

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

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Abstract:

We herein examine the only known non-planispirally coiled early Devonian ammonoid, the holotype specimen of *Ivoites opitzi*, to investigate if the host was encrusted *in vivo* and if these sclerobionts were responsible for the trochospiral coiling observed in this unique specimen. To test if the presence of runner-like sclerobionts infested the historically collected specimen of *Ivoites opitzi* during its life, we used microCT to produce a three-dimensional model of the surface of the specimen. Our results indicate that sclerobionts grew across the outer rim (venter) on both sides of the ammonoid conch at exactly the location where the deviation from the planispiral was recognized, and where subsequent ammonoid growth would likely preclude encrustation. This indicates *in vivo* encrustation of the *I. opitzi* specimen, and represents the earliest documentation of the phenomenon. Further, this suggests that non-planispiral coiling in *I. opitzi* was pathologically induced and does not represent natural morphological variation in the species. Despite the observed anomalies in coiling, the specimen reached adulthood and retains important identifying morphological features, suggesting the ammonoid was minimally impacted by encrustation in life. As such, appointing a new type specimen – as suggested by some authors – for the species is not necessary. In addition, we identify the sclerobionts responsible for modifying the coiling of this specimen as hederelloids, a peculiar group of sclerobionts likely related to phoronids. Hederelloids in the Devonian are commonly found encrusting on fossils collected in moderately deep environments within the photic zone and are rarely documented in dysphotic and aphotic samples. This indicates that when the ammonoid was encrusted it lived within the euphotic zone and supports the latest interpretations of the Hunsrück Slate depositional environment.

Introduction

Ammonoids are an extinct group of externally-shelled cephalopods that are often used to study biostratigraphy, diversity and evolutionary patterns (Ritterbush et al. 2014). The ammonoid shell is typically coiled with touching or overlapping whorls, but some forms – so called heteromorphs – deviate from this shape as their shell is not entirely coiled and/or is trochospirally coiled (Landman, Tanabe & Davis 1996). Mesozoic 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 were loosely coiled and can therefore also be considered heteromorphs from a morphological perspective. However, early ammonoids differ in important ways from Mesozoic

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43 heteromorphs as their embryonic shell is also uncoiled (House 1996; De Baets et al. 2012; De
44 Baets et al. 2013; De Baets, Landman & Tanabe 2015), and not all types of coiling known
45 from the Mesozoic have been reported from the Paleozoic (e.g., trochospiral coiling is
46 thought to be absent). The sole known possible exception was a specimen of *Ivoites opitzi*
47 from the Hunsrück Slate of Germany, which showed evidence for non-planispiral coiling (De
48 Baets et al. 2013). Originally, the holotype specimen was interpreted to exhibit a transitional
49 morphology in the natural variation from gyroconic to trochospiral coiling as observed in the
50 Jurassic heteromorph *Spiroceras* (Dietl 1978).

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51 However, this specimen is also encrusted by epicoles – “any organism that spent its life
52 attached to or otherwise inhabiting the exterior of any more or less hard object” (Davis,
53 Klofak & Landman 1999). In biology, the term chosen for the encrusting organism implies the
54 relationship it has with its host (e.g. *in vivo*, post mortem), and a wide variety of terminology
55 has been employed for encrusters in the paleontological literature (see discussion in Taylor
56 & Wilson 2002). A general term for encrusting or boring organism being used with growing
57 popularity is ‘sclerobiont’ and means “organisms living in or on any kind of hard substrate”
58 (Taylor and Wilson, 2002). If these epicoles, or sclerobionts, settled on the ammonoid host
59 shell during its life, they could be called epizoa (Davis, Klofak & Landman 1999; Klug & Korn
60 2001) and may cause deviations from planispiral coiling (oscillations of the shell around the
61 median plane to trochospiral coiling) to abnormalities in the whorl cross section when
62 overgrowing the epizoa (Merkt 1966; Keupp 1992; Checa, Okamoto & Keupp 2002) and
63 various other pathologies (Larson 2007; Keupp 2012; De Baets, Keupp & Klug 2015; Keupp &
64 Hoffmann 2015). Cephalopod workers have commonly used the term epicoles to refer to
65 organisms which encrust ammonoids post-mortem (Davis, Klofak & Landman 1999; Klug &
66 Korn 2001; Rakociński 2011; De Baets, Keupp & Klug 2015; Keupp & Hoffmann 2015).
67 Deviations from planispiral coiling in ammonoids have been attributed to sclerobionts in the past
68 (discussed below), yet distinguishing between *in vivo* and post-mortem encrustations is rarely
69 straightforward. In some cases it is impossible to tell if encrustation was *in-vivo* or post
70 mortem, but using various lines of evidence (Seilacher 1960; Seilacher 1982; Baird, Brett &
71 Frey 1989; Davis, Klofak & Landman 1999; Keupp 2012; De Baets, Keupp & Klug 2015; Keupp
72 & Hoffmann 2015) can sometimes elucidate a live-live interaction between host and
73 encruster. The main criteria used by researchers to identify likely cases of *in vivo*
74 colonization of cephalopod shell are (compare Rakús & Zítt 1993; Davis, Klofak & Landman
75 1999; Klug & Korn 2001; Luci & Cichowolski 2014):

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- 76 1. both flanks are encrusted but the apertural region remains free of encrusters
- 77 2. encrusters growth stops precisely at a whorl or are otherwise outpaced by the conch
- 78 growth of the cephalopod
- 79 3. encrusters show a dominant growth direction consistent with shape and putative life
- 80 position of the cephalopod shell and may express changes in growth direction as the
- 81 host life position changes
- 82 4. the cephalopod reacts to its encrusters during growth by developing some kind of
- 83 behaviour that is reflected in the shell (usually nonplanispiral coiling and other
- 84 deformations).

86 Cases in which deformation of the shell and/or deviation from the normal planispiral coiling
 87 were caused by encrusters provide incontrovertible evidence that the encrusters colonized
 88 the shell while the host lived (Checa, Okamoto & Keupp 2002; Luci & Cichowolski 2014).
 89 Asymmetrical encrustations during life result in deviations from the planispiral; this has been
 90 experimentally demonstrated in gastropods and has been observed in various taxa of
 91 ammonoids (Merkt 1966; Klug & Korn 2001; Keupp 2012). Patterns related with Criteria 1
 92 and 3 are the only criteria which can be used to infer in-vivo encrustation when host growth
 93 has already stopped (Seilacher 1960; Keupp 2012), but could potentially also develop in
 94 postmortem sclerobiont attachment during necroplanktonic drift. However, post-mortem
 95 drift seems unlikely when ammonoid shells are small (< 200 mm: Wani et al. 2005;
 96 Rakociński 2011). Large, well-preserved or heavily colonized ammonoids were likely also
 97 encrusted *in-vivo*, because the length of time required for significant encrustation to occur is
 98 greater than the length of necroplanktonic drift, even when the additional weight of the
 99 sclerobiont is not considered (Keupp 2012). Furthermore, a vertical position resembling the
 100 living position of the ammonoid is not always preserved in necroplanktonic drift, and a
 101 subhorizontal position can be achieved after *asymmetrical* postmortem encrustation as a
 102 result of added weight (e.g., loosely coiled *Spirula*; Donovan 1989).

103 Although post-mortem encrustations of ammonoids on the seafloor can be common
 104 (Rakociński 2011), there are many examples for different organisms settling on the shells of
 105 living and fossil cephalopods including foraminifers, bivalves, sponges and corals (Baird,
 106 Brett & Frey 1989; Davis & Mapes 1999; Keupp 2012; Wyse Jackson & Key Jr 2014). These
 107 live-live interactions are not necessarily beneficial for the host or the sclerobiont. Often the
 108 cephalopods are disadvantaged, because encrustation increases drag and provides an
 109 additional weight burden that the cephalopod must carry, potentially limiting speed and
 110 mobility (Keupp 2012). In some cases the encrusters have a disadvantage. As the host
 111 cephalopod grows, the encruster may rotate away from their preferred position, losing
 112 access to valuable currents for filter feeding, and might eventually be overgrown by the shell
 113 in coiled ammonoids (Meischner 1968). However, encrusters largely profit from establishing
 114 on a pelagic host. Sessile organisms obtain a pseudoplanktic method of locomotion,
 115 providing the potential for greater and more varied nutrition and increased reproductive
 116 breadth.

117 Mobile organisms can potentially use the shell as temporary pasture (Keupp 2012), while
 118 sclerobionts can use it as benthic island surrounded by soft and unconsolidated sediment
 119 (Seilacher 1982). For pathological reactions in shell form and growth to occur, the
 120 sclerobionts must settle on still growing, younger hosts. Sclerobionts that settle on the shell
 121 of adult animals that have already reached their final shell size do not induce a pathological
 122 change in the host. In those situations, it is only possible to infer that these sclerobionts
 123 encrusted *in-vivo* because of their preferential orientation with respect to water currents or
 124 the life position of its host (Seilacher 1960; Seilacher 1982; Keupp, Röper & Seilacher 1999;
 125 Hauschke, Schöllmann & Keupp 2011).

126 If encrustation happens after the host's death, the organisms can colonize both the exterior
 127 and interior of empty shells (Bartels, Briggs & Brassel 1998). Shells which are lying on the sea

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129 bottom are typically substantially overgrown on one side (the portion above the sediment-
130 water interface) and is usually taken as good evidence for post-mortem encrustation
131 (Seilacher 1982; Schmid-Röhl & Röhl 2003; Lukeneder 2008; Keupp 2012). Encrustation on
132 both sides can potentially also develop in reworked shells and internal moulds; however
133 these typically show a more complex history of encrustation involving multiple generations
134 and a variety of taxa (Macchioni 2000; Luci & Cichowolski 2014; Luci, Cichowolski & Aguirre-
135 Urreta 2016). More importantly, resedimentation typically results in shell breakage and
136 reworked ammonoids (sensu Fernández-López 1991) differ considerably from normally
137 preserved ammonoids (e.g., abrasional features, differences in infilling and preservation:
138 Fernández-López & Meléndez 1994). Post-mortem encrustation can also be recognized when
139 structures normally believed to be covered with soft-parts (inside of the shell) or additional
140 objects are encrusted by the epicoles (Bartels, Briggs & Brassel 1998; Klug & Korn 2001).
141 Different generations of sclerobionts with clearly diverging orientations or different taxa on
142 both sides of the ammonoid are also indicative of a post-mortem encrustation (Macchioni
143 2000; Klug & Korn 2001; Luci & Cichowolski 2014).

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144 Our main goal is to test if the sclerobionts settled on the ammonoid during lifetime, which
145 can tested by investigating the criteria listed above – particularly if they are growing on both
146 sides of the shell (criterium 1) and if the beginning of non-planispiral coiling (criterium 4)
147 correlates with the settling of these sclerobionts. If these encrustations happened during
148 lifetime and can be linked with severe pathological reactions (e.g., non-planispiral coiling),
149 this might have important implications for taxonomy and indirectly for biostratigraphy
150 (Spath 1945). Pathological specimens with strongly different morphologies have occasionally
151 been described as different species (Spath 1945; Keupp 2012).

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152 An additional goal is to identify the identity of the sclerobionts, which were preliminary
153 determined to be aulopodid tabulate corals (De Baets et al. 2013). Some taxa of aulopodid
154 corals have traditionally been confused with other sclerobionts with runner-like
155 morphologies (Lescinsky 2001) like hederelloids and cyclostomate bryozoans (Fenton &
156 Fenton 1937; Elias 1944; Bancroft 1986).

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157 In testing these questions, it was important to avoid using destructive analyses because the
158 specimen is an important historical specimen (Opitz 1932) and the holotype of *Ivoites opitzi*
159 (De Baets et al. 2013) from the famous Hunsrück Lagerstätte. The Hunsrück Slate is a facies
160 typical for the Lower Devonian (Emsian) of the Rhenish Massif which consists predominantly
161 of dark fine-grained argillites metamorphosed into slates (Bartels, Briggs & Brassel 1998). In
162 the Bundenbach-Gemünden area, these strata can contain fossils with remarkable
163 preservation including articulated echinoderms and vertebrates as well as preserved soft
164 tissues of arthropods and other groups without hard tissues (Bartels [Briggs & Brassel, 1998](#)).

