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Permian lobed Zoophycos as the product of the terrestrialization process: Behavioral innovation in the Tahkandit Limestone (Yukon River, Alaska, USA)

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# Palaeogeography, Palaeoclimatology, Palaeoecology

## Permian lobed Zoophycos as the product of the terrestrialization process: behavioral innovation in the Tahkandit Limestone Formation (Yukon River, Alaska, USA)

--Manuscript Draft--

<b>Manuscript Number:</b>	PALAEO-D-21-00864
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<b>Manuscript Region of Origin:</b>	North America
<b>Abstract:</b>	<p>Paleontological survey in the remote Yukon-Charley Rivers National Preserve in Alaska led to the discovery of lobed Zoophycos from the lower Tahkandit Limestone Formation (informally named Sandstone unit), an interval characterized by grayish-green glauconitic sandstone and conglomerate of coastal origin. The studied Zoophycos consists of a lobate skirt-like spreite bounded by a marginal tube. Smaller tongue-shaped lobes branch off from larger parent lobes that share the same tongue-like shape. Sedimentological features, together with body fossils and associated trace fossils ( Planolites, Chondrites ), indicate a shoreface habitat for the Zoophycos producer. This shallow-marine environmental setting is in contrast with the deeper bathymetries in which lobed Zoophycos are recovered in post-Paleozoic times. The producer of the lobed Zoophycos of the Yukon River is interpreted as a deposit-feeder that used sensory-driven, directed search for locating heterogeneously distributed trophic resources. The Zoophycos producer filled its burrow with Coprolus- like fecal pellets, possibly complementing deposit feeding with microbial gardening and/or food caching. Data presented here provide useful insight into the morphological evolution and bathymetric distribution of Zoophycos , suggesting two 'Golden Ages' for lobed Zoophycos: (1) Devonian-Permian and (2) Jurassic-Neogene. This stratigraphic distribution supports the important ecological role of major terrestrialization events, that are, the Palaeozoic expansion of land plants and the Mesozoic expansion of angiosperms. The consequent increased input of nutrients to coastal areas <del>has been</del> an important contributor to declining trends in porewater oxygen concentrations. This phenomenon favored adaptive traits to exploit nutrient-rich but oxygen-poor niches, among which the U-shaped marginal tube of lobed Zoophycos was an efficient adaptation to bring oxygenated water into low-oxygen substrates.</p>

## Highlights

- 1) This report adds new ichnological information to a poorly understood, and prominent, Permian rock unit that crops out along the Yukon River near the US-Canadian border.
- 2) This report illustrates the important role of terrestrialization events in driving the *Zoophycos* morphology.
- 3) Traditionally it ~~has been~~ interpreted that more stable or favorable environments such as offshore settings are conducive to the preservation of larger spirals of *Zoophycos*, and this study shows them preserved in more inshore environments.
- 4) This is one of the oldest known trace morphologies of *Zoophycos* with such a complex vertical structure.

1 Permian lobed *Zoophycos* as the product of the terrestrialization process: behavioral innovation in  
2 the Tahkandit Limestone Formation (Yukon River, Alaska, USA)

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26 ABSTRACT

27 Paleontological survey in the remote Yukon-Charley Rivers National Preserve in Alaska led to the  
28 discovery of lobed *Zoophycos* from the lower Tahkandit Limestone Formation (informally named  
29 Sandstone unit), an interval characterized by grayish-green glauconitic sandstone and conglomerate  
30 of coastal origin. The studied *Zoophycos* consists of a lobate skirt-like spreite bounded by a  
31 marginal tube. Smaller tongue-shaped lobes branch off from larger parent lobes that share the same  
32 tongue-like shape. Sedimentological features, together with body fossils and associated trace fossils  
33 (*Planolites*, *Chondrites*), indicate a shoreface habitat for the *Zoophycos* producer. This shallow-  
34 marine environmental setting is in contrast with the deeper bathymetries in which lobed *Zoophycos*  
35 are recovered in post-Paleozoic times. The producer of the lobed *Zoophycos* of the Yukon River is  
36 interpreted as a deposit-feeder that used sensory-driven, directed search for locating  
37 heterogeneously distributed trophic resources. The *Zoophycos* producer filled its burrow with  
38 *Coprolus*-like fecal pellets, possibly complementing deposit feeding with microbial gardening  
39 and/or food caching. Data presented here provide useful insight into the morphological evolution  
40 and bathymetric distribution of *Zoophycos*, suggesting two ‘Golden Ages’ for lobed *Zoophycos*: (1)  
41 Devonian-Permian and (2) Jurassic-Neogene. This stratigraphic distribution supports the important  
42 ecological role of major terrestrialization events, that are, the Palaeozoic expansion of land plants  
43 and the Mesozoic expansion of angiosperms. The consequent increased input of nutrients to coastal  
44 areas ~~has been~~ an important contributor to declining trends in porewater oxygen concentrations.  
45 This phenomenon favored adaptive traits to exploit nutrient-rich but oxygen-poor niches, among  
46 which the U-shaped marginal tube of lobed *Zoophycos* was an efficient adaptation to bring  
47 oxygenated water into low-oxygen substrates.

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52 1. Introduction

53 One of the most iconic, enigmatic and widespread ichnofossils is *Zoophycos*, a spreite  
54 structure comprising protrusive burrows of variable length and orientation, arranged in helicoid  
55 spirals with an overall circular, elliptical or lobate outline (Frey, 1970; Häntzschel, 1975;  
56 Löwemark and Schafer, 2003; Rodríguez-Tovar and Uchman, 2004; Löwemark et al., 2005;  
57 Kotake, 2014; Löwemark, 2015). *Zoophycos* has been a subject of scientific interest since the 19<sup>th</sup>  
58 century, when Johann Gotthelf Fischer von Waldheim (1811) first described *Zoophycos* as  
59 *Umbellularia logimna* and interpreted it as a fossil plant (Baucon et al., 2012; Bessudnova, 2013).  
60 The botanical hypothesis of *Zoophycos* was prominent in the 1800s, e.g., the influential researcher  
61 Brogniart (1828) introduced it as *Fucoides circinnatus* (Plička, 1968). The botanist Massalongo  
62 (1851) established the genus *Zoophycos*, supporting the botanical origin of the trace fossil. The  
63 botanical interpretation of *Zoophycos* was still popular in the 1900s (e.g., Barsanti, 1902), whereas  
64 Kryschtofowitsch (1911) interpreted *Zoophycos* from eastern Siberia as a trace fossil. The  
65 ichnological interpretation of *Zoophycos* gained increased support by the 1950s (e.g., Seilacher,  
66 1954), although Plička (1968) interpreted it as fossil prostomia of sabellids.

67 Despite over 190 years of studies on *Zoophycos*, its taxonomy, tracemaker and ethology, as  
68 well as its palaeoenvironmental significance, remain still mostly unresolved (Olivero, 2007;  
69 Löwemark, 2015; Zhang et al., 2015b; Monaco et al., 2016). No extant organism has been observed  
70 producing incipient *Zoophycos* (Zhang et al., 2015b). Sipunculids, polychaete annelids, arthropods  
71 and echiuran worms ~~have been~~ proposed as possible producers of *Zoophycos* (Kotake, 1992;  
72 Rodríguez-Tovar and Uchman, 2004). Recently proposed explanations for *Zoophycos* include (1)  
73 deposit feeding, (2) detritus feeding, (3) refuse dumping, (4) caching surface material and (5)  
74 gardening microorganisms (Kotake 1989; Bromley and Hanken 2003; Löwemark et al., 2004;  
75 Olivero and Gaillard 2007; Löwemark, 2015; Monaco et al. 2016; Zhang et al. 2015a; Giannetti et  
76 al. 2017). This Phanerozoic ichnotaxon has a widespread and global occurrence in the geological  
77 record, appearing first in the Cambrian (Jensen 1997; Sappenfield et al. 2012) and continuing

78 through the Quaternary (McGugan 1963; Logan and McGugan 1968; Löwemark and Schäfer 2003;  
79 Seilacher 2007).

80 Two interesting macroecological trends characterize *Zoophycos* (recently reviewed by Zhang  
81 et al. 2015b). Firstly, this ichnotaxon shifts from more proximal, shallow environments in the early  
82 Phanerozoic (Paleozoic) to more distal, closer to the continental rise, settings in the Mesozoic and  
83 finally to the deeper, bathyal realm in the Palaeogene to recent times (Zhang et al. 2015b). This  
84 habitat migration ~~has been~~ interpreted as a response to biotic pressures, particularly related to global  
85 biodiversity expansion after the Permo–Triassic, Triassic–Jurassic and Cretaceous–Paleogene mass  
86 extinctions (Olivero 2003; Knaust 2009; Löwemark 2012) or redistribution due to  
87 paleogeographical reorganization of the continents (Martin 1996; Martin 2003; Martin et al. 2008).  
88 Parallel to these biotopic changes, an increase in complexity of the pattern in these trace fossils can  
89 be observed, from simple, small tubes arranged in circular or elliptical patterns to complex,  
90 spiralling multi-branched and lobated structures (Zhang et al. 2015b). While the simple  
91 morphotypes are prevalently Paleozoic, more elaborated structures appeared from the Mesozoic to  
92 dominate the Cenozoic deep-marine record (Zhang et al. 2015b), with structural lobes oriented in  
93 different directional planes (Seilacher 1974, 2007). As such, lobed *Zoophycos* are rare in the  
94 Palaeozoic but common in post-Palaeozoic times.

