

1     **INSIGHTS INTO THE MORPHOLOGY OF *SPHENOTHALLUS* (CNIDARIA): NEW FEATURES IDENTIFIED**  
2     **IN AN OLD GENUS, FROM THE CARBONIFEROUS (PENNSYLVANIAN, BASHKIRIAN) OF WESTERN**  
3     **IRELAND**

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6                     **Abstract**

7     The recent discovery of well-preserved fragments of *Sphenothallus* in the Central Clare Group  
8     (Pennsylvanian) of western Ireland provides new insights into the morphology of this enigmatic,  
9     putative cnidarian. The specimens demonstrate a morphological plasticity including features not  
10    previously described for *Sphenothallus*, such as the presence of flat sides and angular lateral  
11    margins, non-bilateral symmetry in sigmoidal cross-sections suggestive of growth torsion, and a new  
12    type of bifurcating branching (new term ‘railtrack junction branching’ introduced herein), not related  
13    to known budding. We propose that these structures were all growth-related features during life,  
14    not post-mortem artefacts of collapse or compaction. The flat sides and growth torsion are  
15    compared with similar features in conulariids, supporting the previously proposed phylogenetic  
16    linkage between the two groups, which may be an example of atavism. However, the bifurcating  
17    ‘railtrack junction branching’ is unknown in conulariids or other similar organisms.

18  
19                     **Introduction**

20    The fossil record is replete with many tube-like organisms composed of a variety of substances. Their  
21    morphology, ecology and phylogenetic affinity are commonly described as problematic.  
22    Nevertheless these ‘Problematica’ form important components of many marine communities in  
23    terms of their abundance and diversity. One such tube, *Sphenothallus* Hall, originally described as  
24    *Serpulites longissimus* J. de C. Sowerby from the Silurian of England, and its allies, has been the  
25    subject of much discussion, particularly regarding its taxonomic affinities. Only one previous record  
26    of *Sphenothallus* is known from Ireland, *S. carbonarius* (M’Coy, 1844) from the Carboniferous of  
27    Manorhamilton, County Leitrim. Originally assigned to *Serpulites* the lectotype (NMING:F7357/C)  
28    and counterpart (NMING:F7357/B) are in the National Museum Ireland, Natural History, Dublin.

29         The new Irish material assigned to the genus *Sphenothallus* occurs in the Pennsylvanian  
30    (Bashkirian/Regional Substage: Kinderscoutian) rocks of the Clare Basin (Fig. 1). The specimens are  
31    relatively abundant and well preserved although fragmentary. All described and illustrated  
32    specimens are repositated at the National Museum Ireland, Natural History, Dublin (Accession  
33    numbers NG:F35396–NG:F35407).

37 *Sphenothallus* is generally described as an enigmatic, flattened tuboid fossil and has been recorded  
38 from rocks of Cambrian to Triassic age, although it has not been documented from the Permian  
39 System (Bolton 1994; Fatka *et al.* 2012; Chang *et al.* 2018; Van Iten *et al.* 2023). The taxon was first  
40 described from the Silurian of England by J. de C. Sowerby (as *Serpulites longissimus*) under the  
41 direction of Sir Roderick Murchison during the latter's investigations of the Silurian System  
42 (Murchison 1839). James Hall first introduced the generic name *Sphenothallus* in 1847 for what he  
43 believed to be plant material. Ruedemann (1896) considered the taxon to be related to the  
44 conulariids, although Mason and Yochelson (1985) stated that Ruedemann confused flattened  
45 *Sphenothallus* tubes with flattened conulariids. The generic names *Enchostoma*, *Serpulites*, and  
46 *Campylites* were also used for similar flattened or tuboid chitinous fossils until the first major  
47 revision of the genus *Sphenothallus* by Schmidt and Teichmüller (1956), which covered most  
48 European records. The type species of *Sphenothallus* Hall is from the Ordovician of New York;  
49 however, it was not until the study by Mason and Yochelson (1985) that the distribution of this  
50 genus (which they considered an annelid) throughout the Devonian to Pennsylvanian rocks of North  
51 America was documented.

52 *Sphenothallus* is remarkably widespread both geographically and stratigraphically. Following the  
53 initial interest by 19<sup>th</sup> Century scientists, based on records predominantly from Europe and the  
54 subsequent work of Mason and Yochelson (1985) from the USA, *Sphenothallus* has been recorded  
55 from Cambrian to Triassic deposits, except in the Permian, at a wide variety of other locations: South  
56 Korea (Choi 1990), Bolivia (Babcock 1993; Hannibal *et al.* 1993), Canada (Bolton 1994), Argentina  
57 (Taboada 1997), China (Zhu *et al.* 2000; Wang Yi *et al.* 2003), Estonia (Vinn and Kirsimae 2015),  
58 Sweden (Nathorst 1883; Stewart *et al.* 2015), Morocco (Van Iten *et al.* 2016), Ukraine (Dernov 2023),  
59 and Slovenia (Van Iten *et al.* 2023).

