

IN DEFENCE OF AN ICONIC ICHNOGENUS – *OICHNUS* BROMLEY, 1981

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Wisshak, M., Kroh, A., Bertling, M., Knaust, D., Nielsen, J. K., Jagt, J. W. M., Neumann, C. & Nielsen, K. S. S. 2015. In defence of an iconic ichnogenus – *Oichnus* Bromley, 1981. *Annales Societatis Geologorum Poloniae*, 85: 445–451.

Abstract: By establishing the bioerosion ichnogenus *Oichnus*, Richard Bromley (1981) addressed ‘small round holes in shells’ and catalysed a series of still ongoing discussions on ichnotaxonomical principles. In a recent revision by Zonneveld and Gingras (2014), *Oichnus* was rejected, together with *Tremichnus* Brett, 1985 and *Fossichnus* Nielsen, Nielsen and Bromley, 2003, by means of subjective synonymisation with the presumed senior synonym *Sedilichnus* Müller, 1977. However, *Sedilichnus* is nomenclaturally unavailable, because it is an atelonym (conditionally proposed). In addition, reinvestigation of the type material of ‘*Sedilichnus*’ shows that it probably describes variably shaped oscula and thus is a genuine morphological character of the host sponge *Prokaliapsis janus*, rather than a bioerosion trace fossil. The ichnogenera *Oichnus* and *Tremichnus* are revised, leading to the synonymisation of *Balticapunctum* Rozhnov, 1989 with *Tremichnus*, and of *Fossichnus* with *Oichnus*. The refined ichnogenetic diagnoses return *Oichnus* to complete or incomplete bioerosive penetrations in calcareous skeletal substrates, commonly interpreted as praedichnia with or without signs of attachment, while *Tremichnus* (now including *O. excavatus*) exclusively refers to shallow pits passing into echinoderm skeletons that are interpreted as domichnia or fixichnia.

Key words: Ichnology, ichnotaxonomy, *Oichnus*, *Tremichnus*, *Sedilichnus*, bioerosion, predation.

Manuscript received 8 July 2015, accepted 3 August 2015

INTRODUCTION

Few trace fossils are as iconic as *Oichnus*, erected with two ichnospecies in 1981 by Richard Bromley for ‘small round holes in shells’, in conjunction with a cornerstone discussion of concepts in ichnotaxonomy. Since then, several additional ichnospecies of *Oichnus* have been established and the original diagnosis has been subjected to multiple amendments and revisions (Bromley, 1993; Nielsen and Nielsen, 2001; Donovan and Jagt, 2002; Nielsen *et al.*, 2003; Neumann and Wisshak, 2009; Ruggiero and Raia, 2014). During this ichnotaxonomical progress, *Oichnus* and its disputed potential junior synonym *Tremichnus* Brett, 1985 have continued to fuel ichnological discussions (e.g., Pickerill and Donovan, 1998; Feldman and Brett, 1998;

Nielsen and Nielsen, 2001; Todd and Palmer, 2002; Nielsen and Nielsen, 2002; Donovan and Pickerill, 2002; Neumann and Wisshak, 2006; Wilson *et al.*, 2014). This dialogue has been kept alive by a recent revision of *Oichnus* by Zonneveld and Gingras (2014). These authors suggested subjective synonymisation of *Oichnus* (together with *Tremichnus* and *Fossichnus* Nielsen, Nielsen and Bromley, 2003) with the presumed senior synonym *Sedilichnus* Müller, 1977. The aim of the present review is to demonstrate that *Sedilichnus* is not a nomenclaturally available ichnotaxon and that neither *Sedilichnus* nor *Tremichnus* are suitable for synonymisation with *Oichnus*.

ICHNOTAXONOMIC DISCUSSION

Sedilichnus is an atelonym (a term for unavailable names *sensu* Dubois, 2011) because it was proposed on conditional terms only, as clearly indicated by the phrase “Should it [a taxonomic characterization] become necessary...” (Müller, 1977, p. 890, translated from German). Such conditionally proposed names are addressed by article 15.1 of the International Code of Zoological Nomenclature (ICZN, 1999), which applies to names established after 1960. This renders the ichnogenus name *Sedilichnus*, the ichnospecies name *spongiophilus* and the two subspecific nomina *minus* and *maximus* nomenclaturally unavailable. Hence, beyond doubt, *Oichnus* is to be retained.