95 This study reports an unusually lobate *Zoophycos* from the early Permian Tahkandit   
96 Limestone Formation (*sensu* Beauchamp, 1995) of the Yukon–Charley Rivers National Preserve,  
97 east-central Alaska. These traces numerous vertically oriented whorls and marginal lobes, as it is  
98 usually found in Cenozoic traces, anticipating the evolution of these structures by at least ~50  
99 million years (Olivero 2003; Zhang et al. 2015b). Systematic studies on the trace fossils of the  
100 Yukon River and their paleoenvironmental significance are lacking, with regard to the environment  
101 structure. Specifically, three major questions are posed: (1) what are the trace fossils of the  
102 Tahkandit Limestone Formation, a prominent but incompletely understood marine unit found



103 through the region? (2) What is the shape of the Yukon River *Zoophycos*? (3) Why lobed  
104 *Zoophycos* are found in the Permian Tahkandit Limestone Formation?

105


## 106 2. Methods

107 Data presented in this study were collected in 2010 during a National Park Service Alaska  
108 Region sponsored geological and paleontological survey of the Yukon-Charley Rivers National  
109 Preserve in east-central Alaska (Fig. 1A-B). The section described in this study (Fig. 2) partially  
110 overlaps with the type section of the Tahkandit Limestone Formation described by Brabb and Grant  
111 (1971, Fig. 6) and the outcrop is located on the west (left) side of the Yukon River just south of the  
112 ~~merge~~ of the Nation River (GPS: N65°10'915"; W141°42'205"), approximately 30 km west of the  
113 U.S. – Canada border. The lower section of the Tahkandit Limestone Formation, informally named  
114 Sandstone unit, is the subject of the bulk of this study. Tahkandit deposits are described in terms of  
115 overall architecture, sedimentology, and major paleontological characteristic, with particular  
116 attention on identified ichnocenoses. General overall geological data used in this study are provided  
117 in the geological map of Brabb and Grant (1965). Specimens referred here were collected on the  
118 ancestral homeland of the Han Hwëch'in Athabascans and are housed at the Perot Museum of  
119 Nature and Science, Dallas, Texas. The morphology of *Zoophycos* is described according the  
120 terminology of Olivero (2003).

121

## 122 3. Geological Setting

123 The rocks in this study accumulated at the margin of Ishbel Trough and belong to the poorly  
124 defined Tahkandit Limestone which comprises outer shelf to basinal carbonates, sandstones, and  
125 shales (Bamber and Waterhouse, 1971; Beauchamp, 1995). In the Charley River and Eagle  
126 quadrangles (Fig. 1B), a major unconformity that represents the latest Devonian, Carboniferous, and  
127 basal Permian, separates the Devonian Nation River Formation (Brabb 1967; Brabb and Churkin  
128 1967; Scott and Doher 1967; Gehrels et al. 1999) from the overlying Permian Tahkandit Limestone

129 deposits. The Nation River beds exposed at the locality discussed here are represented by 16 meters  
130 of deposits characterized by ~~alternated~~ siliciclastic beds and finely laminated, organic-rich shale.  
131 Both the Nation River and the Tahkandit Limestone formations ~~have been~~ folded by a relatively  
132 small ~~anticline~~ structure and consequently affected by vertical normal faulting; consequently,  
133 Tahkandit deposits show a dip of 62 degrees toward the north-west. The Tahkandit Limestone  
134 ~~Formation~~ (Fig.1) ~~has been~~ informally divided into two lithostratigraphic unit, the basal Sandstone  
135 unit, and the overlying Limestone unit (Brabb and Grant 1971). The lower interval is represented by  
136 approximately 15 meters of grayish-green, glauconitic sandstone and conglomerate consisting  
137 primarily of chert and quartz grains. Brachiopods are by large the most abundant fossils, whereas  
138 bivalves, corals, arenaceous foraminifera, and bryozoans are scarce. The occurrence of the  
139 brachiopods *Yakovlevia mammata* and *Thamnosia* sp. as well as trilete spores, bisaccate pollen  
140 grains, hystrichosphaerids, and megaplant remains in the glauconitic sandstones at the top of the  
141 lower unit (Brabb and Grant 1971, and references therein, this study) support an Early Permian  
142 (Cisuralian) age and shallow marine to estuarine/tidal environments. Brabb and Grant (1971) also  
143 reported structures “similar to *Zoophycos* sp.” and “the so called *Spirophyton* sp.” from this interval  
144 and confirm that such structures are widely distributed in rocks of Pennsylvanian and Permian age  
145 in the Yukon territory (Nelson 1961). Sandstone and conglomeratic beds (Fig. 2B) of the lower unit  
146 grade conformably into very pale, relatively sand- and glauconite-free limestone that forms cliffs  
147 and pinnacles typical of the morphology of the area. At a microscopic scale, the bioclastic limestone  
148 is a **packstone** with fragments of brachiopod and thin-shelled bivalves, bryozoans, and foraminifera.  
149 Finally, the Tahkandit Limestone ~~Formation~~ is overlain by the Glenn Shale which represents the  
150 entire Middle Triassic – Early Cretaceous interval and consists primarily in grayish-black  
151 carbonaceous shale with minor siltstone and quartzite. 

152

153 4. Sedimentology and Paleontology

154 The basal contact between the Nation River and Tahkandit Limestone formations is only  
155 partially exposed (Fig. 2A): however, the sharp juxtaposing of dark, plastic clay and well sorted,  
156 glauconitic sandstones clearly mark the boundary between the two formations and is here used as 0  
157 datum for the facies description (Fig. 3). Based on the lithological and sedimentological  
158 characteristics, paleontological data, and fossil trace assemblages, depositional facies are identified  
159 in the type section of the Tahkandit Limestone Formation as follows.

160

#### 161 4.1 Foreshore Facies (F)

162 This facies association is represented by massive, tabular conglomerate grading upward into  
163 gravelly sands (Fig. 3). Single beds range in thickness between 20 and 45 cm and generally display  
164 sharp-erosional base floored by extensively bioturbated, coarse gravel to coarse pebbly sandstone.  
165 These deposits are very well sorted, without any coaly fragment nor sandy or muddy matrix, and  
166 rare shell fragments. With minor exceptions, conglomerates show pervasive secondary  
167 glauconization and carbonate cement. Burrowing structures are referred to the firm ground  
168 ichnogenera *Conostichus*, *Bergaueria* and *Skolithos*; vertical burrowing structures are generally  
169 robust, dwelling as deep as 80 cm into the underlying sandy deposits, and reach 5 cm in diameter.

170 The sedimentological and ichnological characteristics of this facies association suggest a high-  
171 energy coastal environment: the basal erosion surface is interpreted to be the result of wave  
172 ravinement that cut across shoreface to offshore deposits. Glauconite generally develops under  
173 oxygenated to slightly reducing conditions close to the sediment/water interface and is considered  
174 to represent a powerful (but not exclusive) indicator of stratigraphic condensation within marine  
175 sediments (Loutit et al. 1988; Kidwell 1991). Well-developed firm ground *Thalassinoides*,  
176 *Conostichus*, *Bergaueria*, *Planolites*, and *Skolithos* are here referred to the *Glossifungites*  
177 ichnofacies, which develops exclusively in firm, unlithified substrates such as dewatered muds or  
178 compacted sands. Relevant to this study is the occurrence at 9.6 m and 14.2 m of the measured  
179 section of plant remains, coaly fragments, and organic rich laminated bed that were observed and

180 sampled for palynological analyses. Such beds document subaerial conditions or the proximity to a  
181 non-marine source of sediments.

182

#### 183 4.2 Shoreface Facies (S)

184 This sedimentary facies is arranged in fining-upward cross-laminated sandstone intercalated  
185 with conglomeratic beds (Fig. 3). Conglomeratic beds are sharp-based, largely bioclastic and with  
186 minor sandy matrix: strata are tabular to low-angle cross-stratified, reaching individual maximum  
187 thickness of 30 cm. Finer-grained conglomeratic deposits are occasionally arranged in elongated  
188 lenses and display a rhythmic alternation with laminar sands, suggesting a possible wave to tidal  
189 influence during deposition. Alike conglomeratic deposits referred to facies F (Fig. 3), none of these  
190 bed display evidence of glauconization. Fossil remains are extremely abundant and represented by  
191 the brachiopods *Yakovlevia mammata*, *Thamnosia* sp., and *Megousia* sp., which account for the  
192 80% of the deposits and are also found in undisturbed life position/assemblages. No ichnofossils  
193 have been observed in finer-grained conglomeratic deposits, with the exception of *Skolithos* traces  
194 in a single lenticular bed (12.1 m in the measured section). Sandstones are fine- to medium-grained,  
195 high-angle cross-bedded lamination, and display an overall fining upward trend with minor silty  
196 deposits. In addition, coarser sandy and bioclastic beds characterized by sharp and erosive basal  
197 contact and scattered with gastropod and bivalve shell fragments (1 cm in average) have been  
198 observed and interpreted as tempestite deposits. Sandstones are also characterized by a rich and  
199 diverse soft-ground related fossil trace assemblage which are referred to the *Skolithos* ichnofacies.  
200 Identifiable ichnogenera traces include *Skolithos*, and *Bergaueria*. The central shoreface facies  
201 (*sensu* Antia et al. 1994) shows a high proportion of shells, a broad range of sediment size (from  
202 fine-grained sandstones to pebble) and marked diversity in sedimentary structures (Fig. 4). The  
203 *Skolithos* ichnofacies is indicative of relatively high levels of wave or current energy characterized  
204 by changes in deposition rates and physical reworking of sediments. Graded storm beds, fossil

205 distribution and the *Skolithos* ichnofacies are here considered as indicative of upper shoreface  
206 deposits.