60 Radiograph images of specimens from the Lower Devonian Hunsrück Slate of Germany, published  
61 by Fauchald *et al.* (1986) were interpreted as showing two tentacles and a spool-like body in the  
62 open cavity of *Sphenothallus*. To date, these remain the only putative soft-body parts described for  
63 the genus, however they were inconclusive in determining its taxonomic position; but the authors  
64 stated that these structures 'would seem to prove beyond question that *Sphenothallus* was indeed  
65 wormlike'; they noted, however, that the sleeve of tissue that purportedly supported the two  
66 tentacles is similar to the supportive structure at the base of the tentacular crown of extant sabellid  
67 polychaetes. Nevertheless, subsequently Fauchald and Yochelson (1990) agreed that *Sphenothallus*  
68 was not an annelid based on the lack of segmentation of its soft parts.

69 Van Iten *et al.* (1992) placed *Sphenothallus* firmly within the Phylum Cnidaria, based on material  
70 from the Mississippian Bear Gulch Formation in central Montana, in particular noting the presence  
71 of schotts, multilamellar thecae, holdfasts and clonal-branching; all of which are features which can  
72 be identified in modern hydrozoans and scyphozoans. Comprehensive reviews by Mason and  
73 Yochelson (1985), Van Iten *et al.* (1992) and Neal and Hannibal (2000) have discussed the changing  
74 taxonomic position of *Sphenothallus* during the 20<sup>th</sup> Century, and Zhu *et al.* (2000) provided a very  
75 thorough review of the historical nomenclature of the genus. Since then, *Sphenothallus* has  
76 generally been accepted as a medusozoan, despite the lack of diagnostic soft-body parts.

77 More recently, Vinn and Mironenko (2021) have described phosphatic lamellar fibrous ‘plywood’  
78 layers in *Sphenothallus* from the Mississippian of central Russia. They conclude that this layering  
79 could indicate an originally organic layered structure that has been diagenetically phosphatized  
80 (similar organic structures are known in cnidarians, polychaete annelids and phoronids) or the  
81 phosphatic composition was an original feature (which they consider less likely), indicating a closer  
82 affinity with vertebrates. In either case, they acknowledged that while these organic lamellar fibrous  
83 ‘plywood’ layers occur in some cnidarian (anthozoan) tubes (Stampar *et al.* 2015), they are unknown  
84 in medusozoans.

85 Dzik *et al.* (2017) described radial septa and tetradial symmetry in juvenile *Sphenothallus* and  
86 noted a change to a bilateral symmetry in adult specimens. They compared the early ontogenetic  
87 growth to coronate scyphozoan polyps and proposed that the ancestor of cnidarians was also a  
88 bilaterally symmetrical animal.

89

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### Palaeoecology

91 *Sphenothallus* has been universally considered a marine animal; it has been recorded from dysoxic,  
92 oxic, shallow to deeper-water marine environments, including hardgrounds. The sole exception of an  
93 occurrence in non-marine deposits (upper Pennsylvanian lacustrine sediments of New Mexico) has  
94 been attributed to allochthonous fragments, carried inshore from a nearby marine environment  
95 (Lerner and Lucas 2011). When associated with hardgrounds, the holdfasts of *Sphenothallus* have  
96 been reported on presumably dead brachiopods, as well as other *Sphenothallus*. Vinn and  
97 Mironenko (2021) linked the appearance of *Sphenothallus* in the Mississippian of Russia to the  
98 maximum height of rising relative sea level which coincided with the spread of anoxic conditions in  
99 the bottom water layers. Otherwise, it appears to have been an opportunist, usually occurring with  
100 few other benthic animals (Bodenbender *et al.* 1989; Van Iten *et al.* 1996; Neal and Hannibal, 2000;  
101 Wang *et al.* 2003). The new Irish material similarly occurs with a low number of other benthic

102 organisms (scarce inarticulate brachiopods, unidentified burrowing organisms and demosponges) at  
103 the base of a cyclothemic shallowing-upwards unit (Kilkee cyclothem). The specimens are found in  
104 grey shale, and there is no evidence of anoxic bottom water conditions as indicated by the presence  
105 of infaunal burrowing. Ammonoids (*Anthracoceras* sp. and *Reticuloceras* sp.) also occur rarely in the  
106 same horizon but they are generally not considered part of the benthic fauna due to their pelagic,  
107 swimming lifestyle; however, a nektobenthic habit has been proposed for some Carboniferous  
108 ammonoids (Tanabe *et al.* 1995), so they may have spent some time on the seafloor. Numerous  
109 holdfast-like structures embedded in the muddy substrate occur along the same horizon. They are  
110 not attached to hard substrates which, apart from the substrates provided by *Sphenothallus*  
111 themselves, are almost entirely lacking. Several specimens bear circular or subcircular scars of  
112 possible attachments but no specimens of *Sphenothallus* attached to the holdfasts have been found.  
113 However, based on the similarity to *Sphenothallus* holdfasts described from elsewhere (Peel, 2021) it  
114 is reasonable to assume they are the disconnected holdfasts of *Sphenothallus* which tethered the  
115 animals to the seafloor during life.

116

#### 117 **Systematic palaeontology**

118

119 Phylum Cnidaria Verrill, 1865

120 Subphylum Medusozoa Peterson, 1979

121 Class, Order, Family uncertain

122 Genus *Sphenothallus* Hall, 1847

123

124 *Type species.* *Sphenothallus angustifolius* Hall, 1847, originally described from the Upper Ordovician  
125 of eastern New York State, USA.