Apart from this nomenclatural circumstance, even if these nomina were available, in practice *Sedilichnus* would be a *nomen dubium*: It is unclear whether the holes it refers to are a native morphological feature of the sponge *Prokaliapsis janus* (Roemer, 1864), a bioerosion trace, or an example of bioclaustration (as specified by Müller, 1977 in his diagnosis). While the arguments for a *syn-vivo* genesis put forward by Ulbrich (1974) and Müller (1977) are convincing, their lines of reasoning for commensal bioclaustration are not (e.g., the presence of surface pores at the bottom of the pits). In the opinion of the present authors, *Sedilichnus* most likely is a quite variable morphological feature of the sponge itself, as already indicated in the original diagnosis by Roemer (1864). Müller’s holotype (Fig. 1A, B) and a selection of sectioned specimens from Müller’s and Ulbrich’s original material (Fig. 1C, D) show complete silicification of those sponges. In the best preserved parts, they nevertheless exhibit a number of features in support of the interpretation of the present authors. The holotype of *Sedilichnus* displays astrorhiza, i.e. canals (addressed by Ulbrich as apophyses) radiating from the *Sedilichnus* pits. According to Ulbrich (1974), they are a typical feature that also surrounds the main osculum (paragaster) in *Prokaliapsis janus*. The surface structure of *Sedilichnus* is reminiscent of that of the main osculum, being densely covered with small pores along the entire circumference (rendering the bioerosion hypothesis untenable). The internal architecture of the sponge’s spiculate skeleton is largely overprinted by silicification. No growth increments are visible, but a central bundle of densely spaced, silicified canals connecting to the bottom of the main osculum, as well as similar canals radiating from the main osculum and the *Sedilichnus* pits, can be recognised. On most of the specimens that were depicted by Ulbrich (1974) and Müller (1977), including the specimen bearing the holotype, the distribution of *Sedilichnus* is rather regular. Even though Ulbrich argued that some sponges had a more irregular cover, or were devoid of such depressions, the authors consider this observation probably to reflect a considerable morphological (and perhaps partly also preservational) variability in *Prokaliapsis*, as is also expressed by a marked variability in overall shape. To conclude, the present authors interpret most of the *Sedilichnus* traces (including the holotype) as oscula of *Prokaliapsis janus*. Such a morphological feature is not uncommon in Cretaceous and other sponges, e.g. species of *Jerea* or *Becksia* (e.g. Rauff, 1933; Małeck, 1980; Świerczewska-Gładysz,

2010). In contrast, Müller’s ‘Type II’ traces, which were not included in his definition of *Sedilichnus* (= ‘Type I’), describe tapering pits with an elongated and almond-shaped opening, and may represent bioerosive structures, perhaps produced by endolithic bivalves. Furthermore, fossil sponges of similar early Campanian age from other sites close to the type locality additionally show straight, deep (depth:width = 5:1) *Trypanites* borings, which in contrast to *Sedilichnus* clearly cut across the sponge’s canal system and might even have been formed *post mortem*.

