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An updated classification of animal behaviour preserved in substrates

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During the last few decades, many new ethological categories for trace fossils have been proposed in addition to the original five given by Seilacher. In this article, we review these new groups and present a version of the scheme of fossil animal behaviour originally published by Bromley updated with regard to modern ethological concepts, especially those of Tinbergen. Because some behaviours are more common in certain environments than others, they are useful in palaeoecological reconstructions, forming the original basis of the ichnofacies concept. To simplify, we summarise some ethological categories as previously done by others. However, the tracemaker's behaviour in some cases is so distinctive that subcategories should be employed, especially in ecological interpretations of certain environments where a special behaviour may be dominant.

Keywords: trace fossils; ethological categories; animal behaviour; palaeoecology; ichnology

1. Introduction

The classification of fossil animal behaviour is necessary to its utilisation in palaeoecology and stratigraphy but also presents procedural challenges not faced by researchers on modern organisms. Ethologists (and neoichnologists) nearly always know the species whose behaviour they study, whereas palaeoichnologists almost never do. Palaeoichnologists are restricted to the geologic record, leading to an emphasis on behaviours that involve movement or erosion of sediment, such as burrowing and boring, rather than important behaviours that ordinarily do not, such as swimming and flying. Detailed studies of trace fossils analyse the contextual substrate together with the deduced anatomy and behaviour of the tracemaker drawing appropriate analogies with modern examples (Martin, 2013, pp. 19–25).

Unfortunately, the Kuhnian paradigm in which ichnologists work has drifted so far from that of modern ethology that it can act as a barrier to the understanding of ancient behaviour (Miller, 2007; Plotnick, 2012). Even neoichnologists and ethologists do not speak the same language, let alone palaeoichnologists, but these scientists have much to tell each other. In this article, we attempt to adjust the palaeoichnological paradigm rather than to replace it, by simplifying the system of ethological categories that is currently in use, and by testing the utility of each category in reference to basic ethological principles (Martin & Bateson, 2007).

The ethological classification of Seilacher (1953a), as refined by Frey and Seilacher (1980), is part of the paradigm within which palaeoichnologists work today in order to describe trace fossils. The paradigm requires biogenic structures to be described simultaneously in regard to four aspects: (1) toponomically, according to the relationship that the structures have with contrasting substrate materials; (2) biologically, according to their relationship to their makers; (3) ethologically, according to their biological function; and (4) systematically, according to their morphology. In this article, we focus on point three.

The categorisation of trace fossils according to their ethology is a very useful tool in ecological analyses of ancient environments and in the reconstruction of interactions among tracemakers. Because we cannot observe ancient animals, trace fossils are the only signs of life that show us how these animals moved, ate, hunted or dwelled. Many morphological criteria of trace fossils are ecologically informative. Thorough observation of trace fossils leading towards a behavioural interpretation of their makers is therefore a valuable tool in bringing the fossilised animals back to life.

Seilacher (1953a) recognised that similar behaviour results in similar morphology of trace fossils (convergent evolution or homoplasy), so they may be classified according to their ethological function. His original classification for invertebrates in marine environments recognises five groups: resting traces (cubichnia), dwelling traces (domichnia), combined dwelling and feeding traces (fodinichnia), crawling or, better, locomotion traces (repichnia), and the combined feeding and locomotion traces called grazing traces (pascichnia). He also suggested that nesting, swimming and other specialised traces (e.g. nets and pitfalls; cf. irretichnia Lehane & Ekdale, 2013) might later be recognised as categories, but did not name them formally. Accordingly, several new ethological categories have been proposed

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since 1953 to cover other animal behaviour (Table 1). However, some have not been fully accepted by the ichnological community, mainly because they reflect highly specialised behaviour that is only rarely preserved, or consist of special cases within existing categories. Many ichnotopes, especially terrestrial ones, are dominated by trace fossils reflecting a single highly specialised behaviour (e.g. breeding in subterraneous brood structures). In such cases, these rarely seen categories have been incorporated here as subcategories of broader categories (cf. Buatois & Mángano, 2012, p. 18).

The ethological classification system must not be used as a taxonomical classification system as it occasionally has been since its introduction (e.g. Rindsberg (1994) experimented with this). As such, it only works in exceptional cases, e.g. distinguishing between similar ichnotaxa (e.g. repichnion *Cruziana* vs. cubichnion *Rusophycus*). Seilacher himself, however, did not employ his scheme in such a strict sense (e.g. his use of *'Cruziana'* in 2007). Too many trace fossils have overlapping functions, and the morphologic diversity of any ethological category is too broad to make the two systems compatible. A modification of Knaust's (2012) determinative key to ichnogenera based on purely morphological features will probably serve much better in this regard.

In the following pages, we discuss the categories proposed after 1953 (cf. Table 1) and propose a new, updated scheme of animal behaviour based on that of Bromley (1996, figure 9.2) (Figure 1). For a classification system of traces produced by plants, consult Mikuláš (1999).

2. Ethology, the study of behaviour

Ethology derives from Ancient Greek ἦθος [ethos], meaning *character, manners, habit* and the suffix -λογία

Table 1. Ethological categories proposed for use in ichnology within the framework of Seilacher's (1953a) classification.

Ethological category in order of usage	Author(s)	Google Scholar citations, 6 April 2015	Current status
Domichnia	Seilacher (1953a)	808	Original categories (Seilacher, 1953a); generally accepted (Bromley, 1996)
Fodinichnia		637	
Pascichnia		509	
Repichnia		447	
Cubichnia		433	
Fugichnia	Frey (1973)	341	Generally accepted categories (Bromley, 1996)
Agrichnia	Ekdale et al. (1984)	171	
Praedichnia	Ekdale (1985)	142	
Equilibrichnia	Frey and Pemberton (1985)	104	Reassigned to domichnia and fodinichnia
Calichnia	Genise and Bown (1994a)	56	Generally accepted category (Bromley, 1996)
Fixichnia	De Gibert et al. (2004)	47	Generally accepted category
Chemichnia	Bromley (1996)	43	Generally accepted category (Bromley, 1996)
Mortichnia	Seilacher (2007)	33	Reassigned to repichnia, praedichnia and ecdysichnia
Pupichnia	Genise et al. (2007)	32	Subcategory of ecdysichnia
Navichnia	Gingras et al. (2007)	30	Subcategory of repichnia
Cursichnia	Müller (1962)	16	Subcategory of repichnia
Natichnia		16	
Aedificichnia	Bown and Ratcliffe (1988)	16	Reassigned to domichnia and calichnia
Volichnia	Müller (1962)	16	Subcategory of repichnia and cubichnia
Polychresichnia	Hasiotis (2003)	14	Reassigned to calichnia and domichnia
Sphenoichnia	Mikuláš (1999)	11	Attributed to plants
Impedichnia	Tapanila (2005)	10	Body fossils; recommended term ***impeditaxa***
Taphichnia	Pemberton et al. (1992)	9	Reassigned to fugichnia
Xylichnia	Genise (1995)	9	Subcategory of fodinichnia
Corrosichnia	Mikuláš (1999)	9	Attributed to plants
Movichnia	Müller (1962)	9	Equivalent to our usage of repichnia
Mordichnia		8	Subcategory of praedichnia
Cibichnia	Müller (1962)	6	Equivalent to our usage of fodinichnia
Cecidoichnia	Mikuláš (1999)	5	Attributed to plants, considered as body fossils (Bertling et al., 2006); recommended term ***cecidotaxa***
Irretichnia	Lehane and Ekdale (2013)	4	Subcategory of praedichnia
Digestichnia	Vallon (2012), Vialov (1972)	3	Recently revived category
Aestivichnia	Verde et al. (2007)	1	Subcategory of domichnia
Quietichnia	Müller (1962)	1	Supercategory proposed for domichnia + cubichnia; not in current use
Ecdysichnia	Vallon et al. (in press)	0	Recently proposed category

Notes: Categories are arranged in descending order of usage as reflected by citations on the Google Scholar search engine on 6 April 2015. In general, the older an accepted term is, the greater the number of citations; unaccepted terms never develop a large number of citations. Accepted terms are boldfaced.