126

127 *Amended diagnosis (after Van Iten et al. 2013).* *Sphenothallus* specimens generally consist of a  
128 single, slender, gently tapered hollow tube constructed of numerous, very thin (approximately 1–2  
129  $\mu\text{m}$ ) lamellae that parallel the exterior surface of the tube (e.g., Van Iten *et al.* 1992, 2002; Muscente  
130 and Xiao 2015; Vinn and Kirsimäe 2015). In addition there may be a plywood-style structure with  
131 alternating layers of lamellae orientated at high angles (Vinn and Morenenko, 2021). Most  
132 specimens contain substantial amounts of the mineral apatite, but others are largely or entirely  
133 organic (see Muscente and Xiao 2015 and references cited therein). Tube shape changes during  
134 ontogeny from circular in juvenile/immature specimens to ellipsoidal to broadly sigmoidal in some  
135 adults. This sigmoidal shape may include the development of flat lateral faces and sharp corners



136 between adjoining faces. The pair of marginal thickenings are asymmetrical and the result of the  
137 sigmoidal shape of the adult test. The wide or oral end of the tube is open, and the oral margin of  
138 each face is gently curved. The narrow, aboral (apical) end of the tube exhibits a small, sub-conical  
139 expansion floored by a thin membrane cemented in life to hard substrates including hardgrounds.

140 |  
141 *Sphenothallus* aff. *carbonarius* M'Coy, 1844

142 Figs. 2–7

143 aff. 1844 *Serpulites carbonarius*; M'Coy, p. 170, pl. 23, fig. 32.

144 aff. 1844 *Serpulites membranaceus*; M'Coy, p. 170, pl. 23, fig. 31.

145 aff. 1967 *Campylites carbonarius* (McCoy); Wilson, pp. 470–471, pl. 1, figs. 8–16.

146  
147  
148 *Discussion.* The specimens described herein are broadly similar to *S. carbonarius*, originally described  
149 | from the Carboniferous of Ireland by M'Coy (1844). This species was redescribed by Wilson (1967)  
150 on the basis of M'Coy's type material and new material from the Carboniferous of central Scotland,  
151 and he concluded that *S. membranaceus* (M'Coy, 1844) should be regarded as a junior synonym of *S.*  
152 *carbonarius*. There is a real difficulty in comparing our new material with previously described  
153 species, as many published species are differentiated purely on width, size and surface structure,  
154 with no other differentiating features. Some authors have used the angle of expansion (Peng *et al.*  
155 2005; Fatka *et al.* 2012), however as Neal and Hannibal (2000) pointed out, the rate of expansion  
156 varies intraspecifically and cannot be used to distinguish species. The usefulness of the new features  
157 described herein to distinguish species is currently unknown as these features have not been  
158 described in other species of *Sphenothallus*, and further work on new material is required to  
159 | understand the levels of intraspecific variation within this genus.

160  
161 *Material and occurrence.* 50 incomplete specimens were extracted from a coastal cliff section  
162 exposing the uppermost part of the Tullig cyclothem and the base of the Kilkee cyclothem of the  
163 Central Clare Group. The Tullig cyclothem is defined as the lithological unit immediately overlying  
164 the Gull Island Formation, with the upper boundary defined by the middle of three *Reticuloceras* cf.  
165 *stubblefieldi* ammonoid bands (Wignall and Best 2000), which also marks the base of the overlying  
166 Kilkee cyclothem. Rider (1974) initially defined the base of each cyclothem as 'the base of the black  
167 shale interval at the boundary between the sandy deposition of the cyclothem below and the clay  
168 deposition of the cyclothem above'. We favour Rider's initial definition and therefore place the

169 | *Sphenothallus* horizon at the base of the Kilkee cyclothem, which is 25–100cm below the first  
170 | *Reticuloceras* horizon.

171

172 | *Description and remarks.* The new fauna shows examples of typical *Sphenothallus* features as  
173 | described and illustrated throughout the literature (e.g. Mason and Yochelson 1985; Van Iten *et al.*  
174 | 1992; Peel 2021) including, gently expanding thecae, clonal budding, transversely ridged and  
175 | wrinkled surfaces, thickened lateral margins, lamellar layering, diagonal fractures in test and the  
176 | presence of closely associated holdfasts, although no specimens were found attached to holdfasts  
177 | (Fig. 2). The Irish specimens show, however, several diagnostic features, notably flat sides and  
178 | ‘angles’, sigmoidal cross-sections and ‘railtrack junction branching’. These three new characters are  
179 | described below.

180 | The material provides evidence of the development of flat sides in the adult theca. These flat  
181 | sides are not immediately obvious in many specimens as they are developed on the lateral margins  
182 | only and are rarely seen in bedding plane views. In some of the specimens the test is preserved such  
183 | that it falls out as a separate piece when the specimens are split along bedding planes (Fig. 3). They  
184 | preserve the organo-phosphatic tube (dark shiny outer layer) with very obvious flat lateral sides as  
185 | well as the development of diagonally opposed thickened ‘angles’. The internal part shows some  
186 | layering and may have been rigid during life based on the preservation of some sections of test  
187 | preserved rotated at a very high angle to bedding, such that the flattened part of the test is  
188 | perpendicular to bedding, indicating they have not been flattened after burial. The thickened lateral  
189 | margins commonly described in *Sphenothallus* warrant further study, because in the adult  
190 | specimens displayed here (Figs. 3 and 4) they do not appear as thickened curved margins (see  
191 | Stewart *et al.* 2015, fig. 3 for an example from a juvenile Cambrian specimen) but clearly form sharp  
192 | ‘angles’ on opposite lateral margins of the test. It is also clear that this is not a compactional or  
193 | collapse feature formed from curved thickened margins but is an original growth feature of the test.