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165 Although some fossils reveal remarkable preservation, they are all typically flattened and it is
166 difficult to impossible to prepare such thin, compressed fossils from both sides without
167 destroying parts of it. This is for example illustrated by the only known specimen and
168 holotype of *Palaeoscorpius devonicus*, where some parts of the shale that are thinner than 1
169 mm are very fragile or missing altogether after preparation (Kühl et al. 2012b). This might be
170 one of the reasons why fossils with hard parts commonly studied for biostratigraphic or
171 paleoenvironmental purposes at other sites where they are more three-dimensionally

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173 preserved have been comparable little studied in the Hunsrück Slate (Bartels, Briggs &
174 Brassel 1998; Südkamp 2007). This is also the case for ammonoids, which are important
175 index fossils to date this deposit and are often extremely flattened hampering also their
176 taxonomic assignment (Bartels, Briggs & Brassel 1998; De Baets et al. 2013).

177 Considering the size and the preservation of our specimen, as well as the expected x-ray
178 contrast between pyritic fossils and the slate matrix, we elected micro-CT to create a three-
179 dimensional model to answer these questions. This method is well suited for these purposes
180 (Sutton, Rahman & Garwood 2014). Many CT-studies have focused on analyzing ontogeny or
181 morphological traits for phylogenetic purposes (Monnet et al. 2009; Garwood & Dunlop
182 2014; Naglik et al. 2015a), but they can be used to test ecological or paleobiological aspects
183 (Kruta et al. 2011; Kühl et al. 2012b; Hoffmann et al. 2014) such as the interpretation of
184 pathologies (Anné et al. 2015) and bioerosion (Beuck et al. 2008; Rahman et al. 2015).
185 Tomographic studies in ammonoids have focused on functional morphology, empirical
186 buoyancy calculations and ontogeny of the chambered shell (Lukeneder 2012; Hoffmann et
187 al. 2014; Tajika et al. 2014; Lemanis et al. 2015; Naglik et al. 2015a; Naglik et al. 2015b; Tajika
188 et al. 2015; Lemanis et al. 2016; Lemanis, Zachow & Hoffmann 2016; Naglik, Rikhtegar & Klug
189 2016).

190

191 Material and geological setting

192 The studied fossil specimen is the holotype of *Ivoites opitzi*, which was collected from the
193 Hunsrück Slate in the Central Hunsrück, now known as the Middle Kaub Formation
194 (Schindler et al. 2002), at the Schieleberg-quarry near Herrstein, Germany (De Baets et al.
195 2013; see Fig.1 for a map and stratigraphic provenance of this specimen). It is repositied in
196 the Karl-Geib-Museum in Bad Kreuznach: KGM 1983/147. The Middle Kaub Formation
197 contains some of most completely preserved early ammonoids (De Baets et al. 2013) and
198 belong the oldest known ammonoid faunas (Becker & House 1994) together with similar
199 aged faunas from China (Ruan 1981; 1996) and Morocco (De Baets, Klug & Plusquellec 2010).
200 The exact stratigraphic position of our specimen is not known. However, *Ivoites* is restricted
201 to Early Emsian. This particular species (*I. opitzi*) has been found associated with
202 dacryoconarid *Nowakia praecursor* in samples deriving from Eschenbach-Bocksberg Quarry,
203 but they have also been found in overlying layers of the Obereschenbach quarry
204 (Wingertshell member sensu Schindler et al. 2002), which might range into the Barrandei
205 Zone (De Baets et al. 2013). Other ammonoids, including those from the same genus (*I.*
206 *schindewolfi*, *Erbenoceras solitarium*), which have been reported from the early Emsian
207 strata of the Schieleberg quarry in Herrstein, speak for a Praecursor to the Barrandei zone
208 age of the strata (De Baets et al. 2013).

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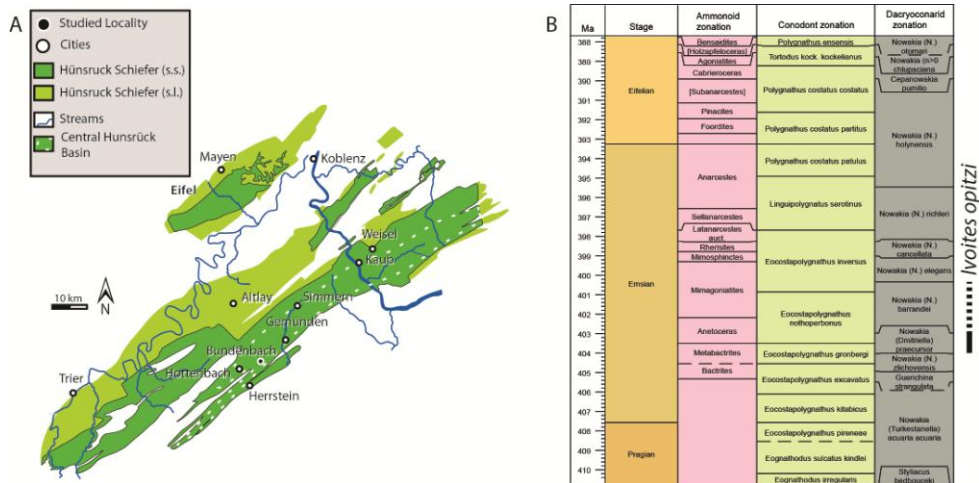


Fig.1: Geographic and Stratigraphic Context. (A) map of the locality (modified from De Baets 2012) and (B) stratigraphic provenance of *Ivoites opitzi* (time-scale based on Becker, Gradstein & Hammer 2012: created with time-scale creator 6.4: <http://engineering.purdue.edu/Stratigraphy/tscreator/>)

We investigated the taxonomy, provenance and taphonomy of 342 ammonoids from the Central Hunsrück Basin in a recent monograph (De Baets et al. 2013) including 82 specimens of *Ivoites* and 7 additional specimens of closely related *Metabactrites*.

The investigated specimen was chosen as the holotype above 19 other specimens of *Ivoites opitzi* as it was 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 evidenced by traces of suture lines and other structures (e.g., opitzian pits) internal to the shell (taphonomic category IIB of De Baets et al., 2013). The last half-whorl probably corresponds to the body chamber as indicated by faint traces of a suture in hand piece and x-ray images (Kneidl 1984), lack of pyrite infilling of the last whorl, terminal uncoiling as well as the large lateral extension of the end of the whorl interpreted to be the apertural edge (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 and before the dissolution, compaction, and breakage of the shell. These observations were used successfully to interpret preservation of ammonoids in the Jurassic bioturbated shales (Hudson 1982), and were additionally supported by fracture patterns (De Baets et al. 2013).

The whorls of this specimen 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). Oblique embedding can result in one bit of whorl lying on top of one whorl, but the opposite side should then lie below this whorl (see for example De Baets et al. 2013, Plate 5, Fig. 3 for an example), which is not the case in our specimen. Compaction on an umbilical concretion can also results in asymmetric deformation, but affect similar quadrants is the same way and the concretion should still be

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239 present, which is not the case in our specimen (see De Baets et al. 2013, Plate 10, Fig. 11 for
240 an example). Compaction of a horizontally embedded specimen would result in subsequent
241 whorl (with a thicker whorl section) to lie above previous whorls. The only way the
242 preservation observed in KGM 1983/147 could occur is if the specimen was already
243 torticonic before burial.

244 | During the initial investigation of the holotype of *I. opitzi*, the possibility of a live-live
245 relationship between the host and the sclerobionts was excluded because of an inferred lack
246 of conclusive evidence (De Baets et al. 2013). The sclerobionts nearer the aperture did not
247 provide any evidence that could support *in situ* or post-mortem encrustation. The
248 sclerobiont colony on the phragmacone near the point of non-planispiral coiling was
249 seemingly not growing across both sides of the whorl, and again, the authors were unable to
250 infer the relationship between host and sclerobiont. But only the left side was prepared in
251 this historically collected material (Opitz, 1932, p. 121, Fig. 117). A microCT of the specimen
252 | allowing [studying](#) the specimens from both sides, now gives us the unique opportunity to
253 reevaluate this interpretation.

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Fig. 2: Holotype of *Ivoites opitzi*. Several sclerobionts can be seen encrusting specimen KGM 1983/147. [Scale bar: 1 cm.](#)

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262 Methods

263 The specimen of *I. opitzi* under investigation is a holotype, and thus could not be
264 investigated destructively. Thus, the specimen was well-suited to be studied with X-ray
265 microtomography. X-ray microtomography uses x-rays to acquire radiographs (or
266 projections) of an object at multiple angles. From these projections, a sequence of parallel
267 and evenly spaced tomograms (individual slice images mapping the X-ray attenuation within
268 a sample) is computed indirectly. This tomographic dataset in turn can be used to recreate a
269 virtual model (3D model) without destroying the original object. The prefix micro- refers to
270 the fact that pixel sizes of the cross-sections are in the micrometre range (Sutton, Rahman &
271 Garwood 2014). Markus Poschmann (Mainz) kindly borrowed the specimen from the Karl-
272 Geib-Museum and brought it to the Steinmann Institute, where it was investigated with X-
273 ray micro-tomography. KGM 1983/147 was scanned on a Phoenix v|tome|x s at 150 kV and
274 160 µA with 0.400 s of exposure time by Alexandra Bergmann (Steinmann Institute). This
275 resulted in two thousand two hundred unfiltered projections providing a voxel size of 118
276 µm (~ pixel size of 118µm). Three-dimensional reconstructions and an animation were
277 produced using the 107 images (tomograms) in the x-z-plane by Julia Stalkerich using the
278 free software SPIERS (Sutton et al. 2012; <http://spiers-software.org>). A video as well as files
279 essential for verification can be found in the supplementary material, the latter include the
280 used image stack and a scansheet with description of scan setting and specimen information
281 (Davies et al. 2017). The fixed threshold value was manually chosen to maximally separate
282 pyritic fossils from the shale matrix, because the objects of focus (ammonoid and epicoles)
283 are pyritic (see material and methods); Regions of interest were defined using the masking
284 system in SPIERS, allowing them to be rendered separately to have the most conservative
285 interpretation of the position of the pyritic ammonoid vs. epicoles (Sutton, Rahman &
286 Garwood 2014). Coloured masks were used in the final representation to distinguish the
287 various features captured: ammonoid (yellow), runner-like epicoles (green), orthoconic
288 nautiloid (red), brachiopod (blue) and dacryoconarids (yellow). This model was important
289 into Blender v 7.28 and enlarged 200% on the z-axis to measure the deviation from the
290 plani-spiral.

291

292 Results

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

294 In the model, the first whorl lies on top of the second whorl. The median plane of the first
295 whorl seems to lie between 1 and 2 mm above that of the second whorl in the model, which
296 must have been even greater before compaction (see discussion). The 3D-model (see Figs. 3,
297 4) therefore substantiates the previously hypothesized suspicion (De Baets et al. 2013) that
298 the specimen is not entirely coiled planispirally. Five clusters (A-E) of colonial sclerobionts
299 can be recognized in the 3D-model (see arrows in Figs. 3, 4).