[-logia], standing for *study (of)*. Neither in biology nor in palaeontology is there a proper definition of the term *behaviour*. Perhaps Kappeler (2012, p. 4) presented one of the better definitions: 'internally coordinated control of movements or signals with which an intact organism interacts with conspecifics or other components of its animated or inanimated environment as well as activities that serve the individual's homeostasis'. In biology, the term also includes psychological aspects such as instinct, learning, teaching or social interactions among individuals of the same species (Kappeler, 2012). However, as palaeoichnologists, we can only observe behaviour in which the tracemaker interacted with and modified a substrate (see definition of trace fossils in Bertling et al., 2006, p. 266).

Tinbergen (1963) indirectly formulated four questions that have become the foundation of behavioural studies in biology (e.g. Martin & Bateson, 2007, pp. 2–4) and that are routinely addressed in Recent studies when observing, describing or explaining a given behaviour:

(1) *What is the function of this behaviour?* That is, what consequences does the behaviour have for the survival and the reproductive success of the individual?

(2) *What internal and external factors* ('proximate causal mechanisms') *control the behaviour and through which mechanisms* (such as hormones, pheromones, neurones and muscles)*?* That is, how does it work?

(3) *How did the behaviour develop during the ontogeny of the individual?* What factors influenced the development of the behaviour and how did genetic and external influences interact?

(4) *How did the behaviour originate during the phylogeny of the species?* What is its adaptive importance – its 'ultimate or evolutionary explanation'?

A behavioural biologist would answer the question, 'Why does a male frog croak in spring?' by saying: The croaking attracts females that are ready to mate, serving the frog's biological need to pass on his genes to the next generation. It may also deter other males from entering his territory (ultimate explanations). The male frog croaks because his larynx muscles are activated by the connected motor neurons. The behaviour is initiated by the higher level of testosterone in spring (which corresponds to Tinbergen's question about the proximate causal mechanisms). The male has probably learnt the 'melody', 'rhythm', etc. during a receptive phase of his ontogeny from other adult conspecifics. The frog also croaks in this way because his ancestors did; males that do not engage in this behaviour have scant success with females (phylogenetic explanation).

Because we are rarely certain of the tracemaker in palaeoichnology and no direct observation is possible,

Tinbergen's four questions and their answers are modified for their use in this field:

(1) *What was the function of the behaviour that was recorded as a trace?* What did the tracemaker try to achieve? Examples here are reproduction, predation, resting, protection, feeding or defaecation. These are in principle the ethological categories of Seilacher (1953a) as updated by Bromley (1996) and Buatois and Mángano (2012), and now again in the current article.

(2) *What external factors controlled or were controlled by this behaviour?* This question is to be answered from the surrounding sediment and/or substrate or to some extent by comparison of the trace fossils with modern equivalents. What do we know about the physical characteristics of the environment in which the trace was produced (oxygen content, salinity, water temperature, currents, etc.)? Which other tracemakers (of the same or different species) inhabited this or other ecological niches? Did they avoid one another (e.g. phobotaxis) or interact more closely (e.g. traces within traces)? How did the tracemaker control or optimise these factors, e.g. Bernoulli effect in irrigation of burrows, microclimate maintenance in brooding structures?

(3) *How did the trace develop during the ontogeny of an individual tracemaker?* This aspect of ichnology has barely been addressed, but as usual Seilacher (1967: figure 4) pioneered with a careful description of how the spreite burrow *Diplocraterion parallelum* changes through time. Basan and Frey (1977) described how modern fiddler crab (*Uca* spp.) burrows change through I-, J-, U-, and W-shapes; Hill and Hunter (1973) similarly described the morphological changes of ghost crab (*Ocypode quadrata*) burrows during the makers' ontogeny. Borings (e.g. *Entobia*, *Gastrochaenolites*, *Teredolites*) commonly show evidence of the growth of their makers (e.g. Bromley, 1970). The fact that most burrows do *not* show changes in width corresponding to the growth of their makers suggests either that they are continuously modified through time or do not represent more than a fraction of the maker's lifespan (e.g. Frey & Seilacher, 1980, p. 202, table 2).

(4) *How did this behaviour originate during the phylogeny of the tracemaker?* This may be difficult to answer because the tracemaker and its evolution remain unknown or the same trace fossils could be produced by different species. However, viewed over longer time ranges, trace fossils have indeed evolved within environments or shifted from one environment to another (e.g. *Zoophycos* from shallow and deep-sea environments to deep seas during the Phanerozoic; Knaust, 2004).

In addition to Tinbergen's four, we propose another question:

(5) *How was the trace fossil created?* Describe the overall morphology. For burrows, what clues can you find to the mode of excavation? What is the sum of physical evidence leading towards identification of the maker (bioprint), including sculptural elements (bioglyphs)? Is the burrow's wall supported by a lining? For borings, was the bioerosion process chemical or mechanical? etc.

A palaeoichnologist therefore would answer the question, 'Why did a *Troodon* dinosaur build this nest?' as follows: The dinosaur built the nest to serve its biological need for reproduction and to give its offspring a certain amount of protection (e.g. nesting in colonies). Raising the eggs above-ground and orienting them vertically with their pointed ends down optimised the microclimate and exposed a larger eggshell area with pores for perfect development of the embryos by reducing temperature fluctuation and enhancing airflow. The raised nest might also have protected the eggs from flooding. Accumulation of soil into a circular embankment was probably accomplished by the *Troodon* pushing up sediment with its feet, hands and snout. To achieve the round shape the dinosaur must have moved clockwise or counterclockwise around the centre of the nest. The rim was then patted down to make it firmer. It probably cemented shortly after construction. The offspring were contained inside a manageable space when very young. Nesting behaviour evolved from simple pits in the ground to raised platforms, perhaps even cushioned with plant matter (cf. Martin, 2014, pp. 100–109).

3. Ethological categories

In this section, we list the currently recognised ethological categories in alphabetical order with recommendations on their use. We propose to employ several of the less cited ones as subcategories of already existing groups or groups describing a higher-level behaviour to keep the overall number small. This is in accordance with Frey and Pemberton (1985), who noted that the ethological classification is intentionally restricted to a small number of categories and that new ones should be added sparingly. Bromley (1996) began the process of condensation by combining all locomotion traces (cursichnia, natichnia and volichnia *sensu stricto*) under the already existing repichnia. Our goal is to strengthen the categories that are useful in ecology and palaeoecology.

The concept of superior and subordinate categories is not new. Early on, Müller (1962) proposed several groups of higher and lower ranked trace fossils to augment Seilacher's (1953a) scheme. For example, his supercategory 'quietichnia' (from Latin *quiēscere*, to rest) comprised Seilacher's cubichnia and domichnia.

However, this early advance was largely ignored by Western scientists.

3.1. Agrichnia – farming traces

Erected by Ekdale, Bromley, and Pemberton (1984), this category consists mostly of burrows built in a highly regular or patterned layout to maximise their inner surface area. Their strict, often handwriting-like symmetry earned them the name graphoglyptids. These burrows usually show true branching and therefore must have been open structures for repeated transit by the tracemaker. Much is still unknown about the function of agrichnia, because these traces mainly occur in deep-sea environments today. Most of our knowledge is based on palaeoichnological studies of turbidites, where these traces are well preserved. Seilacher (1977) suggested two functions for such burrows and regarded the simpler structures (commonly having only few apertures) as traps for migrating meiofauna (for further discussion, see Lehane & Ekdale, 2013) and those having numerous apertures at the seafloor as gardening systems similar to the galleries in which leafcutter ants (e.g. *Atta colombica*) cultivate fungi (Bromley, 1996, p. 5).