194 | Two specimens of *Sphenothallus* show examples of a new type of branching, termed ‘railtrack  
195 | junction branching’ herein. In this type of branching the entire test appears to bifurcate across a  
196 | transverse midline and diverge at an angle of 25 degrees, duplicating the entire adult test, effectively  
197 | forming a ‘two-headed’ test (Figs. 5–7).

198 | Some of the specimens of *Sphenothallus* display distinct flat-sided lateral margins. These flat  
199 | sides are most clearly seen in transverse cross-sections (Fig. 3). The facets are clearly part of the so-  
200 | called thickened lateral margins and are only seen in certain examples where the margins are  
201 | exposed laterally. The facets are often oblique to bedding and may be connected to adjoining flat  
202 | sides by sharp, acute, obtuse or perpendicular angles or they may be connected to curved sides. The

203 flat sides sometimes show a left/right asymmetry in cross-section, in their connection to other  
204 surfaces, with connections to more pronounced curved surfaces on diagonally opposite  
205 (upper/lower) sides.

206 The identification of three new characters in a genus may be considered to require the erection  
207 of a new taxon, however we feel that some of the features we describe may have been overlooked  
208 in previous studies in other material (beyond the scope of the present study) and they can be best  
209 accommodated in an amended diagnosis for the genus.

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## Discussion

213 *Sphenothallus* has generally been described as a 'tube', 'tuboid' or 'flattened tube' with thickened  
214 lateral margins and demonstrably tubular forms have been clearly identified in juvenile specimens in  
215 the current fauna as well as by previous authors (Dzik *et al.* 2017). Peel (2021) described the main  
216 morphological features of *Sphenothallus* as 'the long slender phosphatic tube, originating from a  
217 small conical holdfast, and an opposing pair of lateral longitudinal thickenings of the elliptical tube  
218 wall'. However, apart from Dzik *et al.* (2017) and a brief comment in Mason and Yochelson (1985)  
219 there has been little attention paid to the ontogenetic change in morphology that occurs in  
220 *Sphenothallus*; the change from a circular cross-section to a flattened cross-section. It has been  
221 assumed by most other authors that this flattening is related to either sedimentary compaction or  
222 post-mortem collapse of a thin tubular thallus (Wang *et al.* 2003). Very few photographic images of  
223 cross-sections of the adult *Sphenothallus* have been published (Van Iten *et al.* 1992, fig. 1; Wang *et*  
224 *al.* 2003, fig. 8).

225 The adult Clare specimens display a distinctive, variably thickened test. This central thickened test  
226 must have been rigid prior to burial because segments of *Sphenothallus* aff. *carbonarius* preserved  
227 at high angles to bedding maintain the same thickened form as those preserved parallel to bedding  
228 but rotated at a high angle. This indicates that at least the central part of the test was rigid during  
229 life. In addition, two specimens show evidence of brittle fracture prior to burial, again this indicates a  
230 rigid thallus during life.

231 The wrinkled surfaces often described on *Sphenothallus* are well-developed in some of the Clare  
232 specimens. In some specimens transverse 'ripples' are present (Fig. 2.D), in others (Fig. 2.C), these  
233 are largely replaced by irregular 'wrinkles' with only vestiges of the transverse 'ripples' preserved.  
234 While it is easy to ascribe the wrinkling to a collapsed thin membrane, we suggest that the nature of  
235 the test is more complex and that these wrinkles or ripples are a primary feature of the  
236 *Sphenothallus* test, the function of which is unknown.

237 The flat-sided margins (Figs. 3 and 4) have not been described in *Sphenothallus* previously. They  
238 are only found in adult specimens and are variably developed. The flat margins are not connected to  
239 each other to form a rhombus in cross-section but are separated by the irregularly thickened median  
240 test. These flat sides bear some slight resemblance to the flat faces of conulariids, long considered to  
241 be phylogenetically related to *Sphenothallus* (see Van Iten *et al.* 1992). Conulariids have a  
242 tetrahedral (or rarely trihedral or hexahedral test (Sendino *et al.* 2012) composed of (usually) four  
243 flat triangular sides which formed an inverted pyramidal test in life. In cross-section they are usually  
244 square, however Sandino *et al.* (2012) demonstrated that torsion during growth could produce  
245 asymmetrical forms in the Ordovician conulariid *Metaconularia anomala*. Significantly, 56% of their  
246 studied specimens showed sinistral torsion when viewed from the apex, producing a twisted  
247 rhomboid shape in cross-section. As the apex end is unknown in most of the *Sphenothallus*  
248 fragments direct comparison with sinistral or dextral torsion is not possible. However, it is feasible  
249 that growth torsion could explain the shape of some of the flat-sided, sigmoidal *Sphenothallus* cross-  
250 sections described herein. Both *Sphenothallus* and conulariids have been assigned to the polyps of  
251 medusozoan Cnidaria as they both share a similar composition (lamellar, organo-phosphatic test)  
252 and the presence of schotts; in addition *Sphenothallus* is known to have reproduced by clonal  
253 budding.

