Names for trace fossils: a uniform approach

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The taxonomic treatment of trace fossils needs a uniform approach, independent of the ethologic groups concerned. To this aim, trace fossils are rigorously defined with regard to biological taxa and physical sedimentary structures. Potential ichnotaxobases are evaluated, with morphology resulting as the most important criterion. For trace fossils related to bioerosion and herbivory, substrate plays a key role, as well as composition for coprolites. Size, producer, age, facies and preservation are rejected as ichnotaxobases. Separate names for undertracks and other poorly preserved material should gradually be replaced by ichnotaxa based on well-preserved specimens. Recent traces may be identified using established trace fossil taxa but new names can only be based on fossil material, even if the distinction between recent and fossil may frequently remain arbitrary. It is stressed that ichnotaxa must not be incorporated into biological taxa in systematics. Composite trace fossil structures (complex structures made by the combined activity of two or more species) have no ichnotaxonomic standing but compound traces (complex structures made by one individual tracemaker) may be named separately under certain provisions. The following emendations are proposed to the International Code of Zoological Nomenclature: The term 'work of an animal' should be deleted from the code, and ichnotaxa should be based solely on trace fossils as defined herein.
□ *Ichnotaxa, ichnotaxobases, ichnotaxonomy, nomenclature, trace fossils.*

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Naming the traces of fossil organisms is usually a process foreign to the non-specialist, and all too often is a cause for frustration even amongst specialists. The need to name trace fossils, however, has unambiguously been accepted for decades because these structures provide important information for sedimentology (environment) and palaeontology (producer behaviour, ecosystem evolution, stratigraphy) alike (Seilacher 1953). The current lack of both a thorough basis and a general agreement on principles has resulted in a plethora of poorly understood trace fossil names (ichnotaxa).

This paper aims at presenting a comprehensive and uniform approach to ichnotaxonomy with limited excursions into the fields of trace fossil systematic and nomenclature. Currently, many trace fossils are diagnosed inadequately, either by incorporation of too many different forms, or by using such specific criteria that the ichnotaxon remains monotypic. In addition, the absence of a hierarchy of appropriate ichnotaxobases has caused much confusion. For historic development, the reader is referred to comprehensive reviews by Bromley (1990), Magwood (1992) and Pickerill (1994). We review existing positions, give critical examples and try to offer new solutions.

The current paper is based on the consensus of ichnologists from various subdisciplines. The concepts presented here were developed during two especially tailored Workshops on Ichnotaxonomy, the first being

convened by M. Bertling and R. G. Bromley in Aakirkeby, Bornholm, Denmark in August, 1998, and the second by A. Uchman in Kraków and Tymbark, Poland in September, 2002. During the first meeting, ideas were exchanged and disseminated (e.g. Rindsberg 1999; Bertling 1999), and a lively debate followed on the SKOLITHOS listserver (www.listsrv.rediris.es/archives/skolithos.html). We have received considerable input from colleagues and now feel that most authors of future trace fossil publications will share our consensus.

Definitions

Taxonomy, systematics and nomenclature

Taxonomy is the science of giving the best name available to an object, in other words, of placing it at the currently correct position within a given system. Taxonomy does not relate to the structure of this system, which is handled by the science of systematics. Nor does it comprise the rules for handling names, which rather are the objectives of nomenclature. Differing from the two branches of science previously mentioned, nomenclature is merely a technical set of rules. Increasing knowledge about its objects is irrelevant for this set of rules (and *vice versa*) but in order to be applied properly, its objects must be well defined. Taxonomy and systematics therefore may change considerably through time whereas nomenclature should not. The objects of ichnotaxonomy are trace fossils, a group of biogenic phenomena whose exact demarcations are somewhat blurred in current literature. To unify ichnotaxonomy, it is therefore necessary to define what a trace fossil is.

Trace fossils

A both exact and comprehensive definition of 'trace fossil' was lacking until now, adding to the confused situation of ichnotaxonomy. Previous attempts (Blackwelder 1967; Frey 1973; ICZN 1999: Glossary) to delimit trace fossils were useful and are refined here. Generally, a trace fossil is defined as follows: a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate. This definition tries to equalize the status of trace fossils against the objects of biological nomenclature, which are rigidly defined on a routine basis.

The substrate may be rock, soft to firm sediment, dead organic matter (peat, wood, shell, bone), or (then) living organic tissue. Typical and well-known examples include burrows, tracks and trackways in soft substrates and borings in hard substrates. Burrows and borings in

plants (leaves, wood, etc.) undoubtedly are traces. There is a 'grey zone' of dubious structures, however, that some workers include as trace fossils and others do not (Table 1).

With this definition, the following are excluded from the 'grey zone':

- Skeletal parts of organisms that *may exactly* match the full producer morphology, e.g. the tests of agglutinated foraminifera (with all rhizopodia retracted).
- Secretions without subsequent manipulation by the producer, such as eggs, pearls, larval puparia of flies (Diptera), reproductive cocoons of earthworms and leeches (Clitellata), calculi (e.g. kidney stones) – which must be treated as parts of organisms. Their exact taxonomic treatment may vary between organisms and authors: For example, eggs have been named using a separate system of collective taxa (Hirsch 1994), fully analogous to the palaeobotanical parataxonomy for seeds, pollen, etc., and alternatively have been viewed as true body fossils (e.g. Pickford & Dauphin 1993) taking their place in biological systematics. Calcareous linings in borings may not be treated as parts of organisms if their biologically mediated deposition cannot be demonstrated. This would result in considering them as chemically precipitated cement rather than traces. Where they are of clearly organic origin, however, they are integral parts of the producers (Fig. 1).

Structures consisting of sedimentary particles and an enclosed community of organisms (biodeposition structures such as soil and stromatolites) – which are sedimentological objects, highlighting the point that many trace fossils are biogenic sedimentary structures, but by no means all biogenic sedimentary structures are trace fossils. Nonetheless, soils and stromatolites may contain recognizable trace fossils (burrows or borings); we do not follow Sarjeant (1975) here but instead are in line with Pemberton & Frey (1982).

Table 1. Traces and non-traces in the 'grey zone'.

| Traces	Not traces
Coprolites	Eggs
Gastroliths	Calculi
Regurgitaliths	Pearls
All kinds of nests	Embedment structures
Spider webs	
Woven cocoons	Secreted cocoons
Caddisfly cases	Plant reaction tissues
'Sand reefs'	Soils, stromatolites
Bite and gnaw structures (signs of predation)	Pathological structures (signs of diseases)
Signs of human biology	Signs of human technology
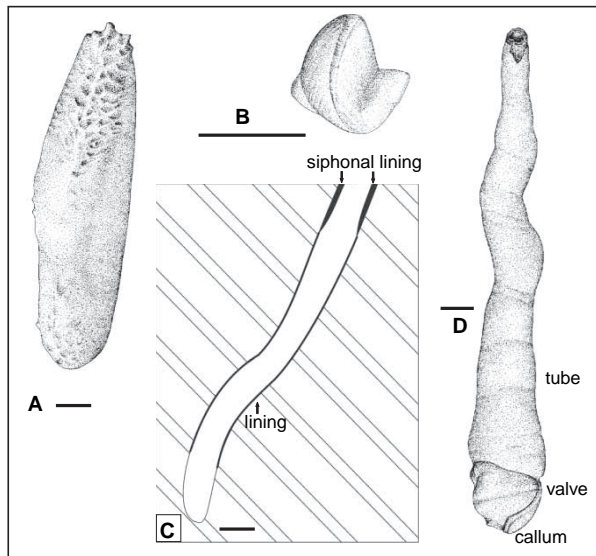
Fig. 1. Calcareous linings in borings and on boring bivalves. □A. Mytilidae: The various subgenera of *Lithophaga* (mostly date mussels) are distinguished based on carbonate deposits on the adult shell (Soot-Ryen 1969), e.g. *Lithophaga (Diberus)* with irregular calcareous deposits on the shell. □B–C. Teredinidae: B. Teredinid valve, note lack of any calcareous deposits. C. Boring of a teredinid bivalve with calcareous linings (schematic). □D. Pholadidae: the Cenozoic wood-boring *Teredina* successively thickens its lined boring until this fuses into a tube with the senile shell (Deshayes 1860); adult *Teredina* has a calcareous tube which envelopes the complete soft body and which is intergrown with much smaller valves; all bivalves oriented anteriorly downward, all scale bars 5 mm.

- Embedment structures in calcareous skeletons that are produced by an actively growing organism around disturbing or irritating objects or living organisms such as, e.g., spionid polychaetes (mud blisters, e.g. Handley & Bergquist 1997). Where two interacting organisms produce embedment structures, their roles have to be discussed in order to avoid misconceptions. The embedding host forms and creates the 'substrate' around the embedded organism, i.e. it varies its shape as a skeletal reaction. Even though one can thus see the relics of a biotic interaction in the fossil record, this does not represent behaviour more than any genetically fixed growth pattern. For the host it does not matter whether the disturbance is caused by an organism or an object; pearls are not trace fossils (see above). Nor are other biotic interactions, e.g. disease and reproduction, to be treated taxonomically. If the host reaction resulting in an embedment structure were considered to be a trace, any variation in growth form of unclear origin could be named, an absurd conclusion. We agree with Goldring *et al.* (1997), who stated that substrate effects during trace construction should not be available as ichnotaxobases.

Embedment structures are distinguished from borings by the intactness of the host skeleton (Pickerill & Donovan 1998); no skeletal particles are crosscut or moved. The embedded organism is not necessarily passive, as it may use certain features (chemical secretions, tentacles, parasitic feeding, etc.) to actively prevent complete overgrowth. Even so, the embedded organism does not actively manipulate the substrate. We therefore reject any ethological category using the suffix –ichnia (see Tapanila 2005).

Another argument against regarding embedment structures as trace fossils is that the boundary between them as so-called bioclaustration (Taylor 1990) *versus* (other) bioimmuration structures is impossible to determine. A living organism overgrowing a living counterpart causes bioclaustration, whereas bioimmuration is defined as the overgrowth of a dead organism (Voigt 1972). Although the distinction can sometimes be made for soft-bodied victims with a discrete body outline, it is not possible to tell whether an exoskeleton, e.g. a shell, still bore its inhabitant at the time of overgrowth. Even if not considered trace fossils, highly characteristic embedment structures of recurrent shape (in this case probably caused by symbionts) may receive names outside ichnotaxonomy. They are not biological taxa, however, because from the biological point of view they represent mere growth variations.

The case is occasionally complicated by a combination of embedment and boring. In the case of a borer, e.g. a bivalve colonizing a living coral, the living coral substrate grows more rapidly than the borer in summer. The bivalve has to shuffle upwards to keep pace with its host coral. In winter, the endozoan may grow more rapidly than the coral. In order to accommodate its increasing size, the bivalve has to bore downwards into the coral. The resulting cavity, after a few alternating seasons, consists partly of boring and partly of embedment structure, forming a compound trace (see below). Structures like these have received their own name in the past (e.g. Edinger & Risk 1994).

