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 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.

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.

Permian lobed *Zoophycos* as the product of the terrestrialization process: behavioral innovation in the Tahkandit Limestone Formation (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 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

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; Häntzschel, 1975; Lowemark and Schafer, 2003; Rodríguez-Tovar and Uchman, 2004; Löwemark et al., 2005; Kotake, 2014; Löwemark, 2015). *Zoophycos* has been a subject of scientific interest since the 19th century, when Johann Gotthelf Fischer von 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 Massalongo (1851) established the genus *Zoophycos*, supporting the botanical origin of the trace fossil. The botanical interpretation of *Zoophycos* was still popular in the 1900s (e.g., Barsanti, 1902), whereas Kryschtofowitsch (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, 2007; Löwemark, 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 ~~have been~~ 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; Löwemark et al., 2004; Olivero and Gaillard 2007; Löwemark, 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; Löwemark and Schäfer 2003; Seilacher 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 (Paleozoic) 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 ~~has been~~ 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; Löwemark 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 Paleozoic, more elaborated 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 Formation (*sensu* Beauchamp, 1995) of the Yukon–Charley Rivers National Preserve, east-central Alaska. These traces 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 Formation, a prominent but incompletely understood marine unit found through the region? (2) What is the shape of the Yukon River *Zoophycos*? (3) Why lobed *Zoophycos* are found in the Permian Tahkandit Limestone Formation?

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 Formation 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 ~~merge~~ of the Nation River (GPS: N65°10’915”; W141°42’205”), approximately 30 km west of the U.S. – Canada border. The lower section of the Tahkandit Limestone Formation, 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 characteristic, with particular attention on identified ichnocenoses. General overall geological data used in this study are provided in the geological map of Brabb and Grant (1965). Specimens referred here were collected on the ancestral homeland of the Han Hwëch'in Athabascans and are housed at the Perot Museum of Nature and Science, Dallas, Texas. The morphology of *Zoophycos* is described according the terminology of Olivero (2003).

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; 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 1967; Brabb and Churkin 1967; 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 meters of deposits characterized by ~~alternated~~ siliciclastic beds and finely laminated, organic-rich shale. Both the Nation River and the Tahkandit Limestone formations ~~have been~~ folded by a relatively small ~~anticline~~ structure and consequently affected by vertical normal faulting; consequently, Tahkandit deposits show a dip of 62 degrees toward the north-west. The Tahkandit Limestone ~~Formation~~ (Fig.1) ~~has been~~ informally divided into two lithostratigraphic unit, the basal Sandstone unit, and the overlying Limestone unit (Brabb and Grant 1971). The lower interval is represented by approximately 15 meters of grayish-green, glauconitic sandstone and conglomerate consisting primarily of chert and quartz grains. Brachiopods are by large the most abundant fossils, whereas bivalves, corals, arenaceous foraminifera, and bryozoans are scarce. The 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 at the top of the lower unit (Brabb and Grant 1971, and references therein, this study) support an Early Permian (Cisuralian) age and shallow marine to estuarine/tidal environments. 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 is a packstone with fragments of brachiopod and thin-shelled bivalves, bryozoans, and foraminifera. Finally, the Tahkandit Limestone ~~Formation~~ 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.

4. Sedimentology and Paleontology

The basal contact between the Nation River and Tahkandit Limestone formations is only partially exposed (Fig. 2A): however, the sharp juxtaposing 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 fossil trace assemblages, depositional facies are identified in the type section of the Tahkandit Limestone Formation 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, dwelling 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 occasionally 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 the 80% of the deposits and are also found in undisturbed life position/assemblages. No ichnofossils have been observed in finer-grained conglomeratic deposits, with the exception of *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) have been observed and interpreted as tempestite deposits. Sandstones are also characterized by a rich and diverse soft-ground related fossil trace 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 silt with large scale, low-angle, hummocky cross-stratification (1–2 meters in average), 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 ~~have been~~ 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 a lower shoreface environment with intense wave influence on sediment distribution and events of abrupt decrease in sediment supply (or sediment by-pass). The *Cruziana* ichnofacies develops on soft-grounds of shallow-marine, permanently subtidal, and unconsolidated substrates. The ichnogenus *Zoophycos* has an extremely broad paleobathymetric range (Zheng 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 circalittoral sites.

