A peer-reviewed version of this preprint was published in PeerJ on 30 June 2017.

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

Julia Stilkerich [1] , **Trisha A Smrecak** [2] , **Kenneth De Baets** Corresp. [1]

[1] Geozentrum Nordbayern, Friedrich-Alexander Universität Erlangen-Nürnberg, Erlangen, Germany

[2] Department of Geology, Grand Valley State University, Allendale, United States

Corresponding Author: Kenneth De Baets
Email address: kenneth.debaets@gmail.com

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 on 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.

1
2
3D-Analysis of a non-planispiral ammonoid from the Hunsrück-Slate: natural or pathological variation?

3
Julia Stilkerich[1], Trisha Smrecak[2], Kenneth De Baets[1,*]

4
5
[1]Geozentrum Nordbayern, Friedrich-Alexander Universität Erlangen-Nürnberg, Erlangen, Germany
6
[2]Department of Geology, Michigan State University, East Lansing

7
*Corresponding author: kenneth.debaets@fau.de

8
Abstract:

9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
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.

30
Introduction

31
32
33
34
35
36
37
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

38   considered heteromorphs from a morphological perspective. However, early ammonoids differ
39   in important ways from Mesozoic heteromorphs as their embryonic shell is also uncoiled (House
40   1996; De Baets et al. 2012; De Baets et al. 2013; De Baets, Landman & Tanabe 2015), and not all
41   types of coiling known from the Mesozoic have been reported from the Paleozoic (e.g.,
42   trochospiral coiling is thought to be absent). The sole known possible exception was a specimen
43   of *Ivoites opitzi* from the Hunsrück Slate of Germany, which showed evidence for non-planispiral
44   coiling (De Baets et al. 2013). Originally, the holotype specimen was interpreted to exhibit a
45   transitional morphology in the natural variation from gyroconic to trochospiral coiling as
46   observed in the Jurassic heteromorph *Spiroceras (Dietl 1978)*.

47   However, this specimen is also encrusted by epicoles – "any organism that spent its life attached
48   to or otherwise inhabiting the exterior of any more or less hard object"(Davis, Klofak & Landman
49   1999). In biology, the term chosen for the encrusting organism implies the relationship it has
50   with its host (e.g. *in vivo*, post mortem), and a wide variety of terminology has been employed
51   for encrusters in the paleontological literature (see discussion in Taylor & Wilson 2002).A general
52   term for encrusting or boring organism being used with growing popularity is 'sclerobiont' and
53   means "organisms living in or on any kind of hard substrate" (Taylor and Wilson, 2002). If these
54   epicoles, or sclerobionts, settled on the ammonoid host shell during its life, they could be called
55   epizoa (Davis, Klofak & Landman 1999; Klug & Korn 2001) and may cause deviations from
56   planispiral coiling (oscillations of the shell around the median plane to trochospiral coiling) to
57   abnormalities in the whorl cross section when overgrowing the epizoa (Merkt 1966; Keupp
58   1992; Checa, Okamoto & Keupp 2002) and various other pathologies (Larson 2007; Keupp 2012;
59   De Baets, Keupp & Klug 2015; Keupp & Hoffmann 2015). Cephalopod workers have commonly
60   used the term epicoles to refer to organisms which encrust ammonoids post-mortem (Davis,
61   Klofak & Landman 1999; Klug & Korn 2001; Rakociński 2011; De Baets, Keupp & Klug 2015;
62   Keupp & Hoffmann 2015). Deviations from planispiral coiling in ammonoids have been attributed to
63   sclerobionts in the past (discussed below), yet distinguishing between *in vivo* and post-mortem
64   encrustations is rarely straightforward. In some cases it is impossible to tell if encrustation was
65   *in-vivo* or post mortem, but using various lines of evidence (Seilacher 1960; Seilacher 1982;
66   Baird, Brett & Frey 1989; Davis, Klofak & Landman 1999; Keupp 2012; De Baets, Keupp & Klug
67   2015; Keupp & Hoffmann 2015) can sometimes elucidate a live-live interaction between host
68   and encruster. The main criteria used by researchers to identify likely cases of *in vivo*
69   colonization of cephalopod shell are (compare Rakús & Zítt 1993; Davis, Klofak & Landman 1999;
70   Klug & Korn 2001; Luci & Cichowolski 2014):

71   1. both flanks are encrusted but the apertural region remains free of encrusters

72   2. encrusters growth stops precisely at a whorl or are otherwise outpaced by the conch
73   growth of the cephalopod

74   3. encrusters show a dominant growth direction consistent with shape and putative life
75   position of the cephalopod shell and may express changes in growth direction as the host
76   life position changes

4. the cephalopod reacts to its encrusters during growth by developing some kind of behaviour that is reflected in the shell (usually nonplanispiral coiling and other deformations).

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

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

Mobile organisms can potentially use the shell as temporary pasture (Keupp 2012), while sclerobionts can use it as benthic island surrounded by soft and unconsolidated sediment (Seilacher 1982). For pathological reactions in shell form and growth to occur, the sclerobionts must settle on still growing, younger hosts. Sclerobionts that settle on the shell of adult animals that have already reached their final shell size do not induce a pathological change in the host. In those situations, it is only possible to infer that these sclerobionts encrusted *in-vivo* because

116   of their preferential orientation with respect to water currents or the life position of its host
117   (Seilacher 1960; Seilacher 1982; Keupp, Röper & Seilacher 1999; Hauschke, Schöllmann & Keupp
118   2011).

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

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

144   An additional goal is to identify the identity of the sclerobionts, which were preliminary
145   determined to be auloporid tabulate corals (De Baets et al. 2013). Some taxa of auloporid corals
146   have traditionally been confused with other sclerobionts with runner-like morphologies
147   (Lescinsky 2001) like hederelloids and cyclostomate bryozoans (Fenton & Fenton 1937; Elias
148   1944; Bancroft 1986).

149   In testing these questions, it was important to avoid using destructive analyses because the
150   specimen is an important historical specimen (Opitz 1932) and the holotype of Ivoites opitzi (De
151   Baets et al. 2013) from the famous Hunsrück Lagerstätte. The Hunsrück Slate is a facies typical
152   for the Lower Devonian (Emsian) of the Rhenish Massif which consists predominantly of dark
153   fine-grained argillites metamorphosed into slates (Bartels, Briggs & Brassel 1998). In the
154   Bundenbach-Gemünden area, these strata can contain fossils with remarkable preservation
155   including articulated echinoderms and vertebrates as well as preserved soft tissues of

156   arthropods and other groups without hard tissues (Bartels et al., 1998). Although some fossils
157   reveal remarkable preservation, they are all typically flattened and it is difficult to impossible to
158   prepare such thin, compressed fossils from both sides without destroying parts of it. This is for
159   example illustrated by the only known specimen and holotype of *Palaeoscorpius devonicus*,
160   where some parts of the shale that are thinner than 1 mm are very fragile or missing altogether
161   after preparation (Kühl et al. 2012b). This might be one of the reasons why fossils with hard
162   parts commonly studied for biostratigraphic or paleoenvironmental purposes at other sites
163   where they are more three-dimensionally preserved have been comparable little studied in the
164   Hunsrück Slate (Bartels, Briggs & Brassel 1998; Südkamp 2007). This is also the case for
165   ammonoids, which are important index fossils to date this deposit and are often extremely
166   flattened hampering also their taxonomic assignment (Bartels, Briggs & Brassel 1998; De Baets
167   et al. 2013).

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

180   **Material and geological setting**

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

195　Emsian strata of the Schieleberg quarry in Herrstein, speak for a Praecursor to the Barrandei

196　zone age of the strata (De Baets et al. 2013).
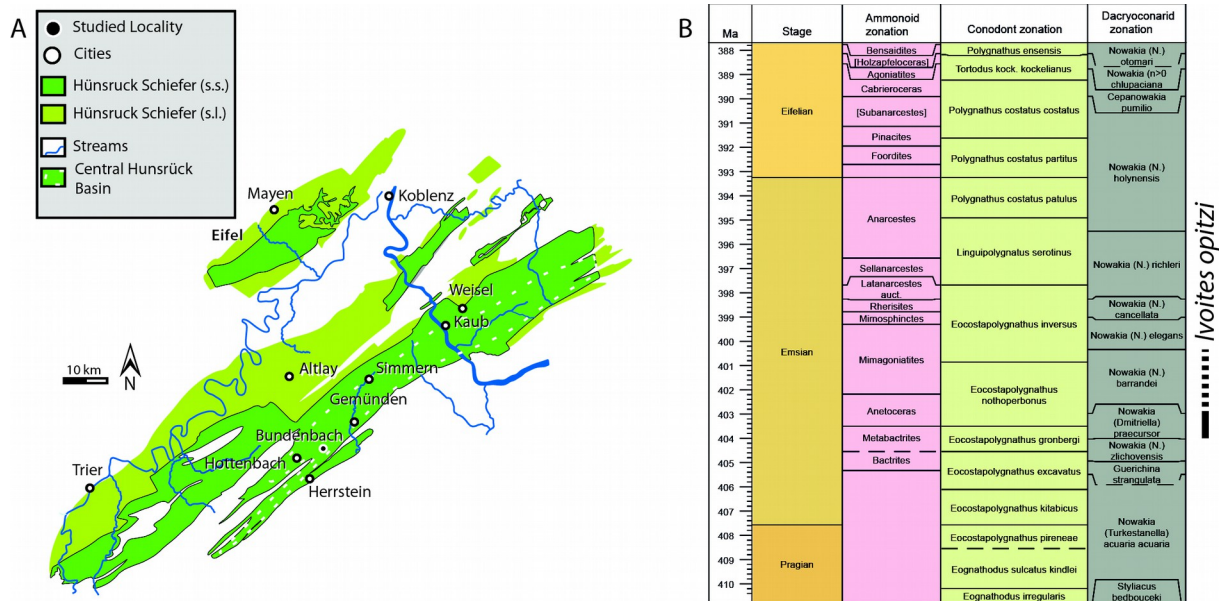
197　Fig.1: Geographic and Stratigraphic Context. (A) map of the locality (modified from De Baets 2012) and (B)
198　stratigraphic provenance of *Ivoites opitzi* (time-scale based on Becker, Gradstein & Hammer 2012: created with
199　time-scale creator 6.4: http://engineering.purdue.edu/Stratigraphy/tscreator/)

200　We investigated the taxonomy, provenance and taphonomy of 342 ammonoids from the Central

201　Hunsrück Basin in a recent monograph (De Baets et al. 2013) including 82 specimens of *Ivoites*

202　and 7 additional specimens of closely related *Metabactrites*.