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Comentario [GP1]: Please, be consistent to spell planispiral or plani-spiral in all cases

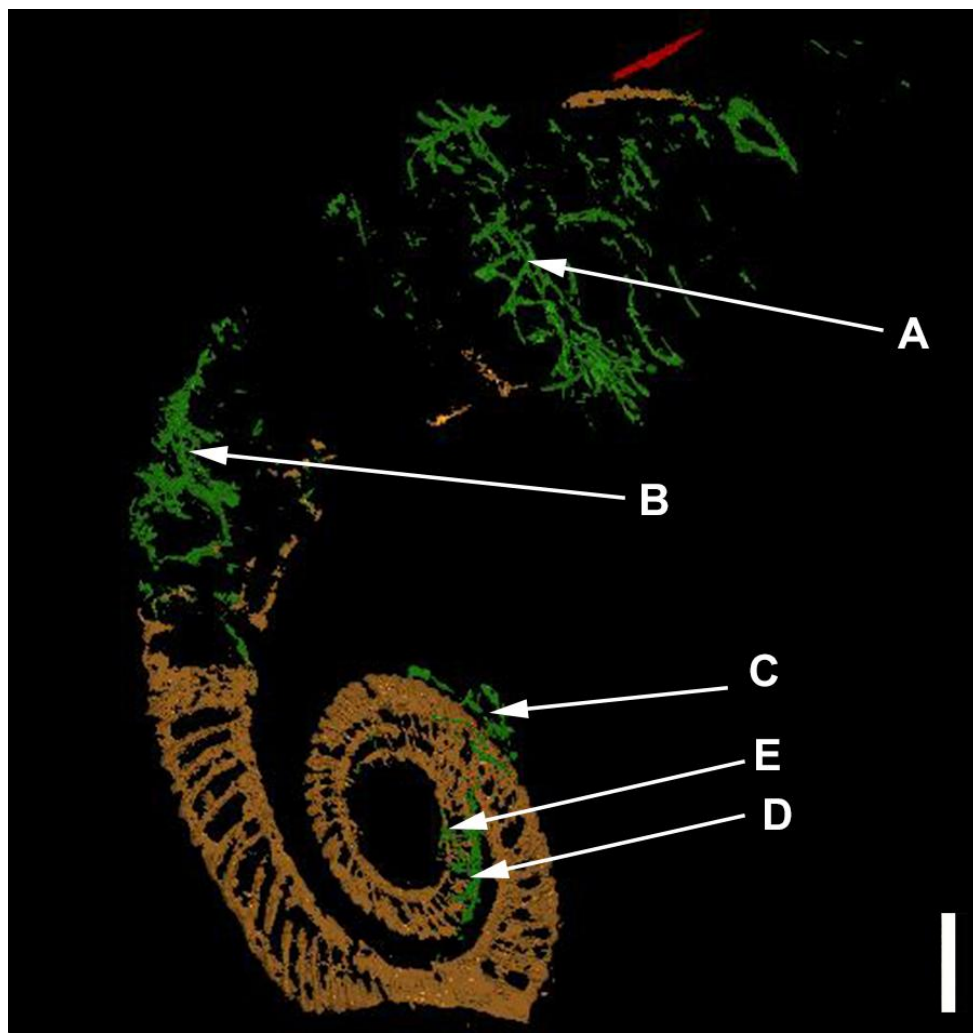


Fig. 3: The ammonoid (brown), the epicoles (green) and the orthoconic nautiloid (red) in the 3D-model. Five sclerobiont clusters (A-E) were distinguished. Scale bar: 1 cm.

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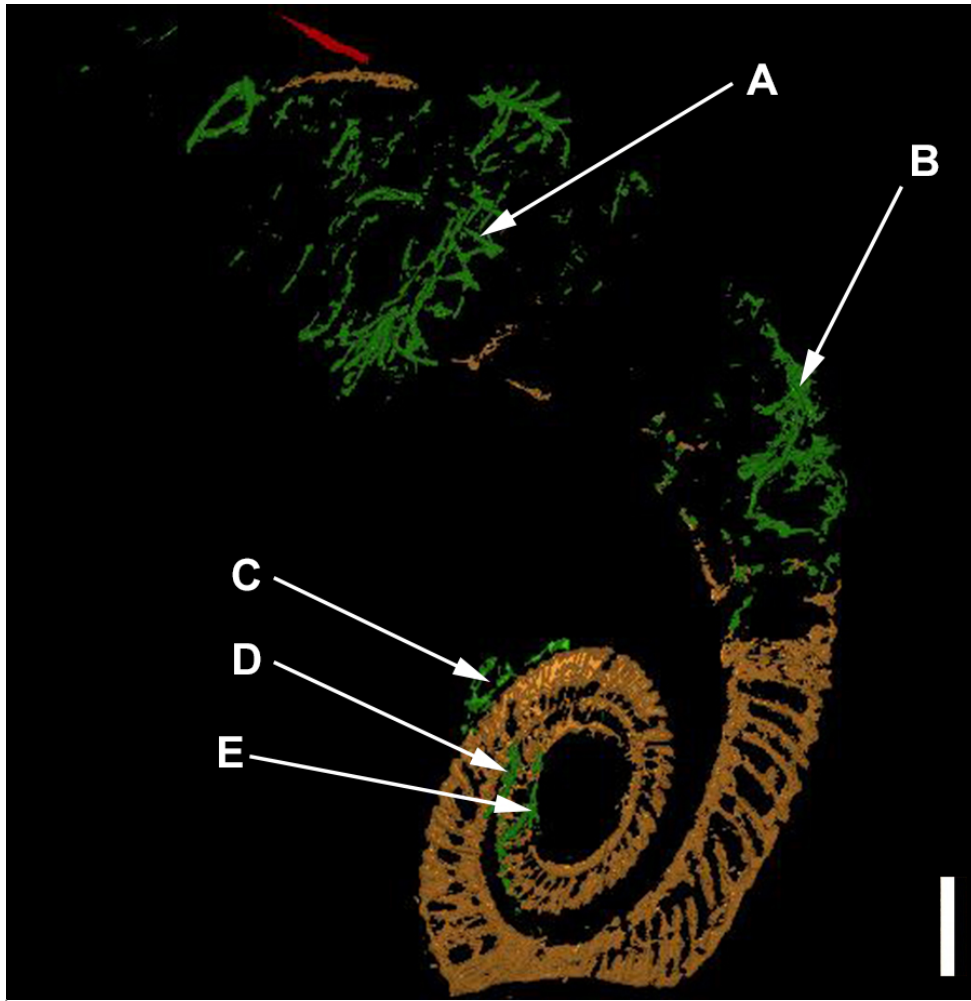


Fig. 4: The ammonoid (brown), the runner-like epicoles (green) and the orthoconic nautiloid (red) rotated 180°. Scale bar: 1 cm.

At least three clusters (C-E) can be recognized on the phragmocone. Additional clusters (A, B) can be found on the final demi-whorl. In the inner whorls, the sclerobionts are located ventrally on both sides of the whorl cross section (see Figs. 3C-E, 4C-E). Their direction of growth and budding follows the spiral axis of the ammonoid shell. The earliest recognizable sclerobionts with respect to the growth direction of the ammonoid (clusters D-E) coincide with the position where non-planispirality can be first recognized (Fig. 5).

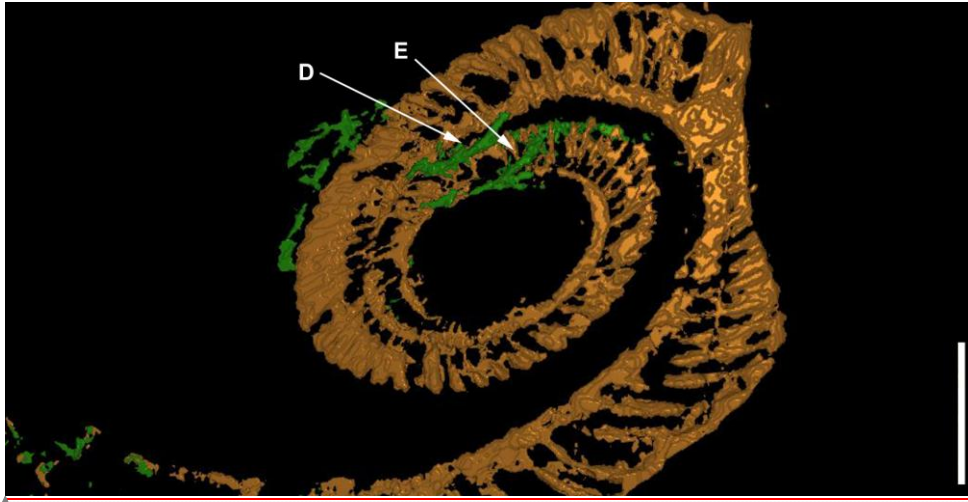
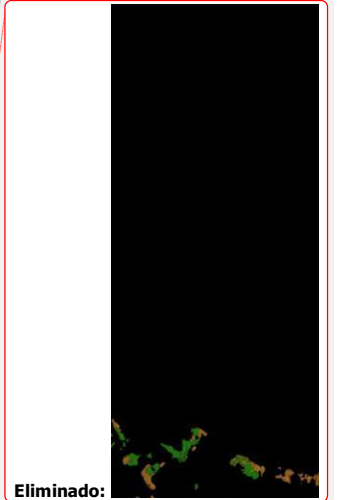
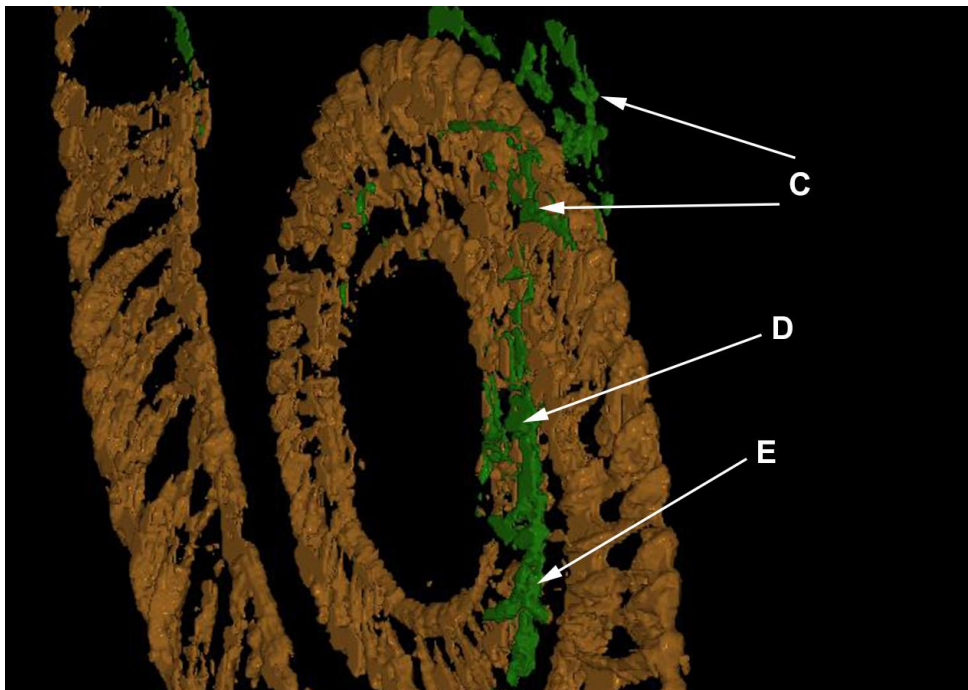


Fig. 5: The white arrows mark the position of the sclerobiont clusters (D and E) close to the position where non-planispiral coiling can be first recognized. Scale bar: 1 cm.

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More importantly, there is evidence that clusters (C, D and E) are growing on both sides of the ammonoid (Fig. 6). The last demi-whorl of the host ammonoid was not infilled with pyrite, therefore the growth patterns of the sclerobionts in clusters A and B cannot be established with certainty.