4.4 Offshore Facies (O)

This facies consists of exclusively silt- and mud-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 finer deposits of shoreface deposits (Fig. 4). When facies O (Fig. 2C) deposits overly very coarse beds of other shallower facies, the transition is abrupt, suggesting a rapid shift in depositional condition. No fossil remains ~~have been~~ 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 ~~have been~~ 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, 2015).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 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. Oliviero 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 sub-parallel 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 140–160 cm.

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; Häntzschel, 1975; Kotake, 2014; Löwemark et al., 2005; Lowemark and Schafer, 2003; Rodríguez-Tovar and Uchman, 2004; Löwemark, 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.

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 faecal pellets (Knaust, 2013). The fecal pellets within the Yukon River *Zoophycos* fit with the characteristics of the ichnofamily Coprulidae, which comprises rounded, smooth or sculptured, structureless or structured coprolites and cololites (Knaust, 2020). Various animals produce Coprulidae, 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 Paleozoic 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 Löwemark and Schäfer, 2003 and Löwemark 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 a deposit feeder, 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 Löwemark and Schäfer, 2003 and Löwemark 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, 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 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 ~~has been~~ implemented 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 calculated (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). The lobed ratio increased from the Devonian to the Permian, dropped in the Triassic, and increased again from the Jurassic onwards (Fig. 7B). Accordingly, two ‘Golden Ages’of lobed *Zoophycos* are distinguished*:* (1) Devonian-Permian and (2) Jurassic-Neogene. Overall, lobed specimens were much commoner in the second interval than during Palaeozoic times (Fig. 7A). It should be noted that these two Golden Ages of lobed *Zoophycos* partially coincide~~s~~ with the first (Devonian) and the last (Cretaceous-Cenozoic) radiation of *Zoophycos*, which ~~have~~ previously ~~been~~ established by Zhang et al. (2015b).

6.2 Lobed *Zoophycos* as a product of terrestrialization

The two Golden Ages of lobed *Zoophycos* (Devonian-Permian and Jurassic-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 ~~have been~~ 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 Paleozoic 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 ~~has been~~ 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; therefore, 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 substrate (Bromley, 1996). For this reason, *Zoophycos* with U-shaped tunnels are linked with poorly oxygenated conditions, whereas *Zoophycos* with J-shaped tunnels, connected with only one opening to the seafloor, ~~have been~~ taken to suggest a well-oxygenated setting (Wetzel and Werner, 1981; Gong et al., 2008). The two Golden Ages of lobed *Zoophycos* are separated by the Triassic, when a decline in the relative (Fig. 7A) and absolute (Fig. 7B) number of lobed *Zoophycos* is observed. This decline in lobed *Zoophycos* 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* take place 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 producers 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 radiations, which plausibly had a more direct impact on deep-sea settings. In fact, the Middle Jurassic was characterized by a major ecological transition 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 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.

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FIGURE CAPTION

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, 1969.

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

FIG. 3: Stratigraphic column of the Nation River Fm. (Devonian, A-B), and composite section of the 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

