The ichnological collection of Georg Gasser (1857–1931): between fucoids and trace fossils

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ABSTRACT

At the end of the 19th century, the naturalist and artist Georg Gasser assembled a rich palaeontological collection, which included several trace fossils. The collection consists of 56 ichnological specimens, which were interpreted either as body or trace fossils by Georg Gasser. Specifically, a conspicuous part of the collection is represented by the dwelling burrow *Laevicyclus parvus*, which was interpreted as a crinoid columnal ("Trochiten"). By contrast, Gasser correctly interpreted the feeding burrow *Planolites beverleyensis* as a trace fossil ("Hieroglyph"), although some specimens were interpreted as body fossils. Gasser supported the botanical interpretation for the burrows *Chondrites intricatus* and *Gyrochorte comosa*, which were considered as a seaweed and a conifer, respectively. The collection of Gasser also includes a well-preserved ophiuroid burrow (*Asteriacites lumbricalis*), the fecal string of an ammonite or a holothurian (*Lumbricaria intestinum*), and possible fish coprolites. The mixed interpretation of Gasser reflects his historical period, during which discussion over the botanical or ichnological nature of trace fossils took on increasing prominence among scientists. Revision of the collection shows that the collection is dominated by trace fossils of the Werfen Formation (Lower Triassic), which indicates that Gasser assembled its ichnological collection without a specific stratigraphic criterion.

KEY WORDS

Ichnology, ichnofossils, Austrian Kingdom, Central Europe

1. INTRODUCTION

Ichnology is a rapidly evolving field of study that focuses on the interactions between organisms and the substrate (Bromley, 1996; Seilacher, 2007; Buatois & Mángano, 2011). The fossilized products of organism-substrate interactions – trace fossils – are a powerful tool in both pure and applied palaeontology. Trace fossils such as burrows, borings and trails are a central tool in the reconstruction of ancient ecosystems (Seilacher, 1953), hydrocarbon exploration (la Croix et al., 2013; Bednarz & McIlroy, 2015), scientific drilling, and characterization of aquifers (Droser & O'Connell, 1992; Cunningham et al., 2009). However, this was not always the case. During most of the 19th century trace fossils indeed received a botanical interpretation, as exemplified by the work of the eminent palaeobotanist Adolphe Brongniart (Osgood, 1975). Following his attitude toward comparative anatomy, Brongniart interpreted the branching trace fossil *Chondrites* as an alga, and according to the resemblance to the brown alga *Fucus*, he used the term fucoid to indicate such fossils (Brogniart, 1823; Baucon et al., 2012). The botanical interpretation was replaced with the ichnological one between the 1880s and the 1930s (Osgood, 1975, Baucon et al., 2012). During the same crucial period, the naturalist Georg Gasser assembled his paleontological collection, which includes several specimens of trace fossils. Apparently, Gasser compiled his catalogues around 1895 and only updated them for a short time, as fossil specimens acquired from 1899 on are not reported in the catalogue (Wagensommer et al., this volume b). Consequently, Gasser's collection represents an open window onto the crucial transition from the botanical to the ichnological interpretation of trace fossils. Surprisingly, the trace fossils of the Gasser collection have never been studied in recent times. The goal of this study is therefore to discuss the historical and scientific significance of the trace fossils in the Georg Gasser collection. To such a scope, three questions arise: (1) What are the trace fossil taxa in the collection? (2) How were the trace fossils interpreted by Georg Gasser? (3) In which locality were the trace fossils collected?

The aims of this study are to provide answers to these questions. For this reason, this paper is organized in three major sections, each of which refers to a specific question.

2. MATERIALS AND METHODS

The trace fossils of the Gasser collection were investigated in 2022. The ichnological collection of Georg Gasser is composed of 56 specimens inventorized. Details about the cleaning and inventorying part of the research project can be found in Kustatscher et al. (this volume). The specimens include trace fossils preserved as full reliefs and semireliefs. All specimens were photographed using a Panasonic DC-FZ82 camera. Trace fossils were referred to existing ichnogenera following the norms of the ICZN (1999). Assignments were made at the

FIG. 1: Digestion traces (digestichnia). Scale bars = 1 cm: A) *Lumbricaria intestinum*, PZO 12604; B) Coprolites labeled as "Koprolithen Excremente" (Coprolites Excrements); C) General view of B, showing various coprolites, PZO 15790-15800.

ichnospecific level. All fossils are inventorized in the paleozoological (suffix PZO) collection of the Museum of Nature South Tyrol (NMS).

3. THE COMPOSITION OF THE COLLECTION

The trace fossil specimens of the Gasser collection are identified at ichnospecies level and are organized in ethological categories (Seilacher, 1953; Vallon et al., 2016). Open nomenclature has been used when the traces are not identifiable neither at ichnospecies nor at ichnogenus level. It should be noted that some traces are compound structures (e.g., *Laevicyclus* is a dwelling and feeding structure; Knaust, 2015) whereas others fit with more than a single behaviour (e.g., *Chondrites* may represent feeding or gardening; Baucon et al., 2020). Accordingly, the ichnological samples of the Gasser collection are attributed to cubichnia (1 specimen), digestichnia (14 specimens), domichnia (7 specimens), fodinichnia (31 specimens) and pascichnia (1 specimen). Few (2) specimens are likely to be ichnofossils, but the preservation precludes a robust identification. The major ichnofossils identified in the collection are as follows:

3.1 DIGESTION TRACES (DIGESTICHNIA; FIG. 1)

Lumbricaria intestinum **Münster, 1831**
Description: This taxon includes looping and meandering string-shaped structures with homogeneous, structureless fill.
Representative material: PZO 12604 (Fig. 1A)
Ichnological remarks: The studied material fit in *Lumbricaria*, which includes rope or string-shaped coprolites or cololites with structureless fill (Knaust & Hoffmann, 2021). We assign the studied specimen to *L. intestinum* because of its elongate and intertwined shape, which are typical features of the ichnospecies; by contrast, *Lumbricaria colon* is a well-confined aggre-

FIG. 2: Dwelling traces (domichnia). Scale bars = 1 cm: A) *Laevicyclus parvus*, PZO 13669; B) *Laevicyclus parvus*, PZO 13160; C) Label of the specimen pictured in A showing the use of the term "Trochites"; D) Second label of the specimen pictured in A showing the use of the term "Trochites".

gate (Knaust & Hoffmann 2021). Holothurians (Kietzmann & Bressan, 2019), cephalopods (e.g., ammonites; Knaust & Hoffmann, 2021), annelids and vertebrates (fishes, flying reptiles) (tab 1, in Knaust & Hoffmann, 2021) have been suggested as the producers of *Lumbricaria.*

Historical remarks: *Lumbricaria* has been recognized more than 300 years ago, being a very common trace fossil in the Upper Jurassic Lithographic Limestones (Plattenkalk) of southern Germany (Knaust & Hoffmann, 2021). The specimen comes from the Solnhofen Plattenkalk.