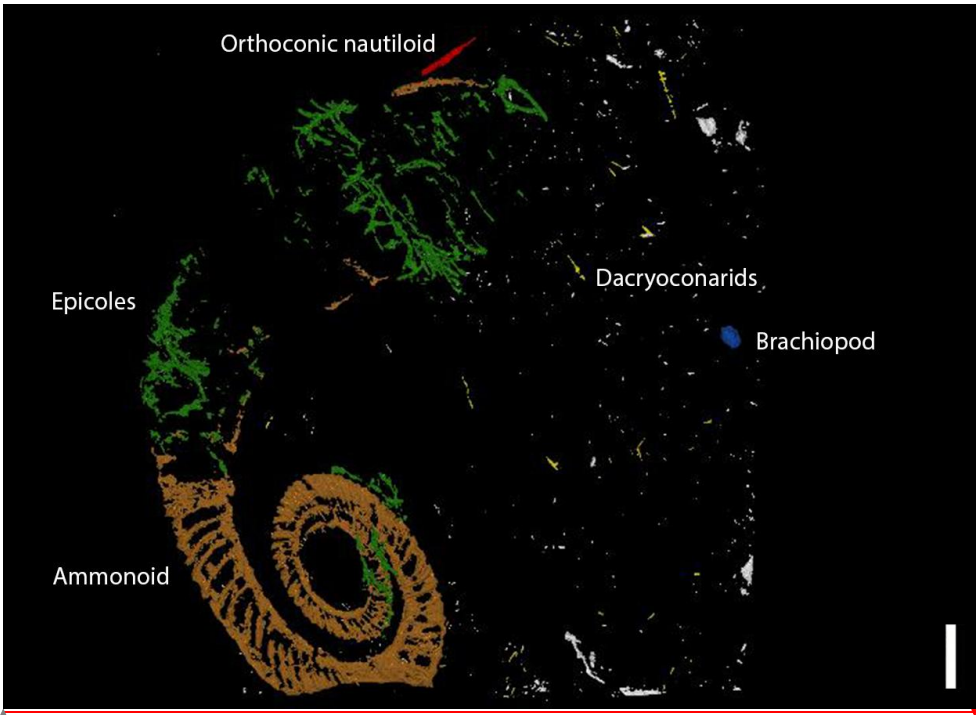
330 Fig. 6: Close-up of the 3D-model showing that sclerobionts are settling on both sides of the shell. Note
331 correlation between asymmetrical sclerobiont encrustation of cluster E and the deviation from planispiral
332 coiling of the host.

333

334 Elongated components like the dacryoconarids present in the substrate (marked in yellow in
335 Figure 7) along with the *I. opitzi* specimen are often orientated along the direction of the
336 paleo-current (Hladil, Čejchan & Beroušek 1991; Hladil et al. 2014; Gügel et al. 2017).
337 Neither the dacryoconarids nor the epicoles show a preferential orientation with respect to
338 the substrate. Sclerobiont clusters C, D, and E do show a preferential orientation with
339 respect to the spiral axis of the ammonoid shell. Unnamed, small, and bulky components
340 visible in the matrix are probably prytic nodules of different sizes.

341

342



343

344 Fig. 7: The 3D-model showing all components. A brachiopod is coloured blue and dacryoconarids are shown in
345 yellow. Runner-like epicoles are marked in green and orthoconic nautiloid in red. Scale bar: 1 cm.

346

347 Morphology of the runner-like sclerobionts

348 The mode of preservation of the *I. opitzi* specimen, pyritization and internal mould
349 preservation, makes examination of fine details or microstructure of the sclerobionts
350 impossible. Yet the microCT permits three dimensional examination of the branching

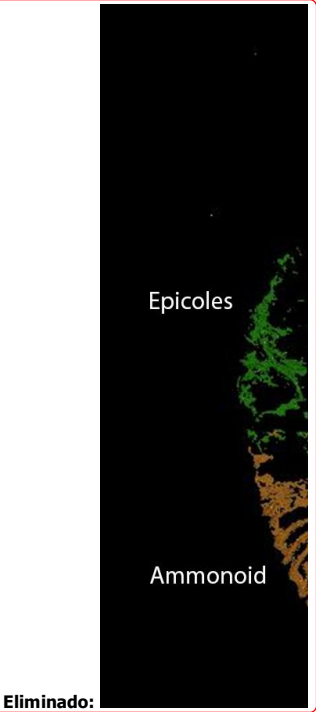
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353 patterns of the sclerobiont colonies. The original settlement location of the colonial
354 organism cannot be distinguished, but the branching pattern of colonies grows in a direction
355 largely parallel to the direction of the aperture of the host.

356 The colonies in all clusters have the same taxonomic affinity. Zooids in the colonies are long
357 and tubular, and curve slightly near the zooecial opening. Zooids are larger than those
358 commonly observed in bryozoans and bud in alternating directions. Diameter of the more
359 3D-preserved tubes is typically around 1.5 mm, but this might have been artificially
360 augmented by compaction (De Baets et al. 2013). The tubes widen in the direction of growth
361 expand distally and slightly contracted at the apex giving them a club-like appearance,
362 characters typical of hederelloids (Elias 1944).

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363 Branching morphology in the established colonies on the host are diverse despite many
364 shared characteristics. Morphologies of zooids exhibited in clusters A through D are
365 generally more elongate and acutely curved away from the uniserial plane to those in cluster
366 E which contain zooids that curve more dramatically along multiple, pluriserial branches of
367 the colony. Some of this variation could have been amplified by differential compaction in
368 shales (Ross 1978; Briggs & Williams 1981).

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370 Discussion

371 The three-dimensional model of *I. opitzi* permitted extensive observation of the relationship
372 between the ammonoid host and the sclerobiont clusters present. The results permit
373 positive identification of the sclerobionts and interpretation of the relationship between
374 them and their host.

375 Synvivo vs. Post-Mortem encrustation

376 Three possible scenarios can explain encrustation on both sides of the ammonoid by a
377 sclerobiont colony, clearly visible in clusters C, D and E:

378 1) In-vivo encrustation: encrustation on both sides of the ammonoid by sclerobiont colonies
379 C, D, and E and the direction of the growth of those sclerobionts matching the growth of the
380 ammonoid, speak for an in-vivo encrustation – at least for sclerobiont clusters C-E. A lack of
381 a similar directional growth for all sclerobiont colonies on the ammonoid and with
382 dacryoconarids in the surrounding substrate, as well as a lack in widespread encrustation
383 across the ammonoid shell, further support the likelihood that the ammonoid was encrusted
384 before the ammonoid settled on the seafloor (see Figure 8).

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385 2) Post-mortem drift: encrustation of such large colonies solely during post-mortem drift
386 seems unlikely due to the small size of our specimen (105 mm diameter). This is below the
387 200 mm limit listed for long floating cephalopod shells by Wani et al. (2005) and Rakociński
388 (2011). Interestingly, our specimen would have even a much smaller phragmocone volume
389 than coiled ammonoids at equal diameters used in these experiments. More importantly,
390 the extra weight of the sclerobionts should have made it sink even sooner than a non-
391 encrusted shells so that it would not have resulted in encrustation on both sides. Post-
392 mortem drift is deemed rare for ammonoids in general; most are implied to sink rather

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396 | rapidly (Maeda & Seilacher 1996). Furthermore its vertical position in the water column
397 | should have been affected by asymmetric encrustation resulting in a non-vertical position of
398 | the shell after loss of soft-part parts which should have led to a more asymmetrical
399 | distribution of the sclerobionts as the preferentially attach to the lower part of drifting shells
400 | (Donovan 1989).

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401 | 3) Resedimentation or reelaboration/reworking on the seafloor: usually encrustation of the
402 | sediment-free side of the ammonoids - which mostly end of horizontally on the seafloor - is
403 | taken to be characteristic unless reelaboration/reworking of shells or internal moulds
404 | happened (Macchioni 2000). In our cases, we have encrustation on both sides by the same
405 | colonies and transport by currents and reworking seems unlikely due the completeness of
406 | our specimen and similarities in preservation with other specimens of its taphonomic group
407 | (De Baets et al. 2013). All their characteristics speak for a relatively rapid burial and infilling
408 | with pyrite only during early diagenesis (before shell dissolution). Furthermore, the same
409 | sclerobionts (C-E) started growing on the venter to both sides of the lateral sides which
410 | speak rather for a simple encrustation history rather than multiple generations of epibionts
411 | encrusting each sediment-free side sequentially (at least one before and after
412 | resedimentation/reworking and possibly more). No evidence for re-sedimentation or
413 | reworking (abrasional features) is present in any of the 82 studied specimens of *Ivoites*.

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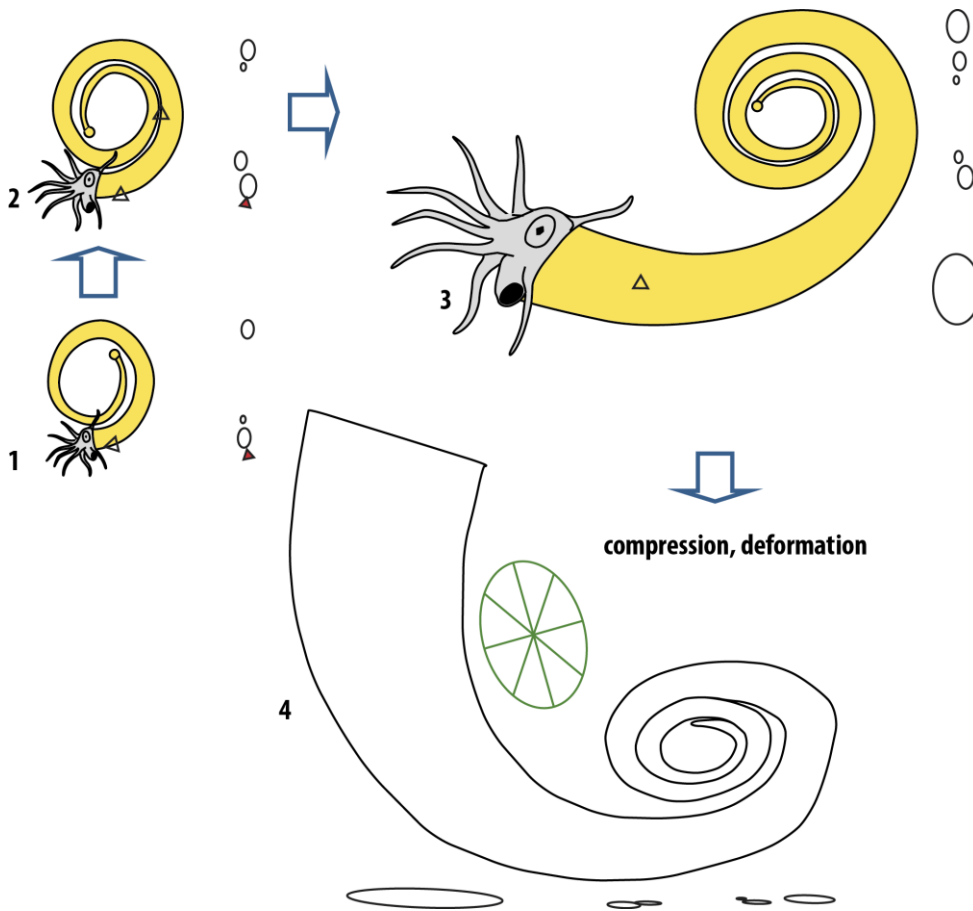


Fig. 8: Model of in-vivo encrustation and subsequent compression and deformation on *Ivoites opitzi*. 1) orientation and morphology of the specimen shortly after asymmetrical encrustation of first generation of epizoa (clusters D and E). 2) orientation and morphology of the specimen shortly after the asymmetrical encrustation of the second generation (cluster C) of epizoa (previous cluster of epizoa are currently lodged between the first and second whorl). 3) orientation and morphology of specimen when becoming encrusted with final epizoa (clusters A and B) or shortly before, 4) specimen after deformation; effect of deformation if specimen would have been initially planispirally coiled, effect in whorl section of specimen which was initially non-planispiral.