Most fossil farming traces were probably irrigated by the tracemakers. Agrichnia are typically produced in deep-sea environments, just below the sediment surface of hemipelagic mud. They are usually preserved in positive hyporelief at the lower surface of sandstones deposited by turbidity currents, which excavate and cast the lower parts of the traces. Burrow morphologies range from branched meanders to spirals or nets.

Boundaries between chemichnia and pascichnia, fodinichnia and probably praedichnia (especially irretichnia) are indistinct, especially in the fossil record. Until Lehane and Ekdale's (2013) work, trapping traces (irretichnia) were included as agrichnia. We agree that trapping prey is clearly a different behaviour than farming. However, modern analogues are poorly understood, making the recognition of trapping traces very difficult at present. We doubt that trapping traces and farming traces will be easy to distinguish in the fossil record. As Bromley (1996, p. 195) noted, 'After all, there is a natural sequence from the trapping of microbes for food, via the culturing of microbes for food, to the culturing of microbes as symbionts.'

3.2. Calichnia – brooding traces

Originally proposed for insect breeding structures by Genise and Bown (1994a), all traces produced for raising and caring of the young by adults of the same species should be incorporated into this category (cf. Bromley, 1996, p. 199; Buatois & Mángano, 2012, p. 24). In Recent examples, these traces may be constructed to achieve several purposes, ranging from pure protection of the offspring to establishing stable microclimates, e.g.
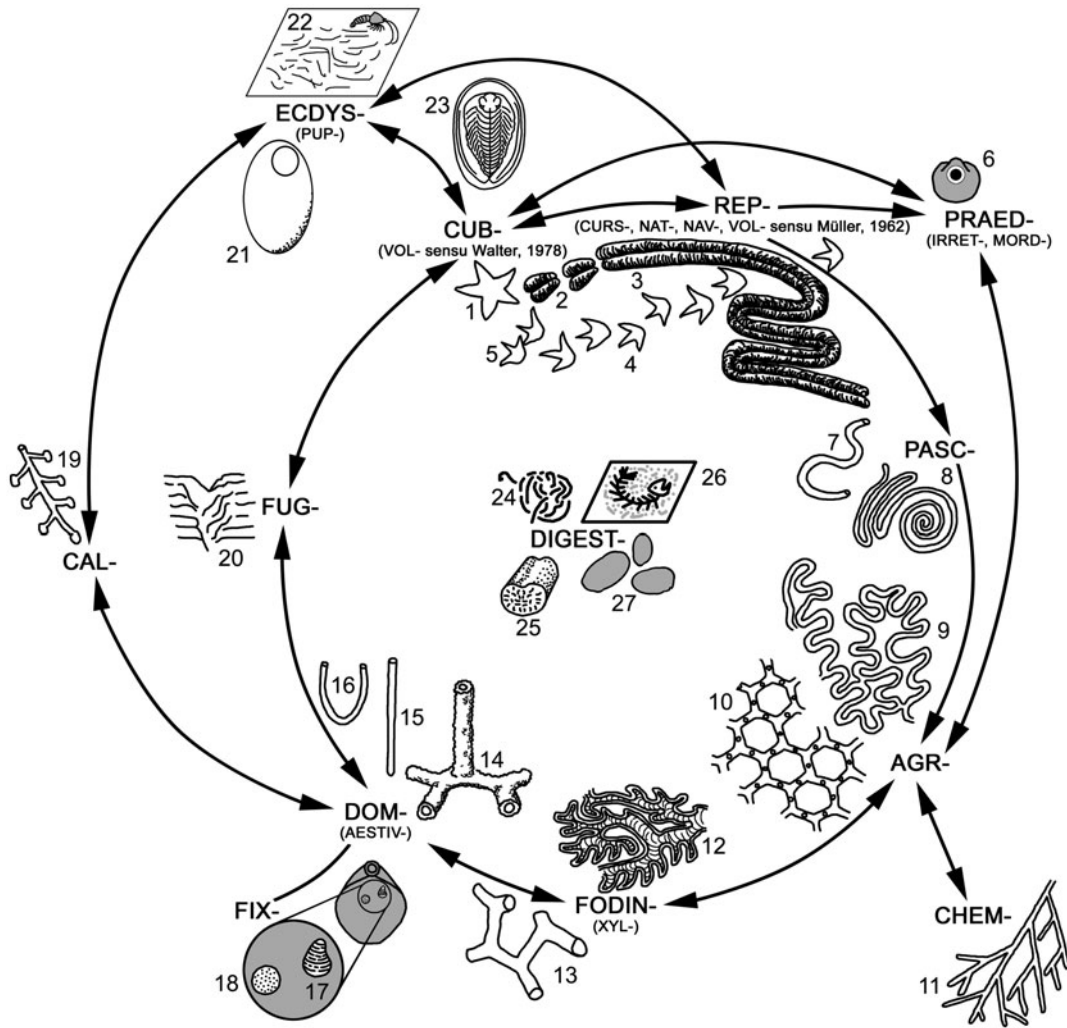
Figure 1. Updated ethological scheme for trace fossils based on the behaviour of their animal tracemakers (modified from Bromley, 1996). The names of the categories are abbreviated (lacking the suffix –*ichnia*), subcategories are mentioned in brackets. Arrows show transitions between ethological categories. Crossovers to digestichnia may occur from any other category; for simplification, these arrows have been omitted. The trace fossils given as examples are as follows: 1: *Asteriacites*; 2: *Rusophycus*; 3: *Cruziana*; 4: bipedal vertebrate trackway; 5: Take-off trace of a bird; 6: *Oichnus*; 7: *Helminthopsis* or *Planolites*; 8: *Helminthoida*; 9: *Cosmorhaphe*; 10: *Paleodictyon*; 11: *Chondrites*; 12: *Phycosiphon*; 13: *Spongeliomorpha* or *Thalassinoides*; 14: *Spongeliomorpha* or *Ophiomorpha*; 15: *Skolithos*; 16: *Arenicolites*; 17: *Centrichnus* on a brachiopod; 18: *Podichnus* on a brachiopod; 19: beetle brooding burrow; 20: escape structure; 21: *Rebuffoichnus*; 22: decapod moulting trace; 23: *Rusophycus morgati*; 24: *Lumbricaria*; 25: *Favreina*; 26: regurgitalite; 27: gastroliths.

constant humidity and temperature (Genise & Bown, 1994a, 1994b; Genise, Mángano, Buatois, Laza, & Verde, 2000). In contrast to Bromley (1996), fossil leaf-mining of insect larvae or bark-mining traces by xylophagous beetle larvae (e.g. Scolytinae) should be placed in the fodinichnia (Müller, 1982, 1989, pp. 688–693). In these cases, only the central gallery needs be regarded as a calichnion, the numerous radiating galleries being fodinichnia because they are produced by the feeding larvae rather than their parents.

Burrows may be simple or complex, commonly consisting of one or more chambers that may be connected to adult-sized tunnels for access, but much smaller exit apertures or tunnels for juveniles may exist. Vertebrate nests may range from shallow pits (e.g. Mueller-Töwe

et al., 2011) to small mounds or tunnels (Martin, 2014; pp. 97–98) or typical 'birds' nests' built of twigs (cf. Lehmann, 2005). Calichnia are usually preserved in full relief.

