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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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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 (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-Palaeozoic 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) Carboniferous–Permian and (2) Cretaceous–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 was 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

One of the most iconic, enigmatic and widespread ichnofossils is *Zoophycos,* a spreite structure comprising protrusive burrows of variable length and orientation, arranged in helicoid spirals with an overall circular, elliptical or lobate outline (Frey, 1970; Hantzschel, 1975; Lowemark and Schafer, 2003; Rodríguez-Tovar and Uchman, 2004; Lowemark et al., 2005; Kotake, 2014; Lowemark, 2015). *Zoophycos* has been a subject of scientific interest since the 19th century, when Johann Gotthelf Fischer de Waldheim (1811) first described *Zoophycos* as *Umbellularia logimna* and interpreted it as a fossil plant (Baucon et al., 2012; Bessudnova, 2013). The botanical hypothesis of *Zoophycos* was

prominent in the 1800s, e.g., the influential researcher Brogniart (1828) introduced it as *Fucoides circinnatus* (Plička, 1968). The botanist Mas-salongo (1855) established the genus *Zoophycos,* supporting the botan-ical origin of the trace fossil. The botanical interpretation of *Zoophycos* was still popular in the 1900s (e.g., Barsanti, 1902), whereas Krysch-tofowitsch (1911) interpreted *Zoophycos* from eastern Siberia as a trace fossil. The ichnological interpretation of *Zoophycos* gained increased support by the 1950s (e.g., Seilacher, 1954), although Plička (1968) interpreted it as fossil prostomia of sabellids.

Despite over 190 years of studies on *Zoophycos,* its taxonomy, tracemaker and ethology, as well as its palaeoenvvironmental significance, remain still mostly unresolved (Olivero and Gaillard, 2007;

Lowemark, 2015; Zhang et al., 2015b; Monaco et al., 2016). No extant organism has been observed producing incipient *Zoophycos* (Zhang et al., 2015b). Sipunculids, polychaete annelids, arthropods and echiuran worms were proposed as possible producers of *Zoophycos* (Kotake, 1992; Rodriguez-Tovar and Uchman, 2004). Recently proposed explanations for *Zoophycos* include (1) deposit feeding, (2) detritus feeding, (3) refuse dumping, (4) caching surface material and (5) gardening microorganisms (Kotake, 1989; Bromley and Hanken, 2003; Lowemark et al., 2004; Olivero and Gaillard, 2007; Lowemark, 2015; Monaco et al., 2016; Zhang et al., 2015a; Giannetti et al., 2017).This Phanerozoic ichnotaxon has a widespread and global occurrence in the geological record, appearing first in the Cambrian (Jensen, 1997; Sappenfield et al., 2012) and continuing through the Quaternary (McGugan, 1963; Logan and McGugan, 1968; Lowemark and Schafer, 2003; Sei-lacher, 2007).

Two interesting macroecological trends characterize *Zoophycos* (recently reviewed by Zhang et al., 2015b). Firstly, this ichnotaxon shifts from more proximal, shallow environments in the early Phanerozoic (Palaeozoic) to more distal, closer to the continental rise, settings in the Mesozoic and finally to the deeper, bathyal realm in the Palaeogene to recent times (Zhang et al., 2015b). This habitat migration was interpreted as a response to biotic pressures, particularly related to global biodiversity expansion after the Permo–Triassic, Triassic–Jurassic and Cretaceous–Paleogene mass extinctions (Olivero, 2003; Knaust, 2009; Lowemark, 2012) or redistribution due to paleogeographical

reorganization of the continents (Martin, 1996; Martin, 2003; Martin et al., 2008). Parallel to these biotopic changes, an increase in complexity of the pattern in these trace fossils can be observed, from simple, small tubes arranged in circular or elliptical patterns to complex, spiralling multi-branched and lobated structures (Zhang et al., 2015b). While the simple morphotypes are prevalently Palaeozoic, more elabo-rated structures appeared from the Mesozoic to dominate the Cenozoic deep-marine record (Zhang et al., 2015b), with structural lobes oriented in different directional planes (Seilacher, 1974, 2007). As such, lobed *Zoophycos* are rare in the Palaeozoic but common in post-Palaeozoic times.

This study reports an unusually lobate *Zoophycos* from the early Permian Tahkandit Limestone (Brabb and Grant, 1971) of the Yukon–Charley Rivers National Preserve, east-central Alaska. These traces consist of numerous vertically oriented whorls and marginal lobes, as it is usually found in Cenozoic traces, anticipating the evolution of these structures by at least ~50 million years (Olivero, 2003; Zhang et al., 2015b). Systematic studies on the trace fossils of the Yukon River and their paleoenvironmental significance are lacking, with regard to the environment structure. Specifically, three major questions are posed: (1) what are the trace fossils of the Tahkandit Limestone, a prominent but incompletely understood marine unit found through the region? (2) What is the shape of the Yukon River *Zoophycos*? (3) Why are lobed *Zoophycos* found in the Permian Tahkandit Limestone?
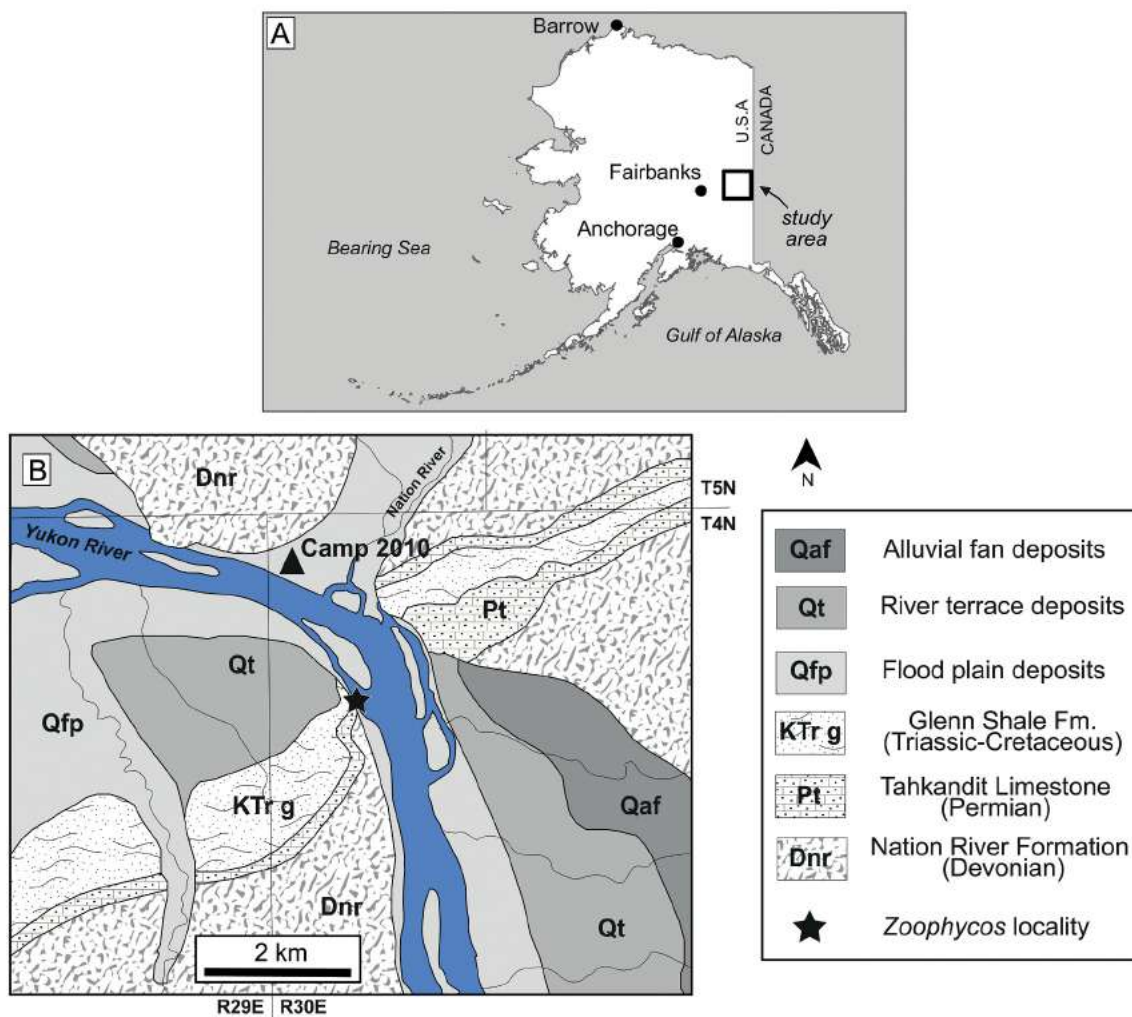