203　The investigated specimen was chosen as the holotype above 19 other specimens of *Ivoites*

204　*opitzi* as it was the most complete, three-dimensional and well-preserved specimen of the

205　species. It has three complete whorls and a diameter of 105 mm (Fig. 2; De Baets et al., 2013).

206　The specimen is mostly preserved as an internal, pyritic mould as evidenced by traces of suture

207　lines and other structures (e.g., opitzian pits) internal to the shell (taphonomic category IIB of De

208　Baets et al., 2013). The last half-whorl probably corresponds to the body chamber as indicated

209　by faint traces of a suture in hand piece and x-ray images (Kneidl 1984), lack of pyrite infilling of

210　the last whorl, terminal uncoiling as well as the large lateral extension of the end of the whorl

211　interpreted to be the apertural edge (De Baets et al. 2013).

212　The infilling of the shell with pyrite in this taphonomic category is interpreted to have happened

213　early in the diagenesis, below the sediment-water interface and before the dissolution,

214　compaction, and breakage of the shell. These observations were used successfully to interpret

215　preservation of ammonoids in the Jurassic bioturbated shales (Hudson 1982), and were

216　additionally supported by fracture patterns (De Baets et al. 2013).

217   The whorls of this specimen touch and overlap each other, but this is interpreted to be a
218   consequence of compression and tectonic deformation as the inner whorl lies completely above
219   the following whorl (De Baets et al. 2013). Oblique embedding can result in one bit of whorl
220   lying on top of one whorl, but the opposite side should then lie below this whorl (see for
221   example De Baets et al. 2013, Plate 5, Fig. 3 for an example), which is not the case in our
222   specimen. Compaction on an umbilical concretion can also results in asymmetric deformation,
223   but affect similar quadrants is the same way and the concretion should still be present, which is
224   not the case in our specimen (see De Baets et al. 2013, Plate 10, Fig. 11 for an example).
225   Compaction of a horizontally embedded specimen would result in subsequent whorl (with a
226   thicker whorl section) to lie above previous whorls. The only way the preservation observed in
227   KGM 1983/147 could occur is if the specimen was already torticonic before burial.

228   During the initial investigation of the holotype of *I. opitzi.* the possibility of a live-live relationship
229   between the host and the sclerobionts was excluded because of an inferred lack of conclusive
230   evidence (De Baets et al. 2013). The sclerobionts nearer the aperture did not provide any
231   evidence that could support *in situ* or post-mortem encrustation. The sclerobiont colony on the
232   phragmacone near the point of non-planispiral coiling was seemingly not growing across both
233   sides of the whorl, and again, the authors were unable to infer the relationship between host
234   and sclerobiont. But only the left side was prepared in this historically collected material (Opitz,
235   1932, p. 121, Fig. 117). A microCT of the specimen allowing to study the specimens from both
236   sides, now gives us the unique opportunity to reevaluate this interpretation.

237   Fig. 2: Holotype of *Ivoites opitzi*. Several sclerobionts can be seen encrusting specimen KGM 1983/147.

238   **Methods**

239   The specimen of *I. opitzi* under investigation is a holotype, and thus could not be investigated
240   destructively. Thus, the specimen was well-suited to be studied with X-ray microtomography. X-
241   ray microtomography uses x-rays to acquire radiographs (or projections) of an object at multiple
242   angles. From these projections, a sequence of parallel and evenly spaced tomograms (individual
243   slice images mapping the X-ray attenuation within a sample) are computed indirectly. This
244   tomographic dataset in turn can be used to recreate a virtual model (3D model) without
245   destroying the original object. The prefix micro- refers to the fact that pixel sizes of the cross-
246   sections are in the micrometre range (Sutton, Rahman & Garwood 2014). Markus Poschmann
247   (Mainz) kindly borrowed the specimen from the Karl-Geib-Museum and brought it to the
248   Steinmann Institute, where it was investigated with X-ray micro-tomography. KGM 1983/147 was
249   scanned on a Phoenix v|tome|x s at 150 kV and 160 µA with 0.400 s of exposure time by Alexandra
250   Bergmann (Steinmann Institute). This resulted in two thousand two hundred unfiltered projections
251   providing a voxel size of 118 µm (~ pixel size of 118um). Three-dimensional reconstructions and an
252   animation were produced using the 107 images (tomograms) [in the x-z-plain by Julia Stilkerich using the
253   free software SPIERS (Sutton et al. 2012; http://spiers-software.org). The fixed threshold value was
254   manually chosen to maximally separate pyritic fossils from the shale matrix, because the objects of focus
255   (ammonoid and epicoles) are pyritic (see material and methods); Regions of interest were defined using
256   the masking system in SPIERS, allowing them to be rendered separately to have the most conservative
257   interpretation of the position of the pyritic ammonoid vs. epicoles (Sutton, Rahman & Garwood 2014).
258   Coloured masks were used in the final representation to distinguish the various features
259   captured: ammonoid (yellow), runner-like epicoles (green), orthoconic nautiloid (red),
260   brachiopod (blue) and dacryoconarids (yellow).