Another aspect of the dubious nature of *Sedilichnus* is that Müller (1977) defined it without providing any morphological criteria. Instead, he explicitly denoted it as an embedment structure, in a very general sense. He excluded any possibility of bioerosion in his original diagnosis (p. 890): ‘Traces of attached and sessile animals that were not produced by mechanical or chemical action of the epibiont, but being a host reaction leading to incomplete immuration, tracing the outline and surface of the epibiont’ [translated from German]. In contrast, the diagnosis of the type species *Sedilichnus spongiophilus* is based on morphological criteria (p. 891): ‘A *Sedilichnus* with a bowl-shaped, smooth-walled depression of circular outline and rounded margin’ [translated from German]. While this diagnosis alone may indicate a relationship to bioerosional trace fossils, its clear reference to an embedment structure does not. Bertling *et al.* (2006, p. 267) defined embedment structures as ‘... structures in calcareous skeletons that are produced by an actively growing organism around disturbing or irritating objects or living organisms ...’. According to Goldring *et al.* (1997), substrate effects during trace construction should not be used as ichnotaxobases. In contrast, Tapanila and Ekdale (2007) review taxa established for bioclaustrations and consider them valid ichnotaxa. However, the consensus put forward by Bertling *et al.* (2006) does not support this approach by stating that embedment structures in general were not compatible with the definition of a trace fossil, defined therein (p. 266) as ‘a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate’ (accompanied by table 1 explicitly excluding embedment structures). However, Bertling *et al.* (2006) admitted that occasionally cases could be complicated by the occurrence of a combination of bioclaustration and boring, in which case those parts that clearly are host reactions should not be addressed ichnotaxonomically.

Indeed, this case applies at least to some ichnospecies established within the ichnogenus *Tremichnus*. Its type ichnospecies *T. paraboloides* Brett, 1985 does not show a host reaction (Fig. 1G, H), whereas *Tremichnus minutus* Brett, 1985 and *T. cysticus* Brett, 1985 can. The shape of the central pit in all three ichnospecies is similar. They differ in size, but this – just like host reactions – is not considered to be a suitable ichnotaxobase in itself (Bertling *et al.*, 2006). Hence, these three ichnospecies can be synonymised with the type ichnospecies *T. paraboloides*. The last among Brett’s (1985) suite of *Tremichnus* ichnospecies, *T. puteolus*, does not reveal a clear host reaction, but bears a strong morphological resemblance to and thus possibly represents a senior synonym of *Centrichnus concentricus* Bromley and

