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

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 terrestralization 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

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 ~~has been~~ 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.

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   Lowemark 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 19th

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 palaeoenvvironmental 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   Rodriguez-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; Lowemark 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

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

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

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

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

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

6.1 The two Golden Ages of lobed *Zoophycos*

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

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

1. Habitat: *Zoophycos* is typically found in shelf deposits in the Palaeozoic, lower shelf-slope in the Mesozoic, and bathyal settings in the Cenozoic (Seilacher, 1986; Bottjer et al., 1988; Olivero, 2003; Zhang et al., 2015b; see also Baucon and Avanzini, 2008);

2. Tiering: *Zoophycos* shifted gradually from the shallow to deep tiers of marine substrates in the Phanerozoic (Zhang et al., 2015b).

3. Morphology: *Zoophycos* evolved from small, simple, helicoidal, rooster-shaped, circular/elliptical spreiten of one to two whorls without marginal lobes in the Palaeozoic, to large, complex, helicoidal, lobate spreiten of several whorls in the Cenozoic (Seilacher, 1986; Bottjer et al., 1988; Olivero, 2003; Zhang et al., 2015b)

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

The most peculiar feature of the studied *Zoophycos* is the lobed morphology of form B. The *Zoophycos* form B described herein is a three-dimensionally arranged structure with complex, 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* trough 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 in

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-Frasinian), 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

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

Acknowledgments

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740

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)

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

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

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

FIG. 7: Lobed *Zoophycos* through time. Data are binned by geologic periods. The source dataset is the Phanerozoic *Zoophycos* database of Zhang et al. (2015b). Sites with no information on the basic morphology of *Zoophycos* ~~have been~~ filtered out from the dataset. The dataset ~~has been~~ implemented by information on the Yukon River *Zoophycos* and two additional *Zoophycos*-bearing sites (Baucon and Carvalho, 2008; Baucon et al., 2015). (A) Lobed *Zoophycos* ratio. The y axis represents the ratio between the number of sites with lobed *Zoophycos* and the total number of sites with *Zoophycos.* (B) Number of sites with lobed *Zoophycos.*
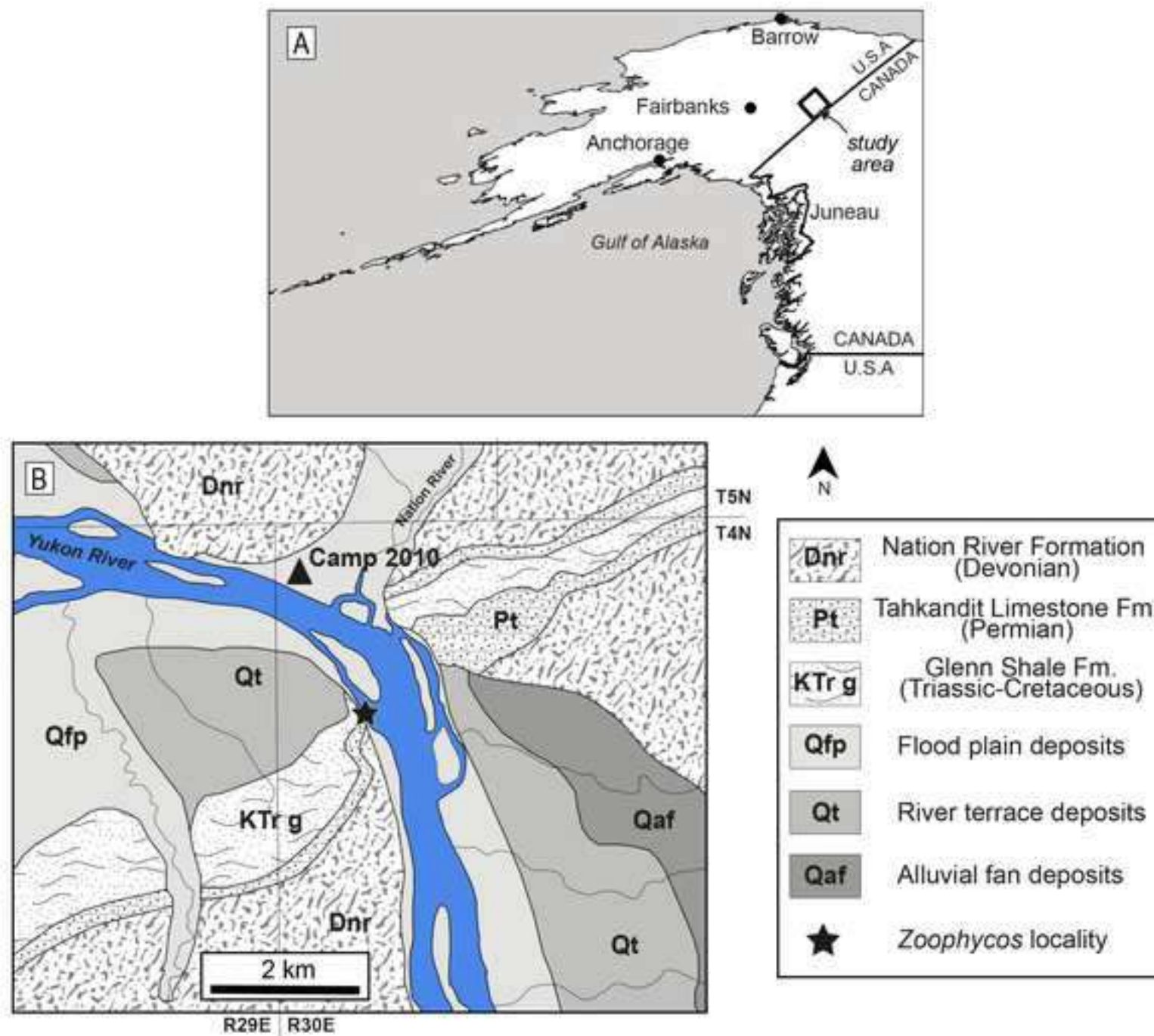
Figure 1
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Figure 1