261   **Results**

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

263   In the model, the first whorl lies on top of the second whorl. The median plane of the first whorl
264   seems to lie between 1 and 2 mm above that of the second whorl in the model, which must
265   have been even greater before compaction (see discussion). The 3D-model (see Figs. 3, 4)
266   therefore substantiates the previously hypothesized suspicion (De Baets et al. 2013) that the
267   specimen is not entirely coiled planispirally. Five clusters (A-E) of colonial sclerobionts can be
268   recognized in the 3D-model (see arrows in Figs. 3, 4).
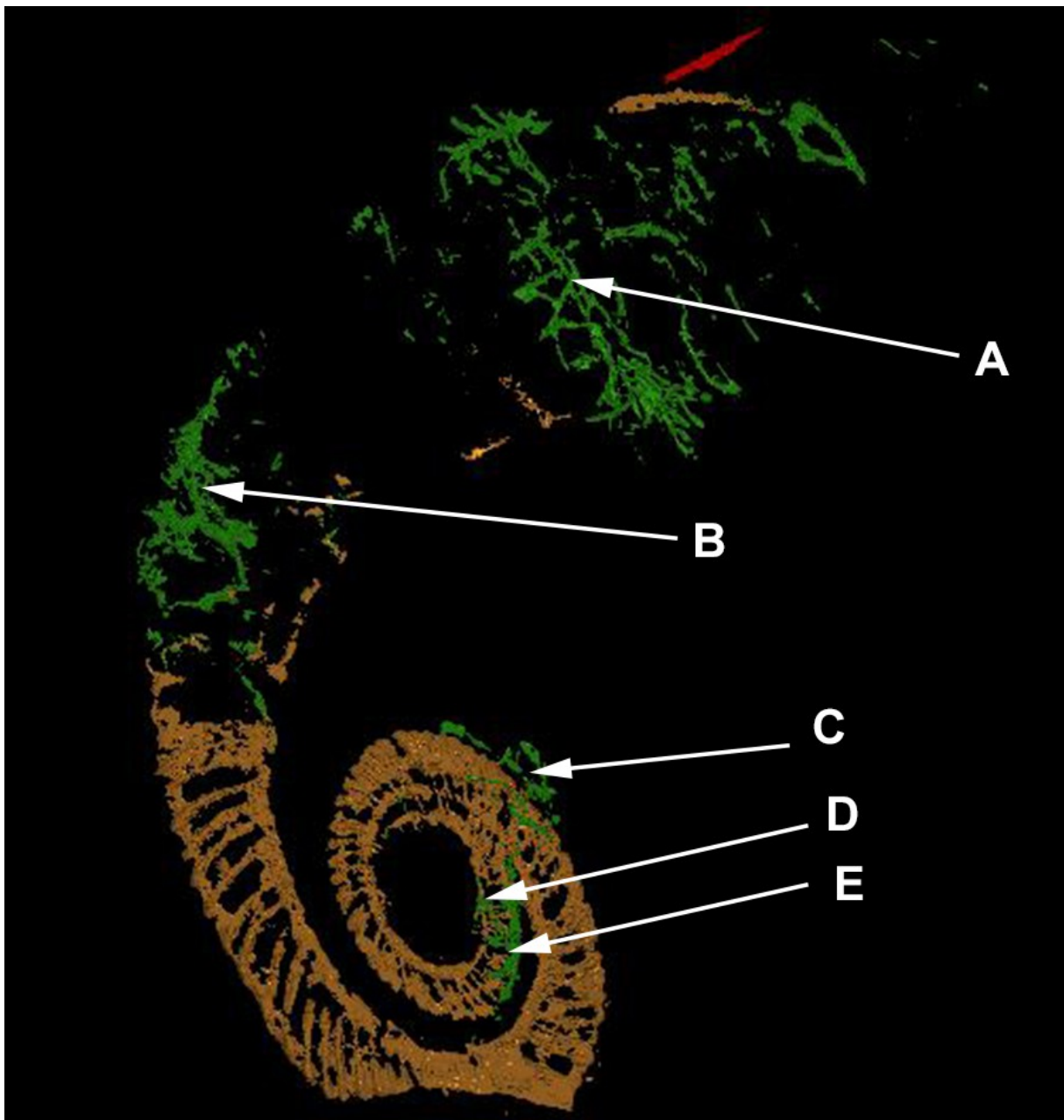
269 Fig. 3: The ammonoid (brown), the epicoles (green) and the orthoconic nautiloid (red) in the 3D-model. Five
270 sclerobiont clusters (A-E) were distinguished.
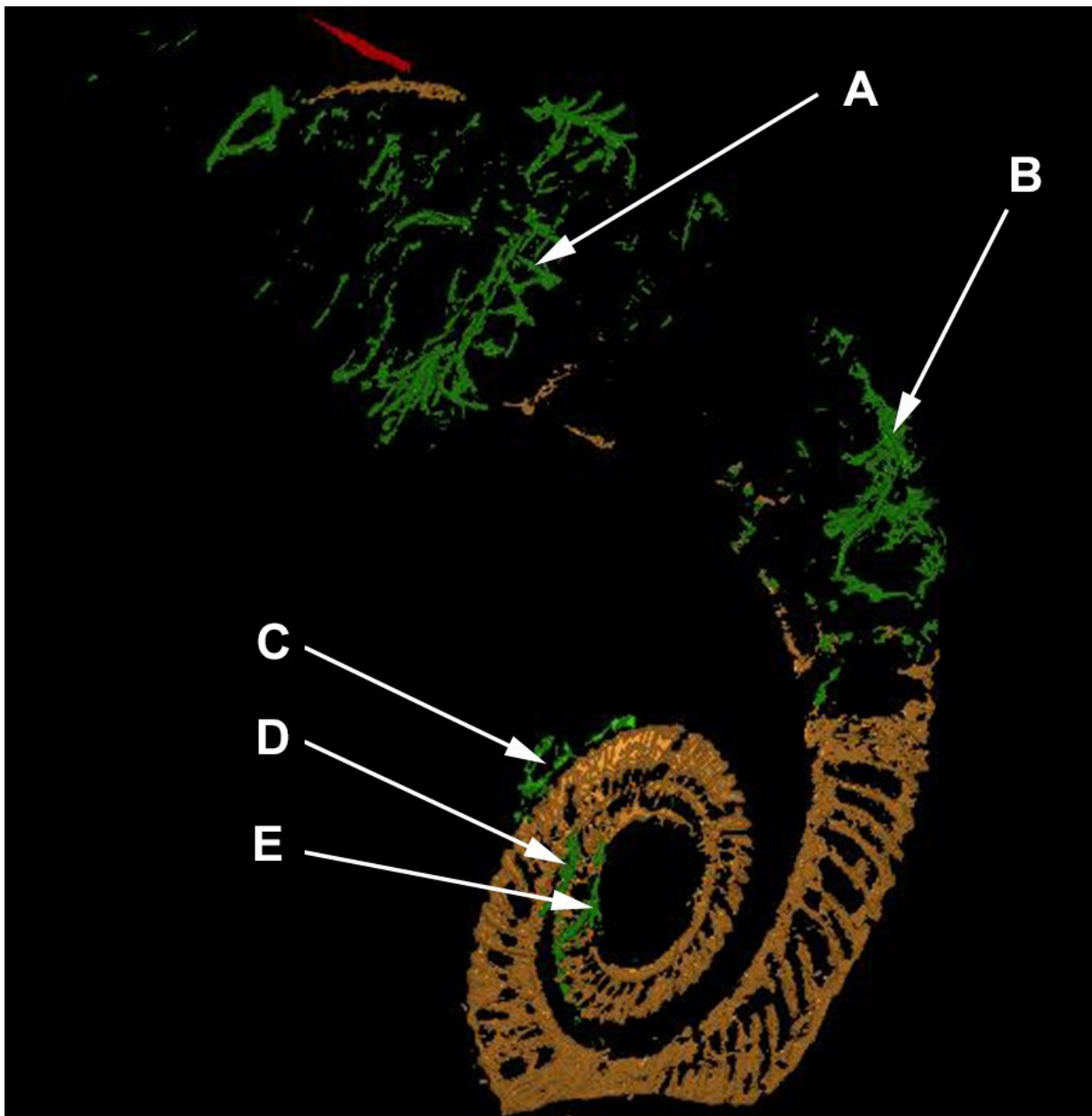
271   Fig. 4: The ammonoid (brown), the runner-like epicoles (green) and the orthoconic nautiloid (red) rotated 180°.

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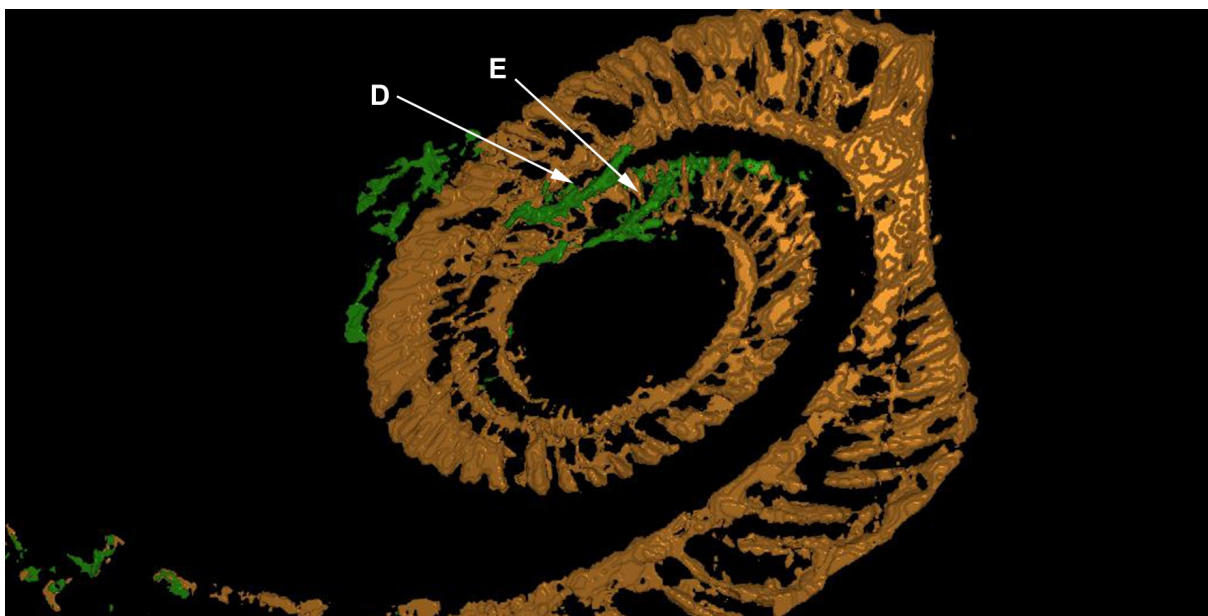
278   Fig. 5: The white arrows mark the position of the sclerobiont clusters (D and E) close to the position where non-
279   planispiral coiling can be first recognized.

