Eckhardt & Henneberg 2010). As the only known non-planispirally coiled specimen is pathological, it is deemed better to designate another specimen as type for this species to avoid ambiguity as non-planispirality does not belong to normal intraspecific variation nor to the taxonomic definition of this taxon. We suggest to select paratype SMF-HF 940 from the same locality as the neotype(De Baets et al. 2013). We are however confident that original type specimen belong to same species as the neotype as it completes the same amount of whorl before uncoiling, has a similar rib spacing and only differs from other specimens in its pathological coiling deviations (De Baets et al. 2013).

Conclusions

With the aid of μCT, we can demonstrate that at least some of the encrustations must have happened during the lifetime of the ammonoid as the epicoles are located on both sides of the ammonoid near place where deviations from planispiral coiling start. This indicates that the non-planispiral, slight trochospiral coiling in this specimen is pathological and does not form a part of the natural variation of as it was observed Mesozoic heteromorphs and originally interpreted in this specimen (Dietl 1978; De Baets et al. 2013). To avoid taxonomic confusion as non-spiral coiling does not form part of the natural variation, we herein suggest to select a non-pathological specimen as neotype for the species *Ivoites opitzi*. As the specimen survived at least 3 different encrustations and associated deformations, until adulthood, the effects on its mode of life were probably negligible. We re-identify these runner-like epizoa as hederelloids (as opposed to auloporid tabulate corals), which make them the first known hederelloids to encrust an ammonoid in vivo and suggest that the ammonoid probably lived within the

at present, you haven't argued this well, which has negative implications for your whole thesis

this is the first time this is clear

phrasing should match previous piece

euphotic zone for most of its life. However, more studies on epicoles and epizoa from the Hunsrück Slate, preferably with µCT, would be necessary to further corroborate these hypotheses.

Author contributions

Julia Stilkerich analyzed the data, wrote the paper, prepared figures, reviewed drafts of the paper.

Kenneth De Baets conceived and designed the experiments, prepared figures and/or tables, reviewed drafts of the paper.

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