- Pathological structures and results of diseases visible in skeletal parts (as opposed to trace fossils resulting from predation such as biting and gnawing punctures and scrapes). Tumorous swellings of bones, caries in teeth, osteoporosis, healed injuries of bones or carbonate skeletons, etc. are more properly considered as subjects of palaeopathology (e.g. Tasnádi-Kubacska 1962; Wells 1964).
- Reaction tissues of plants, e.g. resulting from the puncture by an insect during oviposition. Mikuláš

(1999) established the category cecidoichnia for these structures commonly referred to as galls. This term is ichnologically ambiguous, however, as galls may preserve a trace or not. If they do contain a recognizable trace fossil, e.g. a boring, faecal pellets, a pupal chamber, or an exit hole etc., they may be named as such. The disproportionate development of reaction tissue is no reason to discard galls as traces in principle. Without a recognizable trace contained, they are only reaction tissues of plants, and as such they do not qualify as trace fossils. Rather they consist of an actively growing substrate similar to embedment structures.

As a rough analogy, consider a mosquito boring through a mammal's skin. It produces a trace, but if this results in a swelling this is only a pathological reaction. The swelling is not the trace. Likewise, when a gall maker punctures a leaf, neither the egg deposited nor the plant tissue originating from chemicals secreted by the larva or the plant is a trace. This is independent of the intention of the gall-maker, i.e. whether the gall production occurs accidentally or is fully intended. Swollen tissue and plant reaction tissues may at best be considered 'traces of traces' having an original tracemaker, whose trace (the puncture) is obliterated by the induced plant growth. The same situation prevails with the animal that caused '*Tremichnus*' (Brett 1985) in Palaeozoic crinoids. Some crinoid hosts reacted with deposition of skeletal material around the hole, as a swelling, whereas others did not. The swelling is not a trace fossil, only the actual hole that it surrounds. All these swellings are merely pathological and as such, objects of palaeopathology (see above).

Plant galls consist of nothing but plant tissue should be named within a separate scheme of collective taxa, analogous to the treatment of oötaxa (eggs, etc.) and larvae (see above). Galls nonetheless must not be considered zoological taxa because they are made up of plant tissue; hence they cannot receive the name of the insect responsible.

- Hominid artefacts are excluded because it would be impracticable to claim the trace fossil nature for archaeological objects. This is independent of their age or taphonomic situation. Fossilized signs of hominid biology, however, are included, i.e. footprints and faeces. Non-hominid tools are also included even if their nature is difficult to prove.

Objects such as coprolites (where the modified substrate consists of food), gastroliths (where substrate stones are modified by digestive action and acids) and regurgitaliths (regurgitated, undigested material such as

the pellets of certain birds, deposited in a recognizable form) are included as trace fossils. Pectinariid tubes and caddisfly (Trichoptera) cases are also included (e.g. Vyalov 1973). Both consist of various amounts of sedimentary particles (e.g. Sukacheva 1982) and they do not exactly match the producer body outline. Caddisfly cases are built by the animals around their proper chitinous skeletons and hence cannot be considered biotaxa. Similarly, the so-called sand reefs (e.g. Ekdale & Lewis 1993), structures created by sabellariid polychaetes from sand grains, are architectural structures (aedificichnia) and conform with the definition of a trace fossil as given above.

Some structures superficially considered as secretions are also accommodated in trace fossils, viz. nets and cocoons woven by larval and adult arthropods such as Araneae, Hymenoptera or Lepidoptera. The substrate (silk) here is secreted by the producer itself. In a second step, the silk is manipulated to form recurrent structures. This type of cocoon must not be confused with the mere secretions of Diptera and Clitellata. In addition, it may contain foreign material such as leaves or soil particles, which is a type of substrate in terms of our definition above.

The discussion of embedment structures, plant reaction tissues and other swellings shows that there are hybrid structures resulting from combinations of boring and growth in a mutual interaction of partner organisms. These structures are, at least partially, the work of animals and may contain a clear trace. The whole structures, however, are not traces as defined above. For convenience and in order to maintain stability of names with a high ecological meaning, we advocate nomenclaturally (not taxonomically) treating them as if they were ichnotaxa.

Some of the items not considered trace fossils here may nonetheless receive names outside the biological system. Being produced by animals, their nomenclature has to be governed by the International Code of Zoological Nomenclature (ICZN). As a consequence, we propose to amend the current idiom 'work of an animal' as used in the Code (ICZN 1999: Glossary) by a clearly worded list of categories under 'trace fossils', including burrows, borings and etchings, tracks and trackways, coprolites, gastroliths, regurgitaliths, nests, woven cocoons, spider webs, leaf mines, bite and gnaw structures.

Fossil versus Recent structures

It is important to distinguish between fossil and Recent traces because the International Code of Zoological Nomenclature, since its second edition, has only allowed the use of names for modern traces established prior to 1931 (Stoll *et al.* 1964; ICZN 1999, Art. 1.2.1). This

restriction has to be understood as a beneficial pre-ventative measure against the erection of taxa for structures that only have minute preservation potential. Reineck & Flemming (1997), for example, described tyre traces in the muddy tidal flats of the German Wadden Sea, water-surface structures made by birds starting to fly, and human urinating traces, fortunately only creating nomina nuda. However, the ICZN (1999) does not define 'fossil' (Nielsen & Nielsen 2001). Does it mean 'found in lithified sediment', 'found in pre-Holocene strata', or 'found below the taphonomically active zone'? These three possibilities may serve as practical criteria to judge whether use of ichnotaxa is justified under the current ICZN (1999) but they are not always applicable. Modern deep-sea burrowers may penetrate deeply into Pleistocene sediment (Fig. 2A) so that dating an active burrow with microfossils or radiocarbon from the surrounding matrix could be

Fig. 2. Problematic age (fossil or Recent) identification of traces. □A. Recent marine burrows (*Skolithos* and *Chondrites)* reaching down deep through the fully bioturbated 'mixed layer' (I, Recent) into the 'transitional layer' (II) or even into the fossil 'historical layer' (III). □B. Bored clasts which may have borings contemporaneous with the matrix sediment or may have fallen from a cliff above; not to scale.

misleading (e.g. Löwemark & Schäfer 2003), and reworked hard parts of fossils can be bored today without any possibility for accurate dating.

A fossilization barrier for trace fossils in sediments is almost impossible to define. Borings in lithic substrates may be considered as fossilized following the death of their producers; Neogene and Holocene borings can hardly be told apart sometimes as the substrate contains no information about the age of a boring (e.g. Radwański 1977) (Fig. 2B). It is highly questionable whether this circumstance should permit the naming of modern borings. This practice would be welcomed by ichnologists working on carbonate bioerosion. It would however lead to innumerable cases where a modern trace that in principle could have been assigned to a modern organism from the start, is left in a taxonomic limbo with more than one possible maker. Because the aim of this paper is to unify ichnotaxonomy, we do not advocate the naming of modern borings, as the modern-to-fossil transition may be blurred in this case. This model is followed by at least some specialists in borings (e.g. Glaub 2004 and references therein).

In addition, there are several instances where traces in modern substrates are morphologically indistinguish-able from their fossil counterparts. They have sometimes been described using the (officially forbidden) names of trace fossils, e.g. by Ekdale (1980); Pemberton & Frey (1982); Bromley (1990); Wetzel (1991); Gaillard (1991); Vogel *et al*. (2000) and Fu & Werner (2000). These authors used the trace fossil names in order to point out biological affinities and ecological or sedimentological implications without awkward constructions such as 'a burrow of the *Zoophycos* type'. Following Bromley & Fürsich (1980) and Bromley (1990), the usage of existing and well-defined trace fossil names for modern structures are supported, whereas the establishment of ichnotaxa based on modern material is not, being well aware of the difficulties in defining the modern-to-fossil transition.
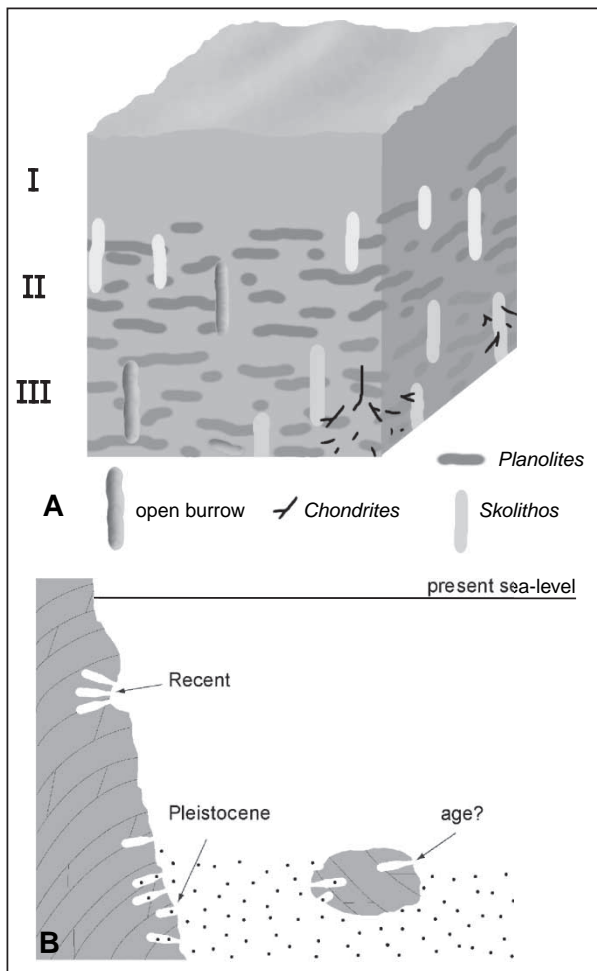
Trace fossil nomenclature

Status of ichnotaxa

The nomenclature of organisms is governed by a set of International Codes, legislative volumes for botany, zoology and bacteria generally abbreviated as ICBN, ICZN and ICNB, respectively. Names for 'the work of animals' (in the wording of ICZN) have always been protected by the zoological code. Ichnotaxa of plant and fungal origin on the other hand had no legal standing under any of the codes until 1999. A call to formalize general practice among ichnologists and extend the regulations of the ICZN to all trace fossils (following

earlier proposals by Sarjeant & Kennedy (1973) and Pemberton & Frey (1982)) has resulted in a major improvement in the 4th edition (ICZN 1999, Art. 1.2.1). Names of 'animals' may now be based on the 'fossilized work of organisms', which means that protistan, plant and fungal trace fossils (e.g. their microborings) are included in 'animals' for the purposes of the code.

Trace fossils as type specimens

Requirement of types. – With the publication of the 4th edition of the ICZN (1999, Art. 16.4), trace fossil species (ichnospecies) require holotypes just as biological taxa do. Tubbs (2003) has clarified that the principle of typification extends to the levels of newly established ichnogenera (ICZN 1999, Art. 42.3.2; but see Arts. 13.3.3 and 66.1 for opposite treatment of ichnogenera proposed prior to 2000) and ichnofamilies (ICZN 1999, Art. 29 and 63), i.e. each ichnofamily must have a type ichnogenus. In practice, most ichnologists have based new descriptions of taxa on actual fossils, and sometimes even explicitly designated morphotypes as the types of new ichnospecies (e.g. Bromley 1981; Bertling 1992; Rindsberg 1994; Uchman 1995; Genise 1995; Schlirf 2000; Mikuláš 2000; Nielsen & Nielsen 2001; Braddy & Briggs 2002).

Inaccurate or incomplete descriptions occasionally necessitate reexamination of types. Much more often than with type specimens of biological species, the type of an ichnospecies turns out to be too badly preserved for proper identification at the increased level of knowledge after the time of its introduction. This is because differently preserved trace fossils may exhibit different features, not merely because of the lack of certain features expressed only in well-preserved specimens. Items of particular interest include poorly preserved tracks and eroded burrows. The Code allows photographs and (natural) casts as references to holotypes (ICZN 1999, Art. 72.5.3; 73.1.4) potentially leading to additional uncertainty in isolated cases.