207

#### 208 4.3 Upper Shoreface Facies (US)

209 This facies primarily comprises fine-grained sandstone and silt with large scale, low-angle,  
210 hummocky cross-stratification (1–2 meters in average), parallel lamination and an overall fining-  
211 upward trend (Fig. 3). Sandstone beds are also characterized by extensive planar and sub-planar  
212 fossil traces, whereas no macroscopic shell remains ~~have been~~ observed. No mudstone intercalation  
213 ~~has been~~ observed, whereas glauconitic intervals are recurrent. *Zoophycos* traces (Fig 5) are by far  
214 the most frequent of this facies: despite the vast majority range between 35 and 45 cm in size,  
215 several intervals preserve feeding traces that exceed 140 cm in diameter, with a measured maximum  
216 planar extension of 165 cm. Other identified soft-ground ichnogenera include *Thalassinoides*,  
217 *Planolites*, and *Chondrites* and therefore, together with *Zoophycos* are referred to the *Cruziana*  
218 ichnofacies. Sedimentological data suggest a lower shoreface environment with intense wave  
219 influence on sediment distribution and events of abrupt decrease in sediment supply (or sediment  
220 by-pass). The *Cruziana* ichnofacies develops on soft-grounds of shallow-marine, permanently  
221 subtidal, and unconsolidated substrates. The ichnogenus *Zoophycos* has an extremely broad  
222 paleobathymetric range (Zheng et al., 2015b), but are commonly restricted to intervals characterized  
223 by fine, muddy sands and less effected by turbidity flows or significant bottom currents.  
224 Lithological characteristic and the occurrence of *Zoophycos* are consistent with deposition in  
225 circalittoral sites.

226

#### 227 4.4 Offshore Facies (O)

228 This facies consists of exclusively silt- and mud-dominated deposits, showing thin-bedded  
229 laminar stratification (between 3 and 25 mm). There are no wave-formed structures, and intense  
230 bioturbation in mudstone intervals (tubular structures are identifiable) obliterated all sedimentary

231 structures. This facies occurs in close association with finer deposits of shoreface deposits (Fig. 4).  
232 When facies O (Fig. 2C) deposits overly very coarse beds of other shallower facies, the transition is  
233 abrupt, suggesting a rapid shift in depositional condition. No fossil remains ~~have been~~ observed in  
234 this facies. Fine-grained siltstone and mudstone beds present in this facies suggest inner shelf  
235 environment, unaffected by the action of waves and major currents.

236

## 237 5, Morphology of the *Zoophycos* from the Yukon River

238 *Zoophycos* start occurring at 20 cm above the base of the section together with a rich  
239 ichnoassemblage of *Conichnus* (between other traces, Fig. 4 and Table 1). Two different  
240 morphotypes ~~have been~~ observed, i.e., form A (unlobed) and B (lobed). The morphotypes share  
241 common architectural and textural features. Specifically, both morphotypes consist of a thin layer of  
242 bioturbated sediment (lamina or spreite *sensu* Olivero and Gaillard, 2007 ; see also Zhang,  
243 2015).The lamina is helically coiled around a central axis and tapers vertically from a flat area to an  
244 apical point (apex). As such, the 3D structure is roughly conical. The maximum number of whorls  
245 is 2. The lamina is characterized by arched structures (primary lamellae) that represent the positions  
246 of a single forming tunnel moving though the sediment (see Olivero, 2003). There is no evidence of  
247 secondary lamellae, i.e., arched structures located in the spaces between the primary lamellae  
248 (Olivero, 2003). When preserved, the burrow fill is darker than the host rock and consists of  
249 millimetric ellipsoidal pellets. The structures, especially the lobed form B, frequently display a  
250 marginal tube. Many traces present the typical central tube which marginally spread creating a fan-  
251 like lobe of coarser (Fig. 5), more spaced spreiten and a more dorsally pronounced axis of coiling,  
252 which forms a sort of proximal “stem” (Fig. 5; e.g. Oliviero and Gaillard 2007). The depth of this  
253 axis can range to 20 cm and up to two coils can be counted in the three dimensionally preserved  
254 traces (Fig. 5). The two morphotypes differ in the shape of the lamellae and of the lamina outline.

255

### 256 5.1 Form A (unlobed; Fig. 5A, E, F).

257 Form A comprises several J-shaped lamellae that form the spreite. Each lamella departs  
258 from a common apical point and follows a sub-parallel arrangement with regard to the other  
259 lamellae. The lamellae arrangement results in a roughly circular outline of the lamina. The studied  
260 specimens display sinistral coiling, but dextral coiling cannot be excluded because of limited  
261 number of specimens observed. No secondary lamellae ~~have been~~ documented. The diameter of the  
262 structures is approximately 20 cm, although the fragmentary nature of the material precludes an  
263 exact estimate of the lamina size.

264

## 265 5.2 Form B (lobed; Fig. 5B, C, D)

266 Form B consists of several U-shaped primary lamellae that form the spreite. The lamellae  
267 arrangement results in a skirt-like lamina with lobate outline. The lamina (Figs. 5, 6) is bounded by  
268 a marginal tube (Fig. 5B, C). Centrally to the marginal tube, the primary lamellae develop  
269 according to the same planar orientation the U-shaped structure. While secondary lamellae are  
270 absent (Fig. 6A, B), an irregular surface is present on some traces (Fig. 6C). Large unbioturbated  
271 areas are found in-between adjacent lobes (Fig. 5B). Some lobes are tongue-like, being long and  
272 distinct from the rest of the lamina (Fig. 5C). Smaller tongue lobes (child lobes) can branch off  
273 from larger tongue lobes (parent lobes) (Fig. 5C). The axis of the child lobe in Fig. 5C forms an  
274 angle of 84° with the axis of its parent lobe. The structures measured at this section (Fig. 3) range in  
275 size from 140–160 cm.

276

## 277 6. Taxonomy, tracemaker and behavior of the Yukon River *Zoophycos*

278 The studied spreite structures share the major architectural elements with the ichnogenus  
279 *Zoophycos*, which is characterized by (1) a spreite; (2) protrusive burrows of variable length and  
280 orientation, arranged in helicoid spirals; (3) circular, elliptical or lobate outline; (4) a marginal tube,  
281 which is often, but not always, present (Frey, 1970; Häntzschel, 1975; Kotake, 2014; Löwemark et  
282 al., 2005; Löwemark and Schafer, 2003; Rodríguez-Tovar and Uchman, 2004; Löwemark, 2015).

283 As such, the studied structures are attributed to the ichnogenus *Zoophycos*. The morphological  
284 heterogeneity of *Zoophycos* is so large that, perhaps, it would be better to refer to a ‘*Zoophycos*  
285 group’ rather than to a single ichnogenus (Uchman, 1999; see also Olivero, 2003). Early description  
286 of ichnoassemblages from estuarine Permian beds in the arctic (Miller, 1991) reported the  
287 occurrence of *Spirophyton*, an ichnotaxon characterized by spiral-like structures and opportunistic  
288 strategies (Bromley, 1996). Although superficially similar to *Zoophycos*, *Spirophyton* presents  
289 unlobed edges lacking marginal tubes (Jensen, 1997; Miller, 2003; Seilacher, 2007).  
290 Following Knaust (2004), no determination at the ichnospecies ~~have been~~ done for the studied  
291 specimens because of the poor ichnotaxonomic status of *Zoophycos*. However, the studied  
292 *Zoophycos* can be readily compared with the morphotypes described in previous studies.  
293 Accordingly, the here studied form A resembles morphotypes A and B of Olivero (2003), which  
294 present simple or very slightly lobate outline. Similarly, form A resembles the “cock-tail shaped  
295 spreiten with J-shaped primary lamellae” described by Zhang et al. (2015b). The cock-tail  
296 *Zoophycos* of Zhang et al. (2015) is typical of Palaeozoic nearshore to offshore settings. By  
297 contrast, the here studied form B resembles morphotype D of Olivero (2003), which is characterized  
298 by strongly lobate margins and lack of secondary lamellae. Morphotype D is typical of Late  
299 Cretaceous units deposited in deep slope to basin environments (Olivero, 2003). It should also be  
300 noted that the size range of the studied *Zoophycos* matches the width size range (140 – 160 cm) of  
301 the largest *Zoophycos* traces recorded in the Phanerozoic (Zhang et al. 2015b). According to Zhang  
302 et al. (2015b), the width of the *Zoophycos* spreite increased from 18 cm in the Lower Palaeozoic to  
303 43 cm in the Cenozoic.