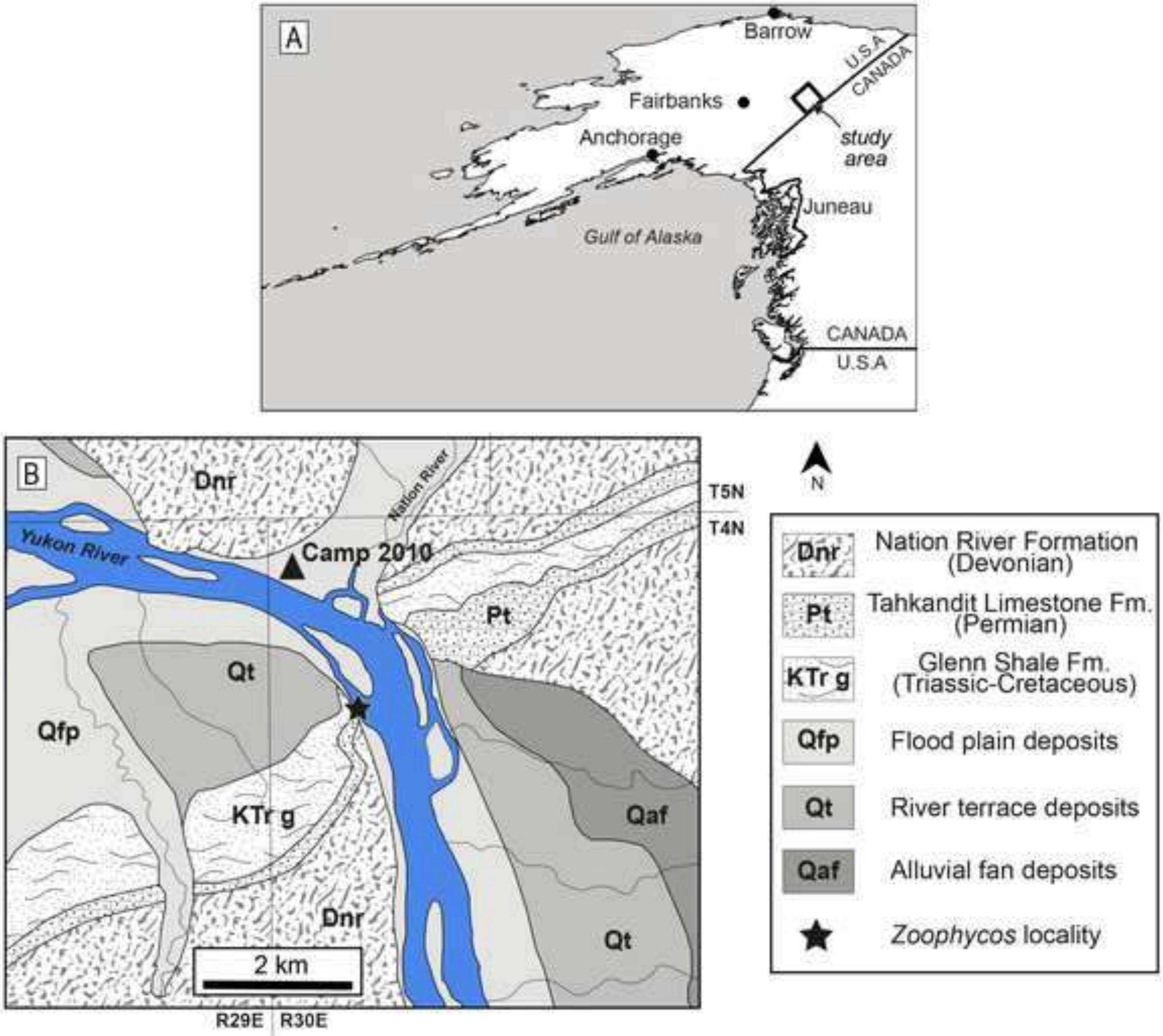

A
Barrow
U.S.A
CANADA
Fairbanks
Anchorage
study area
Juneau
Gulf of Alaska
CANADA
U.S.A
B
Dnr
Nation River
Yukon River
Camp 2010
Pt
Qt
Qfp
KTr g
Qaf
Dnr
Qt
2 km
T5N
T4N
R29E
R30E
N
Dnr
Nation River Formation (Devonian)
Pt
Tahkandit Limestone Fm. (Permian)
KTr g
Glenn Shale Fm. (Triassic-Cretaceous)
Qfp
Flood plain deposits
Qt
River terrace deposits
Qaf
Alluvial fan deposits
Zoophycos locality

