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## 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

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).

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):

- 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).

85

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

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

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

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

156 In testing these questions, it was important to avoid using destructive analyses because the  
157 specimen is an important historical specimen (Opitz 1932) and the holotype of *Ivoites opitzi*  
158 (De Baets et al. 2013) from the famous Hunsrück Lagerstätte. The Hunsrück Slate is a facies  
159 typical for the Lower Devonian (Emsian) of the Rhenish Massif which consists predominantly  
160 of dark fine-grained argillites metamorphosed into slates (Bartels, Briggs & Brassel 1998). In  
161 the Bundenbach-Gemünden area, these strata can contain fossils with remarkable  
162 preservation including articulated echinoderms and vertebrates as well as preserved soft  
163 tissues of arthropods and other groups without hard tissues (Bartels et al., 1998). Although  
164 some fossils reveal remarkable preservation, they are all typically flattened and it is difficult  
165 to impossible to prepare such thin, compressed fossils from both sides without destroying  
166 parts of it. This is for example illustrated by the only known specimen and holotype of  
167 *Palaeoscorpius devonicus*, where some parts of the shale that are thinner than 1 mm are  
168 very fragile or missing altogether after preparation (Kühl et al. 2012b). This might be one of  
169 the reasons why fossils with hard parts commonly studied for biostratigraphic or  
170 paleoenvironmental purposes at other sites where they are more three-dimensionally

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

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

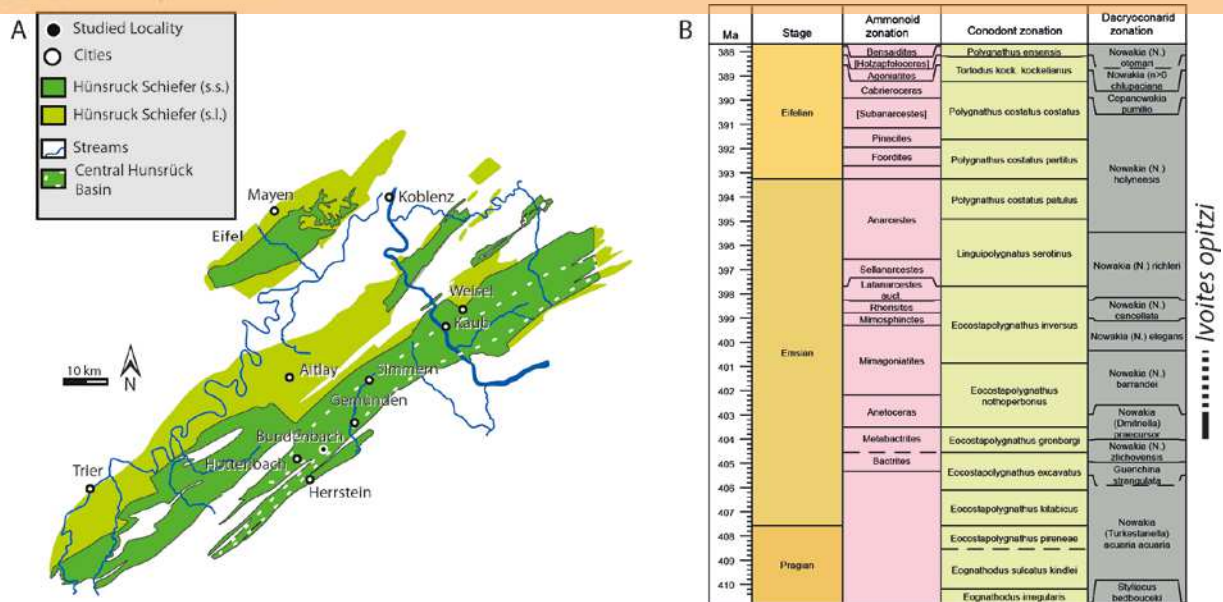
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### 189 **Material and geological setting**

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

207





208

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

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

215 The investigated specimen was chosen as the holotype above 19 other specimens of *Ivoites*  
 216 *opitzi* as it was the most complete, three-dimensional and well-preserved specimen of the  
 217 species. It has three complete whorls and a diameter of 105 mm (Fig. 2; De Baets et al.,  
 218 2013). The specimen is mostly preserved as an internal, pyritic mould as evidenced by traces  
 219 of suture lines and other structures (e.g., opitzian pits) internal to the shell (taphonomic  
 220 category IIB of De Baets et al., 2013). The last half-whorl probably corresponds to the body  
 221 chamber as indicated by faint traces of a suture in hand piece and x-ray images (Kneidl  
 222 1984), lack of pyrite infilling of the last whorl, terminal uncoiling as well as the large lateral  
 223 extension of the end of the whorl interpreted to be the apertural edge (De Baets et al. 2013).

224

225 The infilling of the shell with pyrite in this taphonomic category is interpreted to have  
 226 happened early in the diagenesis, below the sediment-water interface and before the  
 227 dissolution, compaction, and breakage of the shell. These observations were used  
 228 successfully to interpret preservation of ammonoids in the Jurassic bioturbated shales  
 229 (Hudson 1982), and were additionally supported by fracture patterns (De Baets et al. 2013).

230 The whorls of this specimen touch and overlap each other, but this is interpreted to be a  
 231 consequence of compression and tectonic deformation as the inner whorl lies completely  
 232 above the following whorl (De Baets et al. 2013). Oblique embedding can result in one bit of  
 233 whorl lying on top of one whorl, but the opposite side should then lie below this whorl (see  
 234 for example De Baets et al. 2013, Plate 5, Fig. 3 for an example), which is not the case in our  
 235 specimen. Compaction on an umbilical concretion can also result in asymmetric  
 236 deformation, but affect similar quadrants in the same way and the concretion should still be

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

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

252





253

254 Fig. 2: Holotype of *Ivoites opitzi*. Several sclerobionts can be seen encrusting specimen KGM 1983/147.  
255 Scalebar: 1 cm.