304 Both forms of *Zoophycos* from the Yukon River are filled by elliptical pellets. These are  
305 interpreted as a **bioprint**, that is, the “tracemaker’s signature”, a set of characters that allow  
306 recognition of the producer (Kopaska-Merkel and Rindsberg, 2015). Because both forms of  
307 *Zoophycos* share the same bioprint, they plausibly shared the same tracemaker. A vermiform, soft-  
308 bodied producer is a viable hypothesis in light of the pellet-filled tunnels of the modern polychaete



309 *Nereis* (Kulkarni and Panchang, 2015). This hypothesis is also supported by the modern terebellid  
310 polychaete *Terebellides stroemi*, constructing inclined, *Rhizocorallium*-like spreite burrows with  
311 *Coprolus*-like faecal pellets (Knaust, 2013). The fecal pellets within the Yukon River *Zoophycos* fit  
312 with the characteristics of the ichnofamily Coprulidae, which comprises rounded, smooth or  
313 sculptured, structureless or structured coprolites and cololites (Knaust, 2020). Various animals  
314 produce Coprulidae, foremost polychaetes and other annelids, as well as enteropneusts, gastropods,  
315 bivalves, tunicates and insects (Knaust, 2020). Pellets are also associated with Bohemian  
316 Ordovician body fossils (Bruthansová and Kraft, 2003) and they are found in Paleozoic burrows as  
317 well (Uchman et al., 2005; Baucon et al., 2020). The excellent preservation of fecal pellets in the  
318 Yukon River *Zoophycos* suggests low-oxygen conditions in the interstitial waters, which are known  
319 to play a role in preserving fecal pellets (Podhalańska, 2007; Neto de Carvalho et al., 2016; Baucon  
320 et al., 2020).

321         The presence of pellets has also an important behavioral significance because it shows that  
322 the tracemaker actively filled its tunnels. According to the reviews of Löwemark and Schäfer, 2003  
323 and Löwemark et al., 2004, the behavioral models of *Zoophycos* are the (1) deposit feeder model;  
324 (2) detritus feeder model; (3) refuse dump model; (4) gardening model; (5) cache model. The  
325 morphology of the Yukon River structures is compatible with several of the proposed ethological  
326 models for *Zoophycos*, with specific emphasis on the deposit feeding, gardening and cache models.  
327 In the deposit feeder model, the tracemaker is a deposit feeder, feeding on the outer wall, and  
328 excreting its feces on the inner wall (e.g., Wetzel and Werner, 1981; see also the reviews of the  
329 *Zoophycos* models in Löwemark and Schäfer, 2003 and Löwemark et al., 2004). This model can  
330 explain the morphology of the Yukon River *Zoophycos*, with specific reference to the lobed form B.  
331 In fact, the general morphology of form B is compatible with a sensory-driven, directed search for  
332 heterogeneously distributed trophic resources within the substrate. Animals seek to maximize their  
333 net rate of energy intake, that is, the difference between energetic benefit and their energetic  
334 expenditure while searching for, handling, consuming, and digesting food (LaScala-Gruenewald et

335 al., 2019). To do so, they spend more time in food-rich areas than in areas with scarce resources,  
336 also benefiting from sensory information on local resource density (Mårell et al., 2002; Stenberg  
337 and Persson, 2005; Chapperon and Seuront, 2011; Sinervo, 2013). In this regard, the presence of  
338 vast unbioturbated areas between the *Zoophycos* lobes is compatible with areas with scarce  
339 resources. Tongue lobes and the wide angles between parent and child lobes are indicative of  
340 sensory-directed movement towards food-rich areas. Overall, these features suggest that the  
341 producer of the Yukon River *Zoophycos* developed movement patterns adapted to the distribution  
342 of food to maximize its net energy intake through time. It should also be noted that the construction  
343 of well-developed and defined lobes ~~has been~~ interpreted as either an explorative function of the  
344 tracemaker (as previously suggested) or the effect of avoiding an obstacle (Fig. 6D), like a coarser  
345 grain, in the sediment (Oliviero and Gaillard 2007; Gong et al. 2010).

346 In the detritus feeding model, the producer deposits fecal pellets in the sediment in order to  
347 remove them from the feeding area on the surface (Kotake, 1991). This model does not explain the  
348 presence of vast unbioturbated areas between lobes, the characteristic tongue lobes, and the wide  
349 angles between child and parent lobes. The detritus feeding model also does not explain the  
350 requirement of having an open U-shaped marginal tube, as shown by the Yukon River *Zoophycos*.  
351 A similar objection ~~has been~~ proposed by Löwemark et al. (2004). However, the detritus feeding  
352 hypothesis should be reconsidered in light of the similarity between *Zoophycos* form B and the  
353 incipient *Rhizocorallium* produced by the modern polychaete *Terebellides stroemi*, which feeds on  
354 suspended detritus (Moverley et al., 1986). In fact, *Terebellides stroemi* produces inclined, spreite  
355 burrows filled with *Coprolus*-like faecal pellets (Knaust, 2013).

356 According to the refuse dump model, the tracemaker is a deposit feeder sitting head-down in  
357 the burrow and introducing pelleted surface material as ballast to compensate for the material  
358 ingested and excreted at the surface (Bromley, 1991; see also the reviews of the *Zoophycos* models  
359 in Löwemark and Schäfer, 2003, and Löwemark et al., 2004). This model does not fit with the  
360 hypothesized fecal origin of the pellets of the Yukon River *Zoophycos*. Specifically, the pellets of

361 the Yukon River *Zoophycos* are very dark in colour, suggesting a high organic content which, in  
362 turn, may indicate a fecal origin. For instance, the fresh pellets of the modern polychaete  
363 *Heteromastus filiformis* display an organic content 2.4-fold higher than in the feeding zone  
364 sediment because of selective uptake of organic-rich matter (Neira and Höpner, 1994; see also  
365 Baucon et al., 2020). According to the gardening model, the producer feeds on detritus on the  
366 seafloor and deposits its fecal pellets in the sediment. Oxygenated water is pumped through the  
367 burrow along the marginal tube, allowing micro-organisms to thrive. The producer then feeds on the  
368 microbial content (Bromley, 1991; see also the reviews of the *Zoophycos* models in Löwemark and  
369 Schäfer, 2003 and Löwemark et al., 2004). In the cache model, the *Zoophycos* producer collects  
370 food during good times and stores it for bad times (Bromley, 1991; Miller III and D'Alberto, 2001;  
371 see also Löwemark and Schäfer, 2003 and Löwemark et al., 2004). The gardening and cache model  
372 only partially fit with the Yukon River *Zoophycos* because there is no evidence of feeding on  
373 previously stored material.

374 In sum, the morphology of the lobed *Zoophycos* of the Yukon River is suggestive of a  
375 deposit feeder that filled its tunnels with fecal pellets. Marine invertebrates commonly switch  
376 between different feeding modes, therefore, deposit feeding does not exclude gardening and caching  
377 behavior(s) using the fecal products of deposit feeding. The interpretation proposed for the Yukon  
378 River specimens does not necessarily apply to each and every *Zoophycos*, especially because the  
379 morphological heterogeneity of *Zoophycos* is large (Uchman, 1999; Olivero, 2003), which suggests  
380 a wide ethological heterogeneity.

381

## 382 6.1 The two Golden Ages of lobed *Zoophycos*

383 This report not only provides new stratigraphic data for a Permian rock unit that crops out  
384 along the Yukon River but contributes new insights on the macroevolutionary history of one of the  
385 most iconic and widespread ichnotaxon in paleoichnology. An Early Permian age for this section is  
386 supported by the co-occurrence of the brachiopods *Yakovlevia mammata* and *Thamnosia* sp. as well

387 as trilete spores, bisaccate pollen grains, hystrichosphaerids, and megaplant remains in the  
388 glauconitic sandstones as typically described for the Tahkandit Limestone Formation (Brabb and  
389 Grant 1971). Because of its Permian age, and lobed morphology, the *Zoophycos* form B occupies a  
390 place of prominence in the evolution of the ichnogenus, as defined by previous authors (Seilacher,  
391 1986; Bottjer et al., 1988; Olivero, 2003; Zhang et al., 2015b). According to these authors, three  
392 aspects of *Zoophycos* changed markedly across the Phanerozoic:

- 393 1. Habitat: *Zoophycos* is typically found in shelf deposits in the Palaeozoic, lower shelf-  
394 slope in the Mesozoic, and bathyal settings in the Cenozoic (Seilacher, 1986; Bottjer et  
395 al., 1988; Olivero, 2003; Zhang et al., 2015b; see also Baucon and Avanzini, 2008);
- 396 2. Tiering: *Zoophycos* shifted gradually from the shallow to deep tiers of marine substrates  
397 in the Phanerozoic (Zhang et al., 2015b).
- 398 3. Morphology: *Zoophycos* evolved from small, simple, helicoidal, rooster-shaped,  
399 circular/elliptical spreiten of one to two whorls without marginal lobes in the Palaeozoic,  
400 to large, complex, helicoidal, lobate spreiten of several whorls in the Cenozoic  
401 (Seilacher, 1986; Bottjer et al., 1988; Olivero, 2003; Zhang et al., 2015b)

402 The form B of the Yukon River *Zoophycos* fit well with the typical habitat of Palaeozoic  
403 *Zoophycos*, i.e., the sedimentological features associated with *Zoophycos*, together with the body  
404 and trace fossil content, indicate a shoreface setting. The studied *Zoophycos* provide no  
405 unquestionable evidence of tiering depth, although their excellent preservation may indicate a deep-  
406 tier nature. In fact, shallow-tier structures tend to be obliterated by bioturbation, whereas deep-tier  
407 structures tend to dominate an ichnofabric (Bromley, 1996). In addition, the preservation of pellets  
408 within *Zoophycos* suggests that the burrow system ~~has been~~ produced in low-oxygen conditions,  
409 which are usually (but not exclusively) associated with deeper tiers.