Fig. 1. A, map showing the study area in the Yukon-Charley Rivers National Preserve near the U.S.-Canada border; B, simplified geological map showing the location of the Permian beds discussed in this manuscript Modified from Brabb and Churkin Jr, 1969.

2. Methods

Data presented in this study were collected in 2010 during a National Park Service Alaska Region sponsored geological and paleontological survey of the Yukon-Charley Rivers National Preserve in east-central Alaska (Fig. 1A-B). The section described in this study (Fig. 2) partially overlaps with the type section of the Tahkandit Limestone described by Brabb and Grant (1971), Fig. 6) and the outcrop is located on the west (left) side of the Yukon River just south of the confluence with the Nation River (GPS: N65°10′915″; W141°42′205″), approxi-mately 30 km west of the U.S. – Canada border. The lower section of the Tahkandit Limestone, informally named Sandstone unit, is the subject of the bulk of this study. Tahkandit deposits are described in terms of overall architecture, sedimentology, and major paleontological charac-teristic, with particular attention on identified ichnocenoses. General overall geological data used in this study are provided in the geological map of Brabb and Churkin Jr (1969). Specimens referred here were collected on the ancestral homeland of the Han Hwech'in Athabascans and are housed at the Perot Museum of Nature and Science, Dallas, Texas.

In this paper, we follow the review of Baucon (2015: Table 2) for naming groups of trace fossils. Accordingly, an ichnocoenose is regarded as a group of traces that have been formed by the action of what ap-proximates a single benthic community or a succession of similar com-munities. An ichnoassemblage comprises all trace fossils occurring within a single unit of rock. An ichnoassociation is regarded as a recurrent association of ichnotaxa in a group of ichnoassemblages. These definitions are after Davitashvili (1945), Lessertisseur (1955), Ekdale et al. (1984), Pickerill (1992), Pickerill and Brenchley (1975), McIlroy (2004), Bromley (1996), Legendre (2005), Buatois and Mángano (2011). The morphology of *Zoophycos* is described according the terminology of Olivero (2003).

To analyze how *Zoophycos* changed across the Phanerozoic, we analyzed the comprehensive "Phanerozoic *Zoophycos* database" (Zhang et al., 2015b: Supplementary Table S1). The original database includes 448 entries, each of which refers to a specific *Zoophycos*-bearing palae-ontological site. These data have been filtered by selecting only those

records presenting information about *Zoophycos* morphology. The resulting dataset includes 285 entries. The dataset has been supple-mented with information about lobed *Zoophycos* of the Pramollo Basin *Zoophycos* (Baucon and Carvalho, 2008; Baucon et al., 2015) and the Yukon River *Zoophycos* described in this report. As a result, the database used here includes 288 entries. More specifically, the database used here includes 22 sites containing lobed *Zoophycos* and 266 sites with unlobed *Zoophycos* only.

3. Geological setting

The rocks in this study accumulated at the margin of Ishbel Trough and belong to the poorly defined Tahkandit Limestone which comprises outer shelf to basinal carbonates, sandstones, and shales (Bamber and Waterhouse, 1971; Brabb and Grant, 1971; Beauchamp, 1995). In the Charley River and Eagle quadrangles (Fig. 1B), a major unconformity that represents the latest Devonian, Carboniferous, and basal Permian, separates the Devonian Nation River Formation (Brabb and Churkin Jr, 1969; Scott and Doher, 1967; Gehrels et al., 1999) from the overlying Permian Tahkandit Limestone deposits. The Nation River beds exposed at the locality discussed here are represented by 16 m of deposits characterized by alternating siliciclastic beds and finely laminated, organic-rich shale. Both the Nation River and the Tahkandit Limestone formations were folded by a relatively small anticline structure and consequently affected by vertical normal faulting; consequently, Tah-kandit deposits show a dip of 62 degrees toward the north-west. The Tahkandit Limestone (Fig. 1) was informally divided into two lithos-tratigraphic unit, the basal Sandstone unit, and the overlying Limestone unit (Brabb and Grant, 1971). The basal interval is represented by approximately 15 m of grayish-green, glauconitic sandstone and conglomerate consisting primarily of chert and quartz grains. Brachio-pods are by large the most abundant fossils, whereas bivalves, corals, arenaceous foraminifera, and bryozoans are scarce (Brabb and Grant, 1971). The occurrence of the brachiopods *Yakovlevia mammata* and *Thamnosia* sp. as well as trilete spores, bisaccate pollen grains, hys-trichosphaerids, and megaplant remains in the glauconitic sandstones at the top of the lower unit (Brabb and Grant, 1971, and references therein,
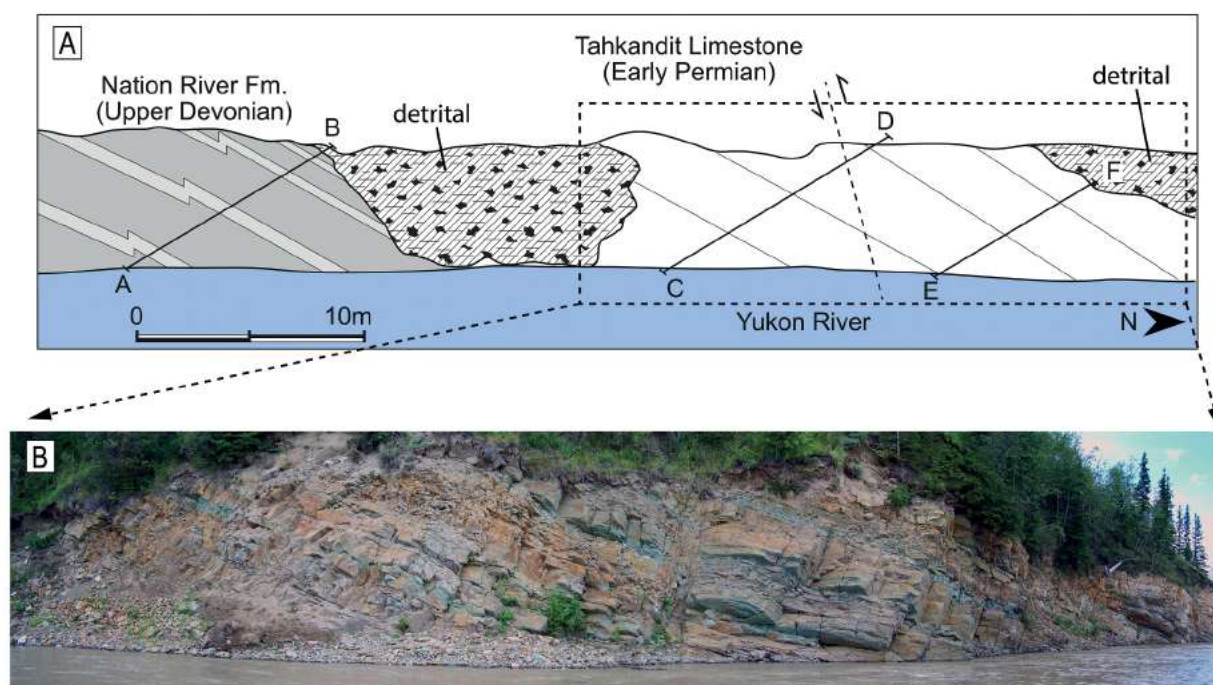