Figure 2

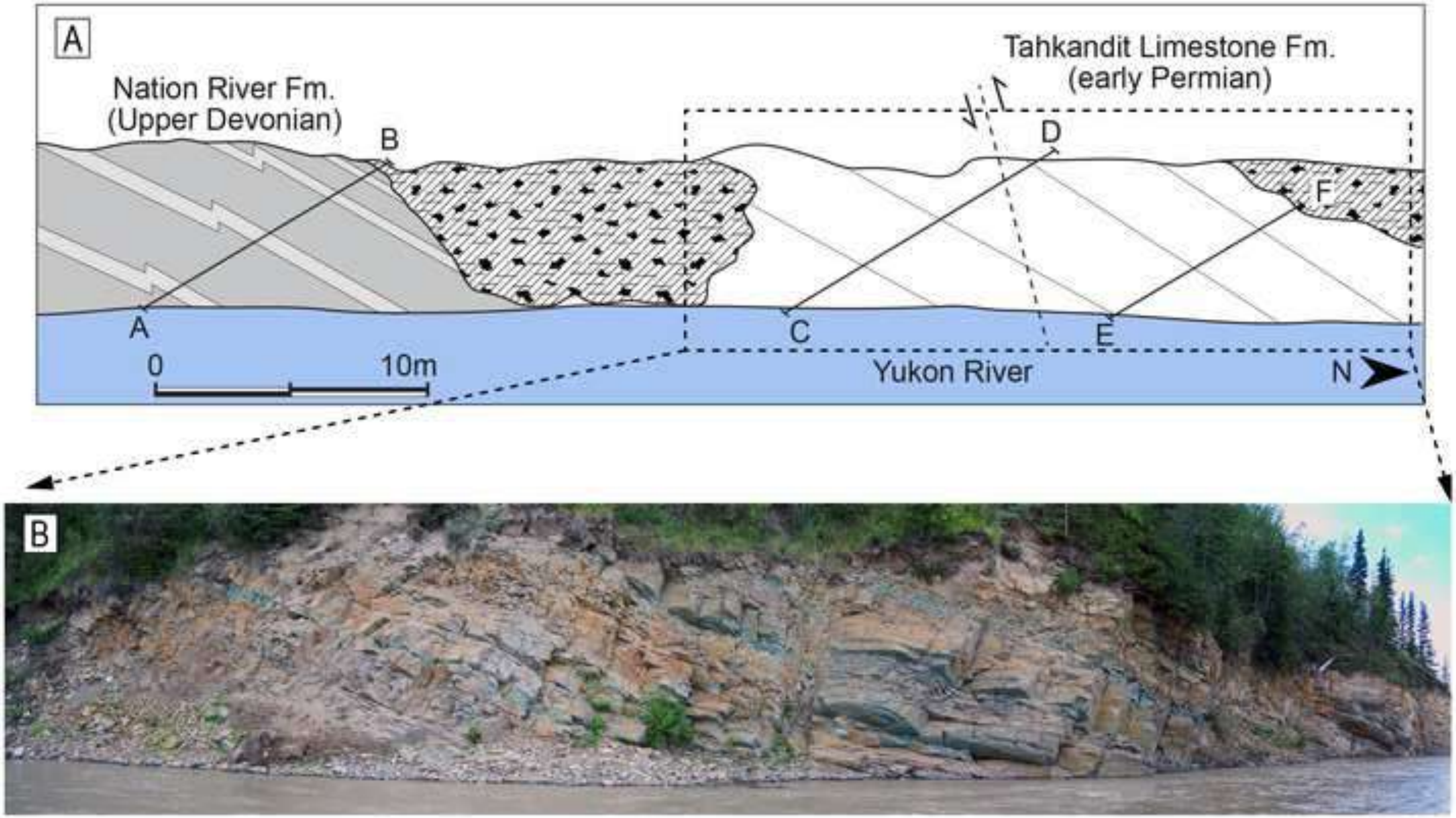

A
Nation River Fm.
(Upper Devonian)
Tahkandit Limestone Fm.
(early Permian)
B
D
F
A
C
E
0
10m
Yukon River
N
B