280   More importantly, there is evidence that clusters (C, D and E) are growing on both sides of the
281   ammonoid (Fig. 6). The last demi-whorl of the host ammonoid was not infilled with pyrite,
282   therefore the growth patterns of the sclerobionts in clusters A and B cannot be established with
283   certainty.
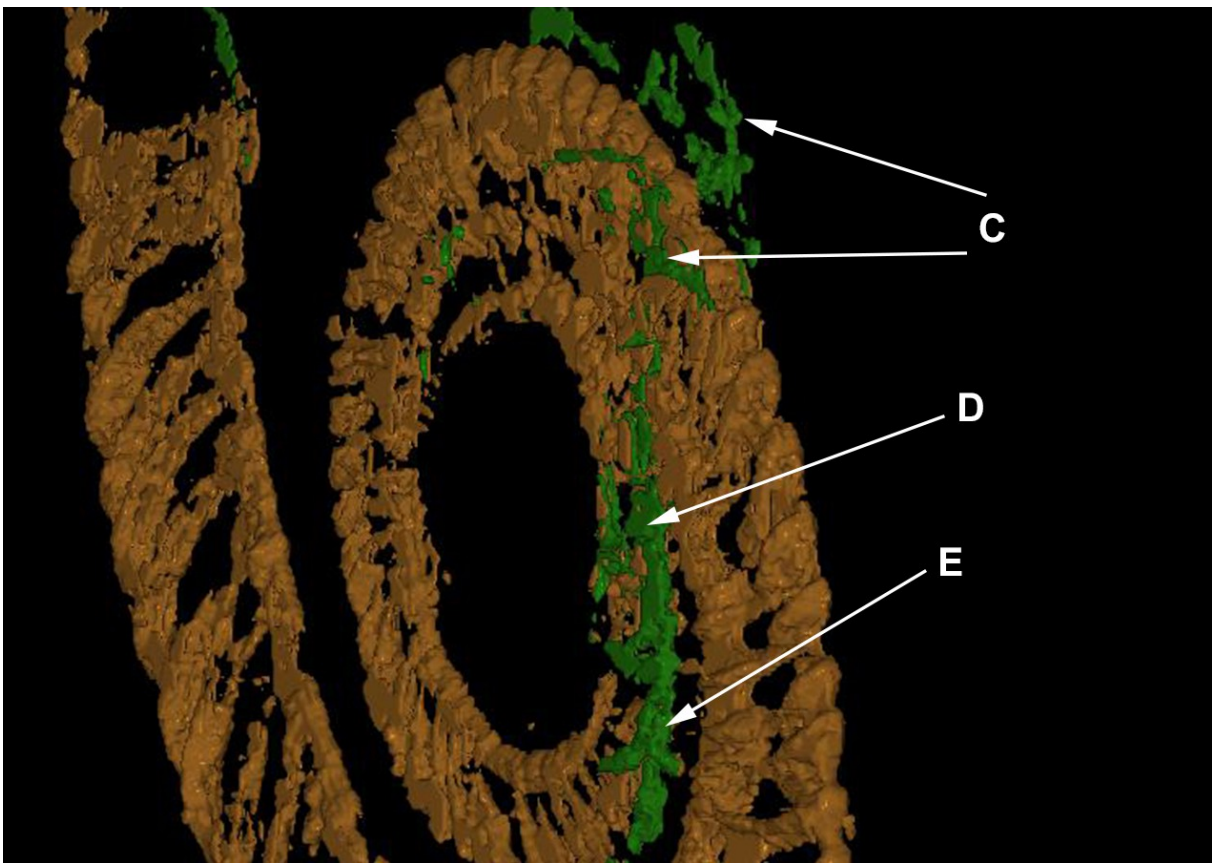
284   Fig. 6: Close-up of the 3D-model showing that sclerobionts are settling on both sides of the shell. Note correlation
285   between asymmetrical sclerobiont encrustation of cluster E and the deviation from planispiral coiling of the host.

286   Elongated components like the dacryoconarids present in the substrate (marked in yellow in
287   Figure 7) along with the *I. opitzi* specimen are often orientated along the direction of the paleo-
288   current (Hladil, Čejchan & Beroušek 1991; Hladil et al. 2014). Neither the dacryoconarids nor the
289   epicoles show a preferential orientation with respect to the substrate. Sclerobiont clusters C, D,
290   and E do show a preferential orientation with respect to the spiral axis of the ammonoid shell.
291   Unnamed, small, and bulky components visible in the matrix are probably pryitic nodules of
292   different sizes.
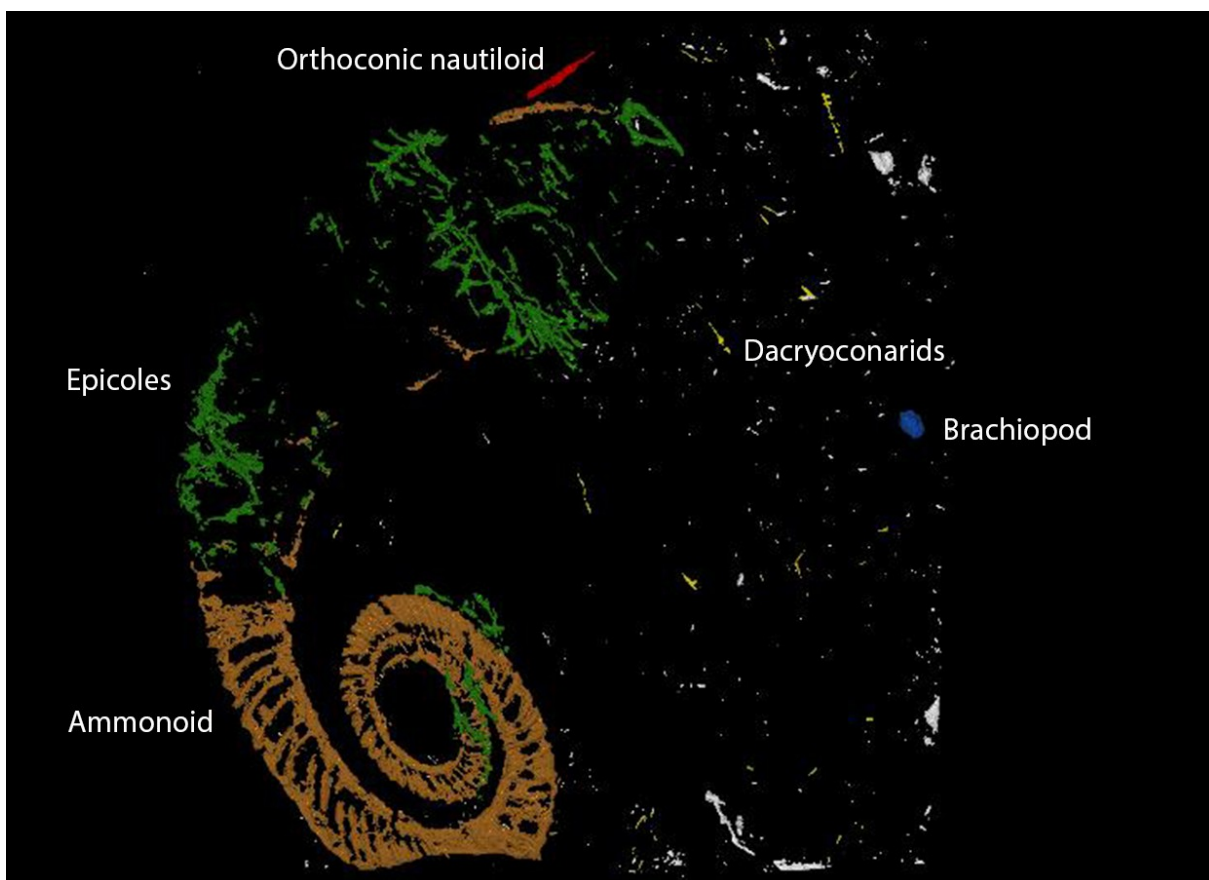
293 Fig. 7: The 3D-model showing all components. A brachiopod is coloured blue and dacryoconarids are shown in
294 yellow. Runner-like epicoles are marked in green and orthoconic nautiloid in red.

295 Morphology of the runner-like sclerobionts

296 The mode of preservation of the *I. opitzi* specimen, pyritization and internal mould preservation,
297 makes examination of fine details or microstructure of the sclerobionts impossible. Yet the
298 microCT permits three dimensional examination of the branching patterns of the sclerobiont
299 colonies. The original settlement location of the colonial organism cannot be distinguished, but
300 the branching pattern of colonies grow in a direction largely parallel to the direction of the
301 aperture of the host.

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

309 Branching morphology in the established colonies on the host are diverse despite many shared
310 characteristics. Morphologies of zooids exhibited in clusters A through D are generally more

311   elongate and acutely curved away from the uniserial plane to those in cluster E which contain
312   zooids that curve more dramatically along multiple, pluriserial branches of the colony. Some of
313   this variation could have been amplified by differential compaction in shales (Ross 1978; Briggs
314   & Williams 1981).

315

316   **Discussion**

317   The three-dimensional model of *I. opitzi* permitted extensive observation of the relationship
318   between the ammonoid host and the sclerobiont clusters present. The results permit positive
319   identification of the sclerobionts and interpretation of the relationship between them and their
320   host.

321   Synvivo vs. Post-Mortem encrustation

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

324   1) In-vivo encrustation: encrustation on both sides of the ammonoid by sclerobiont colonies C,
325   D, and E and the direction of the growth of those sclerobionts matching the growth of the
326   ammonoid, speak for an in-vivo encrustation – at least for sclerobiont clusters C-E. A lack of a
327   similar directional growth for all sclerobiont colonies on the ammonoid and with
328   dacryoconarids in the surrounding substrate, as well as a lack in widespread encrustation across
329   the ammonoid shell, further support the likelihood that the ammonoid was encrusted before
330   the ammonoid settled on the seafloor.

331   2) Post-mortem drift: encrustation of such large colonies solely during post-mortem drift seems
332   unlikely due to the small size of our specimen (105 mm diameter). This is below the 200 mm
333   limit listed for long floating cephalopod shells by Wani et al. (2005) and Rakociński (2011).
334   Interestingly, our specimen would have even a much smaller phragmocone volume than coiled
335   ammonoids at equal diameters used in these experiments. More importantly, the extra weight
336   of the sclerobionts should have made it sink even sooner than a non-encrusted shells so that it
337   would not have resulted in encrustation on both sides. Post-mortem drift is deemed rare for
338   ammonoids in general; most are implied to sink rather rapidly and would have preferentially
339   encrusted the lower parts of the ammonoid. Furthermore its vertical position in the water
340   column should have been affected by asymmetric encrustation resulting in a non-vertical
341   position of the shell after loss of soft-part parts which should have led to a more asymmetrical
342   distribution of the sclerobionts as the preferentially attach to the lower part of drifting shells
343   (Donovan 1989).