Undertracks and overtracks. – Footprints pose a special taxonomic problem because they frequently include blurred or morphologically deviating undertracks or overtracks, produced by the animal sinking into more than just the top layer of sediment, or by sediment later filling a deeply concave track, respectively (Demathieu 1970; Goldring & Seilacher 1971) (Fig. 3). The loss of detail in overtracks is less than in undertracks but in general, the thicker the layer of sediment, the more details are missing in either case. These 'phantom tracks' (Haubold 1996) exhibit considerable variation in shape due to diagenesis and preservation. Sometimes this

aspect of tracks has been overlooked by authors of ichnotaxa, resulting in much confusion about the form of related but better-preserved tracks.

To complicate the situation, several instances are known in which different track ichnotaxa have identical undertracks (Manning 2004). These may occasionally still be recognized at a higher systematic level, even if not identifiable at the ichnospecific or –generic level, and may have received separate names in the past. These names qualify as collective ichnotaxa, e.g. the early '*Ichnium*' as used by Pabst (1896; see also Häntzschel 1975).

We strongly encourage authors to use only complete tracks as a basis for the establishment of an ichnotaxon. Where undertracks are recognized these should be referred to as 'undertrack of < *Ichnotaxon* >'. Information about undertracks and overtracks should always be included in the description, not the diagnosis.

In cases where much better preserved material is discovered in intimate connection with previously named undertracks (Fig. 3), we suggest that the new material be given a new name and the ill-defined ichnotaxon be allowed to fall into disuse as a nomen dubium (ICZN 1999: Art. 23.9). This procedure must obey all provisions of the Code for this situation, including comprehensive systematic restudy of the group to which the ichnotaxon belongs. When new material is only slightly better it is preferable to emend the older ichnotaxon. It is not acceptable to declare ichnotaxa as nomina dubia as soon as better preserved specimens are found; this procedure is against good nomenclatural practice and is not sanctioned by ICZN (1999, Art. 75.3, 75.5).

Poorly preserved types. – On numerous occasions, previous authors have based ichnotaxa on poorly preserved material, especially strongly scoured, weathered or eroded specimens. Material like this should never serve as type specimens for ichnospecies because it may later turn out that precisely the missing criteria are important ichnotaxobases (Fig. 4). In these cases, we advise authors to use open nomenclature (see below).

Taphonomic features, e.g. concretions, chemical or physical deformation haloes, may convey interesting information about the tracemaker. Analogously with the suggested treatment of undertracks, these characters should be included in the description rather than in the diagnosis. In general, diagnoses of ichnotaxa should always be based on the most complete available material. It is much easier later to assign fragmentary samples to a particular ichnotaxon than to emend or synonymize ichnotaxa based on rudimentary diagnoses.
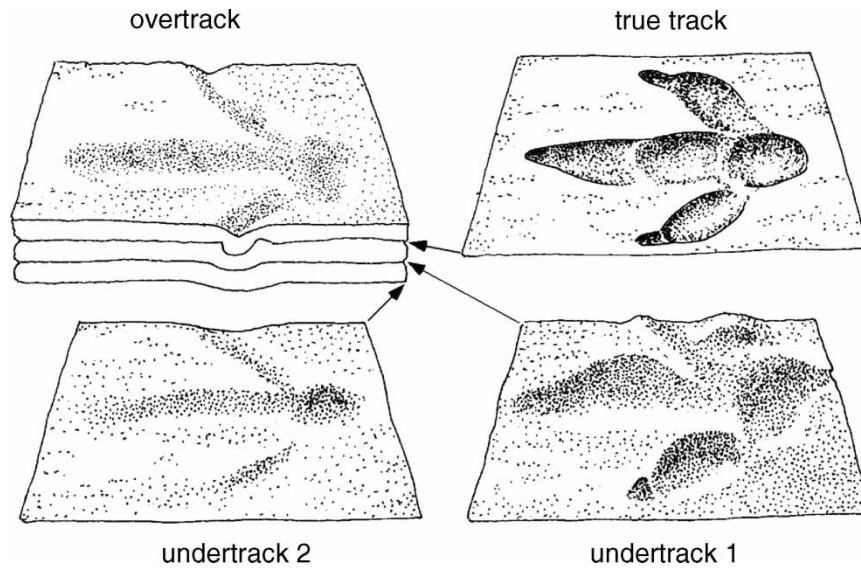
overtrack   true track

undertrack 2   undertrack 1

Fig. 3. Overtracks, undertracks and their relationship to the true track. Overtrack in a thin covering of sand deposited subsequently over the tracking surface, two compressional undertracks shown here on parting planes beneath the tracking surface, exhibiting decreasing detail downward (schematic results of experiments of Milàn & Bromley with wet cement using an emu as trackmaker).

Open nomenclature

Ichnologists have applied open nomenclature very sparsely, and this has resulted in numerous poorly identified records of trace fossils. Assignment of a descriptive code to traces of uncertain affinity is undesirable as this often results in them becoming lost in the literature. Palaeoecological interpretation is particularly hampered this way. To increase stability and utility of ichnotaxa we recommend that authors employ open nomenclature (Richter 1948; Bengtson 1988). This includes the use of 'aff.' to relate well-preserved but undescribed material to a named ichnotaxon, 'cf.' as a provisional identification for poorly preserved material, and '?' for uncertain identification. For further details refer to Bengtson (1988).

In order to clearly distinguish ichnotaxa from biological names, we propose to follow the usage of Bromley & D'Alessandro (1987) who introduced 'isp.' and 'igen.'

for open nomenclature as well as for the original description of new trace fossils.

Ichnosystematics

Systematic levels

For the goals of ichnotaxonomy, it is important to keep in mind that more systematic ranks are available than just ichnospecies and ichnogenus. Subgenera and subspecies are permitted in the systematics of trace fossils as well, although they are rarely used (Rindsberg 1990). No new systematic scheme for trace fossils is presented here, because the question of naming an individual (trace) fossil or any other organism is independent of its position within the system.

We welcome in principle the tentative attempts of previous authors to establish ichno-orders and higher
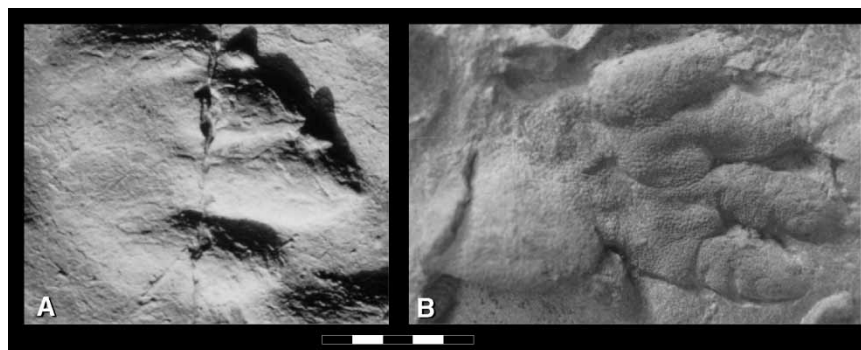
Fig. 4. Complete and incomplete registration of digits in *Brachychirotherium*. □A. Left foot impression of *Brachychirotherium circaparvum* Demathieu, Ladinian (Middle Triassic) of Mont d'Or Lyonnais near Lyon, France. □B. Left foot impression of *Brachychirotherium gallicum* Willruth, Anisian (Middle Triassic) of Lodève, France (specimen in the Museé de Lodève); scale bar for both 5 cm.

categories (Seilacher 1953; Vyalov 1966, 1972). These ranks have been established beyond the system of name-bearing types, i.e. rules of priority and homonymy do not apply. Ichnotaxa may be incorporated into a higher-rank classification if this is independent of biological systematics. Because these taxa are established outside the realms of the ICZN, each subsequent author is free to adopt or dismiss them. Our main concern here is the ichnofamily rank, because it is governed by the ICZN.

Ichnofamilies

Establishment of ichnofamilies. – The ICZN (1999, Art. 10.3) explicitly allows the use of ichnofamilies, for which it is applied in the same way as for the lowest ranks. It is proposed that ichnofamilies be used more widely as they aid hierarchical classification of the increasing number of ichnogenera. Not every ichnogenus needs to be placed in an ichnofamily; we expect that most will remain incertae sedis. Ichnofamilies should be named sparingly and preferably after consensus on included ichnogenera is reached among relevant ichnologists. For example, many of the morphological groups of flysch ichnotaxa developed by Książkiewicz (1977) and subsequently modified by Uchman (1995, 1998) could be formalized as ichnofamilies. Also, most insect trace fossils in palaeosols are arranged in ichnofamilies (Genise 2000).

Ichnofamilies and biological affinity. – Ichnofamilies should be based on trace morphology alone, not on producer biology (Bromley 1996). Ichnofamilies such as 'traces made by crabs' or 'tracks of ornithopods' are not acceptable. This makes their artificial character very clear and shows that they should not be confounded with biological families. Sadly, some vertebrate ichnologists have adopted ichnofamilies established by Vyalov (1966) without typification (see above) and continue to erect suprageneric taxa parallel to biological grouping of their producers.

The ICZN (1999, Art. 23.7.3) clearly states that biological names and ichnotaxa must be kept strictly apart: "A name established for an ichnotaxon does not compete in priority with a name established for an animal (even for the animal that formed, or may have formed, the trace fossil)." For example, recent borings may exhibit such detailed morphology that they have routinely been used as the basis of biologic taxa (e.g. Soule & Soule 1969). The 'ctenostome bryozoan families' Spathiporidae and Terebriporidae were founded on the nominate borings *Spathipora* and *Terebripora*, respectively (d'Orbigny 1847; Pohowsky 1978), and are therefore ichnofamilies, not biologic taxa.

Ichnotaxonomy

Principles

As shown above, trace fossils form a highly heterogeneous group of structures derived from various biological activities. It is therefore not advisable to impose too detailed procedures for identifying and naming trace fossils as a whole. Tracks, burrows, borings, coprolites etc. each require their special sets of characteristics (ichnotaxobases, Bromley 1990) for identification. We therefore do not suggest using identical sets of ichnotaxobases for all trace fossils and at any systematic level. We do propose, however, uniform validity and invalidity of certain kinds of ichnotaxobases independent of which ichnotaxon is concerned.

Ichnotaxobases

Approach. – In the past, various workers have used diverse ichnotaxobases even within identical groups of ichnotaxa. Depending on the main aspect, ichnotaxobases have been weighted differently, which sometimes led to contradictory naming. A well-known example is the group of arthropod or worm burrows that has been described as *Thalassinoides*, *Ophiomorpha*, *Teichichnus* and *Gyrolithes* based on wall structure and morphology, and as *Spongeliomorpha* based on overall morphology (Fürsich 1973; Schlirf 2000). A major problem throughout taxonomy, distinguishing criteria relevant at the various systematic ranks, is aggravated in ichnotaxonomy: Where relationships are dubious, it is up to the personal decision of the researcher which ichnotaxobase to choose for each hierarchy (e.g. Braddy 1995). In a classic paper, Fürsich (1974) presented a solution to this quandary, suggesting that features indicating highly significant behaviour should be ichnogeneric ichnotaxobases, while less significant behaviour, e.g. that controlled by the environment, should provide ichnospecific ichnotaxobases. Goldring *et al*. (1997) opposed this solution, citing its inherent subjectivity. No objective system of ichnotaxobases has yet been agreed upon by ichnologists.