256

257

**258 Methods**

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

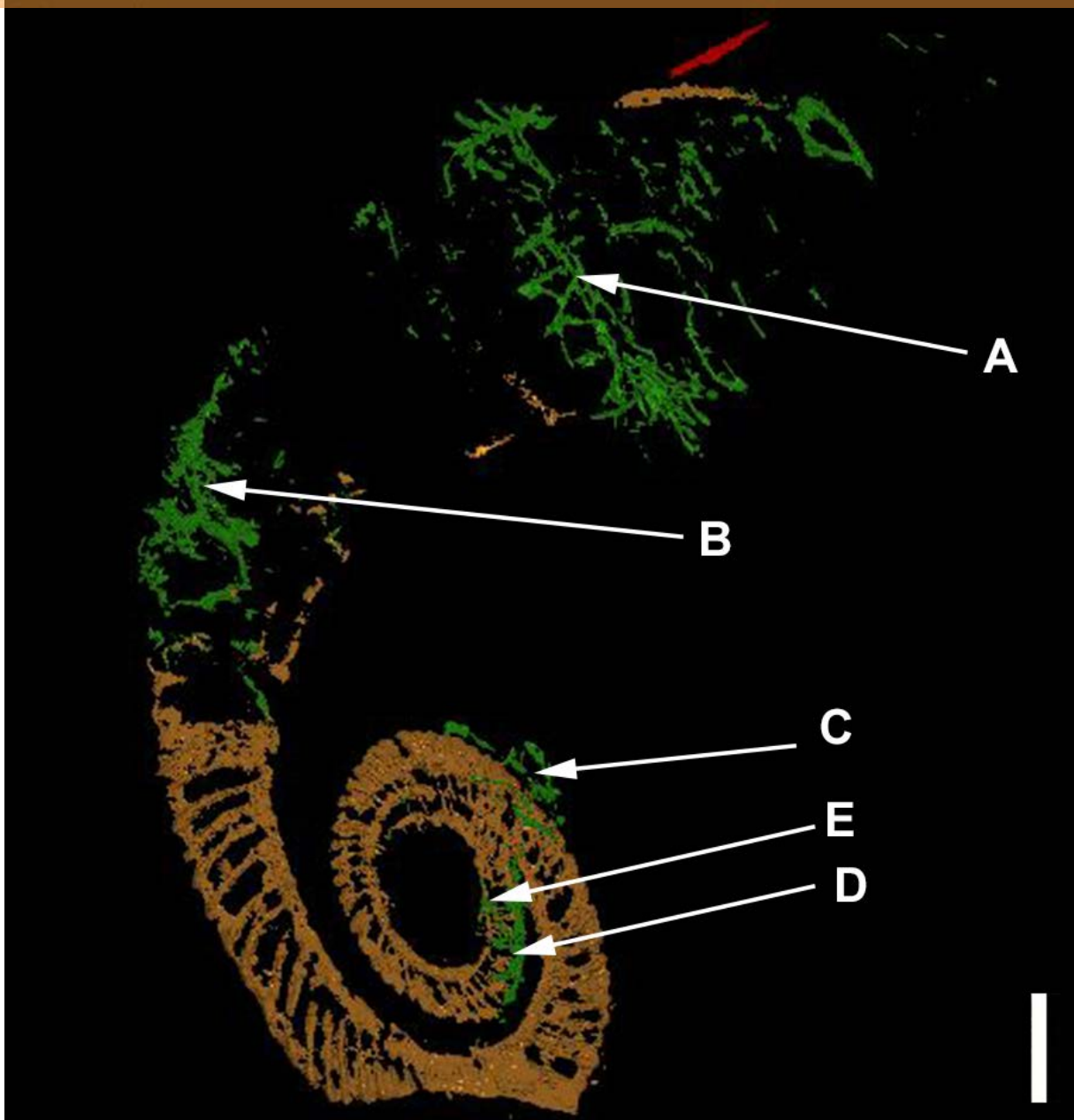
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**288 Results**