Fig. 2. A, simplified geological section of the Devonian-Permian beds exposed in the study area. The detrital material is a mix of rock debris and vegetation. B, photomosaic showing the *Zoophycos* locality, Tahkandit Limestone.

this study) support an Early Permian (Cisuralian) age and shallow marine to estuarine/tidal environments (Brabb and Grant, 1971). Brabb and Grant (1971) also reported structures "similar to *Zoophycos* sp." and "the so called *Spirophyton* sp." from this interval and confirm that such structures are widely distributed in rocks of Pennsylvanian and Permian age in the Yukon territory (Nelson, 1961). Sandstone and conglomeratic beds (Fig. 2B) of the lower unit grade conformably into very pale, relatively sand- and glauconite-free limestone that forms cliffs and pinnacles typical of the morphology of the area. At a microscopic scale,

the bioclastic limestone contains fragments of brachiopod and thin-shelled bivalves, bryozoans, and foraminifera. Finally, the Tahkandit Limestone is overlain by the Glenn Shale which represents the entire Middle Triassic–Early Cretaceous interval and consists primarily in grayish-black carbonaceous shale with minor siltstone and quartzite (Brabb and Churkin Jr, 1969).
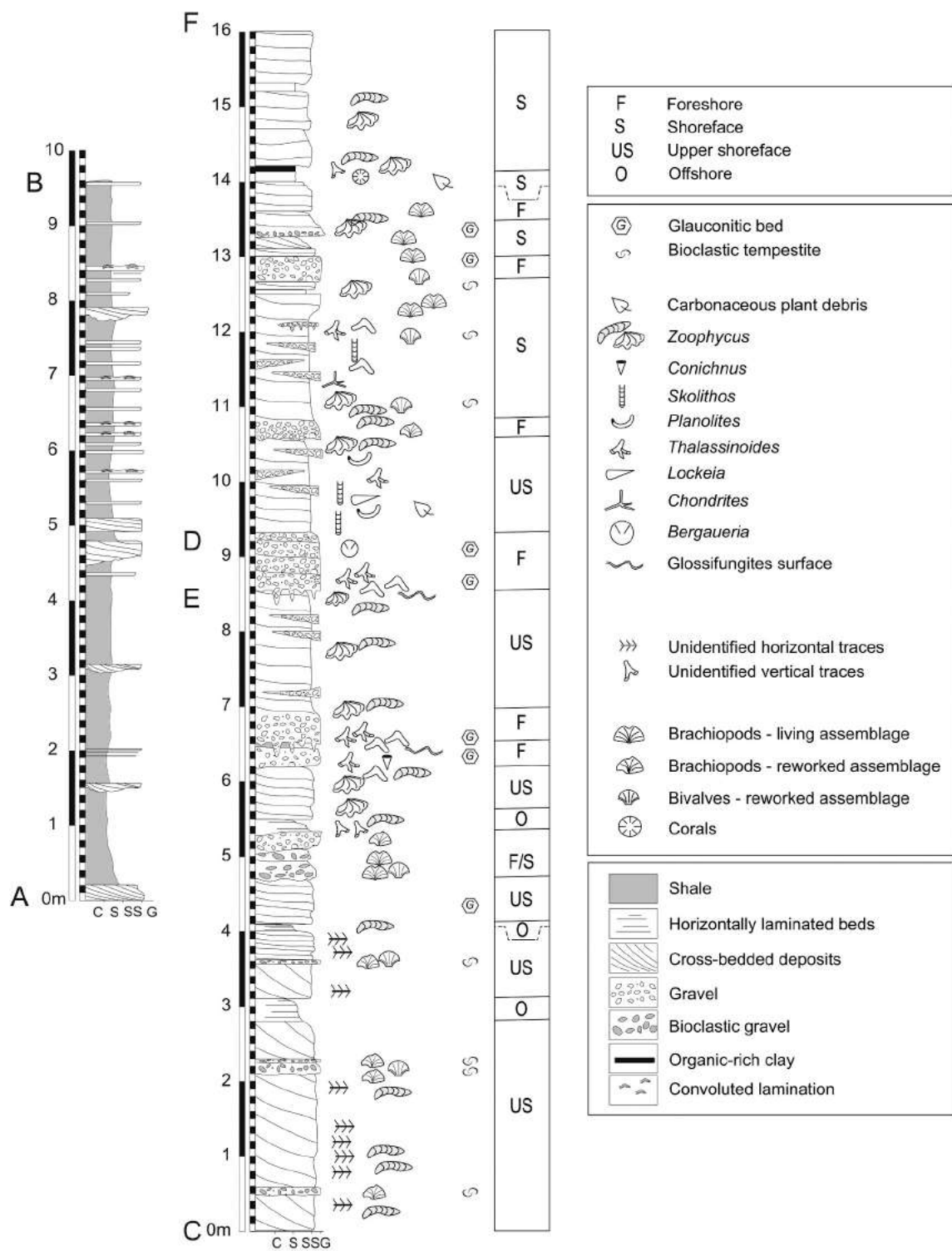

Fig. 3. Stratigraphic column of the Nation River Fm. (Devonian, A-B), and composite section of the Tahkandit Limestone (Permian, C-F).