254 It is therefore tempting to suggest that the presence of flat sides in *Sphenothallus* may be  
255 another indication of the phylogenetic connection between conulariids and *Sphenothallus*. However,  
256 it is difficult to explain how the flat sides are only partially developed, i.e. on lateral margins only and  
257 irregularly at that, and the extent of the flat sides towards the aperture is unknown. The nature of  
258 the apical-? openings of the *Sphenothallus* specimens described herein is unknown.

259 Tube flattening of a thallus wall on death by collapse or shrinkage is equally unlikely to produce  
260 the preserved fossilized forms, which are very consistent. Sigmoidal cross-sections have not been  
261 described previously for *Sphenothallus* and it would be easy to dismiss this shape as a result of  
262 compaction or flattening, however the preservation of the Clare specimens (Fig. 3) leaves little doubt  
263 that it is an original growth feature. While it may be that torsion during growth could produce some  
264 of the cross-sectional shapes displayed herein, the changing ontogenetic variability in the shape of  
265 *Sphenothallus* means that is difficult to confirm. It is clear however that the flat sides, 'angles' and  
266 sigmoidal cross-section are intimately linked.

267 It may be that the broad similarity between the flat sides, sharp angle and the evidence for  
268 torsion may be evidence for atavism. Atavism is the occurrence of ancestral traits long thought to  
269 have been lost in the phylogenetic lineage. These characters which, are known in conulariids, may  
270 derive from a common ancestor. Geux (2001) hypothesized for Mesozoic ammonites that sub-lethal

271 stress during extinction events favoured primitive looking forms which are similar to remote  
272 ancestors. It may be that the stress of rapidly changing sea-levels in restricted basins (which appears  
273 to have driven ammonoid evolution during the Pennsylvanian) also triggered a particular atavism in  
274 *Sphenothallus*. However, it is unclear what the evolutionary advantage of the flat sides and sharp  
275 angles could have been, or why this one particular glacio-eustatic sea-level change recorded in the  
276 rocks of the Kilkee cyclothem should have triggered it.

277 The 'railtrack junction branching' could be dismissed as two adult specimens overlying each other  
278 (twice), but the preservation leaves little doubt that such an explanation is not tenable as it would  
279 require an extraordinary coincidence of overlying that is not supported by the evidence in the  
280 several specimens showing the feature (Figs. 5–7). This ability to generate replicas of adult tests by  
281 'simple' splitting is a form of cloning. It may be that the conditions were stressful and this type of  
282 cloning made reproduction much quicker, speeding up population replacement. However, the size of  
283 some specimens (12cm) would suggest that they were able to reach a mature length successfully,  
284 although the amount of time it took to achieve maturity is unknown.

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### Conclusions

288 Previously undescribed features of *Sphenothallus*, including, flat lateral sides, marginal 'angles'  
289 sigmoidal cross-sections and 'railtrack junction branching' demonstrate a morphological plasticity in  
290 this enigmatic cnidarian genus. The flat lateral sides and marginal angles may be comparable to the  
291 flat sides and corners of conulariids, with which they have commonly been phylogenetically linked.  
292 However, an exact comparison cannot be made as the flat sides and angles are only developed on  
293 two sides in *Sphenothallus*. The development of flat sides and marginal 'angles' is coincident with  
294 the development of a sigmoidal cross-section. This sigmoidal shape may be a modification of an  
295 underlying bilaterally symmetrical bauplan, possibly the result of the development of flattened sides  
296 which are usually rotated with respect to the median thallus surface. This may represent growth  
297 torsion, similar to that described elsewhere for conulariids. The development of these features may  
298 be a rare example of atavism in the fossil record.

299 'Railtrack junction branching' is a newly described form of branching for *Sphenothallus*, that  
300 appears to allow duplication of an adult thallus. The mechanism of how this happens is unknown,  
301 however it is a form of cloning, which could have significant survival value in a stressful  
302 environment.

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311

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446 Figure captions

447 Fig. 1—(A) Map of location in Ireland. (B) Regional geology indicating *Sphenothallus* location site. (C)

448 Local stratigraphy. \* indicates *Sphenothallus* horizon. ALPORT = Alportian regional substage; Amm.

449 Biozone = Regional ammonoid biozones.

450

451 Fig. 2—*Sphenothallus* aff. *carbonarius* from the Central Clare Group, County Clare, Ireland. (A)

452 NG:F35396; showing the typical gently expanding lower section. Scale bar = 5cm. (B) NG:F35397;

453 showing mature *Sphenothallus* aff. *carbonarius* with attached budding immature daughter tube

454 (arrow). Scale bar = 4mm. (C) NGF:35398; showing faint transverse bands on thallus as well as

455 wrinkling. Scale bar = 3mm. (D) NG:F35399; showing well-developed transverse bands with no

456 wrinkling. Scale bar = 3mm. (E) NG:F35400; example of diagonal fractures in thallus. Scale bar =

457 1mm. (F) NG:F35401; probable *Sphenothallus* aff. *carbonarius* holdfast. Scale bar = 2mm.

458

459 Fig. 3—A—D; NG:F35402—NG:F35405. Examples of tranverse cross-sections through *Sphenothallus*

460 aff. *carbonarius* tests from west Clare, Ireland. Note the flat oblique lateral sides with thickened

461 diagonally opposite corners/angles and sigmoidal appearance. Black arrows indicate diagonal

462 thickened angles, white arrows indicate flat lateral sides. Scale bar = 1mm.