Notably, structures built by social insects also serve other purposes such as dwelling (domichnia), ventilation or farming (agrichnia), and transitions to the respective ethological categories exist. Additional transitions may occur to ecdysichnia (pupichnia, see Vallon, Schweigert, Bromley, Röper, & Ebert, in press).

3.3. Chemichnia – chemosymbiotic traces

Bromley (1996) proposed **chemichnia** for traces left by tracemakers that live in symbiosis with chemoautotrophic

bacteria. This category might be much larger than previously assumed, judging from the high diversity of Recent tracemakers living in this way. Burrow morphology is similarly diverse, because in order to make use of redox differences between oxic and reducing tiers, the tracemaker's and internal symbionts' needs must both be fullfilled. In general, the makers of chemichnia stay connected to oxygenated water through apertures at the sediment surface, but also penetrate anoxic sediments sufficiently to mine sulphide- or ammonium-rich porewaters that are required for microbial respiration (e.g. in *Chondrites*, *Solemyatuba*, *Trichichnus*). Some tracemakers simply commute between the oxic surface sediment and the anoxic tier below (Ott, 1993), whereas others construct deep mines to pump up H_2S-rich pore water (Kędzierski, Uchman, Sawlowicz, & Briguglio, 2014; Seilacher, 1990). Sulphide oxidation by various sulphur bacteria may produce framboidal aggregates of pyrite within the trace fossils (Jørgensen & Gallardo, 1999; Jørgensen & Nelson, 2004), e.g. in *Trichichnus* (Kędzierski et al., 2014). A halo of lighter coloured surrounding sediment may also be present, and its formation being linked to oxidation of pyrite or iron monoxides during diagenesis (Kędzierski et al., 2014).

Many bivalves living in symbiosis with sulphur-oxidising bacteria produce essentially Y-shaped burrows (e.g. Lucinidae, Thyasiridae and Solemyidae; Seilacher, 1990, 2007). The bivalves live in the upper, more or less U- to V-shaped part of the burrow. The vertical shaft usually reaches far down to the anoxic layers of the sediment from which H_2S-rich pore water is pumped up and made available for the bivalve's symbionts. These deep shafts may have multiple branches and are highly patterned. Here, many suspected chemichnia show pronounced distancing between branches, the diametre of each burrow is fairly constant and the burrows are phobotactic (Fu, 1991; Seilacher, 1990, 2007). In principle, no newly produced burrow element should crosscut an older part or a neighbouring burrow of the same ichnotaxon. The regular branching pattern optimises both surface area and influx of H_2S-rich porewaters (Fu, 1991). Some chemichnia are backfilled with sediment differing from the surrounding sediment (mainly in colour owing to different content of organic matter).

Chemosymbiosis may well be active in other types of burrows. Therefore, transitions to other behavioural groups exist, especially to agrichnia, but also to fodinichnia (especially in the fossil record where the tracemaker usually cannot be named and symbiosis with chemoautotrophs remains speculative).

3.4. Cubichnia – resting traces (including volichnia sensu Walter, 1978)

Resting traces, one of the original five categories defined by Seilacher (1953a), include traces that are created during short-term stationary behaviour. This may be resting, hiding, respiration, rehydration, hibernation, etc. but also feeding (marking the transition to praedichnia) as done by some predators, e.g. asterozoans (producing *Asteriacites*). More often, however, than surface traces, cubichnia are produced endogenically by animals that live within a superficial sand layer, e.g. many bivalves (producing e.g. *Lockeia*). The trace is created when they dig down to establish themselves by disturbing the top of the underlying substrate (e.g. Bromley, 1996; Seilacher, 1953b). In hardgrounds, limpets and sea urchins may create resting traces by boring shallow pits (Bromley, 1970; Mikuláš, 1992).

Lessertisseur (1956) distinguished informally between resting and hiding traces. In the second group, the tracemakers would usually be concealed by a thin layer of sediment. Distinction between these, however, is difficult in the fossil record.

Walter (1978) redefined the volichnia as landing and take-off traces of flying or leaping organisms. Although intended as locomotion traces by Müller (1962, see also repichnia), Walter's category fits best within the cubichnia (see also Buatois & Mángano, 2012, p. 20). Volichnia (sensu Walter, 1978) should only be used exceptionally for genuine touching-down and lifting-off traces (surface disturbances) of swimming or flying tracemakers (e.g. *Tonganoxichnus*). To be recognisable as such, volichnia should ideally be combined with an abruptly starting or ending repichnion (Martin, 2013, p. 470).

Cubichnia (s. l.) are trough-like depressions, shallower than they are broad, typically preserved as positive hypichnia, but with negative epichnia occurring as well. No lining or other reinforcement is usually present because the surrounding sediment is supported by the tracemaker's body, except perhaps around the respiratory organs to maintain an unimpeded water flow (Rindsberg, 2012). They are produced by vagile animals digging or boring into the substrate and lingering there temporarily. When the structures are abandoned, the maker may create an exit trace. Resting traces reflect to some extent the outline and ventral morphology of their makers. Together with the retained impressions of digging by appendages such as feet, fins, claws and podia, this fact provides clues to the identity of the tracemaker (i.e. bioprint). Thus, they are the trace fossil group in which a tracemaker assignment has the highest probability of success. Vertical and horizontal repetition or overlapping is common in this ethological category. Transitions exist to repichnia, fugichnia, equilibrichnia, ecdysichnia and praedichnia.

3.5. Digestichnia – digestion traces

Digestichnia (Vallon, 2012) include all traces that are made by digestive processes. Behavioural modifications made to material that has been acted on within the digestive tract of the tracemaker, leaving orally or anally or even being retained as gut contents, are regarded as digestion traces. In contrast to the term *bromalite*

(fossilised remains of digested material; Hunt, 1992, p. 221), *digestichnion* is an ethological rather than descriptive term; compare the usage of *coprolite*. Coprolites are the most common examples, but regurgitalites, cololites and gastroliths also belong to the digestion traces. The category was originally defined by Vialov (1972) but was little used before its revival by Vallon (2012) (Table 1).

Identifiable coprolites usually have a distinct shape. Examples and methodology were presented by Häntzschel, El-Baz, and Amstutz (1968). Coprolites commonly consist of a faecal groundmass that may be phosphatic, calcitic, purely organic or a mix of these types. Remains of body fossils may be present (e.g. Vallon, 2012).

Regurgitalites are mainly produced by vertebrates (especially reptiles, birds and some fish); some molluscs (e.g. cephalopods, suspension-feeding bivalves and gastropods) also regurgitate indigestible matter. These resemble coprolites to some extent, but lack a faecal groundmass and therefore only consist of remains of hard body parts of the tracemaker's prey or incidentally ingested sediment particles. Some avian regurgitalites (e.g. of hawks and owls) are moulded into a form that may itself be recognised as a trace of activity (Elbroch & Marks, 2001, pp. 167–186). Hard parts may show fractures from biting and chewing and/or etching, and dissolution features caused by stomach acids and enzymes (e.g. Vallon, 2012).

Fossilised faecal matter that has not been discarded from the intestinal tract, yet has been named cololite (or more correct, but rarely used *cololith*; Agassiz, 1833, p. 676). The term is not only used for faeces-filled intestines that are preserved within a body cavity, but also for faecal matter in the shape of intestines isolated from a body fossil (in contrast to coprolite). At least, one example of a cololite has been formally named (*Ambergrisichnus* Monaco et al., 2014).