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

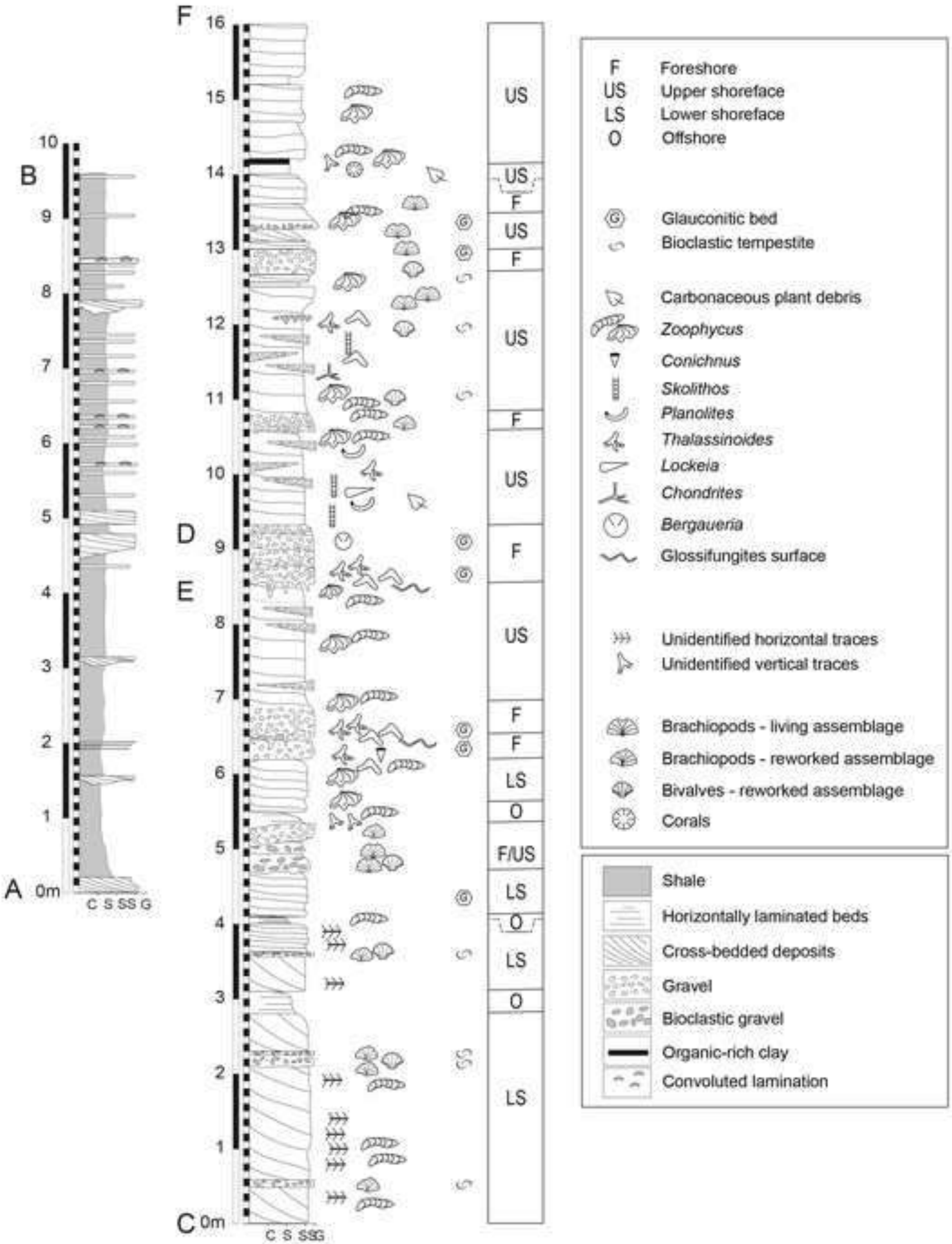
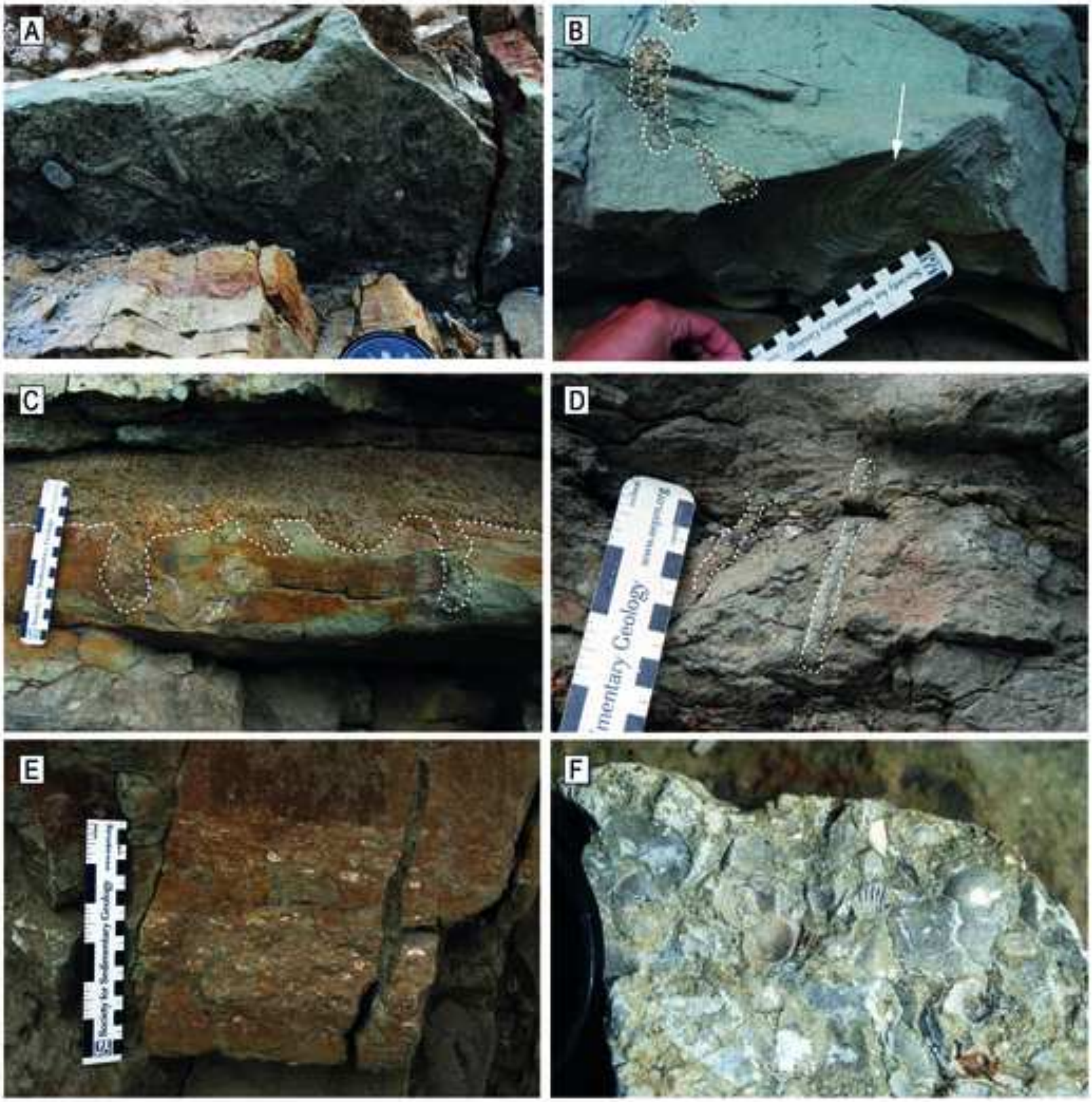


