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ORIGINAL ARTICLE

Bioerosion ichnotaxa: review and annotated list

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Abstract

A remarkable diversity of bioerosion trace fossils is reflected by the plethora of ichnotaxa that has been proposed for these structures during the past two centuries. Bioerosion traces include microborings, macroborings, grazing traces, attachment etchings, and predation traces. They occur in calcareous, siliceous, osteic, and xylic substrates, and are known or interpreted to be produced by tracemakers as diverse as bacteria, fungi, algae, invertebrates, and vertebrates. This review presents the status quo of an inventory of all bioerosion ichnotaxa currently recognized as valid, comprising 123 ichnogenera and 339 ichnospecies, including 45 *combinationes novae*, the majority of which on account of fossil sponge bioerosion traces formerly grouped within the sponge biotaxon *Cliona*. In addition, the spelling of several ichnotaxa has to be corrected, leading to eight *nomina corrigenda*, and three cases of primary or secondary homonymy require establishing *nomina nova,* i.e., the new ichnogenus name *Irhopalia* replacing *Rhopalia* Radtke, 1991, as well as the new ichnospecies names *Entobia morrisi* replacing *E. glomerata* (Morris, 1851) and *Entobia tuberculata* replacing *E. mammillata* Bromley and D'Alessandro, 1984, respectively. Ichnotaxa of dubious or invalid nomenclatural status currently include an additional 76 ichnogenera and 157 ichnospecies. The invalid ichnogenus *Ipites* is herein reinstated as new ichnogenus. Considering that only four valid (and one invalid) ichnofamilies had previously been established for bioerosion ichnotaxa, we here introduce a suite of 14 additional ichnofamilies: Gastrochaenolitidae, Talpinidae, Entobiaidae, Planobulidae, Ichnoreticulinidae, Saccomorphidae, Centrichnidae, Renichnidae, Podichnidae, Gnathichnidae, Circolitidae, Oichnidae, Belichnidae, and Machichnidae. During the past five decades, the number of valid bioerosion ichnotaxa has more than quadrupled, reflecting a boost in bioerosion research, but also indicating the need for ichnotaxonomic consolidation in concert with a revision of key ichnogenera. In this context, the aim of this overview is to call for feedback from the research community in order to foster completeness of this list and to provide ichnotaxonomic stability. Furthermore, we want to raise awareness of the existence of the listed ichnotaxa, many of which obviously have remained unconsidered or forgotten for a long time.

Keywords Trace fossil · Bioerosion · Ichnotaxonomy · Ichnofamily · Ichnogenus · Ichnospecies

Introduction

Structures resulting from bioerosion of calcareous, siliceous, osteic, and xylic hard substrates classify as trace fossils and comprise various microborings, macroborings, grazing traces, attachment etchings and predation traces (e.g., Neumann 1966; Bromley 1994; Wisshak and Tapanila 2008; Tribollet et al. 2011). They are the work of a wide range of organisms across kingdoms and scales, and include traces made by bacteria, fungi, algae, invertebrates, and vertebrates. Trace fossils are named using a conceptual framework referred to as ichnotaxonomy, based on the Linnaean binominal nomenclature, with their names being governed by the 'International Code of Zoological Nomenclature' (International Commission on Zoological Nomenclature,

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ICZN 1999, in its current 4th edition; online version partially updated). Even though bioerosion ichnotaxa include the work not only of animals (explicitly protected by the ICZN), but also of plants, fungi, and bacteria (whose nomenclatural codes do not recognize trace fossils), they are commonly named within the framework of the ICZN as if they were protected (Bertling et al. 2004; Rindsberg 2012). Concepts and reviews on ichnotaxonomic principles, such as the validity and hierarchy of suitable ichnotaxobases, were provided, for instance by Pickerill (1994), Bertling et al. (2006), and Bertling (2007). Overview papers on trace-fossil systematics and the history of ichnotaxonomy were given by Magwood (1992), Bromley (1996), Knaust (2012), and Rindsberg (2012).

The dawn of taxonomical treatment of bioerosion trace fossils dates back almost two centuries (Fig. 1). Bronn (1837: p. 691) was the first to establish a still valid bioerosion ichnotaxon, *Entobia*, produced by excavating sponges. He did so, however, without introducing a species name, which was not a prerequisite at that time. The first of the many entobian ichnospecies was not described until 1843 as *Entobia cretacea* Portlock, 1843; it was subsequently designated as the type ichnospecies of *Entobia* by Häntzschel (1962). The first published and still valid bioerosion ichnospecies is *Talpina ramosa* von Hagenow, 1840, which was established together with *Talpina solitaria* von Hagenow, 1840, now cited as *Trypanites solitarius* (von Hagenow, 1840). Since these classical bioerosion trace fossils were established, more than a hundred ichnogenera and several hundred ichnospecies were described.

The primary objective of this contribution is to present an inventory of the currently recognized bioerosion ichnotaxa (Table 1), including taxa of dubious or invalid status (Table 2). While these lists were compiled, numerous redundant or otherwise invalid ichnotaxa were identified and consequently recombined, synonymized, and/or rejected. It is the very nature of such a taxonomic inventory that it is work in progress, and we hereby call for feedback from the research community. Input on errors of fact, conceptual pitfalls, and missing or potentially invalid ichnotaxa is highly appreciated: it would aid ichnotaxonomic stability and improve the completeness of this list. A web-based interactive bioerosion ichnotaxonomy database is currently under construction.

Concepts and methods

The present compilation is the result of an extensive literature query that primarily included searching and browsing the available publications on bioerosion trace fossils for records of ichnotaxa. In addition, a general Internet search was performed for all ichnogenera, and key online databases were consulted, such as the Index of Organism Names (ION;

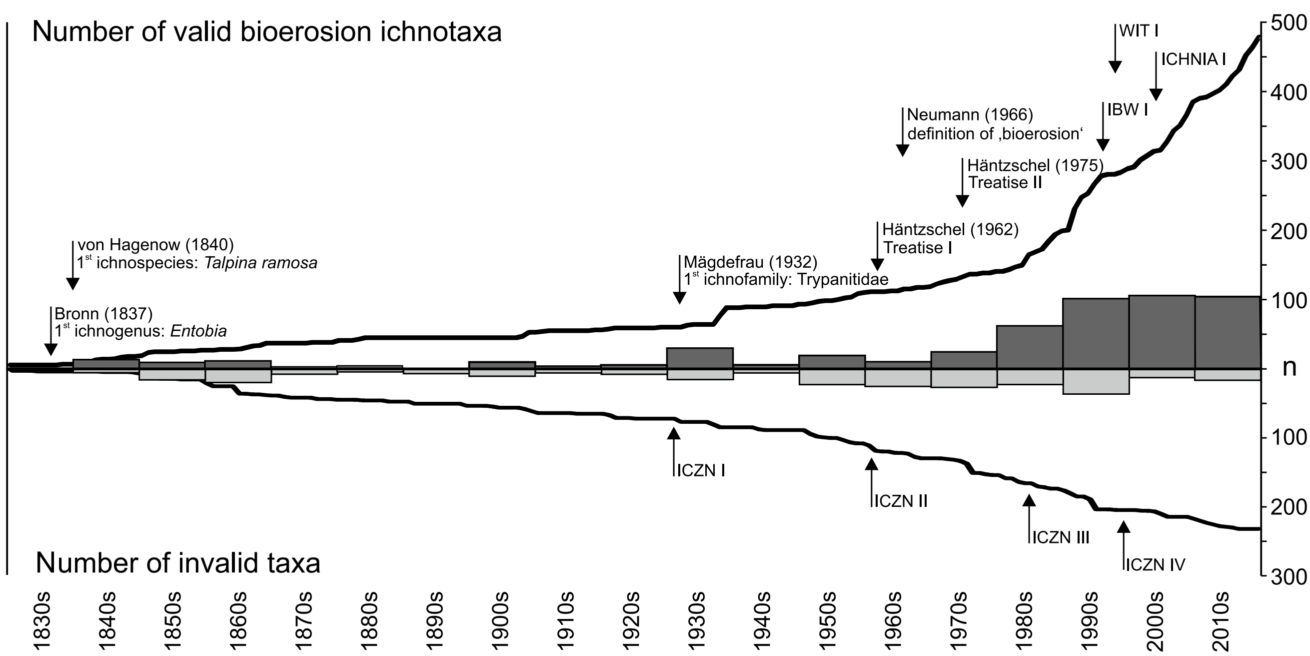

Fig. 1 The timeline of bioerosion ichnotaxonomy, showing the number of valid as well as invalid ichnotaxa established per decade (bars) and cumulative per year (line). Arrows indicate landmark publications, initiations of workshop/conference series (IBW = International Bioerosion Workshop, WIT = Workshop on Ichnotaxonomy, ICHNIA = International Congress on Ichnology), and the various editions of the 'Trace Fossils' part of the 'Treatise on Invertebrate Paleontology' and the 'International Code of Zoological Nomenclature' (ICZN)

including all entries of the Zoological Record; http://www.organismnames.com), the Global Names Index (GNI; http://gni.globalnames.org), the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/species), and ZooBank (http://zoobank.org). An earlier version of this list was presented as an interactive poster at the 9th International Bioerosion Workshop in Rome, October 2017, and feedback from the participants is considered in this review.

With respect to the definition of a trace fossil, we follow Bertling et al. (2006), defining it as ‘a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate’. For confining bioerosion ichnotaxa, we acknowledge the original definition of the term by Neumann (1966), who defined bioerosion as ‘the removal of consolidated mineral or lithic substrate by the direct action of organisms’. We follow Bromley (1994), however, who refined the definition of bioerosion as ‘… the process by which animals, plants and microbes sculpt or penetrate surfaces of hard substrates’. With respect to traces in ‘hard substrate’, this definition includes bioerosion of calcareous substrates (biogenic and abiogenic carbonates), siliceous substrates (sensu lato; biogenic and abiogenic silica, silicate minerals and rocks, siliciclastic rocks), osteic substrates (bone, teeth, scales), and xylic substrates (wood, seeds, amber; soft plant tissues are excluded due to their consistency). These four principal substrate types (and more constrained substrates in some instances) are herein accepted as relevant ichnotaxobases on ichnospecies and especially on ichnogenus level, whereas ichnofamilies address primarily morphological categories across substrate types.

For clarification and complementation, Table 2 also lists those ichnotaxa that are not bioerosion ichnotaxa, but which were considered as such in the editions of the ‘Trace Fossils’ part of the ‘Treatise on Invertebrate Paleontology’ (Häntzschel 1962, 1975). The way ichnogenera and affiliated ichnospecies are presented largely follows the latest revision of the respective ichnotaxa. For those cases where (1) ichnotaxa are synonymized or otherwise rejected, (2) new combinations are established herein, or (3) nomenclatural acts are performed (introduction of *nomina nova* or emendations in spelling), this is briefly justified and discussed in a dedicated section.

Infrasubspecific varieties, such as Schloz’s (1972) *Talpina ramosa* var. *curvata*, *recta*, and *subtilis*, or the various varieties of Müller’s (1968) *Conchifora zylindriformis,* are not considered here, because such names are not regulated by the Code, if established after 1960 (ICZN 1999: Art. 15.2, 45.6.1). Similarly, the very few existing ichnosubspecies such as Müller’s (1977) *Sedilichnus spongiophilus minus* and *maximus*, are not considered herein, although such a subspecific rank is valid according to the Code (ICZN 1999).

The validity and availability of the ichnotaxa were assessed to the best of our knowledge following the jurisdiction of the ICZN (1999), thereby treating those ichnotaxa established in the years of ichnotaxonomic limbo (1931–1985) as if they were protected by the Code. Most relevant cut-off dates are the validity of extant animal traces and of illustrations without description prior to 1931, the validity of conditionally proposed ichnotaxa prior to 1961, and the validity of ichnogenera without a designated type ichnospecies, as well as nominal ichnotaxa established without designation of a holotype or syntypes prior to 2000.

As for traces of ctenostome bryozoans, there is a longstanding and still unresolved debate over which taxa to consider as biotaxa and which as ichnotaxa (e.g., Bertling 1995; Bromley 2004; Bertling et al. 2006; Rosso 2008; Buatois et al. 2017). The group remains in need of a revision that is beyond the scope of this paper. Consequently, we only list those taxa that were established as ichnotaxa in the first place (see Rosso 2008 for the latest review). Other (ichno-) genera that would need to be considered in a reevaluation include at least *Electra* Lamouroux, 1816; *Terebripora* d’Orbigny, 1847; *Haimeina* Terquem and Piette, 1865; *Spathipora* Fischer, 1866; *Ropalonaria* Ulrich, 1879; *Vinella* Ulrich, 1890; *Penetrantia* Silén, 1946; *Immergentia* Silén, 1946; *Condranema* Bassler, 1952; *Foraripora* Voigt and Soule, 1973; *Casteropora* Pohowsky, 1978; *Cookobryozoon* Pohowsky, 1978; *Fischerella* Pohowsky, 1978; *Marcusopora* Pohowsky, 1978; *Orbignyopora* Pohowsky, 1978; and *Voigtella* Pohowsky, 1978.

The distinction between true bioerosion traces and so-called ‘pseudoborings’ is of paramount importance. The latter are embedment structures termed ‘bioclaustrations’ (Palmer and Wilson 1988). They form when a living skeleton-secreting organism overgrows a living symbiont (sensu lato). This process has to be distinguished from ‘bioimmuration’ (Voigt 1972), where a dead organism is being overgrown. There is an ongoing discussion whether bioclaustration structures should be considered trace fossils. According to Bertling et al. (2006), they are not, because they were formed by means of a host reaction rather than active modification of the substrate by a tracemaker. It was (and is again here) consequently suggested that such structures be addressed as parataxa outside ichnotaxonomy in a yet to be defined ‘collective group’ within the framework of the ICZN. Nevertheless, numerous taxa have been established for bioclaustration structures prior to and after this rejection (see Tapanila and Ekdale 2007 and Klompmaker et al. 2014 for discussion), including the establishment of an ethological class ‘impedichnia’ by Tapanila (2005). This makes the standpoint expressed in Bertling et al. (2006) controversial.

Further complicating the matter, combinations of bioclaustration and bioerosion do occur, leading to so-called 'compound boring-bioclaustrations' (Tapanila and Ekdale 2007), as exemplified by *Klemmatoica linguliforma* Tapanila and Holmer, 2006 and *Kanthyloma crusta* Klompmaker et al., 2014. However, only those cases are herein considered as bioerosion trace fossils, where bioerosive action is predominant and identified as largely independent from the host reaction. These instances are the ichnogenus *Tremichnus* Brett, 1985 (see Wisshak et al. 2005), and the ichnospecies *Gastrochaenolites vivus* Edinger and Risk, 1994. All other bioclaustration structures proposed as trace fossils are not considered ichnotaxa here: *Streptindytes* Calvin, 1888; *Gitonia* Clarke, 1908; *Hicetes* Clarke, 1908; *Chaetosalpinx* Sokolov, 1948; *Phragmosalpinx* Sokolov, 1948; *Diorygma* Biernat, 1961; *Torquaysalpinx* Plusquellec, 1968; *Helicosalpinx* Oekentorp, 1969; *Burrinjuckia* Chatterton, 1975; *Palaeophytobia* Süss and Müller-Stoll, 1975; *Protophytobia* Süss, 1979; *Catellocaula* Palmer and Wilson, 1988; *Clavatulicola* Radwański and Bałuk, 1997; *Eodiorygma* Bassett et al., 2004; *Klemmatoica* Tapanila and Holmer, 2006; *Caupokeras* McKinney, 2009; *Imbutichnus* Santos et al., 2012; *Ostiocavichnus* Bohaty et al., 2012; *Kanthyloma* Klompmaker et al., 2014; *Galacticus* Klompmaker et al., 2016, and *Thatchtelithichnus* Zonneveld et al., 2015. The same applies to the related group of galls formed in calcareous skeletons, namely the ichnogenera *Castexia* Mercier, 1936; *Endosacculus* Voigt, 1959; and *Heckerina* Alekseev and Endelman, 1989.

The list of valid bioerosion ichnotaxa (Table 1) is organized in alphabetical order (ichnogenera) and year of publication (ichnospecies) instead of morphological criteria or higher taxonomic rank (existing and new ichnofamilies are characterized in a separate section). In addition, the type ichnospecies of each ichnogenus is indicated, as is the original combination of regrouped ichnospecies. The list is complemented by information about the nature of the bioeroded hard substrate, the general type of bioerosion trace, and the known or inferred tracemaker. Original publications are listed in the reference section.

The compilation of dubious or invalid ichnogenera and ichnospecies (Table 2) likewise is ordered alphabetically (ichnogenera) and according to the year of publication (ichnospecies). For each taxon, the reasoning for its present nomenclatural status and the respective reference are given.

This published work and the nomenclatural acts therein have been registered in ZooBank: http://zoobank.org/references/8FB87191-588F-47AD-8C0A-8957EAF3D6C8.

Bioerosion ichnofamilies

Only a limited number of the currently recognized bioerosion ichnotaxa is grouped within the higher systematic unit of an ichnofamily, although such a classification is supported by the ICZN (1999) and common for other groups of trace fossils (Bertling 2007). Some of the categories of architectural designs in trace fossils, as defined by Buatois et al. (2017), largely coincide with the currently recognized ichnofamilies (for instance the Dendrinidae), and were suggested by the latter authors as representing a suitable basis for the establishment of further ichnofamilies.