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

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



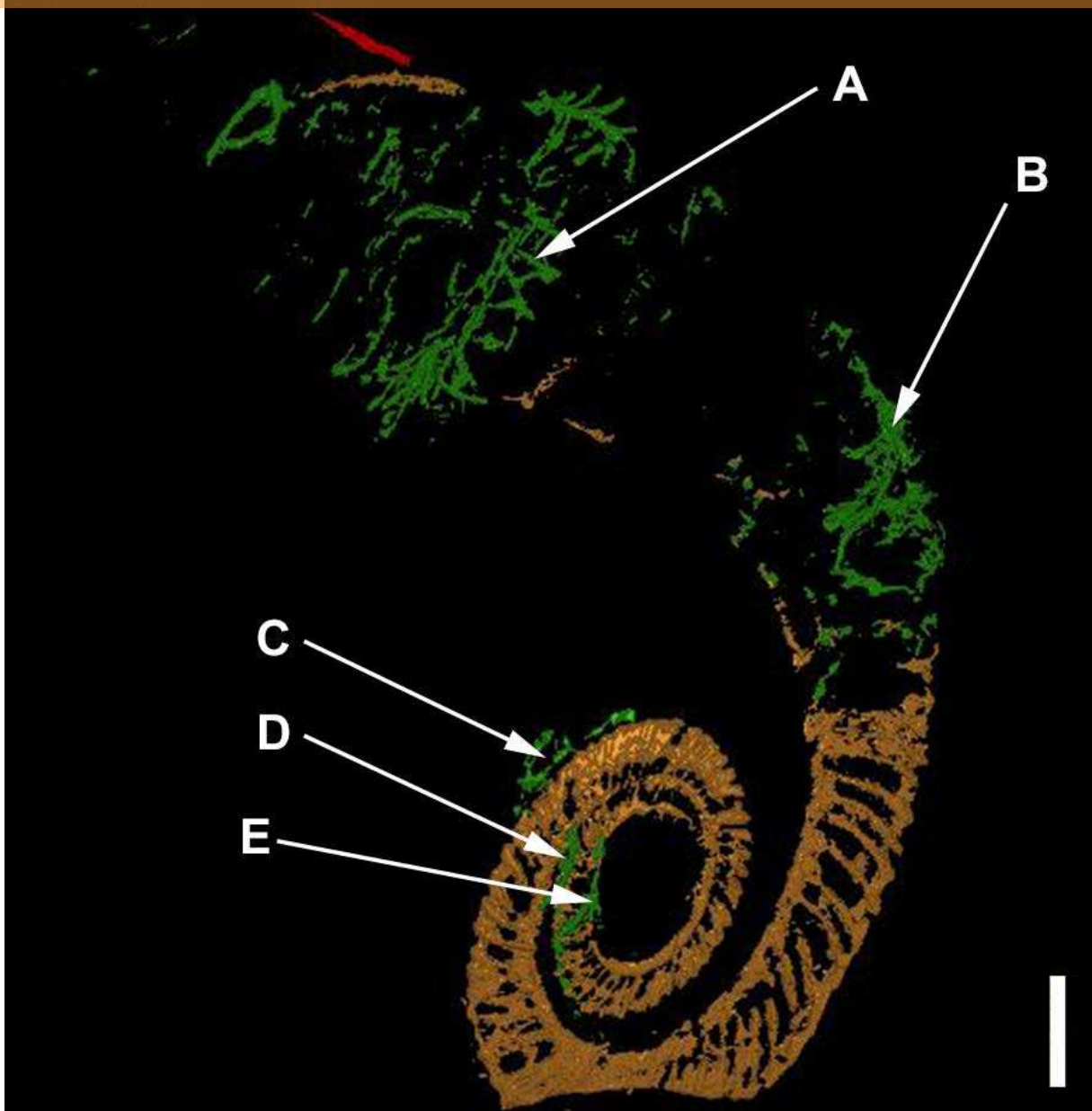


296

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

299

300



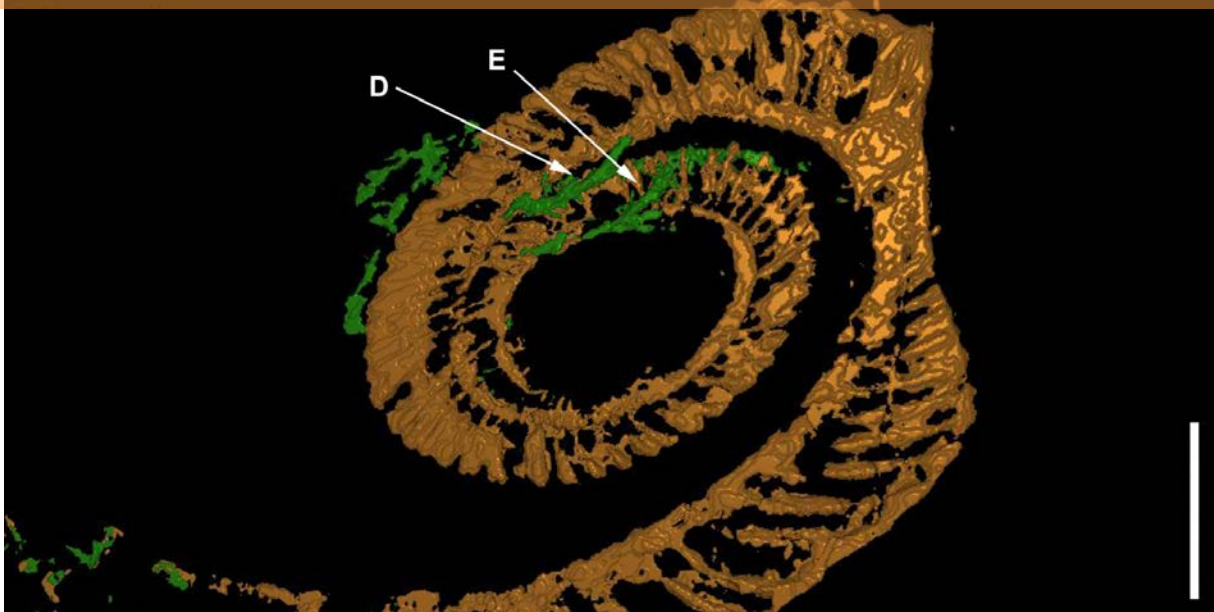
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302 Fig. 4: The ammonoid (brown), the runner-like epicoles (green) and the orthoconic nautiloid (red) rotated 180°.  
303 Scalebar: 1 cm.