Figure 4



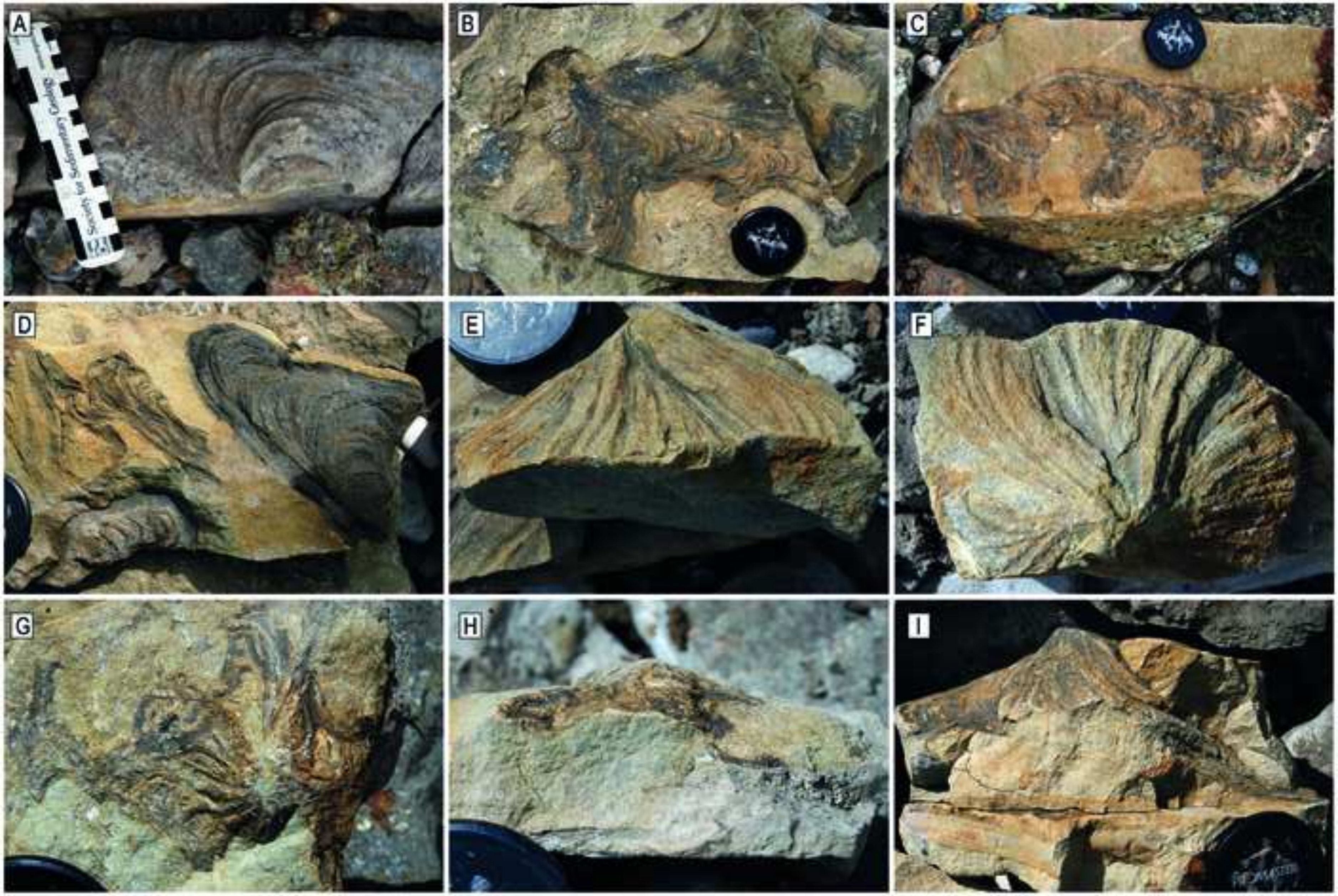


Figure 6

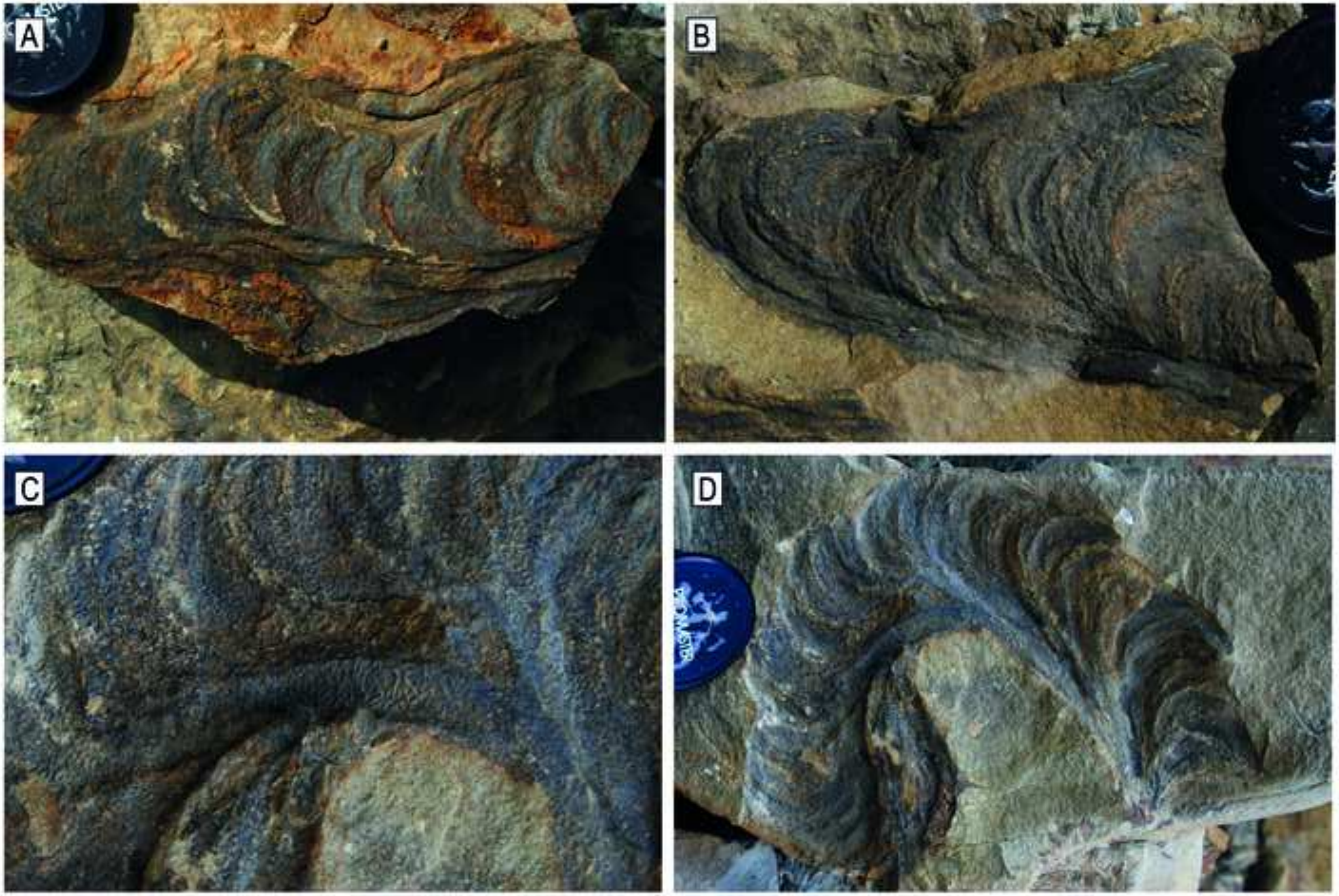


Figure 7

Click here to access/download;Figure;Fig 7A and B.jpg