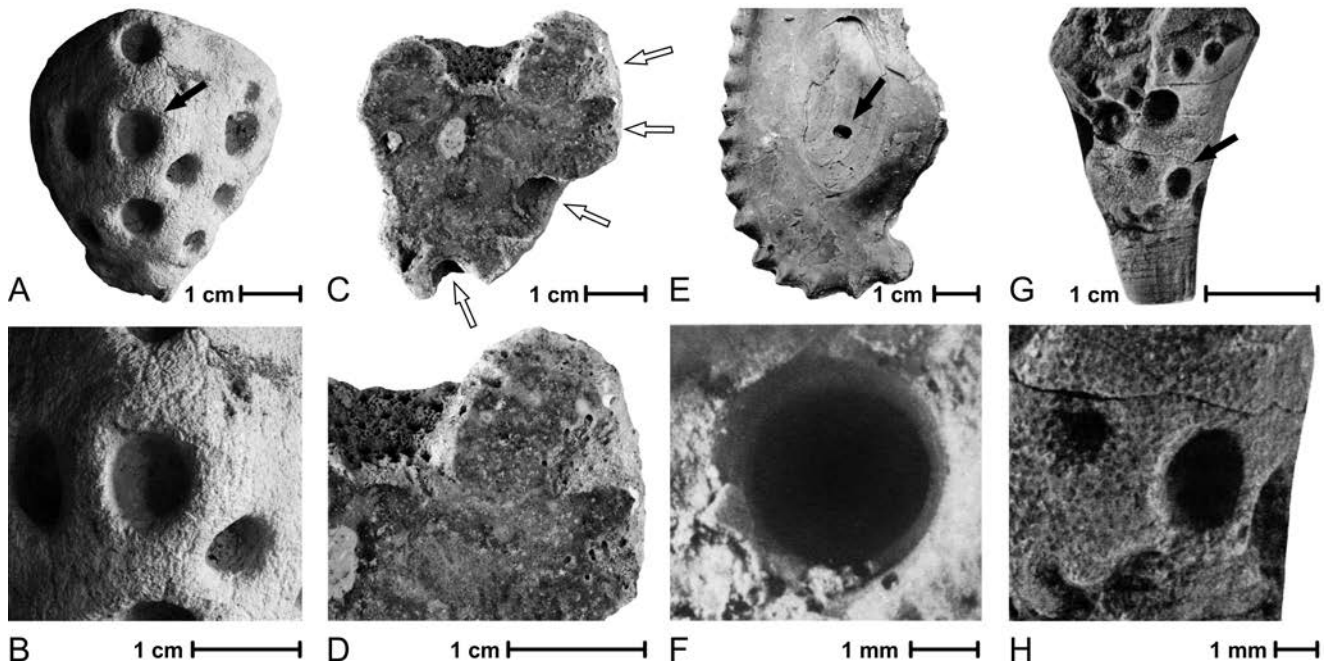


Fig. 1. Revisiting holotypes of the type ichnospecies of *Sedilichnus* Müller, 1977, *Oichnus* Bromley, 1981, and *Tremichnus* Brett, 1985. **A, B.** Overview and close-up of an early Campanian sponge *Prokaliapsis janus* (Roemer, 1864) from Wernigerode, Harz, Germany, with multiple pits addressed by Müller (1977) as embedment structures, including the holotype (arrow) of *Sedilichnus spongiophilus* (rejected atelonym), herein regarded as most probably primary sponge features; Palaeontological Collection of the TU Bergakademie Freiberg, Germany, No. FG 210/284. **C, D.** A sectioned topotypical and heavily silicified *Prokaliapsis janus* (original to Ulbrich, 1974 and Müller, 1977), illustrating the surface texture of the *Sedilichnus* walls (right-hand side in close-up) with radiating pores and canals, reminiscent of the texture in the main osculum (upper left in close-up); Palaeontological Collection of the TU Bergakademie Freiberg, Germany, No. FG 210/285. **E.** An early Campanian oyster *Arctostrea diluviana* from Ivö Klack, southern Sweden, with the exit of an *Oichnus simplex* topotype (holotype currently inaccessible, owing to collection renovation) on the inner side of the valve (arrow). **F.** Close-up of *Oichnus simplex* holotype in another *Arctostrea diluviana* from Ivö Klack, southern Sweden; Geological Museum, University of Copenhagen, Denmark, No. MGUH 15351 (reproduced from Bromley, 1981). **G, H.** The crinoid *Ichtyocrinus laevis* from the Silurian Rochester Shale, Lewinston, NY, USA, bearing numerous *Tremichnus paraboloides*, including the lectotype (arrow) shown in close-up; Buffalo Museum of Science, Buffalo, NY, USA, No. BMS E23971 (reproduced from Brett, 1985).

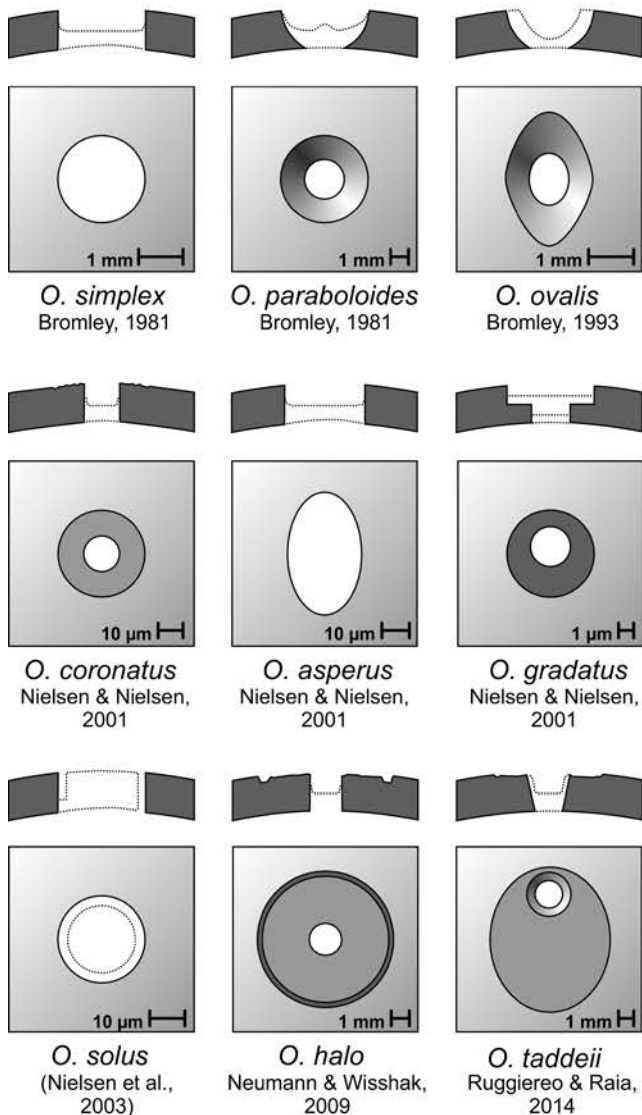
Martinell, 1991 and the very similar trace *Anellusichnus circularis* Santos, Mayoral and Muñiz, 2005. Resolving this ichnotaxonomical issue is beyond the scope of the present paper, however.