463

464 Fig. 4—Outline comparison drawings of six *Sphenothallus* aff. *carbonarius* -cross-sections displaying

465 variable but broadly sigmoidal shape with flat edges and 'angles'. Not to scale.

466

467 Fig. 5—NG:F35406 (A). NG:F35407 (B). Two specimens of *Sphenothallus* aff. *carbonarius* from

468 County Clare, Ireland, displaying 'Railtrack junction branching'. Scale bar = 5mm. Inset boxes A,B

469 shown in detail in figures 6 and 7.

470

471 | Fig. 6—Inset box A from Figure 5. ‘Railtrack junction branching’ in *Sphenothallus* aff. *carbonarius*  
472 | from County Clare, Ireland. The entire adult splits in two and diverges resulting in a duplicated  
473 | thallus. Scale in mm.

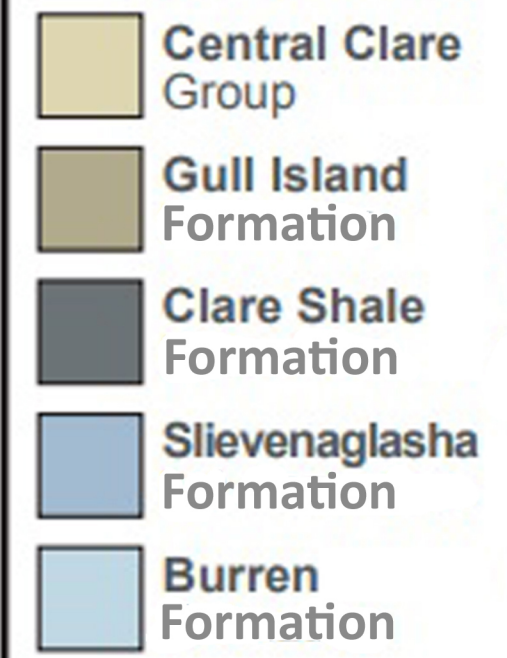
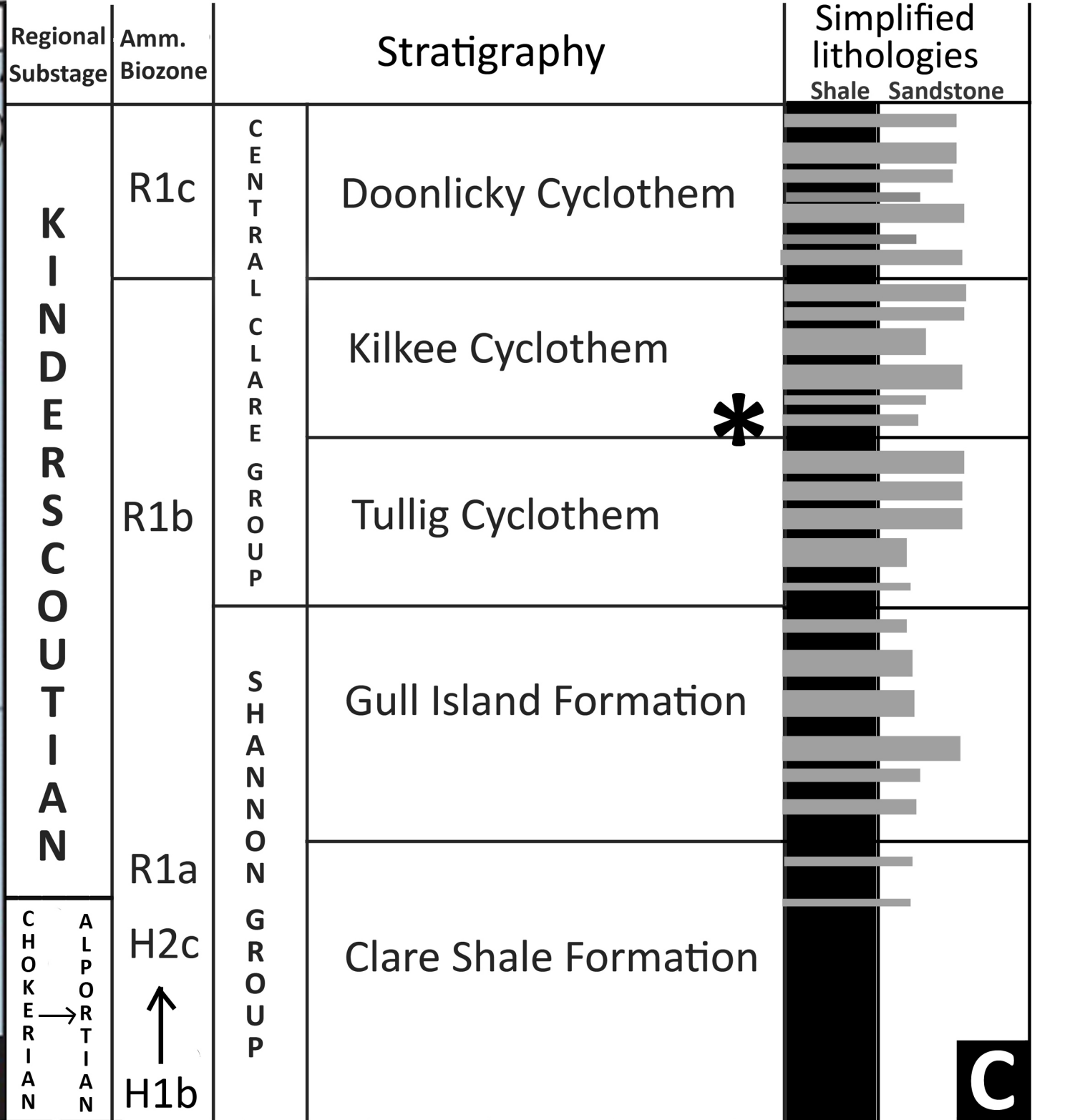
474