Although perfect agreement among taxonomists seems unlikely, we can at least avoid some of the pitfalls. In the following paragraphs, we cite typical examples to discuss potential ichnotaxobases (morphology in its broadest sense, size, substrate, diagenesis and preservation, producer ethology, biology or evolution, geological age, location and facies) and distinguish between useful and impermissible criteria.

Morphology. – Most trace fossils are initially recognized because of their distinct morphology within a host

substrate. This includes several groups of criteria, both external (1 through 3) and internal (4 and 5), any of which may be characteristic:

(1) The overall shape is most readily recognized but is not necessarily the most relevant ichnotaxobase. It comprises general course or path, pattern of arrangement and form of subunits in more complex structures, branching (presence or absence and type, e.g. order, angle, size relations) and cross-sectional outline (e.g. Bromley 1990).

(2) Even more important can be the orientation with regard to the substrate (vertical, oblique, horizontal) and the position in or on the substrate.

(3) Surface features (sculpture) usually play a rather subordinate role and are diagnostic mostly at the ichnospecific level, e.g. as etched sculpture on gastroliths or as wall ornament in burrows. As knowledge about modern producers increases, surface features may become more important in the ichnotaxonomy of some groups (Genise 2004). In fossil insect nests, micromorphological characters may be of higher significance (Genise & Hazeldine 1998).

(4) The internal structure may be highly diverse; it is important especially for burrows and coprolites. Burrows are distinguished by the wall (presence or absence and structure of wall) and the type of fill (active *versus* passive). Passive fill results in no additional biogenic features and is rejected as an ichnotaxobase on this ground. Active fill may imply ichnotaxobases such as spreite structure, lamination or other textures exhibiting grain sorting.

(5) The architecture of insect nests provides even more relevant ichnotaxobases than their outward appearance. For instance, associated tunnel systems and spatial arrangement of chambers in multi-chamber nests are important features here (Genise & Bown 1994).

Not all of these features have to be relevant for naming a trace fossil, as the use of characters with little preservation potential is a critical point. Vertical tubes as top parts of *Paleodictyon* or funnels in vertical trace fossils (*Diplocraterion* or *Skolithos*) of sand-dwelling producers will all be eroded rapidly and hence are unsuitable ichnotaxobases (Fig. 5). Likewise, skin impressions in vertebrate tracks are too rarely preserved to base an ichnotaxon on this character. Equally, the course or path of a trackway is irrelevant as is speed or size of the animal making the trackway (Braddy 1995). Sediment backpush mounds, although useful directional or palaeoslope indicators (e.g. Sadler 1993), are of no diagnostic value. Rather, the arrangement of individual

tracks (internal *versus* external width, number and angle of foot or claw imprints, etc.) is important here (Anderson 1981; Trewin 1994). Computer simulations may be of great value in identifying suitable ichnotaxobases in such cases.

For the distinction of closely related ichnospecies, quantitative data may be needed; we thus strongly encourage the use of morphometric analysis at this level (e.g. Demathieu 1970; Lockley 1998). We do not refer to undertracks here as they do not constitute namable entities, and as their features vary with the depth of the undertrack (Manning 2004). Several approaches to morphometry exist, especially for morphologically complex ichnotaxa such as vertebrate tracks, the most common being multivariate statistics and the landmark method. In any case, the number of measurements to be taken depends on the number of criteria available. It is not necessary to have all possible data at hand but usually half of the theoretically measurable criteria are needed. According to information theory, three is always the minimum number (Demathieu & Demathieu 2002). Ichnogenera, however, are better described using qualitative aspects.

Great care has to be taken in the selection of appropriate characters here, especially in tracks that exhibit several measurable criteria (e.g. Demathieu 1986; Lockley 1998). This is not done lightly. The ichnologist attempting to distinguish ichnotaxa morphometrically should have advanced skills in information theory in addition to considerable ichnologic experience. The qualitative analysis of large samples of tracks is at least as important as morphometric studies in recognizing distinctive morphologies (e.g. Demathieu 1970; Lockley 1998).

Size. – Size for the purpose of ichnotaxonomy is understood as a single morphometric parameter. It has been used as an ichnotaxobase mostly at the ichnospecies level, and it may help (among other morphological criteria) to distinguish ichnogenera as well, e.g. the vertically coiled burrows *Gyrolithes* (diameter of tens of mm) and *Daimonelix* (diameter of tens of cm; Fig. 6). However, this example, and most other examples known to us, are better expressed in terms of proportions of morphometric parameters, i.e. as a matter of shape rather than size alone.

Historically, ichnospecies erected solely on size characteristics have generally been either synonymized or distinguished by morphologic criteria. Where a suite of traces differs only in size, the suspicion is strong that the suite represents an ontogenetic series (e.g. *Brachychirotherium*, see Demathieu 1970, 46 ff., 131 ff., 1981; Courel & Demathieu 1976) or preservational variants (Manning 2004). Gaps in a series of measurements need not indicate separate ichnospecies, as the preservation
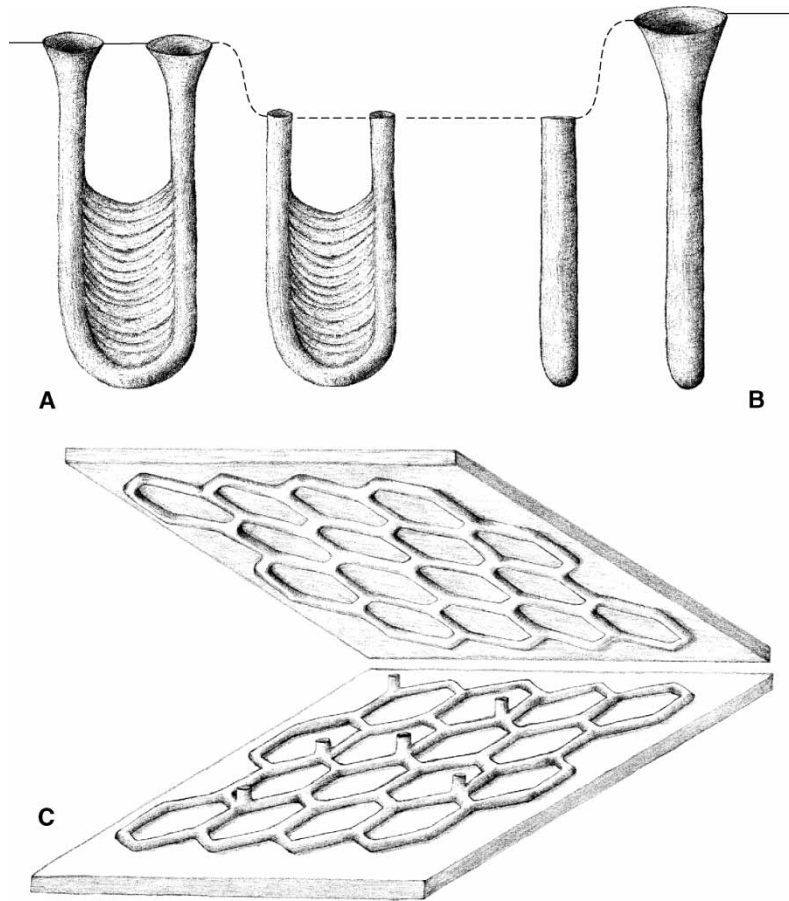
Fig. 5. Morphological characters that are easily eroded do not form useful ichnotaxobases. □A. Funnels of *Diplocraterion*. □B. Funnels of *Skolithos* (broken horizontal lines represent depth of erosion). □C. Vertical shafts on *Palaeodictyon* nets which are lost during parting; not to scale.

potential of juvenile structures is low. These commonly are positioned in the shallowest tiers and will easily be wiped out by surface abrasion (mainly in the case of borings) or by subsequent bioturbation by larger animals. Also, the possibility that the tracemaker had distinct growth stages, such as instars, must be considered. Bimodal or multimodal distribution curves based on a single morphometric parameter (size) thus do not necessarily indicate the actual existence of separate ichnospecies. For these reasons we are reluctant to use size at the ichnospecies rank and reject it altogether at higher ranks.

Substrate. – Historically, ichnogenera have been distinguished on the basis of the type of substrate: Simple shafts are called *Skolithos linearis* Haldeman when found
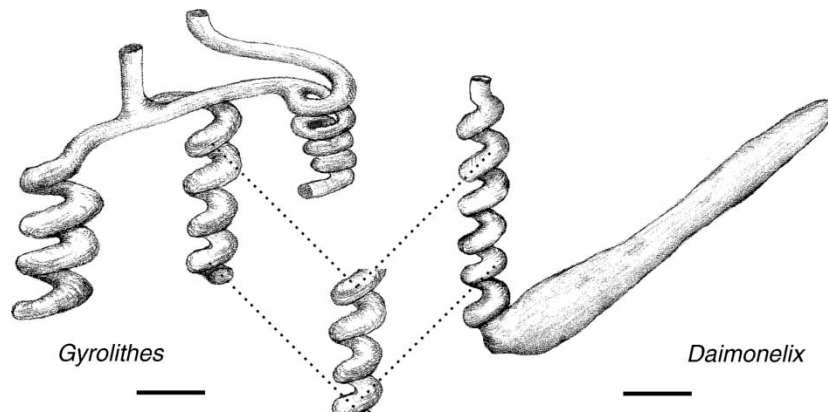

Fig. 6. Size as an ichnotaxobase. Morphologically similar corkscrew sections in *Gyrolithes* (scale bar 5 cm) and *Daimonelix* (scale bar 50 cm).

in various soft sedimentary substrates and *Trypanites weisei* Mägdefrau in lithic substrates. Flask-shaped structures are named *Teredolites clavatus* Leymerie as wood borings, *Gastrochaenolites lapidicus* Kelly & Bromley as rock borings and *Amphorichnus papillatus* Männil as firmground burrows (Fig. 7). Within this system, the most important point is the substrate consistency (soft or firm *versus* hard) because it implies a different producer behaviour: organisms boring into hard substrate use different techniques (scraping with hard parts, e.g. Rice 1969; Blake 1969; Röder 1977 or etching, e.g. Bromley 1994) from those burrowing in unconsolidated sediment (grain displacement by extensions and contractions of the body, e.g. Bromley 1990). The grain size ichnotaxonomically does not matter either in soft and firm sediment or in hard substrates.

We recognize that borings and burrows are fundamentally different. Recognition of these differences is essential in ichnofacies analysis. Faunal and floral divides between soft, firm and hard substrates are real but not sufficiently distinct; a few exceptional boring organisms may attack stiff mud as well as lithic substrates (e.g. Pemberton & Frey 1985). There is no clear boundary within soft substrates, however (clay, silt, sandy mud, muddy sand, sand), which prohibits the use of such differences as ichnotaxobases. They certainly are not suitable for tracks, contrary to the proposal of Haubold (1996).

Some kinds of traces (and tracemakers) are restricted to very particular substrates, but others are less restricted. As a result, substrate is an important consideration in the classification of some groups of trace fossils but not in others. Using neoichnology as a guide for bioerosion studies, we generally see clear divides between the infaunas of lithic, woody and other hard substrates. Very few living borer species are common to more than one such substrate (Fig. 8) but some are restricted to very particular substrates such as

leaves of individual species of plants (e.g. Hering 1951; Vité 1952; Genise 1995). Borings in lithic and xylic substrates form two nearly exclusive groups and we expect their ichnotaxonomy to be almost entirely separate. Borings in hard clastic *versus* carbonate substrates, however, overlap somewhat. Bioerosion structures on and in bones are usually sufficiently distinguished morphologically. Where the morphology of these traces is close to ichnotaxa typical of lithic substrates, we recommend a careful search for subtle differences. Bone should therefore be considered as 'lithic' in the usage of this terminology.