304

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

311



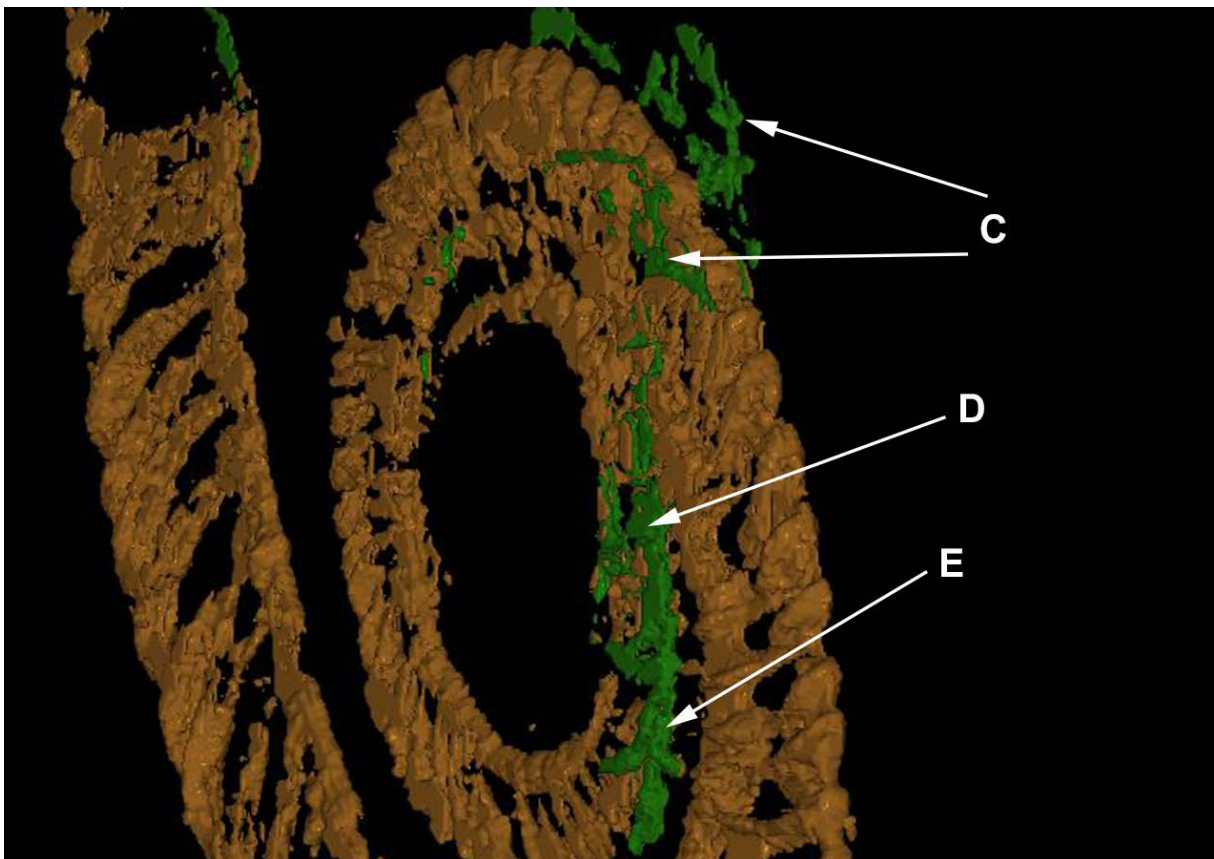
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313 Fig. 5: The white arrows mark the position of the sclerobiont clusters (D and E) close to the position where non-  
314 planispiral coiling can be first recognized. Scalebar: 1 cm.

315

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

320



321

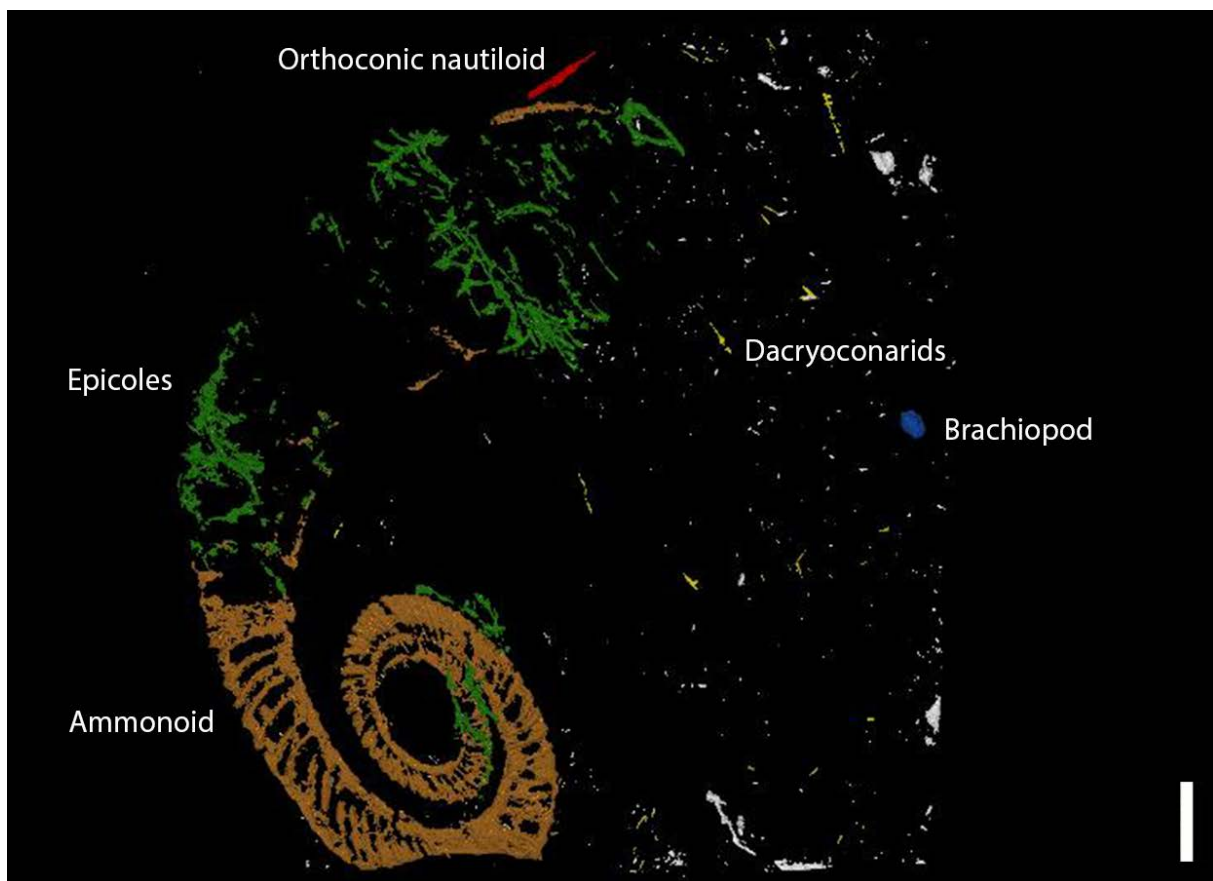
322 Fig. 6: Close-up of the 3D-model showing that sclerobionts are settling on both sides of the shell. Note  
323 correlation between asymmetrical sclerobiont encrustation of cluster E and the deviation from planispiral  
324 coiling of the host.