Wings (2004, 2007) divided gastroliths into 'bio-gastroliths', 'patho-gastroliths' and 'geo-gastroliths'. Biogastroliths are concretions produced prior to moulting in some crustacean species to store calcium (Vallon, 2012) and so are not regarded as trace fossils. Pathogastroliths ('bezoars') are mainly generated in the stomachs of herbivorous mammals and are agglomerations of swallowed and felted hair or plant fibres. Geogastroliths are deliberately or accidentally swallowed pebbles and sand. These rocks are not traces, but the modifications of their surfaces by stomach processes are (Bertling et al., 2006; Vallon, 2012). Because gastroliths stay within the stomach for a relatively long time, they typically show abrasion and etching of the surfaces in the form of sub-parallel grooves, resulting from muscle contractions and other stones contained in the stomach (Schmeisser & Flood, 2008). Polishing, however, does not take place (Wings, 2004).

Defaecation and regurgitation may happen in conjunction with all kinds of behaviours, so transitions to each of the other ethological categories may occur. Digestichnia (except on geogastroliths) are preserved as full reliefs and often contain remains of body fossils (hard parts of the prey).

3.6. Domichnia – dwelling traces (including aestivichnia)

Domichnia consist of open burrows, borings, simple hollows or cavities occupied by the tracemaker and created as permanent or semi-permanent domiciles (Bromley, 1996; Seilacher, 1953a). The structures protect not only from competitors and predators, but also from temporary changes in the local environment (Rindsberg, 2012). Forms range from simple, shallow pits (e.g. *Bergaueria*) or vertical tubes (e.g. *Skolithos*) via J-, U- or Y-shaped burrows (e.g. *Arenicolites*, *Diplocraterion*) to complexly branched traces (e.g. *Thalassinoides*). A spreite may be present. Most domichnia are vertical to oblique, but the more complex structures are dominated by horizontal elements having only a few shafts connecting several tiers of the burrow with one another or the sediment surface. Open burrows in firmgrounds or borings in hard substrates typically need little reinforcement, but the walls may be sculpted with bioglyphs reflecting the tracemaker's appendages or its method of excavating (e.g. *Entobia*, *Spongeliomorpha*). Other interior surfaces may be smoothly finished or perhaps lined to limit influx of pore water from the surrounding substrate (e.g. some *Gastrochaenolites* in porous corals, LHV observation; Aller, 1983). Walls of burrows in substrates that collapse easily are commonly lined (e.g. *Ophiomorpha*) to ensure stability, to fend off other burrowers or to control pore water flow. After abandonment, domichnia within soft substrates typically collapse or are passively filled with sediment; alternatively, unused elements of burrow systems may be backfilled.

The tracemakers need to possess special adaptations in order to excavate, irrigate and maintain an open burrow. This topic is dealt with in an extensive literature (for further reading see, e.g. Bromley, 1996; Buatois & Mángano, 2012). The producers of domichnia may be sessile suspension feeders (marking the transition to fixichnia), active carnivores waiting in ambush for their prey or detritivores. The trace fossil, however, emphasises the stationary dwelling function and not the trophic group (in contrast to Recent ethological studies). Specialisation exists in different burrows. Burrows with more than one aperture (e.g. U tubes) often improve the oxygen and nutrient flow for the inhabitant. If the tracemaker does not actively irrigate its burrow by movement of its gills or other appendages, then other burrow modifications are often present (Bromley, 1996). In such cases, one aperture may be raised higher above the sediment surface than the other, which causes a difference in current velocity generating a constant passive flow through the burrow (Vogel, 1978). Different angles at junctions help to irrigate complex burrows. Currents are also produced

by the tracemaker moving within the burrow, pushing air or water in front of it. This pressure wave is easier divided at junctions having 120° angles resulting in an even distribution of oxygen-rich fluids within the burrow (cf. Vallon & Kjeldahl-Vallon, 2011).

Another specialisation, preserved especially in palaeosols, was described by Verde, Ubilla, Jiménez, and Genise (2007). Spherical chambers having a lined wall of imbricated pellets and a filling of rounded to meniscate pellets arranged in winding strings were convincingly interpreted as aestivation chambers of earthworms. Verde et al. (2007) grouped these chambers with other aestivation burrows of amphibians (Hembree, Hasiotis, & Martin, 2005) and lungfish (Voorhies, 1975) and recommended either the establishment of a new ethological category (aestivichnia) or incorporation within the domichnia. We prefer to maintain the aestivichnia as a subcategory of domichnia because the tracemakers construct these structures for protection against temporary worsening of local environmental conditions (cf. Rindsberg, 2012, p. 55).

Some domichnial burrows may be inhabited by several individuals, not necessarily belonging to the same species (e.g. callianassid shrimps and innkeeper worms *Urechis caupo*; Bromley, 1996; Fisher & MacGinitie, 1928). Because they are subsurface structures created sometimes at considerable depths below the sediment-water or sediment-air interface, they have a high preservational potential. But they also may be inhabited for very long periods, sometimes even several generations. Owing to this fact, the morphology of domichnia may vary during ontogeny of the tracemaker (Frey & Seilacher, 1980; table 2). Burrows of the fiddler crab *Uca pugnax* are initially constructed as a simple shaft and only later expanded to a U-shaped burrow (Basan & Frey, 1977). Other examples of burrow morphologies changing with time include increasing size of bioglyphs and burrow or boring diameter (Bromley, 1970, 1996), adding segments to a burrow system, and filling or closing off segments (Schäfer, 1972). Further modifications of domichnial morphology include reinforcement of the burrow's lining that also might be opened for expansion, repair, etc. Careful observation of these parts is vital in order to answer Tinbergen's third question.

Several possibilities obtain where a spreite is present. Either sediment feeding is involved (marking a transition to fodinichnia), the tracemaker has adjusted its relative position to the sediment surface during erosion or sedimentation events (equilibrated domichnia) or enlargement of the burrow was needed with the growth of the tracemaker (e.g. in U tubes). Similarities exist with fixichnia, especially in bioerosional domichnia.

3.7. *Ecdysichnia – moulting traces (including pupichnia)*

Abel (1935, pp. 280–287) had already defined a category for all kinds of moulting. He saw traces of moulting

behaviour (ecdysis) in the exuviae of arthropods, shed feathers, hatched eggs or cocoons, etc. As in the case of digestichnia, it must be emphasised that ecdysichnia consist of evidence of *behaviour*, not merely the exuviae or other body remains. Especially in arthropods, which apart from 'worms' are the most common tracemakers, ecdysis must be done on a regular basis to allow for growth. Vallon et al. (in press) have revived Abel's idea, redefining the category of moulting traces and giving it the formal name ecdysichnia. Included are all traces left in or on any substrate by animals that are connected with moulting. This may include pupation (see Genise, Melchor, Bellosi, González, & Krause, 2007 for the recognition of these traces), ecdysis in arthropods or shedding of the skin (e.g. a deer rubbing his newly grown antlers on a tree trunk creating scratches in the bark). However, in the fossil record, probably only insect pupation and arthropod ecdysis will be commonly preserved or recognisable (Vallon et al., in press). A few detailed observations of fossil moulting traces exist (e.g. Bishop, 1986; Brandt, 2002; Seilacher, 2007; Tetlie, Brandt, & Briggs, 2008; Vallon et al., in press). Trilobites pressed themselves into sticky mud to fix their old cuticula in one position, thus easing their exit (Seilacher, 2007). Modern decapods tend to toss and turn to rid themselves of old cuticulae during ecdysis (Vallon et al., in press). In contrast to trilobites, moulting traces of modern arthropods tend to be more complex and exhibit a greater variety of movements, making it difficult to erect ichnotaxa for these structures.

Pupation chambers were summarised as pupichnia by Genise et al. (2007), who showed how these structures could be distinguished from similar calichnia. This behaviour only applies to a small number of insects, because pupation in cocoons, chrysalides or puparia is much more common. Since pupation is a special case of ecdysis (Abel, 1935), the pupichnia are best included as a subcategory of the ecdysichnia.

