



The ichnogenus *Teichichnus* Seilacher, 1955

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ABSTRACT

The ichnotaxonomy of the Phanerozoic trace fossil *Teichichnus* Seilacher, 1955 is revised and its ethology, producers and environmental affiliation are re-evaluated. Newly studied material reveals that *Teichichnus* is a sub-vertical spreite burrow with an arcuate shape, containing stacked laminae and a passively filled terminal causative burrow. Funnel-like extension of the terminal causative burrow and wall ornamentation may occur. High variation of burrow morphology is common and has resulted in the erection of 18 ichnospecies, of which only four are herein regarded as valid: *Teichichnus rectus*, *T. zigzag*, *T. patens* and *T. duplex*. These ichnospecies are characterised by their overall burrow shape, spreite morphology and, more subordinate, occurrence of branching and sculpture as recommended ichnotaxobases. Combined modes of feeding become evident, including deposit- and suspension-feeding, suggesting that *Teichichnus* is a dwelling trace rather than a feeding trace. Aside from the classical interpretation of polychaetes as producers, many features accord with an interpretation of dwelling echiurans and holothurians. This interpretation may apply for many post-Palaeozoic *T. rectus* and *T. zigzag*, whereas *T. duplex* and partly *T. patens* are likely produced by arthropods (i.e. trilobites and crustaceans). Bivalves are also considered for producing *Teichichnus*-like traces. *Teichichnus* is a marine trace fossil with predominance in shallow-marine environments. Low-diversity and high-density occurrences of *Teichichnus* characterise marginal-marine (paralic) environments with reduced salinity (i.e. brackish water) and oxygen (i.e. dysoxia), whereas in shoreface and offshore settings *Teichichnus* occurs in association with many other ichnotaxa and in low density. Deep-marine occurrences of *Teichichnus* are comparably sparse, and isolated records may indicate dysoxic bottom conditions.

1. Introduction

After its introduction from the Lower Cambrian of Pakistan, the ichnogenus *Teichichnus* Seilacher, 1955 became frequently recognised as a common trace fossil in paralic to shallow-marine, but also deep-marine deposits throughout the entire Phanerozoic and from many parts of the world.

As with many other ichnogenera, *Teichichnus* has needed a thorough revision for a long time for sustaining its ichnotaxonomic stability, and previous workers have called for it repeatedly (e.g. Frey and Howard, 1985; Corner and Fjalstad, 1993; Jensen, 1997; Mángano et al., 2002; Mángano and Buatois, 2011; Buatois et al., 2017). After such a revision, only a few well-defined ichnospecies may be applied with confidence for palaeontological, sedimentological and evolutionary interpretations. Furthermore, gradational forms to other ichnospecies and ichnogenera are common and require clearly defined ichnotaxobases for the assignment of such hybrids. Various preservation of *Teichichnus* has also given reason to assign such forms to different ichnogenera, which however are junior synonyms of *Teichichnus*.

A long-standing paradigm is the assumption that *Teichichnus*

consists of burrows produced by deposit-feeding vermiform animals, probably polychaetes, although burrowing organisms of different phyla are the likely trace makers in different periods of their geological record. An abundance of new and well-preserved material, mainly from Jurassic well cores from offshore Norway, provides insight into the burrow architecture of *Teichichnus* and the overall trace-fossil reconstruction.

This review aims chiefly for an ichnotaxonomic consolidation of valid *Teichichnus* ichnospecies based on a set of well-defined ichnotaxobases, which in the future may allow more precise description and interpretation of this common trace fossil. In addition, potential producers of *Teichichnus* are considered based on previous work and on newly analysed material, in the context of behavioural interpretations. Finally, the environmental importance of the various ichnospecies of *Teichichnus* is emphasised.

Unfortunately, many of the ichnospecies of *Teichichnus* were erected without a holotype or syntypes, whereas other holotypes are lost, inaccessible, fragmentary or difficult to obtain. Therefore, most of the evaluation is based on figured types, and the relevant specimen information, if available, is stated.

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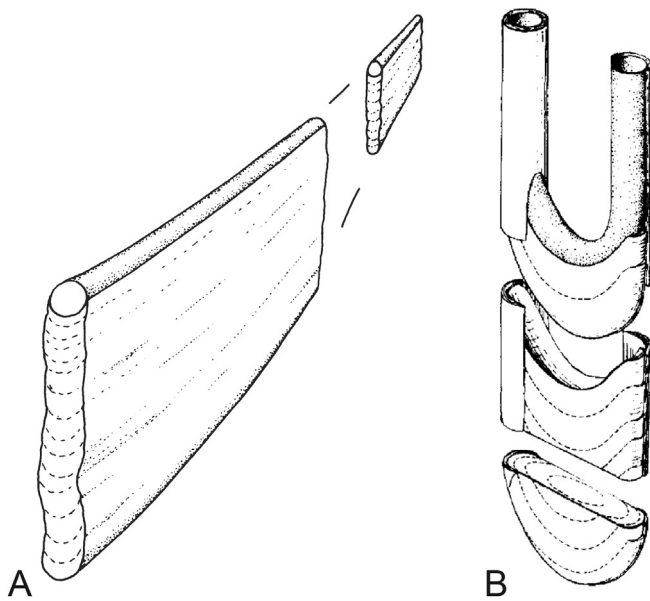


Fig. 1. Part of a retractive burrow of *Teichichnus rectus* Seilacher, 1955 with its arcuate morphology (A) in comparison with the similar U-shaped trace fossil *Diplocraterion parallelum* Torell, 1870 (B), the latter containing paralleling marginal burrow parts (A from Frey and Bromley, 1985, republished with permission of NRC Research Press; and B from Seilacher, 1967, republished with permission of Elsevier; permission conveyed through Copyright Clearance Center, Inc.).