Rozhnov (1989) described pits that exhibit host reactions by eocrinoids as *Balticapunctum inchoatus*. Herein, *Balticapunctum* is synonymised with *Tremichnus paraboloides* Brett, 1985, thus rejecting it as a valid ichnotaxon. In any case, host reactions such as cysts, swellings, rims or regeneration structures, observed together with *Tremichnus* or isolated (bioclastrations), may nevertheless be addressed taxonomically outside the concept of ichnotaxonomy, similar to other taxa denoting embedment structures (see Tapanila, 2005, 2008; Tapanila and Ekdale, 2007 for reviews). Accordingly, in a recent revision of ethological categories, Vallon *et al.* (2015) reject the term impedichnia (Tapanila, 2005) and suggest replacement by impeditaxa.

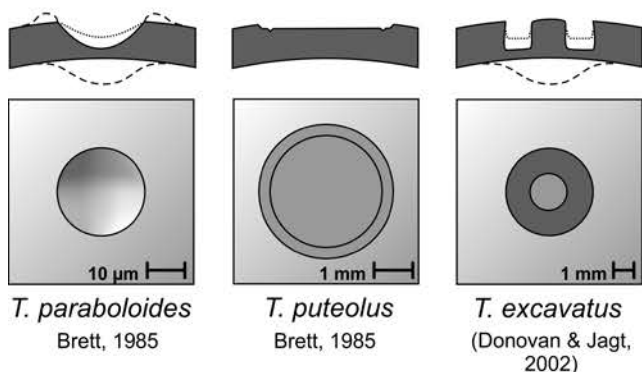
In order to clarify further the relationship and distinction between *Oichnus* and *Tremichnus*, it is necessary to revisit the original diagnoses (see below) and name-bearing holotypes of the respective type ichnospecies (Fig. 1), and to redefine morphological limits (Fig. 2). Originally, *Oichnus* was established exclusively for bioerosion traces and these were interpreted as resulting from drilling preda-

tion. Successful predation inevitably leads to a full penetration of the host skeleton. This is reflected in ‘small round holes in shells’ in Bromley’s (1981) title, as well as in the first sentence of his original ichnogenetic diagnosis. In order to accommodate unsuccessful or incomplete predation traces as well, Bromley opened the door for incompletely penetrative specimens in the form of shallow depressions or pits, as reflected in the second sentence of his diagnosis (the term ‘non-penetrative’, as applied by Zonneveld and Gingras, 2014, should be avoided, because ‘penetrate’ is defined as finding or forcing a way into *or* through something; see the Oxford Dictionary (Tulloch, 1995)). A complete penetration and its corresponding incomplete counterpart were (and should) be given the same ichnospecies name. In ichnotaxonomy, this common practice is in accordance with other ichnotaxa, for instance *Entobia* Bronn, 1837, in which various ontogenetic stages (growth phases A to E *sensu* Bromley and D’Alessandro, 1984) are included within each ichnospecies. If unfinished specimens cannot be identified with certainty on the basis of their outline and shape, they should be addressed as *Oichnus* isp. instead. The coherence of this concept was weakened with the establishment of *Oichnus excavatus* Donovan and Jagt, 2002, which is the sole ichnospecies of *Oichnus* that has never been found to