344   3) Resedimentation or reelaboration/reworking on the seafloor: usually encrustation of the
345   sediment-free side of the ammonoids - which mostly end of horizontally on the seafloor - is
346   taken to be characteristic unless reelaboration/reworking of shells or internal moulds happened
347   (Macchioni 2000). In our cases, we have encrustation on both sides by the same colonies and

348 transport by currents and reworking seems unlikely due the completeness of our specimen and
349 similarities in preservation with other specimens of its taphonomic group. All their
350 characteristics speak for a relatively rapid burial and infilling with pyrite only during early
351 diagenesis (before shell dissolution). Furthermore, the same sclerobionts (C-E) started growing
352 on the venter to both sides of the lateral sides which speak rather for a simple encrustation
353 history rather than multiple generations of epibionts encrusting each sediment-free side
354 sequentially (at least one before and after resedimentation/reworking and possibly more). No
355 evidence for re-sedimentation or reworking (abrasional features) are present in any of the 82
356 studied specimens of *Ivoites*.

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

358 The non-planispiral coiling of this specimen, a unique occurrence in the species, occurs at the
359 position of the sclerobiont clusters D and E. This pathological variation in host growth is also
360 consistent with encrustation of the cephalopod during its life-time. Even if the deviation in
361 coiling plane is only 1 to 2 mm now, it would have been substantially greater before burial and
362 compaction. Whorl thickness has estimated to reduce up to 248 % in some specimens (De Baets
363 et al. 2013), so originally these deviations could have been up to 2.5 to 5 mm.

364 Sclerobionts in clusters D and E are in a position that would have been hard to encrust if the
365 subsequent whorl had already grown at the time of encrustation (e.g., when it was lying on the
366 seafloor, the space between whorls around the venter would only have been between 2.5 to 5
367 mm, complicating sclerobiont settling. Our specimen suggests that the second whorl lies on top
368 of the first whorl (e.g., in the direction of the more heavily encrusted side, see Figure 3) while
369 the last whorl probably lies again below the second whorl (e.g., the coiling had almost
370 normalized until the next encrustation by sclerobiont cluster C). The encrustation and its slightly
371 different weight distribution across the venter would predict a deviation of the whorl initially in
372 the direction of the encrusters weight and subsequently in the opposite direction (this seems to
373 be still visible in our specimen despite it been heavily flattened). Such a pattern would thus be
374 expected if the specimen was encrusted in-vivo for the first time slightly before it completed
375 about one whorl (Checa, Okamoto & Keupp 2002). The non-planispiral coiling observed in this
376 specimen could not be produced by flattening or deformation – not even if the specimen was
377 embedded obliquely (see discussion in Material and Methods). Furthermore, clusters D-E are
378 positioned closely before the position where deviation of planispiral coiling can first be
379 recognized and indicates that the coiling was induced by the sclerobiont encrustation. If these
380 clusters grew on the ammonoid during life, as is also suggested by growth on both sides of the
381 shell, the deviations from planispiral coiling would have been unavoidable (Checa, Okamoto &
382 Keupp 2002).

383 The fact that sclerobiont clusters C, D, and E of runner-like epicoles are growing on both sides of
384 the ammonoid and that clusters (D-E) occur slightly before the position where the deviations
385 from planispiral coiling – where a whorl lies directly on top of the subsequent whorl – can be
386 first recognized speak for an encrustation of the ammonoid during its lifetime.

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

392   Identity of the encrusters

393   Hederelloids are a problematic group of runner-like sclerobionts, which occur in the fossil record
394   from the Silurian through Permian and are most diverse in the Devonian (Solle 1952; Solle 1968;
395   Taylor & Wilson 2007). Hederelloids have traditionally been treated as cyclostome bryozoans
396   (Bassler 1939; Elias 1944; Solle 1952; Solle 1968; Dzik 1981), but were redefined based upon
397   differences in branching patterns, skeletal microstructure, lack of an astogenetic gradient, and
398   wide range in tube diameters (Bancroft 1986; Wilson & Taylor 2001; Taylor & Wilson 2007). They
399   are currently mostly interpreted to be closely related to phoronids (Taylor & Wilson 2007; Taylor,
400   Vinn & Wilson 2010; Frey et al. 2014). Both auloporid corals and hederelloids are uncommon in
401   the middle Kaub Formation as their life habit requires a solid substrate upon which to settle;
402   these were rare within the clay environments of the Hunsrück Slate (Bartels, Briggs & Brassel
403   1998).

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

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

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

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

435   Implications for paleoenvironment of *Ivoites*

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

451   Hederelloids are typical encrusters found in Devonian photic zone environments (Brett et al.
452   2012). They are most diverse and abundant in shallower facies, but persist into the deep
453   euphotic zone (Smrecak 2016). The presence of hederelloids on the specimen, in combination
454   with other evidence described earlier, support an interpretation of *in vivo* encrustation. The
455   pelagic life habit of *I. opitzi* would allow colonies of hederelloids to settle and grow on the shell
456   with some success. In contrast, at depths of 100+ meters, hederelloid encrustation, and
457   sclerobiont encrustation in general, is significantly less common (e.g., Brett et al. 2011; Brett et
458   al. 2012; Smrecak & Brett 2014)). Thus, presence of multiple colonies of hederelloids on the
459   specimen support *in vivo* encrustation at depths within the photic zone, and lends further
460   support for depositional conditions in line with current interpretations that the Hunsrück Slate
461   interpreted was deposited near storm-wave base (Bartels, Briggs & Brassel 1998; Sutcliffe, Tibbs
462   & Briggs 2002).

463   De Baets et al. (2013) found encrusted ammonoid shells to be rare (only 6 of 342 studied
464   ammonoids: about 2%). Only two specimens of 82 specimens of *Ivoites* (2%) were found to be

465   encrusted with hederelloids – our specimen and an additional specimen of *Ivoites* sp. which was
466   interpreted to be encrusted post-mortem (Bartels, Briggs & Brassel 1998). So far, bivalves,
467   brachiopods, bryozoans, crinoids, hederelloids and tabulate corals have been reported to
468   encrust conchs of ammonoids or other externally shelled cephalopods from the Hunsrück Slate
469   s.s. or middle Kaub Formation (Brassel 1977; Bartels, Briggs & Brassel 1998; Jahnke & Bartels
470   2000; Kühl et al. 2012a; De Baets et al. 2013), but these have mostly thought to have happened
471   post-mortem due to their heavy encrustation on one side of the fossils or the encrustation of
472   the structures which would normally be covered with soft-parts (Bartels, Briggs & Brassel 1998;
473   Jahnke & Bartels 2000; De Baets et al. 2013). Heavy encrustations seems to be more common in
474   nautiloids (Bartels, Briggs & Brassel 1998; Jahnke & Bartels 2000; Kühl et al. 2012a), but these
475   have so far only been qualitatively studied. In environments between 100 and 200m
476   encrustation is generally low, which also consistent with a rare *in-vivo* encrustation of our
477   specimen swimming in shallower depths rather than the commonly reported post-mortem
478   encrustation. Additional studies on epicoles on ammonoid shells and other shells from the
479   Hunsrück Slate would be necessary to further test these hypotheses.

480   Implication for mode of life

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

491   We cannot entirely rule out a post-mortem encrustation of clusters A-B. Hederelloid growth in
492   those clusters are preferentially orientated away from the aperture of the ammonoid conch, as
493   opposed to those of the inner whorls (cluster C-E) which are preferentially orientated towards it.
494   Associated dacryoconarids do not show a preferential orientation with respect to the substrate
495   (as would be expected in the case of current alignment: Hladil, Čejchan & Beroušek 1991) or the
496   hederelloids. This does not necessarily speak against encrustation during the lifetime of the
497   ammonoid by clusters A and B as the terminal uncoiling of the ammonoid is interpreted to have
498   influenced the life orientation from an upturned aperture in the inner whorls to a downturned
499   aperture during the terminal uncoiling at the end of the ontogeny (Klug & Korn 2004; De Baets
500   et al. 2013; Klug et al. 2015a). We know the ammonoid specimen reached adulthood because it
501   terminally uncoils, which is typical for many taxa of Anetoceratinae and interpreted as a sign of
502   adulthood (De Baets, Klug & Korn 2009; De Baets et al. 2013; De Baets, Klug & Monnet 2013;
503   Klug et al. 2015b).

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

511　　Implications for taxonomy

512　　Defining pathological specimens as species can have important taxonomic implications (Spath
513　　1945). According to Spath (1945), such ammonoid species should remain valid, but no new type
514　　can be chosen while the holotype is still in existence. Others, like Haas (1946), claim assigning a
515　　pathological specimen might undermine the status of the species, considering the morphology
516　　of the species is described based on a pathological specimen, and that a new neotype should be
517　　selected. As the only known non-planispirally coiled specimen of *I. opitzi* is pathological, Haas
518　　(1946) would have suggested to designate another specimen as type for this species to avoid
519　　ambiguity. Non-planispirality does not belong to normal intraspecific variation of this species,
520　　nor to the taxonomic definition of this taxon. Paratype SMF-HF 940, which was collected from
521　　the same locality as the holotype (De Baets et al. 2013), would be the best candidate among the
522　　paratypes. Reassigning a neotype has recently been intensively discussed for the holotype of
523　　*Homo floriensis (Kaifu et al. 2009; Eckhardt & Henneberg 2010)*, but the severity of deviation has
524　　to be considered in this specimen. However, both aspects (electing a neotype for pathological
525　　specimens and its dependence of the severity of the pathology) are not specifically discussed in
526　　the International Code of Zoological Nomenclature (ICZN). According to Article 75.1 of ICZN, "the
527　　neotype is ... designated under conditions ... when no name-bearing type specimen is believed
528　　to be extant ...". In this case, if the holotype, even when pathologically deformed, is extant, the
529　　proposal of neotype is not granted. A proposal could be submitted to the ICZN to resolve the use
530　　of pathologically-induced morphological variation of holotypes, but this falls outside the aim of
531　　our study. Furthermore, we are confident that original type specimen belongs to same species
532　　as the paratypes as it completes the same amount of whorl before uncoiling, has a similar rib
533　　spacing and only differs from other specimens in its minor pathological coiling deviations (De
534　　Baets et al. 2013). As non-planispiral coiling was not part of the original diagnosis, we feel it is
535　　unnecessary to submit a proposal to appoint a new type specimen, which might not be allowed
536　　anyway.