4. Sedimentology and paleontology

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

4.1. Foreshore facies (F)

This facies association is represented by massive, tabular conglomerate grading upward into gravelly sands (Fig. 3). Single beds range in thickness between 20 and 45 cm and generally display sharp-erosional base floored by extensively bioturbated, coarse gravel to coarse pebbly sandstone. These deposits are very well sorted, without any coaly fragment nor sandy or muddy matrix, and rare shell fragments. With minor exceptions, conglomerates show pervasive secondary glauconization and carbonate cement. Burrowing structures are referred to the firm ground ichnogenera *Conostichus*, *Bergaueria* and *Skolithos*; vertical burrowing structures are generally robust, penetrating as deep as 80 cm into the underlying sandy deposits, and reach 5 cm in diameter. The sedimentological and ichnological characteristics of this facies association suggest a high-energy coastal environment: the basal erosion surface is interpreted to be the result of wave ravinement that cut across shoreface to offshore deposits. Glauconite generally develops under oxygenated to slightly reducing conditions close to the sediment/water interface and is considered to represent a powerful (but not exclusive) indicator of stratigraphic condensation within marine sediments (Loutit et al., 1988; Kidwell, 1991). Well-developed firm ground *Thalassinoides*, *Conostichus*, *Bergaueria*, *Planolites*, and *Skolithos* are here referred to the *Glossifungites* ichnofacies, which develops exclusively in firm, unlithified substrates such as dewatered muds or compacted sands. Relevant to this study is the occurrence at 9.6 m and 14.2 m of the measured section of plant remains, coaly fragments, and organic rich laminated bed that were observed and sampled for palynological analyses. Such beds document subaerial conditions or the proximity to a non-marine source of sediments.

4.2. Shoreface facies (S)

This sedimentary facies is arranged in fining-upward cross-laminated sandstone intercalated with conglomeratic beds (Fig. 3). Conglomeratic beds are sharp-based, largely bioclastic and with minor sandy matrix: strata are tabular to low-angle cross-stratified, reaching individual maximum thickness of 30 cm. Finer-grained conglomeratic deposits are locally arranged in elongated lenses and display a rhythmic alternation with laminar sands, suggesting a possible wave to tidal influence during deposition. Alike conglomeratic deposits referred to facies F (Fig. 3), none of these bed display evidence of glauconization. Fossil remains are extremely abundant and represented by the brachiopods *Yakovlevia mammata*, *Thamnosia* sp., and *Megousia* sp., which account for 80% of the deposits and are also found in undisturbed life position/assemblages. No ichnofossils were observed in finer-grained conglomeratic deposits, except for *Skolithos* traces in a single lenticular bed (12.1 m in the measured section). Sandstones are fine- to medium-grained, high-angle cross-bedded lamination, and display an overall fining upward trend with minor silty deposits. In addition, coarser sandy and bioclastic beds characterized by sharp and erosive basal contact and scattered with gastropod and bivalve shell fragments (1 cm in average) were observed and interpreted as tempestite deposits. Sandstones are also characterized by a rich and diverse soft-ground related trace fossil assemblage which are referred to the *Skolithos* ichnofacies. Identifiable ichnogenera traces include *Skolithos*, and *Bergaueria*. The central shoreface facies

(sensu Antia et al., 1994) shows a high proportion of shells, a broad range of sediment size (from fine-grained sandstones to pebble) and marked diversity in sedimentary structures (Fig. 4). The *Skolithos* ichnofacies is indicative of relatively high levels of wave or current energy characterized by changes in deposition rates and physical reworking of sediments. Graded storm beds, fossil distribution and the *Skolithos* ichnofacies are here considered as indicative of upper shoreface deposits.

4.3. Upper shoreface facies (US)

This facies primarily comprises fine-grained sandstone and siltstone with large scale, low-angle, hummocky cross-stratification (1–2 m in average wavelength), parallel lamination and an overall fining-upward trend (Fig. 3). Sandstone beds are also characterized by extensive planar and sub-planar fossil traces, whereas no macroscopic shell remains were observed. No mudstone intercalation has been observed, whereas glauconitic intervals are recurrent. *Zoophycos* traces (Fig 5) are by far the most frequent of this facies: despite the vast majority range between 35 and 45 cm in size, several intervals preserve feeding traces that exceed 140 cm in diameter, with a measured maximum planar extension of 165 cm. Other identified soft-ground ichnogenera include *Thalassinoides*, *Planolites*, and *Chondrites* and therefore, together with *Zoophycos* are referred to the *Cruziana* ichnofacies. Sedimentological data suggest an upper shoreface environment with intense wave influ-ence on sediment distribution and events of abrupt decrease in sediment supply (or sediment bypass). The *Cruziana* ichnofacies develops on soft- grounds of shallow-marine, permanently subtidal, and unconsolidated substrates. The ichnogenus *Zoophycos* has an extremely broad paleo-bathymetric range (Zhang et al., 2015b), but are commonly restricted to intervals characterized by fine, muddy sands and less effected by turbidity flows or significant bottom currents. Lithological characteristic and the occurrence of *Zoophycos* are consistent with deposition in cir-calittoral sites.

4.4. Offshore facies (O)

This facies consists of exclusively siltstone- and mudstone-dominated deposits, showing thin-bedded laminar stratification (between 3 and 25 mm). There are no wave-formed structures, and intense bioturbation in mudstone intervals (tubular structures are identifiable) obliterated all sedimentary structures. This facies occurs in close association with shoreface deposits (Fig. 4). When facies O (Fig. 2C) deposits overly very coarse beds of other shallower facies, the transition is sharp, suggesting a rapid shift in depositional condition. No fossil remains were observed in this facies. Fine-grained siltstone and mudstone beds present in this facies suggest inner shelf environment, unaffected by the action of waves and major currents.