325

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

333

334



335

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

338

339 Morphology of the runner-like sclerobionts

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



343 patterns of the sclerobiont colonies. The original settlement location of the colonial  
344 organism cannot be distinguished, but the branching pattern of colonies grow in a direction  
345 largely parallel to the direction of the aperture of the host.

346 The colonies in all clusters have the same taxonomic affinity. Zooids in the colonies are long  
347 and tubular, and curve slightly near the zooecial opening. Zooids are larger than those  
348 commonly observed in bryozoans and bud in alternating directions. Diameter of the more  
349 3D-preserved tubes are typically around 1.5 mm, but this might have been artificially  
350 augmented by compaction (De Baets et al. 2013). The tubes widen in the direction of growth  
351 expand distally and slightly contracted at the apex giving them a club-like appearance,  
352 characters typical of hederelloids (Elias 1944).

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

359

## 360 Discussion

361 The three-dimensional model of *I. opitzi* permitted extensive observation of the relationship  
362 between the ammonoid host and the sclerobiont clusters present. The results permit  
363 positive identification of the sclerobionts and interpretation of the relationship between  
364 them and their host.

### 365 Synvivo vs. Post-Mortem encrustation

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

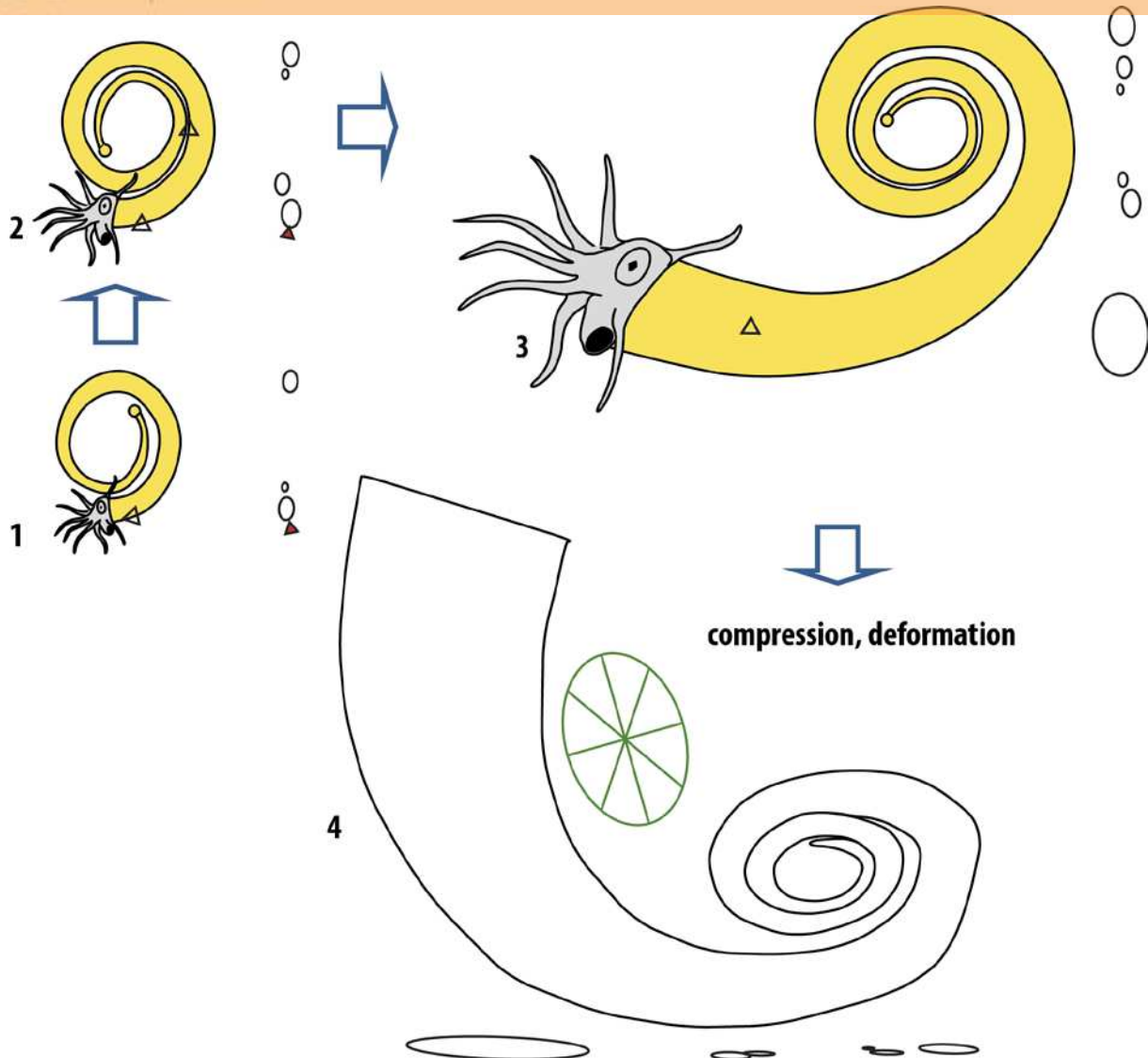
368 1) In-vivo encrustation: encrustation on both sides of the ammonoid by sclerobiont colonies  
369 C, D, and E and the direction of the growth of those sclerobionts matching the growth of the  
370 ammonoid, speak for an in-vivo encrustation – at least for sclerobiont clusters C-E. A lack of  
371 a similar directional growth for all sclerobiont colonies on the ammonoid and with  
372 dacroconarids in the surrounding substrate, as well as a lack in widespread encrustation  
373 across the ammonoid shell, further support the likelihood that the ammonoid was encrusted  
374 before the ammonoid settled on the seafloor (see Figure 8).