537　　**Conclusions**

538　　With the aid of µCT, we can demonstrate that at least some of the encrustations must have
539　　happened during the lifetime of the ammonoid as the sclerobionts are located on both sides of
540　　the ammonoid at the place where deviation from planispiral coiling starts. This indicates that the
541　　non-planispiral, slight trochospiral coiling in this specimen is probably pathological and does not
542　　form a part of the natural variation (De Baets et al. 2013). To avoid taxonomic confusion

543 resulting from non-spiral coiling in this taxon, which is not part of the natural variation as initially
544 thought, one could select a neotype. While this practice has been suggested for other taxa (e.g.
545 Haas (1946), this is, in our opinion, not necessary as non-planispiral coiling did not form part of
546 the original diagnosis. As the specimen survived at least 3 different encrustations and associated
547 deformations through adulthood, the effects on its daily life were probably negligible. We re-
548 identify these runner-like epizoa as hederelloids (as opposed to auloporid tabulate corals), which
549 make them the first known hederelloids to encrust an ammonoid *in vivo* and suggests that the
550 ammonoid probably lived within the photic zone for most of its life. However, more studies on
551 sclerobionts from the Hunsrück Slate, preferably with μCT, are necessary to further corroborate
552 these hypotheses.

References

565 Anné J, Garwood RJ, Lowe T, Withers PJ, and Manning PL. 2015. Interpreting pathologies in extant and
566   extinct archosaurs using micro-CT. *PeerJ* 3:e1130.
567 Baird GC, Brett CE, and Frey RC. 1989. "Hitchhiking" epizoans on orthoconic cephalopods: preliminary
568   review of evidence and its implications. *Senckenbergiana Lethaea* 69:439-465.
569 Bancroft AJ. 1986. Hederella carbonaria Condra and Elias, a rare ?bryozoan from the Carboniferous of
570   Great Britain. *Proceedings of the Geologists' Association* 97:243-248.
571 Bartels C, Briggs DEG, and Brassel G. 1998. *The fossils of the hunsrück slate - Marine Life in the devonian*.
572 Bassler RS. 1939. The Hederelloidea: A Suborder of Paleozoic Cyclostomatous Bryozoa. *Proceedings of*
573   *the United States National Museum* 87:25-91.
574 Becker RT, Gradstein FM, and Hammer O. 2012. Chapter 22 - The Devonian Period. In: Gradstein FM, Ogg
575   JG, Schmitz MD, and Ogg GM, eds. *The Geologic Time Scale*. Boston: Elsevier, 559-601.
576 Becker RT, and House MR. 1994. International Devonian goniatite zonation, Emsian to Givetian, with new
577   records from Morocco. *Courier Forschungsinstitut Senckenberg* 169:79-135.
578 Beuck L, Wisshak M, Munnecke A, and Freiwald A. 2008. A Giant Boring in a Silurian Stromatoporoid
579   Analysed by Computer Tomography. *Acta Palaeontologica Polonica* 53:149-160.

580   Brassel G. 1977. Der erste Fund von Hederelloideen (Bryozoa) im Hunsrückschiefer von Bundenbach
581   (Unterdevon, Rheinisches Schiefergebirge). *Notizblatt des Hessischen Landesamtes für*
582   *Bodenforschung* 105:41-45.
583   Brett CE, Parsons-Hubbard KM, Walker SE, Ferguson C, Powell EN, Staff G, Ashton-Alcox KA, and Raymond
584   A. 2011. Gradients and patterns of sclerobionts on experimentally deployed bivalve shells:
585   Synopsis of bathymetric and temporal trends on a decadal time scale. *Palaeogeography,*
586   *Palaeoclimatology, Palaeoecology* 312:278-304.
587   Brett CE, Smrecak T, Parsons Hubbard K, and Walker S. 2012. Marine Sclerobiofacies: Encrusting and
588   Endolithic Communities on Shells Through Time and Space. In: Talent JA, ed. *Earth and Life*.
589   Dordrecht: Springer, 129-157.
590   Briggs DE, and Williams SH. 1981. The restoration of flattened fossils. *Lethaia* 14:157-164.
591   Cecca F. 1997. Late jurassic and early cretaceous uncoiled ammonites: Trophism-related evolutionary
592   processes. *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science*
593   325:629-634.
594   Checa AG, Okamoto T, and Keupp H. 2002. Abnormalities as natural experiments: a morphogenetic
595   model for coiling regulation in planispiral ammonites. *Paleobiology* 28:127-138.
596   Davis RA, Klofak SM, and Landman NH. 1999. Epizoa on Externally Shelled Cephalopods. In: Rozanov AY,
597   and Shevyrev AA, eds. *Fossil Cephalopods: Recent Advances In Their Study*. Moscow: Russian
598   Academy of Sciences Paleontological Institute, 32-51.
599   Davis RA, and Mapes RH. 1999. Pits in internal molds of cephalopods. *Berichte der Geologischen*
600   *Bundesanstalt* 46:31.
601   De Baets K. 2012. Early Emsian Ammonoidea: stratigraphy, intraspecific variability and macroevolution
602   PhD Thesis. Universität Zürich.
603   De Baets K, Keupp H, and Klug C. 2015. Parasites of ammonoids. In: Klug C, Korn D, De Baets K, Kruta I,
604   and Mapes RH, eds. *Ammonoid Paleobiology: From anatomy to paleoecology Topics in*
605   *Geobiology 43*. Dordrecht: Springer, 837-875.
606   De Baets K, Klug C, and Korn D. 2009. Anetoceratinae (Ammonoidea, Early Devonian) from the Eifel and
607   Harz Mountains (Germany), with a revision of their genera. *Neues Jahrbuch für Geologie und*
608   *Paläontologie - Abhandlungen* 252:361-376.
609   De Baets K, Klug C, Korn D, Bartels C, and Poschmann M. 2013. Emsian Ammonoidea and the age of the
610   Hunsrück Slate (Rhenish Mountains, Western Germany). *Palaeontographica A* 299:1-113.
611   De Baets K, Klug C, Korn D, and Landman NH. 2012. Early Evolutionary Trends in Ammonoid Embryonic
612   Development. *Evolution* 66:1788-1806.
613   De Baets K, Klug C, and Monnet C. 2013. Intraspecific variability through ontogeny in early ammonoids.
614   *Paleobiology* 39:75-94.
615   De Baets K, Klug C, and Plusquellec Y. 2010. Zlichovian faunas with early ammonoids from Morocco and
616   their use for the correlation of the eastern Anti-Atlas and the western Dra Valley. *Bulletin of*
617   *Geosciences* 85:317-352.
618   De Baets K, Landman NH, and Tanabe K. 2015. Ammonoid Embryonic Development. In: Klug C, Korn D, De
619   Baets K, Kruta I, and Mapes RH, eds. *Ammonoid Paleobiology: From anatomy to ecology Topics in*
620   *Geobiology 43*. Dordrecht: Springer, 113-205.
621   Dietl G. 1978. Die heteromorphen Ammoniten des Dogger. *Stuttgarter Beiträge Zur Naturkunde B* 33:1-
622   97.
623   Donovan SK. 1989. Taphonomic significance of the encrustation of the dead shell of recent Spirula spirula
624   (Linné) (Cephalopoda: Coleoidea) by Lepas anatifera Linné (Cirripedia: Thoracia). *Journal of*
625   *Paleontology* 63:698-702.
626   Dzik J. 1981. Evolutionary relationships of the early Palaeozoic 'cyclostomatous' Bryozoa. *Palaeontology*
627   24:827-861.
628   Eckhardt RB, and Henneberg M. 2010. LB1 from Liang Bua, Flores: Craniofacial asymmetry confirmed,
629   plagiocephaly diagnosis dubious. *American Journal of Physical Anthropology* 143:331-334.