5. Morphology of the *Zoophycos* from the Yukon River

Zoophycos start occurring at 20 cm above the base of the section together with a rich ichnoassemblage of *Conichnus* (between other traces, Fig. 4 and Table 1). Two different morphotypes were observed, i. e., form A (unlobed) and B (lobed). The morphotypes share common architectural and textural features. Specifically, both morphotypes consist of a thin layer of bioturbated sediment (lamina or spreite sensu Olivero and Gaillard, 2007; see also Zhang et al., 2015a). The lamina is helically coiled around a central axis and tapers vertically from a flat area to an apical point (apex). As such, the 3D structure is roughly conical. The maximum number of whorls is 2. The lamina is characterized by arched structures (primary lamellae) that represent the positions of a single forming tunnel moving though the sediment (see Olivero, 2003). There is no evidence of secondary lamellae, i.e., arched structures located in the spaces between the primary lamellae (Olivero, 2003). When preserved, the burrow fill is darker than the host rock and consists of millimetric ellipsoidal pellets. The structures, especially the
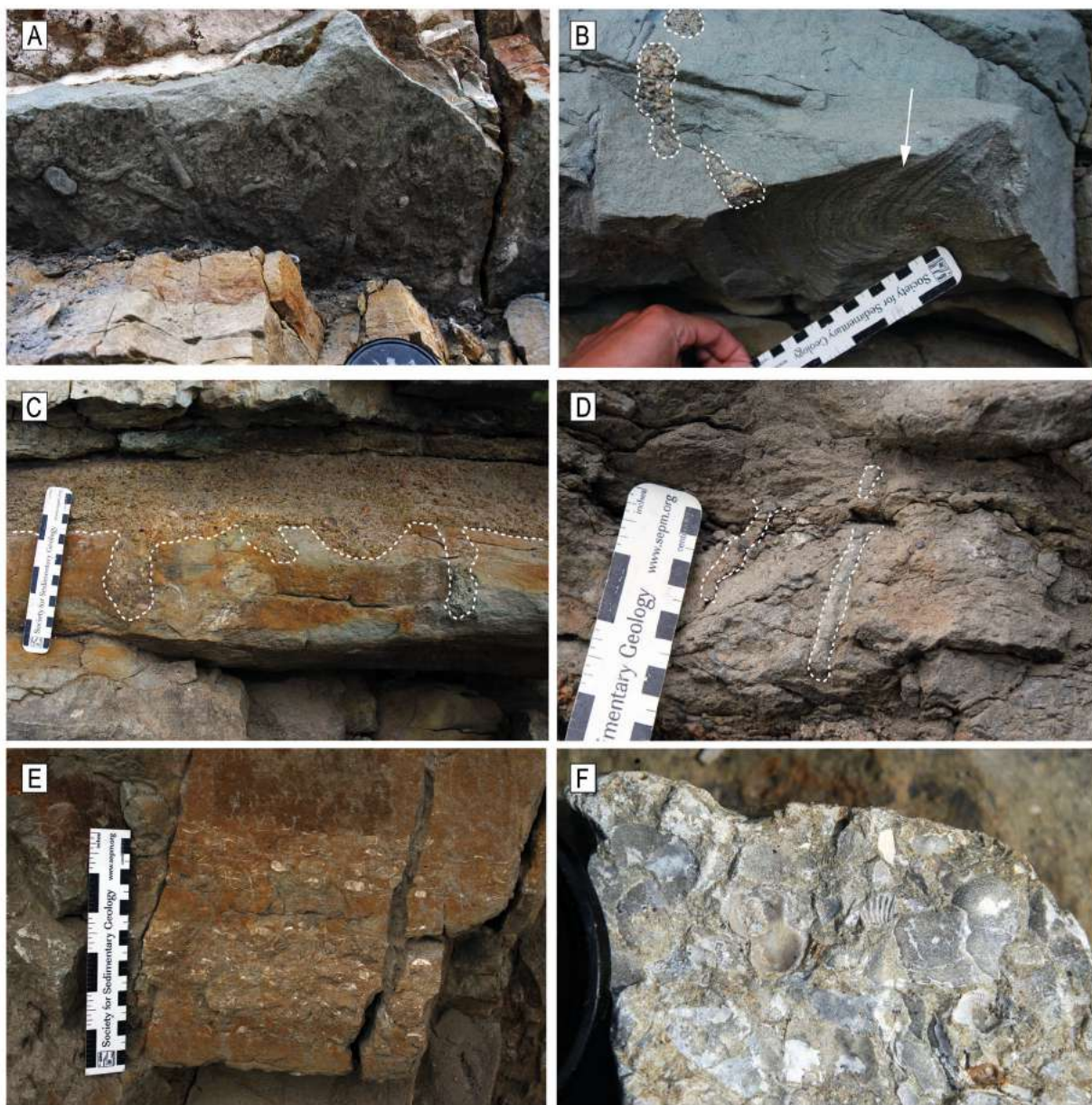
Fig. 4. A–D, trace fossils (*Conichnus*) and body fossils (E, F, brachiopods, bryozoans) co-occurring in the *Zoophycos*-bearing ichnocoenosis.

lobed form B, frequently display a marginal tube. Many traces present the typical central tube which marginally spread creating a fan-like lobe of coarser (Fig. 5), more spaced spreiten and a more dorsally pronounced axis of coiling, which forms a sort of proximal "stem" (Fig. 5; e. g. Olivero and Gaillard, 2007). The depth of this axis can range to 20 cm and up to two coils can be counted in the three dimensionally preserved traces (Fig. 5). The two morphotypes differ in the shape of the lamellae and of the lamina outline.

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

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

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

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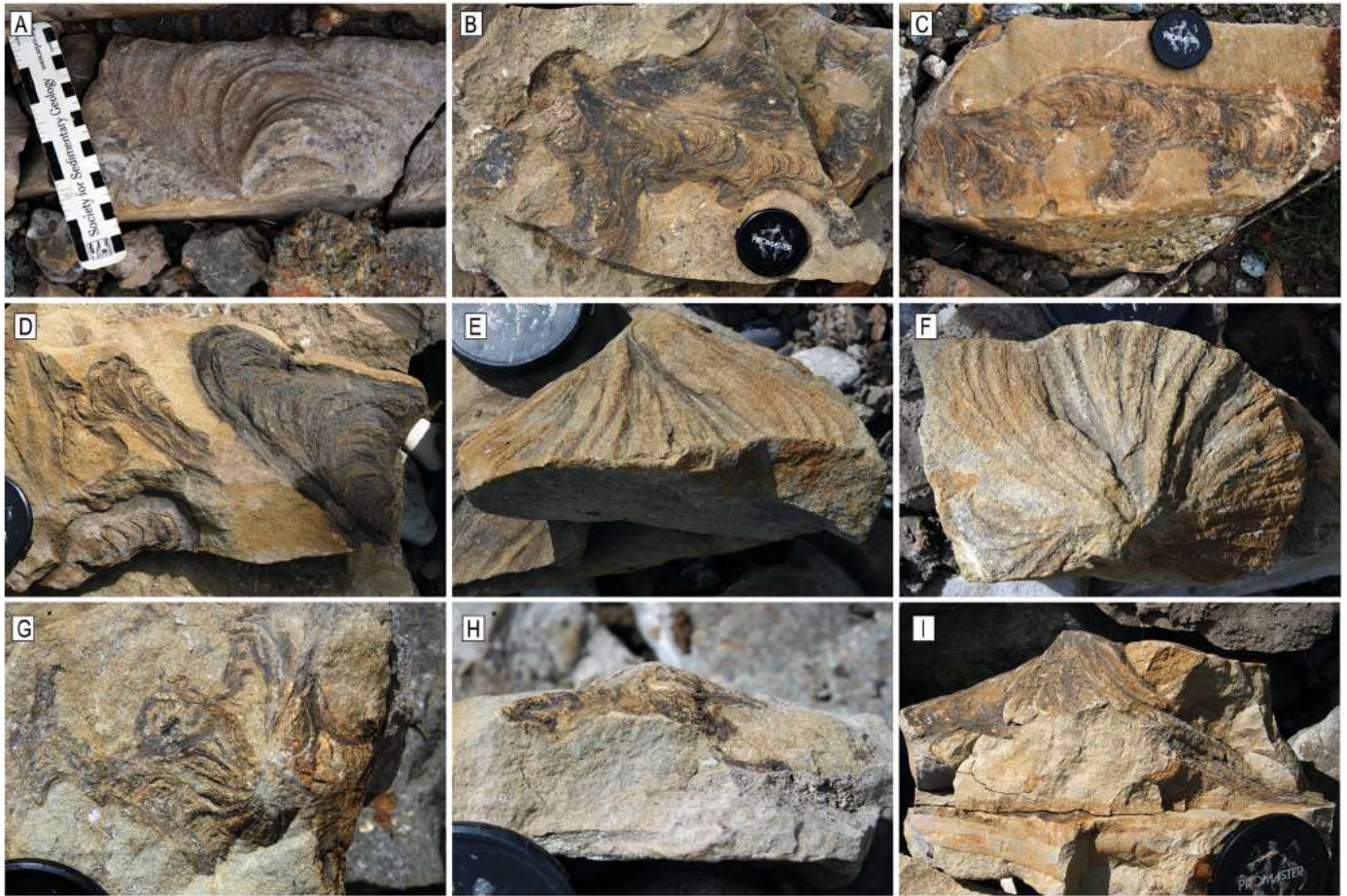
Fig. 5. A–D, *Zoophycos* traces with well-developed spreiten and lobes; E–I, details from the three-dimensionally developed *Zoophycos*.