Pathological variation in the morphology of *I. opitzi*

The non-planispiral coiling of this specimen, a unique occurrence in the species, occurs at the position of the sclerobiont clusters D and E. This pathological variation in host growth is also consistent with encrustation of the cephalopod during its life-time. Even if the deviation in coiling plane is only 1 to 2 mm now, it would have been substantially greater before burial

and compaction. Whorl thickness alone has estimated to reduce up to 248 % in some specimens (De Baets et al. 2013), so originally these deviations could have been up at least 2.5 to 5 mm. If we artificially the thickness with 200 %, we obtain a maximum deviation of the median plane of one whorl to the next of about 2 mm (2,5 mm if we augment the thickness to 250 %). The same deviations can be observed within a single whorl (Fig. 10). Considering that the specimen has been extremely flattened (one whorl has been pressed on the other). At least another whorl thickness, the differences in whorl thickness between this whorl and the next which would make it a total of about 2 times this amount, ca. 4 mm (5 mm is we artificially augment the whorl thickness to 250%). This is a rather conservative estimate, as we cannot know exactly how the specimen was compressed between the whorls.

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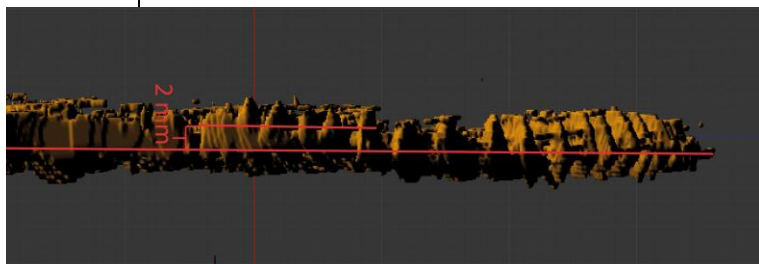


Figure 9. Retrodeformed whorl cross section to 200% results in a 2 mm distance between the mid-point of a particular part of the whorl (lateral view).

448 Sclerobionts in clusters D and E are in a position that would have been hard to encrust if the
449 subsequent whorl had already grown at the time of encrustation (e.g., when it was lying on
450 the seafloor, the space between whorls around the venter would only have been between
451 around 5 mm, complicating sclerobiont settling. Our specimen suggests that the second
452 whorl lies on top of the first whorl (e.g., in the direction of the more heavily encrusted side,
453 see Figure 3) while the last whorl probably lies again below the second whorl (e.g., the
454 coiling had almost normalized until the next encrustation by sclerobiont cluster C). The
455 encrustation and its slightly different weight distribution across the venter would predict a
456 deviation of the whorl initially in the direction of the encrusters weight and subsequently in
457 the opposite direction (this seems to be still visible in our specimen despite it been heavily
458 flattened). Such a pattern would thus be expected if the specimen was encrusted in-vivo for
459 the first time slightly before it completed about one whorl (Checa, Okamoto & Keupp 2002).
460 The non-planispiral coiling observed in this specimen could not be produced by flattening or
461 deformation – not even if the specimen was embedded obliquely (see discussion in Material
462 and Methods). Furthermore, clusters D-E are positioned closely before the position where
463 deviation of planispiral coiling can first be recognized and indicate that the coiling was
464 induced by the sclerobiont encrustation. If these clusters grew on the ammonoid during life,
465 as is also suggested by growth on both sides of the shell, the deviations from planispiral
466 coiling would have been unavoidable (Checa, Okamoto & Keupp 2002).

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467 The fact that sclerobiont clusters C, D, and E of runner-like epicoles are growing on both
468 sides of the ammonoid and that clusters (D-E) occur slightly before the position where the
469 deviations from planispiral coiling – where a whorl lies directly on top of the subsequent
470 whorl – can be first recognized are also consistent with an encrustation of the ammonoid
471 during its lifetime.

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472 This specimen, therefore, documents the oldest direct evidence for *in-vivo* encrustation of
473 ammonoids. The previous record holders were *Paranarcestes*, *Latanarcestes* and
474 *Sellanarcestes* from the Upper Emsian interpreted to be encrusted with aulopod corals
475 during their lifetime, also evidenced by deviations from normal planispiral coiling in the host
476 and by the subsequent growth of the ammonoid over the coral (Klug & Korn 2001; De Baets,
477 Keupp & Klug 2015).

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479 Identity of the encrusters

480 Hederelloids are a problematic group of runner-like sclerobionts, which occur in the fossil
481 record from the Silurian through Permian and are most diverse in the Devonian (Solle 1952;
482 Solle 1968; Taylor & Wilson 2007). Hederelloids have traditionally been treated as
483 cyclostome bryozoans (Bassler 1939; Elias 1944; Solle 1952; Solle 1968; Dzik 1981), but were
484 redefined based upon differences in branching patterns, skeletal microstructure, lack of an
485 astogenetic gradient, and wide range in tube diameters (Bancroft 1986; Wilson & Taylor
486 2001; Taylor & Wilson 2007). They are currently mostly interpreted to be closely related to
487 phoronids (Taylor & Wilson 2007; Taylor, Vinn & Wilson 2010; Frey et al. 2014). Both
488 aulopod corals and hederelloids are uncommon in the middle Kaub Formation as their life

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490 habit requires a solid substrate upon which to settle; these were rare within the clay
491 environments of the Hunsrück Slate (Bartels, Briggs & Brassel 1998).

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492 The nature of the pyritic preservation of the host specimen, *I. opitzi*, does not make it
493 possible to look at the microstructure or fine details of the sclerobionts, but the general
494 morphology supports that all clusters of sclerobionts share a taxonomic affinity. Runner-like
495 sclerobionts common in the Devonian include auloporidae coral, paleotubuliporidae bryozoans,
496 and hederelloids. The sclerobionts encrusting *I. opitzi* are colonial, with elongated zooids,
497 lateral branching/budding patterns, and relatively large tube diameters which speak for their
498 identification as hederelloids rather than auloporidae or bryozoans (Elias 1944; Bancroft 1986;
499 Wilson & Taylor 2006; Taylor & Wilson 2007).

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500 The runner-like encrusters were initially thought to be auloporidae corals (De Baets et al.
501 2013), which are known to encrust brachiopods (Zapalski 2005; Mistiaen et al. 2012) and
502 ammonoids (Klug & Korn 2001) during their lifetime. Some auloporidae taxa have been
503 confused with hederelloids in the past (Fenton & Fenton 1937; Elias 1944) and can be hard
504 to differentiate when taphonomic conditions have degraded the quality of the specimen due
505 to gross morphological similarities.

506 Hederelloids have been reported to encrust externally shelled cephalopods before (Thayer
507 1974; Brassel 1977; Bartels, Briggs & Brassel 1998; Frey et al. 2014), but these are, to our
508 knowledge, the first reported to encrust an ammonoid *in vivo*. Sclerobionts can provide also
509 important information on paleoecology, sedimentary environments and taphonomy, both
510 when they encrust shells *in vivo* or after death of their host (Baird, Brett & Frey 1989; Kacha
511 & Šaric 2009; Rakociński 2011; Brett et al. 2012; Wilson & Taylor 2013; Luci & Cichowolski
512 2014; Wyse Jackson, Key & Coakley 2014; Luci, Cichowolski & Aguirre-Urreta 2016).

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513 The presence of five distinct clusters of hederelloids suggests that colonization of the host by
514 sclerobionts happened numerous times (see Figures 4 and 6). Not all colonizations show
515 clear evidence of *in vivo* encrustation; clusters A and B were likely the last to settle on the
516 specimen – based upon their location on the shell and the ontogeny of the host – but also do
517 not show evidence of *post-mortem* encrustation. Clusters A and B, however, are the largest,
518 which suggest that they had sufficient nutrients to settle, establish, and grow for an
519 extended period of time. This is unlikely to have occurred in the benthos after the death of
520 the *I. opitzi* specimen, but is not impossible. However, because the size of the hederelloid
521 colonies in clusters A and B exceed that of the other colonies, clusters C, D and E were likely
522 not living concurrently with clusters A and B.

523 Implications for paleoenvironment of *Ivoites*

524 Some authors have attributed the rarity of encrusters in coiled ammonoids compared with Paleozoic
525 (orthoconic) nautiloids to their ability to (keep) clean or chemical defenses against encrusters
526 (Donovan 1989; Davis, Klofak & Landman 1999; Keupp 2012). Potentially, early ammonoids were
527 more similar to their orthoconic nautiloid and bactritoid relatives. Furthermore, mechanical removal
528 of epizoans might have proven more difficult in loosely coiled ammonoids like *Ivoites* as the previous
529 whorl might have been out of reach of the cephalopod-arm complex (see Figure 8). However, these
530 suggestions are all quite speculative – it is impossible to find direct evidence for chemical or
531 mechanical cleaning or defensive behavior in this fossil group. More importantly, these mechanisms

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532 are also unnecessary to be invoked for such differences which could equally be explained by the fact
533 that many nautiloids would have lived in more shallow environments – which show higher
534 encrustation rates in general (Brett et al. 2012; Šmrecak & Brett 2014; Šmrecak 2016). Modern
535 Nautilus shows differences in encrustations between different environments too (Landman et al.
536 1987).

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538 The sedimentary environment of the Hunsrück Slate have been widely interpreted, ranging
539 from shallow sedimentation on tidal flats, at depths from around storm-wave base to
540 significantly deeper (Solle 1950; Seilacher & Hemleben 1966; Erben 1994; Bartels, Briggs &
541 Brassel 1998). The sedimentary environment in the central Hunsrück Basin is now thought to
542 be rather complex; depressions between sedimentary fans provided environments below
543 storm wave base and sills which could locally extend into the intertidal zone (Etter 2002).
544 The beds with the exceptionally preserved fossils and hemipelagic fauna (ammonoids,
545 dactyloconarids) in the Bundenbach-Gemünden area have been interpreted to be mostly
546 deposited below storm-wave base and/or at depths around 100m (Sutcliffe, Tibbs & Briggs
547 2002; Stets & Schäfer 2009). Even in these regions, more sandy layers with neritic
548 brachiopods are intercalated, suggesting occasional shallower depths above storm wave
549 base. It is now generally accepted that the maximum depth was within the photic zone due
550 to the presence in some layers of receptaculitid algae, which are interpreted to be closely
551 related to green algae, and good visual capabilities of arthropods (Bartels, Briggs & Brassel
552 1998; Etter 2002; Selden & Nudds 2012). Based on the latter, maximum depths of 200 m
553 have suggested (Rust et al. 2016).

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554 Hederelloids are typical encrusters found in Devonian photic zone environments (Brett et al.
555 2012). They are most diverse and abundant in shallower facies, but persist into the deep
556 euphotic zone (Šmrecak 2016). The presence of hederelloids on the specimen, in
557 combination with other evidence described earlier, support an interpretation of *in vivo*
558 encrustation. The pelagic life habit of *I. opitzi* would allow colonies of hederelloids to settle
559 and grow on the shell with some success. In contrast, at depths of 100+ meters, hederelloid
560 encrustation, and sclerobiont encrustation in general, is significantly less common (e.g.,
561 Brett et al. 2011; Brett et al. 2012; Šmrecak & Brett 2014). Thus, presence of multiple
562 colonies of hederelloids on the specimen support *in vivo* encrustation at depths within the
563 photic zone, and lends further support for depositional conditions in line with current
564 interpretations that the Hunsrück Slate interpreted was deposited near storm-wave base
565 (Bartels, Briggs & Brassel 1998; Sutcliffe, Tibbs & Briggs 2002).