630   Elias MK. 1944. Auloporidae and Hederelloidea (And a System to Avoid Ambiguous Use of Generic
631   Names). *Journal of Paleontology* 18:529-534.
632   Erben H. 1994. Das Meer des Hunsrückschiefers. *Erdgeschichte im Rheinland Fossilien und Gesteine aus*
633   400:49-56.
634   Etter W. 2002. Hunsrück slate: widespread pyritization of a Devonian fauna. *Exceptional fossil*
635   *preservation*, eds Bottjer, DJ, W Etter, JW Hagadorn, and CM Tang:143-165.
636   Fenton MA, and Fenton CL. 1937. Aulopora: A Form-Genus of Tabulate Corals and Bryozoans. *American*
637   *Midland Naturalist* 18:109-115.
638   Fernández-López S, and Meléndez G. 1994. Abrasion surfaces on internal moulds of ammonites as
639   palaeobathymetric indicators. *Palaeogeography, Palaeoclimatology, Palaeoecology* 110:29-42.
640   Fernández-López SR. 1991. Taphonomic concepts for a theoretical biochronology. *Revista Espanola de*
641   *Paleontologia* 6:37-49.
642   Frey L, Naglik C, Hofmann R, Schemm-Gregory M, FRÝDA J, Kroeger B, Taylor PD, Wilson MA, and Klug C.
643   2014. Diversity and palaeoecology of Early Devonian invertebrate associations in the Tafilalt
644   (Anti-Atlas, Morocco). *Bulletin of Geosciences* 89:75-112.
645   Garwood RJ, and Dunlop J. 2014. Three-dimensional reconstruction and the phylogeny of extinct
646   chelicerate orders. *PeerJ* 2:e641.
647   Haas O. 1946. Neotypes for Species Based on Pathological Specimens. *Nature* 157:700.
648   Hauschke N, Schöllmann L, and Keupp H. 2011. Oriented attachment of a stalked cirripede on an
649   orthoconic heteromorph ammonite - implications for the swimming position of the latter. *Neues*
650   *Jahrbuch für Geologie und Paläontologie - Abhandlungen* 262:199-212.
651   Hladil J, Čejchan P, and Beroušek P. 1991. Orientation of the conical tests of tentaculites: internal waves in
652   aqueous environment. *Čas Mineral Geol* 36:115-130.
653   Hladil J, Simcik M, Ruzicka MC, Kulaviak L, and Lisy P. 2014. Hydrodynamic experiments on dacryoconarid
654   shell telescoping. *Lethaia* 47:376-396.
655   Hoffmann R, Schultz JA, Schellhorn R, Rybacki E, Keupp H, Gerden SR, Lemanis R, and Zachow S. 2014.
656   Non-invasive imaging methods applied to neo- and paleo-ontological cephalopod research.
657   *Biogeosciences* 11:2721-2739.
658   House MR. 1996. Juvenile goniatite survival strategies following Devonian extinction events. *Geological*
659   *Society, London, Special Publications* 102:163-185.
660   Jahnke H, and Bartels C. 2000. Der Hunsrückschiefer und seine Fossilien, Unter-Devon. In: Pinna G, and
661   Meischner D, eds. *Europäische Fossillagerstätten*. Dordrecht: Springer, 36-44.
662   Kacha P, and Šaric R. 2009. Host preferences in Late Ordovician (Sandbian) epibenthic bryozoans:
663   example from the Zahorany Formation of Prague Basin. *Bulletin of Geosciences* 84:169-178.
664   Kaifu Y, Baba H, Kurniawan I, Sutikna T, Saptomo EW, Jatmiko, Awe RD, Kaneko T, Aziz F, and Djubiantono
665   T. 2009. Brief communication: "Pathological" deformation in the skull of LB1, the type specimen
666   of Homo floresiensis. *American Journal of Physical Anthropology* 140:177-185.
667   Keupp H. 1992. Wachstumsstörungen bei Pleuroceras und anderen Ammonoidea durch Epökie. *Berliner*
668   *Geowissenschaftliche Abhandlungen E* 3:113-119.
669   Keupp H. 2012. Atlas zur Paläopathologie der Cephalopoden. *Berliner Paläobiologische Abhandlungen*
670   12:1-392.
671   Keupp H, and Hoffmann R. 2015. Ammonoid paleopathology. In: Klug C, Korn D, De Baets K, Kruta I, and
672   Mapes RH, eds. *Ammonoid Paleobiology: from anatomy to ecology*. Dordrecht: Springer, 877-
673   926.
674   Keupp H, Röper M, and Seilacher A. 1999. Paläobiologische Aspekte von syn vivo-besiedelten
675   Ammonoideen im Plattenkalk des Ober-Kimmeridgiums von Brunn in Ostbayern. *Berliner*
676   *Geowissenschaftliche Abhandlungen Reihe E Palaeobiologie* 30:121-145.
677   Klug C, and Korn D. 2001. Epizoa and post-mortem epicoles on cephalopod shells–examples from the
678   Devonian and Carboniferous of Morocco. *Berliner geowissenschaftliche Abhandlungen (E)*
679   36:145-155.

680   Klug C, and Korn D. 2004. The origin of ammonoid locomotion. *Acta Palaeontologica Polonica* 49:235-
681   242.
682   Klug C, Kröger B, Vinther J, Fuchs D, and De Baets K. 2015a. Ancestry, Origin and Early Evolution of
683   Ammonoids. In: Klug C, Korn D, De Baets K, Kruta I, and Mapes RH, eds. *Ammonoid Paleobiology:*
684   *From macroevolution to paleogeography Topics in Geobiology 44*, 3-24.
685   Klug C, Zatoń M, Parent H, Hostettler B, and Tajika A. 2015b. Mature modifications and sexual
686   dimorphism. In: Klug C, Korn D, De Baets K, Kruta I, and Mapes RH, eds. *Ammonoid Paleobiology:*
687   *from anatomy to ecology*. Dordrecht: Springer, 253-320.
688   Kneidl V. 1984. *Hunsrück und Nahe: Geologie, Mineralogie und Paläontologie. Ein Wegweiser für den*
689   *Liebhaber*. Stuttgart: Kosmos Verlag.
690   Kruta I, Landman N, Rouget I, Cecca F, and Tafforeau P. 2011. The Role of Ammonites in the Mesozoic
691   Marine Food Web Revealed by Jaw Preservation. *Science* 331:70-72.
692   Kühl G, Bartels C, Briggs DEG, and Rust J. 2012a. *Visions of a Vanished World: The Extraordinary Fossils of*
693   *the Hunsrück Slate*: Yale University Press.
694   Kühl G, Bergmann A, Dunlop J, Garwood RJ, and Rust JES. 2012b. Redescription and palaeobiology of
695   Palaeoscorpius devonicus Lehmann, 1944 from the Lower Devonian Hunsrück Slate of Germany.
696   *Palaeontology* 55:775-787.
697   Landman NH, Tanabe K, and Davis RA. 1996. *Ammonoid paleobiology*. New York: Plenum Press.
698   Larson N. 2007. Deformities in the Late Callovian (Late Middle Jurassic) Ammonite Fauna from Saratov,
699   Russia. In: Landman NH, Davis RA, and Mapes RH, eds. *Cephalopods Present and Past: New*
700   *Insights and Fresh Perspectives*. Netherlands: Springer 344-374.
701   Lemanis R, Korn D, Zachow S, Rybacki E, and Hoffmann R. 2016. The Evolution and Development of
702   Cephalopod Chambers and Their Shape. *PLoS ONE* 11:e0151404.
703   Lemanis R, Zachow S, Fusseis F, and Hoffmann R. 2015. A new approach using high-resolution computed
704   tomography to test the buoyant properties of chambered cephalopod shells. *Paleobiology*
705   FirstView:1-17.
706   Lemanis R, Zachow S, and Hoffmann R. 2016. Comparative cephalopod shell strength and the role of
707   septum morphology on stress distribution. *PeerJ* 4:e2434.
708   Lescinsky HI. 2001. Epibionts. In: Briggs DEG, and Crowther PR, eds. *Palaeobiology II*. Oxford: Blackwell
709   Publishing, 460-464.
710   Luci L, and Cichowolski M. 2014. Encrustation in nautilids: a case study in the Cretaceous species
711   Cymatoceras peristriatum, Neuquén Basin, Argentina. *Palaios* 29:101-120.
712   Luci L, Cichowolski M, and Aguirre-Urreta MB. 2016. Sclerobionts, shell morphology and biostratinomy on
713   ammonites: two Early Cretaceous cases from the Neuquén Basin, Argentina. *Palaios* 31:41-54.
714   Lukeneder A. 2008. The ecological significance of solitary coral and bivalve epibionts on Lower
715   Cretaceous (Valanginian-Aptian) ammonoids from the Italian Dolomites. *Acta Geologica Polonica*
716   58:425-436.
717   Lukeneder A. 2012. Computed 3D visualisation of an extinct cephalopod using computer tomographs.
718   *Computers & Geosciences* 45:68-74.
719   Macchioni F. 2000. Bioeroded and/or encrusted ammonite moulds and their taphonomic implications.
720   *Rivista Italiana di Paleontologia e Stratigrafia* 106:337-352.
721   Meischner D. 1968. Perniciöse Epökie von *Placunopsis* auf *Ceratites*. *Lethaia* 1:156-174.
722   Merkt J. 1966. Über Austern und Serpeln als Epöken auf Ammonitengehäusen. *Neues Jahrbuch für*
723   *Geologie und Paläontologie - Abhandlungen* 125:467-479.
724   Mistiaen B, Brice D, Zapalski M, and Loones C. 2012. Brachiopods and Their Auloporid Epibionts in the
725   Devonian of Boulonnais (France): Comparison with Other Associations Globally. In: Talent J, ed.
726   *Earth and Life*: Springer Netherlands, 159-188.
727   Monnet C, Zollikofer C, Bucher H, and Goudemand N. 2009. Three-dimensional morphometric ontogeny
728   of mollusc shells by micro-computed tomography and geometric analysis. *Paleontologia*
729   *Electronica* 12:1-13.