475 | Fig. 7—Inset box B from Figure 5. ‘Railtrack junction branching’ in *Sphenothallus* aff. *carbonarius*  
476 | from- County Clare, Ireland. The entire adult splits in two and diverges resulting in a duplicated adult  
477 | thallus. Scale in mm.

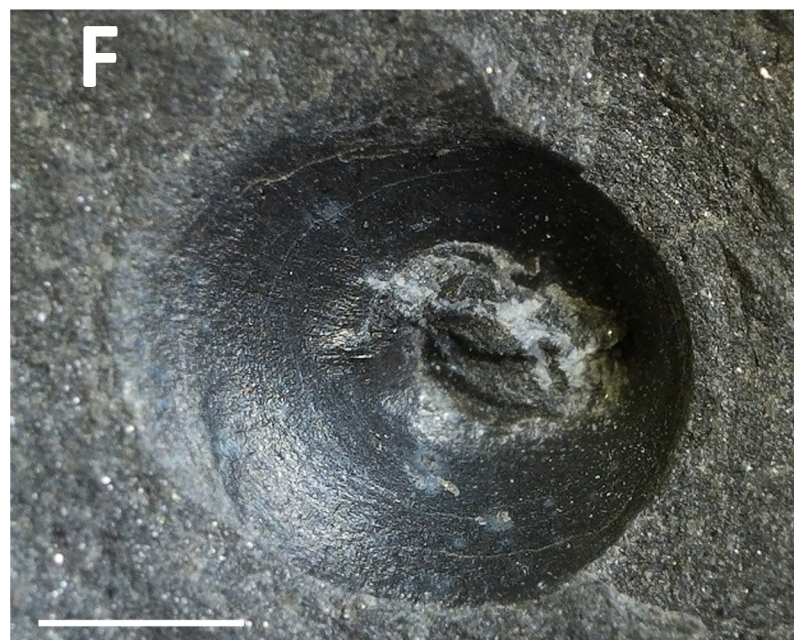
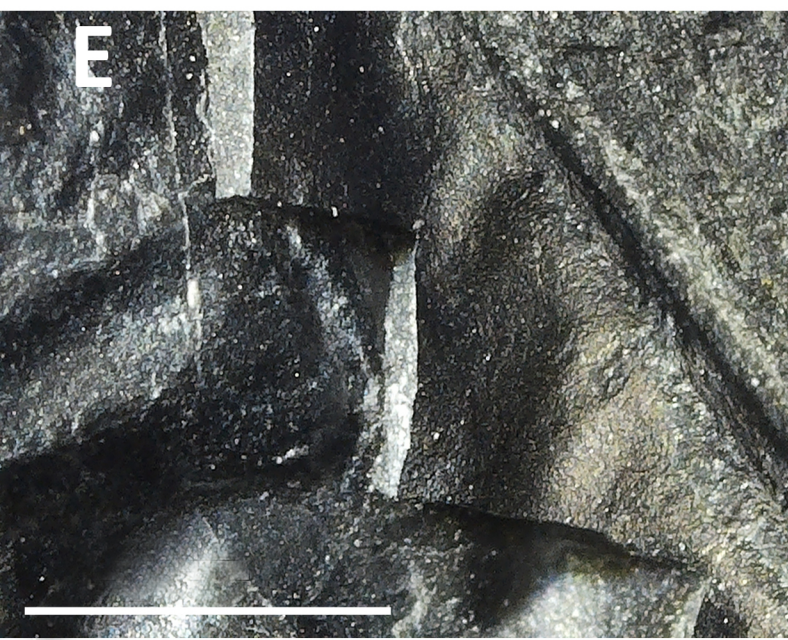
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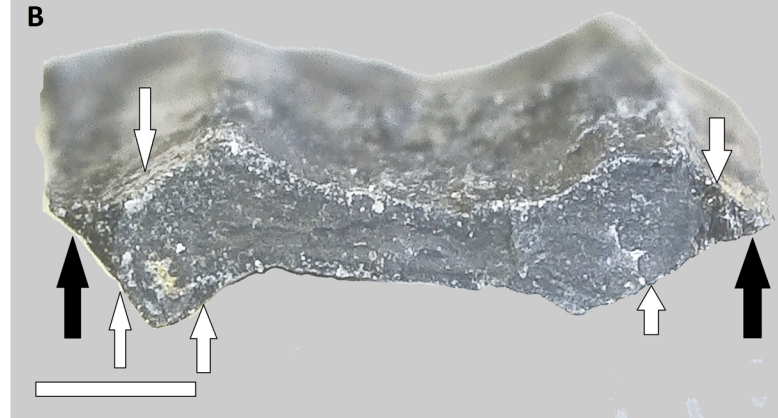
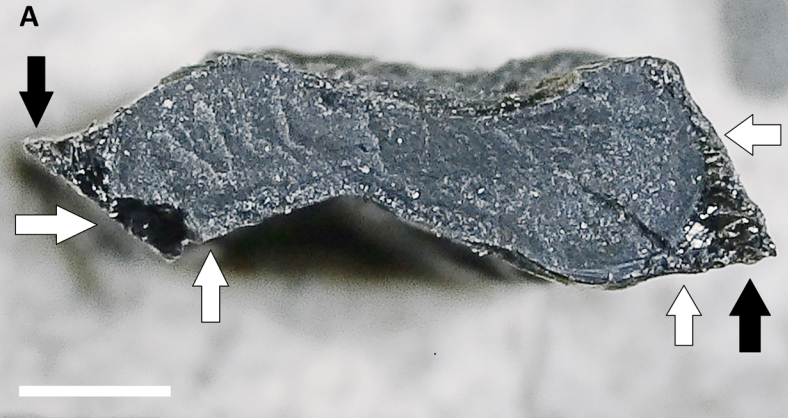
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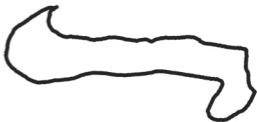