'Spherical and cylindrical coprolites'

Description: Spherical and cylindrical structures with smooth surface.

Representative material: PZO 15790–15800 (Fig. 1B–C)

Ichnological remarks: The specimens PZO 15790–15800 are strongly reminiscent of the iconic fish coprolites from the latest Triassic of the United Kingdom (see Cueille et al., 2020). The coprolites from the British Triassic have been featured in classic early researches by luminaries such as William Buckland (Cueille et al., 2020).

However, the studied material does not present clear structural patterns (e.g., spiral marks, food remains), which makes the ichnotaxonomic assignment difficult. In addition, fossilized faeces (bromalites) include ejected faecal material (coprolites) and faecal material preserved in the gut (cololites) (Prasad, 2005; Hunt et al., 2007; Brachaniec et al., 2015; Knaust, 2020). Distinguishing between coprolites and cololites may be difficult since they can be morphologically and compositionally similar (Knaust, 2020). For these reasons, we use open nomenclature to describe the here discussed material (PZO 15790–15800).

Historical remarks: The specimens PZO 15790 to 15800 are pasted on a single glass plate labelled as coprolites ("Koprolithen Excremente") and come from England and "Podolia", a historical region between Ukraine and Moldova.

3.2 DWELLING TRACES (DOMICHNIA; FIG. 2)

***Laevicyclus parvus* (Desio, 1940)**

Description: The vertical burrows consist of a small central core and an outer lining. The burrows are preserved on bedding planes as ring-like structures.

Representative material: PZO 13160, PZO 13669 (Fig. 2).

Ichnological remarks: The studied traces are attributable to the ichnofamily Siphonichnidae, comprising simple to complex burrows of varying morphology consisting of one or more sub-vertical tube(s) with passively filled core and commonly actively filled mantle or lining (Knaust, 2015). Among siphonichnids, *Laevicyclus* and *Siphonichnus* are similar, i.e. *Laevicyclus* is a cylindrical vertical burrow with an actively filled mantle and a passively filled core, whereas *Siphonichnus* comprises vertical,

FIG. 3: Feeding traces (fodinichnia). Scale bars = 1 cm: A) *Chondrites intricatus*, PZO 13416; B) Detail of A. C) *Chondrites intricatus* labelled as "Algen" (seaweed), PZO 13663; D) *Planolites beverleyensis* (arrowed), PZO 13664; E) Label of the specimen illustrated in D, showing the use of the term "Hieroglyphen" (hieroglyphs).

oblique or horizontal cylindrical burrows characterised by a laminated meniscate mantle (active fill), which is penetrated by a homogeneous core (Knaust, 2015). The traces of the Gasser collection do not show evidence of meniscate mantle, therefore we assign them to *Laevicyclus*. *Laevicyclus* is a monotypic taxon, hence the Gasser traces fit in *L. parvus* (Knaust, 2015). *Laevicyclus* is a compound trace fossil resulting from dwelling and suspension- or deposit-feeding of polychaetes or bivalves (Knaust, 2015). In the case of worm-like producers, the outer ring-like structure represent tentacle swirlmarks around the top of the burrow (Alpert & Moore, 1975; Seilacher, 1953). The studied material does not present features that allow distinguishing between bivalve and worm-like producers.

Historical remarks: Gasser labelled *Siphonichnus* as "Trochiten" (e.g., PZO 13669), that are, crinoid columnals. *Siphonichnus* and columals share a concentric structure with a well-defined central area, i.e., the lumen in the columnalia, and the core in *Siphonichnus*). According to his labels, Gasser collected *Siphonichnus* in the "Werfener Schichten", that is, the Lower Triassic Werfen Formation. The studied samples share the same preservation style with the specimens of *Siphonichnus* in the historical collection of the University of Heidelberg, which come from the Lower Triassic lithostratigraphic units of South Tyrol (Knaust, 2015, fig. 2E–F).

3.3 FEEDING TRACES (FODINICHNIA; FIG. 3)

Chondrites intricatus **(Brongniart 1828)**

Description: The regularly branching system consist of straight branches that typically form branching angles smaller than 45°. Full-relief preservation.

Representative material: PZO 13416, PZO 13663 (Fig. 3A–C)

Ichnological remarks: The studied trace fossils are assigned to *Chondrites*, which is a "regularly branching tunnel system consisting of a small number of sub-vertical master-shafts, connected to the ancient sediment-water interface, that branches at depth to form a dendritic network" (Baucon et al., 2020, p. 3; see also Fu, 1991). Specifically, the studied trace fossils are comparable with *Chondrites intricatus* (Brogniart, 1823), which is characterized by downward radiating straight branches and branching angle less than 45° (Uchman, 1998).
Actualistic studies (Dufour & Felbeck, 2003, Hertweck et al., 2007) show that burrows of modern bivalves (thyasirids) and annelids are the closest morphological analogues of *Chondrites*. By analogy, bivalves produced *Chondrites* by pushing their extensile foot into the sediment; sulfur-pumping bivalves backfilled inactive tunnels to ensure pumping efficiency in the new tunnel. Annellids produced *Chondrites* by extending their proboscis and intruding into the sediment or by ingesting the sediment particles in front of them. According to the most recent ethological review of the taxon (Baucon et al., 2020), the *Chondrites* tracemakers built their burrows to obtain food:
(1) Subsurface deposit feeding annelids produced *Chondrites*-like traces when searching for food in the sediment;
(2) Chemosymbiotic thyasirid bivalves produced *Chondrites* to provision sulfur-oxidizing symbionts with the chemical reductants they required for metabolism;
(3) Asymbiotic thyasirids built *Chondrites* for cultivating bacteria and directly ingesting them.
As such, *Chondrites* can be regarded as a feeding trace (fodinichnion), a chemosymbiotic trace (chemichnion) or a farming trace (agrichnion), although there are no known morphological features to attribute a specimen of *Chondrites* to one ethological class or the other.
Historical remarks: Gasser's labelled the specimen PZO 13663 as 'Algen' (algae). During the 19th century, most scientists associated branching trace fossils (e.g., *Chondrites*) to algae, or 'fucoids'. The term 'fucoid' may derive from Pliny's 'phycites' (alga-like stone) through the Italian 'fucite'. Specifically, the term fucite was adopted to indicate bioturbated rocks (Baucon et al., 2012). For instance, Targioni-Tozzetti (1777) compared 'fuciti' to 'Pietre Lombricarie' (Worm-Stones), saying that "when they are split-off … They reveal impressions of algae (Fuci)" (Baucon et al., 2012). It should be noted that Tozzetti questioned the vegetal nature of fuciti, of which the origin "botanical or animal, is not known" (Targioni-Tozzetti, 1777). After the 1830s, the term fucite fell into disuse, being replaced by the etymologically analogous fucoid.