375 2) Post-mortem drift: encrustation of such large colonies solely during post-mortem drift  
376 seems unlikely due to the small size of our specimen (105 mm diameter). This is below the  
377 200 mm limit listed for long floating cephalopod shells by Wani et al. (2005) and Rakociński  
378 (2011). Interestingly, our specimen would have even a much smaller phragmocone volume  
379 than coiled ammonoids at equal diameters used in these experiments. More importantly,  
380 the extra weight of the sclerobionts should have made it sink even sooner than a non-  
381 encrusted shells so that it would not have resulted in encrustation on both sides. Post-  
382 mortem drift is deemed rare for ammonoids in general; most are implied to sink rather

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

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

401



402

403

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

412

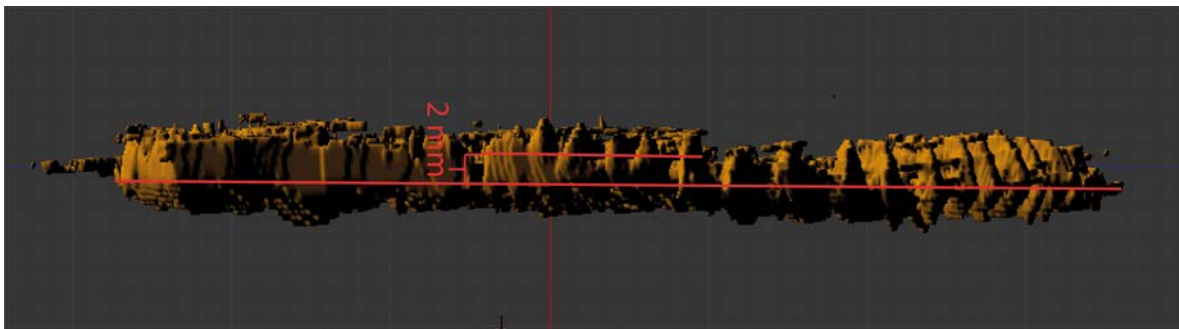
413

414 Pathological variation in the morphology of *I. opitzi*

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

419 and compaction. Whorl thickness alone has estimated to reduce up to 248 % in some  
420 specimens (De Baets et al. 2013), so originally these deviations could have been up at least  
421 2.5 to 5 mm. If we artificially the thickness with 200 %, we obtain a maximum deviation of  
422 the median plane of one whorl to the next of about 2 mm (2,5 mm if we augment the  
423 thickness to 250 %). The same deviations can be observed within a single whorl (Fig. 10).  
424 Considering that the specimen has been extremely flattened (one whorl has been pressed on  
425 the other). At least another whorl thickness, the differences in whorl thickness between this  
426 whorl and the next which would make it a total of about 2 times this amount, ca. 4 mm (5  
427 mm is we artificially augment the whorl thickness to 250%). This is a rather conservative  
428 estimate, as we cannot know exactly how the specimen was compressed between the  
429 whorls.

430



431

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

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

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

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

464

465 Identity of the encrusters

466 Hederelloids are a problematic group of runner-like sclerobionts, which occur in the fossil  
467 record from the Silurian through Permian and are most diverse in the Devonian (Solle 1952;  
468 Solle 1968; Taylor & Wilson 2007). Hederelloids have traditionally been treated as  
469 cyclostome bryozoans (Bassler 1939; Elias 1944; Solle 1952; Solle 1968; Dzik 1981), but were  
470 redefined based upon differences in branching patterns, skeletal microstructure, lack of an  
471 astogenetic gradient, and wide range in tube diameters (Bancroft 1986; Wilson & Taylor  
472 2001; Taylor & Wilson 2007). They are currently mostly interpreted to be closely related to  
473 phoronids (Taylor & Wilson 2007; Taylor, Vinn & Wilson 2010; Frey et al. 2014). Both  
474 auloporid corals and hederelloids are uncommon in the middle Kaub Formation as their life  
475 habit requires a solid substrate upon which to settle; these were rare within the clay  
476 environments of the Hunsrück Slate (Bartels, Briggs & Brassel 1998).

477 The nature of the pyritic preservation of the host specimen, *I. opitzi*, does not make it  
478 possible to look at the microstructure or fine details of the sclerobionts, but the general  
479 morphology supports that all clusters of sclerobionts share a taxonomic affinity. Runner-like  
480 sclerobionts common in the Devonian include auloporid coral, paleotubuliporid bryozoans,  
481 and hederelloids. The sclerobionts encrusting *I. opitzi* are colonial, with elongated zooids,  
482 lateral branching/budding patterns, and relatively large tube diameters which speak for their  
483 identification as hederelloids rather than auloporids or bryozoans (Elias 1944; Bancroft 1986;  
484 Wilson & Taylor 2006; Taylor & Wilson 2007).

485 The runner-like encrusters were initially thought to be auloporid corals (De Baets et al.  
486 2013), which are known to encrust brachiopods (Zapalski 2005; Mistiaen et al. 2012) and  
487 ammonoids (Klug & Korn 2001) during their lifetime. Some auloporid taxa have been  
488 confused with hederelloids in the past (Fenton & Fenton 1937; Elias 1944) and can be hard  
489 to differentiate when taphonomic conditions have degraded the quality of the specimen due  
490 to gross morphological similarities.