We recommend that, within reason, trace fossils found in the principal types of lithic, woody and soft substrates be kept separate regardless of morphologic similarity (not identity). It would usually be a mistake, however, to name a new ichnotaxon based solely on a difference in substrate. Substrate certainly is not acceptable as an ichnotaxobase within these major categories.

Coprolites may be considered as having a substrate (i.e. constituting material) even if they are usually found disrupted from their origins. The food consumed by their producer is processed, i.e. biologically modified, in its intestines and excreted as coprolites. With this approach, substrate (wood, sediment, fish scales, insect wings, echinoderm plates etc.) may form an important ichnotaxobase for this special group of trace fossils, apart from their morphology. This is not compulsory, however, as predators are not necessarily prey-specific; e.g. crocodile dung can include bird or fish remains.

Diagenesis and preservation. – Even though many trace fossils are produced within the sediment they may undergo severe change during taphonomy. Erosion, deformation and diagenetic enhancement are some of the processes to consider here. Four examples are provided in order to illustrate their importance:
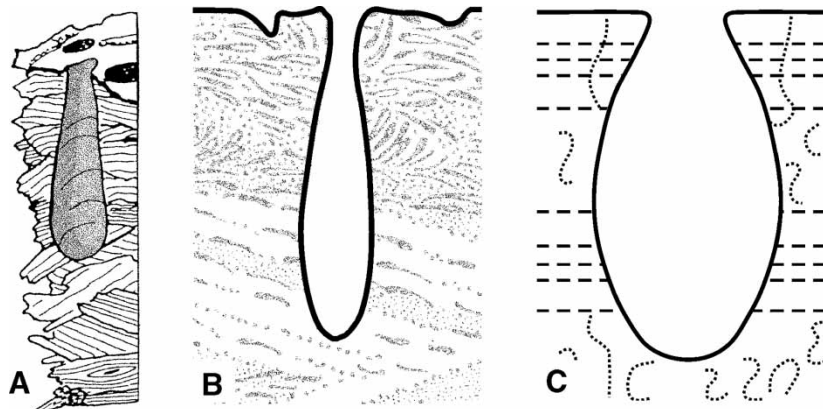

Fig. 7. Substrate as an ichnotaxobase. Morphologically similar flask-shaped trace fossils distinguished by principal type of substrate. □A. *Teredolites* in wood. □B. *Gastrochaenolites* in rock. □C. *Amphorichnus* in mud; not to scale.
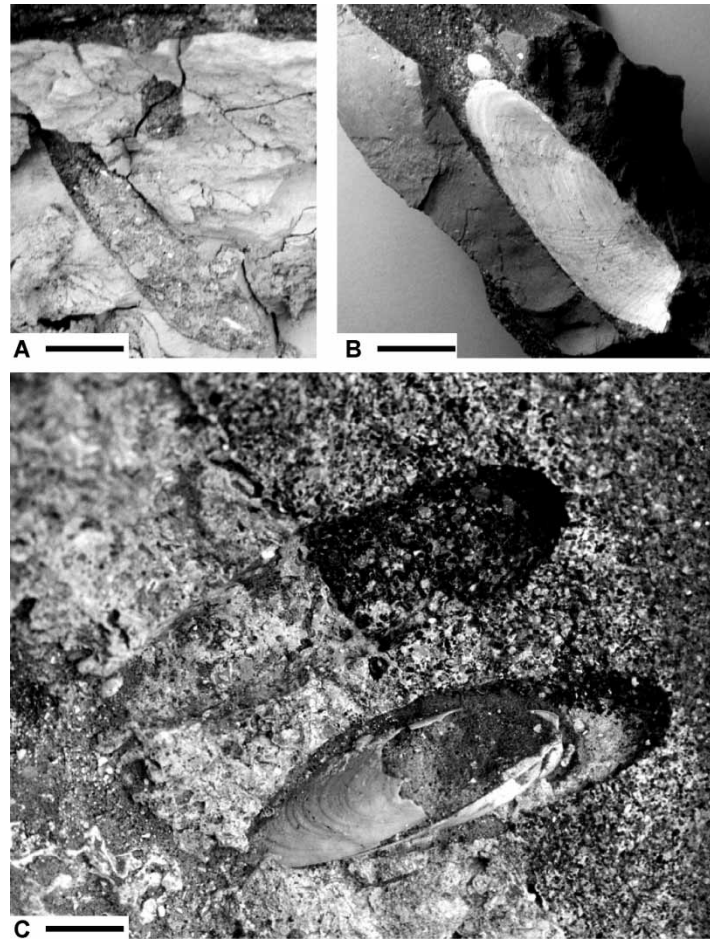
Fig. 8. Substrate as an ichnotaxobase. *Gastrochaenolites* crossing the hard-soft substrate boundary without notable changes of shape. □A. Silt firmground with *Gastrochaenolites* isp. overlain by quartz sand (Pliocene Kritika Formation, Rhodes, Greece). □B. *In-situ* body fossil of the bivalve tracemaker, *Pholas dactylus* Linné, at same locality. □C. Two *Gastrochaenolites torpedo* Kelly & Bromley, one of them containing the in-situ bivalve tracemaker, *Lithophaga lithophaga* Röding, boring from high-Mg calcite coralline-algal skeleton (left) into well-cemented calcarenite (right) (Pleistocene Rhodos Formation, Rhodes, Greece); scale bars 1 cm.

(1) Arthropod trackways commonly comprise several ichnospecies that in turn may belong to different ichnogenera, an undesirable situation. Myriapod trackways may grade from *Diplichnites* via *Diplopodichnus* to *Dendroidichnites* (Fig. 9; Braddy 1998). This obviously conveys little information apart from substrate consistency and consequent differences in preservation. The track ways cannot be considered compound trace fossils (see below) because they did not arise from different producer behaviour. Vertebrate trackways pose similar problems: It may be difficult to tell whether an individual track is just poorly preserved due to originally soft substrate or whether it represents another ichnotaxon (Baird 1957; Lockley 1998; Fornos *et al*. 2002).

(2) The modern sea urchin *Echinocardium cordatum* burrows horizontally in sand using mucus and spines (Fig. 10). It maintains contact with the water column above via a hair-thin shaft that is successively reestablished as the echinoid proceeds through the sediment. This shaft usually is obliterated by other burrowers but under certain taphonomic conditions within sandy sediments it
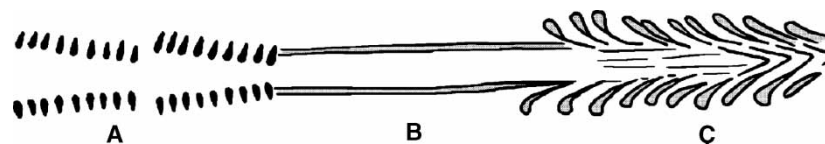

Fig. 9. Preservation as an ichnotaxobase. Intergradation of □A. *Diplopodichnus*: into □B. *Diplichnites* and □C. *Dendroidichnites* as an effect of changing substrate, schematic.
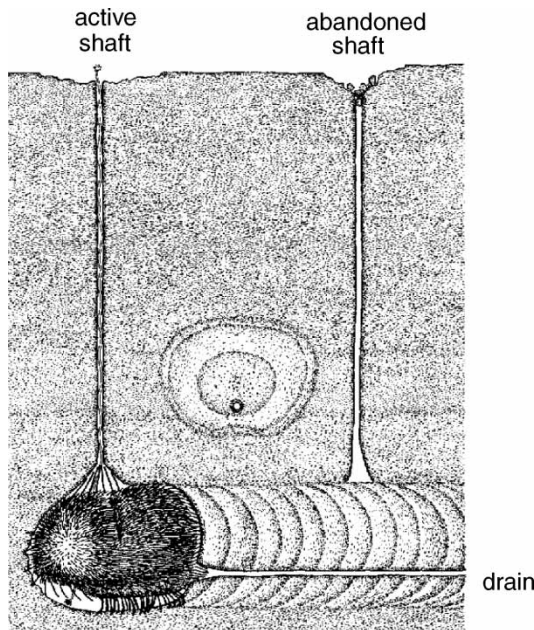
Fig. 10. Preservation as an ichnotaxobase. Burrow, backfill, shaft and drain structures of the spatangoid echinoid *Echinocardium cordatum* (Pennant); echinoid is about 2 cm high; modified after Bromley (1996).
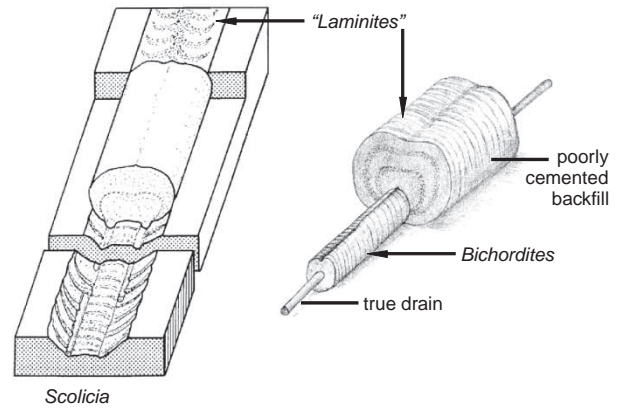

Fig. 11. Preservation as an ichnotaxobase: Main types of echinoid burrows and their preservational variants (from Uchman 1995). *Bichordites*, the inner well cemented part of the burrow surrounding the true drain may resemble *Bolonia*. The median groove on top may form when the true drain collapses, whereas the median crest is a result of excessive cementation.

may be enlarged and enhanced diagenetically (Bromley & Asgaard 1975). Oxidation of previously dysoxic sediment results in a brownish stain easily seen in both Recent and fossil examples. The shaft as preserved in fossils, however, may be considerably larger than in modern traces, suggesting that its size (and perhaps shape?) should only be used with caution as an ichnotaxobase. Without knowledge of the recent counterpart, however, this would not have been discovered.

(3) Locomotion trace fossils of echinoids are characterized by one or a pair of thin, horizontal cords of sediment. These represent the drainage canals, which are preserved preferentially by diagenetic enhancement of its mucous lining. In *Bichordites sensu* Plaziat & Mahmoudi (1988), the inner well-cemented part, surrounding the true drain, may resemble *Bolonia* in full relief (Fig. 11). A median groove on top may form when the true drain collapses; the median crest is a result of excessive cementation (Schlirf 2002).

(4) Burrows of irregular echinoids have been identified as *Scolicia, Subphyllochorda, Taphrhelminthopsis* and *Bichordites*. Uchman (1995) and Goldring *et al*. (1997) claimed that these ichnotaxa were established on preservational variants of largely identical burrows, with their taphonomic history depending on the tier they were produced in. The full hyporelief expression of

Scolicia (lacking the 'roof') used to be identified as *Subphyllochorda*. Very shallow-tier examples cast subsequent to erosion were formerly identified as *Taphrhelminthopsis* (Fig. 12). Therefore both ichnogenera are incompletely preserved echinoid burrows, toponomic variants of *Scolicia* (Uchman 1995). This gives them a character comparable to undertraces: the whole structure is not preserved, only parts that have escaped taphonomic obliteration. (This argument assumes, following Uchman, 1995, that early Palaeozoic trace fossils labelled as *Taphrhelminthopsis* were misidentified.)