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

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

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

The studied spreite structures share the major architectural elements with the ichnogenus *Zoophycos*, which is characterized by (1) a spreite; (2) protrusive burrows of variable length and orientation, arranged in helicoid spirals; (3) circular, elliptical or lobate outline; (4) a marginal tube, which is often, but not always, present (Frey, 1970; Hantzschel, 1975; Kotake, 2014; Lowemark et al., 2005; Lowemark and Schafer, 2003; Rodríguez-Tovar and Uchman, 2004; Lowemark, 2015). As such, the studied structures are attributed to the ichnogenus *Zoophycos*. The morphological heterogeneity of *Zoophycos* is so large that, perhaps, it would be better to refer to a 'Zoophycos group' rather than to a single ichnogenus (Uchman, 1999; see also Olivero, 2003). Early description of ichnoassemblages from estuarine Permian beds in the arctic (Miller, 1991) reported the occurrence of *Spirophyton*, an ichnotaxon characterized by spiral-like structures and opportunistic strategies (Bromley, 1996). Although superficially similar to *Zoophycos*, *Spirophyton* presents unlobed edges lacking marginal tubes (Jensen, 1997; Miller, 2003;

Seilacher, 2007).

Following Knaust (2004), no determination at the ichnospecies have been done for the studied specimens because of the poor ichnotaxonomic status of *Zoophycos*. However, the studied *Zoophycos* can be readily compared with the morphotypes described in previous studies. Accordingly, the here studied form A resembles morphotypes A and B of Olivero (2003), which present simple or very slightly lobate outline. Similarly, form A resembles the "cock-tail shaped spreiten with J-shaped primary lamellae" described by Zhang et al. (2015b). The cock-tail *Zoophycos* of Zhang et al. (2015) is typical of Palaeozoic nearshore to offshore settings. By contrast, the here studied form B resembles morphotype D of Olivero (2003), which is characterized by strongly lobate margins and lack of secondary lamellae. Morphotype D is typical of Late Cretaceous units deposited in deep slope to basin environments (Olivero, 2003). It should also be noted that the size range of the studied *Zoophycos* matches the width size range (140–160 cm) of the largest *Zoophycos* traces recorded in the Phanerozoic (Zhang et al., 2015b). According to Zhang et al. (2015b), the width of the *Zoophycos* spreite increased from 18 cm in the Lower Palaeozoic to 43 cm in the Cenozoic.
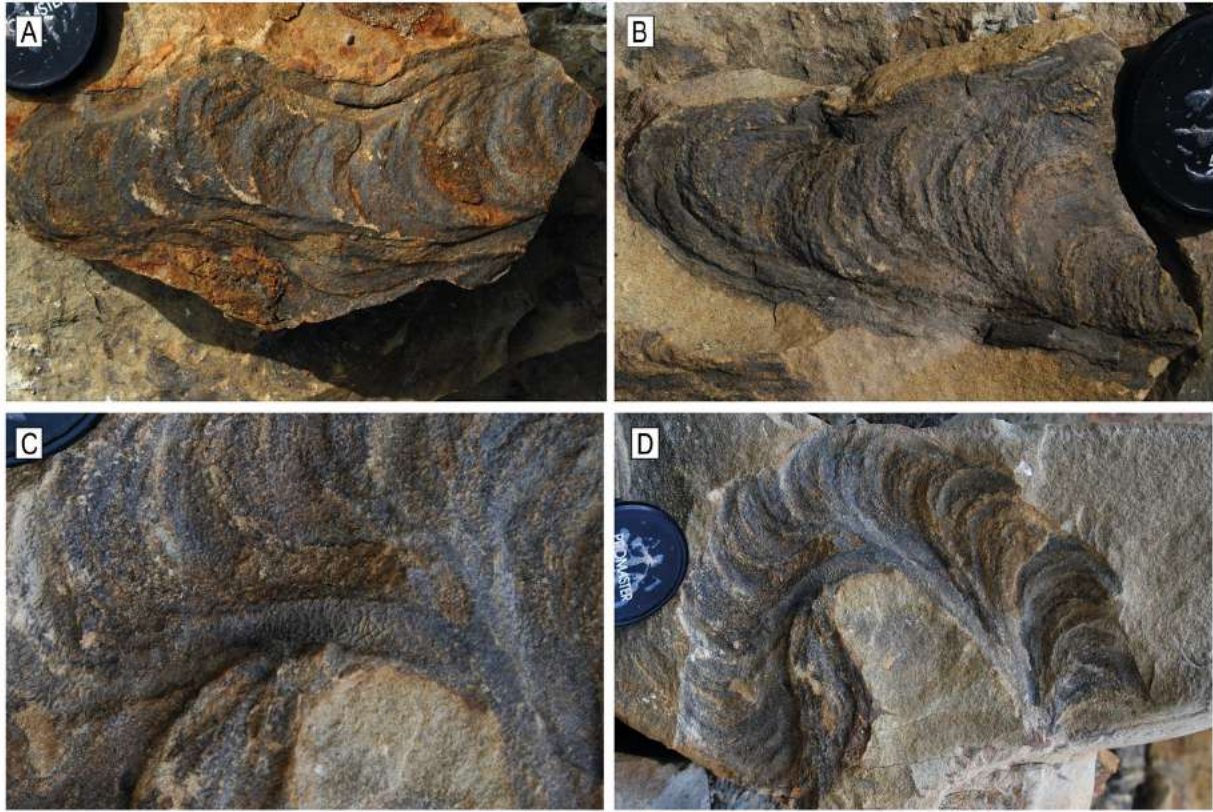
Fig. 6. Close-up of some of the best preserved *Zoophycos* laminae from this section showing textural details from the lamellae and marginal tube.