Planolites beverleyensis (Billings 1862)

Description: Straight to winding, unbranched, cylindrical unlined burrows. The burrow margin is smooth.
Representative material: PZO 13345 (Fig. 3D–E)
Ichnological remarks: The studied burrows are comparable to the 'worm burrows' *Planolites* and *Palaeophycus*, which include cylindrical, straight to winding, mostly unbranched burrows. *Planolites* and *Palaeophycus* are distinguished by the presence (*Palaeophycus*) or absence (*Planolites*) of a burrow lining (Pemberton & Frey, 1982; Keighley & Pickerill, 1995; Marenco & Bottjer, 2008). The studied burrows are unlined, being comparable to *Planolites*. It should be noted that several specimens are fragmentary (e.g., PZO 13678 and PZO 14159 consist of 9 and 11 cylindrical fragments, respectively). Consequently, the preservation precludes to determine whether the original trace fossils were branched or not, which is a key ichnotaxobase (Bertling et al., 2006). In conclusion, the fragmentary specimens are attributed to *Planolites*, but the original burrows may have pertained to other ichnotaxa. Currently recognized ichnospecies of *Planolites* include *P. montanus* (small, curved to tortuous burrows), *P. beverleyensis* (large, straight to gently curved burrows) and *P. annularis* (transversely annulated burrows) (Pemberton & Frey, 1982). Accordingly, we assign the studied burrows to *P. beverleyensis.* A wide range of deposit-feeding organisms can produce *Planolites*, including not only worm-like tracemakers (annellids, priapulids, hemichordates) but also crustaceans and bivalves (Knaust, 2017). A single specimen (PZO 13298) displays a faint longitudinal ornamentation, which make it comparable to the ornamented taxon *Scoyenia*. However, the preservation does not allow a robust assignment of the specimen.
Historical remarks: Gasser frequently (but not exclusively) uses the term 'hieroglyph' to describe *Planolites*. Most likely he brought the term from the work of Fuchs (1895), entitled "Fucoiden und Hieroglyphen Denkschriften" ("Memorandum about fucoids and hieroglyphs"). Fuchs (1895) distinguishes three family groups of trace fossils (Häntzschel, 1975, Baucon et al., 2012):

1. Vermiglyphen: threadlike, straight or winding reliefs occurring mostly on bed soles;
2. Rhabdoglyphen: straight bulges on lower bedding surfaces;
3. Graphoglypten: reliefs resembling ornaments or letters. The term partly corresponds to the similar term Hieroglyphen.

It should be noted that the traces of the Gasser collection are not 'Graphoglypten' *sensu stricto*. In fact, the term Graphoglypten has had a considerable success since its introduction and its English analog (graphoglyptid) is still used for indicating a group of ornamental trace fossils occurring at the base of sandstone beds in flyschoid successions (Seilacher, 2007). By contrast, the specimens described as 'hieroglyphen' by Gasser are straight to winding burrows preserved as full-reliefs or hyporeliefs. Gasser describes the specimen PZO 13345 as "Hieroglyph Kriechspur?", that means, "crawling hieroglyph?". This further supports the idea that Gasser recognized the ichnological nature of some trace fossils. However, it should be noted that Gasser often identified *Planolites* as a body fossil, i.e., as a coral ("Koralle"; label of PZO 14253), or as vertebrae ("Rippentheile von grossen Wirbel" meaning costal fragment of a big vertebra; inventory notes respectively of PZO 13020 and PZO 13021).

3.4 GRAZING TRACES (PASCICHNIA; FIG. 4B)

Gyrochorte comosa (Heer, 1865)

Description: Horizontal epirelief consisting of a bilobed, winding trace.
Representative material: PZO 15812
Ichnological remarks: The studied specimen is assigned to *Gyrochorte*, which is a burrow with a top part (positive epirelief) consisting of two convex lobes with a median furrow and a bottom part (negative hyporelief) consisting of two grooves and a median ridge (de Gibert & Bonner, 2002). In the Gasser's specimen the bottom part is not preserved. The most important characteristic for identifying *Gyrochorte* is the recognition

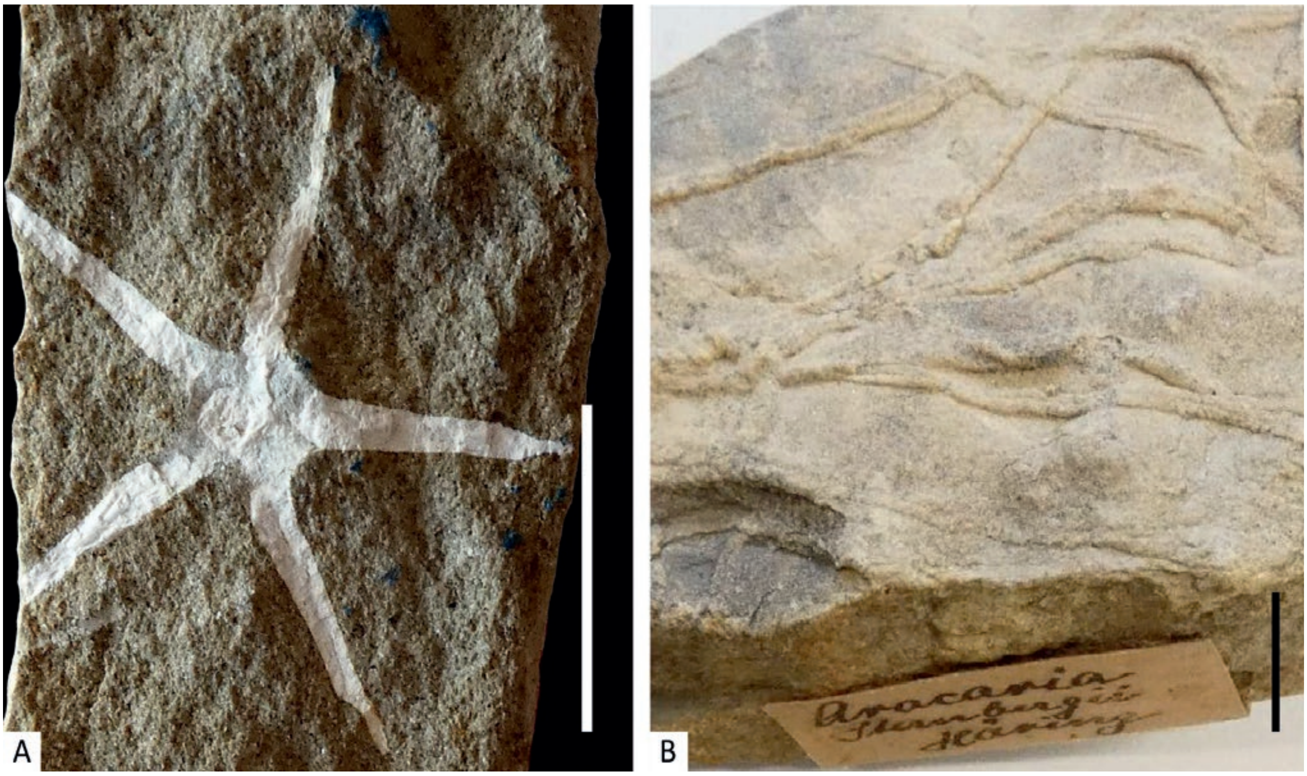

FIG. 4: Cubichnia and pascichnia (resting and grazing traces). Scale bars = 1 cm: A) *Asteriacites lumbricalis*, PZO 13827; B) *Gyrochorte comosa*, PZO 15812; note the label "*Aracaria sternbergii*", referring to the plant genus *Araucaria*.

of the vertical dimension of the burrow (de Gibert & Bonner, 2002). This aspect is faintly shown in the chipped side of the sample.