Some other examples of biogeochemically mediated diagenesis as in *Bichordites* are the well-known chalk ichnofossil *Bathichnus*, which is most remarkable because of its massive, barrel-shaped flint ring (Bromley *et al*. 1975), the domichnion *Tisoa* (Frey & Cowles 1972) as well as *Trichichnus* (Uchman 1999). In each case, the burrows gain contrast against the surrounding sediment due to diagenesis (Fig. 13). They do exhibit, however, characteristic morphologic features that would make them recognizable even without their spectacular preservation; hence preservation is not necessarily an ichnotaxobase.

We concede that preservational variants of trace fossils may convey biological, toponomic and perhaps sedimentological information, but with numerous transitions between 'ordinary' and 'special' preservation, this alone cannot be accepted as an ichnotaxobase. We feel that we are in line here with previous authors (e.g. Bromley 1990; Magwood 1992). Just as separate ichnotaxa should not be established or retained for undertracks, diagenetically altered trace fossils should not receive independent ichnotaxonomic status. For this
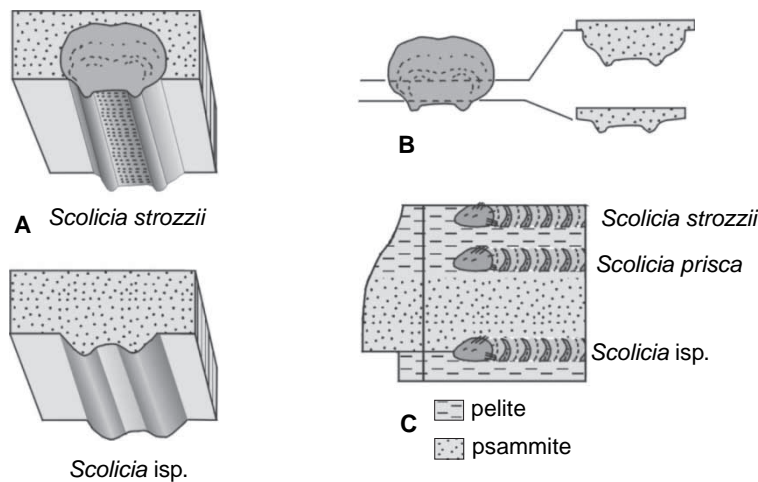
Fig. 12. Preservation as an ichnotaxobase: Preservational aspects of *Scolicia* (based on Uchman 1995). □A. *Scolicia* in full relief on sole of turbiditic bed (formerly called *Subphyllochorda*, top) and washed-out and cast form (formerly called *Taphrhelminthopsis* or *Taphrhelminthoida*, now *Scolicia strozzii*; bottom). □B. Depth of erosion influencing burrow morphology of the washed-out and cast preservational variants. □C. Different ichnospecies produced at different depths in turbiditic deposits.

reason, *Subphyllochorda* and *Taphrhelminthopsis* should be considered as junior synonyms of *Scolicia*. Trace fossils preserved in this way can in principle be described in open nomenclature as belonging to a certain ichnofamily.

Producer-related criteria. – The relationship between trace fossils and their producers usually is ambiguous (Fig. 14). Several groups of trace fossils, however, are so highly characteristic of their producers that they may be taken as proxy data to reconstruct their phylogeny, biology and of course, ethology. They include vertebrate tracks (e.g. Haubold 1971, 1996; Demathieu & Haubold 1974; Lockley 1998), leaf mines (e.g. Hering 1951), insect nests (e.g. Genise 1999) and most borings (e.g.

Fig. 13. Preservation as an ichnotaxobase: Chemically diagnosed ichnogenera. □A. *Tasselia* in phosphatic concretion (vertical section). □B. Detail of axial tube of *Tasselia*, (A and B modified from van Tassel 1965). □C. *Tisoa* in horizontal cross-section. □D. *Tisoa* in concretion originally interpreted as mucoid reinforcement of burrow walls (vertical section); all drawings schematic, scale bars 1 cm.

Bromley 1994). Occasionally the interrelationship is so tight that ichnotaxa have been erroneously placed within the biological system by authors until recently (e.g. Haubold 1971; Labandeira 2000; Foster 2001).

The most obvious producers have repeatedly entered into trace fossil taxonomy in the early years with ichnogenera such as *Teredolites, Merostomichnites, Rhynchosauroides,* or *Sabellarifex*, to name only a few. It has later turned out that many such names were coined in error (although any taxon name is just an array of letters and need not imply any meaning, according to the ICZN). *Teredolites* may be produced by many other wood-boring bivalves than just *Teredo* (Bromley *et al.* 1984); *Merostomichnites* is probably made by crustaceans rather than merostomes (Braddy 2001); *Sabellarifex* was probably produced by polychaetes other than sabellariid worms, etc. For these reasons, it is preferable that ichnotaxa should not be named with reference to supposed producers.

The examples listed here show that a supposed close relationship between trace and tracemaker may later have to be modified more or less drastically. For this reason, conclusions about producers always depend on the complexity of trace fossils and the current knowledge of producer biology. The producers of several groups of trace fossils have remained enigmatic, in some cases even with regard to kingdom. In summary, only in exceptional cases can ichnotaxa be reliably linked to the corresponding biological taxa at low systematic levels.

We acknowledge that information about tracemaker biology and affinity may provide important clues for the proper selection of ichnotaxobases (Fürsich 1974), especially as we expect knowledge about producer relationships to increase in the future. Closely watching modern trace producers is of great help in the search for
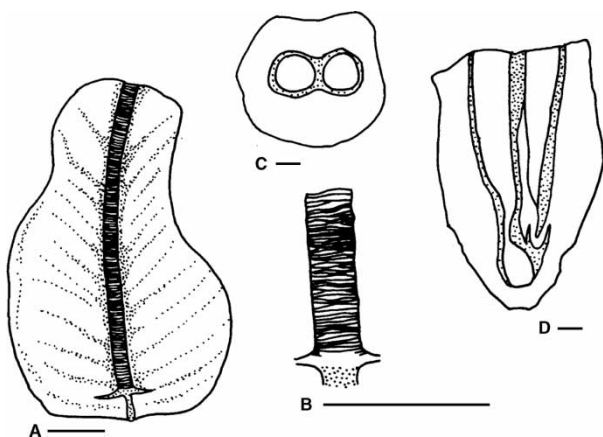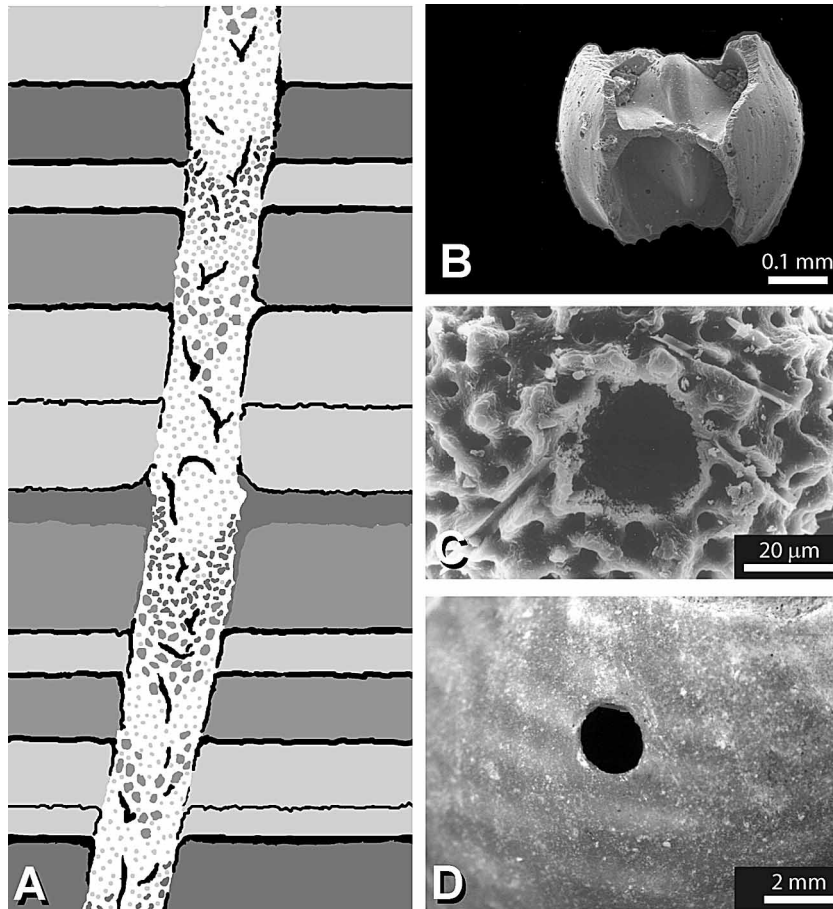
Fig. 14. One organism may form different traces (A, B), and different organisms may leave similar traces (C, D). □A. Trace produced by Recent scaphopod moving upward through sediment, schematic. □B. Gnawing trace on foraminiferal test, characteristic of feeding scaphopods; (SEM photo; Pleisto-Holocene, off West Greenland at 68° N 55° W in 190-200 m depth). □C. *Oichnus simplex* Bromley in test of planktic foraminifer, probably caused by a nematode (SEM photo; Holocene, Gulf of Aqaba at 27°54′ N 34°28′ E in 1200 m depth). □D. *Oichnus simplex* Bromley in shell of benthonic gastropod bored by a muricid gastropod (SEM photo; Holocene, beach of Tromsø, Norway).

ichnotaxobases relevant for distinction of ichnotaxa. Any producer-based criteria as such, however, may not be considered relevant for ichnotaxonomy, because the assignment generally is too ambiguous.

Geological Age. – Some trace fossils mirror animal behaviour that has not changed in principle through time. Given our knowledge of biological evolution, it becomes obvious that different tracemakers were responsible for similar traces at different times. In this case it may be tempting to assign different names to ichnotaxa with supposed different producers in mind, i.e. to use stratigraphic considerations to delimit ichnotaxa. A well-known example is *Isopodichnus*, which Bromley & Asgaard (1972) placed in synonymy with *Cruziana*. *Cruziana* is almost exclusively a marine Palaeozoic trace fossil attributed chiefly to trilobite activity. The morphologically identical *Isopodichnus*, however, occurs in nonmarine Devonian and Triassic sediments and is represented today by the work of

notostracan crustaceans (Bromley 1996). Such examples should direct attention to details that might distinguish trace fossils of strongly different age. Parallel to established procedures in biological fossils, we follow Bromley (1990), Magwood (1992) and others in proposing that stratigraphic age should never be an ichnotaxobase. It should be noted that some ichnotaxa appear to be restricted to rocks of a particular age, notably, most vertebrate trackways. Again, this information is not to be discarded by the ichnotaxonomist looking for distinguishing characters, but diagnoses must be solely morphological.

Location and facies. – Haubold (1996) has claimed facies as an important ichnotaxobase for vertebrate tracks. This is contrary to the widely accepted use of some invertebrate traces as facies-breaking structures, i.e. their makers are eurytopic (Seilacher 1964). In addition, if temporal distribution is not recognized as a valid criterion, the same should logically be the case for

spatial distribution. As long as the behaviour of whichever producer did not change, it is irrelevant where and when it made a trace. Thus, trace fossils occurring in strongly different facies should be re-examined carefully in order to ascertain whether they are truly identical morphologically or just differ taphonomically. Palaeogeographical distribution is also not an ichnotaxobase though trace fossils are in some cases geographically limited.