Ichnogenus *Oichnus* Bromley, 1981
complete borings penetrate through
various calcareous skeletal substrates;
(praedichnia)



Ichnogenus *Tremichnus* Brett, 1985
complete borings pass into
echinoderm skeletal substrates;
(fixichnia or domichnia)



penetrate through its host skeleton. Considering the fair number of specimens recorded to date, an interpretation as permanent drilling failure can be excluded and, consequently, *O. excavatus* is now thought to be a domichnion rather than a praedichnion (Donovan and Jagt, 2004). Morphological and ethological criteria alike strongly indicate that *O. excavatus* is better placed in a separate ichnogenus. Since *Tremichnus* is never completely penetrating through the host substrate, it cannot be synonymised with *Oichnus*, but the former is a suitable ichnogenus for *O. excavatus* under the new combination *Tremichnus excavatus* (Donovan and Jagt, 2002). Furthermore, this match is supported by the fact that *Tremichnus* is so far only known from echinoderm host substrates. The diagnosis of *Tremichnus* is condensed and revised below for better accommodation of *T. excavatus* and for exclusion of invalid ichnotaxobases. These nomenclatural steps confine *Oichnus* once more to complete or incomplete penetrations, commonly interpreted as praedichnia with or without signs of attachment. They foster the distinction from *Tremichnus*, now comprising exclusively pits in echinoderm skeletons that do not pass through the host substrate and are commonly interpreted as domichnia or fixichnia.

The advocated retention of the ichnogenus *Oichnus* and re-establishment of ichnotaxonomic stability may serve as a solid base for addressing (ichno-) diversity and processes of drilling predation and parasitism – as initiated more than two millennia ago when Aristotle formulated, ‘*The ceryx and the purple murex have this organ firm and solid; and just as the myops, or horse-fly, and the oestrus, or gadfly, can pierce the skin of a quadruped, so is that proboscis proportionately stronger in these testaceans; for they bore right through the shells of other shell-fish on which they prey.*’ [from *Historia Animalium*, written by Aristotle in about 350 B.C., translated by Thompson (1910)].

SYSTEMATIC ICHNOTAXONOMY

Ichnogenus *Oichnus* Bromley, 1981 Figs 1E, F, 2

- non 1977 *Sedilichnus* – Müller, pp. 890–891, pl. I, figs 1–13, pl. II, figs 1–4 [atelonym; ?part of sponge body fossil].
*1981 *Oichnus* – Bromley, pp. 60–62, pls 1–3.
2003 *Fossichnus* – Nielsen, Nielsen and Bromley, pp. 3–6, figs 1–3 [subjective junior synonym].

Type ichnospecies. *Oichnus simplex* Bromley, 1981 from the lower Campanian at Ivö Klack, Sweden, by original designation.

Fig. 2. Scheme compiling characters of the various ichnospecies of *Oichnus* Bromley, 1981 and *Tremichnus* Brett, 1985, as seen in plan view and cross-section, arranged in order of ichnospecies establishment. Dotted lines in cross-sections indicate known or inferred incomplete stages and dashed line outlines facultative host reactions (not part of the trace). Light grey shading in plan views indicates shallow etching scars; dark grey indicates deeper relief. Although not of diagnostic value, note the considerable range in approximate size of the respective holotypes.

Other ichnospecies. *Oichnus paraboloides* Bromley, 1981; *O. ovalis* Bromley, 1993; *O. coronatus* Nielsen and Nielsen, 2001; *O. gradatus* Nielsen and Nielsen, 2001; *O. asperus* Nielsen and Nielsen, 2001; *O. solus* (Nielsen, Nielsen and Bromley, 2003) comb. nov.; *O. halo* Neumann and Wisshak, 2009; *O. taddeii* Ruggiero and Raia, 2014.