Gyrochorte is interpreted as being produced by a worm-like organism burrowing obliquely (Seilacher, 1955). *Gyrochorte* producers tended to re-burrow previously formed traces of the same species (Wetzel et al., 2020). *Gyrochorte* is restricted to moderate energy nearshore and shallow marine environments (de Gibert & Bonner, 2002; Baucon & Neto de Carvalho, 2016)

Historical remarks: Gasser labelled *Gyrochorte* as "*Aracaria sternbergii*" (sic), interpreting it as the plant genus *Araucaria.*

3.5 RESTING TRACES (CUBICHNIA; FIG. 4A)

Asteriacites lumbricalis **von Schlotheim, 1820**

Description: Star-shaped burrows consisting of five arms departing from a central discoid area. The fill is white and markedly differs from the host rock.

Representative material: PZO 13827 (Fig. 4A).

Ichnological remarks: The morphology of PZO 13827 is consistent with the ichnospecies *Asteriacites lumbricalis*, represented by star-shaped traces with five or more arms (Baucon & Neto de Carvalho, 2016; Knaust & Neumann, 2016). The ichnospecies of *Asteriacites* are, with decreasing length/width ratio of their arm imprints, *A. lumbricalis*, *A. stelliformis* and *A. quinquefolius* (Knaust & Neumann, 2016). The studied material is assigned to *A. lumbricalis* because of the particularly slender arms. The ichnogenus *Asteriacites* is interpreted as a resting trace (cubichnion) produced by Asterozoan producers, including either Ophiuroidea ('brittle stars') or Asteroidea ('sea stars'; Mángano et al., 2007; Seilacher, 2007; Knaust & Neumann, 2016). Since the arms of the studied *Asteriacites* depart from a central area and they present a vermiform shape, we refer them to brittle star producers. Body and trace fossils of brittlestars are relatively uncommon in most of the Phanerozoic, but they are relatively abundant in Early Triassic deposits (e.g., Werfen Formation) (Baucon & Neto de Carvalho, 2016). Modern brittlestars include both suspension- or deposit-feeders that extend their arms to trap nutrient particles (Hughes, 1998).

Historical remarks: *Asteriacites* has attracted the interest of scientists since the 1700s (Knaust & Neumann, 2016).

4. CHRONOSTRATIGRAPHIC DISTRIBUTION OF THE SPECIMENS

The ichnological collection of Georg Gasser does not continuously document the chronostratigraphic scale, but it focuses on specific geological intervals that range from the Triassic to the Neogene (Fig. 5). Specifically, several specimens come from the Lower Triassic Werfen Formation. Intriguingly, the Werfen Formation is still nowadays acknowledged as a major source of invertebrate trace fossils (e.g., Twitchett & Wignall, 1996; Twitchett, 1999; Hofmann et al., 2014; Baucon & Neto de Carvalho, 2016). The Gasser collection also comprises Cretaceous and Cenozoic specimens. Among the latter, a specimen of *Chondrites* is labelled "Tertiaere" (Tertiary), plausibly pertaining to Cenozoic flysches of the Alps.

The large number of Triassic trace fossils indicates that Georg Gasser assembled his ichnological collection on a locality-based