Figure 2

A Nation River Fm. (Upper Devonian)

Tahkandit Limestone Fm. (early Permian)

B

D

F

A

C

E

0   10m

Yukon River

N

B

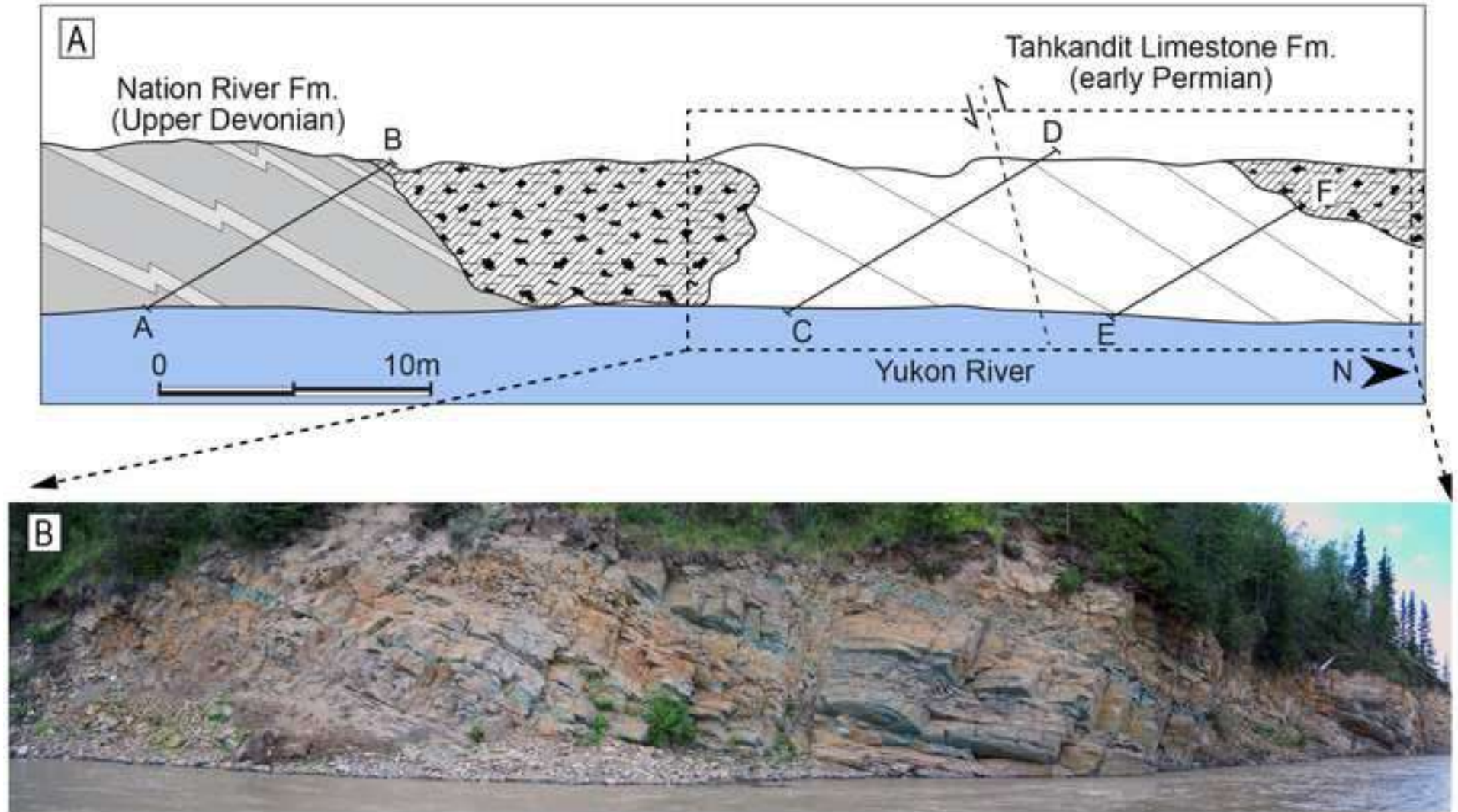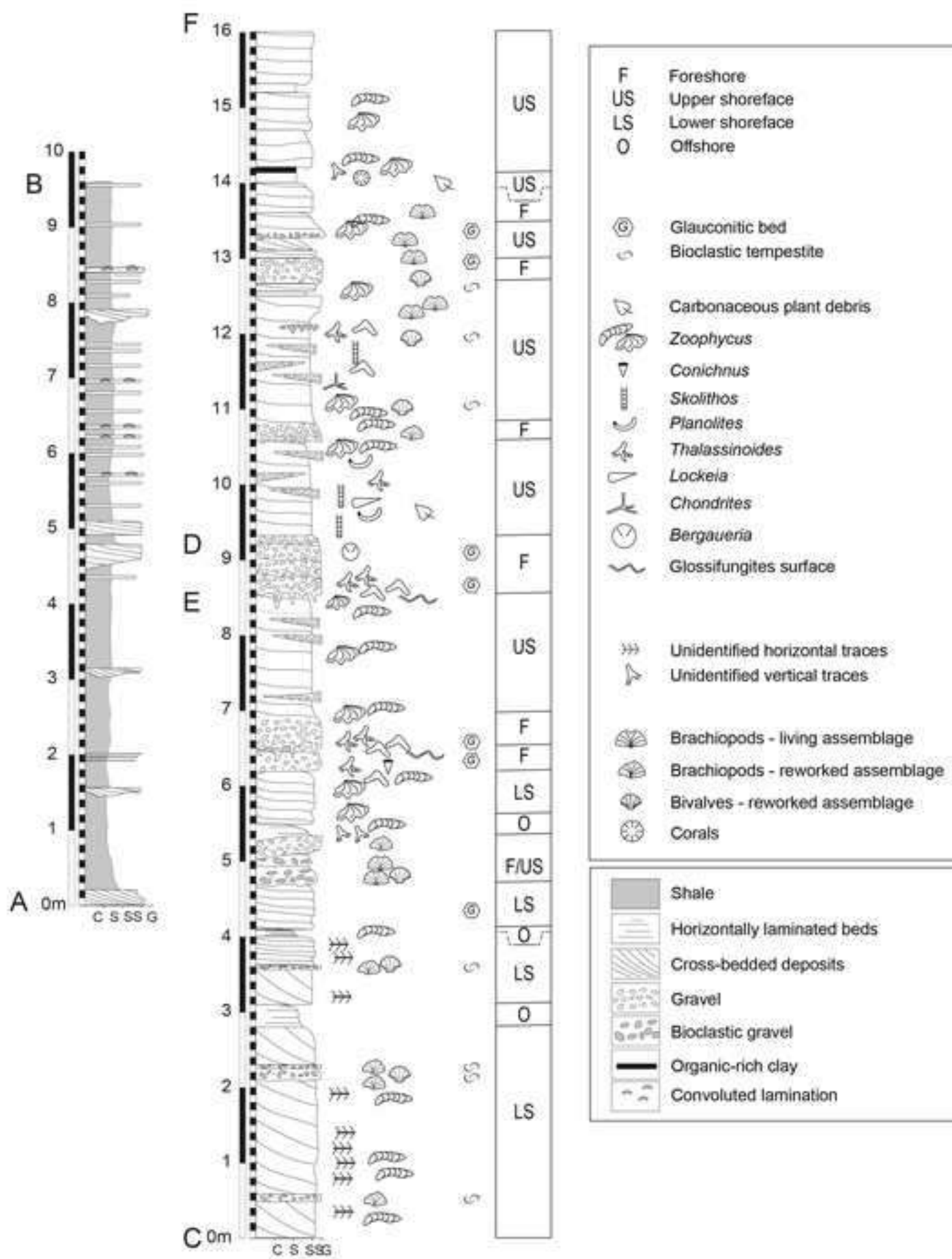Figure 3   Click here to access/download;Figure;Fig. 3.jpg ⬇