Original diagnosis. Circular to subcircular holes of biogenic origin bored into hard substrates. The hole may pass right through the substrate as a penetration, where the substrate is a thin shell; or end within the substrate as a shallow to deep depression or short, subcylindrical pit.

Emended diagnosis. Holes with rounded outline, bored into calcareous skeletal substrates. The solitary and commonly perpendicular traces usually pass right through the substrate, or end as pit (incomplete penetration), wider than deep.

Differential diagnosis. Distinguished from *Tremichnus* Brett, 1985 by invariably complete penetration, except in aborted borings, and occurrence in a wide range of calcareous skeletal substrates. *Dipatulichnus* Nielsen and Nielsen, 2001 is characterised by holes in pairs. While *Oichnus* is defined as completely penetrative or, when incomplete, as pits that are wider than deep, *Trypanites* Mägdefrau, 1932 is distinctly deeper than wide and does not pass through the substrate. *Anellusichnus* Santos, Mayoral and Muñiz, 2005, *Centrichnus* Bromley and Martinell, 1991, and *Ophthalmichnus* Wisshak, Alexandrakis and Hoppenrath, 2014 are very shallow attachment etchings of variable outline, with shallow concentric grooves, and they never pass through the substrate. Further bioerosion traces with this property that are clearly distinguished from incomplete *Oichnus* are the echinoid boring trace *Circolites* Mikuláš, 1992 and the cyanobacterial microboring *Planobola* Schmidt, 1992.

Remarks. The diagnosis was revised in order to (1) include all observed outlines, (2) confine the substrate type to calcareous skeletons, (3) distinguish single from multiple penetrations, (4) specify the orientation with respect to the substrate surface, and (5) condense the diagnosis. *Oichnus bavincourti* (Vaillant, 1909), introduced as a new combination by Dunlop and Braddy (2011), is here excluded from *Oichnus*, because it is a burrow in siliciclastic sediment, rather than a boring in a skeletal or lithic substrate. *Cteniza bavincourti* (Vaillant, 1909) is regarded a *nomen dubium* on account of its incomplete preservation and its original tentative assignment to a biotaxon (i.e. the spionid polychaete *Sabella*). There seem to be no features to warrant placement of *Fossichnus solus* in an ichnogenus separate from *Oichnus*. Therefore, the authors follow Zonneveld and Gingras (2014) in synonymising these two, formally introducing *O. solus* as a new combination herein.

Ichnogenus *Tremichnus* Brett, 1985

Figs 1G, H, 2

- non 1977 *Sedilichnus* – Müller, pp. 890–891, pl. I, figs 1–13, pl. II, figs 1–4 [atonym; ?part of sponge body fossil].
- *1985 *Tremichnus* – Brett, pp. 626–631, figs 1–6.
- 1989 *Balticapunctum* – Rozhnov, p. 52–54, pl. II, figs 1–11 [subjective junior synonym].

Type ichnospecies. *Tremichnus paraboloides* Brett, 1985 from the Silurian Rochester Shale, Lewiston, NY, USA, by original designation.

Other ichnospecies. *Tremichnus puteolus* Brett, 1985; *T. excavatus* (Donovan and Jagt, 2002) comb. nov.

Original diagnosis. Circular pits or embedment structures of varying diameter (about 0.1 to 4.0 mm) occurring on the plates of echinoderms, primarily crinoids, with or without associated thickening or gall-like deformation of the plates. Pits regularly parabolic in cross section, with diameter/depth ratios variable from about 0.1–1.0; no internal expansion or other ramifications. Holes

always oriented perpendicularly to external plate surfaces, tapering inward; generally not penetrating through plates. Adjacent pits may overlap one another.

Emended diagnosis. Circular pits, generally wider than deep, perpendicularly bored into ossicles of echinoderms.