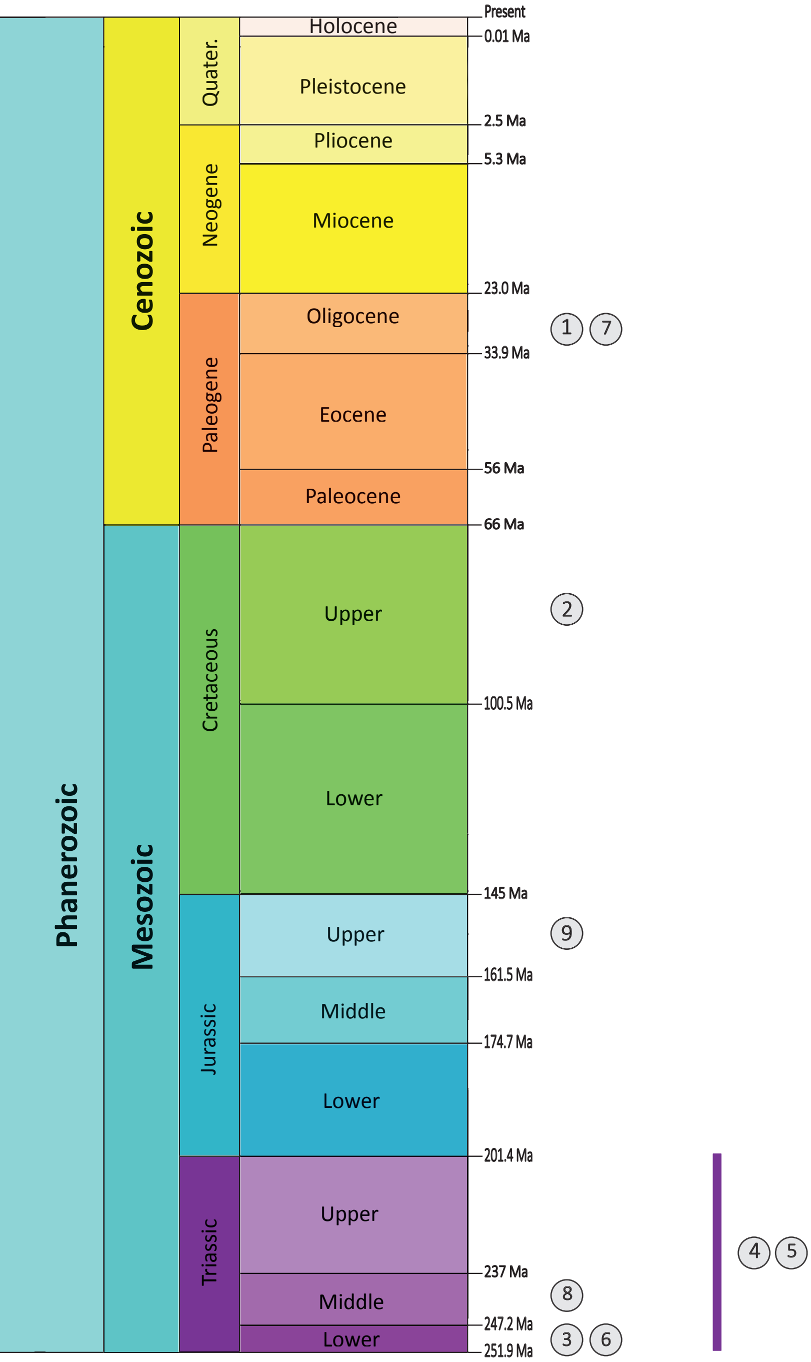

FIG. 5: Chronostratigraphic distribution of Gasser's ichnological specimens. 1. Bad Häring; 2. Bregenz; 3. Eppan/Appiano; 4. Fassa Valley; 5. Hafling/Avelengo; 6. Ratzes/Razzes – Kastelruth/Castelrotto; 7. Monte Brione; 8. Seiser Alm/Alpe di Siusi; 9. Solnhofen

criterion. As indicated by his labels, most specimens pertain to the Fassa Valley and the Seiser Alm/Alpe di Siusi. This parallels the process by which Gasser assembled the paleobotanical and remaining paleozoological collection, i.e., the collection is a geographical representation of the most important outcrops during the lifetime of Georg Gasser (Wagensommer et al., this volume a; Kustatscher et al., this volume; Tomelleri et al., this volume a). Gasser did not collect the specimens by himself, but probably relied on local collectors.

5. GEOGRAPHIC DISTRIBUTION OF THE SPECIMENS

Here we discuss some of the fossil sites mentioned in the collection. Figure 6 shows only those that can be placed in a fairly defined area.

5.1 AUSTRIA

Bad Häring
Age: Early Oligocene
This place in the Tyrol is one of the most famous fossiliferous localities for the European Paleogene both for paleobotanical and paleozoological specimens.
Collection Georg Gasser: PZO 15812

Bregenz
Age: Late Cretaceous
Georg Friebe (2009) describes in an abstract of the Norman Douglas Symposium that in 2007 was recovered the "Naturalien-Sammlung" (collection of natural fossils) of Norman Douglas (1868–1952), although in bad preservation. The collection of the writer included also three specimens of "Fukoiden" collected from the Eocene Flysch of Vorarlberg. These strata are nowadays considered Upper Cretaceous in age (Friebe, 2009, p. 9).
Collection Georg Gasser: PZO 13663
Remarks: The specimen from Bregenz is a chondritid (*Chondrites intricatus*). Most likely, it is referrable to the Helvetic Zone, which has prominent outcrops south of Bregenz (Janoschek & Matura, 1980).

Tirol
Age: Not determined_
Collection Georg Gasser: PZO 13160
Remarks: The specimen from Tirol derives from a donation and is attributed to the ichnospecies *Laevicyclus parvus.*

5.2 ENGLAND

Locality unknown
Age: Cretaceous
Collection Georg Gasser: PZO 15798–15800
Remarks: The specimens are digestichnia, that are strongly reminiscent of the iconic fish coprolites from the latest Triassic of the UK (Cueille et al., 2020). However, the label indicate a Cretaceous age.

5.3 ITALY

Eppan/Appiano sulla Strada del Vino (Trentino-Alto Adige)
Age: Early Triassic
Westwards of Eppan/Appiano a succession that starts with the Upper Permian Gröden/Val Gardena Formation crops out, extending up to the Middle Triassic Dolostone. Considering the lithology of the samples and the outcropping successions, the

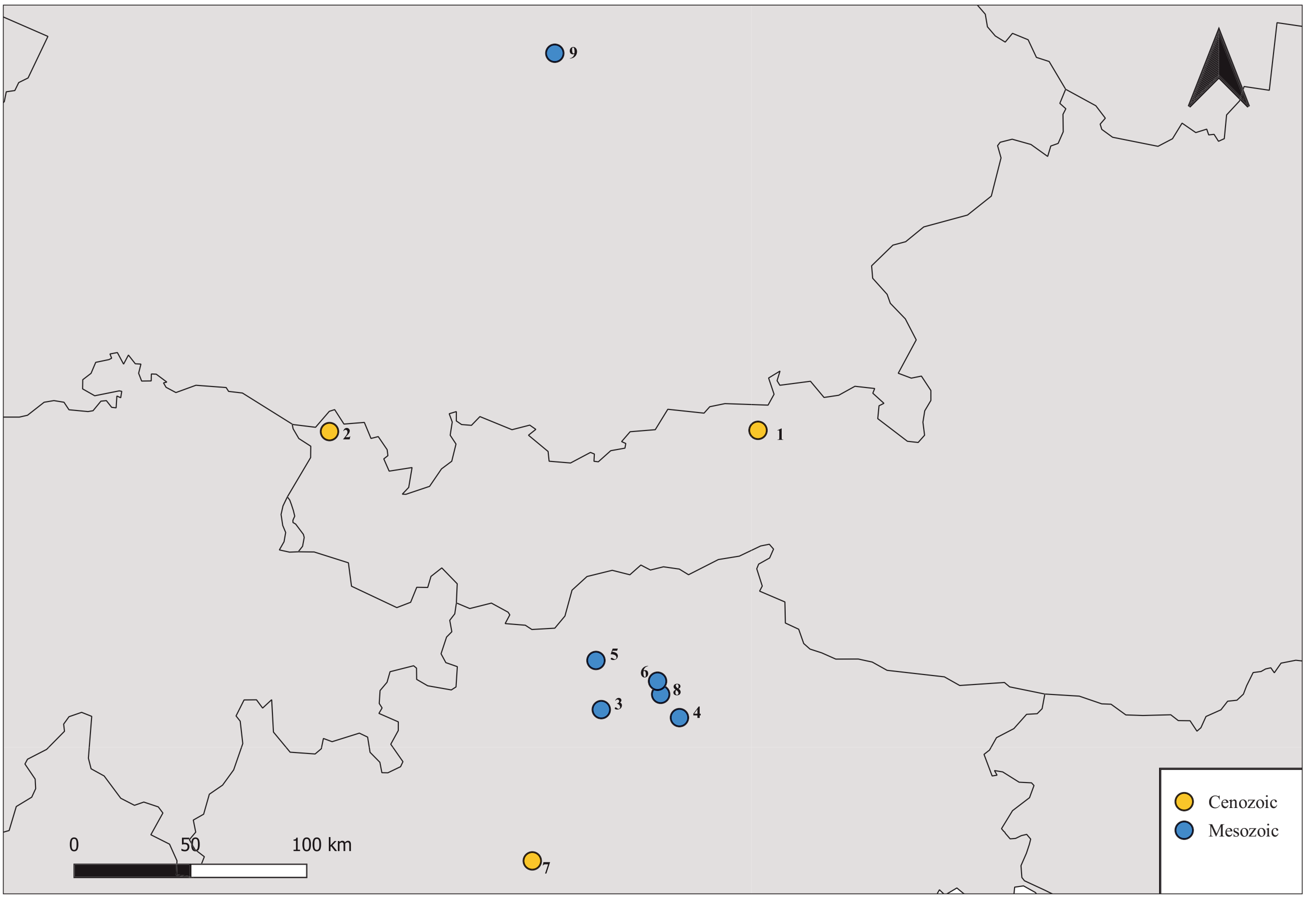

FIG. 6: Map of Europe with the localities from which Gasser's ichnological specimens come. 1. Bad Häring; 2. Bregenz; 3. Eppan/Appiano; 4. Val di Fassa; 5. Hafling/Avelengo; 6. Ratzes/Razzes – Kastelruth/Castelrotto; 7. Monte Brione; 8. Seiser Alm/Alpe di Siusi; 9. Solnhofen