410 The most peculiar feature of the studied *Zoophycos* is the lobed morphology of form B. The  
411 *Zoophycos* form B described herein is a three-dimensionally arranged structure with complex,  
412 marginally lobed spreiten, morphologically similar to those described for Cenozoic bathyal

413 sediments (e.g. Monaco et al. 2016). To analyze the distribution of lobed *Zoophycos* through time,  
414 we used the “Phanerozoic *Zoophycos* database” (Zhang et al., 2015b: Supplementary Table S1), as  
415 a source dataset. This comprehensive dataset reveals two Palaeozoic sites with lobed *Zoophycos*,  
416 namely the Catskill Mountains (Devonian, USA) and Malý Rabštýn (Carboniferous, Czech  
417 Republic). The dataset ~~has been~~ implemented with the Carboniferous and Permian lobed *Zoophycos*  
418 of the Pramollo Basin (Italy-Austria) (Baucon and Carvalho, 2008; Baucon et al., 2015) and the  
419 here studied Yukon River ones. By contrast, sites with no information on the basic morphology of  
420 *Zoophycos* ~~have been~~ filtered out from the source dataset.

421 To evaluate the evolution of lobed *Zoophycos*, we calculated (1) the lobed ratio (Fig. 7A),  
422 that is the proportion between the number of sites with lobed *Zoophycos* and (2) the total number of  
423 sites with lobed *Zoophycos* (Fig. 7B). Although the oldest *Zoophycos* of the dataset is Cambrian in  
424 age, no lobed *Zoophycos* are documented before the Devonian (Fig. 7). The lobed ratio increased  
425 from the Devonian to the Permian, dropped in the Triassic, and increased again from the Jurassic  
426 onwards (Fig. 7B). Accordingly, two ‘Golden Ages’ of lobed *Zoophycos* are distinguished: (1)  
427 Devonian-Permian and (2) Jurassic-Neogene. Overall, lobed specimens were much ~~commoner~~  
428 the second interval than during Palaeozoic times (Fig. 7A). It should be noted that these two Golden  
429 Ages of lobed *Zoophycos* partially coincides with the first (Devonian) and the last (Cretaceous-  
430 Cenozoic) radiation of *Zoophycos*, which ~~have~~ previously ~~been~~ established by Zhang et al. (2015b).

431

## 432 6.2 Lobed *Zoophycos* as a product of terrestrialization

433 The two Golden Ages of lobed *Zoophycos* (Devonian-Permian and Jurassic-Neogene) are  
434 both linked with changes in nutrient dynamics. The widespread appearance of lobed *Zoophycos* is  
435 contemporaneous with the oceanographic changes that ~~have~~ occurred during the Middle Jurassic,  
436 when deep-sea bottom nutrient conditions were greatly improved by increased particulate organic  
437 carbon and dissolved organic carbon derived from surface plankton bloom (Zhang et al., 2015b). It  
438 should be noted that this event was followed by a major radiation of land plants in the Cretaceous,

439 which also increased the supply of nutrients to the oceans (Allmon and Martin, 2014). The  
440 increased shelf areas and plankton blooms ~~have been~~ hypothesized to have driven the high  
441 occurrence frequencies of *Zoophycos* in the Cretaceous–Cenozoic (Zhang et al., 2015b).  
442 Another profound change in nutrient cycling begun with the Paleozoic origin of wood in plants,  
443 permanently shifting the distribution of active carbon species within the global carbon cycle by the  
444 end of the Mississippian (Strother et al., 2010). This phase of the terrestrialization process has its  
445 roots in the Devonian (Givetian-Frasnian), with the rise of lignophytes (Strother et al., 2010;  
446 Kenrick et al., 2012). Large trees with well-developed rooting systems are unlikely to predate the  
447 Middle Devonian (Kenrick et al., 2012). Intriguingly, the earliest documented lobed *Zoophycos*  
448 dates back to the Givetian (Miller, 1979). The Devonian radiation of lobed *Zoophycos* coincides  
449 with the first *Zoophycos* radiation, which ~~has been~~ linked to the rise of deep-rooted plants (Zhang et  
450 al., 2015b). Before of the major intervals of diversification of land plants (Devonian expansion of  
451 land plants and the Cretaceous expansion of angiosperms), the supply of nutrients to the oceans by  
452 terrestrial runoff was lower than it was afterward (Allmon and Martin, 2014).

453         Contemporaneous events do not necessarily mean causality; therefore, a question might  
454 arise: How can nutrient enrichment favor the evolution of lobed *Zoophycos*? The answer is provided  
455 by the U-shaped marginal tube of *Zoophycos*, which represents an efficient adaptation to dwell into  
456 nutrient-rich but oxygen-poor substrates. Specifically, the increased input of nutrients to coastal  
457 areas ~~has been~~ suggested as an important contributor to declining trends in bottom water oxygen  
458 concentrations (Diaz and Rosenberg, 1995). Indeed, there is a known interaction between supply of  
459 nutrients, primary production, sedimentation and oxygen consumption (Rydberg et al., 1990).  
460 Consequently, from a macroevolutionary perspective, any global increase in seawater nutrients is  
461 expected to favor biological adaptations to cope with low-oxygen substrates. Among such  
462 adaptations, U-shaped burrows allow to efficiently induce the flow of oxygenated seawater within  
463 the substrate (Bromley, 1996). For this reason, *Zoophycos* with U-shaped tunnels are linked with  
464 poorly oxygenated conditions, whereas *Zoophycos* with J-shaped tunnels, connected with only one

465 opening to the seafloor, ~~have been~~ taken to suggest a well-oxygenated setting (Wetzel and Werner,  
466 1981; Gong et al., 2008). The two Golden Ages of lobed *Zoophycos* are separated by the Triassic,  
467 when a decline in the relative (Fig. 7A) and absolute (Fig. 7B) number of lobed *Zoophycos* is  
468 observed. This decline in lobed *Zoophycos* is plausibly explained by the effects of the end-Permian  
469 extinction on biodiversity and nutrient dynamics. In fact, the aridity of the Late Permian climate, the  
470 collapse of the peat mire ecosystem at the Permian-Triassic boundary and the protracted arid  
471 conditions during the Early Triassic reduced the terrigenous influx of nutrients into the ocean  
472 (Zharkov and Chumakov, 2001; Michaelsen, 2002; Benton and Newell, 2014).

473         The two Golden Ages of lobed *Zoophycos* take place in different environmental settings.  
474 The Yukon River *Zoophycos* well exemplifies this phenomenon, since its shoreface setting differs  
475 from the typical deep-sea environment of the Mesozoic and Cenozoic lobed specimens. Lobed  
476 forms of *Zoophycos* have a bathymetric range spanning from the lower shelf-slope in the Mesozoic  
477 to the bathyal realm in the Cenozoic. In particular, the here studied form B resembles the lobed  
478 *Zoophycos* without secondary lamellae described by Olivero (2003), who suggests that lobed  
479 *Zoophycos* are typical of Late Cretaceous units deposited in deep slope to basin environments. This  
480 different scenario can be explained with the Mesozoic increase in competition in shallow-marine  
481 settings. In fact, according to Zhang et al. (2015b), the accelerated competition in the Mesozoic  
482 neritic seas might have forced the producers of *Zoophycos* to migrate to bathyal environments. In  
483 addition, the Devonian rise of lignophytes may have had a more profound impact on shallow-  
484 marine environments than on the deep-sea, since the nutrient increase was linked to the land-sea  
485 supply of nutrients. By contrast, the Cretaceous expansion of angiosperms was predated by  
486 plankton radiations, which plausibly had a more direct impact on deep-sea settings. In fact, the  
487 Middle Jurassic was characterized by a major ecological transition within the coccolithophores, and  
488 the radiation of one of the principal families of cyst-forming dinoflagellates (Wiggan et al., 2018).

489

490 7. Conclusions

491 A paleontological reconnaissance survey of an Early Permian unit along the Yukon River in  
492 east-central Alaska has provided new ichnological data for the unit as well as new information on  
493 macroevolution of complex *Zoophycos*-group trace fossils. The producer of the here studied  
494 *Zoophycos* is regarded as a deposit-feeder using sensory-driven, directed search for locating  
495 heterogeneously distributed trophic resources. It filled its burrow with *Coprolus*-like fecal pellets,  
496 possibly integrating deposit feeding with microbial gardening and/or food caching. However, the  
497 proposed hypothesis cannot be tested against a neoichnological analogue of *Zoophycos*, which has  
498 not been described yet. Further neoichnological research is therefore encouraged in this direction.  
499 Two ‘Golden Ages’ of lobed *Zoophycos* are distinguished in this study: (1) Devonian-Permian and  
500 (2) Jurassic-Neogene. This distribution supports the important role of terrestrialization events in  
501 driving the *Zoophycos* morphology, i.e., radiations of land plants increased nutrient input to the  
502 oceans and decreased porewater oxygenation, thus favoring biological adaptations to exploit  
503 nutrient-rich but oxygen-poor substrates. The characteristic U-shaped marginal tube of lobed  
504 *Zoophycos* is among these adaptations. Further research in other Paleozoic units is needed to  
505 confirm the observed trend and derive a more detailed model of the relationship between *Zoophycos*  
506 and terrestrialization events. Finally, this study shows a fruitful integration between detailed  
507 lithostratigraphy with ichnological analysis, allowing to enlighten the macroevolution of this  
508 enigmatic ichnotaxon for the whole Phanerozoic.