Acknowledging the demand for additional ichnofamilies that are primarily morphologically based (Bromley 1996; Bertling 2007) yet ecologically and ethologically meaningful, we additionally define a number of new ichnofamilies for bioerosion ichnotaxa accordingly. This way, emphasis is put on covering the most common and important ichnotaxa on the one hand, and on recognizing those groups that share enough morphological characters to allow inclusion of a fair amount of ichnogenera on the other hand. Several ichnogenera with a unique form remain without ichnofamily for the time being. Borings of ctenostome bryozoans are not considered here, because a revision of this group of bioerosion trace fossils is needed in order to clarify which of the established family names actually are to be regarded as ichnofamilies (see above).

Trypanitidae Mägdefrau, 1932

Type ichnogenus: *Trypanites* Mägdefrau, 1932.

Diagnosis: 'Unbranched, straight tubes' [original diagnosis, translated], here revised to: unbranched, cylindrical borings of approximately constant diameter with straight, winding, or spiraling course.

Members: *Anobichnium* Linck, 1949; *Australocerambyx* Peña, 1971; *Carporichnus* Genise, 1995; *Eocavum* Buchholz, 1986; *Helicotaphrichnus* Kern et al., 1974; *Linckichnus* Schlirf, 2006; *Osprioneides* Beuck and Wisshak in Beuck et al., 2008b; *Paleobuprestis* Walker, 1938; *Paleoipidus* Walker, 1938; *Pecinolites* Mikuláš and Dvořák, 2002; *Spirichnus* Fürsich et al., 1994; *Stipitichnus* Genise, 1995; *Trypanites* Mägdefrau, 1932; *Tubulohyalichnus* McLoughlin et al., 2009.

Ethological category: Domichnia (dwelling traces).

Rogerellidae Codez and de Saint-Seine, 1958

Type ichnogenus: *Rogerella* de Saint-Seine, 1951.

Diagnosis: 'stalked slit, marginal bulge' [original diagnosis, translated], here revised to: pouch-shaped borings.

Members: *Aurimorpha* Wisshak et al., 2008; *Cubiculum* Roberts et al., 2007; *Cuenulites* Rodríguez-Tovar et al., 2015; *Cuniculichnus* Höpner and Bertling, 2017; *Petroxestes* Wilson and Palmer, 1988; *Rogerella* de Saint-Seine, 1951; *Sanctum* Erickson and Bouchard, 2003; *Umbichnus* Martinell et al., 1999.

Ethological category: Domichnia (dwelling traces).

Remarks: Bromley and D'Alessandro (1987) considered the ichnogenus *Zapfella* de Saint-Seine, 1954 as a subjective junior synonym of *Rogerella* de Saint-Seine, 1951. They did not touch upon the question of synonymy at the ichnofamily level, even though Codez and de Saint-Seine (1958) erected the ichnofamily Zapfellidae in the same paper as their Rogerellidae, with *Zapfella* as its type ichnogenus. With synonymous type ichnogenera, the two ichnofamilies are synonymous as well. As it is up to the first reviser to clarify the synonymy of synchronously erected taxa (ICZN 1999: Art. 24.2), we here select Rogerellidae Codez and de Saint-Seine, 1958 as the valid ichnotaxon, rendering Zapfellidae invalid.

Dendrinidae Bromley et al., 2007

Type ichnogenus: *Dendrina* Quenstedt, 1849.

Diagnosis: Originally defined as 'microborings having a rosetted or incompletely rosetted (i.e., fan-shaped) morphology, with or without a central or marginal main chamber', slightly revised here to: dendritic or rosetted to fan-shaped borings, with or without a central or marginal main chamber.

Members: *Abeliella* Mägdefrau, 1937; *Antodendrina*, Wisshak, 2017; *Calcideletrix* Mägdefrau, 1937; *Clionolithes* Clarke, 1908; *Dendrina* Quenstedt, 1849; *Dictyoporus* Mägdefrau, 1937; *Neodendrina* Wisshak and Neumann, 2018; *Nododendrina* Vogel et al., 1987; *Pyrodendrina* Tapanila, 2008; *Rhopalondendrina* Wisshak, 2017.

Ethological category: Domichnia (dwelling traces), fodinichnia? (combined dwelling and feeding traces).

Osteichnidae Höpner and Bertling, 2017

Type ichnogenus: *Osteichnus* Höpner and Bertling, 2017.

Diagnosis: Originally defined as 'non-branched borings in bone substrates irrespective of their orientation', here revised to: cylindrical borings with fused U-loops.

Members: *Asthenopodichnium* Thenius, 1979; *Canaliparva* Furlong and McRoberts, 2014; *Caulostrepsis* Clarke, 1908; *Maeandropolydora* Voigt, 1965; *Osteichnus* Höpner and Bertling, 2017; *Pseudopolydorites* Głazek et al., 1971; *Sertaterebrites* Ekdale et al., 1989.

Remarks: Originally erected with osteic substrate as a main criterion, the ichnofamily can no longer be defined this way and is consequently redefined here based on the U-shaped morphology of its type ichnogenus.

Ethological category: Domichnia (dwelling traces).

Gastrochaenolitidae ifam. nov.

Type ichnogenus: *Gastrochaenolites* Leymerie, 1842.

Diagnosis: Unbranched, distally widened borings.

Members: *Apectoichnus* Donovan, 2018; *Clavichnus* Höpner and Bertling, 2017; *Gastrochaenolites* Leymerie, 1842; *Palaeosabella* Clarke, 1921; *Phrixichnus* Bromley and Asgaard, 1993; *Teredolites* Leymerie, 1842.

Ethological category: Domichnia (dwelling traces).

Talpinidae ifam. nov.

Type ichnogenus: *Talpina* von Hagenow, 1840.

Diagnosis: Branched cylindrical borings that may anastomose.

Members: *Cunctichnus* Fürsich et al., 1994; *Cycalichnus* Genise, 1995; *Ipites* igen. nov.; *Lapispecus* Voigt, 1970; *Paleoscolytus* Walker, 1938; *Talpina* von Hagenow, 1840; *Xylonichnus* Genise, 1995.

Ethological category: Domichnia (dwelling traces) or agrichnia (farming traces).

Entobiaidae ifam. nov.

Type ichnogenus: *Entobia* Bronn, 1837.

Diagnosis: Uni-camerate borings to multi-camerate boxwork borings, connected to the substrate surface by several apertures.

Members: *Entobia* Bronn, 1837; *Unellichnus* Breton, 2015a.

Ethological category: Domichnia (dwelling traces).

Remarks: The family name Entobiidae is already preoccupied by a family of copepods, established by Ho (1984) based on the type genus *Entobius* Dogiel, 1908. In order to avoid homonymy between family-group names, we follow recommendation 29A of the ICZN (1999) and use the entire ichnogeneric name as the stem for the new ichnofamily.

Planobolidae ifam. nov.

Type ichnogenus: *Planobola* Schmidt, 1992.

Diagnosis: Spherical, hemispherical or clavate microborings with a single or multiple connection(s) to the substrate surface.

Members: *Cavernula* Radtke, 1991; *Cyclopuncta* Elias, 1958; *Granulohyalichnus* McLoughlin et al., 2009; *Planobola* Schmidt, 1992.

Ethological category: Domichnia (dwelling traces).

Ichnoreticulinidae ifam. nov.

Type ichnogenus: *Ichnoreticulina* Radtke and Golubić, 2005.

Diagnosis: Systems of strongly ramifying microborings composed of cylindrical tunnels that often show intercalary, lateral, or terminal swellings.

Members: *Conchocelichnus* Radtke et al., 2016; *Eurygonum* Schmidt, 1992; *Filuroda* Solle, 1938; *Ichnoreticulina* Radtke and Golubić, 2005; *Irhopalia* nom. nov.; *Orthogonum* Radtke, 1991; *Palaeomycelites* Bystrov, 1956.

Ethological category: Domichnia (dwelling traces) or fodinichnia (combined dwelling and feeding traces).

Saccomorphidae ifam. nov.

Type ichnogenus: *Saccomorpha* Radtke, 1991.

Diagnosis: Spherical, sac-shaped, or multilobate microborings interconnected by thin tunnels.

Members: *Polyactina* Radtke, 1991; *Saccomorpha* Radtke, 1991.

Ethological category: Fodinichnia (combined dwelling and feeding traces).

Centrichnidae ifam. nov.

Type ichnogenus: *Centrichnus* Bromley and Martinell, 1991.

Diagnosis: Single to multiple, roughly circular depressions on the surface of hard substrates, shallower than wide, with individual grooves often arranged concentrically or excentrically.

Members: *Augoichnus* Arendt, 2012; *Centrichnus* Bromley and Martinell, 1991; *Lacrimichnus* Santos et al., 2003; *Ophthalmichnus* Wisshak et al., 2014; *Solealites* Uchman et al., 2018a; *Tremichnus* Brett, 1985.

Ethological category: Fixichnia (attachment traces).

Renichnidae ifam. nov.

Type ichnogenus: *Renichnus* Mayoral, 1987a.

Diagnosis: Spiral to elongate depressions on the surface of hard substrates, shallower than wide.

Members: *Camarichnus* Santos and Mayoral, 2006; *Canalichnus* Santos and Mayoral, 2006; *Renichnus* Mayoral, 1987; *Spirolites* Uchman et al., 2018a; *Sulcichnus* Martinell and Domènech, 2009.

Ethological category: Fixichnia (attachment traces).

Podichnidae ifam. nov.

Type ichnogenus: *Podichnus* Bromley and Surlyk, 1973.

Diagnosis: Multiple round or oval depressions on the surface of hard substrates, regularly spaced in a cluster.

Members: *Finichnus* Taylor et al., 2013; *Flosculichnus* Donovan and Jagt, 2005; *Podichnus* Bromley and Surlyk, 1973.

Ethological category: Fixichnia (attachment traces).

Gnathichnidae ifam. nov.

Type ichnogenus: *Gnathichnus* Bromley, 1975.

Diagnosis: Repetitive sets of linear, shallow grooves on the surface of hard substrates.

Members: *Gnathichnus* Bromley, 1975; *Radulichnus* Voigt, 1977.

Ethological category: Pascichnia (combined locomotion and grazing traces).

Circolitidae ifam. nov.

Type ichnogenus: *Circolites* Mikuláš, 1992.

Diagnosis: Circular to irregular-shaped depressions in hard substrates, with steep to overhanging marginal walls that may show sets of linear, shallow grooves.

Members: *Circolites* Mikuláš, 1992; *Ericichnus* Santos and Mayoral in Santos et al., 2015; *Osteocallis* Roberts et al., 2007; *Planavolites* Mikuláš, 1992.

Ethological category: Combined paschichnia (combined locomotion and grazing traces) and domichnia (dwelling traces).

Oichnidae ifam. nov.

Type ichnogenus: *Oichnus* Bromley, 1981.

Diagnosis: Complete circular penetrations or sets thereof in biogenic hard substrates, in some cases surrounded by shallow etchings.

Members: *Dipatulichnus* Nielsen and Nielsen, 2001; *Kardopomorphos* Beuck et al., 2008a; *Lamniporichnus* Mikulaš et al., 1998; *Loxolenichnus* Breton et al., 2017; *Oichnus* Bromley, 1981; *Stellatichnus* Nielsen and Nielsen, 2001.

Ethological category: Praedichnia (predation traces; but also in xylic seeds), occasionally combined with fixichnia (attachment traces).

Belichnidae ifam. nov.

Type ichnogenus: *Belichnus* Pether, 1995.

Diagnosis: Recurrent fracture patterns in shells and other skeletal material.

Members: *Belichnus* Pether, 1995; *Bicrescomanducator* Donovan et al. in Andrew et al., 2010.

Ethological category: Praedichnia (predation traces).

Machichnidae ifam. nov.

Type ichnogenus: *Machichnus* Mikuláš et al., 2006.

Diagnosis: Punctures to grooves, both of somewhat irregular outline, often in sets, in bone.

Members: *Knethichnus* Jacobsen and Bromley, 2009; *Linichnus* Jacobsen and Bromley, 2009; *Machichnus* Mikuláš et al., 2006; *Mandaodonites* Cruickshank, 1986; *Nihilichnus* Mikuláš et al., 2006.

Ethological category: Praedichnia (predation or scavenging traces).

Nomenclatural acts, invalidations, synonymizations and new combinations

This section contains the justification and discussion of all nomenclatural acts (i.e., introduction of *nomina nova* and *nomina corrigenda*), new combinations, and invalidations performed in this review, with represented ichnotaxa in alphabetical order.

Aggregatella Elliott, 1962, with its type ichnospecies *A. pseudohieroglyphicus* Elliott, 1962, was erected based on a thin-section and interpreted as a microcoprolite (pellet). However, these 'small, flexuous curved or twisted elongate solid bodies' are more likely microborings, but they cannot be identified with certainty based on the two-dimensional thin-section image. Accordingly, the two ichnotaxa must be considered *nomina dubia*.

Anellusichnus Santos et al., 2005 is herein regarded as subjective junior synonym of *Centrichnus* Bromley and Martinell, 1991 and its two ichnospecies are well accommodated within the original diagnosis of *Centrichnus*. Because they differ in morphology from the other ichnospecies, they are considered valid as new combinations.

Anoigmaichnus Vinn et al., 2014 and its type ichnospecies *A. odinsholmensis* Vinn et al., 2014 include a cylindrical shaft with an elevated aperture, the latter interpreted as an embedment structure. Being mainly a boring, *A. odinsholmensis* resembles *Trypanites weisei* Mägdefrau, 1932, whose type material occasionally shows elevated apertures (so-called 'Ringwälle', Mägdefrau, 1932), and is therefore regarded as junior synonym of it.

Table 1 List of all bioerosion ichnotaxa currently recognized as valid, with author(s), indication of the type ichnospecies (*asterisk*), original name or combination, principal type of bioerosion trace fossil, nature of infested hard substrate, and known or inferred tracemaker (Abbreviations: comb. nov. = *combinatio nova*; nom. corr. = *nomen corrigendum*; nom. nov. = *nomen novum*)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
Abeliella Mägdefrau, 1937		Microboring; osteic; invertebrate?
A. riccioides Mägdefrau, 1937*		Microboring; osteic; invertebrate?
A. procera Mägdefrau, 1937		Microboring; osteic; invertebrate?
Amphifaoichnus Pirrone & Buatois, 2016		Macroboring; osteic; invertebrate
A. seilacheri Pirrone & Buatois, 2016*		Macroboring; osteic; invertebrate
Anobichnium Linck, 1949		Macroboring; xylic; invertebrate
A. simile Linck, 1949*		Macroboring; xylic; invertebrate
Antodendrina Wisshak, 2017		Microboring; calcareous; invertebrate?
A. ligula Wisshak, 2017*		Microboring; calcareous; invertebrate?
Apectoichnus Donovan, 2018		Macroboring; xylic; invertebrate
A. longissimus (Kelly & Bromley, 1984)*	*Teredolites longissimus*	Macroboring; xylic; invertebrate
Asthenopodichnium Thenius, 1979		Macroboring; xylic; invertebrate
A. xylobiontum Thenius, 1979*		Macroboring; xylic; invertebrate
A. lithuanicum Uchman et al., 2007		Macroboring; xylic; invertebrate
A. lignorum Genise et al., 2012		Macroboring; xylic; invertebrate
Augoichnus Arendt, 2012		Attachment; calcareous; invertebrate?
A. dituberculatus Arendt, 2012*		Attachment; calcareous; invertebrate?
Aurimorpha Wisshak et al., 2008		Microboring; calcareous; unknown
A. varia Wisshak et al., 2008*		Microboring; calcareous; unknown
Australocerambyx Peña, 1971		Macroboring; xylic; invertebrate
A. chilensis Peña, 1971*		Macroboring; xylic; invertebrate
Belichnus Pether, 1995		Predation; calcareous; invertebrate
B. monos Pether, 1995*		Predation; calcareous; invertebrate
Bicrescomanducator Donovan et al. in Andrew et al., 2010		Predation; calcareous; invertebrate
B. rolli Donovan et al. in Andrew et al., 2010*		Predation; calcareous; invertebrate
B. serratus (Zamora et al., 2011)	*Mandibulichnus serratus*	Predation; calcareous; invertebrate
B. spiralis (Stafford et al., 2015) comb. nov.	*Caedichnus spiralis*	Predation; calcareous; invertebrate
Calcideletrix Mägdefrau, 1937		Microboring; calcareous; invertebrate?
C. flexuosa Mägdefrau, 1937*		Microboring; calcareous; invertebrate?
C. anomala (Mägdefrau, 1937)	*Dendrina anomala*	Microboring; calcareous; invertebrate?
C. breviramosa Mägdefrau, 1937		Microboring; calcareous; invertebrate?
C. fastigata (Radtke, 1991)	*Polyactina fastigata*	Microboring; calcareous; invertebrate?
Camarichnus Santos & Mayoral, 2006		Attachment; calcareous; invertebrate
C. arcuatus Santos & Mayoral, 2006		Attachment; calcareous; invertebrate
C. subrectangularis Santos & Mayoral, 2006*		Attachment; calcareous; invertebrate
Canalichnus Santos & Mayoral, 2006		Attachment; calcareous; invertebrate
C. tenuis Santos & Mayoral, 2006*		Attachment; calcareous; invertebrate
Canaliparva Furlong & McRoberts, 2014		Microboring; calcareous; invertebrate
C. circularis Furlong & McRoberts, 2014*		Microboring; calcareous; invertebrate
Carporichnus Genise, 1995		Macroboring; xylic; invertebrate
C. maximus Genise, 1995*		Macroboring; xylic; invertebrate
Caulostrepsis Clarke, 1908		Macroboring; calcareous; invertebrate
C. taeniola Clarke, 1908*		Macroboring; calcareous; invertebrate
C. biforans (Gripp, 1967)	*Polydora biforans*	Macroboring; calcareous; invertebrate
C. cretacea (Voigt, 1971)	*Dodecaceria cretacea*	Macroboring; calcareous; invertebrate
C. avipes Bromley & D'Alessandro, 1983		Macroboring; calcareous; invertebrate
C. contorta Bromley & D'Alessandro, 1983		Macroboring; calcareous; invertebrate
C. spiralis Pickerill et al., 2001		Macroboring; calcareous; invertebrate