specimen identified as *Planolites* could come from the Lower Triassic Werfen Formation of the area.
Collection Georg Gasser: PZO 13349, 13351

Hafling/Avelengo (Trentino-Alto Adige)
Age: Triassic
Collection Georg Gasser: PZO 13350
Remarks: The specimens are identified as *Planolites.*

Bad Ratzes/Bagno Razzes near Kastelruth/Castelrotto (Trentino-Alto Adige)
Age: Lower Triassic
On the western slope of the Schlern/Sciliar a succession, starting with the Lopingian Gröden/Val Gardena Formation and extending up to the Middle Triassic Dolostone, crops out. Considering the lithology of the samples and the outcropping successions, the specimen identified as *Planolites* could come from the Lower Triassic Werfen Formation of the area.
Collection Georg Gasser: PZO 13283
Remarks: The specimens are identified as *Chondrites.*

Monte Brione-Riva del Garda (Trentino-Alto Adige)
Age: Rupelian (Oligocene)
Although there have been carried out only few studies on the bioturbations of this area, the CARG (cartographic project in Italy) map 80 Riva del Garda shows on the Monte Brione two formations of Cenozoic age. These are the Linfano Limestone (Rupelian in age) and the Monte Brione Formation (Chattian/early Miocene in age). Moreover, the Linfano Limestone has been described as containing distinct bioturbations. This suggests that the fossil could come from the Linfano Limestone.
Collection Georg Gasser: PZO 13678, 14159, 14160, 14544
Remarks: The specimens are identified as *Planolites.*

Seiser Alm/Alpe di Siusi (Trentino-Alto Adige)
Age: Middle Triassic
The Seiser Alm/Alpe di Siusi is well-known for its Middle Triassic successions. The specimens are identified as *Laevicyclus* and *Planolites*.
Collection Georg Gasser: PZO 12893, 13664, 15758, 15760

Fassa Valley (Trentino-Alto Adige)
Age: Triassic
A large variety of geological units crops out in Val di Fassa, including a sedimentary succession that ranges from Permian terrigenous deposits (e.g., Gröden/Val Gardena Formation) to Triassic marine successions (e.g., Werfen Formation, Dolomia Principale) (Frattini & Crosta, 2013). The ichnotaxa discovered in the Gasser Collection (*Laevicyclus parvus, Planolites beverleyensis*), due to the lithologic features of the specimens, can be confidently attributed to the Werfen Formation and lithologic features of the specimens are reminiscent of the Werfen Formation.
Collection Georg Gasser: PZO 12892, 13145, 13146, 13344, 13345, 14527

5.4 GERMANY

Solnhofen (Bavaria)
Age: Upper Jurassic
The Plattenkalk of the Solnhofen Fossil-Lagerstätte is famous for its rich paleofauna, collected for hundreds of years and exhibited in museums of natural history around the world.
Collection Georg Gasser: PZO 12604
Remarks: The specimen is identified as *Lumbricaria,* which is indeed a common trace fossil in the Upper Jurassic "Plattenkalke" of Germany (Knaust & Hoffmann, 2021).

6. GASSER'S INTERPRETATION OF TRACE FOSSILS

Georg Gasser assembled his collection at the transition between the 19th and the 20th century, which corresponds to the transition between two crucial stages in the history of ichnology. Specifically, the history of ichnology is subdivided in five ages (Osgood, 1975, Pemberton et al., 2007, Baucon et al., 2012). During the Age of Naturalists stage, several Renaissance intellectuals depicted trace fossils, including Leonardo da Vinci, Ulisse Aldrovandi, and Konrad Gesner (Baucon, 2009, 2010a, 2010b). Nevertheless, ichnology has existed as disconnected ideas about traces until the Age of Fucoids (1823–1881), during which invertebrate trace fossils were regarded as plants, e.g., seaweed ('fucoids'). Successively, Nathorst (1881) argued that many fucoids were trace fossils, arousing a consistent debate between scientists (Osgood, 1975). This debate characterized the Period of Reaction (or Age of Controversy) (1881–1925) (Osgood, 1975). The Development of the Modern Approach (1925–1953) started with the establishment of the Senckenberg Laboratory, a marine institute devoted to neoichnology (Cadée & Goldring, 2007), whereas the Modern Era of Ichnology (1953–present day) saw the foundation of the central concepts of modern ichnology, starting with Seilacher's (1953) seminal publication on the methods of ichnology (Pemberton et al., 2007).
From a merely chronologic viewpoint, Gasser assembled in his collection in the Period of Reaction, between the Age of Fucoids and the Development of the Modern Approach. Results show that Gasser was a true son of his time, i.e., he interpreted some trace fossils as algae (*Chondrites*) or body fossils, whereas he correctly interpreted others (*Planolites*) as biogenic sedimentary structures. In fact, he labelled a specimen of *Planolites* (PZO 13345) as "Hieroglyph Kriechspur?", that is, "crawling hieroglyph?".

7. CONCLUSIONS

Revision of the Georg Gasser collection revealed 56 specimens of trace fossils, which received a mixed interpretation as body and trace fossils. A botanical interpretation was proposed for *Chondrites intricatus* and *Gyrochorte comosa*, which were regarded as seaweed and conifers, respectively. A zoological interpretation was given to *Laevicyclus parvus,* which was identified as a crinoid columnal. *Planolites beverleyensis* was interpreted as a locomotion trace fossil, although some specimens were referred to body fossils of corals or vertebrates. As such, the Gasser collection is an open window onto the Period of Reaction, i.e., the crucial period of time during which the ichnological nature of trace fossils was hotly debated. The results of this paper encourage further research on other historical collections of trace fossils, aiming to reveal what was the status of ichnological knowledge outside from the academic clique.