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566 De Baets et al. (2013) found encrusted ammonoid shells to be rare (only 6 of 342 studied
567 ammonoids: about 2%). Only two specimens of 82 specimens of *Ivoites* (2%) were found to
568 be encrusted with hederelloids – our specimen and an additional specimen of *Ivoites* sp.
569 which was interpreted to be encrusted post-mortem (Bartels, Briggs & Brassel 1998).
570 Taphonomic or collection biases (Wyse Jackson & Key Jr 2014) are unlikely to explain the low
571 percentages of encrustation as the ammonites and epibionts are principally preserved in the way
572 (e.g., pyritic compound moulds in our case). So far, bivalves, brachiopods, bryozoans, crinoids,
573 hederelloids and tabulate corals have been reported to encrust conchs of ammonoids or
574 other externally shelled cephalopods from the Hunsrück Slate s.s. or middle Kaub Formation

576 (Brassel 1977; Bartels, Briggs & Brassel 1998; Jahnke & Bartels 2000; Kühl et al. 2012a; De
577 Baets et al. 2013), but these have mostly thought to have happened post-mortem due to
578 their heavy encrustation on one side of the fossils or the encrustation of the structures
579 which would normally be covered with soft-parts (Bartels, Briggs & Brassel 1998; Jahnke &
580 Bartels 2000; De Baets et al. 2013). Heavy encrustations seems to be more common in
581 nautiloids (Bartels, Briggs & Brassel 1998; Jahnke & Bartels 2000; Kühl et al. 2012a), but
582 these have so far only been qualitatively studied. In environments between 100 and 200m
583 encrustation is generally low, which also consistent with a rare *in-vivo* encrustation of our
584 specimen which has swam in shallower depths when the first encrusters settled rather than
585 the commonly reported post-mortem encrustation. Additional studies on epicoles on
586 ammonoid shells and other shells from the Hunsrück Slate would be necessary to further
587 corroborate these hypotheses.

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588 Implication for mode of life

589 Loosely coiled early ammonoids are mostly treated as poor swimmers based on their poor
590 streamlining with high drag (Westermann 1996; Klug & Korn 2004; Klug et al. 2015a);
591 additional limitations imposed by epizoa on streamlining and shell orientation might be
592 (even) less important in these forms than in normally coiled ammonoids. The fact that our
593 specimen survived at least three separate encrustations – as evidenced by different
594 settlement locations of the clusters of hederelloids – and growth deformations associated
595 with earlier encrustation further corroborates this idea, although further investigations on
596 additional specimens would be necessary to confirm this hypothesis. Most hederelloid
597 colonies generally grow along the spiral direction and do not cross from one whorl to the
598 next, which provide additional evidence that they encrusted the ammonoid during its
599 lifetime.

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600 We cannot entirely rule out a post-mortem encrustation of clusters A-B. Hederelloid growth
601 in those clusters is preferentially orientated away from the aperture of the ammonoid
602 conch, as opposed to those of the inner whorls (cluster C-E) which are preferentially
603 orientated towards it. Associated dacryoconarids do not show a preferential orientation with
604 respect to the substrate (as would be expected in the case of current alignment: Hladil,
605 Čejchan & Beroušek 1991) or the hederelloids. This does not necessarily speak against
606 encrustation during the lifetime of the ammonoid by clusters A and B as the terminal
607 uncoiling of the ammonoid is interpreted to have influenced the life orientation from an
608 upturned aperture in the inner whorls to a downturned aperture (see Figure 8) during the
609 terminal uncoiling at the end of the ontogeny (Klug & Korn 2004; De Baets et al. 2013; Klug
610 et al. 2015a). We know the ammonoid specimen reached adulthood because it terminally
611 uncoils, which is typical for many taxa of Anetoceratinae and interpreted as a sign of
612 adulthood (De Baets, Klug & Korn 2009; De Baets et al. 2013; De Baets, Klug & Monnet 2013;
613 Klug et al. 2015b).

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614 *Hederella* is known to encrust another ammonoid from the Hunsrück Slate, but this is
615 interpreted to have happened post-mortem (Brassel 1977; Bartels, Briggs & Brassel 1998).
616 There is no evidence that this happened in-vivo in the second specimen as these are located
617 on an incompletely preserved body chamber, and have been interpreted as encrusting the
618 inside of the shell (Bartels, Briggs & Brassel 1998) – but this should be further tested with

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621 μ CT. Additional studies would be necessary to confirm if our specimen is an isolated case of
622 in vivo encrustation or part of a more common phenomenon.

623 Implications for taxonomy

624 Defining pathological specimens as species can have important taxonomic implications
625 (Spath 1945). According to Spath (1945), such ammonoid species should remain valid, but no
626 new type can be chosen while the holotype is still in existence. Others, like Haas (1946),
627 claim assigning a pathological specimen might undermine the status of the species,
628 considering the morphology of the species is described based on a pathological specimen,
629 and that a new neotype should be selected. It is important to note that several authors have
630 erected different ammonoid species based on small differences in coiling. As the only known
631 non-planispirally coiled specimen of *I. opitzi* is pathological, an author like Haas (1946) might
632 have suggested to designate another specimen as type for this species to avoid ambiguity.
633 However, our study highlights that non-planispirality does not belong to normal intraspecific
634 variation of this species, nor to the taxonomic definition of this taxon. Paratype SMF-HF 940,
635 which was collected from the same locality as the holotype (De Baets et al. 2013), would be
636 the best candidate among the paratypes. Reassigning a neotype has recently been
637 intensively discussed for the holotype of *Homo floresiensis* (Kaifu et al. 2009; Eckhardt &
638 Henneberg 2010), but the severity of deviation has to be considered in this specimen.
639 However, both aspects (electing a neotype for pathological specimens and its dependence of
640 the severity of the pathology) are not specifically discussed in the International Code of
641 Zoological Nomenclature (ICZN). According to Article 75.1 of ICZN, "the neotype is ...
642 designated under conditions ... when no name-bearing type specimen is believed to be
643 extant ...". In this case, if the holotype, even when pathologically deformed, is extant, the
644 proposal of neotype is not granted. A proposal could be submitted to the ICZN to resolve the
645 use of pathologically-induced morphological variation of holotypes, but this falls outside the
646 aim of our study. Furthermore, we are confident that the original type specimen belongs to
647 the same species as the paratypes as it completes the same amount of whorls before
648 uncoiling, has a similar rib spacing and only differs from other specimens in its minor coiling
649 deviations (De Baets et al. 2013). As non-planispiral coiling was not part of the original
650 diagnosis, we feel it is unnecessary to submit a proposal to appoint a new type specimen,
651 which might not be allowed anyway.

652

653 **Conclusions**

654 With the aid of μ CT, we can demonstrate that at least some of the encrustations must have
655 happened during the lifetime of the ammonoid as the sclerobionts are located on both sides
656 of the ammonoid at the place where deviation from planispiral coiling starts. This indicates
657 that the non-planispiral, slight trochospiral coiling in this specimen is probably pathological
658 and does not form a part of the natural variation (De Baets et al. 2013). To avoid taxonomic
659 confusion resulting from non-spiral coiling in this taxon, which is not part of the natural
660 variation as initially thought, one could select a neotype. While this practice has been
661 suggested for other taxa (e.g. Haas, 1946), this is, in our opinion, not necessary as non-
662 planispiral coiling did not form part of the original diagnosis. As the specimen survived at

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least 3 different encrustations and associated deformations through adulthood, the effects on its daily life were probably negligible. We re-identify these runner-like epizoa as hederelloids (as opposed to auloporidae tabulate corals), which make them the first known hederelloids to encrust an ammonoid *in vivo* and suggests that the ammonoid probably lived within the photic zone for most of its life. However, more studies on sclerobionts from the Hunsrück Slate, preferably with μ CT, are necessary to further corroborate these hypotheses.

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References that are not cited in text:

Becker RT, Gradstein FM, and Hammer O. 2012. Chapter 22 - The Devonian Period. In: Gradstein FM, Ogg JG, Schmitz MD, and Ogg GM, eds. *The Geologic Time Scale*. Boston: Elsevier, 559-601.

References

- Anné J, Garwood RJ, Lowe T, Withers PJ, and Manning PL. 2015. Interpreting pathologies in extant and extinct archosaurs using micro-CT. *PeerJ* 3:e1130.
- Baird GC, Brett CE, and Frey RC. 1989. "Hitchhiking" epizoa on orthoconic cephalopods: preliminary review of evidence and its implications. *Senckenbergiana Lethaea* 69:439-465.
- Bancroft AJ. 1986. *Hederella carbonaria* Condra and Elias, a rare ?bryozoan from the Carboniferous of Great Britain. *Proceedings of the Geologists' Association* 97:243-248.
- Bartels C, Briggs DEG, and Bräse G. 1998. *The fossils of the Hunsrück slate - Marine Life in the Devonian*.
- Bassler RS. 1939. The Hederelloidea: A Suborder of Paleozoic Cyclostomatous Bryozoa. *Proceedings of the United States National Museum* 87:25-91.
- Becker RT, Gradstein FM, and Hammer O. 2012. Chapter 22 - The Devonian Period. In: Gradstein FM, Ogg JG, Schmitz MD, and Ogg GM, eds. *The Geologic Time Scale*. Boston: Elsevier, 559-601.
- Becker RT, and House MR. 1994. International Devonian goniatite zonation, Emsian to Givetian, with new records from Morocco. [Courier Forschungsinstitut Senckenberg 169:79-135.](#)
- Beuck L, Wisshak M, Munnecke A, and Freiwald A. 2008. A Giant Boring in a Silurian Stromatoporoid Analysed by Computer Tomography. *Acta Palaeontologica Polonica* 53:149-160.
- Bräse G. 1977. Der erste Fund von Hederelloiden (Bryozoa) im Hunsrückschiefer von Bundenbach (Unterdevon, Rheinisches Schiefergebirge). *Notizblatt des Hessischen Landesamtes für Bodenforschung* 105:41-45.

707 Brett CE, Parsons-Hubbard KM, Walker SE, Ferguson C, Powell EN, Staff G, Ashton-Alcox KA, and
708 Raymond A. 2011. Gradients and patterns of sclerobionts on experimentally deployed bivalve
709 shells: Synopsis of bathymetric and temporal trends on a decadal time scale.
710 *Palaeogeography, Palaeoclimatology, Palaeoecology* 312:278-304.

711 Brett CE, Smrecak T, Parsons Hubbard K, and Walker S. 2012. Marine Sclerobiofacies: Encrusting and
712 Endolithic Communities on Shells Through Time and Space. In: Talent JA, ed. *Earth and Life*.
713 Dordrecht: Springer, 129-157.

714 Briggs DE, and Williams SH. 1981. The restoration of flattened fossils. *Lethaia* 14:157-164.

715 Cecca F. 1997. Late jurassic and early cretaceous uncoiled ammonites: Trophism-related evolutionary
716 processes. *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary*
717 *Science* 325:629-634.

718 Checa AG, Okamoto T, and Keupp H. 2002. Abnormalities as natural experiments: a morphogenetic
719 model for coiling regulation in planispiral ammonites. *Paleobiology* 28:127-138.

720 Davies TG, Rahman IA, Lautenschlager S, Cunningham JA, Asher RJ, Barrett PM, Bates KT, Bengtson S,
721 Benson RBJ, Boyer DM, Braga J, Bright JA, Claessens LPAM, Cox PG, Dong X-P, Evans AR,
722 Falkingham PL, Friedman M, Garwood RJ, Goswami A, Hutchinson JR, Jeffery NS, Johanson Z,
723 Lebrun R, Martínez-Pérez C, Marugán-Lobón J, O'Higgins PM, Metscher B, Orliac M, Rowe TB,
724 Rücklin M, Sánchez-Villagra MR, Shubin NH, Smith SY, Starck JM, Stringer C, Summers AP,
725 Sutton MD, Walsh SA, Weisbecker V, Witmer LM, Wroe S, Yin Z, Rayfield EJ, and Donoghue
726 PCJ. 2017. Open data and digital morphology. *Proceedings of the Royal Society B: Biological*
727 *Sciences* 284.

728 Davis RA, Klofak SM, and Landman NH. 1999. Epizoa on Externally Shelled Cephalopods. In: Rozanov
729 AY, and Shevryev AA, eds. *Fossil Cephalopods: Recent Advances In Their Study*. Moscow:
730 Russian Academy of Sciences Paleontological Institute, 32-51.