491 Hederelloids have been reported to encrust externally shelled cephalopods before (Thayer  
492 1974; Brassel 1977; Bartels, Briggs & Brassel 1998; Frey et al. 2014), but these are, to our  
493 knowledge, the first reported to encrust an ammonoid *in vivo*. Sclerobionts can provide also

494 important information on paleoecology, sedimentary environments and taphonomy, both  
495 when they encrust shells *in vivo* or after death of their host (Baird, Brett & Frey 1989; Kacha  
496 & Šaric 2009; Rakociński 2011; Brett et al. 2012; Wilson & Taylor 2013; Luci & Cichowolski  
497 2014; Wyse Jackson, Key & Coakley 2014; Luci, Cichowolski & Aguirre-Urreta 2016).

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

#### 508 Implications for paleoenvironment of *Ivoites*

509 Some authors have attributed the rarity of encrusters in coiled ammonoids compared with Paleozoic  
510 (orthoconic) nautiloids to their ability to (keep) clean or chemical defenses against encrusters  
511 (Donovan 1989; Davis, Klofak & Landman 1999; Keupp 2012). Potentially, early ammonoid were  
512 more similar to their orthoconic nautiloid and bactritoid relatives. Furthermore, mechanical removal  
513 of epizoans might have proven more difficult in loosely coiled ammonoids like *Ivoites* as the previous  
514 whorl might have been out of reach of the cephalopod-arm complex (see Figure 8). However, these  
515 suggestions are all quite speculative – it is impossible to find direct evidence for chemical or  
516 mechanical cleaning or defensive behavior in this fossil group. More importantly, these mechanisms  
517 are also unnecessary to be invoked for such differences which could equally be explained by the fact  
518 that many nautiloids would have lived in more shallow environments – which show higher  
519 encrustation rates in general (Brett et al. 2012; Smrecak & Brett 2014; Smrecak 2016). Modern  
520 *Nautilus* shows differences in encrustations between different environments too (Landman et al.  
521 1987).

522

523 The sedimentary environment of the Hunsrück Slate have been widely interpreted, ranging  
524 from shallow sedimentation on tidal flats, at depths from around storm-wave base to  
525 significantly deeper (Solle 1950; Seilacher & Hemleben 1966; Erben 1994; Bartels, Briggs &  
526 Brassel 1998). The sedimentary environment in the central Hunsrück Basin is now thought to  
527 be rather complex; depressions between sedimentary fans provided environments below  
528 storm wave base and sills which could locally extend into the intertidal zone (Etter 2002).  
529 The beds with the exceptionally preserved fossils and hemipelagic fauna (ammonoids,  
530 dacroconarids) in the Bundenbach-Gemünden area have been interpreted to be mostly  
531 deposited below storm-wave base and/or at depths around 100m (Sutcliffe, Tibbs & Briggs  
532 2002; Stets & Schäfer 2009). Even in these regions, more sandy layers with neritic  
533 brachiopods are intercalated, suggesting occasional shallower depths above storm wave  
534 base. It is now generally accepted that the maximum depth was within the photic zone due  
535 to the presence in some layers of receptaculitid algae, which are interpreted to be closely  
536 related to green algae, and good visual capabilities of arthropods (Bartels, Briggs & Brassel



537 1998; Etter 2002; Selden & Nudds 2012). Based on the latter, maximum depths of 200 m  
538 have suggested (Rust et al. 2016).

539 Hederelloids are typical encrusters found in Devonian photic zone environments (Brett et al.  
540 2012). They are most diverse and abundant in shallower facies, but persist into the deep  
541 euphotic zone (Smrecak 2016). The presence of hederelloids on the specimen, in  
542 combination with other evidence described earlier, support an interpretation of *in vivo*  
543 encrustation. The pelagic life habit of *I. opitzi* would allow colonies of hederelloids to settle  
544 and grow on the shell with some success. In contrast, at depths of 100+ meters, hederelloid  
545 encrustation, and sclerobiont encrustation in general, is significantly less common (e.g.,  
546 Brett et al. 2011; Brett et al. 2012; Smrecak & Brett 2014)). Thus, presence of multiple  
547 colonies of hederelloids on the specimen support *in vivo* encrustation at depths within the  
548 photic zone, and lends further support for depositional conditions in line with current  
549 interpretations that the Hunsrück Slate interpreted was deposited near storm-wave base  
550 (Bartels, Briggs & Brassel 1998; Sutcliffe, Tibbs & Briggs 2002).

551 De Baets et al. (2013) found encrusted ammonoid shells to be rare (only 6 of 342 studied  
552 ammonoids: about 2%). Only two specimens of 82 specimens of *Ivoites* (2%) were found to  
553 be encrusted with hederelloids – our specimen and an additional specimen of *Ivoites* sp.  
554 which was interpreted to be encrusted post-mortem (Bartels, Briggs & Brassel 1998).  
555 Taphonomic or collection biases (Wyse Jackson & Key Jr 2014) are unlikely to explain the low  
556 percentages of encrustation as the ammonites and epibionts are principally preserved in the way  
557 (e.g., pyritic compound moulds in our case). So far, bivalves, brachiopods, bryozoans, crinoids,  
558 hederelloids and tabulate corals have been reported to encrust conchs of ammonoids or  
559 other externally shelled cephalopods from the Hunsrück Slate s.s. or middle Kaub Formation  
560 (Brassel 1977; Bartels, Briggs & Brassel 1998; Jahnke & Bartels 2000; Kühl et al. 2012a; De  
561 Baets et al. 2013), but these have mostly thought to have happened post-mortem due to  
562 their heavy encrustation on one side of the fossils or the encrustation of the structures  
563 which would normally be covered with soft-parts (Bartels, Briggs & Brassel 1998; Jahnke &  
564 Bartels 2000; De Baets et al. 2013). Heavy encrustations seems to be more common in  
565 nautiloids (Bartels, Briggs & Brassel 1998; Jahnke & Bartels 2000; Kühl et al. 2012a), but  
566 these have so far only been qualitatively studied. In environments between 100 and 200m  
567 encrustation is generally low, which also consistent with a rare *in-vivo* encrustation of our  
568 specimen which have swam in shallower depths when the first encrusters settled rather  
569 than the commonly reported post-mortem encrustation. Additional studies on epicoles on  
570 ammonoid shells and other shells from the Hunsrück Slate would be necessary to further  
571 corroborate these hypotheses.