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
Cavernula Radtke, 1991		Microboring; calcareous; plant
C. pediculata Radtke, 1991*		Microboring; calcareous; plant
C. zancobola Schmidt, 1992		Microboring; calcareous; plant?
C. coccidia Glaub, 1994		Microboring; calcareous; plant?
Centrichnus Bromley & Martinell, 1991		Attachment; calcareous; invertebrate
C. eccentricus Bromley & Martinell, 1991*		Attachment; calcareous; invertebrate
C. concentricus Bromley & Martinell, 1991		Attachment; calcareous; invertebrate
C. circularis (Santos et al., 2005) comb. nov.	*Anellusichnus circularis*	Attachment; calcareous; invertebrate
C. undulatus (Santos et al., 2005) comb. nov.	*Anellusichnus undulatus*	Attachment; calcareous; invertebrate
Circolites Mikuláš, 1992		Macroboring; calcareous; invertebrate
C. kotoucensis Mikuláš, 1992*		Macroboring; calcareous; invertebrate
Clavichnus Höpner & Bertling, 2017		Macroboring; osteic; invertebrate
C. ionasi (Muñiz et al., 2010)*	*Trypanites ionasi*	Macroboring; osteic; invertebrate
Clionolithes Clarke, 1908		Microboring; calcareous; invertebrate?
C. radicans Clarke, 1908*		Microboring; calcareous; invertebrate?
C. palmatus Clarke, 1908		Microboring; calcareous; invertebrate?
C. pannosus (Solle, 1938)	*Olkenbachia pannosa*	Microboring; calcareous; invertebrate?
C. alcicornis (Vogel et al., 1987)	*Ramodendrina alcicornis*	Microboring; calcareous; invertebrate?
C. cervicornis (Vogel et al., 1987)	*Ramodendrina cervicornis*	Microboring; calcareous; invertebrate?
C. convexus (Hofmann, 1996)	*Platydendrina convexus*	Microboring; calcareous; invertebrate?
Conchocelichnus Radtke et al., 2016		Microboring; calcareous; plant
C. seilacheri Radtke et al., 2016*		Microboring; calcareous; plant
Cubiculum Roberts et al., 2007		Macroboring; osteic; invertebrate
C. ornatum (Roberts et al., 2007)*	*Cubiculum ornatus*	Macroboring; osteic; invertebrate
C. leve Pirrone et al., 2014 nom. corr.	*Cubiculum levis*	Macroboring; osteic; invertebrate
C. inornatum Xing et al., 2015 nom. corr.	*Cubiculum inornatus*	Macroboring; osteic; invertebrate
C. cooperi Parkinson, 2016		Macroboring; osteic; invertebrate
Cuenulites Rodríguez-Tovar et al., 2015		Macroboring; siliceous; invertebrate
C. sorbasensis Rodríguez-Tovar et al., 2015*		Macroboring; siliceous; invertebrate
C. amygdaloides Uchman et al., 2018b		Macroboring; siliceous; invertebrate
Cunctichnus Fürsich et al., 1994		Macroboring; calcareous; invertebrate
C. probans Fürsich et al., 1994*		Macroboring; calcareous; invertebrate
Cuniculichnus Höpner & Bertling, 2017		Macroboring; osteic; invertebrate
C. variabilis Höpner & Bertling, 2017*		Macroboring; osteic; invertebrate
Curvichnus Nielsen, 2002		Macroboring; calcareous; invertebrate
C. semorbis Nielsen, 2002*		Macroboring; calcareous; invertebrate
C. pediformis Blissett & Pickerill, 2007		Microboring; calcareous; invertebrate
Cycalichnus Genise, 1995		Macroboring; xylic; invertebrate
C. garciorum Genise, 1995*		Macroboring; xylic; invertebrate
Cyclopuncta Elias, 1958		Attachment; calcareous; unknown
C. girtyi Elias, 1958*		Attachment; calcareous; unknown
Dendrina Quenstedt, 1849		Microboring; calcareous; invertebrate?
D. dendrina (Morris, 1851)*	*Talpina dendrina*	Microboring; calcareous; invertebrate?
D. belemniticola Mägdefrau, 1937		Microboring; calcareous; invertebrate?
D. lacerata Hofmann, 1996		Microboring; calcareous; invertebrate?
Dictyoporus Mägdefrau, 1937		Microboring; calcareous; invertebrate?
D. nodosus Mägdefrau, 1937*		Microboring; calcareous; invertebrate?
D. balani (Tavernier et al., 1992)	*Dendrorete balani*	Microboring; calcareous; invertebrate?
Dipatulichnus Nielsen & Nielsen, 2001		Predation; calcareous; unknown
D. rotundus Nielsen & Nielsen, 2001*		Predation; calcareous; unknown

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
Endoconchia Runnegar in Bengtson et al., 1990		Microboring; calcareous; bacterium
E. lata Runnegar in Bengtson et al., 1990*		Microboring; calcareous; bacterium
E. angusta Runnegar in Bengtson et al., 1990		Microboring; calcareous; bacterium
Entobia Bronn, 1837		Macroboring; calcareous; invertebrate
E. cretacea Portlock, 1843*		Macroboring; calcareous; invertebrate
E. michelini (Nardo, 1845) comb. nov.	*Vioa michelini*	Macroboring; calcareous; invertebrate
E. glomerata (Michelin, 1846) comb. nov.	*Vioa glomerata*	Macroboring; calcareous; invertebrate
E. nardina (Michelin, 1846) comb. nov.	*Vioa nardina*	Macroboring; calcareous; invertebrate
E. duvernoyi (Michelin, 1847) comb. nov.	*Vioa duvernoyi*	Macroboring; calcareous; invertebrate
E. irregularis (d'Orbigny, 1850) comb. nov.	*Cliona irregularis*	Macroboring; calcareous; invertebrate
E. ramosa (d'Orbigny, 1850) comb. nov.	*Cliona ramosa*	Macroboring; calcareous; invertebrate
E. parisiensis (d'Orbigny, 1850)	*Cliona parisiensis*	Macroboring; calcareous; invertebrate
E. dissociata (Duchassaing, 1850)	*Vioa dissociata*	Macroboring; calcareous; invertebrate
E. duvernoysii (Duchassaing, 1850)	*Vioa duvernoysii*	Macroboring; calcareous; invertebrate
E. pectita (Michelotti, 1861) comb. nov.	*Vioa pectita*	Macroboring; calcareous; invertebrate
E. strombi (Duchassaing de Fonbressin & Michelotti, 1864)	*Vioa strombi*	Macroboring; calcareous; invertebrate
E. megastoma (Fischer in d'Archiac et al., 1866)	*Cliona megastoma*	Macroboring; calcareous; invertebrate
E. falunica (Fischer in d'Archiac et al., 1866) comb. nov.	*Cliona falunica*	Macroboring; calcareous; invertebrate
E. cerithii (Fraas, 1867) comb. nov.	*Vioa cerithii*	Macroboring; calcareous; invertebrate
E. paradoxa (Fischer, 1868)	*Cliona paradoxa*	Macroboring; calcareous; invertebrate
E. praecursor (Fischer, 1868) comb. nov.	*Cliona praecursor*	Macroboring; calcareous; invertebrate
E. cerithiorum (Fischer, 1868) comb. nov.	*Cliona cerithiorum*	Macroboring; calcareous; invertebrate
E. tubulosa (Seguenza, 1879) comb. nov.	*Cliona tubulosa*	Macroboring; calcareous; invertebrate
E. perforata (Seguenza, 1882) comb. nov.	*Cliona perforata*	Macroboring; calcareous; invertebrate
E. intricata (Seguenza, 1882) comb. nov.	*Cliona intricata*	Macroboring; calcareous; invertebrate
E. catenata (Frič, 1883) comb. nov.	*Vioa catenata*	Macroboring; calcareous; invertebrate
E. exogyrarum (Frič, 1883)	*Vioa exogyrarum*	Macroboring; calcareous; invertebrate
E. mammillata (Chapman, 1907) comb. nov.	*Cliona mammillata*	Macroboring; calcareous; invertebrate
E. peregrinator (Chapman, 1907) comb. nov.	*Cliona peregrinator*	Macroboring; calcareous; invertebrate
E. bullini (Annandale, 1920) comb. nov.	*Cliona bullini*	Macroboring; calcareous; invertebrate
E. devonica (Clarke, 1921)	*Topsentia devonica*	Macroboring; calcareous; invertebrate
E. radiciformis (Lehner, 1937) comb. nov.	*Cliona radiciformis*	Macroboring; calcareous; invertebrate
E. microtuberum (Stephenson, 1941) comb. nov.	*Cliona microtuberum*	Macroboring; calcareous; invertebrate
E. retiformis (Stephenson, 1952)	*Cliona retiformis*	Macroboring; calcareous; invertebrate
E. cateniformis Bromley & D'Alessandro, 1984		Macroboring; calcareous; invertebrate
E. geometrica Bromley & D'Alessandro, 1984		Macroboring; calcareous; invertebrate
E. laquea Bromley & D'Alessandro, 1984		Macroboring; calcareous; invertebrate
E. ovula Bromley & D'Alessandro, 1984		Macroboring; calcareous; invertebrate
E. volzi Bromley & D'Alessandro, 1984		Macroboring; calcareous; invertebrate
E. depressa Ghare, 1985		Macroboring; calcareous; invertebrate
E. dendritica Pleydell & Jones, 1988		Macroboring; calcareous; invertebrate
E. gigantea Bromley & D'Alessandro, 1989		Macroboring; calcareous; invertebrate
E. magna Bromley & D'Alessandro, 1989		Macroboring; calcareous; invertebrate
E. parva Bromley & D'Alessandro, 1989		Macroboring; calcareous; invertebrate
E. astrologica Mikuláš, 1992		Macroboring; calcareous; invertebrate
E. solaris Mikuláš, 1992		Macroboring; calcareous; invertebrate
E. goniodes Bromley & Asgaard, 1993		Macroboring; calcareous; invertebrate
E. cervicornis Fürsich et al., 1994		Macroboring; calcareous; invertebrate
E. convoluta Edinger & Risk, 1994		Macroboring; calcareous; invertebrate
E. micra Wisshak, 2008		Microboring; calcareous; invertebrate

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
E. nana Wisshak, 2008		Microboring; calcareous; invertebrate
E. cracoviensis Bromley & Uchman in Bromley et al., 2009		Macroboring; calcareous; invertebrate
E. resinensis Santos et al., 2011		Macroboring; calcareous; invertebrate
E. colaria Wisshak et al., 2017		Macroboring; calcareous; invertebrate
E. morrisi nom. nov.	*Clionites glomerata*	Macroboring; calcareous; invertebrate
E. tuberculata nom. nov.	*Entobia mammillata*	Macroboring; calcareous; invertebrate
Eocavum Buchholz, 1986		Macroboring; xylic; vertebrate
E. picifactum Buchholz, 1986*		Macroboring; xylic; vertebrate
Ericichnus Santos & Mayoral in Santos et al., 2015		Grazing; siliceous; invertebrate
E. bromleyi Santos & Mayoral in Santos et al., 2015*		Grazing; siliceous; invertebrate
E. asgaardi Santos & Mayoral in Santos et al., 2015		Grazing; siliceous; invertebrate
Eurygonum Schmidt, 1992		Microboring; calcareous; bacterium
E. nodosum Schmidt, 1992*		Microboring; calcareous; bacterium
E. pennaforme Wisshak et al., 2005		Microboring; calcareous; plant
Fascichnus Radtke & Golubić, 2005		Microboring; calcareous; bacterium
F. dactylus (Radtke, 1991)*	*Fasciculus dactylus*	Microboring; calcareous; bacterium
F. frutex (Radtke, 1991)	*Fasciculus frutex*	Microboring; calcareous; bacterium
F. grandis (Radtke, 1991)	*Fasciculus grandis*	Microboring; calcareous; plant
F. parvus (Radtke, 1991)	*Fasciculus parvus*	Microboring; calcareous; bacterium
F. acinosus (Glaub, 1994)	*Fasciculus acinosus*	Microboring; calcareous; bacterium
F. rogus (Bundschuh & Balog, 2000)	*Fasciculus rogus*	Microboring; calcareous; bacterium
F. bellafurcus (Radtke et al., 2010)	*Abeliella bellafurca*	Microboring; calcareous; bacterium
Feldmannius Low & Guinot, 2010		Microboring; calcareous; invertebrate
F. cavernosus (Casadío et al., 2001)* nom. corr.	*Feldmannia cavernosa*	Microboring; calcareous; invertebrate
Filuroda Solle, 1938		Microboring; calcareous; unknown
F. reptans (Clarke, 1908)*	*Clionolithes reptans*	Microboring; calcareous; unknown
Finichnus Taylor et al., 2013		Attachment; calcareous; invertebrate
F. peristoma (Taylor et al., 1999)*	*Leptichnus peristoma*	Attachment; calcareous; invertebrate
F. dromeus (Taylor et al., 1999)	*Leptichnus dromeus*	Attachment; calcareous; invertebrate
F. tortus (Rosso, 2008)	*Leptichnus tortus*	Attachment; calcareous; invertebrate
Flagrichnus Wisshak & Porter, 2006		Microboring; calcareous; fungus
F. profundus Wisshak & Porter, 2006*		Microboring; calcareous; fungus
F. baiulus Wisshak & Porter, 2006		Microboring; calcareous; fungus?
Flosculichnus Donovan & Jagt, 2005		Attachment; calcareous; invertebrate?
F. tectus Donovan & Jagt, 2005*		Attachment; calcareous; invertebrate?
Gastrochaenolites Leymerie, 1842		Macroboring; calcareous; invertebrate
G. japonicus (Hatai et al., 1974)	*Moniopterus japonicus*	Macroboring; calcareous; invertebrate
G. lapidicus Kelly & Bromley, 1984*		Macroboring; calcareous; invertebrate
G. ampullatus Kelly & Bromley, 1984		Macroboring; calcareous; invertebrate
G. cluniformis Kelly & Bromley, 1984		Macroboring; calcareous; invertebrate
G. dijugus Kelly & Bromley, 1984		Macroboring; calcareous; invertebrate
G. orbicularis Kelly & Bromley, 1984		Macroboring; calcareous; invertebrate
G. turbinatus Kelly & Bromley, 1984		Macroboring; calcareous; invertebrate
G. ornatus Kelly & Bromley, 1984		Macroboring; calcareous; invertebrate
G. raigadensis (Badve & Ghare, 1984) comb. nov.	*Paleolithopholas raigadensis*	Macroboring; calcareous; invertebrate
G. cor Bromley & D'Alessandro, 1987		Macroboring; calcareous; invertebrate
G. vivus Edinger & Risk, 1994		Macroboring; calcareous; invertebrate
G. anauchen Wilson & Palmer, 1998		Macroboring; calcareous; invertebrate
G. oelandicus Ekdale & Bromley, 2001		Macroboring; calcareous; invertebrate
G. pickerilli Donovan, 2002		Macroboring; calcareous; invertebrate