2. The term ‘spreite’

The term ‘spreite’ (plural ‘spreiten’ or, less common ‘spreites’) originated from German language and means ‘layer, lamina’ (Stevenson, 2010). In ichnology, the term spreite relates to the laminated structure of burrow fills and its areal extent. It was adapted from the botanic literature, where this expression has been used to define the leaf blade since the 19th century or earlier. In the age of fucoids (middle of the 19th century), many burrows were interpreted as plants and the term ‘spreite’ became applied in the description of such trace fossils and remained there even with a subsequently changing interpretation (e.g. Fuchs, 1895). In the 1950-s, ‘spreite’ had its revitalisation as a common term in ichnology, after it was applied by Seilacher (1955).

3. Systematic ichnology

The ichnogenus *Teichichnus* can be included in the ichnofamily Alectoruridae Schimper in Schimper and Schenk, 1890, but has been also attributed more informally to teichichnians (Martinsson, 1965) or teichichnids (Chisholm, 1970; Fürsich, 1974a; Seilacher, 2007).

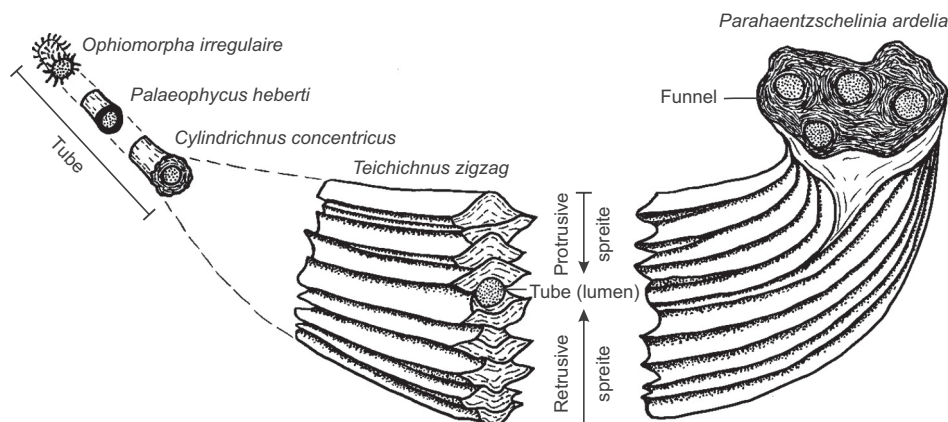


Fig. 2. Idealised reconstruction of a complete *Teichichnus zigzag* spreite burrow based on observations on Jurassic core material (mainly sandstone) from offshore Norway and inspired by Frey and Bromley (1985). Major burrow components are labelled. Individual burrow parts could give reason to be attributed to different ichnotaxa if found in isolation.

3.1. Ichnogenus *Teichichnus* Seilacher, 1955

Type ichnospecies: *Teichichnus rectus* Seilacher, 1955 (p. 378; pl. 24, fig. 1), by monotypy.

Original diagnosis: Lange, mauerförmige Versatzbauten, die aus einem Stapel von rinnenförmigen Lamellen bestehen. (Long, wall-shaped backfill minings consisting of a pile of gutter-shaped laminae. [Translation from German]).

Diagnosis (after Häntzschel, 1975, p. W114): Spreiten-bauten formed by series of long horizontal burrows stacked vertical to bedding, resembling stacked flat U-shaped roof gutters with pipe at top; wall-shaped laminar body straight or slightly sinuous; generally not branching; commonly retrusive built but can also be protrusive, up to about 50 cm. long (in M. Cam. of Öland up to 135 cm.), about 10 cm. or more in height.

Diagnosis (emended by Frey and Howard, 1985, p. 391): Bladelike to gently curved, rarely branched spreiten structures consisting of several closely concentric, horizontal or inclined, longitudinally nested burrows inosculating to simple, singular tunnels. Burrows within a given spreite displaced upward (retrusive) or downward (protrusive), and oriented at various angles with respect to bedding.

Diagnosis (emended by Orłowski, 1989, p. 222): Trace fossils with spreite, formed by few or many long, horizontal burrows stacked vertical to bedding; burrows from solid structures commonly retrusive inside sandstones. Lower and upper surfaces well preserved, commonly smooth but sometimes covered by longitudinal ridges and grooves.

Diagnosis (emended by Buckman, 1992, p. 121): Unbranched vertical wall structures comprising parallel stacked horizontal or gently inclined lamellae.

Diagnosis (emended by Schlirf and Bromley, 2007, p. 135): Long, straight, sinuous to zigzag-shaped, unbranched or branched, wall-like spreite structures, formed by vertical displacement of horizontal or oblique, erect to undulose tubes lacking wall-lining, resulting in single gutter-shaped or double gutter-shaped spreite lamellae as seen in transverse cross section. Bioglyphs may be present.

Diagnosis (emended herein): Vertical to oblique, unbranched or branched, elongated to arcuate spreite burrow with stacked convex-down and/or convex-up laminae and a passively filled terminal causative burrow. Funnel-like extension of the tube and wall ornamentation may be present.

Remarks: The development of numerous diagnoses of *Teichichnus* reflects the difficulty of creating a meaningful diagnosis capturing all characteristics. Furthermore, subsequently introduced ichnospecies have also required adjustments of the ichnogenetic diagnosis. A common issue for a consistent description of ichnospecies of *Teichichnus* is the lack of uniform ichnotaxobases by which ichnotaxa can be differentiated (Bertling et al., 2006; Knaust, 2012). *Teichichnus* serves as a good example where diverse categories of features have been applied to describe individual ichnospecies, such as overall shape (e.g. arcuate, U-

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