Moulting traces can either be superficial disturbances of the substrate, transitional to cubichnia, or burrow-like subsurface structures (e.g. pupichnia). When produced by arthropods, transitions may exist to other ethological categories. A fugichnion connected to an exuvia was reported by Schweigert and Frattigiani (2004), but transitions to repichnia and cubichnia will probably turn out to be more common.

3.8. *Fixichnia – attachment traces*

Fixichnia (de Gibert, Domènech, & Martinell, 2004) represent a special behaviour on hard substrates. These attachment traces bind the epilithic tracemaker at an early ontogenetic stage to a fixed anchor point where they live for the rest of their lives. Therefore, the produced structures are closely related behaviourally to the domichnia (Bromley, 1992; Ekdale et al., 1984; Martinell, 1989). Many makers of domichnia apart from bioeroders, however, can leave their dwelling structures

and produce a new structure somewhere else. Thus, fixichnial morphology is completely different from domichnial morphology, and very special adaptations are necessary to produce these traces. In most attachment traces, the substrate is mechanically or chemically roughened so the tracemaker has a better grip on the surface. Anchoring is achieved by soft or hard body parts (exoskeleton). They are usually surface structures, preserved as shallow negative epichnia. Morphologies range from concentric furrows (*Centrichnus*) via radially arranged tiny pits (*Podichnus*) to kidney-shaped (*Renichnus*), star-shaped (*Stellichnus*) or serpentiform furrows (made by Recent polychaetes on pebble surfaces; LHV observation).

3.9. Fodinichnia – feeding traces (including xylichnia)

Seilacher (1953a) incorporated within this category mainly burrows (and subsequently borings) that are constructed by deposit-feeders while ingesting the substrate. Usually, a dwelling structure that is left open during the lifetime of the tracemaker is combined with a far more extensive feeding structure that may be open or progressively filled (spreite). Burrows may be simple (*Planolites*, *Scoyenia*, *Taenidium*), branched (some *Arthrophycus*), U-shaped (*Rhizocorallium*), radial (*Dactyloidites, Gyrophyllites*) or complex (*Treptichnus*) with various orientations. A spreite originates by shifting the open part of the burrow (lumen) to one side while depositing the excavated material on the other after extracting its nutrition. The traces are most commonly preserved as full-relief endichnia.

Close relations exist with domichnia and pascichnia as well as agrichnia. Depending on preservation and interpretation, these structures are sometimes difficult to place into only one of the mentioned categories.

Kelly and Bromley (1984), Genise (1995) and Bertling et al. (2006) amongst others regarded substrate selection as an important ichnotaxobase. Thus, Genise (1995) introduced xylichnia for wood borings (e.g. *Teredolites*) as a subcategory of fodinichnia. We agree with this placement because substrate feeding has to be regarded as a more important behaviour than the selection of any particular substrate.

3.10. Fugichnia – escape traces

Escape structures are produced by tracemakers that have been buried by sudden sediment accumulations (Frey, 1973, p. 14). They are temporary structures, producing only disturbed sedimentary lamination and therefore are not originally open or reinforced, but instead show undefined boundaries. Owing to the panic reactions of the tracemakers during sudden burial, the traces usually are vertical to oblique and show vertical repetition. In case of originally simple domichnia like *Skolithos* or *Diplocraterion*, cone-in-cone or U-in-U structures are

produced, respectively (Buatois & Mángano, 2012). In addition to these vertical escape traces, a few horizontal examples have been documented from Recent studies where the tracemakers were trying to escape infaunal predators (Behrends & Michaelis, 1977; Bromley, 1996). In the fossil record, these will not be recognisable, so we restrict fugichnia to traces produced during escape from burial, as Frey (1973) originally intended. Fugichnia are generally preserved as full-relief endichnia.

Transitions may exist with ecdysichnia (Vallon et al., in press) and repichnia. The category 'taphichnia' (Pemberton, MacEachern, & Frey, 1992) was defined as traces of unsuccessful attempts to escape burial. We regard this category as an unnecessary subset of fugichnia, because the reactive behaviour reflected by taphichnia is the same as in fugichnia. Whether the attempted escape from being buried alive is successful is irrelevant, as escape traces are produced in either case. Additionally, the recognition of taphichnia depends in practice on the tracemaker having hard parts. Soft-bodied tracemakers are not ordinarily preserved, and in such cases, the trace will look like a 'lucky-escape' fugichnion, when in fact it was a tragedy.

3.11. Pascichnia – grazing traces

The combination of locomotion and feeding is mostly expressed as spiral or meandering trails. This movement allows the tracemaker to efficiently exploit a particular area of a substrate for food. Defined by Seilacher (1953a) as surface to near-surface traces, most of his original and subsequent examples, have since been proved to be subsurface structures produced by epifaunal detritus- or infaunal deposit-feeders, respectively (Rindsberg, 2012); accordingly, the term is redefined here to fit usage during the past sixty years. Modern ecologists distinguish surface and subsurface feeding (e.g. Lopez & Levinton, 1987) because specific life strategies and adaptions are required for each feeding method. In the fossil record, this differentiation is hardly achievable because surface traces have such a low preservation potential compared to subsurface traces. Here again, we must ask in Tinbergen's spirit: What was the function of the traces? Because the overall morphology of the traces is similar despite their different position with regard to the substrate surface, and all were made in pursuit of surficial or near-surficial detritus, distinction between surface and shallow subsurface traces seems unnecessary and artificial. If the distinction would be meaningless to the organisms that made the traces, then why should ichnologists insist on it?

Traces are usually preserved in positive hyporelief, less commonly in negative epirelief. The usually meandering (*Nereites*) or spiral (*Spirorhaphe*) course of many such traces points to the exploitation of a food source. Pascichnia are generally horizontal and constructed parallel to the sea floor. They are unbranched and constructed more regularly than repichnia. Simpler

forms (curved to looped structures) may cross each other, but traces with a strict pattern and more complex morphologies (spirals and meanders) do usually not. The latter pascichnia include guided meanders in which the boundary of the newer part of the constructed trace touches the previously produced part (thigmotaxis). In most cases, pascichnia are continuous trails, though tracemakers that can lift their feeding organ or entire body off the substrate may produce discontinuous feeding traces. The above-mentioned examples are subsurface grazing traces. Genuinely surficial pascichnia are rare in the fossil record, and few have been named. The clearest examples are bioerosional grazing traces such as *Radulichnus* and *Gnathichnus*.

Müller (1982, 1989) classified and characterised several insect and insect larval feeding traces in leaves, below the bark or within the wood and placed them within the fodinichnia. We agree with this placement, because their food source is exploited systematically in highly patterned forms and the resulting traces are parallel to the substrate surface.

Boundaries between repichnia (in genuine surface traces), fodinichnia (in subsurface traces) and agrichnia (in very regular examples) may be hard to draw in specific cases.

3.12. *Praedichnia – predation traces (including mordichnia and irretichnia)*

Traces of predation (Ekdale, 1985, p. 67) show interactions between a predator and its prey. Often the hard body parts of the prey carry the traces of predation, such as round drillholes (*Oichnus*) and chipped margins in shells or gnawing and biting traces on bones (named 'mordichnia' by Müller, 1962). Most praedichnia are therefore bioerosional structures (Bromley, 1981, 1993). Soft-substrate predation causing only indistinct sedimentary disturbances might not be recognised as praedichnia, but rather be interpreted as endogenic repichnia or fugichnia. A few examples from soft substrates have been documented, e.g. trilobites preying on 'worms' (e.g. Bergström, 1973; Jensen, 1990) and fish preying on unidentified invertebrates (*Osculichnus* Demircan & Uchman, 2010).