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
G. hospitium Kleemann, 2009		Macroboring; calcareous; invertebrate
Glirotremmorpha Collinson & Hooker, 2000		Macroboring; xylic; invertebrate
G. entecta Collinson & Hooker, 2000* nom. corr.	*Glirotremmorpha entectus*	Macroboring; xylic; invertebrate
Gnathichnus Bromley, 1975		Grazing; calcareous; invertebrate
G. pentax Bromley, 1975*		Grazing; calcareous; invertebrate
Granulohyalichnus McLoughlin et al., 2009		Microboring; siliceous; bacterium
G. vulgaris McLoughlin et al., 2009*		Microboring; siliceous; bacterium
Helicotaphrichnus Kern et al., 1974		Macroboring; calcareous; invertebrate
H. commensalis Kern et al., 1974*		Macroboring; calcareous; invertebrate
H. helicus (Nielsen & Görmüş, 2004) comb. nov.	*Trypanites helicus*	Macroboring; calcareous; invertebrate
Ichnogutta Botquelen & Mayoral, 2005		Microboring; calcareous; invertebrate
I. erecta Botquelen & Mayoral, 2005* nom. corr.	*Ichnogutta erectus*	Microboring; calcareous; invertebrate
Ichnoreticulina Radtke & Golubić, 2005		Microboring; calcareous; plant
I. elegans (Radtke, 1991)*	*Reticulina elegans*	Microboring; calcareous; plant
Ichnotorula Tavernier & Golubić, 1993		Microboring; calcareous; unknown
I. inequalis Tavernier & Golubić, 1993*		Microboring; calcareous; unknown
Ipites igen nov.		Macroboring; xylic; invertebrate
I. bobrowskianus Karpiński, 1962*		Macroboring; xylic; invertebrate
Iramena Boekschoten, 1970		Microboring; calcareous; invertebrate
I. danica Boekschoten, 1970*		Microboring; calcareous; invertebrate
I. bonaresi Mayoral, 1988		Microboring; calcareous; invertebrate
Irhopalia nom. nov.	*Rhopalia*	Microboring; calcareous; plant
I. catenata (Radtke, 1991)* comb. nov.	*Rhopalia catenata*	Microboring; calcareous; plant
I. spinosa (Radtke & Golubić, 2005) comb. nov.	*Rhopalia spinosa*	Microboring; calcareous; plant
I. clavigera (Golubić & Radtke, 2008) comb. nov.	*Rhopalia clavigera*	Microboring; calcareous; plant
Kardopomorphos Beuck et al., 2008a		Predation; calcareous; invertebrate
K. polydioryx Beuck et al., 2008a*		Predation; calcareous; invertebrate
Karethraichnus Zonneveld et al., 2015		Macroboring; osteic; invertebrate
K. lakkos Zonneveld et al., 2015*		Macroboring; osteic; invertebrate
K. fiale Zonneveld et al., 2015		Macroboring; osteic; invertebrate
Knethichnus Jacobsen & Bromley, 2009		Predation; osteic; vertebrate
K. parallelus Jacobsen & Bromley, 2009* nom. corr.	*Knethichnus parallelum*	Predation; osteic; vertebrate
Lacrimichnus Santos et al., 2003		Attachment; calcareous; invertebrate
L. cacelensis Santos et al., 2003*		Attachment; calcareous; invertebrate
L. bonarensis Santos et al., 2003		Attachment; calcareous; invertebrate
Lamniporichnus Mikuláš et al., 1998		Macroboring; xylic; invertebrate
L. vulgaris Mikuláš et al., 1998*		Macroboring; xylic; invertebrate
Lapispecus Voigt, 1970		Macroboring; calcareous; invertebrate
L. cuniculus Voigt, 1970*		Macroboring; calcareous; invertebrate
L. hastatus Wisshak et al., 2017		Macroboring; calcareous; invertebrate
Linckichnus Schlirf, 2006		Macroboring; xylic; invertebrate
L. terebrans Schlirf, 2006*		Macroboring; xylic; invertebrate
Linichnus Jacobsen & Bromley, 2009		Predation; osteic; vertebrate
L. serratus Jacobsen & Bromley, 2009*		Predation; osteic; vertebrate
Loxolenichnus Breton et al., 2017		Predation; calcareous; invertebrate
L. halo (Neumann & Wisshak, 2009)	*Oichnus halo*	Predation; calcareous; invertebrate
L. taddeii (Ruggiero & Raia, 2014)	*Oichnus taddeii*	Predation; calcareous; invertebrate
L. stellatocinctus Breton et al., 2017*		Predation; calcareous; invertebrate
Machichnus Mikuláš et al., 2006		Predation; osteic; vertebrate
M. regularis Mikuláš et al., 2006*		Predation; osteic; vertebrate

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
M. bohemicus Mikuláš et al., 2006		Predation; osteic; vertebrate
M. multilineatus Mikuláš et al., 2006		Predation; osteic; vertebrate
M. normani Chumakov et al., 2013		Grazing; siliceous; vertebrate
M. harlandi Chumakov et al., 2013		Grazing; siliceous; vertebrate
M. jeansi Chumakov et al., 2013		Grazing; siliceous; vertebrate
M. fatimae de Araújo-Júnior et al., 2017		Predation; osteic; vertebrate
Maeandropolydora Voigt, 1965		Macroboring; calcareous; invertebrate
M. vermicularis (Seguenza, 1879) comb. nov.	*Cliona vermicularis*	Macroboring; calcareous; invertebrate
M. lenticula (Gruber, 1933) comb. nov.	*Cliona lenticula*	Macroboring; calcareous; invertebrate
M. decipiens Voigt, 1965*		Macroboring; calcareous; invertebrate
M. sulcans Voigt, 1965		Macroboring; calcareous; invertebrate
M. elegans Bromley & D'Alessandro, 1983		Macroboring; calcareous; invertebrate
M. barocca Bromley & D'Alessandro, 1987		Macroboring; calcareous; invertebrate
M. crassa Bromley & D'Alessandro, 1987		Macroboring; calcareous; invertebrate
M. osmaneliensis Nielsen & Görmüş, 2004		Macroboring; calcareous; invertebrate
Mandaodonites Cruickshank, 1986		Predation; osteic; vertebrate
M. coxi Cruickshank, 1986*		Predation; osteic; vertebrate
Munitusichnus Parkinson, 2016		Macroboring; osteic; invertebrate
M. pascens Parkinson, 2016*		Macroboring; osteic; invertebrate
Neodendrina Wisshak & Neumann, 2018		Microboring; calcareous; unknown
N. carnelia Wisshak & Neumann, 2018*		Microboring; calcareous; unknown
Nihilichnus Mikuláš et al., 2006		Predation; osteic; vertebrate
N. nihilicus Mikuláš et al., 2006*		Predation; osteic; vertebrate
N. covichi Rasser et al., 2016		Predation; calcareous; vertebrate
Nododendrina Vogel et al., 1987		Microboring; calcareous; invertebrate?
N. europaea (Fischer, 1875)	*Dendrina europæa*	Microboring; calcareous; invertebrate?
N. incomposita (Mägdefrau, 1937)	*Dendrina incomposita*	Microboring; calcareous; invertebrate?
N. paleodendrica (Elias, 1957)	*Cliona paleodendrica*	Microboring; calcareous; invertebrate?
N. nodosa Vogel et al., 1987*		Microboring; calcareous; invertebrate?
Oichnus Bromley, 1981		Predation; calcareous; invertebrate
O. simplex Bromley, 1981*		Predation; calcareous; invertebrate
O. paraboloides Bromley, 1981		Predation; calcareous; invertebrate
O. ovalis Bromley, 1993		Predation; calcareous; invertebrate
O. asperus Nielsen & Nielsen, 2001		Predation; calcareous; invertebrate
O. coronatus Nielsen & Nielsen, 2001		Predation; calcareous; invertebrate
O. gradatus Nielsen & Nielsen, 2001		Predation; calcareous; invertebrate
O. solus (Nielsen et al., 2003)	*Fossichnus solus*	Predation; calcareous; invertebrate
Ophthalmichnus Wisshak et al., 2014		Attachment; calcareous; plant
O. lyolithon Wisshak et al., 2014*		Attachment; calcareous; plant
Orthogonum Radtke, 1991		Microboring; calcareous; fungus?
O. scalariformis (Ghare, 1982) comb. nov.	*Talpina scalariformis*	Microboring; calcareous; fungus?
O. tubulare Radtke, 1991*		Microboring; calcareous; fungus?
O. fusiferum Radtke, 1991		Microboring; calcareous; fungus?
O. spinosum Radtke, 1991		Microboring; calcareous; fungus?
O. tripartitum Schmidt, 1992		Microboring; calcareous; fungus?
O. appendiculatum Glaub, 1994		Microboring; calcareous; fungus?
O. giganteum Glaub, 1994		Microboring; calcareous; fungus?
O. lineare Glaub, 1994		Microboring; calcareous; fungus?
Osedacoides Karl et al., 2012		Macroboring; osteic; invertebrate
O. jurassicus Karl et al., 2012*		Macroboring; osteic; invertebrate

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
Osprioneides Beuck & Wisshak in Beuck et al., 2008b		Macroboring; calcareous; invertebrate
O. kampto Beuck & Wisshak in Beuck et al., 2008b*		Macroboring; calcareous; invertebrate
Osteichnus Höpner & Bertling, 2017		Macroboring; osteic; invertebrate
O. ossibiontum (Thenius, 1988)*	*Asthenopodichnium ossibiontum*	Macroboring; osteic; invertebrate
Osteocallis Roberts et al., 2007		Grazing; osteic; invertebrate
O. mandibulus Roberts et al., 2007*		Grazing; osteic; invertebrate
O. infestans Paes Neto et al., 2016		Grazing; osteic; invertebrate
Palaeomycelites Bystrov, 1956		Microboring; osteic; fungus
P. lacustris Bystrov, 1956*		Microboring; osteic; fungus
Palaeosabella Clarke, 1921		Macroboring; calcareous; invertebrate
P. prisca (McCoy, 1855)*	*Vioa prisca*	Macroboring; calcareous; invertebrate
Paleobuprestis Walker, 1938		Macroboring; xylic; invertebrate
P. maxima Walker, 1938*		Macroboring; xylic; invertebrate
P. minima Walker, 1938		Macroboring; xylic; invertebrate
P. sudeticus Muszer & Uglik, 2013		Macroboring; xylic; invertebrate
Paleoipidus Walker, 1938		Macroboring; xylic; invertebrate
P. perforatus Walker, 1938*		Macroboring; xylic; invertebrate
P. marginatus Walker, 1938		Macroboring; xylic; invertebrate
Paleoscolytus Walker, 1938		Macroboring; xylic; invertebrate
P. divergus Walker, 1938*		Macroboring; xylic; invertebrate
Pecinolites Mikuláš & Dvořák, 2002		Macroboring; xylic; invertebrate
P. boreki Mikuláš & Dvořák, 2002*		Macroboring; xylic; invertebrate
Pennatichnus Mayoral, 1988		Microboring; calcareous; invertebrate
P. moguerenicus Mayoral, 1988* nom. corr.	*Pennatichnus moguerenica*	Microboring; calcareous; invertebrate
P. luceni Mayoral, 1988		Microboring; calcareous; invertebrate
Petroxestes Wilson & Palmer, 1988		Macroboring; calcareous; invertebrate
P. pera Wilson & Palmer, 1988*		Macroboring; calcareous; invertebrate
P. altera Jagt et al., 2009		Macroboring; calcareous; invertebrate
Phrixichnus Bromley & Asgaard, 1993		Macroboring; calcareous; invertebrate
P. phrix Bromley & Asgaard, 1993*		Macroboring; calcareous; invertebrate
Pinaceocladichnus Mayoral, 1988		Microboring; calcareous; invertebrate
P. onubensis Mayoral, 1988*		Microboring; calcareous; invertebrate
P. bulbosus Mayoral, 1991		Microboring; calcareous; invertebrate
P. perplexus Mayoral et al., 1994		Microboring; calcareous; invertebrate
P. cristatus Botquelen & Mayoral, 2005		Microboring; calcareous; invertebrate
Planavolites Mikuláš, 1992		Grazing; calcareous; invertebrate
P. homolensis Mikuláš, 1992*		Grazing; calcareous; invertebrate
Planobola Schmidt, 1992		Microboring; calcareous; bacterium?
P. microgota Schmidt, 1992*		Microboring; calcareous; bacterium?
P. cebolla Schmidt, 1992		Microboring; calcareous; bacterium?
P. macrogota Schmidt, 1992		Microboring; calcareous; bacterium?
P. radicata Schmidt, 1992 nom. corr.	*Planobola radicatus*	Microboring; calcareous; bacterium?
Podichnus Bromley & Surlyk, 1973		Attachment; calcareous; invertebrate
P. centrifugalis Bromley & Surlyk, 1973*		Attachment; calcareous; invertebrate
P. obliquus Robinson & Lee, 2008		Attachment; calcareous; invertebrate
P. perpendicularis Robinson & Lee, 2008		Attachment; calcareous; invertebrate
P. conicus Santos & Mayoral in Santos et al., 2014		Attachment; calcareous; invertebrate
Polyactina Radtke, 1991		Microboring; calcareous; fungus
P. araneola Radtke, 1991*		Microboring; calcareous; fungus
Pseudopolydorites Głazek et al., 1971		Macroboring; calcareous; invertebrate

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
P. radwanskii Głazek et al., 1971*		Macroboring; calcareous; invertebrate
Pyrodendrina Tapanila, 2008		Microboring; calcareous; invertebrate?
P. cupra Tapanila, 2008*		Microboring; calcareous; invertebrate?
P. arctica Wisshak, 2017		Microboring; calcareous; invertebrate?
P. belua Wisshak, 2017		Microboring; calcareous; invertebrate?
P. villosa Wisshak, 2017		Microboring; calcareous; invertebrate?
Radulichnus Voigt, 1977		Grazing; calcareous; invertebrate
R. inopinatus Voigt, 1977*		Grazing; calcareous; invertebrate
R. transversus Lopes & Pereira, 2018		Grazing; calcareous; invertebrate
Renichnus Mayoral, 1987a		Attachment; calcareous; invertebrate
R. arcuatus Mayoral, 1987a*		Attachment; calcareous; invertebrate
Rhopalondendrina Wisshak, 2017		Microboring; calcareous; invertebrate?
R. avis Wisshak, 2017*		Microboring; calcareous; invertebrate?
R. acanthina Wisshak, 2017		Microboring; calcareous; invertebrate?
R. contra Wisshak, 2017		Microboring; calcareous; invertebrate?
R. tigris Wisshak, 2017		Microboring; calcareous; invertebrate?
Rodocanalis Schloz, 1972		Attachment; calcareous; unknown
R. reticulatus Schloz, 1972*		Attachment; calcareous; unknown
Rogerella de Saint-Seine, 1951		Macroboring; calcareous; invertebrate
R. oostoma (Seguenza, 1879) comb. nov.	*Cliona oostoma*	Macroboring; calcareous; invertebrate
R. arbiglandensis (Smith, 1910) comb. nov.	*Clionoida arbiglandensis*	Macroboring; calcareous; invertebrate
R. sacculus (Mägdefrau, 1937) comb. nov.	*Nygmites sacculus*	Macroboring; calcareous; invertebrate
R. lecointrei de Saint-Seine, 1951*		Macroboring; calcareous; invertebrate
R. linii (Hyde, 1953) comb. nov.	*Seminolithes linii*	Macroboring; calcareous; invertebrate
R. mathieui de Saint-Seine, 1955		Macroboring; calcareous; invertebrate
R. pattei (de Saint-Seine, 1955)	*Zapfella pattei*	Macroboring; calcareous; invertebrate
R. elliptica (Codez in Codez & de Saint-Seine, 1958) comb. nov.	*Brachyzapfes elliptica*	Macroboring; calcareous; invertebrate
R. elongata (Codez & de Saint-Seine, 1958) comb. nov.	*Simonizapfes elongata*	Macroboring; calcareous; invertebrate
R. cragini Schlaudt & Young, 1960		Macroboring; calcareous; invertebrate
R. caveata (Tomlinson, 1963) comb. nov.	*Trypetesa caveata*	Macroboring; calcareous; invertebrate
R. caudata Voigt, 1967		Macroboring; calcareous; invertebrate
R. davenporti (Tomlinson, 1969) comb. nov.	*Simonizapfes davenporti*	Macroboring; calcareous; invertebrate
R. polonica (Bałuk & Radwański, 1991) comb. nov.	*Trypetesa polonica*	Macroboring; calcareous; invertebrate
Runia Marek, 1982		Macroboring; calcareous; unknown
R. runica Marek, 1982*		Macroboring; calcareous; unknown
Saccomorpha Radtke, 1991		Microboring; calcareous; fungus
S. clava Radtke, 1991*		Microboring; calcareous; fungus
S. sphaerula Radtke, 1991		Microboring; calcareous; fungus
S. terminalis Radtke, 1991		Microboring; calcareous; fungus?
S. stereodiktyon Golubić et al., 2014		Microboring; calcareous; fungus?
S. guttulata Wisshak et al., 2018		Microboring; calcareous; fungus?
Sanctum Erickson & Bouchard, 2003		Macroboring; calcareous; invertebrate
S. laurentiensis Erickson & Bouchard, 2003*		Macroboring; calcareous; invertebrate
Scolecia Radtke, 1991		Microboring; calcareous; bacterium?
S. maeandria Radtke, 1991*		Microboring; calcareous; bacterium?
S. botulifera Radtke, 1991		Microboring; calcareous; bacterium?
S. filosa Radtke, 1991		Microboring; calcareous; bacterium?
S. serrata Radtke, 1991		Microboring; calcareous; bacterium?
Scolytolarvariumichnus Guo, 1991		Macroboring; xylic; invertebrate
S. sussexensis (Jarzembowski, 1990) comb. nov.	*Paleoscolytus sussexensis*	Macroboring; xylic; invertebrate