Both forms of *Zoophycos* from the Yukon River are filled by elliptical pellets. These are interpreted as a bioprint, that is, the "tracemaker's signature", a set of characters that allow recognition of the producer (Kopaska-Merkel and Rindsberg, 2015). Because both forms of *Zoophycos* share the same bioprint, they plausibly shared the same tracemaker. A vermiform, soft-bodied producer is a viable hypothesis in light of the pellet-filled tunnels of the modern polychaete *Nereis* (Kulkarni and Panchang, 2015). This hypothesis is also supported by the modern terebellid polychaete *Terebellides stroemi,* constructing inclined, *Rhizocorallium*-like spreite burrows with *Coprolus*-like fecal pellets (Knaust, 2013). The fecal pellets within the Yukon River *Zoophycos* are morphologically comparable with coprulid pellets. According to Knaust (2020), Coprulidae comprise rounded, smooth or sculptured, structureless or structured coprolites and cololites. Various animals produce similar pellets, foremost polychaetes and other annelids, as well as enteropneusts, gastropods, bivalves, tunicates and insects (Knaust, 2020). Pellets are also associated with Bohemian Ordovician body fossils (Bruthansová and Kraft, 2003) and they are found in Palaeozoic burrows as well (Uchman et al., 2005; Baucon et al., 2020). The excellent preservation of fecal pellets in the Yukon River *Zoophycos* suggests low-oxygen conditions in the interstitial waters, which are known to play a role in preserving fecal pellets (Podhalańska, 2007; Neto de Carvalho et al., 2016; Baucon et al., 2020).

The presence of pellets has also an important behavioral significance because it shows that the tracemaker actively filled its tunnels. According to the reviews of Lowemark and Schafer, 2003 and Lowemark et al., 2004, the behavioral models of *Zoophycos* are the (1) deposit feeder model; (2) detritus feeder model; (3) refuse dump model; (4) gardening model; (5) cache model. The morphology of the Yukon River structures is compatible with several of the proposed ethological models for *Zoophycos,* with specific emphasis on the deposit feeding, gardening and cache models.

In the deposit feeder model, the tracemaker is feeding on the outer wall, and excreting its feces on the inner wall (e.g., Wetzel and Werner, 1981; see also the reviews of the *Zoophycos* models in Lowemark and Schafer, 2003 and Lowemark et al., 2004). This model can explain the morphology of the Yukon River *Zoophycos,* with specific reference to the lobed form B. In fact, the general morphology of form B is compatible with a sensory-driven, directed search for heterogeneously distributed trophic resources within the substrate. Animals seek to maximize their net rate of energy intake, that is, the difference between energetic benefit and their energetic 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, 2006). 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 toward 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 (Olivero 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 Lowemark 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 *T. stroemi,* which feeds on suspended detritus (Moverley et al., 1986). In fact, *T. stroemi* produces inclined, spreite burrows filled with *Coprolus*-like fecal 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 Lowemark and Schafer, 2003, and Lowemark 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 Hopner, 1994; see also Baucon et al., 2020). According to the gardening model, the pro-ducer 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 Lowemark and Schafer, 2003 and Lowemark 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 Lowemark and Schafer, 2003 and Lowemark 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 neces-sarily 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 morphological evolution of one of the most iconic and widespread ichnotaxon in paleoichnology. It should be highlighted that in this section we focus on the morphological evolution of *Zoophycos*, intended as the process by which *Zoophycos* gradually changed in shape across the Phanerozoic. This morphological evolution plausibly reflects the evolution of the *Zoophycos* tracemakers via natural selection, but, at present, it is not possible to connect morphological changes in *Zoophycos* to genetic changes in the tracemakers.

Specifically, several burrows can be regarded as 'extended pheno-types' (sensu Dawkins, 1989), that are, traits influenced by genetics but extended outside the body of the individual organism (Dawkins, 1989; Lewarch and Hoekstra, 2018; Turner, 2003). Accordingly, burrows can be regarded as traits that can evolve through natural selection (Hu and Hoekstra, 2017; Turner, 2003; Weber et al., 2013). For instance, the burrow of the modern *Peromyscus* mice has undergone recent morpho-logical innovations during the diversification of this genus, and discrete genetic modules are responsible for complex burrow evolution (Weber et al., 2013). Among trace fossils, *Zoophycos* is often proposed as an extended phenotype of its producer(s) (e.g., Miller III, 2002; Miller III, 2003; Olivero, 2003).

It is therefore tempting to establish a direct link between the morphological evolution of *Zoophycos* and the (Darwinian) evolution of its tracemakers. However, convergent evolution complicates the

evolutionary understanding of trace fossils. Different tracemakers can produce similar traces when behaving similarly (Bromley, 1996), therefore, structures identified with *Zoophycos* were possibly produced by different lineages of marine invertebrates during the Phanerozoic. In light of the challenges posed by convergent evolution, in this section we primarily focus on morphological evolution only.

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

To evaluate the evolution of lobed *Zoophycos,* we produced graphs of (1) the lobed ratio (Fig. 7A), that is the proportion between the number of sites with lobed *Zoophycos* and (2) the total number of sites with lobed *Zoophycos* (Fig. 7B). Although the oldest *Zoophycos* of the dataset is Cambrian in age, no lobed *Zoophycos* are documented before the Devonian (Fig. 7). In the Palaeozoic, the lobed ratio increased from the Devonian to the Permian (Fig. 7A). The Triassic experiences a marked drop in the number of sites with *Zoophycos* (Fig. 7B), although the lobed ratio reaches a local peak (Fig. 7A). The lobed ratio and the number of *Zoophycos*-bearing sites increase from the Jurassic onwards (Fig. 7B).

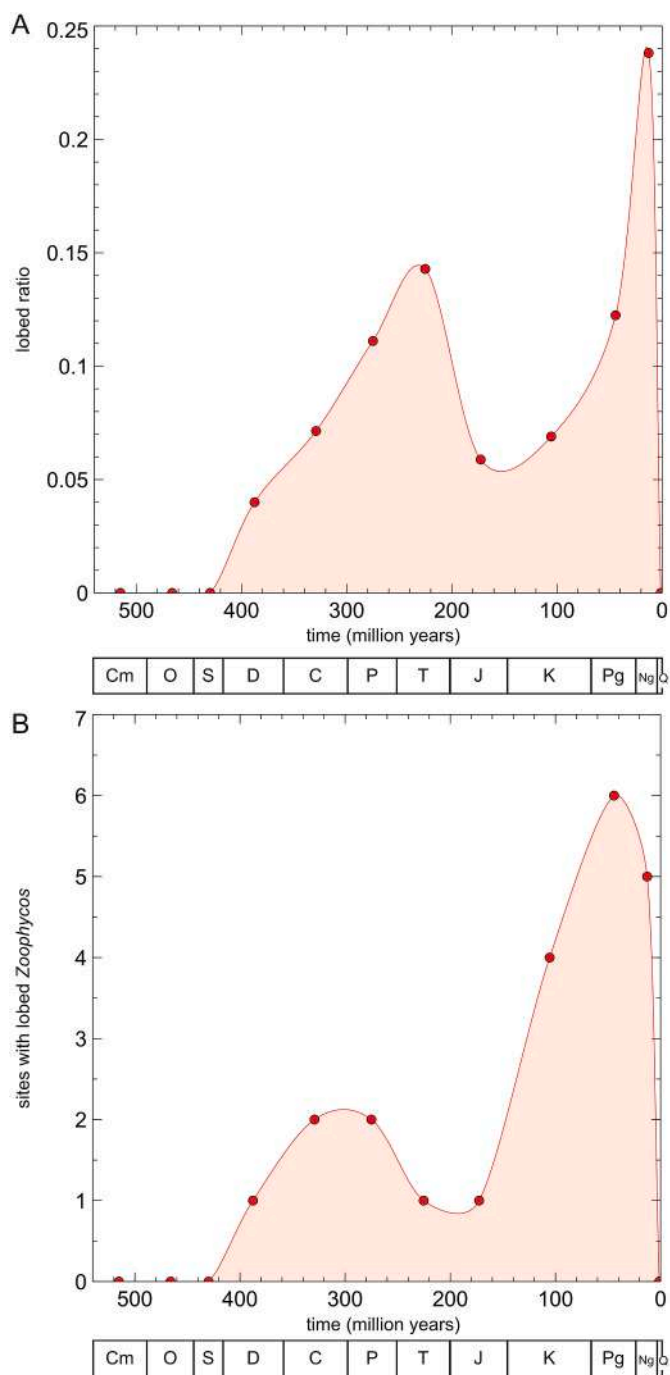Accordingly, two 'Golden Ages' of lobed *Zoophycos* are defined: (1)

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*.