ACKNOWLEDGMENTS

This research project would never have been carried out without the support of the Research funds of the Betrieb Landesmuseum ("Die Fossiliensammlung von Georg Gasser (1857–1931)", CUP H54I19000540005). Benno Baumgarten moved the historical collection in 1992 to the Museum of Nature South Tyrol and stored both the collection and historical documents, making them available for study. Silvio Renesto (University of Varese) provided a first revision identifying what was considered a vertebrate remain as ichnofossils. We thank also the collaborators of the museum Francesca Conci, Francesca Uzzo, Roberta Branz, Barbara Lanthaler, Hendrik Nowak, and several short-time internships that helped with the logistic move of the collection as well as during the inventarisation process. We thank Fabio Massimo Petti (Rome) for the constructive and helpful review of this paper and Giuseppa Forte for her engagement in the composition of part of the figures here displayed.

BIBLIOGRAPHY

Alpert S. P. & Moore J. N., 1975: Lower Cambrian trace fossil evidence for predation on trilobite. Lethaia, 223–230.

Baucon A., 2010a: Da Vinci's *Paleodictyon*: the fractal beauty of traces. Acta Geologica Polonica, 60: 3–17.

Baucon A., 2010b: Leonardo Da Vinci, the Founding Father of Ichnology. Palaios, 25: 361–367.

Baucon A., 2009: Ulisse Aldrovandi (1522–1605): The Study of Trace Fossils During the Renaissance.Ichnos, 16: 245–256.

Baucon A., Bednarz M., Dufour S., Felletti F., Malgesini G., Neto de Carvalho C., Niklas K. J., Wehrmann A., Batstone R., Bernardini F., Briguglio A., Cabella R., Cavalazzi B., Ferretti A., Zanzerl H. & McIlroy D., 2020: Ethology of the trace fossil *Chondrites*: Form, function and environment. Earth-Science Reviews, 202: 1-37.

Baucon A., Bordy E., Brustur T., Buatois L. A., Cunningham T., De C., Duffin C., Felletti F., Gaillard C., Hu B., Hu L., Jensen S., Knaust D., Lockley M., Lowe P., Mayor A., Mayoral E., Mikulas R., Muttoni G., Neto de Carvalho C., Pemberton S., Pollard J., Rindsberg A., Santos A., Seike K., Song H., Turner S., Uchman A., Wang Y., Yi-ming G., Zhang L. & Zhang W., 2012: A History of Ideas in Ichnology. In: Knaust D. & Bromley R. G. (Eds.): Trace Fossils as Indicators of Sedimentary Environments. Developments in Sedimentology, 64. Elsevier, Amsterdam, pp. 3–43.

Baucon A. & Neto de Carvalho C., 2016: Stars of the aftermath: *Asteriacites* beds from the Lower Triassic of the Carnic Alps (Werfen Formation, Sauris di Sopra), Italy. Palaios, 31: 161–176.

Bednarz M. & McIlroy D., 2015: Organism-sediment interactions in shale-hydrocarbon reservoir facies – Three-dimensional reconstruction of complex ichnofabric geometries and pore-networks. International Journal of Coal Geology, 150–151: 238–251.

Bertling M., Braddy S., Bromley R., Demathieu G., Genise J., Mikuláš R., Nielsen J., Nielsen K., Rindsberg A., Schlirf M. & Uchman A., 2006: Names for trace fossils: a uniform approach. Lethaia, 39: 265–286.

Billings E., 1862: New species of fossils from different parts of the Lower, Middle and Upper Silurian rocks of Canada. In: Palaeozoic fossils. Geological Survey of Canada, Ottawa, pp. 96-168.

Brachaniec T., Niedźwiedzki R., Surmik D., Krzykawski T., Szopa K., Gorzelak P. & Salamon M. A., 2015: Coprolites of marine vertebrate predators from the Lower Triassic of southern Poland. Palaeogeography, Palaeoclimatology, Palaeoecology, 435: 118–126.

Brogniart A. T., 1823: Observations sur les Fucoïdes et sur quelques autres plantes marines fossiles. Mémoire de la Société d'Histoire Naturelle de Paris, 1: 301–320.

Bromley R. G., 1996: Trace fossils: biology, taphonomy and applications. 2nd edition. Chapman & Hall, London, 361 pp.

Brongniart A. T., 1828: Histoire des Végétaux Fossiles ou Recherches Botaniques et Géologiques sur les Végétaux Renfermés dans les Diverses Couches du Globe, Volume 1. G. Dufour & E. d'Ocagne, Paris, 136 pp.

Buatois L. A. & Mángano M. G., 2011: Ichnology: Organism-Substrate Interactions in Space and Time. Cambridge University Press, Cambridge / New York, 358 pp.

Cadée G. & Goldring R., 2007: The Wadden Sea, Cradle of Invertebrate Ichnology. In: Miller W. I. (Ed.): Trace Fossils. Concepts, Problems, Prospects. Elsevier, Amsterdam, pp. 3–13.

Croix A. D. la, Gingras M. K., Pemberton S. G., Mendoza C. A., Maceachern J. A. & Lemiski R. T., 2013: Biogenically enhanced reservoir properties in the Medicine Hat gas field, Alberta, Canada. Marine and Petroleum Geology, 43: 464–477.

Cueille M., Green E., Duffin C. J., Hildebrandt C. & Benton M. J., 2020: Fish and crab coprolites from the latest Triassic of the UK: From Buckland to the Mesozoic Marine Revolution. Proceedings of the Geologists' Association, 131: 699–721.

Cunningham K. J., Sukop M. C., Huang H., Alvarez P. F., Curran H. A., Renken R. A. & Dixon J. F., 2009: Prominence of ichnologically influenced macroporosity in the karst Biscayne aquifer: Stratiform "super-K" zones. Bulletin of the Geological Society of America, 121: 164–180.

Desio A., 1940: Vestigia problematiche paleozoiche della Libia. Pubblicazioni dell'Istituto di Geologia, Paleontologia e Geografia Fisica della R. Università di Milano, Serie P., 20: 47–92.

Droser M. L. & O'Connell S., 1992: Trace fossils and ichnofabric in Triassic sediments from cores recovered on Leg 122. In: Rad U. Von, Haq B. U. et al. (Eds.): Proceedings of the Ocean Drilling Program, Scientific Results, 122. Ocean Drilling Program, College Station, TX, pp. 201–213.

Dufour S. C. & Felbeck H., 2003: Sulphide mining by the superextensile foot of symbiotic thyasirid bivalves. Nature, 101: 65–67.

Frattini P. & Crosta G. B., 2013: The role of material properties and landscape morphology on landslide size distributions. Earth and Planetary Science Letters, 361: 310–319.

Friebe J. G., 2009: Die Naturalien-Sammlung von Norman Douglas. Norman Douglas Symposium, 5: 7–34.

Fu S., 1991: Funktion, Verhalten und Einteilung fucoider und lophocteniider Lebensspuren. Courier Forschungsinstitut Senckenberg, 135: 1–79.

Gibert J. M. de & Bonner J. S., 2002: The trace fossil *Gyrochorte*: ethology and paleoecology. Revista Espanola de Paleontologia, 17: 1–12.