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
S. radiatus Guo, 1991*		Macroboring; xylic; invertebrate
S. zherikhini (Petrov, 2013) comb. nov.	*Megascolytinus zherikhini*	Macroboring; xylic; invertebrate
Sertaterebrites Ekdale et al., 1989		Macroboring; calcareous; invertebrate
S. nachukui Ekdale et al., 1989*		Macroboring; calcareous; invertebrate
Spirichnus Fürsich et al., 1994		Macroboring; calcareous; invertebrate
S. spiralis Fürsich et al., 1994*		Macroboring; calcareous; invertebrate
Solealites Uchman & Rattazzi, 2018		Attachment; calcareous; invertebrate
S. ovalis Uchman & Rattazzi, 2018*		Attachment; calcareous; invertebrate
Spirolites Uchman et al., 2018a		Attachment; calcareous; invertebrate
S. radwanskii Uchman et al., 2018a*		Attachment; calcareous; invertebrate
Stellatichnus Nielsen & Nielsen, 2001		Predation; calcareous; unknown
S. radiatus Nielsen & Nielsen, 2001*		Predation; calcareous; unknown
Stellichnus Mayoral, 1987b		Attachment; calcareous; invertebrate
S. radiatus Mayoral, 1987b*		Attachment; calcareous; invertebrate
Stipitichnus Genise, 1995		Macroboring; xylic; invertebrate
S. koppae Genise, 1995*		Macroboring; xylic; invertebrate
Sulcichnus Martinell & Domènech, 2009		Macroboring; calcareous; invertebrate
S. maeandriformis Martinell & Domènech, 2009*		Macroboring; calcareous; invertebrate
S. helicoidalis Martinell & Domènech, 2009		Macroboring; calcareous; invertebrate
S. sigillum Martinell & Domènech, 2009		Macroboring; calcareous; invertebrate
Sulculites Vialov & Nessov, 1974		Macroboring; osteic, invertebrate
S. bellus Vialov & Nessov, 1974*		Macroboring; osteic, invertebrate
Talpina von Hagenow, 1840		Macroboring; calcareous; invertebrate?
T. ramosa von Hagenow, 1840*		Macroboring; calcareous; invertebrate?
T. eduliformis Quenstedt, 1858		Macroboring; calcareous; invertebrate?
T. squamosa Terquem & Piette, 1865		Macroboring; calcareous; invertebrate?
T. hackberryensis (Thomas, 1911)	*Cliona hackberryensis*	Macroboring; calcareous; invertebrate?
T. lizardensis (Lees & Thomas, 1918)	*Clionolithes lizardensis*	Macroboring; calcareous; invertebrate?
T. tenuis (Teichert, 1945) comb. nov.	*Conchotrema tenuis*	Macroboring; calcareous; invertebrate?
T. tubulosa (Teichert, 1945) comb. nov.	*Conchotrema tubulosa*	Macroboring; calcareous; invertebrate?
T. gruberi Mayer, 1952		Macroboring; calcareous; invertebrate?
T. annulata Voigt, 1975		Macroboring; calcareous; invertebrate?
T. hirsuta Voigt, 1975		Macroboring; calcareous; invertebrate?
T. bromleyi Fürsich et al., 1994		Macroboring; calcareous; invertebrate?
T. porrecta Terquem & Piette, 1865		Macroboring; calcareous; invertebrate?
T. hunanensis Stiller, 2005		Macroboring; calcareous; invertebrate?
Tarrichnium Wanner, 1938		Attachment; calcareous; invertebrate?
T. balanocrini Wanner, 1938*		Attachment; calcareous; invertebrate?
Teredolites Leymerie, 1842		Macroboring; xylic; invertebrate
T. clavatus Leymerie, 1842*		Macroboring; xylic; invertebrate
Tremichnus Brett, 1985		Macroboring; calcareous; invertebrate
T. paraboloides Brett, 1985*		Macroboring; calcareous; invertebrate
T. puteolus Brett, 1985		Macroboring; calcareous; invertebrate
T. excavatus (Donovan & Jagt, 2002)	*Oichnus excavatus*	Macroboring; calcareous; invertebrate
Trypanites Mägdefrau, 1932		Macroboring; calcareous; invertebrate
T. solitarius (von Hagenow, 1840)	*Talpina solitaria*	Macroboring; calcareous; invertebrate
T. weisei Mägdefrau, 1932*		Macroboring; calcareous; invertebrate
T. fosteryeomani Cole & Palmer, 1999		Macroboring; calcareous; invertebrate
T. mobilis Neumann et al., 2008		Macroboring; calcareous; invertebrate
Tubulohyalichnus McLoughlin et al., 2009		Microboring; siliceous; bacterium

Table 1 (continued)

Ichnotaxon	Original name or combination	Type; substrate; tracemaker
T. simplus McLoughlin et al., 2009*		Microboring; siliceous; bacterium
T. annularis McLoughlin et al., 2009		Microboring; siliceous; bacterium
T. spiralis McLoughlin et al., 2009		Microboring; siliceous; bacterium
T. stipes McLoughlin et al., 2009		Microboring; siliceous; bacterium
Umbichnus Martinell et al., 1999		Macroboring; calcareous; invertebrate
U. inopinatus Martinell et al., 1999*		Macroboring; calcareous; invertebrate
Unellichnus Breton, 2015a		Macroboring; calcareous; invertebrate
U. calciforans Breton, 2015a*		Macroboring; calcareous; invertebrate
Xylokrypta Tapanila & Roberts, 2012		Macroboring; xylic; invertebrate
X. durossi Tapanila & Roberts, 2012*		Macroboring; xylic; invertebrate
Xylonichnus Genise, 1995		Macroboring; xylic; invertebrate
X. trypetus Genise, 1995*		Macroboring; xylic; invertebrate
X. meniscatus (Genise & Hazeldine, 1995) comb. nov.	*Dekosichnus meniscatus*	Macroboring; xylic; invertebrate

Table 2 List of all bioerosion ichnotaxa currently considered dubious or invalid, their senior synonym or homonym, as well as the reason and the reference for the rejection

Ichnotaxon	Senior synonym/homonym	Reason for rejection	References
Aggregatella Elliott, 1962		*nomen dubium* (microboring assemblage?)	Herein
A. pseudohieroglyphicus Elliott, 1962		*nomen dubium* (microboring assemblage?)	Herein
Anellusichnus Santos et al., 2005	*Centrichnus*	Subjective junior synonym	Herein
Anoigmaichnus Vinn et al., 2014	*Trypanites*	Subjective junior synonym	Herein
A. odinsholmensis Vinn et al., 2014	*T. weisei*	Subjective junior synonym	Herein
Archaeomycelites Bystrow, 1959	*Palaeomycelites*	Subjective junior synonym	Herein
A. odontophagus Bystrow, 1959	*P. lacustris*	Subjective junior synonym	Herein
Asthenopodichnium fallax Francischini et al., 2016	*Petroxestes altera*	Subjective junior synonym	Herein
Asteriastoma Breton, 1992	*Gnathichnus*	Subjective junior synonym	Herein
A. cretaceum Breton, 1992	*G. pentax*	Subjective junior synonym	Herein
Balticapunctum Rozhnov, 1989	*Tremichnus*	Subjective junior synonym	Wisshak et al. (2015)
B. inchoatus Rozhnov, 1989	*T. paraboloides*	Subjective junior synonym	Wisshak et al. (2015)
Bascomella Morningstar, 1922		*nomen dubium* (composite trace fossil)	Bromley & D'Alessandro (1987)
B. gigantea Morningstar, 1922		*nomen dubium* (composite trace fossil)	Herein
B. fusiformis Condra & Elias, 1944		*nomen dubium* (composite trace fossil)	Herein
B. subsphaerica Condra & Elias, 1944		*nomen dubium* (composite trace fossil)	Herein
Belichnus dusos Pether, 1995	*Belichnus monos*	Subjective junior synonym	Herein
Bothrioichnus Palmer & Plewes, 1993		*nomen nudum* (no diagnosis)	Taylor et al. (1999)
Brachyzapfes Codez in Codez & de Saint-Seine, 1958	*Rogerella*	Subjective junior synonym	Bromley & D'Alessandro (1987)
Brutalichnus Mikuláš et al., 2006		*nomen dubium* (producer action not obvious)	Herein
B. brutalis Mikuláš et al., 2006		*nomen dubium* (producer action not obvious)	Herein
Caedichnus Stafford et al., 2015	*Bicrescomanducator*	Subjective junior synonym	Herein
C. spiralis Stafford et al., 2015	*B. spiralis*	Subjective junior synonym	Herein
Calciroda Mayer, 1952	*Talpina*	*nomen dubium* (composite trace fossil)	Herein

Table 2 (continued)

Ichnotaxon	Senior synonym/homonym	Reason for rejection	References
C. kraichgoviae Mayer, 1952	*T. ramosa*	*nomen dubium* (composite trace fossil)	Herein
C. tubulata Hary, 1975	*T. ramosa*	Subjective junior synonym	Herein
Carporichnus bertheorum Genise, 1995	*Carporichnus maximus*	Subjective junior synonym	Genise 2017
C. minimus Genise, 1995	*C. maximus*	Subjective junior synonym	Genise 2017
Caulostrepsis dunbari Condra & Elias, 1944	*Caulostrepsis taeniola*	Subjective junior synonym	Bromley & D'Alessandro (1983)
Chaetophorites Pratje, 1922		*nomen dubium* (poorly defined; types lost)	Herein
C. gomontoides Pratje, 1922		*nomen dubium* (poorly defined; types lost)	Herein
C. tenuis Mägdefrau, 1937		*nomen dubium* (poorly defined)	Herein
"*Chondrites*" *symmetricus* Solle, 1938		*nomen nudum* (not a trace fossil; brachiopod)	Wisshak (2017)
"*Chondrites*" *multifilum* Solle, 1938		*nomen nudum* (not a trace fossil; mould of epilith?)	Wisshak (2017)
Cicatricula Palmer & Palmer, 1977	*Dictyoporus*	Subjective junior synonym	Wisshak (2017)
C. retiformis Palmer & Palmer, 1977	*D. nodosus*	Subjective junior synonym	Wisshak (2017)
Cliona distans Étallon in Thurmann & Étallon, 1864		*nomen dubium* (acrothoracican borings?)	Fischer (1868)
C. multicava Étallon in Thurmann & Étallon, 1864		*nomen dubium* (acrothoracican borings?)	Fischer (1868)
C. ovata Étallon in Thurmann & Étallon, 1864		*nomen dubium* (acrothoracican borings?)	Fischer (1868)
C. duchassaingi Fischer, 1868		*nomen nudum* (no description or indication)	Herein
C. studeri Mayer, 1872		*nomen nudum* (no description or indication)	Herein
C. micropora Seguenza, 1879		*nomen dubium* (microboring assemblage; types lost)	Herein
C. kelheadensis Smith, 1910		*nomen dubium* (poor illustration; types lost)	Herein
C. cretacica Fenton & Fenton, 1932	*Entobia megastoma*	Subjective junior synonym	Bromley & D'Alessandro (1984)
C. stellata Elias, 1957		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
C. fenestralis Elias, 1957	*Dictyoporus nodosus*	Subjective junior synonym	Wisshak (2017)
Clionites Morris in Mantell, 1850	*Entobia*	Subjective junior synonym	Bromley (1970a)
C. parkinsoni Morris in Mantell, 1850		*nomen dubium* (poor description; poor illustration)	Herein
C. conybeari Morris in Mantell, 1850	*E. cretacea*	Subjective junior synonym	Bromley (1970a)
C. glomerata Morris, 1851	*E. glomerata* (Michelin)	Junior homonym; nom. nov.: *E. morrisi*	Herein
C. mantelli Wetherell, 1852	*Rogerella mathieui*	Subjective junior synonym	Häntzschel (1975)
Clionoida Smith, 1910		*nomen dubium* (no definition)	Herein
C. arbiglandensis Smith, 1910		*nomen dubium* (poor illustration; types lost)	Herein
Clionoides Fenton & Fenton, 1932	*Trypanites*	Subjective junior synonym	Herein
C. thomasi Fenton & Fenton, 1932	*T. solitarius*	Subjective junior synonym	Herein
C. utaturensis Ghare, 1982	*T. solitarius*	Subjective junior synonym	Herein
Clionolithes canna Price, 1916	*Talpina hackberryensis*	Subjective junior synonym	Wisshak (2017)
C. quaerens Ruedemann, 1925		Not a trace fossil (unidentified epilith)	Wisshak (2017)
C. fossiger Fenton & Fenton, 1932		Not a bioerosion trace fossil (burrow)	Wisshak (2017)
C. irregularis Fenton & Fenton, 1932	*Talpina hackberryensis*	Subjective junior synonym	Wisshak (2017)
C. pricei Branson, 1937		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
C. ramosus Hyde, 1953		*nomen dubium* (unidentified tubular boring)	Wisshak (2017)
C. implicatus Hyde, 1953	*Palaeosabella prisca*	Subjective junior synonym	Wisshak (2017)
C. hunanensis Chow, 1957		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
C. sollei Talent, 1963	*Clionolithes palmatus*	Subjective junior synonym	Wisshak (2017)
C. bullahirsuta Plewes, 1996		*nomen nudum* (unpublished thesis)	Wisshak (2017)

Table 2 (continued)

Ichnotaxon	Senior synonym/homonym	Reason for rejection	References
Cobalia Étallon, 1859		*nomen dubium* (no illustration; types lost)	Wisshak (2017)
C. jurensis Étallon, 1859		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
C. grayensis Étallon, 1864		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
Conchifora Müller, 1968	*Trypanites*	Subjective junior synonym	Bromley (1972)
C. zylindriformis Müller, 1968	*T. solitarius*	Subjective junior synonym	Herein
Conchotrema Teichert, 1945	*Talpina*	Subjective junior synonym	Herein
Cunicularis isodiametricus Li, 1997	*Endoconchia lata*	Subjective junior synonym	Herein
Cylindricavus Borkar & Kulkarni, 1987		*nomen dubium* (root cast?)	Herein
C. perplexus Borkar & Kulkarni, 1987		*nomen dubium* (root cast?)	Herein
Cylindrocavites Ghare, 1982	*Trypanites*	Subjective junior synonym	Pemberton et al. (1988)
C. cretacea Ghare, 1982	*T. weisei*	Subjective junior synonym	Herein
Dekosichnus Genise & Hazeldine, 1995	*Xylonichnus*	Subjective junior synonym	Herein
Dendrina elongata Étallon, 1859		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
D. scoparia Étallon, 1859		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
D. stellata Étallon, 1859	*Dendrina dendrina*	Subjective junior synonym	Wisshak (2017)
D. punctata Étallon in Thurmann & Étallon, 1864		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
D. fodicans Étallon in Thurmann & Étallon, 1864		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
D. dumosa Étallon in Thurmann & Étallon, 1864		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
D. ramulifera Étallon in Thurmann & Étallon, 1864		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
D. lichenoidea Étallon, 1864		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
D. gracilis Étallon, 1864		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
D. minor Mägdefrau, 1937	*Nododendrina incomposita*	Subjective junior synonym	Wisshak (2017)
D. ordoplana Plewes, 1996	*Dendrina dendrina*	*nomen nudum* (unpublished thesis)	Wisshak (2017)
D. crassa Hofmann, 1996	*Dendrina dendrina*	Subjective junior synonym	Wisshak (2017)
D. fluensis Hofmann, 1996	*Dendrina dendrina*	Subjective junior synonym	Wisshak (2017)
D. orbiculata Hofmann, 1996	*Dendrina belemniticola*	Subjective junior synonym	Wisshak (2017)
D. constans Hofmann, 1996	*Dendrina belemniticola*	Subjective junior synonym	Wisshak (2017)
D. brachiopodicola Hofmann, 1996	*Calcideletrix flexuosa*	Subjective junior synonym	Wisshak (2017)
Dendrorete Tavernier et al., 1992	*Dictyoporus*	Subjective junior synonym	Wisshak (2017)
Dictyoporus garsonensis Elias, 1980	*Dictyoporus nodosus*	Subjective junior synonym	Wisshak (2017)
Entobia antiqua Portlock, 1843		*nomen dubium* (ctenostome bryozoan boring?)	Fischer (1866)
E. conybeari Bronn, 1848	*Entobia cretacea*	Subjective junior synonym	Bromley (1970a)
E. mammillata Bromley & D'Alessandro, 1984	*Entobia mammillata* (Chapman)	Junior homonym; nom. nov.: *E. tuberculata*	Herein
Fasciculus Radtke, 1991	*Fascichnus*	Invalid junior homonym	Radtke & Golubić (2005)
Fossichnus Nielsen et al., 2003	*Oichnus*	Subjective junior synonym	Wisshak et al. (2015)
Gaspeichnus Hunt et al., 2018		*nomen dubium* (likely a burrow)	Herein
G. complexus Hunt et al., 2018		*nomen dubium* (likely a burrow)	Herein
Gastrochaenolites torpedo Kelly & Bromley, 1984	*Gastrochaenolites japonicus*	Subjective junior synonym	Haga et al. (2010)
Gitonia sipho Clarke, 1908	*Palaeosabella prisca*	Subjective junior synonym	Cameron (1969b)
Globodendrina Plewes et al., 1993		Not a trace fossil (foraminiferan body fossil)	Bromley et al. (2007)
G. monile Plewes et al., 1993		Not a trace fossil (foraminiferan body fossil)	Bromley et al. (2007)

Table 2 (continued)

Ichnotaxon	Senior synonym/homonym	Reason for rejection	References
Gnathichnus stellarum Breton et al., 1992	*Gnathichnus pentax*	Subjective junior synonym	Breton (2017)
Granarborus Plewes, 1996		Based on a *nomen nudum*	Wisshak (2017)
G. teicherti Plewes, 1996		*nomen nudum* (unpublished thesis)	Wisshak (2017)
G. nervosus Plewes, 1996		*nomen nudum* (unpublished thesis)	Wisshak (2017)
Graysonia Stephenson, 1952		*nomen dubium* (composite trace fossil)	Bromley & D'Alessandro (1987)
G. bergquesti Stephenson, 1952		*nomen dubium* (composite trace fossil)	Bromley & D'Alessandro (1987)
G. anglica Casey, 1961		*nomen dubium* (composite trace fossil)	Bromley (1970a)
Haguenowia Étallon, 1859		*nomen dubium* (no illustration; types lost)	Wisshak (2017)
H. calloviensis Étallon, 1859		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
H. minima Étallon in Thurmann & Étallon, 1864		*nomen dubium* (poor illustration; holotype lost)	Wisshak (2017)
H. oxfordiensis Étallon, 1864		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
H. kelloviana Étallon, 1864		*nomen dubium* (no illustration; holotype lost)	Wisshak (2017)
Hemicanalis Chiplonkar & Ghare, 1977	*Arachnostega*	Subjective junior synonym (burrow)	Herein
H. reticulata Chiplonkar & Ghare, 1977	*A. fossiger*	Subjective junior synonym (burrow)	Herein
H. prolius Chiplonkar & Ghare, 1977	*A. fossiger*	Subjective junior synonym (burrow)	Herein
Heterodontichnites Rinehart et al., 2006	*Mandaodonites*	Subjective junior synonym	Herein
H. hunti Rinehart et al., 2006	*M. coxi*	Subjective junior synonym	Herein
Hyellomorpha microdendritica Vogel et al., 1987	*Nododendrina incomposita*	Subjective junior synonym	Wisshak (2017)
H. acuminata Tavernier & Golubić, 1993	*Nododendrina europaea*	Subjective junior synonym	Wisshak (2017)
H. magna Tavernier & Golubić, 1993	*? Nododendrina europaea*	Subjective junior synonym	Wisshak (2017)
H. cheimadendritica Plewes, 1996	*Nododendrina nodosa*	*nomen nudum* (unpublished thesis)	Wisshak (2017)
Ipites Karpiński, 1962		*nomen nudum* (reference to biotaxon only)	Herein
Karethraichnus kulindros Zonneveld et al., 2015	*Karethraichnus lakkos*	Subjective junior synonym	Herein
Leptichnus Taylor et al., 1999	*Finichnus*	Invalid junior homonym	Taylor et al. (2013)
Maeandropolydora filosa Chiplonkar & Ghare, 1977	*Maeandropolydora sulcans*	Subjective junior synonym	Herein
Mandibulichnus Zamora et al., 2011	*Bicrescomanducator*	Subjective junior synonym	Sá & Gutiérrez-Marco (2015)
Martesites Vitális, 1961	*Teredolites*	Subjective junior synonym	Kelly & Bromley (1984)
M. vadaszi Vitális, 1961	*T. clavatus*	Subjective junior synonym	Kelly & Bromley (1984)
Megascolytinus Petrov, 2013	*Scolytolarvariumichnus*	Subjective junior synonym	Herein
M. zherikhini Petrov, 2013	*S. zherikhini*	Subjective junior synonym	Herein
Microptychoites Dong in Dong et al., 1984		Based on a *nomen nudum*	Olempska & Wacey (2016)
M. fuquanensis Dong in Dong et al., 1984		*nomen nudum* (ambient inclusion trails)	Olempska & Wacey (2016)
Moniopterus Hatai et al., 1974	*Gastrochaenolites*	Subjective junior synonym	Haga et al. (2010)
Mycelites Roux, 1887		*nomen dubium* (fungus body fossil?)	Herein
M. ossifragus Roux, 1887		*nomen dubium* (fungus body fossil?)	Herein
M. conchifragus Schindewolf, 1962		*nomen nudum* (conditional proposed atelonym)	Herein
Mycobystrovia Goujet & Locquin, 1979		Not a trace fossil (fungus body fossil)	Herein