509

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525

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527

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741

#### FIGURE CAPTION

742

743 FIG. 1: A, map showing the study area in the Yukon-Charley Rivers National Preserve near the  
744 U.S.-Canada border; B, simplified geological map showing the location of the Permian beds  
745 discussed in this manuscript Modified from Brabb and Churkin, 1969.

746 FIG. 2: A, simplified geological section of the Devonian-Permian beds exposed in the study area. B,  
747 photomosaic showing the *Zoophycos* locality, Tahkandit Limestone Formation.

748 FIG. 3: Stratigraphic column of the Nation River Fm. (Devonian, A-B), and composite section of the  
749 Tahkandit Limestone Formation (Permian, C-F)

750 FIG. 4: A–D, trace fossils (*Conichnus*) and body fossils (E, F, brachiopods, bryozoans) co-occurring  
751 in the *Zoophycos*-bearing ichnocoenosis.

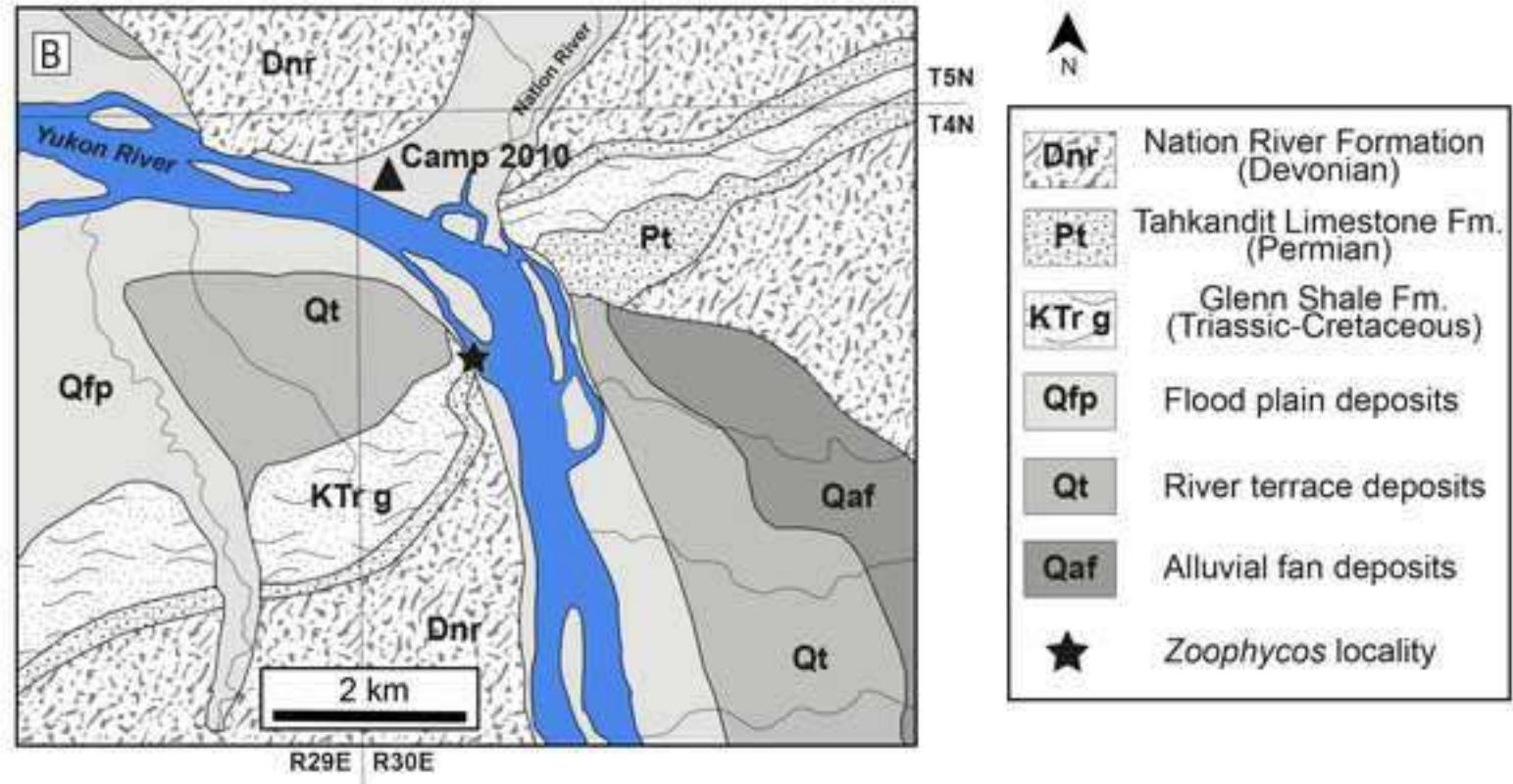
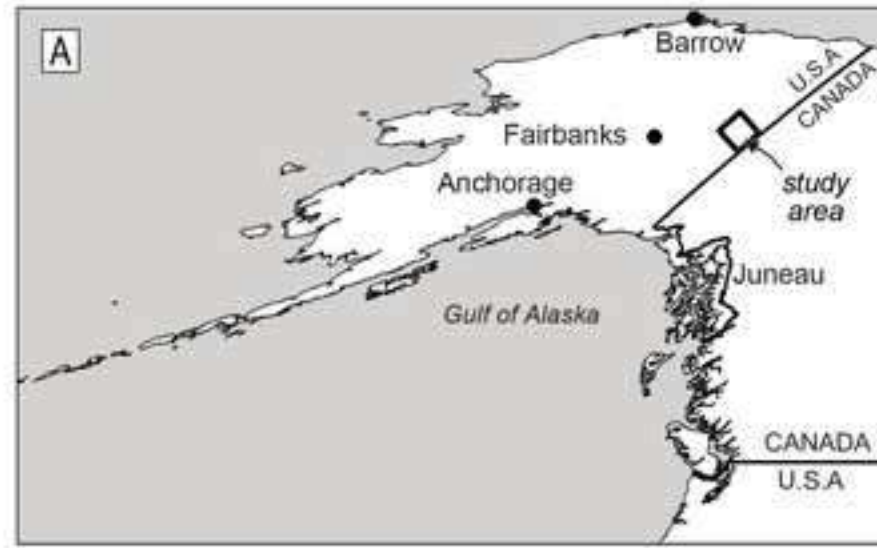
752 FIG. 5: A–D, *Zoophycos* traces with well-developed spreiten and lobes; E–I, details from the three-  
753 dimensionally developed *Zoophycos*.

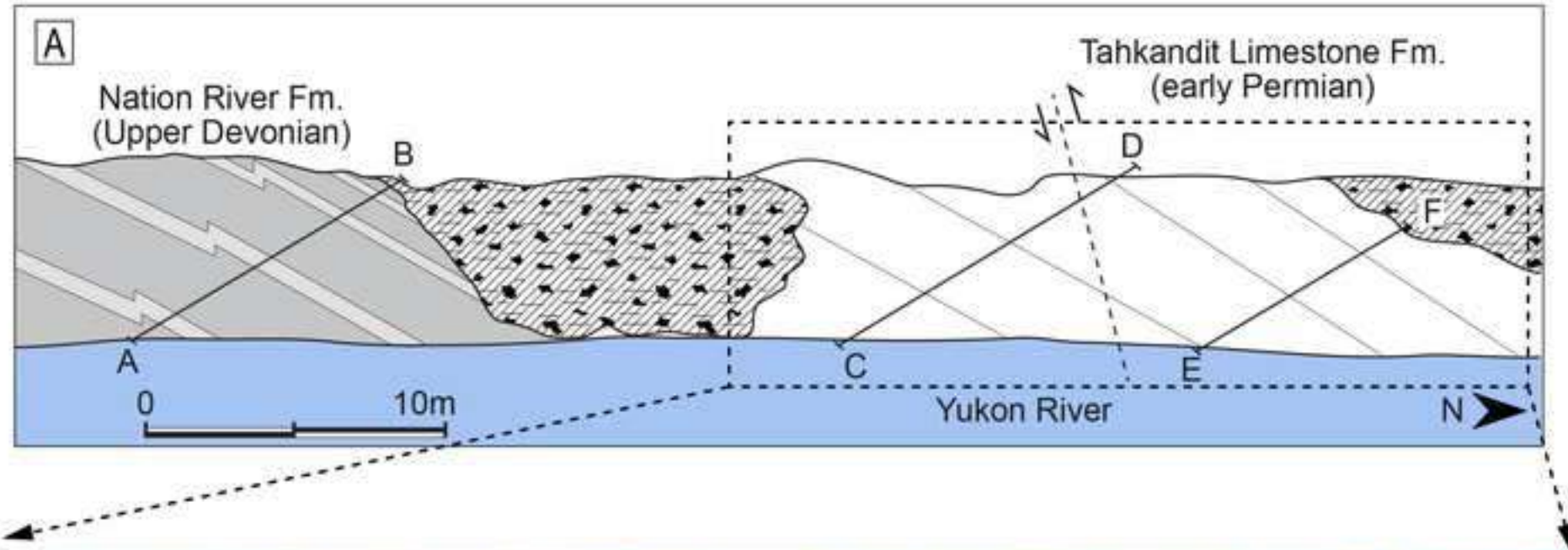
754 FIG. 6: Close-up of some of the best preserved *Zoophycos* laminae from this section showing  
755 textural details from the lamellae and marginal tube.