Häntzschel W., 1975: Trace fossils and problematica. In: Teichert, C. (Ed.): Treatise on Invertebrate Paleontology. Geological Society of America, University of Kansas, Boulder, Colorado and Lawrence, Kansas, p. WI-W269.

Heer O., 1865: Die Umwelt der Schweiz. F. Schulthess., Zürich, 622 pp.

Hertweck G., Wehrmann A. & Liebezeit G., 2007: Bioturbation structures of polychaetes in modern shallow marine environments and their analogues to *Chondrites* group traces. Palaeogeography, Palaeoclimatology, Palaeoecology, 245: 382–389.

Hofmann R., Hautmann M. & Bucher H., 2014: Recovery dynamics of benthic marine communities from the Lower Triassic Werfen Formation, northern Italy. Lethaia, 48: 1–23.

Hughes D. J., 1998: Subtidal brittlestar beds. An overview of dynamics and sensitivity characteristics for conservation management of marine sacs. Scottish Association for Marine Science (UK Marine sacs Project), 78 pp.

Hunt A. P., Lucas S. G., Spielmann J. A. & Lerner A. J., 2007: A Review of Vertebrate Coprolites of the Triassic With Descriptions of New Mesozoic Ichnotaxa. Natural History: 88–107.

ICZN 1999: INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE. Fourth. The International Trust for Zoological Nomenclature, London.

Janoschek W. R. & Matura A., 1980: Outline of the Geology of Austria. Abhandlungen der Geologischen Bundesanstalt, 34: 7–98.

Keighley D. G. & Pickerill R. K., 1995: The ichnotaxa *Palaeophycus* and *Planolites*: historical perspectives and recommendations. Ichnos, 3: 301–309.

Kietzmann D. A. & Bressan G. S., 2019: The coprolite *Lumbricaria* Münster in the Early Tithonian of the Neuquén Basin, Argentina: new evidence for a holothurian producer. PalZ, 93: 357–369.

Knaust D., 2017: Atlas of Trace Fossils in Well Core: Appearance, Taxonomy and Interpretation. Springer, Alphen aan den Rijn, 209 pp.

Knaust D., 2020: Invertebrate coprolites and cololites. Papers in Palaeontology, 6: 385–423.

Knaust D., 2015: Siphonichnidae (new ichnofamily) attributed to the burrowing activity of bivalves: Ichnotaxonomy, behaviour and palaeoenvironmental implications. Earth-Science Reviews, 150: 497–519.

Knaust D. & Hoffmann R., 2021: The ichnogenus *Lumbricaria* Münster from the Upper Jurassic of Germany interpreted as faecal strings of ammonites. Papers in Palaeontology, 7: 807–823.

Knaust D. & Neumann C., 2016: *Asteriacites* von Schlotheim, 1820 – the oldest valid ichnogenus name – and other asterozoan-produced trace fossils. Earth-Science Reviews, 157: 111–120.

Kustatscher E., Tomelleri I., Wagensommer A., this volume: The plant fossils in the paleontological collection of Georg Gasser (1857–1931). Geo.Alp, 19.

Mángano M. G., Buatois L. A., West R. R. & Maples C. G., 2007: The origin and paleoecologic significance of the trace fossil *Asteriacites* in the Pennsylvanian of Kansas and Missouri. Lethaia, 32: 17–30.

Marenco K. N. & Bottjer D. J., 2008: The importance of *Planolites* in the Cambrian substrate revolution. Palaeogeography, Palaeoclimatology, Palaeoecology, 258: 189–199.

Münster G., 1831: Die Lumbricarien enthaltende Lieferung. In: A. Goldfuss (Eds.): Arnz & Co., Düsseldorf, pp. 165–240.

Nathorst A. G., 1881: Om spar af några evertebrerade djur mm och deras paleontologiska betydelse. Norstedt & Söner, Stockholm, 104 pp.

Osgood R. G., 1975: The history of invertebrate ichnology. In: Frey, R. W. (Eds.): The Study of Trace Fossils. Springer Verlag, New York, pp. 3–12.

Pemberton S. G. & Frey R. W.,1982: Trace Fossil Nomenclature and the *Planolites-Palaeophycus* Dilemma. Journal of Paleontology, 56: 843–881.

Pemberton S. G., MacEachern J. A. & Gingras M. K., 2007: The antecedents of invertebrate ichnology in North America: the Canadian and Cincinnati schools. In: Miller III, W. (Eds.): Trace Fossils. Concepts, Problems, Prospects. Elsevier, Amsterdam, pp. 32–51.

Prasad V., 2005: Dinosaur Coprolites and the Early Evolution of Grasses and Grazers. Science 310: 1177–1180.

Schlotheim F. Von, 1820: Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt. Becker, Gotha, 438 pp.

Seilacher A., 1955: Spuren und Fazies im Unterkambrium. Akademie der Wissenschaften und der Literatur, Mainz. Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, 10: 373–399.

Seilacher A., 1953: Studien zur Palichnologie. I. Über die Methoden der Palichnologie. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 96: 421–452.

Seilacher A., 2007: Trace fossil analysis. Springer, Berlin, Heidelberg, 238 pp.

Targioni-Tozzetti G., 1777: Relazioni d'Alcuni Viaggi Fatti in Diverse Parti della Toscana. Tomo decimo. Stamperia Granducale, Firenze, 466 pp.

Tomelleri I., Butzmann R., Cleal C., Forte G. & Kustatscher E., this volume a: The plant fossils in the palaeontological collection Georg Gasser (1857–1931). Geo.Alp, 19.

Twitchett R. J., 1999: Palaeoenvironments and faunal recovery after the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 154: 27–37.

Twitchett R. J. & Wignall P. B., 1996: Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. Palaeogeography, Palaeoclimatology, Palaeoecology, 124: 137-151.

Uchman A., 1998: Taxonomy and ethology of flysch trace fossils: revision of the Marian Książkiewicz collection and studies of complementary material. Annales Societatis Geologorum Poloniae, 68: 105–218.

Vallon L. H., Rindsberg A. K. & Bromley R. G., 2016: An updated classification of animal behaviour preserved in substrates. Geodinamica Acta, 28: 1–16.

Wagensommer A., Tomelleri I., Baumgarten B. & Kustatscher E., this volume a: Die paläontologische Sammlung von Georg Gasser (1857–1931). Geo.Alp, 19.

Wagensommer A., Tomelleri I., Baumgarten B. & Kustatscher E., this volume b: Die Kataloge der „Naturhistorischen Sammlungen“ von Georg Gasser (1857–1931). Geo.Alp, 19.

Wetzel A., Carmona N. & Ponce J., 2020: *Gyrochorte* "highways" and their environmental significance in shallow-marine sediments. Acta Palaeontologica Polonica, 65.

Eingereicht am: 24.10.2022
Angenommen am: 15.11.2022