Table 2 (continued)

Ichnotaxon	Senior synonym/homonym	Reason for rejection	References
M. lepidophaga Goujet & Locquin, 1979		Not a trace fossil (fungus body fossil)	Herein
Myzostomites Clarke, 1921		*nomen nudum* (hypothetical tracemaker)	Brett (1985)
Nygmites Mägdefrau, 1937	*Trypanites*	Subjective junior synonym	Bromley (1972)
Olkenbachia hirsuta Solle, 1938	*Clionolithes radicans*	Subjective junior synonym	Wisshak (2017)
O. simplex Solle, 1938	*Clionolithes radicans*	Subjective junior synonym	Wisshak (2017)
Osedacoides cretaceus Karl & Nyhuis, 2012		*nomen dubium* (synonym of *Karethraichnus*?)	Herein
Ostreoblabe Voigt, 1965	*Palaeosabella*	Subjective junior synonym	Herein
O. perforans Voigt, 1965	*P. prisca*	Subjective junior synonym	Herein
Palaeachlya Duncan, 1876		*nomen dubium* (alga body fossil?)	Herein
P. perforans Duncan, 1876		*nomen dubium* (alga body fossil?)	Herein
P. tortuosa Etheridge, 1891		*nomen dubium* (fungus body fossil?)	Herein
P. torquis Etheridge, 1899		*nomen dubium* (alga body fossil?)	Herein
Palaeoconchocelis Campbell et al., 1979	*Conchocelichnus*	Not a trace fossil (red alga body fossil)	Radtke et al. (2016)
P. starmachii Campbell et al., 1979	*C. seilacheri*	Not a trace fossil (alga body fossil)	Radtke et al. (2016)
Palaeopede Etheridge, 1899		*nomen dubium* (alga body fossil?)	Herein
P. whiteleggei Etheridge, 1899		*nomen dubium* (alga body fossil?)	Herein
Palaeoperone Etheridge, 1891		*nomen dubium* (fungus or sponge body fossil?)	Herein
P. endophytica Etheridge, 1891		*nomen dubium* (fungus or sponge body fossil?)	Herein
Palaeosabella arrogarum Plewes, 1996		*nomen nudum* (unpublished thesis)	Herein
Paleolithophaga Chiplonkar & Ghare, 1976	*Gastrochaenolites*	Subjective junior synonym	Kelly & Bromley (1984)
P. andurensis Chiplonkar & Ghare, 1976		*nomen dubium* (block with pits of varying shape)	Kelly & Bromley (1984)
P. velasensis Badve & Ghare, 1984		Not a bioerosion trace fossil (burrow cf. *Tisoa*)	Herein
Paleolithopholas Badve & Ghare, 1984	*Gastrochaenolites*	Subjective junior synonym	Herein
Platydendrina platycentrum Vogel et al., 1987	*Clionolithes pannosus*	Subjective junior synonym	Wisshak (2017)
Podichnus silesiacus Malkowski, 1975	*Podichnus centrifugalis*	Subjective junior synonym	Santos et al. (2014)
P. donovani Breton, 2011		*nomen nudum* (not a trace fossil; mould of epilith)	Breton (2015b)
Polydorichnus Ishikawa & Kase, 2007	*Helicotaphrichnus*	Subjective junior synonym	Herein
P. subapicalis Ishikawa & Kase, 2007	*H. commensalis*	Subjective junior synonym	Herein
Pyritonema McCoy, 1850		Not a trace fossil (sponge body fossil)	Wisshak (2017)
P.?gigas Fritsch, 1908	*Clionolithes radicans*	Subjective junior synonym	Wisshak (2017)
Radiarites Ghare, 1982		Based on a *nomen nudum*	Wisshak (2017)
R. minutus Ghare, 1982		*nomen nudum* (not a trace fossil; diagenetic halo)	Wisshak (2017)
Ramodendrina Vogel et al., 1987	*Clionolithes*	Subjective junior synonym	Furlong & McRoberts (2014)
Ramosulcichnus Hillmer & Schulz, 1973	*Caulostrepsis*	Subjective junior synonym	Bromley & D'Alessandro (1983)
Repentella Müller, 1968		Based on a *nomen nudum*	Wisshak (2017)
R. maior Müller, 1968		*nomen nudum* (not a trace fossil; mould of epilith)	Wisshak (2017)
R. fragilis Müller, 1968		*nomen nudum* (not a trace fossil; mould of epilith)	Wisshak (2017)
Reticulina Radtke, 1991	*Ichnoreticulina*	Invalid junior homonym	Radtke & Golubić (2005)
Rhopalia Radtke, 1991	*Rhopalia* Macquart, 1838	Junior homonym; nom. nov.: *Irhopalia*	Herein

Table 2 (continued)

Ichnotaxon	Senior synonym/homonym	Reason for rejection	References
Roderosignus Michalík, 1977	*Gnathichnus*	Subjective junior synonym	Michalík (1980)
R. quinqueradialis Michalík, 1977	*G. pentax*	Subjective junior synonym	Michalík (1980)
Sabella bavincourti Vaillant, 1909		Not a bioerosion trace fossil (burrow)	Wisshak et al. (2015)
Sedilichnus Müller, 1977		*nomen nudum* (conditional proposed atelonym)	Wisshak et al. (2015)
S. spongiophilus Müller, 1977		*nomen nudum* (conditional proposed atelonym)	Wisshak et al. (2015)
S. smiley Pokorný & Štofik, 2017	*Oichnus paraboloides*	Subjective junior synonym	Herein
Semidendrina Bromley et al., 2007	*Nododendrina*	Subjective junior synonym	Wisshak (2017)
S. pulchra Bromley et al., 2007	*N. europaea*	Subjective junior synonym	Wisshak (2017)
Seminolithes Hyde, 1953	*Rogerella*	Subjective junior synonym	Bromley & D'Alessandro (1987)
Simonizapfes Codez & de Seint-Seine, 1958	*Rogerella*	Subjective junior synonym	Bromley & D'Alessandro (1987)
Specus Stephenson, 1952	*Palaeosabella*	Subjective junior synonym	Herein
S. frimbriatus Stephenson, 1952	*P. prisca*	Subjective junior synonym	Herein
Spiracavites Chiplonkar & Ghare, 1977	*Trypanites*	Subjective junior synonym	Pemberton et al. (1988)
S. vermicularis Chiplonkar & Ghare, 1977	*T. solitarius*	Subjective junior synonym	Herein
S. radialis Chiplonkar & Ghare, 1977	*T. solitarius*	Subjective junior synonym	Herein
S. marginaria Chiplonkar & Ghare, 1977	*T. solitarius*	Subjective junior synonym	Herein
Spirichnus contentus Plewes, 1996		*nomen nudum* (unpublished thesis)	Herein
S. vacillarum Plewes, 1996		*nomen nudum* (unpublished thesis)	Herein
Stichus Etheridge, 1904		*nomen dubium* (poor illustration)	Herein
S. mermisoides Etheridge, 1904		*nomen dubium* (poor illustration)	Herein
Talpina sentiformis von Hagenow		*nomen nudum* (not formally published)	Wisshak et al. (2017)
T. foliacea von Hagenow		*nomen nudum* (not formally published)	Wisshak et al. (2017)
T. pungens Quenstedt, 1849	*Terebripora pungens*	Subjective junior synonym	Voigt (1972)
T. rotunda Müller, 1851		*nomen dubium* (no description; no illustration)	Wisshak (2017)
T. astartina Étallon in Thurmann & Étallon, 1864		*nomen dubium* (poor illustration; holotype lost)	Herein
Terebripora (?) portlocki Fischer, 1866	*Entobia antiqua*	Objective junior synonym	Herein
Thalamophaga Rhumbler, 1909		Not a trace fossil (foraminiferan body fossil)	Loeblich & Tappan (1964)
T. ramosa Rhumbler, 1909		Not a trace fossil (foraminiferan body fossil)	Loeblich & Tappan (1964)
Topsentia Clarke, 1921		Invalid junior homonym	de Laubenfels (1955)
Topsentopsis de Laubenfels, 1955	*Entobia*	Subjective junior synonym	Tapanila (2006)
Tremichnus minutus Brett, 1985	*Tremichnus paraboloides*	Subjective junior synonym	Wisshak et al. (2015)
T. cysticus Brett, 1985	*Tremichnus paraboloides*	Subjective junior synonym	Wisshak et al. (2015)
T. cystoidiphilus Frest & Strimple in Frest et al., 2011		*nomen nudum* (no holotype designated)	Wisshak et al. (2015)
Trifurcus Plewes, 1996		*nomen nudum* (unpublished thesis)	Wisshak (2017)

Table 2 (continued)

Ichnotaxon	Senior synonym/homonym	Reason for rejection	References
Trypetesa Norman, 1903	*Rogerella*	not a trace fossil (acrothoracican body fossil)	Buatois et al. (2017)
T. lampas Hancock, 1849		Not a trace fossil (acrothoracican body fossil)	Murphy & Williams (2013)
T. lateralis Tomlinson, 1953		Not a trace fossil (acrothoracican body fossil)	Murphy & Williams (2013)
T. habei Utinomi, 1962		Not a trace fossil (acrothoracican body fossil)	Murphy & Williams (2013)
T. nassarioides Turquier, 1967		Not a trace fossil (acrothoracican body fossil)	Murphy & Williams (2013)
T. spinulosa Turquier, 1976		Not a trace fossil (acrothoracican body fossil)	Murphy & Williams (2013)
Uniglobites Pleydell & Jones, 1988	*Entobia*	Subjective junior synonym	Bromley (2004)
Vermiforichnus Cameron, 1969a	*Palaeosabella*	Subjective junior synonym	Herein
V. clarkei Cameron, 1969a	*P. prisca*	Subjective junior synonym	Herein
Vioa Nardo, 1833	*Cliona*	Not a trace fossil (sponge biotaxon)	Vosmaer (1887)
V. michelini Terquem, 1855	*Vioa michelini* Nardo	Invalid junior homonym	Terquem & Piette (1865)
V. ostrearum Fraas, 1869		*nomen dubium* (unspecific description; no type)	Herein
V. rependa Sismonda, 1871		*nomen dubium* (poor description; poor illustration)	Herein
V. superficialis Sismonda, 1871		*nomen dubium* (poor description; no illustration)	Herein
V. millaris Frič, 1883		*nomen dubium* (poor description; no illustration)	Herein
Zapfella de Saint-Seine, 1954	*Rogerella*	Subjective junior synonym	Bromley & D'Alessandro (1987)

Archaeomycelites Bystrow, 1959 and its type ichnospecies *A. odontophagus* Bystrow, 1959 are herein synonymized with *Palaeomycelites* Bystrov, 1956 and its type ichnospecies *P. lacustris* Bystrov, 1956, respectively, based on identical shape of the borings; neither the position in bone/enamel nor facies should be used as ichnotaxobases (Bertling et al. 2006).

Asthenopodichnium fallax Francischini et al., 2016 does not belong to this ichnogenus, which is restricted to xylic substrates (Höpner and Bertling 2017). Rather, its substrate is calcareous; given this and the well-defined shape, it belongs to *Petroxestes* and is here considered a junior synonym of *Petroxestes altera* Jagt et al., 2009.

Asteriastoma Breton, 1992 and its type ichnospecies *A. cretaceum* Breton, 1992 are subjective junior synonyms of *Gnathichnus* Bromley, 1975 and its type ichnospecies *G. pentax* Bromley, 1975, respectively, as suggested by Buatois et al. (2017). *Asteriastoma* merely constitutes a composite trace fossil of *G. pentax* oriented around a preexisting boring as a result of grazing and/or predation (see Bromley 1970b and Wisshak 2006 for examples).

Bascomella Morningstar, 1922, represented by its type ichnospecies *B. gigantea* Morningstar, 1922, was originally considered to be a ctenostome bryozoan boring composed of zooidal chambers and interconnecting stolons. Two additional ichnospecies were later proposed, namely *B. fusiformis* Condra and Elias, 1944 and *B. subsphaerica* Condra and Elias, 1944. Their actual composite nature of accidentally co-occurring acrothoracican borings and tubular borings of unknown origin was recognized by Elias (1957), who advocated redefining *Bascomella* as the pouch-shaped borings only. Restricting a composite ichnotaxon to one of its components, however, deviates from the original author's intention: Morningstar (1922) meant to name the composite structure and hence, no single element can and may be isolated from it. The redefinition by Elias (1957) fails for this reason and consequently the composite ichnotaxon is invalidated, as it contains the work of more than one organism (e.g., Bertling et al. 2006). The taxonomic status of the other *Bascomella* ichnospecies is identical, even if they may contain different representatives of *Rogerella* de Saint-Seine, 1951 or other ichnogenera.

Belichnus Pether, 1995 was erected based on Holocene shells, but the determined age of 13.5–12.5 ka now corresponds to a Pleistocene age (Gradstein et al. 2012). Because no type ichnospecies was designated, *B. monos* is herein subsequently designated as type ichnospecies (ICZN 1999: Art. 69). *Belichnus dusos* Pether, 1995 was considered as a potential junior synonym of *B. monos* by Cadée and de Wolf (2013), which is formally confirmed herein.

Brachyzapfes Codez in Codez and de Saint-Seine, 1958 was synonymized with *Rogerella* de Saint-Seine, 1951 by Bromley and D'Alessandro (1987), based on close morphological resemblance. Accordingly, its type ichnospecies *B. elliptica* Codez in Codez and de Saint-Seine, 1958 is herein formally transferred to *Rogerella* as a new combination.

Brutalichnus Mikuláš et al., 2006, with the type ichnospecies *B. brutalis* Mikuláš et al., 2006, was erected on irregular though intense cracks in bones. They were claimed to have been produced by a carnivorous animal but do not exhibit tooth traces. The breakage is at least as likely due to diagenetic effects such as compaction, i.e., the biogenic nature of the structure remains to be demonstrated.

Caedichnus Stafford et al., 2015 and its type ichnospecies *C. spiralis* Stafford et al., 2015 are phenomena of gastropod shell damage of various shape, which are consistent with the diagnosis of *Bicrescomanducator* Donovan et al. in Andrew et al., 2010. *Caedichnus* is therefore synonymized with that ichnogenus, maintaining its type ichnospecies as a new combination.

Calciroda Mayer, 1952 and its type ichnospecies *C. kraichgoviae* Mayer, 1952 consists of 'branched, horizontal tunnels running along the surface of organism hard parts, sometimes going vertically into the depth' [original diagnosis, translated]. No holotype was designated, but the figured specimens indicate an overlapping or cross-cutting relationship of individual tunnels instead of true branching, in addition to unbranched specimens. Plewes (1996: pl. 13, Fig. 5) studied Mayer's type material and confirmed that '…both branching points and avoidance by tunnels can be seen…'; she regarded *Calciroda* as junior synonym of *Talpina* von Hagenow, 1840. In comparison with the recently rediscovered type material of *Talpina* and its revision (Wisshak et al. 2017: Fig. 2.1), the branched specimens of the dubious (because composite) and partly eroded trace fossil *C. kraichgoviae* can be assigned to *Talpina ramosa* von Hagenow, 1840, whereas the unbranched specimens belong to *Trypanites solitarius* (von Hagenow, 1840). The second ichnospecies, *C. tubulata* Hary, 1975, mainly differs by its fill and preservation from branched *C. kraichgoviae* and thus is also synonymized with *T. ramosa*.