It can be problematic to distinguish whether gnawing and scratching traces on bones were produced during a predator's attack or long after the death of the prey. We have therefore included traces resulting from scavenging within praedichnia despite the fact that ecologists draw a distinction between scavenging and predatory behaviours.

Most predation traces are preserved in negative epirelief, but positive hyporelief may occur. Transitions exist towards repichnia for both predators and prey. Prey can be attacked by predators while occupied in all kinds of behaviours, so all traces of other categories may abruptly end in a praedichnion. As for traces left by the predators, they might be mistaken as repichnia or cubichnia.

Concerning irretichnia, we agree with Lehane and Ekdale (2013) that trapping prey and farming are distinct behaviours that should not in principle be combined under the category agrichnia. In contrast to regular preying, trapping involves the use of external resources, such as pitfalls or sticky substrates. However, only a tiny fraction of trapping traces can be recognised in the fossil record, and, more to the point, we should ask *why* the organism made the trace. Because ultimately the function of the trace was predation, we recognise irretichnia as a subcategory of praedichnia. Morphologies therefore comprise conical depressions in loose sediment, open pits and physical snares produced of a sticky substrate such as silk in spider webs. Single traces usually are very regularly spaced with no overlapping.

While regarding irretichnia as a subcategory of praedichnia, we recognise that the complex irretichnia seen in deep-sea environments may be extraordinarily difficult to interpret as such and may easily be confused with agrichnia.

3.13. *Repichnia – locomotion traces (including natichnia, navichnia, cursichnia and volichnia sensu Müller, 1962)*

Seilacher (1953a) introduced this category for 'crawling' traces. However, repichnia are understood in a broader sense today and comprise all traces produced during locomotion (Bromley, 1996). They are generally simple and shallow and can be either continuous or interrupted. However, they mainly reflect directed locomotion and are not visibly combined with other behaviour (in contrast e.g. to pascichnia). Locomotion traces follow bedding planes and are mainly preserved as positive hypichnia or negative epichnia.

Continuous disturbances of sediment with more or less parallel sides are called trails (='repichnia' sensu Seilacher, 1953a; sensu Müller, 1962) and are made by tracemakers without appendages. They may be simple (e.g. *Mermia*), bilobate in cross section (e.g. some *Cruziana*) or show a chevron-like morphology (e.g. some *Protovirgularia*); rarely, they may be meniscate or annulate. Trackways are made up of repeated sets of discontinuous impressions reflecting the tracemakers' appendages and their motion within the substrate (= the unfortunately named, at least for the English-speaking audience, 'cursichnia' Müller, 1962; e.g. vertebrate trackway *Chirotherium,* arthropod trackway *Diplichnites*). Repichnia produced by evolutionarily transitional animals with reduced limbs (e.g. some anguid lizards) have not been named separately.

Natichnia (Müller, 1962, 1989) are produced by tracemakers swimming close to the sediment surface (e.g. *Undichna*) or hovering just above it. Swimming traces were included as repichnia by Bromley (1990, 1996). Diffuse bioturbation of tracemakers swimming through a soupground ('navichnia' of Gingras, Bann, MacEachern, Waldron, & Pemberton, 2007) should

therefore be included in the repichnia as well (cf. Wetzel & Uchman, 1998).

Müller (1962) included natichnia, cursichnia and repichnia as well as volichnia (sensu Müller, 1962) within his movichnia or movement traces. Only very few volichnia (sensu Müller, 1962) where the tracemakers' wings made impressions while flying just above the ground are documented, despite being fairly common in the Recent (Martin, 2013, pp. 468–470). In essence, we have reconstructed Müller's movichnia but called it by the more familiar term repichnia. Although his system received wide attention as a figure reprinted by Osgood (1970) and Häntzschel (1975, figure 10), Müller's original work, published in the German Democratic Republic, remained unread by most ichnologists outside Germany.

Most transitions from repichnia are to cubichnia and when feeding is involved also to pascichnia. Rarely, they can end in praedichnia or ecdysichnia.

4.   Categories not recommended for use

The behaviours included in the following categories are not regarded as sufficiently distinctive to require their own categories, are redundant in other ways or were excluded from trace fossils by Bertling et al. (2006).

- **Aedificichnia**, introduced by Bown and Ratcliffe (1988) for above-ground structures. This is an unnecessary category because such structures may serve diverse purposes such as extension of skeletons, ventilation, protection or, in the case of mud-dauber wasps, nesting. These structures are better grouped in other categories according to the dominant purpose for which these structures were built. Other traces that were subsequently classed as aedificichnia, such as caddisfly larval tubes (Donovan, 1994) and sand 'reefs' constructed by sabellariid polychaetes (Ekdale & Lewis, 1993) fit well into domichnia because they can be considered as isolated burrow linings. In spider webs, we see, contrary to Donovan (1994), praedichnia (irretichnia; cf. Lehane & Ekdale, 2013).
- **Equilibrichna** are burrows of all kinds that have to be vertically moved by the tracemakers (Frey & Pemberton, 1985) in order to re-establish the necessary functions of the burrow (e.g. ventilation) despite sediment accumulation or erosion. Shifting of the burrow results in a spreite. In case of sediment erosion, a protrusive spreite is produced and when sediment is accumulated a retrusive one. As in fugichnia, the tracemaker may have to adjust because of burial, but in this case has more time to shift the depth of its burrow; and equilibrichnia also include adjustments to the more or less continuous changes in sediment surface level. The resulting traces therefore have clear boundaries, unlike fugichnia. When sediment accumulation is fast, however, the transition to fugichnia is smooth

and the traces become less distinct.

Many animals were evidently unable to equilibrate and produced no spreite, e.g. the tracemakers of *Arthraria* in contrast to *Diplocraterion*. Thus, perhaps other ichnospecies of *Diplocraterion* than *D. yoyo* could be considered as equilibration traces.

Bromley (1996) agreed that equilibrichnia constitutes a distinct category of behaviour. The relatively high number of publications using the term (Table 1) probably reflects the ease of recognition of such traces, and their utility in deducing ancient conditions of sedimentation. However, in keeping with our Tinbergen-inspired questions, we must ask why the tracemaker established the trace to begin with, and the answer is clearly not adjustment to persistent erosion or deposition, but dwelling, or in some cases feeding. *Equilibrated domichnia* or *equilibrated fodinichnia* (e.g. *Rosselia socialis*; Nara, 2002), respectively, would serve as better terms for these structures. The category does usefully respond to Tinbergen's second and third questions, i.e. about control of external factors and ontogenetic changes. Thus, the term equilibrichnia should only be used with equivocation! If a bivalve resting in its *Lockeia* is buried, then it might create an indistinct fugichnion atop its cubichnion. But if it responds in a more deliberate fashion, then it creates an extended *Lockeia* (equilibrated cubichnion). The equilibration trace would be created using the same muscular actions that made the original *Lockeia*.

- **Impedichnia** (Tapanila, 2005) was introduced as category for 'symbiotic' bioclaustration, with symbiosis being used in its broad sense to include antagonistic as well as mutually beneficial interactions. This category is at first glance very closely related to domichnia, especially resembling the ones produced by bioeroders. However, neither the host nor the infesting organism actively manipulates the substrate, in contrast to bioeroders. Cases where the embedded organism uses chemicals, appendages etc. locally to prevent tissue growth of the surrounding host organism could be viewed as a special type of bioerosion. Embedment structures, whether produced by a symbiont, commensal or parasite, or to accommodate one, were excluded by Bertling et al. (2006) from trace fossils along with plant reaction tissues (e.g. plant galls induced by wasps) and skin infections or rashes caused by micro-organisms. We therefore do not recommend the use of impedichnia, though we recognise the need for nonichnologic names to accommodate these structures. We recommend that the term impedichnia be replaced by *impeditaxa*, a neutral term specifically for bioclaustrating *taxa* that would encourage research while not including –*ichnia*. Similarly, cecidoichnia (Mikuláš, 1999), a term for

plant reaction tissues, can be replaced by the neutral *cecidotaxa*.