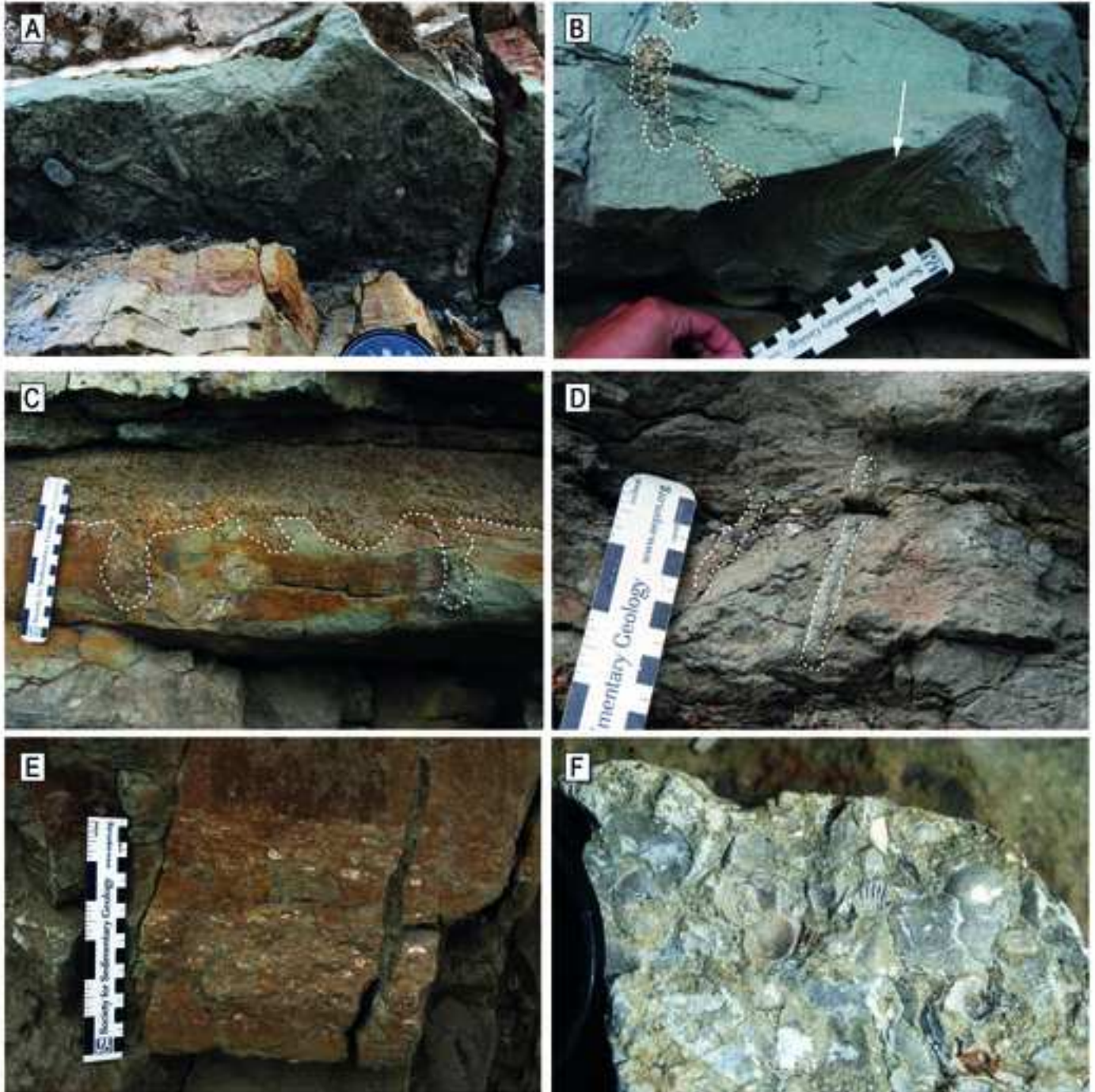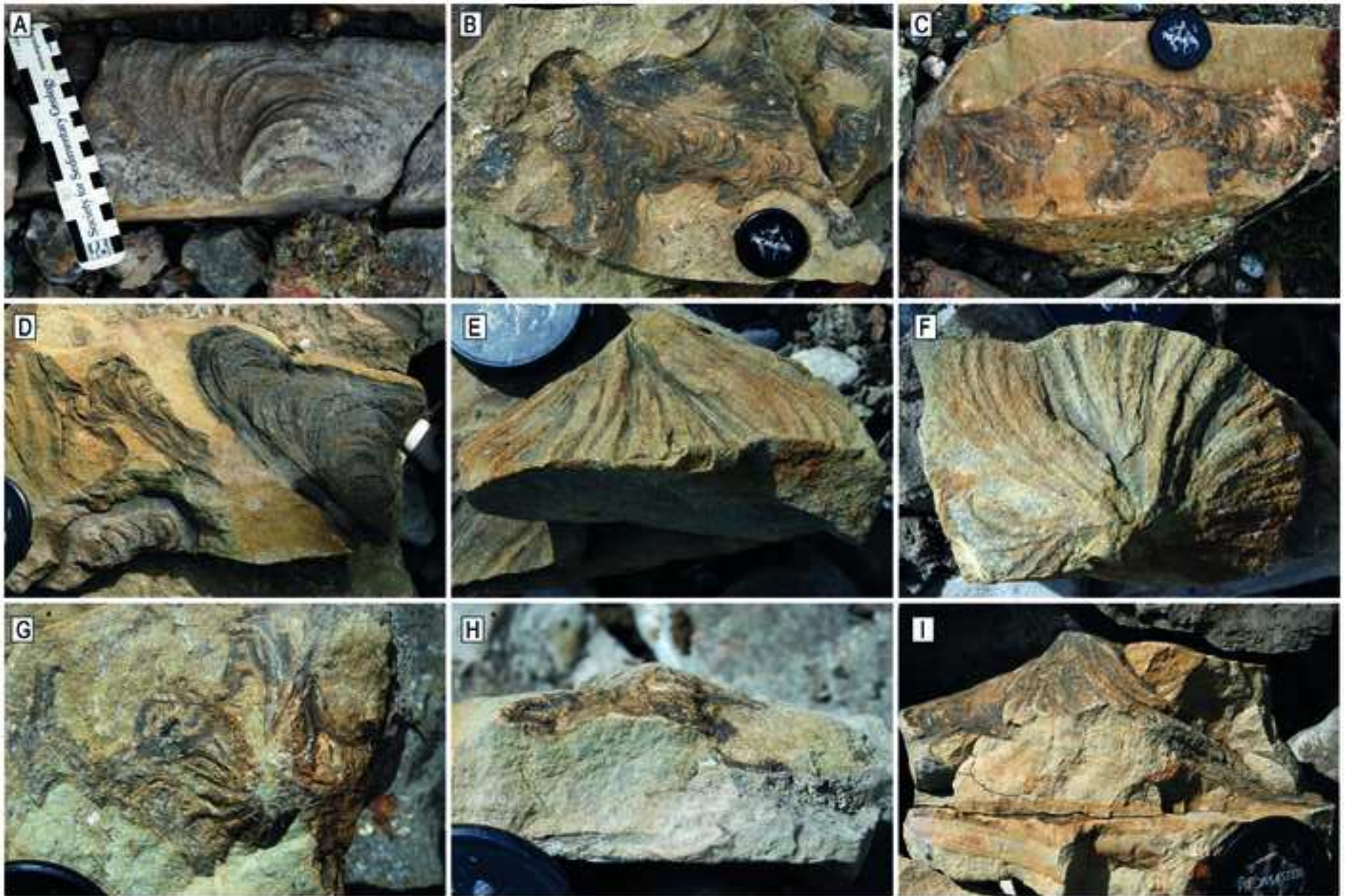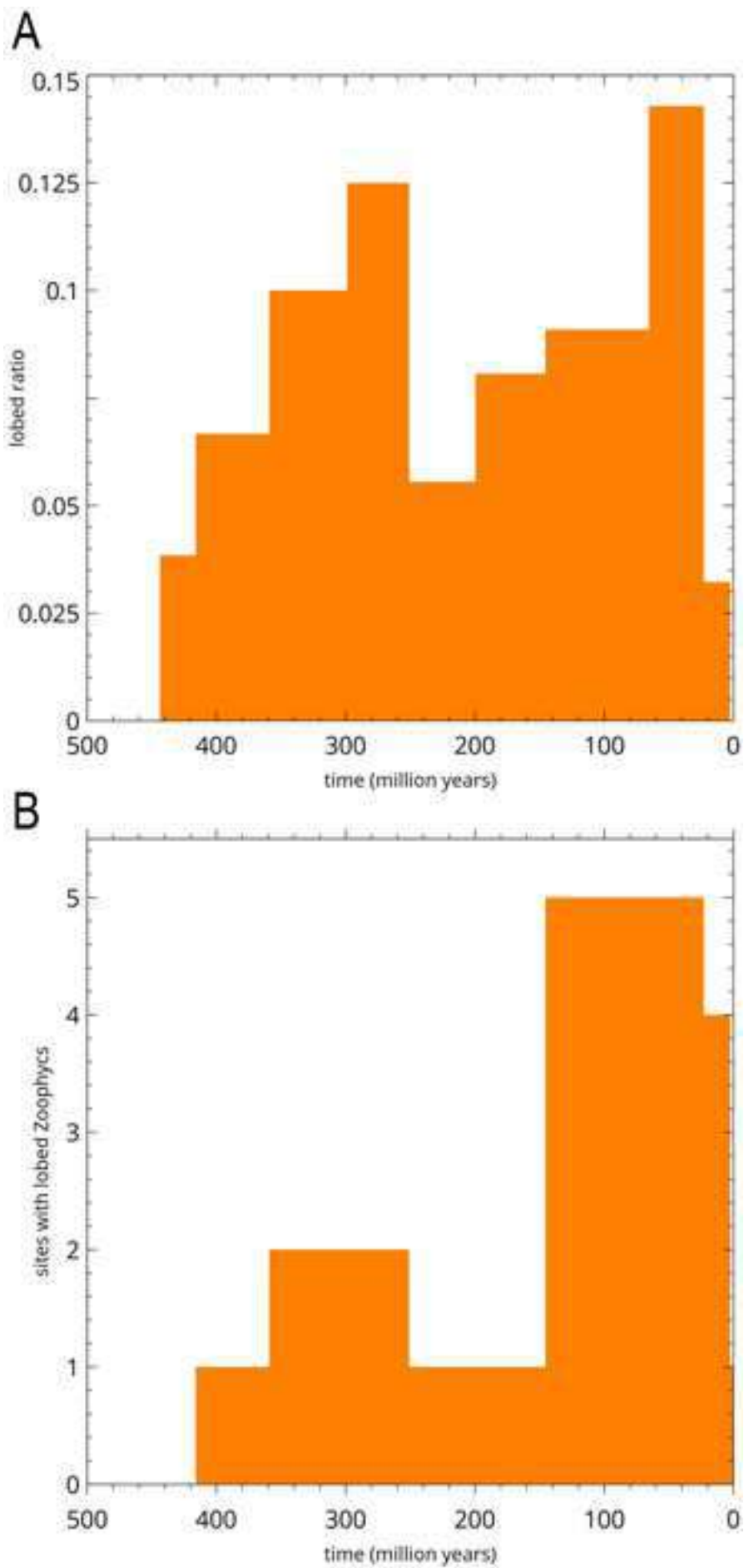
Figure 4

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Figure 5

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Figure 7

A

B

Table 1

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

2

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

3

4