Chaetophorites Pratje, 1922, including the type ichnospecies *C. gomontoides* Pratje, 1922 and *C. tenuis* Mägdefrau, 1937, are *nomina dubia*. A neotype designation for lost type material of the former has proven infeasible (Glaub 1994), and *C. tenuis* is too poorly defined and illustrated to allow an unambiguous application. *Chaetophorites* appears to have represented a storage tank for various microborings, which have only become accessible to reliable morphological characterization with the advent of the epoxy casting method in the 1970s (Golubić et al. 1970). A third ichnospecies, *C. cruciatus* Mägdefrau, 1937, was later recognized as bryozoan trace fossil and was recombined by Voigt (1973) as *Immergentia cruciata* (Mägdefrau, 1937).

Cliona Grant, 1826 -> see *Entobia* Bronn, 1837 below.

Clionites Morris in Mantell, 1850 is an ichnogenus for sponge bioerosion traces with close affinity to *Entobia* Bronn, 1837. Its type ichnospecies *C. conybeari* Morris in Mantell, 1850 was consequently considered by Bromley (1970a) as a subjective junior synonym of *E. cretacea* Portlock, 1843, thus also synonymizing the two ichnogenera. We cannot judge *C. parkinsoni* Morris in Mantell, 1850 because we have not researched and investigated the holotype; it is only rudimentarily described, and the corresponding illustrations do not allow distinction of this ichnospecies. *C. glomerata* Morris, 1851 clearly is a cavernous sponge boring, and thus adequately grouped in the ichnogenus *Entobia* Bronn, 1837. As a result, it becomes a secondary junior homonym to *E. glomerata* (Michelin, 1846) comb. nov., another sponge bioerosion trace herein included in *Entobia*, thus demanding establishment of a *nomen novum* (see below under *Entobia*).

Clionoida Smith, 1910 and its type ichnospecies *C. arbiglandensis* Smith, 1910 are *nomina dubia*, since the original illustration is poor and no type material could be tracked down in the two relevant Glasgow collections. Furthermore, no explicit definition is given for this ichnogenus.

Clionoides Fenton and Fenton, 1932, with *C. thomasi* Fenton and Fenton, 1932 as type ichnospecies, was erected for tubular and infrequently branched borings along the surface of shells. Furlong and McRoberts (2014) erroneously regarded the ichnogenus *Palaeosabella* Clarke, 1921 as a synonym of *Clionoides*, but disregarded the principle of priority (ICZN 1999: Art. 23). Moreover, *Clionoides* is a tubular boring without a club-shaped extension as in *Palaeosabella*. Although no holotype was specified by Fenton and Fenton (1932), their figures show shells with numerous tunnels and grooves running along or close to the surface. Branching occurs but can be regarded as false due to overlapping borings rather than true branching. Given that circumstance, *Clionoides* and *C. thomasi* can be defined as tubular borings along the surface of the substrate and thus become junior synonyms of *Trypanites* Mägdefrau, 1932 and *T. solitarius* (von Hagenow, 1840), respectively. *C. utaturensis* Ghare, 1982 describes 'flexuous or more or less straight borings with circular openings' in belemnite rostra, which is also consistent with the diagnosis of *T. solitarius* (von Hagenow, 1840) (see Bromley 1972), and is therefore included in it as another subjective junior synonym.

Conchifora zylindriformis Müller, 1968, including varieties, is synonymized with *Trypanites solitarius* (von Hagenow, 1840) based on the course more or less parallel to the curvature of the substrate surface.

Conchotrema Teichert, 1945 is an ichnogenus often discussed as probable synonym of *Talpina* von Hagenow, 1840 because of their close morphological similarity and comparable dimensions (e.g., Voigt 1972; Plewes 1996; Bromley 2004). However, to our knowledge its two ichnospecies were, never formally recombined *Talpina*, and thus are formally recombined herein on grounds of the valid arguments put forward by these authors. It still needs to be clarified, however, whether the two ichnospecies are invalid junior synonyms or valid senior synonyms of other Palaeozoic ichnospecies of *Talpina*.

Cubiculum inornatus Xing et al., 2015 as well as the nomen *C. levis* Pirrone et al., 2014 are emended to corresponding gender of genus and species names, i.e., to *C. inornatum* and *C. leve*, respectively, as the gender of the ichnogenus is neuter (ICZN 1999: Art. 31.2).

Cunicularis isodiametricus Li, 1997 was established based on phosphatized natural casts of microborings and thus is to be considered an ichnotaxon as opposed to a cyanobacterium body fossil of the biotaxon *Cunicularis* Green et al., 1988. However, morphologically it is reminiscent of *Endoconchia lata* Runnegar in Bengtson et al., 1990, and thus herein considered a junior synonym of it.

Cylindricavus Borkar and Kulkarni, 1987, based on the type ichnospecies *C. perplexus* Borkar and Kulkarni, 1987, consists of 'cylindrical, unbranched borings with variable disposition' and occurs in freshwater carbonates. It is compared with *Paleolithophaga* (*lapsus calami*; junior synonym of *Gastrochaenolites*), but erected based on its freshwater instead of marine origin. However, facies or environment are not valid ichnotaxobases (Bertling et al. 2006). Moreover, freshwater borings are very rare compared to their marine counterparts, and bioerosion ichnotaxa of this size are essentially unknown. Various shapes and sizes of the figured *C. perplexus* suggest an alternative interpretation, e.g., as fossil root casts, and thus *Cylindricavus* is at present regarded as *nomen dubium*.

Cylindrocavites Ghare, 1982, based on its type ichnospecies *C. cretacea* Ghare, 1982, consists of cylindrical borings penetrating belemnite rostra perpendicular to their surface. Its form is identical with *Trypanites* Mägdefrau, 1932, and it is therefore regarded as junior synonym, following Pemberton et al. (1988). At the ichnospecies level, *C. cretacea* shares all diagnostic features with *T. weisei* Mägdefrau, 1932 and is herein synonymized with it.

Dekosichnus Genise and Hazeldine, 1995, with its type ichnospecies *D. meniscatus* Genise and Hazeldine, 1995, appears to be a junior synonym of *Xylonichnus* Genise, 1995. The diagnoses claim slight differences in the relative height and the more or less oval cross-section, but the figures of the type do not exhibit these characters. The greater density of borings of the *Dekosichnus* type is not an ichnotaxobase (Bertling et al. 2006). Hence, *D. meniscatus* is herein transferred to *Xylonichnus* as new combination.

Entobia Bronn, 1837 is by far the most speciose bioerosion ichnogenus. In the course of this compilation, it has received further accrual of former sponge biotaxa that actually describe empty fossil sponge bioerosion traces. These are to be considered bioerosion ichnotaxa, just as empty recent sponge borings described prior to 1931. This concerns species formerly in the invalid junior synonym *Vioa* Nardo, 1833: *E. michelini* (Nardo, 1845) comb. nov., *E. nardina* (Michelin, 1846) comb. nov., *E. glomerata* (Michelin, 1846) comb. nov., *E. duvernoyi* (Michelin, 1847) comb. nov., *E. pectita* (Michelotti, 1861) comb. nov., *E. cerithii* (Fraas, 1867) comb. nov., and *E. catenata* (Frič, 1883) comb. nov. Three further *Vioa* species were recently transferred to *Entobia* by Schönberg et al. (2017). Two *Vioa* ichnospecies are herein considered *nomina dubia* based on unspecific descriptions and lack of specific types, i.e., *V. ostrearum* Fraas, 1869 and *V. millaris* Frič, 1883. Another two *Vioa* ichnospecies, *V. rependa* Sismonda, 1871 and *V. superficialis* Sismonda, 1871, are herein considered *nomina dubia*, owing to vague descriptions and a poor or no illustration, respectively. Furthermore, the authorship of Sismonda (1871) is unclear: He apparently was the first to record the two taxa in question, but he cited Michelotti as their author. We were unable, however, to find the names in Michelotti's work. In addition, numerous species of the valid sponge genus *Cliona* Grant, 1826 are here transferred to *Entobia*, namely *E. irregularis* (d'Orbigny, 1850) comb. nov., *E. ramosa* (d'Orbigny, 1850) comb. nov., *E. perforata* (Seguenza, 1882) comb. nov., *E. intricata* (Seguenza, 1882) comb. nov., *E. peregrinator* (Chapman, 1907) comb. nov., *E. bullini* (Annandale, 1920) comb. nov., *E. radiciformis* (Lehner, 1937), comb.

nov., and *E. microtuberum* (Stephenson, 1941) comb. nov., the latter tentatively synonymized with *E. megastoma* (Fischer in d'Archiac et al., 1866) by Bromley and D'Alessandro (1984), a view that is not shared here. Two species of *Cliona*, *C. duchassaingi* Fischer, 1868 and *C. studeri* Mayer, 1872, are *nomina nuda*, since they were only listed without any description or indication. Yet four more *Cliona* species were described by Seguenza (1879), only the first one of which appears to be a fossil sponge boring, consecutively recombined as *E. tubulosa* (Seguenza, 1879) comb. nov. herein. The second one is recombined as *Maeandropolydora vermicularis* (Seguenza, 1879) comb. nov., the third is an unspecific assemblage of minute microborings and thus considered a *nomen dubium*, and the last one is an acrothoracid barnacle boring, recombined herein as *Rogerella oostoma* (Seguenza, 1879) comb. nov. However, according to Cleevely (1983) the collections of Seguenza were devastated during the 1908 Messina earthquake, rendering re-investigation of his types impossible. Three *Cliona* species established by Fischer in d'Archiac et al. (1866) and Fischer (1868) were considered *nomina dubia* by Bromley and D'Alessandro (1984). The type material, however, is accessible at the Paris Natural History Museum, and it is sufficiently well preserved to merit further investigation. Hence, these species are formally transferred to *Entobia* as *E. falunica* (Fischer in d'Archiac et al., 1866) comb. nov., *E. praecursor* (Fischer, 1868) comb. nov., and *E. cerithiorum* (Fischer, 1868) comb. nov. Finally, *Cliona kelheadensis* Smith, 1910 is considered a *nomen dubium* since its original illustration is poor and the type material appears to be lost. The ichnospecies *E. glomerata* (Morris, 1851) is clearly distinct from *E. glomerata* (Michelin, 1846) comb. nov., judged by the respective illustrations showing two very different forms of sponge borings. Given that Morris (1851) did not make any reference to Michelin (1846) when erecting his species, *E. glomerata* (Morris, 1851) becomes a secondary junior homonym of *E. glomerata* (Michelin, 1846) comb. nov. The former thus requires a replacement name, and accordingly, *E. morrisi* nom. nov. is hereby introduced for *E. glomerata* (Morris, 1851). The name honours John Morris and his pioneering work on bioerosion trace fossils from the Upper Cretaceous of northern Europe. A similar case is *E. mammillata* Bromley and D'Alessandro, 1984, which is a secondary junior homonym to *E. mammillata* (Chapman, 1907) comb. nov., and is herein transferred from *Cliona* to *Entobia*. We introduce *E. tuberculata* nom. nov. as a replacement name, thereby largely retaining the original reference to the diagnostic mammillate hemispherical tubercles. In any case, in order to identify synonyms, the present plethora of 53 *Entobia* ichnospecies, and in particular the recently transferred early taxa, are in need of revision.

Feldmannius cavernosa (Casadío et al., 2001) is emended in spelling to read *F. cavernosus* (Casadío et al., 2001), in order to comply in gender with the generic name (ICZN 1999: Art. 31.2). This measure is deemed necessary as a result of *Feldmannius* Low and Guinot, 2010 having been introduced as a *nomen novum* for *Feldmannia* Casadío et al., 2001.

Gaspeichnus Hunt et al., 2018 and its type ichnospecies *G. complexus* Hunt et al., 2018 are considered *nomina dubia*, since lithification of the substrate prior to emplacement of traces cannot be demonstrated, and the flattened traces likely represent burrows of uncertain affinity rather than borings.

Gitonia Clarke, 1908, defined by its type ichnospecies *G. corallophila* Clarke, 1908, is a bioclaustration and not a bioerosion trace (Oliver 1983). However, *G. siphon* Clarke, 1908, is a cylindrical bioerosion trace and was synonymized with *Vermiforichnus clarkei* by Cameron (1969b), which in turn is herein synonymized with *Palaeosabella prisca* (McCoy, 1855). Examination of Clarke's (1908) type material of *G. siphon* will show whether it belongs to *Palaeosabella* Clarke, 1921 or to *Trypanites* Mägdefrau, 1932.

Glirotremmorpha entectus Collinson and Hooker, 2000 is emended to *G. entecta*, because the gender of the ichnogenus is feminine (ICZN 1999: Art. 31.2).

Hemicanalis Chiplonkar and Ghare, 1977, including its type ichnospecies *H. reticulata* Chiplonkar and Ghare, 1977, as well as the second ichnospecies *H. prolius* Chiplonkar and Ghare, 1977, are netlike, ramified burrows on the internal moulds of molluscan shells rather than bioerosion trace fossils. This way they have to be considered junior synonyms of *Arachnostega* Bertling, 1992 and *A. fossiger* (Fenton and Fenton, 1932).

Heterodontichnites Rinehart et al., 2006, with its type species *H. hunti* Rinehart et al., 2006, was supposed to differ from *Mandaodonites coxi* Cruickshank, 1986 by alleged round tooth traces of the latter and a more curved pattern. Owing to the incomplete preservation of the single specimen with *Heterodontichnites*, the latter difference cannot be substantiated, whereas the single tooth traces of *Mandaodonites* are ovoid, as in *Heterodontichnites*. With no significant difference remaining, the two ichnogenera and their type ichnospecies are respectively synonymized.

Ichnogutta erectus Botquelen and Mayoral, 2005 is emended to read *I. erecta* Botquelen and Mayoral, 2005 and to comply in gender with the generic name (ICZN 1999: Art. 31.2).

Ipites has been established by Karpiński (1962) explicitly noting twice the supposed close relationship to the Recent '*Ips duplicatus* Sahlb.'. The author introduces the name by stating: 'The genus of the beetle I define with the name *Ipites*.', i.e., without designating it as 'igen. nov.' or similar, after noting that this 'is the first finding of brood galleries of a representatitve resembling the modern genus *I. duplicatus* Sahlb.' Article 20 of the Code (ICZN 1999), however, states that 'A name […] applied to fossils to distinguish them from extant members of that taxon, without clear evidence of intent to establish a new genus-group taxon, […] cannot be used as the valid name of a taxon.' *Ipites* is not an available name therefore, leaving its sole ichnospecies name *bobrowskianus* without ichnogenus name. For this reason, we reintroduce *Ipites* as a new ichnogeneric name here and designate *Ipites bobrowskianus* (Karpiński, 1962) as its type ichnospecies. The etymology is based on the similarity of the trace fossil to the borings of the modern bark beetle genus *Ips*. We diagnose the ichnogenus as follows: Complex boring in xylic substrates, with regularly branched, larger central tunnels and numerous smaller tunnels radiating from the branches; the system lies parallel to the substrate surface. As differential diagnosis we remark that modern bark beetles exhibit a rather wide array of boring architecture, and informed by these patterns, we distinguish *Ipites* igen. nov. from *Scolytolarvariumichnus* Guo, 1991 with just one simple shaft in the centre.

Karethraichnus kulindros Zonneveld et al., 2015 is distinguished from *K. lakkos* Zonneveld et al., 2015 by 'its cylindrical vs hemispherical morphology'. However, this difference can be explained as various developmental stages of the same boring, a situation analogous to the variable penetration depth found in ichnospecies of *Oichnus*. We follow the reasoning of Wisshak et al. (2015) and regard *K. kulindros* as a junior synonym of *K. lakkos*.

Knethichnus parallelum Jacobsen and Bromley, 2009 is emended to *K. parallelus*, because the gender of the ichnogenus is masculine (ICZN 1999: Art. 31.2).

Maeandropolydora filosa Chiplonkar and Ghare, 1977 is based on limited and poorly preserved material in a gastropod shell. The U-shaped tube has no specific orientation, a constant diameter and circular cross-section. As such it may be regarded as part of an originally more extensive boring assignable to *M. sulcans* Voigt, 1965 (cf. Bromley and D'Alessandro 1983).

Megascolytinus Petrov, 2013, with *M. zherikhini* Petrov, 2013 as its type ichnospecies, was established solely because of its large size, which should not be an ichnotaxobase (Bertling et al. 2006). In principle, its shape is identical with *Scolytolarvariumichnus* Guo, 1991, but the ichnospecies deviates from *S. radiatus* Guo, 1991. Therefore, it is herein cited as *S. zherikhini* (Petrov, 2013) comb. nov.

Mycelites Roux, 1887, with *M. ossifragus* Roux, 1887 as its type ichnospecies, was long deemed to be the only available ichnotaxon for fungal borings. Roux' descriptions, at least in part, refer to organic material, as he writes about septa in channels. This excludes a void boring (a trace) but rather points to the presence of an organism. For this reason, the ichnogenus and ichnospecies are rejected. *Mycelites conchifragus* Schindewolf, 1962 was proposed only conditionally and is thus a *nomen nudum* (atelonym): 'Simply in accordance with a handy label, I name them *Mycelites conchifragus*. If one wanted to attach species value to this name, the specimen […] may serve as a holotype' [translated].

Mycobystrovia Goujet and Locquin, 1979 and its type ichnospecies *M. lepidophaga* Goujet and Locquin, 1979 are a taxa combining a fungus biotaxon and the probable boring of the same producer. The diagnosis makes it clear, however, that the name refers to the spores, and thus a fungus body fossil, whereas the boring is not described.