Carboniferous-Permian and (2) Cretaceous-Neogene. Overall, lobed specimens were much commoner in the second interval than during Palaeozoic times (Fig. 7A). It should be noted that the first (Palaeozoic) Golden Age of lobed *Zoophycos* is preceded by the first (Devonian) radiation of *Zoophycos*, which was previously established by Zhang et al. (2015b). The second Golden Age partially coincides with the last

(Cretaceous-Cenozoic) *Zoophycos* radiation established by Zhang et al. (2015b).

6.2. Lobed Zoophycos as a product of terrestrialization

The two Golden Ages of lobed *Zoophycos* (Carboniferous-Permian and Cretaceous-Neogene) are both linked with changes in nutrient dynamics. The widespread appearance of lobed *Zoophycos* is contemporaneous with the oceanographic changes that have occurred during the Middle Jurassic, when deep-sea bottom nutrient conditions were greatly improved by increased particulate organic carbon and dissolved organic carbon derived from surface plankton bloom (Zhang et al., 2015b). It should be noted that this event was followed by a major radiation of land plants in the Cretaceous, which also increased the supply of nutrients to the oceans (Allmon and Martin, 2014). The increased shelf areas and plankton blooms was hypothesized to have driven the high occurrence frequencies of *Zoophycos* in the Cretaceous–Cenozoic (Zhang et al., 2015b).

Another profound change in nutrient cycling begun with the Palaeozoic origin of wood in plants, permanently shifting the distribution of active carbon species within the global carbon cycle by the end of the Mississippian (Strother et al., 2010). This phase of the terrestrialization process has its roots in the Devonian (Givetian-Frasinian), with the rise of lignophytes (Strother et al., 2010; Kenrick et al., 2012). Large trees with well-developed rooting systems are unlikely to predate the Middle Devonian (Kenrick et al., 2012). Intriguingly, the earliest documented lobed *Zoophycos* dates back to the Givetian (Miller, 1979). The Devonian radiation of lobed *Zoophycos* coincides with the first *Zoophycos* radiation, which was linked to the rise of deep-rooted plants (Zhang et al., 2015b). Before of the major intervals of diversification of land plants (Devonian expansion of land plants and the Cretaceous expansion of angiosperms), the supply of nutrients to the oceans by terrestrial runoff was lower than it was afterward (Allmon and Martin, 2014).

Contemporaneous events do not necessarily mean causality; there-fore, a question might arise: How can nutrient enrichment favor the evolution of lobed *Zoophycos*? The answer is provided by the U-shaped marginal tube of *Zoophycos,* which represents an efficient adaptation to dwell into nutrient-rich but oxygen-poor substrates. Specifically, the increased input of nutrients to coastal areas has been suggested as an important contributor to declining trends in bottom water oxygen concentrations (Diaz and Rosenberg, 1995). Indeed, there is a known interaction between supply of nutrients, primary production, sedimentation and oxygen consumption (Rydberg et al., 1990). Consequently, from a macroevolutionary perspective, any global increase in seawater nutrients is expected to favor biological adaptations to cope with low-oxygen substrates. Among such adaptations, U-shaped burrows allow to efficiently induce the flow of oxygenated seawater within the sub-strate (Bromley, 1996). For this reason, *Zoophycos* with U-shaped tun-nels are linked with poorly oxygenated conditions, whereas *Zoophycos* with J-shaped tunnels, connected with only one opening to the seafloor, was taken to suggest a well-oxygenated setting (Wetzel and Werner, 1981; Gong et al., 2008). A decline in the absolute (Fig. 7B) number of lobed *Zoophycos* is observed in the Triassic. This decline in lobed *Zoo-phycos* is plausibly explained by the effects of the end-Permian extinction on biodiversity and nutrient dynamics. In fact, the aridity of the Late Permian climate, the collapse of the peat mire ecosystem at the Permian-Triassic boundary and the protracted arid conditions during the Early Triassic reduced the terrigenous influx of nutrients into the ocean (Zharkov and Chumakov, 2001; Michaelsen, 2002; Benton and Newell, 2014).

The two Golden Ages of lobed *Zoophycos* occur in different environmental settings. The Yukon River *Zoophycos* well exemplifies this phenomenon, since its shoreface setting differs from the typical deep-sea environment of the Mesozoic and Cenozoic lobed specimens. Lobed forms of *Zoophycos* have a bathymetric range spanning from the lower shelf-slope in the Mesozoic to the bathyal realm in the Cenozoic. In

particular, the here studied form B resembles the lobed *Zoophycos* without secondary lamellae described by Olivero (2003), who suggests that lobed *Zoophycos* are typical of Late Cretaceous units deposited in deep slope to basin environments. This different scenario can be explained with the Mesozoic increase in competition in shallow-marine settings. In fact, according to Zhang et al. (2015b), the accelerated competition in the Mesozoic neritic seas might have forced the pro-ducers of *Zoophycos* to migrate to bathyal environments. In addition, the Devonian rise of lignophytes may have had a more profound impact on shallow-marine environments than on the deep-sea, since the nutrient increase was linked to the land-sea supply of nutrients. By contrast, the Cretaceous expansion of angiosperms was predated by plankton radia-tions, which plausibly had a more direct impact on deep-sea settings. In fact, the Middle Jurassic was characterized by a major ecological tran-sition within the coccolithophores, and the radiation of one of the principal families of cyst-forming dinoflagellates (Wiggan et al., 2018).

7. Conclusions

A paleontological reconnaissance survey of an Early Permian unit along the Yukon River in east-central Alaska has provided new ichno-logical 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. How-ever, the proposed hypothesis cannot be tested against a neoichnological analogue of *Zoophycos,* which has not been described yet. Further neo-ichnological research is therefore encouraged in this direction.

Two 'Golden Ages' of lobed *Zoophycos* are distinguished in this study: (1) Carboniferous-Permian and (2) Cretaceous-Neogene. This distribu-tion 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 sub-strates. The characteristic U-shaped marginal tube of lobed *Zoophycos* is among these adaptations. Further research in other Palaeozoic 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 lithos-tratigraphy with ichnological analysis that has added new insight into the macroevolution of this enigmatic ichnotaxon for the whole Phanerozoic.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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