- **Mortichnia** was proposed for traces left by death struggles in the Lithographic Limestones of Solnhofen (Upper Jurassic, southern Germany) by Seilacher (2007, p. 212) (previously called taphoglyphs; Sarjeant, 1975, p. 319; not to be confused with taphichnia). Any tracemaker can be stricken by a sudden death threat, e.g. predation by other animals, exposure to hostile living conditions, disease, etc., although the fossil record will probably yield few traces that are recognisable as mortichnia. This category is to some extent more interpretive than others whose ethology can be directly read from morphological evidence. Seilacher based this new category on holistic interpretation rather than on trace fossil morphology. Vallon et al. (in press) showed that many Solnhofen mortichnia are not 'death marches', because the body fossils at the end of the trackways commonly are exuviae rather than corpses. Genuine mortichnia are rare (e.g. *Telsonichnus* and the spiral or looped trails produced by *Solemya* from the Lithographic Limestones of Solnhofen).

  Without the terminal corpses (owing to incomplete preservation), mortichnia, like taphichnia, are not recognisable. We therefore do not recommend the use of this category.

- **Polychresichnia** (Hasiotis, 2003) encompass structures made by social insects. These complex and frequently large structures are multifunctional, representing different kinds of behaviour simultaneously. We agree with Buatois and Mángano (2012, p. 18) that a discrete ethological category for such multipurpose traces is redundant. Most trace fossils reflect more than one activity or behaviour, and as pointed out in the discussion below and already indicated in the above characterisations of categories, transitions between or overlapping of categories are rather the rule than the exception. Probably most specimens ascribed to polychresichnia could be accommodated at least in part within the calichnia.

5. The diagram

Each category of behaviour ideally results in a trace of a characteristic general morphology (Frey & Seilacher, 1980). In principle, each ichnogenus should fit into a single ethological category, and researchers have in fact occasionally classified ichnogenera within ethological categories (e.g. Rindsberg, 1994). However, the real world is messy, and most organisms perform more than one kind of behaviour; indeed, most change their activity regularly during their lifespan. We have already pointed out intimate relationships between deposit-feeding and dwelling in fodinichnia, and between detritus-feeding and locomotion in pascichnia. Grazing trails may

incorporate occasional resting traces, e.g. echinoid pascichnia *Scolicia prisca* may include cubichnia that have been separately named as *Cardioichnus planus* (Bromley, 1996, p. 179; Smith & Crimes, 1983). The arthropod feeding burrow *Arthrophycus brongniartii* may include cubichnial *Rusophycus* (Rindsberg & Martin, 2003). And *Hillichnus lobosensis* Bromley, Uchman, Gregory, and Martin, 2003, interpreted as the work of a deposit-feeding bivalve, includes a complex mix of behaviours involving locomotion and deposit-feeding. Similarly, some examples of *Thalassinoides suevicus*, a burrow ordinarily interpreted as a crustacean domicile, incorporate palmately branched feeding structures (Miller, 2001). And, as Genise and Bown (1994b) and Hasiotis (2003) have pointed out, the burrows of social insects such as termites may include structures having functions as diverse as dwelling, farming and nesting in addition to others. Although ichnologists have endeavoured as a rule to sort trace fossils into ichnogenera each of which have one dominant behaviour, this is not always possible even in principle, let alone in practice. The gradual development by consensus of a set of morphological groups – ichnofamilies – obviates the need to arrange ichnogenera within ethological categories in a hierarchical ichnotaxonomic system (Rindsberg, 2012).

For pragmatic reasons, in the ethological classification, only the most distinctive behaviour is usually cited for any one ichnogenus. This means that the traces of different behaviours might be connected and/or can form transitions with one another. Thus, a diagram expressing animal behaviour can only show stages during the life cycle according to a single behaviour within a given period of time. In the scheme first presented by Bromley (1996) and emended here (Figure 1), possible transitions between distinct behaviours are indicated by arrows.

According to these possible interactions, the new category digestichnia needs to be placed centrally. Most animals digest their food continuously and also excrete more or less regularly during any kind of behaviour, e.g. the 'faecal ribbons' of *Nereites* and *Scolicia*. Arrows should connect this group with all the others, but for clarity, they are omitted in Figure 1.

The new category ecdysichnia must be placed close to the repichnia and cubichnia. Recent arthropods usually try to find a hidden spot where they can rest without risk of predation until their new carapace has hardened to give them protection. In the described samples, Vallon et al. (in press) showed that repichnia may turn into ecdysichnia and again into repichnia.

The fixichnia are related to just a few categories. This category should be linked at least to the domichnia, because the traces reflect a stationary behaviour similar to dwelling, although the adaptations are different. Feeding traces (fodinichnia) and digesting traces (digestichnia) are usually connected with attaching traces of the organism, but they are not reflected in fixichnia. Because no transitions between fixichnia and other

categories have yet been recorded, we choose to connect the fixichnia only to domichnia.

Compound trace fossils (such as *Hillichnus* Bromley et al., 2003) and complex trace fossils (such as *Zoophycos*) reflect several behaviours, making it impossible to place these complex ichnotaxa into only one category (Miller, 2003, 2003; Pickerill, 1994; Rindsberg, 2012). Moreover, as some researchers have pointed out, complex organism–sediment interactions can even determine the physical properties of the substrate itself (e.g. Bromley, 1996; Miller, 1998). The makers of these traces can be considered in their roles as ecosystem engineers (Jones, Lawton, & Shachak, 1994), or again the traces can be thought of as extended organisms (Miller, 2002; Turner, 2000, 2003, 2004). In such cases, all ethological functions of the trace should be listed and discussed.

6. Conclusions

Since the last generally accepted revision of animal behaviour based on Seilacher's (1953a) ethological categories was made by Bromley in 1996, many new categories have been introduced (Table 1). To keep the number of categories low (cf. Frey & Pemberton, 1985), and following Müller (1962), we suggest the incorporation of some as subcategories within well-established categories that reflect higher-level behaviour. Therefore, we propose with this article a new, updated scheme of animal behaviour (Figure 1). Categories lowered in rank are given in brackets in our diagram. The natichnia for example are placed as a subcategory of repichnia because swimming is a special kind of locomotion (Bromley, 1996, p. 192). Other categories, e.g. the cecidoichnia of Mikuláš (1999), remain controversial (cf. Bertling et al., 2006). We suspect that usage will ultimately determine the fate of some categories (Table 1).

Bromley (1996) arranged all categories established at that time into a flowchart to show transitions between different groups in order to classify and interpret the behaviours of the animals reflected by trace fossils. Transition and close relations among different categories were indicated with arrows. Our current scheme of animal behaviour in substrates (Figure 1) shares these advantages of Bromley's presentation for extending the classification and interpretation of trace fossils in ethological terms.

After more than 60 years, Seilacher's (1953a) ethological classification is still the paradigm in which palaeoichnologists work. The ichnofacies concept was originally developed on the basis of differing proportions of ethological categories within trace fossil assemblages (Seilacher, 1959, 1963, 1964, 1967) and remains focused on the concept of recurrent assemblages of trace fossils (MacEachern et al., 2012). In the past six decades, the classification has become more complex, but with no drastic departure from the standard. Time has shown that these ethological categories are useful for thinking about trace fossils, though there is no need to categorise

everything. What is needed is a clearer connection between biologically inspired ideas (e.g. Tinbergen) and palaeontologically inspired ones (Seilacher).

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