Differential diagnosis. Distinguished from *Oichnus* Bromley, 1981 by not penetrating through the substrate, even in complete traces, and by restriction to echinoderm host substrates. While *Tremichnus* is defined as a pit being generally wider than deep, *Trypanites* Mägdefrau, 1932 is distinctly deeper than wide. *Dipatulichnus* Nielsen and Nielsen, 2001 is characterised by holes in pairs and is completely penetrative. *Anellusichnus* Santos, Mayoral and Muñiz, 2005, *Centrichnus* Bromley and Martinell, 1991, and *Ophthalmichnus* Wisshak, Alexandrakis and Hoppenrath, 2014 are very shallow attachment etchings of variable outline and in part have shallow, concentric grooves. The echinoid boring trace *Circolites* Mikuláš, 1992 has a similar morphology, but often has an undulating edge, is far larger (commonly 1 to 4 cm in diameter), and is largely restricted to non-skeletal calcareous hardgrounds. The cyanobacterial microboring *Planobola* Schmidt, 1992 in turn is much smaller (commonly less than 30 µm in diameter), has a more clavate morphology, and is found in non-echinoderm skeletal carbonate substrates.

Remarks. The diagnosis was revised in order to (1) exclude invalid ichnotaxobases, (2) eliminate specifications to missing features, (3) better accommodate *T. excavatus*, and (4) to condense the diagnosis. *Tremichnus minutus* Brett, 1985 and *T. cysticus* Brett, 1985 are synonymised with *T. paraboloides* Brett, 1985 on account of their prior distinction having been based only on inappropriate ichnotaxobases (size and host reactions). For the latter ichnospecies, one trace on crinoid specimen BMS E23971 is designated as lectotype (see arrow in Fig. 1G). *Tremichnus puteolus* Brett, 1985 is retained; it is possibly a senior synonym of *Centrichnus concentricus* Bromley and Martinell, 1991 and *Anellusichnus circularis* Santos, Mayoral and Muñiz, 2005. *Tremichnus cystoidiphilus* Frest and Strimple (in Frest, Strimple and Paul), 2011 is a *nomen nudum*, because no holotype was designated (an ICZN requirement for ichnotaxa introduced in 2000 or later; ICZN, 1999). *Balticapunctum inchoatus* Rozhnov, 1989 is a subjective junior synonym of *T. paraboloides*. Host reactions observed together with *Tremichnus*, such as cysts, swellings, or rims formed while the tracemaker was still in place (as observed for some *T. paraboloides* on crinoids and *T. excavatus* in echinoids), and regeneration textures formed in abandoned traces (such as echinoid tuberculation observed in *T. excavatus*), are not considered as valid ichnotaxobases (see discussion above) and thus are excluded from the diagnosis. In this context, it should also be noted that, contrary to the discussion of Donovan and Jagt (2004), there is no evidence for interpreting *T. excavatus* as an embedment structure since echinoid tuberculation in abandoned bioerosional traces is a common sign of repair by stereom tissue in living echinoid host substrates (e.g., Neumann and Wisshak, 2006; Wisshak and Neumann, 2006). Also, the sole report of *T. excavatus* from a non-echinoid host substrate (Blissett and Pickerill, 2003) is based on an erroneous interpretation: This occurrence most likely represents moulds of small spiral polychaete tubes (e.g. Spirorbidae) attached to the interior of the last whorl of a gastropod, now preserved as pits in the gastropod mould after diagenetic dissolution of both gastropod and polychaete shells.

Acknowledgements

B. Gaitzsch provided a set of images of the holotype of *Sedilichnus spongiophilus* and arranged a loan of topotypes from the Freiberg collection, and F. Trostheide collected and provided further fossil sponge material. Images of *Oichnus simplex* topotypes

were provided by J. Hagström. We appreciate the valuable discussion with A. Dubois on nomenclatural principles and ICZN matters. We gratefully acknowledge C. E. Brett, M. A. Wilson, and L. H. Vallon for discussions concerning the validity of *Oichnus* and *Tremichnus*, as well as D. Janussen, J. Reitner and N. Hauschke for their expertise on sponge morphology. We thank E. A. Jagt-Yazykova for translating some Russian texts. Valuable reviews were provided by P. H. Kelley and A. K. Rindsberg. Last, but not least, we are indebted to R. G. Bromley for establishing the iconic *Oichnus* and foremost for his friendship and mentorship.

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