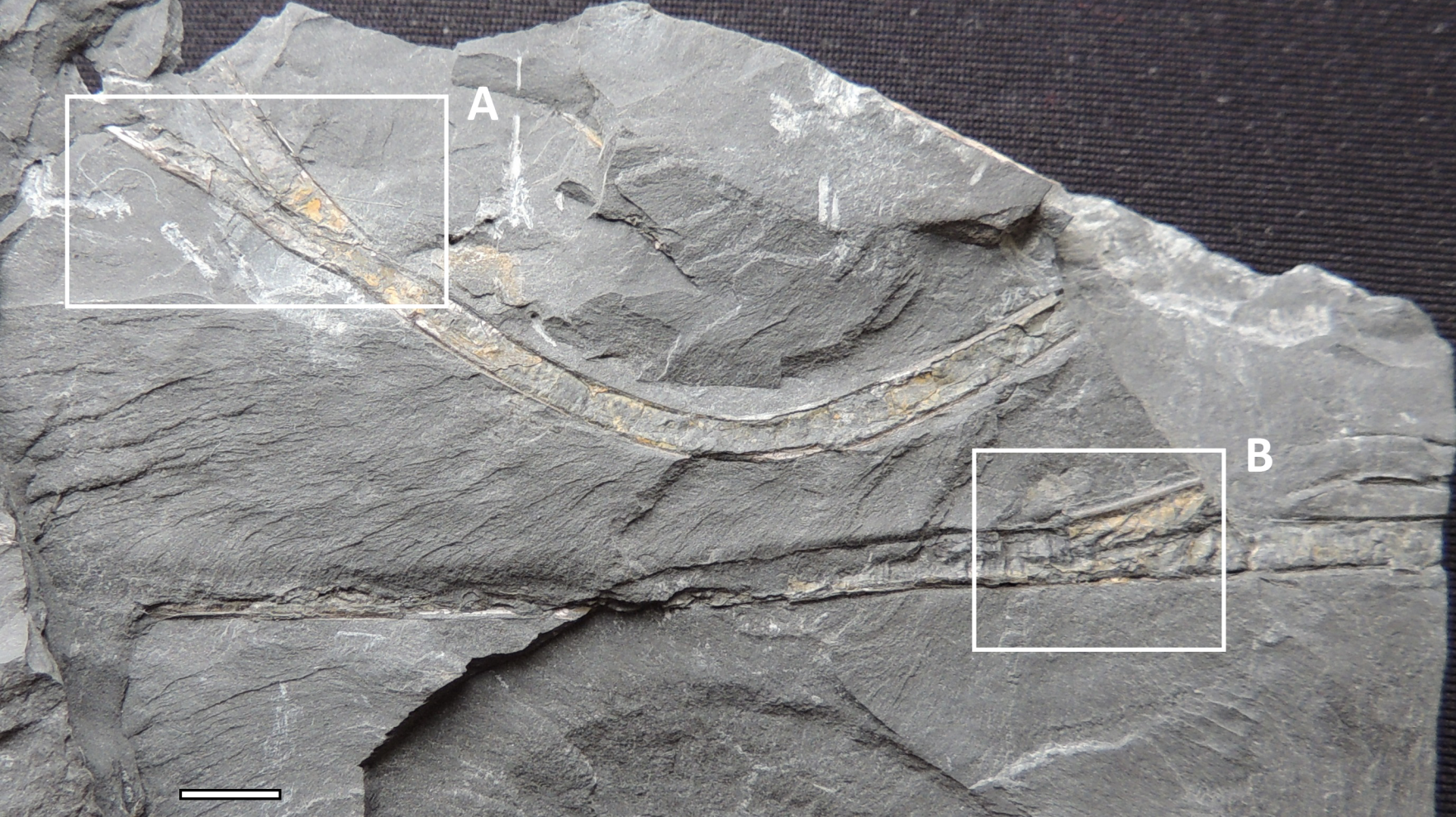






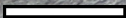






A

B















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