Valid ichnotaxobases. – Summarizing the preceding sections, Table 2 gives potential ichnotaxobases that after careful analysis are recommended or rejected. We conclude that criteria resulting from behaviour are the most important whereas physical, chemical and sedimentological factors should be excluded. This does not mean that ichnotaxa should exclusively be distinguished on the basis of morphology (Pickerill & Donovan 1998); rather, it also includes substrate specificity of producers.

Compound ichnotaxa and composites of trace fossils

Background

Trace fossils often are found not fully isolated from others through their matrix but instead in direct contact. Two types of contact are theoretically possible and have been observed in practice: (a) intergradation (compound structures), and (b) combination (composite structures) (reviewed by Pickerill & Narbonne 1995). (a) Compound traces arise from changing behaviour of a single producer, e.g. a bivalve ploughing through the sediment, resting or feeding (Ekdale & Bromley 2001; Bromley et al. 2003), a sporadically active trilobite, or a shrimp burrowing vertically, in a coiled manner or horizontally (Fig. 15). In most cases, there is no sharp boundary between the sections. (b) Composite structures, on the other hand, are usually made by different producers, usually at different times. This may happen accidentally or may result from changing

substrate characteristics; in either case the ichnotaxa involved are morphologically clearly separated.

Compound and composite structures are not shared with biology, except for the case of clearly defined hybrids. Biology tends to emphasize evolutionary units, not behavioural groupings such as trace fossils, and it can be difficult to free oneself from this background. Joint occurrences of trace fossils have hence resulted in much taxonomic irritation due to confusion about the nomenclatural status of the ichnotaxa concerned, especially if the principal distinction between composite and compound structures is not made. In most instances the definitions above are sufficient to identify a structure as composite or compound. Eiserhardt *et al.* (2001) point out that *Tomaculum* is a set of faecal pellets that each have a characteristic structure previously described as *Coprulus*. This example is neither a typical compound trace (obligate co-occurrence!) nor a typical composite structure (single producer).

Compound structures

The problem. – Compound structures pose two different problems in ichnotaxonomy: (a) An exceptional intergradation of ichnotaxa that are normally found separately would imply synonymization in all other occurrences if methods of biological taxonomy were applied (ICZN 1999: Art. 23.3.2). As shown below, at least one established ichnotaxon would be invalidated this way. (b) If the constituents of a normally compound ichnotaxon are found separately, they would have to be named differently, as they (even exceptionally) form discrete trace fossils.

The questions arising from these problems are whether one should apply the methods of biological taxonomy here (or resort to a special ruling) and how compound structures should be termed. A previous approach, proposed by Pemberton & Frey (1982) was to name compound specimens after the major ichnotaxon in order not to loose too much information. This procedure, however, results in a skewed image of a compound specimen as its nature is not rendered by its identification. It is by no means desirable to synonymize

Table 2. Status of ichnotaxobases.

Recommended	Useful with reservation	Rejected
Morphology:		
overall shape	Host plant (in plant bioerosion)	Size (as defined above)
orientation	Substrate (principal types only)	Taphonomy/preservation
ornamentation		Producer-related criteria
internal structure		Type of passive fill
Composition (of coprolites)		Substrate consistency
		Geological age
		Geographic location/facies

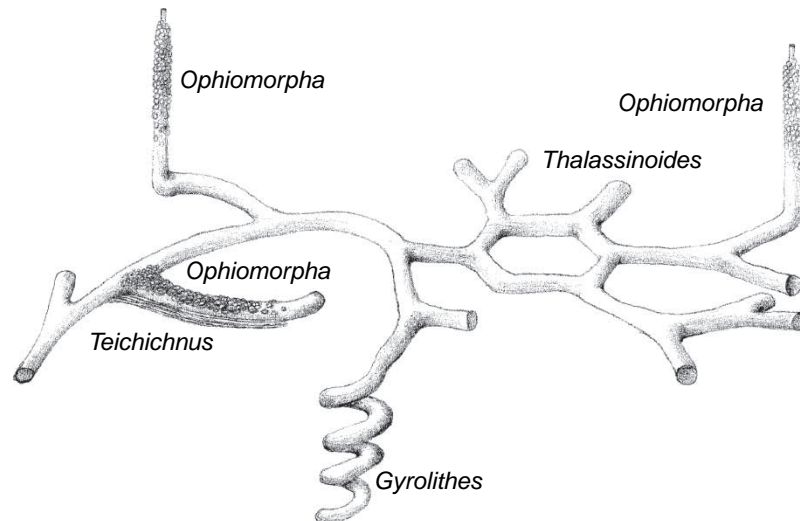*Fig. 15.* Compound structure produced by a malacostracan crustacean comprising the ichnogenera *Ophiomorpha, Thalassinoides, Gyrolithes* and *Teichichnus*; schematic.

all the work of a tracemaker when intergrading specimens are found, nor is it desirable to name "every turn of the worm" (James 1885). We recognize that some investigators are 'lumpers' and some are 'splitters'; a compromise must be struck between these extremes.

Taxonomy of compound traces. – Ichnogenera are established and accepted because they represent notably distinct producer behaviour. For this reason, intergradation of traces belonging to different ichnogenera is not grounds for synonymy. Also, at the current state of knowledge, it is equally not advisable to synonymize intergrading ichnogenera and establish them on an additional ichnosubgeneric rank because then ichnosubgenera could belong to different ichnogenera – an impossible situation from the standpoint of binominal nomenclature.

Usually, compound trace fossils are made up of components that each represent an archetypical behaviour of their own and therefore commonly occur isolated. For this reason, ichnotaxa designating this behaviour are well-established and should remain so (e.g. *Lophoctenium* despite rare intergradation with *Lockeia*, or *Rusophycus* despite uncommon intergradation with *Cruziana*). They lose their individuality, however, within a new superstructure in which subunits cannot be kept apart in practice. If this compound superstructure mirrors a recurrent pattern of behaviour it deserves its own name. This does not invalidate the ichnotaxa assigned to its components when they occur in isolation.

We are aware of two types of behaviour, different in principle, that result in compound trace fossils. (a) The tracemaker may simultaneously behave in two fundamentally distinct ways, e.g. a bivalve uses its foot to dig into the substrate and uses its siphons to collect sediment for food (*Hillichnus*, see Bromley *et al.* 2003, Fig. 16), or a crustacean forms faecal pellets of a certain shape and deposits them on the seafloor in a specific pattern (*Tomaculum*, see Eiserhardt *et al.* 2001). (b) The tracemaker behaves in distinct ways in chronological order, e.g. a trilobite ploughs through the sediment (*Cruziana*) and at times stops to dig deeper when it senses prey (*Rusophycus,* Fig. 17; e.g. Crimes 1970), or a bivalve moves along (*Protovirgularia*) interrupted by resting phases (*Lockeia*) (Ekdale & Bromley 2001; Bromley *et al.* 2003). Both categories of behaviour require a substantial amount of interpretation and are not immediately obvious from the trace fossil morphology or its substrate alone. Because we are reluctant to
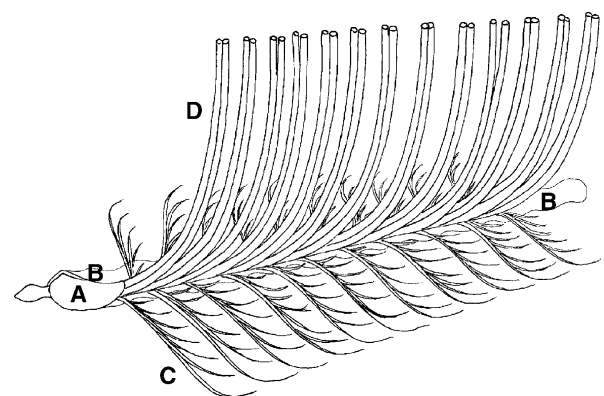

Fig. 16. Compound structures: *Hillichnus lobosensis* Bromley *et al.* as created by simultaneous activity of different producer body parts. □A. The tracemaker, a tellinid or semelid bivalve, moving toward left. □B. burrow structure, largely destroyed by the following, subsequently cross-cutting parts of the trace fossil. □C. Horizontal structures produced by deposit feeding using the inhalant siphon. □D. Vertical tubes created by inhalant and exhalant siphons for respiration; modified after Bromley *et al.* (2003).
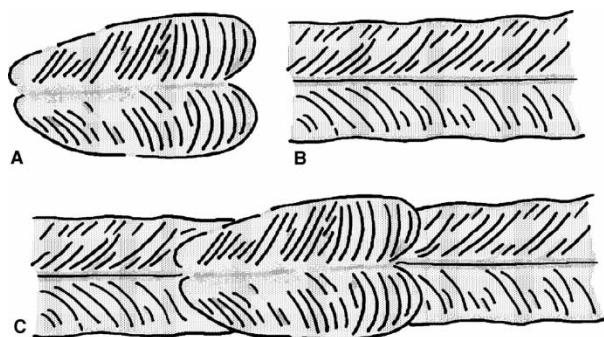
Fig. 17. Compound structures produced by arthropods. □A. 'Resting' (*Rusophycus*). □B. Ploughing (*Cruziana*). □C. Traces usually occur isolated but compound structures showing different producer behaviour at different times also occur; schematic.

allow inferences about producers as an ichnotaxobase we stress that both types of compound trace fossils have to be treated uniformly as given in the examples above. For this reason, we refrain from introducing new technical terms for these different structures.

Diagnoses of compound trace fossils should be based strictly on observation, not on inferences about behaviour. Authors establishing names for superstructures must take great care to avoid comparisons with existing ichnotaxa and should rather restrict the diagnosis to purely morphological terms. Words like 'rusophycoid' or 'protovirgularian' may be useful in the description or discussion, but as they may be invalidated in the future, they should not be used in the diagnosis. The practice advocated here differs from the principles of the zoological code but compound trace fossils have no analogy in biology.

Composite structures

Composites of trace fossils are not valid as ichnotaxa. Various examples of such structures can be given (Fig. 18): *Gastrochaenolites* (bivalve borings) are frequently superimposed on crustacean burrows (*Thalassinoides*) during cementation of a carbonate firm substrate (e.g.
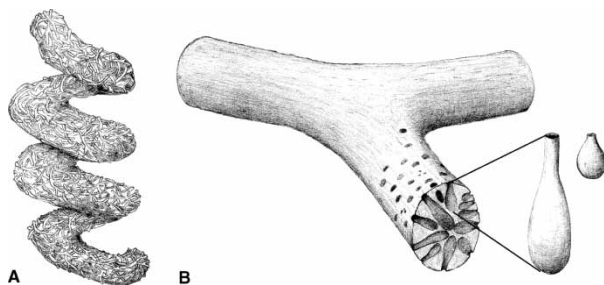

Fig. 18. Composite structures of different producers active at different times. □A. Small *Chondrites* superimposed on *Gyrolithes*. □B. *Gastrochaenolites* superimposed on *Thalassinoides* after filling cementation and exhumation; schematic.

Bromley 1968, 1975), root traces replaced by *Taenidium* after marine flooding (D'Alessandro *et al*. 1992), abandoned worm borings (*Trypanites*) reinhabited by and receiving a secondary ornament (xenomorphy) from an endolithic sponge (ichnogenus *Entobia*), or again, spiral crustacean burrows (*Gyrolithes*) whose wall lining was later recycled by small deposit feeders (ichnogenus *Chondrites*, Bromley & Frey 1974; Fig. 18).