731 Davis RA, and Mapes RH. 1999. Pits in internal molds of cephalopods. *Berichte der Geologischen*
732 *Bundesanstalt* 46:31.

733 De Baets K. 2012. Early Emsian Ammonoidea: stratigraphy, intraspecific variability and
734 macroevolution PhD Thesis. Universität Zürich.

735 De Baets K, Keupp H, and Klug C. 2015. Parasites of ammonoids. In: Klug C, Korn D, De Baets K, Kruta
736 I, and Mapes RH, eds. *Ammonoid Paleobiology: From anatomy to paleoecology Topics in*
737 *Geobiology* 43. Dordrecht: Springer, 837-875.

738 De Baets K, Klug C, and Korn D. 2009. Anetoceratinae (Ammonoidea, Early Devonian) from the Eifel
739 and Harz Mountains (Germany), with a revision of their genera. *Neues Jahrbuch für Geologie*
740 *und Paläontologie - Abhandlungen* 252:361-376.

741 De Baets K, Klug C, Korn D, Bartels C, and Poschmann M. 2013. Emsian Ammonoidea and the age of
742 the Hunsrück Slate (Rhenish Mountains, Western Germany). *Palaeontographica A* 299:1-113.

743 De Baets K, Klug C, Korn D, and Landman NH. 2012. Early Evolutionary Trends in Ammonoid
744 Embryonic Development. *Evolution* 66:1788-1806.

745 De Baets K, Klug C, and Monnet C. 2013. Intraspecific variability through ontogeny in early
746 ammonoids. *Paleobiology* 39:75-94.

747 De Baets K, Klug C, and Plusquellec Y. 2010. Zlichovian faunas with early ammonoids from Morocco
748 and their use for the correlation of the eastern Anti-Atlas and the western Dra Valley. *Bulletin*
749 *of Geosciences* 85:317-352.

750 De Baets K, Landman NH, and Tanabe K. 2015. Ammonoid Embryonic Development. In: Klug C, Korn
751 D, De Baets K, Kruta I, and Mapes RH, eds. *Ammonoid Paleobiology: From anatomy to*
752 *ecology Topics in Geobiology* 43. Dordrecht: Springer, 113-205.

753 Dietl G. 1978. Die heteromorphen Ammoniten des Dogger. *Stuttgarter Beiträge Zur Naturkunde B*
754 33:1-97.

755 Donovan SK. 1989. Taphonomic significance of the encrustation of the dead shell of recent *Spirula*
756 *spirula* (Linné) (Cephalopoda: Coleoidea) by *Lepas anatifera* Linné (Cirripedia: Thoracia).
757 *Journal of Paleontology* 63:698-702.

758 Dzik J. 1981. Evolutionary relationships of the early Palaeozoic 'cyclostomatous' Bryozoa.
759 *Palaeontology* 24:827-861.

760 Eckhardt RB, and Henneberg M. 2010. LB1 from Liang Bua, Flores: Craniofacial asymmetry confirmed,
 761 plagiocephaly diagnosis dubious. *American Journal of Physical Anthropology* 143:331-334.
 762 Elias MK. 1944. Auloporidae and Hederelloidea (And a System to Avoid Ambiguous Use of Generic
 763 Names). *Journal of Paleontology* 18:529-534.
 764 Erben H. 1994. Das Meer des Hunsrückschiefers. *Erdgeschichte im Rheinland Fossilien und Gesteine*
 765 *aus* 400:49-56.
 766 Etter W. 2002. Hunsrück slate: widespread pyritization of a Devonian fauna. *Exceptional fossil*
 767 *preservation, eds Bottjer, DJ, W Etter, JW Hagadorn, and CM Tang*:143-165.
 768 Fenton MA, and Fenton CL. 1937. Aulopora: A Form-Genus of Tabulate Corals and Bryozoans.
 769 *American Midland Naturalist* 18:109-115.
 770 Fernández-López S, and Meléndez G. 1994. Abrasion surfaces on internal moulds of ammonites as
 771 palaeobathymetric indicators. *Palaeogeography, Palaeoclimatology, Palaeoecology* 110:29-
 772 42.
 773 Fernández-López SR. 1991. Taphonomic concepts for a theoretical biochronology. *Revista Espanola*
 774 *de Paleontologia* 6:37-49.
 775 Frey L, Naglik C, Hofmann R, Schemm-Gregory M, FRÝDA J, Kroeger B, Taylor PD, Wilson MA, and
 776 Klug C. 2014. Diversity and palaeoecology of Early Devonian invertebrate associations in the
 777 Tafilt (Anti-Atlas, Morocco). *Bulletin of Geosciences* 89:75-112.
 778 Garwood RJ, and Dunlop J. 2014. Three-dimensional reconstruction and the phylogeny of extinct
 779 chelicerate orders. *PeerJ* 2:e641.
 780 Gügel B, De Baets K, Jerjen I, Schuetz P, and Klug C. 2017. A new subdisarticulated machaeridian from
 781 the Middle Devonian of China: Insights into taphonomy and taxonomy using X-ray
 782 microtomography and 3D-analysis. *Acta Palaeontologica Polonica* 62:237-247.
 783 Haas O. 1946. Neotypes for Species Based on Pathological Specimens. *Nature* 157:700.
 784 Hauschke N, Schöllmann L, and Keupp H. 2011. Oriented attachment of a stalked cirripede on an
 785 orthoconic heteromorph ammonite - implications for the swimming position of the latter.
 786 *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 262:199-212.
 787 Hladil J, Čejchan P, and Beroušek P. 1991. Orientation of the conical tests of tentaculites: internal
 788 waves in aqueous environment. *Casopis pro Mineralogii a Geologii* 36:115-130.
 789 Hladil J, Simcik M, Ruzicka MC, Kulaviak L, and Lisy P. 2014. Hydrodynamic experiments on
 790 dacryoconarid shell telescoping. *Lethaia* 47:376-396.
 791 Hoffmann R, Schultz JA, Schellhorn R, Rybacki E, Keupp H, Gerden SR, Lemanis R, and Zachow S. 2014.
 792 Non-invasive imaging methods applied to neo- and paleo-ontological cephalopod research.
 793 *Biogeosciences* 11:2721-2739.
 794 House MR. 1996. Juvenile goniatite survival strategies following Devonian extinction events.
 795 *Geological Society, London, Special Publications* 102:163-185.
 796 Jahnke H, and Bartels C. 2000. Der Hunsrückschiefer und seine Fossilien, Unter-Devon. In: Pinna G,
 797 and Meischner D, eds. *Europäische Fossilagerstätten*. Dordrecht: Springer, 36-44.
 798 Kacha P, and Šaric R. 2009. Host preferences in Late Ordovician (Sandbian) epibenthic bryozoans:
 799 example from the Zahorany Formation of Prague Basin. *Bulletin of Geosciences* 84:169-178.
 800 Kaifu Y, Baba H, Kurniawan I, Sutikna T, Saptomo EW, Jatmiko, Awe RD, Kaneko T, Aziz F, and
 801 Djubiantono T. 2009. Brief communication: "Pathological" deformation in the skull of LB1,
 802 the type specimen of Homo floresiensis. *American Journal of Physical Anthropology* 140:177-
 803 185.
 804 Keupp H. 1992. Wachstumsstörungen bei Pleuroceras und anderen Ammonoidea durch Epökie.
 805 *Berliner Geowissenschaftliche Abhandlungen E* 3:113-119.
 806 Keupp H. 2012. Atlas zur Paläopathologie der Cephalopoden. *Berliner Paläobiologische*
 807 *Abhandlungen* 12:1-392.
 808 Keupp H, and Hoffmann R. 2015. Ammonoid paleopathology. In: Klug C, Korn D, De Baets K, Kruta I,
 809 and Mapes RH, eds. *Ammonoid Paleobiology: from anatomy to ecology*. Dordrecht: Springer,
 810 877-926.

811 Keupp H, Röper M, and Seilacher A. 1999. Paläobiologische Aspekte von syn vivo-besiedelten
812 Ammonoideen im Plattenkalk des Ober-Kimmeridgiums von Brunn in Ostbayern. *Berliner*
813 *Geowissenschaftliche Abhandlungen Reihe E Palaeobiologie* 30:121-145.

814 Klug C, and Korn D. 2001. Epizoa and post-mortem epicoles on cephalopod shells—examples from the
815 Devonian and Carboniferous of Morocco. *Berliner geowissenschaftliche Abhandlungen (E)*
816 36:145-155.

817 Klug C, and Korn D. 2004. The origin of ammonoid locomotion. *Acta Palaeontologica Polonica* 49:235-
818 242.

819 Klug C, Kröger B, Vinther J, Fuchs D, and De Baets K. 2015a. Ancestry, Origin and Early Evolution of
820 Ammonoids. In: Klug C, Korn D, De Baets K, Kruta I, and Mapes RH, eds. *Ammonoid*
821 *Paleobiology: From macroevolution to paleogeography Topics in Geobiology* 44, 3-24.

822 Klug C, Zatoń M, Parent H, Hostettler B, and Tajika A. 2015b. Mature modifications and sexual
823 dimorphism. In: Klug C, Korn D, De Baets K, Kruta I, and Mapes RH, eds. *Ammonoid*
824 *Paleobiology: from anatomy to ecology*. Dordrecht: Springer, 253-320.

825 Kneidl V. 1984. *Hunsrück und Nahe: Geologie, Mineralogie und Paläontologie. Ein Wegweiser für den*
826 *Liebhaber*. Stuttgart: Kosmos Verlag.

827 Kruta I, Landman N, Rouget I, Cecca F, and Tafforeau P. 2011. The Role of Ammonites in the Mesozoic
828 Marine Food Web Revealed by Jaw Preservation. *Science* 331:70-72.

829 Kühl G, Bartels C, Briggs DEG, and Rust J. 2012a. *Visions of a Vanished World: The Extraordinary*
830 *Fossils of the Hunsrück Slate*: Yale University Press.

831 Kühl G, Bergmann A, Dunlop J, Garwood RJ, and Rust JES. 2012b. Redescription and palaeobiology of
832 *Palaeoscorpis devonicus* Lehmann, 1944 from the Lower Devonian Hunsrück Slate of
833 Germany. *Palaeontology* 55:775-787.

834 Landman NH, Saunders WB, Winston JE, and Harries PJ. 1987. Incidence and kinds of epizoans on the
835 shells of live Nautilus. In: Saunders WB, and Landman NH, eds. *Nautilus: The Biology and*
836 *Paleobiology of a Living Fossil*. New York: Plenum Press, 163-177.

837 Landman NH, Tanabe K, and Davis RA. 1996. *Ammonoid paleobiology*. New York: Plenum Press.

838 Larson N. 2007. Deformities in the Late Callovian (Late Middle Jurassic) Ammonite Fauna from
839 Saratov, Russia. In: Landman NH, Davis RA, and Mapes RH, eds. *Cephalopods Present and*
840 *Past: New Insights and Fresh Perspectives*. Netherlands: Springer 344-374.

841 Lemanis R, Korn D, Zachow S, Rybacki E, and Hoffmann R. 2016. The Evolution and Development of
842 Cephalopod Chambers and Their Shape. *PLoS ONE* 11:e0151404.

843 Lemanis R, Zachow S, Füsseis F, and Hoffmann R. 2015. A new approach using high-resolution
844 computed tomography to test the buoyant properties of chambered cephalopod shells.
845 *Paleobiology FirstView*:1-17.

846 Lemanis R, Zachow S, and Hoffmann R. 2016. Comparative cephalopod shell strength and the role of
847 septum morphology on stress distribution. *PeerJ* 4:e2434.

848 Lescinsky HI. 2001. Epibionts. In: Briggs DEG, and Crowther PR, eds. *Palaeobiology II*. Oxford:
849 Blackwell Publishing, 460-464.