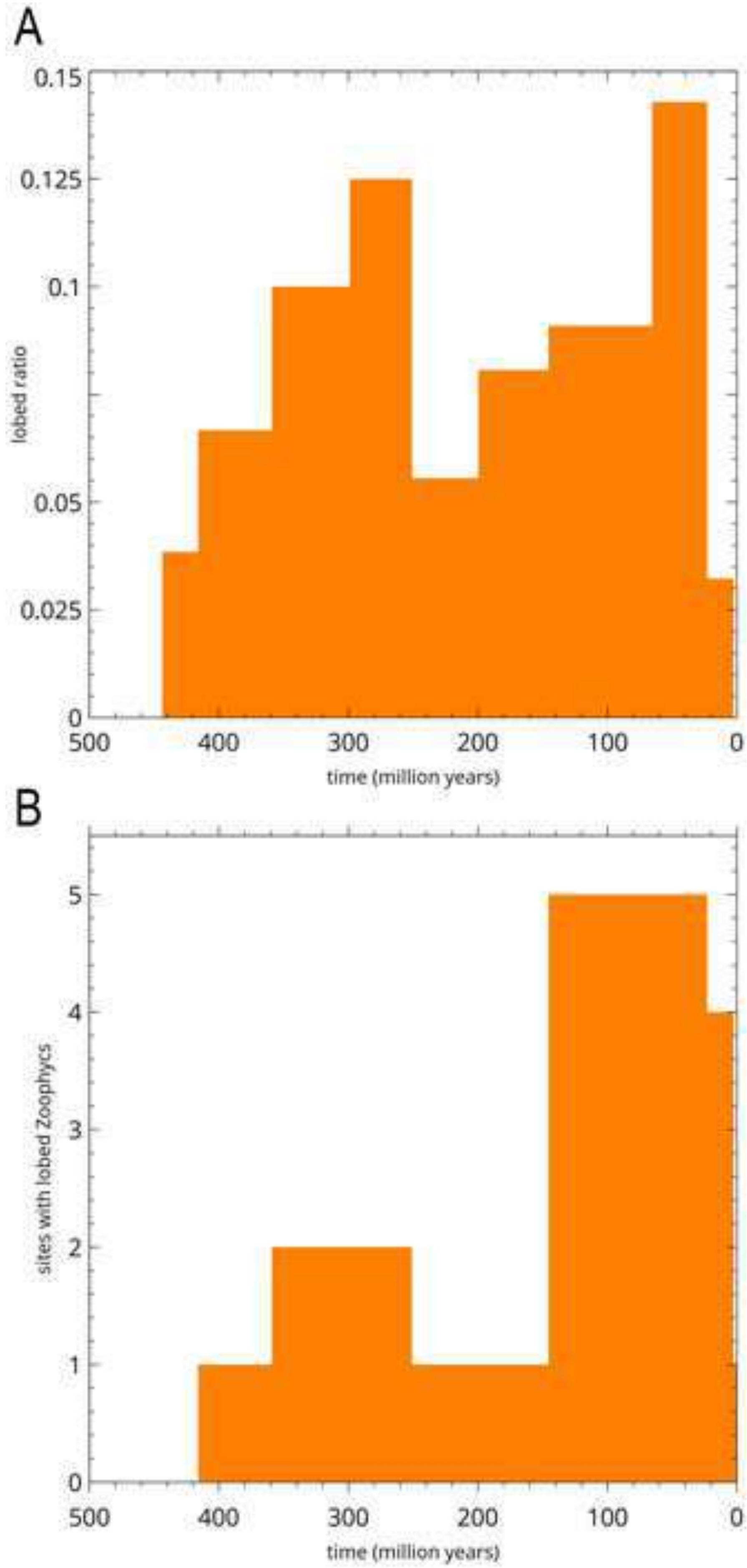


Table 1. Morphology of the trace fossils of the Tahkandit Limestone Formation.

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