756 FIG. 7: Lobed *Zoophycos* through time. Data are binned by geologic periods. The source dataset is  
757 the Phanerozoic *Zoophycos* database of Zhang et al. (2015b). Sites with no information on  
758 the basic morphology of *Zoophycos* ~~have been~~ filtered out from the dataset. The dataset ~~has~~  
759 ~~been~~ implemented by information on the Yukon River *Zoophycos* and two additional  
760 *Zoophycos*-bearing sites (Baucon and Carvalho, 2008; Baucon et al., 2015). (A) Lobed  
761 *Zoophycos* ratio. The y axis represents the ratio between the number of sites with lobed  
762 *Zoophycos* and the total number of sites with *Zoophycos*. (B) Number of sites with lobed  
763 *Zoophycos*.

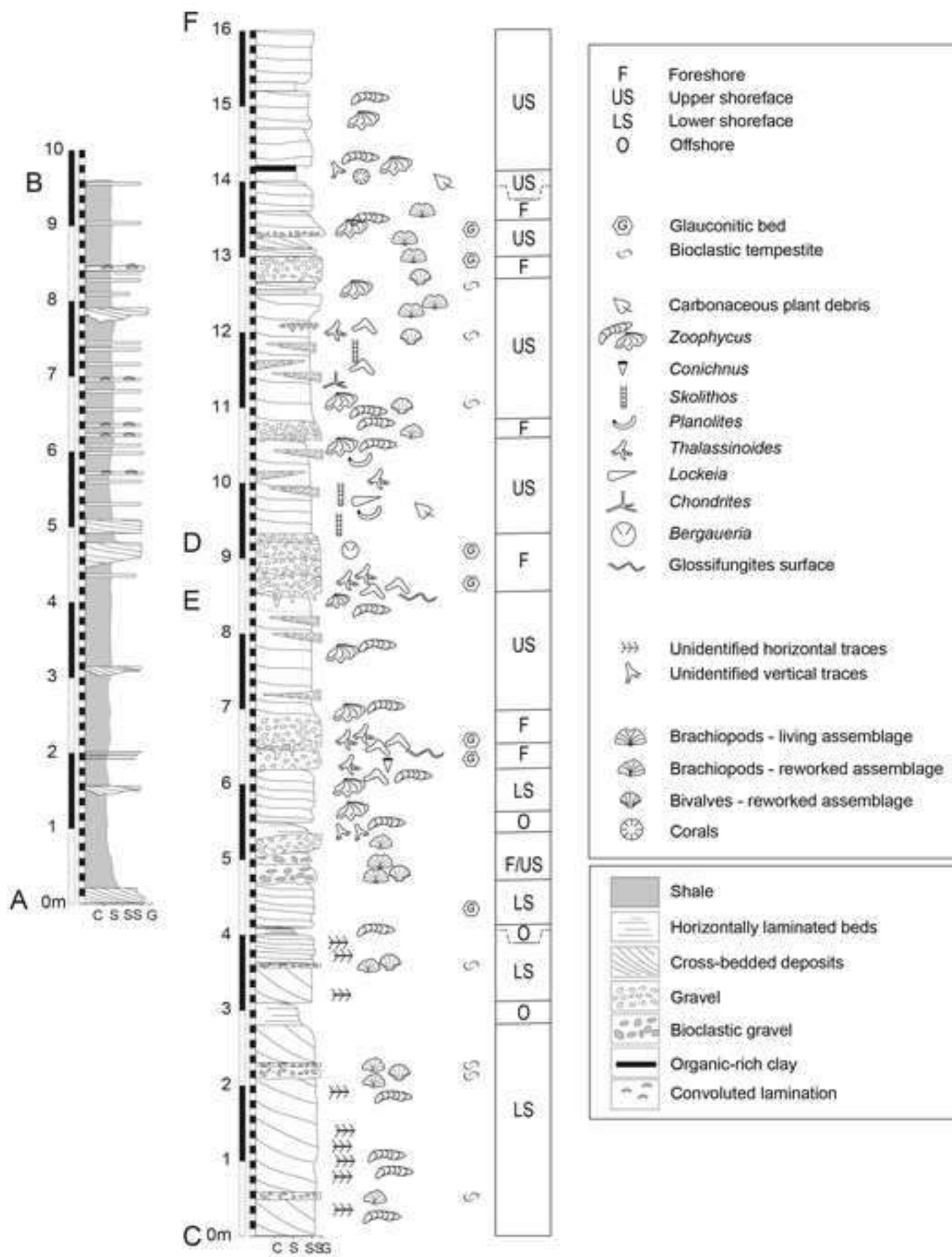
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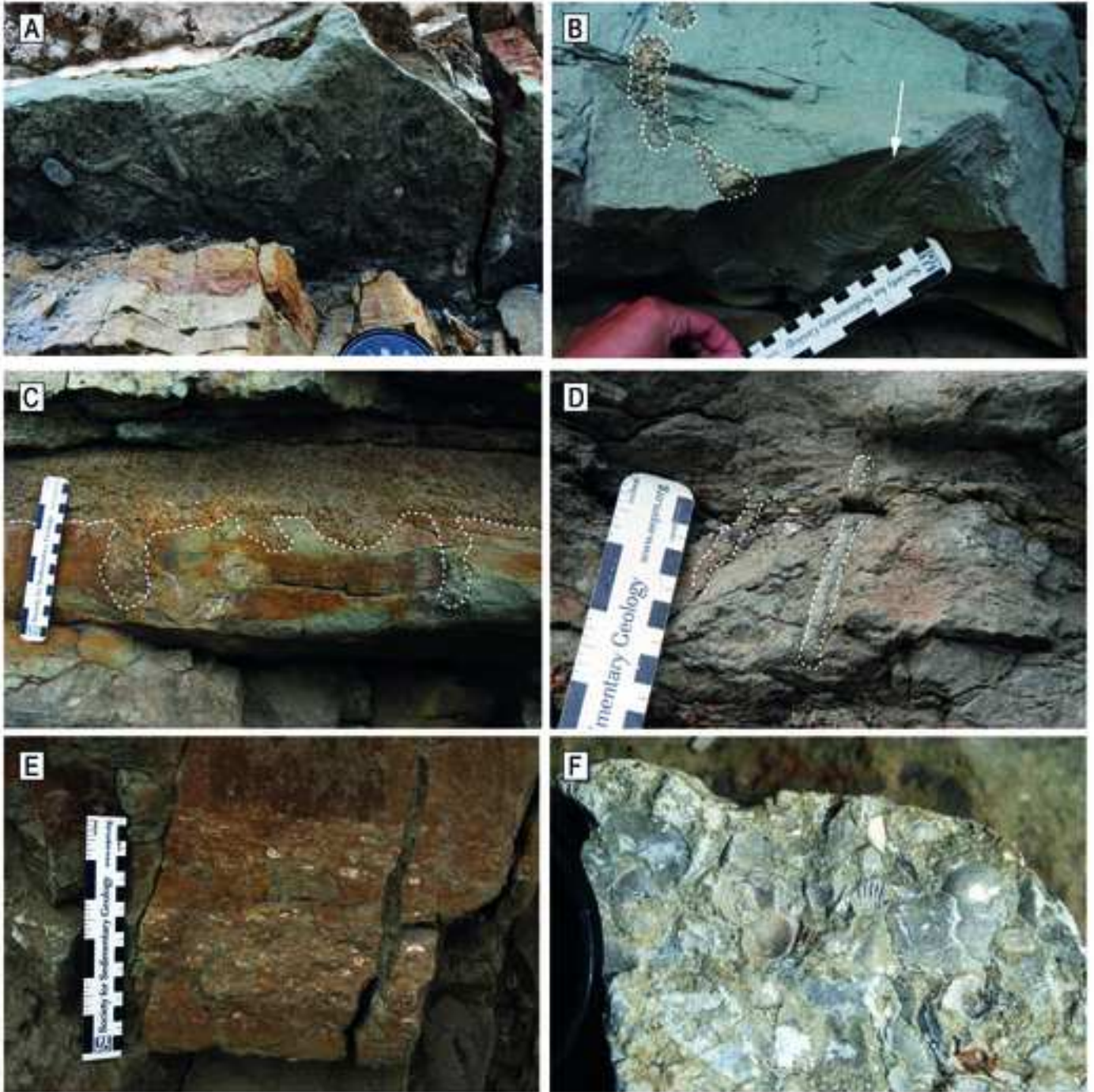
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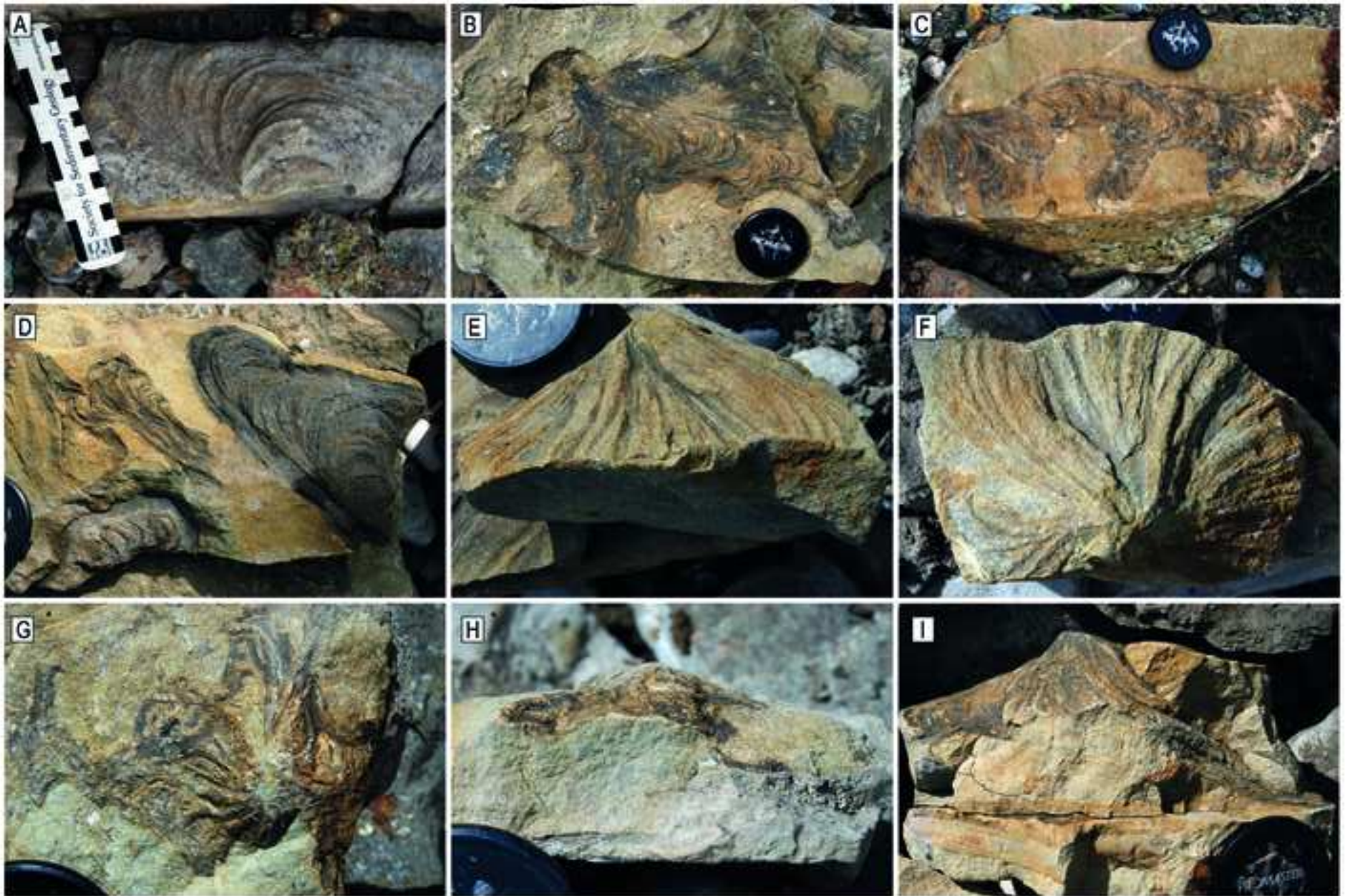