Nygmites Mägdefrau, 1937 and its type ichnospecies *N. solitarius* (von Hagenow, 1840) are junior synonyms of *Trypanites* Mägdefrau, 1937 and *T. solitarius* (von Hagenow, 1840), respectively (Bromley 1972). Mägdefrau (1937) included *N. pungens* (Quenstedt, 1849) (= *Terebripora pungens*) and established the new ichnospecies *N. sacculus*, which differs from the other two ichnospecies by its pouch instead of cylinder shape. Consequently, *N. sacculus* was assigned to *Brachyzapfes elliptica* Codez and de Saint-Seine, 1958 by Seilacher (1968), synonymized with *Zapfella pattei* (de Saint-Seine, 1955) by Tomlinson (1969), and combined as *Brachyzapfes sacculus* (Mägdefrau, 1937) by Voigt (1972). Its nature as the boring of a cirriped was also revealed by Kennedy (1970). Based on its morphology, *N. sacculus* is herein transferred to *Rogerella* de Saint-Seine, 1951 as new combination. A thorough review of *Rogerella* will show its ichnospecific affinity.

Osedacoides cretaceus Karl and Nyhuis, 2012 is a *nomen dubium* since it may be a valid ichnospecies, but the illustrated unique type specimen does not allow to decide whether it belongs to *Karethraichnus* Zonneveld et al., 2015. If this is the case it may form a senior synonym of one of the ichnospecies of *Karethraichnus* as well as of this ichnogenus.

Ostreoblabe Voigt, 1965 and its type ichnospecies *O. perforans* Voigt, 1965 were originally described from the inner valve of oyster shells and are partly embedment structures and partly borings (Bromley 1970a, 2004). The borings are to be identified as *Palaeosabella* Clarke, 1921 and *P. prisca* (McCoy, 1855), respectively, thus being considered junior synonyms here.

Palaeachlya Duncan, 1876, (including the ichnospecies *P. perforans* Duncan, 1876; *P. tortuosa* Etheridge, 1891; and *P. torquis* Etheridge, 1899), *Palaeoperone* Etheridge, 1891 (ichnospecies *P. endophytica* Etheridge, 1891), and *Palaeopede* Etheridge, 1899 (ichnospecies *P. whiteleggei* Etheridge, 1899) were established as biotaxa, but the original descriptions and illustrations combine features of the tracemakers and their borings. The illustrations are, however, too unspecific to justify the status of the ichnotaxa; all are regarded as *nomina dubia* rather than algal or fungal body fossils; the type material needs to be researched and reinvestigated to clarify their status.

Palaeosabella arrogarum Plewes, 1996 was erected in an unpublished thesis and is therefore a *nomen nudum*.

Paleolithophaga Chiplonkar and Ghare, 1976 was synonymized with *Gastrochaenolites* Leymerie, 1842 by Kelly and Bromley (1984). Its type ichnospecies *P. andurensis* Chiplonkar and Ghare, 1976 currently is a *nomen dubium* and would require the definition and inspection of a lectotype out of the several clusters of circular and incomplete borings contained on the type material. *P. velasensis* Badve and Ghare, 1984 appears to be a soft-bottom burrow with affinity to *Tisoa siphonalis* de Serres, 1840, rather than a bioerosion ichnotaxon, and was synonymized with the latter (Knaust 2019).

Paleolithopholas Badve and Ghare, 1984 is defined as 'circular to oblong' borings. The figured material has to be assigned to *Gastrochaenolites* Leymerie, 1842 and is thus synonymized with this ichnogenus. Accordingly, its type ichnospecies *P. raigadensis* Badve and Ghare, 1984 is transferred to *Gastrochaenolites*, awaiting ichnotaxonomic revision to resolve potential synonymy with other ichnospecies in that ichnogenus.

Paleoscolytus sussexensis Jarzembowski, 1990 does not belong to this ichnogenus because it does not display the highly significant branched tunnels. Rather, it is a member of *Scolytolarvariumichnus* Guo, 1991, a scolytid boring with radial unbranched tunnels, leading to the new combination *S. sussexensis* (Jarzembowski, 1990).

Pennatichnus moguerenica Mayoral, 1988 is emended to *P. moguerenicus*, because the gender of the ichnogenus is masculine (ICZN 1999: Art. 31.2).

Planobola radicatus Schmidt, 1992 is emended to *P. radicata*, because the gender of the ichnogenus is feminine (ICZN 1999: Art. 31.2).

Polydorichnus Ishikawa and Kase, 2007 and its type ichnospecies *P. subapicalis* Ishikawa and Kase, 2007 are cylindrical borings in the columella of gastropod shells. They are identical with *Helicotaphrichnus* Kern et al., 1974 and *H. commensalis* Kern et al., 1974, respectively, and thus identified as junior synonyms.

Rhopalia Radtke, 1991 is an invalid junior homonym, because this genus name is preoccupied by the dipteran genus *Rhopalia* Macquart, 1838. This has already seen another junior homonym, the tunicate genus *Rhopalia* Norman, 1897 (now *Rhopalaea* Philippi, 1843). In consequence, we here introduce *Irhopalia* nom. nov., following a suggestion of the original author who had established *Rhopalia* (Radtke pers. comm. 2018). *Irhopalia* now includes the type ichnospecies *Irhopalia catenata* (Radtke, 1991) comb. nov., as well as *I. spinosa* (Radtke and Golubić, 2005) comb. nov. and *I. clavigera* (Golubić and Radtke, 2008) comb. nov.

Sedilichnus smiley Pokorný and Štofik, 2017 is a circular opening in a shell with an inner opening of crescentic outline. Following the review of *Oichnus* by Wisshak et al. (2015), this form represents an incomplete (unfinished) *O. paraboloides*, forming a junior synonym of it.

Seminolithes Hyde, 1953 is a subjective junior synonym of *Rogerella* de Saint-Seine, 1951, as already regarded by Bromley and D'Alessandro (1987). As a consequence, its type ichnospecies *S. linii* Hyde, 1953 (by monotypy) is now listed as the new combination *Rogerella linii* (Hyde, 1953).

Simonizapfes Codez and de Saint-Seine, 1958 is another subjective junior synonym of *Rogerella* de Saint-Seine, 1951, according to Bromley and D'Alessandro (1987), its type ichnospecies *S. elongata* Codez and de Saint-Seine, 1958 to be cited as *R. elongata* (Codez and de Saint-Seine, 1958) comb. nov. Likewise, *S. davenporti* Tomlinson, 1969 is transferred to *Rogerella* until a proper review of this ichnogenus is undertaken.

Specus Stephenson, 1952, based on the type ichnospecies *S. fimbriatus* Stephenson, 1952, includes curved or irregular, club-shaped borings and was synonymized with *Trypanites* Mägdefrau, 1932 by Bromley (1972). After Plewes (1996) reinstated *Palaeosabella* Clarke, 1921, Bromley (2004) suggested to synonymize *Specus* with that ichnogenus, while Furlong and McRoberts (2014) prefer synonymization with *Clionoides* Fenton and Fenton, 1932. With *Clionoides* herein considered a junior synonym of *Trypanites* (see above), however, we follow Bromley's (2004) view and regard *Specus* as a junior synonym of *Palaeosabella. S. fimbriatus* is synonymous with *P. prisca* (McCoy, 1855), although a lectotype is still to be defined.

Spiracavites Chiplonkar and Ghare, 1977 was regarded a junior synonym of *Trypanites* Mägdefrau, 1932 by Pemberton et al. (1988), and its type ichnospecies *S. vermicularis* Chiplonkar and Ghare, 1977 can well be assigned to *T. solitarius* (von Hagenow, 1840). The other two ichnospecies, *S. radialis* and *S. marginaria* Chiplonkar and Ghare, 1977 are recognized as morphological variations and thus synonymous with *T. solitarius*.

Spirichnus contentus Plewes, 1996 and *S. vacillarum* Plewes, 1996 were erected in an unpublished thesis and therefore are *nomina nuda*.

Stichus Etheridge, 1904 and its type ichnospecies *S. mermisoides* Etheridge, 1904 are difficult to judge because the original illustrations lack resolution and spatial detail. We have not investigated the type material, but the structures described may not be bioerosion traces but diagenetically altered pores in the host shell. Consequently, both ichnotaxa are considered *nomina dubia* for the time being.

Talpina astartina Étallon in Thurmann and Étallon, 1864 is a *nomen dubium*, owing to a poor illustration and lost type material. *Talpina scalariformis* Ghare, 1982 does not comply with the characteristics of the ichnogenus *Talpina* von Hagenow, 1840. Instead, the parallel course of its tunnels and the rectangular branching pattern identify this ichnospecies as belonging to the ichnogenus *Orthogonum* Radtke, 1991, and it is here recombined accordingly. A closer investigation of the type material will be necessary to verify whether it is a senior synonym of *O. giganteum* Glaub, 1994.

Terebripora (?) *portlocki* Fischer, 1866 was introduced as a name referring to *Entobia antiqua* Portlock, 1843, thus representing an objective junior synonym only. However, *E. antiqua* indeed is a boring of a ctenostome bryozoan with affinity to *Terebripora* d'Orbigny, 1847.

Trypanites helicus Nielsen and Görmüş, 2004 was erected for planispirally tubular borings, thus not complying with the diagnosis of *Trypanites* Mägdefrau, 1932. It is better accommodated in *Helicotaphrichnus* Kern et al., 1974, despite the different host organism, as the new combination *H. helicus* (Nielsen and Görmüş, 2004). The main difference from *H. commensalis* is its planispiral instead of trochospiral shape.

Trypetesa Norman, 1903 is a genus of acrothoracican body fossils and not an ichnogenus (e.g., Buatois et al. 2017). Similarly, Murphy and Williams (2013) recognized five species of *Trypetesa* as valid acrothoracican cirriped species. *T. caveata* Tomlinson, 1963 and *T. polonica* Bałuk and Radwański, 1991, however, refer to borings and consequently are here transferred to *Rogerella* de Saint-Seine, 1951 as new combinations, until a review of that ichnogenus is performed.

Vermiforichnus Cameron, 1969a and its type ichnospecies *V. clarkei* Cameron, 1969a were established as replacement ichnotaxa for *Palaeosabella* Clarke, 1921 and its type ichnospecies *P. prisca* (McCoy, 1855), respectively. Cameron (1969a) followed McCoy's (1855) original interpretation, repeated by Fenton and Fenton (1932) that the holotype of *Palaeosabella* consists of a single sponge boring with a central cavity and radiating tunnels. This way it would belong to *Topsentia* Clarke, 1921 rather than a cluster of individual clavate worm borings. A thorough reinvestigation of McCoy's holotype by Plewes (1996) and the present authors confirms *Palaeosabella* and its type ichnospecies as valid ichnotaxa for individual clavate borings. A comparison of the holotypes of *V. clarkei* Cameron (1969a) and *P. prisca* (McCoy, 1855) shows that *P. prisca* is the senior synonym of *V. clarkei*, and as a consequence, *Vermiforichnus* is synonymous with *Palaeosabella*.

Vioa Nardo, 1833 -> see *Entobia* Bronn, 1837 above.

Ichnotaxonomy by numbers

A total of 714 bioerosion ichnotaxa have been described since 1837, 480 (67%) of which are currently considered as valid. These are grouped into 18 ichnofamilies and 123 ichnogenera, constituting a total of 339 ichnospecies. The latter include 179 (53%) macroborings, 97 (28%) microborings, 26 (8%) predation traces, 26 (8%) attachment etchings, and 11 (3%) grazing traces (Fig. 2a), described from calcareous (81%), xylic (8%), osteic (8%), and siliceous (3%) substrates (Fig. 2b). Their known or inferred tracemakers (Fig. 2c) are invertebrates (79%), bacteria (6%), fungi (5%), vertebrates (4%), plants (3%), or unknown (3%).

Those 234 ichnotaxa that are currently recognized as invalid include one ichnofamily, 76 ichnogenera, and 157 ichnospecies. Among the latter are 65 (41%) subjective junior synonyms, one (1%) objective junior synonym, one (1%) primary homonym, two (1%) secondary junior homonyms, 55 (35%) *nomina dubia*, 21 (13%) *nomina nuda*, 2 (1%) ichnotaxa that are trace fossils unrelated to bioerosion, and 10 (6%) taxa that actually are to be regarded as body fossils

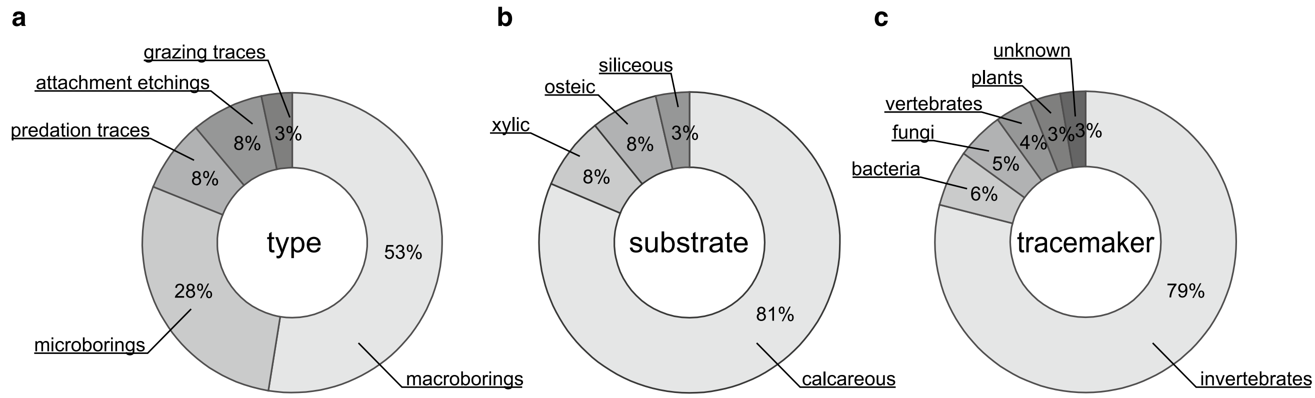

Fig. 2 Quantitative analysis of the 339 valid bioerosion ichnospecies with respect to the type of bioerosion trace (**a**), the preferred substrate (**b**), and their known or inferred tracemaker (**c**)

and thus are biotaxa. As for the current group of *nomina dubia*, it shall be noted that in several cases ichnotaxa can potentially be stabilized by reinvestigation, improved definition and enhanced illustration of the type material with designation of suitable lectotypes where applicable, or, in those cases where the type material remains lost, the definition of neotypes.

Bioerosion ichnotaxonomy appears largely as a European domain, with the most productive protagonists being Richard G. Bromley, who established no fewer than 50 valid bioerosion ichnotaxa between 1970 and 2013, and Max Wisshak (52 ichnotaxa since 2005). Other ichnotaxonomists who established a considerable amount of the currently valid bioerosion ichnotaxa are Gudrun Radtke (33 ichnotaxa since 1991), Eduardo Mayoral (30 ichnotaxa since 1987), Markus Bertling (23 ichnotaxa since 2017), Radek Mikuláš (19 ichnotaxa since 1992), Dirk Knaust (18 ichnotaxa herein), and Ana Santos (15 ichnotaxa since 2003). Together, these eight authors have established more than a third of all valid bioerosion ichnotaxa.

The quantitatively by far most productive decades (Fig. 1) were the 2010s (97 ichnotaxa so far), closely followed by the 2000s (96 valid bioerosion ichnotaxa), and the 1990s (92 ichnotaxa). Milestones in ichnotaxonomy were the two compilations of known bioerosion ichnogenera by Häntzschel (1962, 1975) in the 'Trace Fossils' volumes of the 'Treatise on Invertebrate Paleontology'. This is also in accordance with the marked increase in bioerosion research and publications since Neumann's (1966) definition of the term bioerosion (Schönberg and Tapanila 2006), and was furthermore catalyzed by the initiation of the series of International Bioerosion Workshops (IBW) by Richard Bromley in 1996, the Workshops on Ichnotaxonomy (WIT) by Markus Bertling in 1998, and the International Congress on Ichnology (ICHNIA) by Jorge Genise and others in 2004.

Conclusions and outlook

The past few decades have seen a boost in bioerosion research and the establishment of new ichnotaxa describing bioerosion trace fossils. In fact, the number of valid bioerosion ichnotaxa has nearly quadrupled since the time of the last compilation of ichnogenera in the 'Trace Fossils' part of the 'Treatise on Invertebrate Paleontology' by Häntzschel (1975). The present inventory includes a total of 339 valid ichnospecies, grouped into 123 ichnogenera and 18 ichnofamilies. Such an ichnotaxonomic 'radiation' inevitably bears a tendency for splitting and has created numerous redundant (synonymous) or otherwise invalid ichnotaxa. We see the present compilation as an expression of the current phase of ichnotaxonomic consolidation, by identifying synonymous ichnotaxa, lumping and recombining ichnotaxa, and invalidating or excluding taxa that do not comply with the definition of a trace fossil in general, or a bioerosion trace fossil in particular.

Together with measures performed herein, the list of invalid bioerosion ichnotaxa now includes 157 invalid ichnospecies, 76 rejected ichnogenera, and one invalid ichnofamiliy. However, there remains a strong demand for ichnotaxonomic revisions of certain groups of bioerosion trace fossils, such as the wealth of ichnotaxa and biotaxa that have been erected for traces of ctenostome bryozoans (revision in progress). Likewise, there is a need to reinvestigate the most speciose ichnogenera, foremost *Entobia* Bronn, 1837 (53 ichnospecies), *Gastrochaenolites* Leymerie, 1842 (15 ichnospecies; revision in progress), *Rogerella* de Saint-Seine, 1951 (14 ichnospecies), and *Talpina* von Hagenow, 1840 (13 ichnospecies). Ultimately, this process is expected to maintain ichnotaxonomic stability, to raise awareness of the inventory of available bioerosion ichnotaxa, and to improve the basis for utilizing bioerosion traces as paleoenvironmental indicators.

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