730   Naglik C, Monnet C, Goetz S, Kolb C, De Baets K, Tajika A, and Klug C. 2015a. Growth trajectories of some
731   major ammonoid sub-clades revealed by serial grinding tomography data. *Lethaia* 48:29-46.
732   Naglik C, Rikhtegar F, and Klug C. 2016. Buoyancy of some Palaeozoic ammonoids and their hydrostatic
733   properties based on empirical 3D-models. *Lethaia* 49:3-12.
734   Naglik C, Tajika A, Chamberlain JA, and Klug C. 2015b. Ammonoid Locomotion. In: Klug C, Korn D, De
735   Baets K, Kruta I, and Mapes RH, eds. *Ammonoid Paleobiology: From anatomy to ecology*.
736   Dordrecht: Springer, 649-688.
737   Opitz R. 1932. *Bilder aus der Erdgeschichte des Nahe-Hunsrück-Landes Birkenfeld*. Birkenfeld: Enke.
738   Rahman IA, Belaústegui Z, Zamora S, Nebelsick JH, Domènech R, and Martinell J. 2015. Miocene
739   Clypeaster from Valencia (E Spain): Insights into the taphonomy and ichnology of bioeroded
740   echinoids using X-ray micro-tomography. *Palaeogeography, Palaeoclimatology, Palaeoecology*
741   438:168-179.
742   Rakociński M. 2011. Sclerobionts on upper Famennian cephalopods from the Holy Cross Mountains,
743   Poland. *Palaeobiodiversity and Palaeoenvironments* 91:63-73.
744   Rakús M, and Zítt J. 1993. Crinoid encrusters of Ammonite shells (Carixian, Tunisia). *Geobios* 26:317-329.
745   Ritterbush KA, Hoffmann R, Lukeneder A, and De Baets K. 2014. Pelagic palaeoecology: the importance of
746   recent constraints on ammonoid palaeobiology and life history. *Journal of Zoology* 292:229-241.
747   Ross CA. 1978. Distortion of fossils in shales. *Journal of Paleontology*:943-945.
748   Ruan YP. 1981. Devonian and earliest Carboniferous Ammonoids from Guangxi and Guizhou. *Memoirs of*
749   *the Nanjing Institute of Geology & Paleontology* 15:152.
750   Ruan YP. 1996. Zonation and distribution of the early Devonian primitive ammonoids in South China. In:
751   Wang H-Z, and Wang X-L, eds. *Centennial Memorial Volume of Prof Sun Yunzhen: Paleontology*
752   *and Stratigraphy*. Wuhan: China University of Geosciences Press, 104-112.
753   Rust J, Bergmann A, Bartels C, Schoenemann B, Sedlmeyer S, and Kühl G. 2016. The Hunsrück Biota: A
754   Unique Window into the Ecology of Lower Devonian Arthropods. *Arthropod Structure &*
755   *Development*.
756   Schindler T, Sutcliffe O, Bartels C, Poschmann M, and Wuttke M. 2002. Lithostratigraphical subdivision
757   and chronostratigraphical position of the middle Kaub Formation (Lower Emsian, Lower
758   Devonian) of the Bundenbach area (Hunsrück, SW Germany). *Metalla (Bochum)* 9:73-104.
759   Schmid–Röhl A, and Röhl HJ. 2003. Overgrowth on ammonite conchs: environmental implications for the
760   Lower Toarcian Posidonia Shale. *Palaeontology* 46:339-352.
761   Seilacher A. 1960. Epizoans as a Key to Ammonoid Ecology. *Journal of Paleontology* 34:189-193.
762   Seilacher A. 1982. Ammonite Shells as Habitats — Floats or Benthic Islands? (Abstract). In: Einsele G, and
763   Seilacher A, eds. *Cyclic and Event Stratification*: Springer Berlin Heidelberg, 504-504.
764   Seilacher A, and Hemleben C. 1966. Beiträge sur sedimentation und Fossilführung des Hunsrückschiefers
765   14. *Spurenfauna und Bildungsteife der Hunsrückschiefer (Unterdevon) Notizblatt des Hessischen*
766   *Landesamtes für Bodenforschung zu Wiesbaden* 94:40-53.
767   Selden P, and Nudds J. 2012. *Evolution of fossil ecosystems*: Elsevier.
768   Smrecak TA. 2016. Understanding patterns of sclerobiont encrustation: Methodological review and
769   application of sclerobiont facies model in Middle Devonian Appalachian and Michigan Basin
770   paleodepth gradients PhD. Michigan State University.
771   Smrecak TA, and Brett CE. 2014. Establishing patterns in sclerobiont distribution in a late Ordovician
772   (Cincinnatian) depth gradient: toward a sclerobiofacies model. *Palaios* 29:74-85.
773   Solle G. 1950. Obere Siegener Schichten, Hunsrückschiefer, tiefstes Unterkoblenz und ihre Eingliederung
774   ins Rheinische Unterdevon. *Geol Jb* 65:299-380.
775   Solle G. 1952. Neue Untersuchungen und Arten der Bryozoen-Gattung Hederella und eine Hernodia im
776   rheinischen Unterdevon. *Notzbl hess LA Bodenforsch* 6:35-55.
777   Solle G. 1968. Hederelloidea (Cyclostomata) und einige ctenostome Bryozoen aus dem Rheinischen
778   Devon. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* 54:1-40.

779   Spath LF. 1945. Problems of Ammonite-Nomenclature X. The Naming of Pathological Specimens.
780   *Geological Magazine* 82:251-255.
781   Stets J, and Schäfer A. 2009. The Siegenian delta: land-sea transitions at the northern margin of the
782   Rhenohercynian Basin. *Geological Society, London, Special Publications* 314:37-72.
783   Südkamp WH. 2007. An atypical fauna in the Lower Devonian Hunsrück Slate of Germany.
784   *Paläontologische Zeitschrift* 81:181-204.
785   Sutcliffe O, Tibbs S, and Briggs D. 2002. Sedimentology and environmental interpretation of the fine-
786   grained turbidites in the Kaub Formation of the Hunsrück Slate: analysis of a section excavated
787   for Project Nahecaris. *Metalla (Bochum)* 9:89-104.
788   Sutton MA, Rahman IA, and Garwood RJ. 2014. *Techniques for Virtual Palaeontology*. UK: Wiley-
789   Blackwell.
790   Tajika A, Morimoto N, Wani R, Naglik C, and Klug C. 2015. Intraspecific variation of phragmocone
791   chamber volumes throughout ontogeny in the modern nautilid Nautilus and the Jurassic
792   ammonite Normannites. *PeerJ* 3:e1306.
793   Tajika A, Naglik C, Morimoto N, Pascual-Cebrian E, Hennhöfer D, and Klug C. 2014. Empirical 3D model of
794   the conch of the Middle Jurassic ammonite microconch Normannites: its buoyancy, the physical
795   effects of its mature modifications and speculations on their function. *Historical Biology*:1-11.
796   Taylor PD, Vinn O, and Wilson MA. 2010. Evolution of biomineralisation in 'lophophorates'. *Special Papers*
797   *in Palaeontology* 84:317-333.
798   Taylor PD, and Wilson M. 2007. Morphology and affinities of hederelloid "bryozoans". Bryozoan Studies
799   2007: proceedings of the 14th international bryozoology conference, Boone, North Carolina, July
800   1–8: Virginia Museum of Natural History Special Publication. p 301-309.
801   Taylor PD, and Wilson MA. 2002. A New Terminology for Marine Organisms Inhabiting Hard Substrates.
802   *Palaios* 17:522-525.
803   Thayer CW. 1974. Substrate Specificity of Devonian Epizoa. *Journal of Paleontology* 48:881-894.
804   Wani R, Kase T, Shigeta Y, and De Ocampo R. 2005. New look at ammonoid taphonomy, based on field
805   experiments with modern chambered nautilus. *Geology* 33:849-852.
806   Westermann GEG. 1996. Ammonoid Life and Habitat. In: Landman NH, Tanabe K, and Davis RA, eds.
807   *Ammonoid Paleobiology*. New York: Plenum Press, 607-707.
808   Wiedmann J. 1969. The heteromorphs and ammonoid extinction. *Biological Reviews* 44:563-602.
809   Wilson M, and Taylor P. 2001. Pseudobryozoans" and the problem of encruster diversity in the Paleozoic.
810   *Paleobios* 21:134-135.
811   Wilson MA, and Taylor PD. 2006. Predatory drill holes and partial mortality in Devonian colonial
812   metazoans. *Geology* 34:565-568.
813   Wilson MA, and Taylor PD. 2013. Palaeoecology, Preservation and Taxonomy of Encrusting Ctenostome
814   Bryozoans Inhabiting Ammonite Body Chambers in the Late Cretaceous Pierre Shale of Wyoming
815   and South Dakota, USA. In: Ernst A, Schäfer P, and Scholz J, eds. *Bryozoan Studies 2010*. Berlin,
816   Heidelberg: Springer Berlin Heidelberg, 419-433.
817   Wyse Jackson PN, and Key Jr MM. 2014. Epizoic bryozoans on cephalopods through the Phanerozoic: A
818   review. *Studi Trentini di Scienze Naturali* 94:283-291.
819   Wyse Jackson PN, Key MMJ, and Coakley SP. 2014. Epizoozoan Trepostome Bryozoans on Nautiloids from
820   the Upper Ordovician (Katian) of the Cincinnati Arch Region, U.S.A.: An Assessment of Growth,
821   form, and Water Flow Dynamics. *Journal of Paleontology* 88:475-487.
822   Zapalski MK. 2005. Paleoecology of Auloporida: an example from the Devonian of the Holy Cross Mts.,
823   Poland. *Geobios* 38:677-683.