850 Luci L, and Cichowolski M. 2014. Encrustation in nautilids: a case study in the Cretaceous species
851 *Cymatoceras peristriatum*, Neuquén Basin, Argentina. *Palaio* 29:101-120.

852 Luci L, Cichowolski M, and Aguirre-Urreta MB. 2016. Sclerobionts, shell morphology and
853 biostratigraphy on ammonites: two Early Cretaceous cases from the Neuquén Basin,
854 Argentina. *Palaio* 31:41-54.

855 Lukeneder A. 2008. The ecological significance of solitary coral and bivalve epibionts on Lower
856 Cretaceous (Valanginian-Aptian) ammonoids from the Italian Dolomites. *Acta Geologica*
857 *Polonica* 58:425-436.

858 Lukeneder A. 2012. Computed 3D visualisation of an extinct cephalopod using computer tomographs.
859 *Computers & Geosciences* 45:68-74.

860 Macchioni F. 2000. Bioeroded and/or encrusted ammonite moulds and their taphonomic
861 implications. *Rivista Italiana di Paleontologia e Stratigrafia* 106:337-352.

862 Maeda H, and Seilacher A. 1996. Ammonoid Taphonomy. In: Landman NH, Tanabe K, and Davis RA,
863 eds. *Ammonoid Paleobiology*. New York Plenum Press, 543-578.

864 Meischner D. 1968. Perniciöse Epökie von *Placunopsis* auf *Ceratites*. *Lethaia* 1:156-174.

865 Merkt J. 1966. Über Austern und Serpeln als Epöken auf Ammonitengehäusen. *Neues Jahrbuch für*
866 *Geologie und Paläontologie - Abhandlungen* 125:467-479.

867 Mistiaen B, Brice D, Zapalski M, and Loones C. 2012. Brachiopods and Their Aulopodid Epibionts in
868 the Devonian of Boulonnais (France): Comparison with Other Associations Globally. In: Talent
869 J, ed. *Earth and Life*: Springer Netherlands, 159-188.

870 Monnet C, Zollikofer C, Bucher H, and Goudemand N. 2009. Three-dimensional morphometric
871 ontogeny of mollusc shells by micro-computed tomography and geometric analysis.
872 *Paleontologia Electronica* 12:1-13.

873 Naglik C, Monnet C, Goetz S, Kolb C, De Baets K, Tajika A, and Klug C. 2015a. Growth trajectories of
874 some major ammonoid sub-clades revealed by serial grinding tomography data. *Lethaia*
875 48:29-46.

876 Naglik C, Rikhtegar F, and Klug C. 2016. Buoyancy of some Palaeozoic ammonoids and their
877 hydrostatic properties based on empirical 3D-models. *Lethaia* 49:3-12.

878 Naglik C, Tajika A, Chamberlain JA, and Klug C. 2015b. Ammonoid Locomotion. In: Klug C, Korn D, De
879 Baets K, Kruta I, and Mapes RH, eds. *Ammonoid Paleobiology: From anatomy to ecology*.
880 Dordrecht: Springer, 649-688.

881 Opitz R. 1932. *Bilder aus der Erdgeschichte des Nahe-Hunsrück-Landes Birkenfeld*. Birkenfeld: Enke.

882 Rahman IA, Belaústegui Z, Zamora S, Nebelsick JH, Domènech R, and Martinell J. 2015. Miocene
883 Clypeaster from Valencia (E Spain): Insights into the taphonomy and ichnology of bioeroded
884 echinoids using X-ray micro-tomography. *Palaeogeography, Palaeoclimatology,*
885 *Palaeoecology* 438:168-179.

886 Rakociński M. 2011. Sclerobionts on upper Famennian cephalopods from the Holy Cross Mountains,
887 Poland. *Palaeobiodiversity and Palaeoenvironments* 91:63-73.

888 Rakús M, and Zítt J. 1993. Crinoid encrusters of Ammonite shells (Carixian, Tunisia). *Geobios* 26:317-
889 329.

890 Ritterbush KA, Hoffmann R, Lukeneder A, and De Baets K. 2014. Pelagic palaeoecology: the
891 importance of recent constraints on ammonoid palaeobiology and life history. *Journal of*
892 *Zoology* 292:229-241.

893 Ross CA. 1978. Distortion of fossils in shales. *Journal of Paleontology*:943-945.

894 Ruan YP. 1981. Devonian and earliest Carboniferous Ammonoids from Guangxi and Guizhou.
895 *Memoirs of the Nanjing Institute of Geology & Paleontology* 15:152.

896 Ruan YP. 1996. Zonation and distribution of the early Devonian primitive ammonoids in South China.
897 In: Wang H-Z, and Wang X-L, eds. *Centennial Memorial Volume of Prof Sun Yunzhen:*
898 *Paleontology and Stratigraphy*. Wuhan: China University of Geosciences Press, 104-112.

899 Rust J, Bergmann A, Bartels C, Schoenemann B, Sedlmeyer S, and Kühl G. 2016. The Hunsrück Biota: A
900 Unique Window into the Ecology of Lower Devonian Arthropods. *Arthropod Structure &*
901 *Development*.

902 Schindler T, Sutcliffe O, Bartels C, Poschmann M, and Wuttke M. 2002. Lithostratigraphical
903 subdivision and chronostratigraphical position of the middle Kaub Formation (Lower Emsian,
904 Lower Devonian) of the Bundenbach area (Hunsrück, SW Germany). *Metalla (Bochum)* 9:73-
905 104.

906 Schmid-Röhl A, and Röhl HJ. 2003. Overgrowth on ammonite conchs: environmental implications for
907 the Lower Toarcian Posidonia Shale. *Palaeontology* 46:339-352.

908 Seilacher A. 1960. Epizoans as a Key to Ammonoid Ecology. *Journal of Paleontology* 34:189-193.

909 Seilacher A. 1982. Ammonite Shells as Habitats — Floats or Benthic Islands? (Abstract). In: Einsele G,
910 and Seilacher A, eds. *Cyclic and Event Stratification*: Springer Berlin Heidelberg, 504-504.

911 Seilacher A, and Hemleben C. 1966. Beiträge zur sedimentation und Fossilführung des
912 Hunsrücksschiefers 14. *Spurenfauna und Bildungsteife der Hunsrücksschiefer (Unterdevon)*
913 *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden* 94:40-53.

914 Selden P, and Nudds J. 2012. *Evolution of fossil ecosystems*: Elsevier.

915 Smrecak TA. 2016. Understanding patterns of sclerobiont encrustation: Methodological review and
 916 application of sclerobiont facies model in Middle Devonian Appalachian and Michigan Basin
 917 paleodepth gradients PhD. Michigan State University.
 918 Smrecak TA, and Brett CE. 2014. Establishing patterns in sclerobiont distribution in a late Ordovician
 919 (Cincinnatian) depth gradient: toward a sclerobiofacies model. *Palaaios* 29:74-85.
 920 Solle G. 1950. Obere Siegener Schichten, Hunsrückschiefer, tiefstes Unterkoblenz und ihre
 921 Eingliederung ins Rheinische Unterdevon. *Geol Jb* 65:299-380.
 922 Solle G. 1952. Neue Untersuchungen und Arten der Bryozoen-Gattung Hederella und eine Hernodia
 923 im rheinischen Unterdevon. *Notzbl hess LA Bodenforsch* 6:35-55.
 924 Solle G. 1968. Hederelloidea (Cyclostomata) und einige ctenostome Bryozoen aus dem Rheinischen
 925 Devon. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* 54:1-40.
 926 Spath LF. 1945. Problems of Ammonite-Nomenclature X. The Naming of Pathological Specimens.
 927 *Geological Magazine* 82:251-255.
 928 Stets J, and Schäfer A. 2009. The Siegenian delta: land-sea transitions at the northern margin of the
 929 Rhenohercynian Basin. *Geological Society, London, Special Publications* 314:37-72.
 930 Südkamp WH. 2007. An atypical fauna in the Lower Devonian Hunsrück Slate of Germany.
 931 *Paläontologische Zeitschrift* 81:181-204.
 932 Sutcliffe O, Tibbs S, and Briggs D. 2002. Sedimentology and environmental interpretation of the fine-
 933 grained turbidites in the Kaub Formation of the Hunsrück Slate: analysis of a section
 934 excavated for Project Nahecaris. *Metalla (Bochum)* 9:89-104.
 935 Sutton MA, Rahman IA, and Garwood RJ. 2014. *Techniques for Virtual Palaeontology*. UK: Wiley-
 936 Blackwell.
 937 Tajika A, Morimoto N, Wani R, Naglik C, and Klug C. 2015. Intraspecific variation of phragmocone
 938 chamber volumes throughout ontogeny in the modern nautilid Nautilus and the Jurassic
 939 ammonite Normannites. *PeerJ* 3:e1306.
 940 Tajika A, Naglik C, Morimoto N, Pascual-Cebrian E, Hennhöfer D, and Klug C. 2014. Empirical 3D
 941 model of the conch of the Middle Jurassic ammonite microconch Normannites: its buoyancy,
 942 the physical effects of its mature modifications and speculations on their function. *Historical*
 943 *Biology*:1-11.
 944 Taylor PD, Vinn O, and Wilson MA. 2010. Evolution of biomineralisation in 'lophophorates'. *Special*
 945 *Papers in Palaeontology* 84:317-333.
 946 Taylor PD, and Wilson M. 2007. Morphology and affinities of hederelloid "bryozoans". Bryozoan
 947 Studies 2007: proceedings of the 14th international bryozoology conference, Boone, North
 948 Carolina, July 1–8: Virginia Museum of Natural History Special Publication. p 301-309.
 949 Taylor PD, and Wilson MA. 2002. A New Terminology for Marine Organisms Inhabiting Hard
 950 Substrates. *Palaaios* 17:522-525.
 951 Thayer CW. 1974. Substrate Specificity of Devonian Epizoa. *Journal of Paleontology* 48:881-894.
 952 Wani R, Kase T, Shigeta Y, and De Ocampo R. 2005. New look at ammonoid taphonomy, based on
 953 field experiments with modern chambered nautilus. *Geology* 33:849-852.
 954 Westermann GEG. 1996. Ammonoid Life and Habitat. In: Landman NH, Tanabe K, and Davis RA, eds.
 955 *Ammonoid Paleobiology*. New York: Plenum Press, 607-707.
 956 Wiedmann J. 1969. The heteromorphs and ammonoid extinction. *Biological Reviews* 44:563-602.
 957 Wilson M, and Taylor P. 2001. Pseudobryozoans" and the problem of encruster diversity in the
 958 Paleozoic. *Paleobios* 21:134-135.
 959 Wilson MA, and Taylor PD. 2006. Predatory drill holes and partial mortality in Devonian colonial
 960 metazoans. *Geology* 34:565-568.
 961 Wilson MA, and Taylor PD. 2013. Palaeoecology, Preservation and Taxonomy of Encrusting
 962 Ctenostome Bryozoans Inhabiting Ammonite Body Chambers in the Late Cretaceous Pierre
 963 Shale of Wyoming and South Dakota, USA. In: Ernst A, Schäfer P, and Scholz J, eds. *Bryozoan*
 964 *Studies 2010*. Berlin, Heidelberg: Springer Berlin Heidelberg, 419-433.
 965 Wyse Jackson PN, and Key Jr MM. 2014. Epizoic bryozoans on cephalopods through the Phanerozoic:
 966 A review. *Studi Trentini di Scienze Naturali* 94:283-291.

967 Wyse Jackson PN, Key MMJ, and Coakley SP. 2014. Epizoozoan Trepastome Bryozoans on Nautiloids
968 from the Upper Ordovician (Katian) of the Cincinnati Arch Region, U.S.A.: An Assessment of
969 Growth, form, and Water Flow Dynamics. *Journal of Paleontology* 88:475-487.
970 Zapalski MK. 2005. Paleocology of Auloporida: an example from the Devonian of the Holy Cross
971 Mts., Poland. *Geobios* 38:677-683.

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