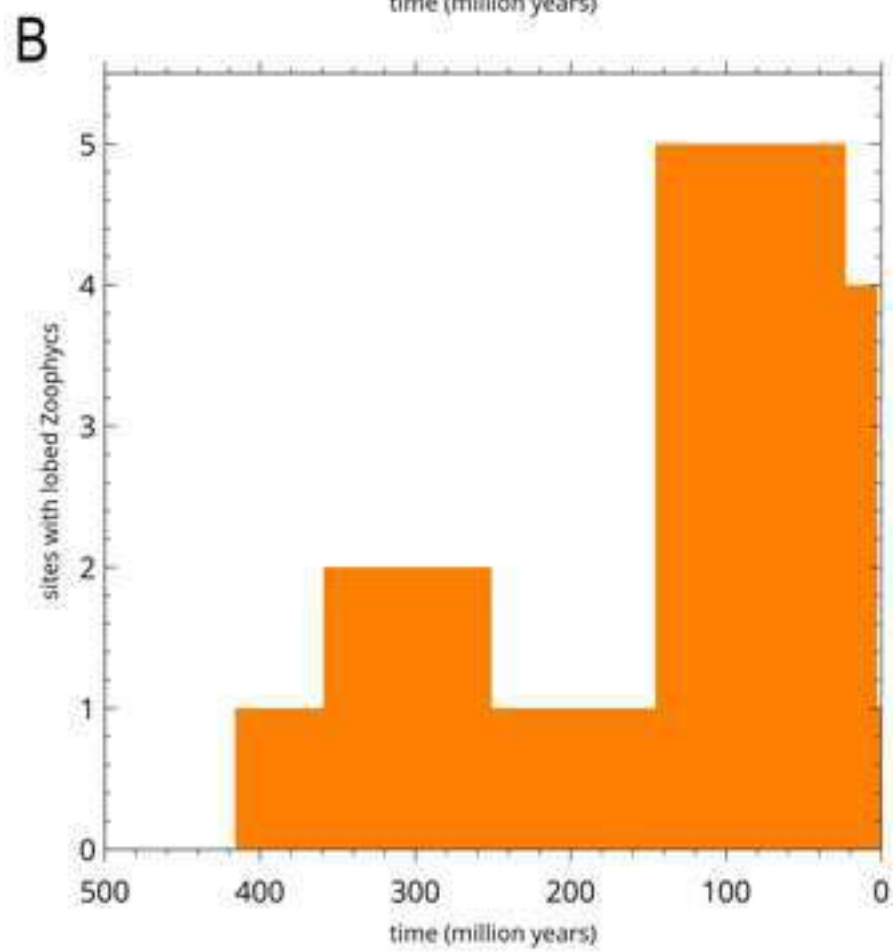
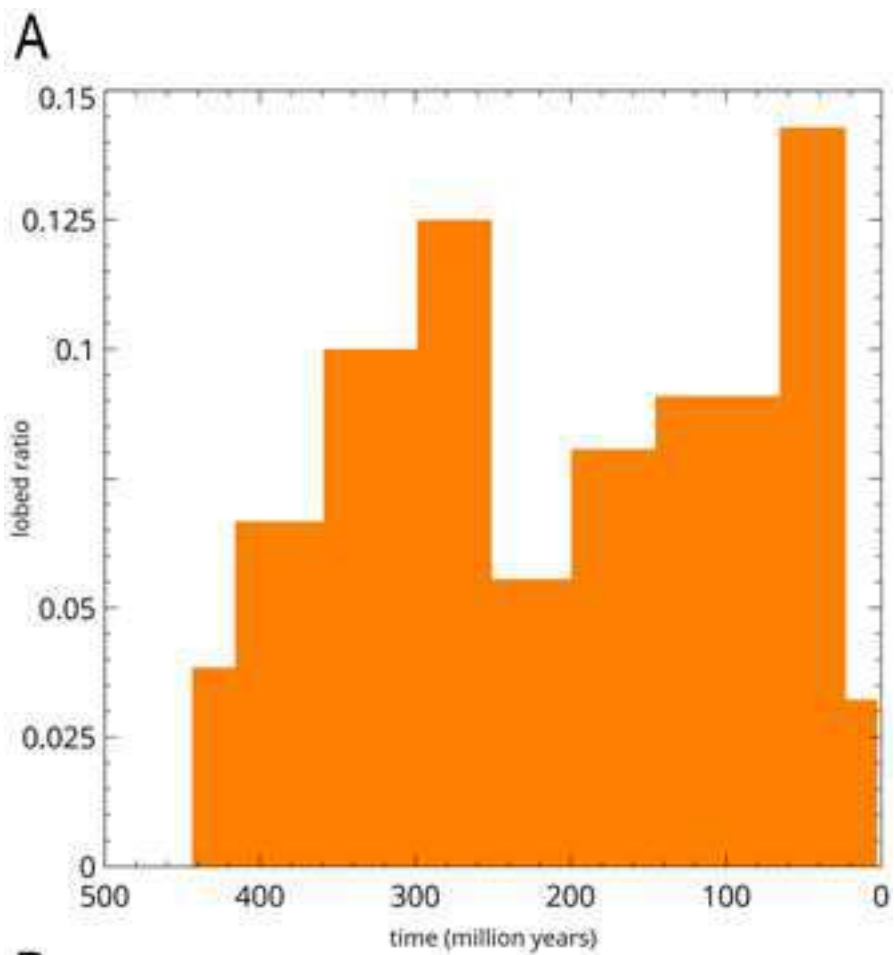












1 Table 1. Morphology of the trace fossils of the Takkandit Limestone Formation.

2

Ichnotaxon	Class	Orientation	Branched	Lining	Fill	Facies
<i>Conostichus</i>	Burrow	Vertical	No	No	Passive?	F
<i>Bergaueria</i>	Burrow	Vertical	No	No	Passive	F, S
<i>Skolithos</i>	Burrow	Vertical	No	No	Passive	F, S
<i>Planolites</i>	Burrow	Vertical	No	No	Active	F, US
<i>Zoophycos</i>	Burrow	Vertical and horizontal	No	No	Active (pelleted)	US
<i>Chondrites</i>	Burrow	Vertical	Yes	No	Active?	US

3

4