572 Implication for mode of life

573 Loosely coiled early ammonoids are mostly treated as poor swimmers based on their poor  
574 streamlining with high drag (Westermann 1996; Klug & Korn 2004; Klug et al. 2015a);  
575 additional limitations imposed by epizoa on streamlining and shell orientation might be  
576 (even) less important in these forms than in normally coiled ammonoids. The fact that our  
577 specimen survived at least three separate encrustations – as evidenced by different  
578 settlement locations of the clusters of hederelloids – and growth deformations associated  
579 with earlier encrustation further corroborates this idea, although further investigations on

580 additional specimens would be necessary to confirm this hypothesis. Most hederelloid  
581 colonies generally grow along the spiral direction and do not cross from one whorl to the  
582 next, which provide additional evidence that they encrusted the ammonoid during its  
583 lifetime.

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

598 *Hederella* is known to encrust another ammonoid from the Hunsrück Slate, but this is  
599 interpreted to have happened post-mortem (Brassel 1977; Bartels, Briggs & Brassel 1998).  
600 There is no evidence that this happened in-vivo in the second specimen as these are located  
601 on an incompletely preserved body chamber, and have been interpreted as encrusting the  
602 inside of the shell (Bartels, Briggs & Brassel 1998) – but this should be further tested with  
603  $\mu$ CT. Additional studies would be necessary to confirm if our specimen is an isolated case of  
604 in vivo encrustation or part of a more common phenomenon.

#### 605 Implications for taxonomy

606 Defining pathological specimens as species can have important taxonomic implications  
607 (Spath 1945). According to Spath (1945), such ammonoid species should remain valid, but no  
608 new type can be chosen while the holotype is still in existence. Others, like Haas (1946),  
609 claim assigning a pathological specimen might undermine the status of the species,  
610 considering the morphology of the species is described based on a pathological specimen,  
611 and that a new neotype should be selected. It is important to note that several authors have  
612 erected different ammonoid species based on small differences in coiling. As the only known  
613 non-planispirally coiled specimen of *I. opitzi* is pathological, an author like Haas (1946) might  
614 have suggested to designate another specimen as type for this species to avoid ambiguity.  
615 However, our study highlights that non-planispirality does not belong to normal intraspecific  
616 variation of this species, nor to the taxonomic definition of this taxon. Paratype SMF-HF 940,  
617 which was collected from the same locality as the holotype (De Baets et al. 2013), would be  
618 the best candidate among the paratypes. Reassigning a neotype has recently been  
619 intensively discussed for the holotype of *Homo floriensis* (Kaifu et al. 2009; Eckhardt &  
620 Henneberg 2010), but the severity of deviation has to be considered in this specimen.  
621 However, both aspects (electing a neotype for pathological specimens and its dependence of  
622 the severity of the pathology) are not specifically discussed in the International Code of

623 Zoological Nomenclature (ICZN). According to Article 75.1 of ICZN, “the neotype is ...  
624 designated under conditions ... when no name-bearing type specimen is believed to be  
625 extant ...”. In this case, if the holotype, even when pathologically deformed, is extant, the  
626 proposal of neotype is not granted. A proposal could be submitted to the ICZN to resolve the  
627 use of pathologically-induced morphological variation of holotypes, but this falls outside the  
628 aim of our study. Furthermore, we are confident that original type specimen belongs to  
629 same species as the paratypes as it completes the same amount of whorl before uncoiling,  
630 has a similar rib spacing and only differs from other specimens in its minor coiling deviations  
631 (De Baets et al. 2013). As non-planispiral coiling was not part of the original diagnosis, we  
632 feel it is unnecessary to submit a proposal to appoint a new type specimen, which might not  
633 be allowed anyway.

634

### 635 **Conclusions**

636 With the aid of  $\mu$ CT, we can demonstrate that at least some of the encrustations must have  
637 happened during the lifetime of the ammonoid as the sclerobionts are located on both sides  
638 of the ammonoid at the place where deviation from planispiral coiling starts. This indicates  
639 that the non-planispiral, slight trochospiral coiling in this specimen is probably pathological  
640 and does not form a part of the natural variation (De Baets et al. 2013). To avoid taxonomic  
641 confusion resulting from non-spiral coiling in this taxon, which is not part of the natural  
642 variation as initially thought, one could select a neotype. While this practice has been  
643 suggested for other taxa (e.g. Haas (1946)), this is, in our opinion, not necessary as non-  
644 planispiral coiling did not form part of the original diagnosis. As the specimen survived at  
645 least 3 different encrustations and associated deformations through adulthood, the effects  
646 on its daily life were probably negligible. We re-identify these runner-like epizoa as  
647 hederelloids (as opposed to auloporidae tabulate corals), which make them the first known  
648 hederelloids to encrust an ammonoid *in vivo* and suggests that the ammonoid probably lived  
649 within the photic zone for most of its life. However, more studies on sclerobionts from the  
650 Hunsrück Slate, preferably with  $\mu$ CT, are necessary to further corroborate these hypotheses.

651

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663

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