We suggest that joint trace fossil occurrences of this type should not have any taxonomic consequences for the ichnotaxa involved. They should be named separately; this way the distinction from compound ichnotaxa is accentuated.

Conclusions

This paper is based on a detailed consensus of 11 active ichnologists from various subdisciplines and includes results of consultations with several other colleagues. After extensive discussions about previously controversial issues in the naming of trace fossils, we propose the following guidelines.

A trace fossil is a morphologically recurrent structure resulting from the life activity of an individual organism (or monospecific group of organisms) modifying the substrate. Based on this definition, several alleged 'trace fossils' are excluded from ichnotaxonomy. Embedment structures, plant reaction tissues, eggs and other secretions may nonetheless be named under the International Code of Zoological Nomenclature (ICZN), as they represent objects suitable for temporary classification besides biological systematics. Nevertheless, trace fossil names are not temporary but represent a parallel taxonomy. Stromatolites, pathologic structures, signs of human technology and soils are not classified as ichnotaxa.

We encourage all ichnologists to use only well-preserved, sufficiently complete material as type specimens for new ichnospecies in order not to increase the current problems with, e.g. named undertracks. The use of open nomenclature is the appropriate means to deal with poorly-preserved samples.

We discourage the use of ichnotaxa established for Recent traces, even where this is allowed by the ICZN. We acknowledge, however, that it may be useful to apply ichnotaxa based on fossil material to recent samples. With this distinction, we are aware of the difficulty or even impossibility to draw a clear line between what is fossil and what is recent. Some specialist groups of biologists are directed to the fact that it is not permissible to group biological taxa in families based

on modern or fossil traces (ichnofamilies), because ichnotaxa and biotaxa do not compete for synonymy.

Among the various ichnotaxobases suggested, morphological criteria resulting from behaviour are the most important. In addition, the principal type of substrate (lithic, xylic or other plant matter, soft sediment, etc.) is crucial for proper identification. Material composition is helpful for coprolites only. Various physical, chemical and sedimentological factors, including substrate consistency and preservation, have to be excluded just as are producer-based criteria. Stratigraphic age, geographical location and facies are equally unsuitable as ichnotaxobases.

Composite structures of different trace fossils that normally occur separately are not valid as ichnotaxa. Compound traces may be covered by one name only when the superstructure mirrors a recurrent pattern of behaviour. The name for the superstructure does not affect the validity of names for its subunits.

We recommend that the International Code of Zoological Nomenclature (ICZN 1999) be amended in several ways following Bertling *et al.* (2003) and Genise *et al.* (2004). Firstly, the term "work of an animal" (ICZN 1999: Glossary) needs refinement or rather replacement by a less ambiguous term to distinguish between various animal products and true trace fossils. The boundary between the 'work' and the 'product' of an animal is very blurred: Consider coprolites versus eggs as 'products' (the first are trace fossils, the latter not) or regurgitaliths and gastroliths, which have an ill-defined position in this equally ill-defined terminology. Fossil eggs and plant reaction tissues, however, are not trace fossils but should rather be named using a separate parataxonomic scheme. Secretions produced by organisms are not trace fossils, i.e. cocoons of flies and clitellates, pearls and calculi. We therefore propose to replace the term 'work of an animal' by 'trace fossils' and subsequently to give a rather comprehensive list of categories of trace fossils. This would mean rewording the glossary of the code in the following way:

- 'ichnotaxon' has to be defined as 'A taxon based on a trace fossil, including fossilized trails, tracks or burrows. See also trace fossil';
- 'work of an animal' should be replaced by 'trace fossil' defined as 'a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate, namely burrows, borings and etchings, tracks and trackways, coprolites, gastroliths, regurgitaliths, nests, woven cocoons, spider webs, leaf mines, and bite and gnaw structures, but not eggs, embedment structures and plant reaction tissues'.

We further advocate that 'igen.' and 'isp.' should be approved as the legitimate abbreviations for ichnogenus and ichnospecies, respectively, for use in open nomenclature and the designation of new ichnotaxa. This requires extension of Appendix E 7 of the code (ICZN 1999) which would then read as 'A new name should be followed immediately by an appropriate statement in abbreviated form, such as 'gen. n.', 'sp. n.', etc., and 'igen. n.', 'isp. n.', etc. for ichnotaxa.'

References

Anderson, A.M. 1981: The *Umfolozia* arthropod trackways in the Permian Dwyka and Ecca series of South Africa. *Journal of Paleontology 55*, 84–108.

Baird, D. 1957: Triassic reptile footprint faunules from Milford, New Jersey. *Bulletin of the Museum of Comparative Zoology 117*, 49–520.

Bengtson, S. 1988: Open nomenclature. *Palaeontology 31*, 223–227.

Bertling, M. 1992: *Arachnostega* n. ichnog. – burrowing traces in internal moulds of boring bivalves (Late Jurassic, northern Germany). *Paläontologische Zeitschrift 66*, 177–185.

Bertling, M. 1999: What's hot in ichnofossils! Report on the International Workshop on Ichnotaxonomy, Bornholm, 3–9 August 1998. *Priscum 9*, 9–10.

Bertling, M., Braddy, S., Bromley, R.G., Demathieu, G.D., Mikuláš, R., Nielsen, J.K., Rindsberg, A.K., Schlirf, M. & Uchman, A. 2003: Draft proposal to emend the Code with respect to trace fossils: request for comments. *Bulletin of Zoological Nomenclature 60*, 141–142.

Blackwelder, R.E. 1967: *Taxonomy: a text and reference book*, 698 pp. Wiley, New York.

Blake, J.A. 1969: Systematics and ecology of shell-boring polychaetes from New England. *American Zoologist 9*, 813–820.

Braddy, S.J. 1995: The ichnotaxonomy of the invertebrate trackways of the Coconino Sandstone (Lower Permian), northern Arizona. *In* Lucas, S.G. & Heckert, A.B. (eds.): Early Permian footprints and facies. *Bulletin of the New Mexico Museum of Natural History and Science 6*, 219–224.

Braddy, S.J. 1998: An overview of the invertebrate ichnotaxa from the Robledo Mountains ichnofauna (Lower Permian), southern New Mexico. *In* Lucas, S.G., Estep, J.W. & Hoffer, J.M. (eds.): Permian stratigraphy and paleontology of the Robledo Mountains, New Mexico. *Bulletin of the New Mexico Museum of Natural History and Science 12*, 93–98.

Braddy, S.J. 2001: Trackways – arthropod locomotion. *In* Briggs, D.E.G. & Crowther, P.R. (eds): *Palaeobiology II*, 389–393. Blackwell Science, Oxford.

Braddy, S.J. & Briggs, D.E.G. 2002: New Lower Permian nonmarine arthropod trace fossils from New Mexico and South Africa. *Journal of Paleontology 76*, 546–557.

Brett, C. E. 1985: *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms. *Journal of Paleontology 59*, 625–635.

Bromley, R.G. 1968: Burrows and borings in hardgrounds. *Meddelelser fra Dansk Geologisk Forening 18*, 247–250.

Bromley, R.G. 1975: Trace fossils at omission surfaces. *In* Frey, R.W. (ed.): *The study of trace fossils*, 399–428. Springer, New York.

Bromley, R.G. 1981: Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geologica Hispanica 16*, 55–64.

Bromley, R.G. 1990: *Trace fossils: biology and taphonomy*, 280 pp. Unwin Hyman, London.

Bromley, R.G. 1994: The palaeoecology of bioerosion. *In* Donovan, S.K. (ed.): *The palaeobiology of trace fossils*, 134–154. Johns Hopkins, Baltimore.

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

Bromley, R.G. & Asgaard, U. 1972: Freshwater *Cruziana* from the Upper Triassic of Jameson Land, East Greenland. *Grønlands Geologiske Undersøgelse Rapport 49*, 7–13.

Bromley, R.G. & Asgaard, U. 1975: Structures produced by spatangoid echinoids: a problem of preservation. *Bulletin of the Geological Society of Denmark 24*, 261–281.

Bromley, R. G. & D'Alessandro, A. 1987: Bioerosion of the Plio-Pleistocene transgression of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia 93*, 379–442.

Bromley, R.G. & Frey, R.W. 1974: Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides, Ophiomorpha* and *Spongeliomorpha*. *Bulletin of the Geological Society of Denmark 23*, 311–335.

Bromley, R.G. & Fürsich, F.T. 1980: Comments on the proposed amendments to the International Code of Zoological Nomenclature regarding ichnotaxa. *Bulletin of Zoological Nomenclature 37*, 6–10.

Bromley, R.G., Schulz, M.-G. & Peake, N.B. 1975: Paramoudras: giant flints, long burrows and the early diagenesis of chalks. *Det Kongelige Danske Videnskabernes Selskabs Biologiske Skrifter 20 (10)*, 1–31.

Bromley, R.G., Pemberton, S.G. & Rahmani, R.A. 1984: A Cretaceous woodground: the *Teredolites* ichnofacies. *Journal of Paleontology 58*, 488–498.

Bromley, R.G., Uchman, A., Gregory, M.R. & Martin, A.J. 2003: *Hillichnus lobosensis* igen. et isp. nov., a complex trace fossil produced by tellinacean bivalves, Paleocene, Monterey, California, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology 192*, 157–186.

Courel, L. & Demathieu, G.D. 1976: Une ichnofaune reptilienne remarquable dans les grès Triasiques de Largentiere (Ardèche, France). *Palaeontographica A 151*, 194–216.

Crimes, T.P. 1970: The significance of trace fossils in sedimentology, stratigraphy, and palaeoecology with examples from Lower Palaeozoic strata. *In* Crimes, T.P. & Harper, J.C. (eds.): *Trace Fossils. Geological Journal, Special Issue 3*, 101–126. Seel House, Liverpool.

D'Alessandro, A., Loiacono, F. & Bromley, R.G. 1992: Marine and nonmarine trace fossils and plant roots in a regressional setting (Pleistocene, Italy). *Rivista Italiana di Paleontologia e Stratigrafia 98*, 495–522.

Demathieu, G.D. 1970: Les empreintes de pas de Vertébrés du Trias de la bordure N.-E. du Massif Central. *Cahiers de Paléontologie* [series without numbering], 1–211. Paris.

Demathieu, G.D. 1986: La notion d'ichnogenre dans le domaine de la palichnologie des Vertébrés. *Bulletin scientifique de Bourgogne 39*, 61–69.

Demathieu, G. & Demathieu, P. 2002: Concerning the erection of ichnogenera and ichnospecies in vertebrate ichnotaxonomy. *Ichnos 9*, 117–121.

Demathieu, G.D. & Haubold, H. 1974: Evolution und Lebensgemeinschaften terrestrischer Tetrapoden nach ihren Fährten in der Trias. *Freiberger Forschungshefte C 298*, 51–72.

Deshayes, G.-P. 1860: *Description des animaux sans vertèbres découverts dans le Bassin de Paris pour servir de supplément a la description des coquilles fossiles des environs de Paris comprenant une revue générale de toute les espèces actuellement connues: mollusques acéphalés I*, 912 pp. Baillière, Paris.

Edinger, E.N. & Risk, M.J. 1994: Oligocene–Miocene extinction and geographic restriction of Caribbean corals: roles of turbidity, temperature, and nutrients. *Palaios 9*, 576–579.

Eiserhardt, K.-H., Koch, L. & Eiserhardt, W.L. 2001: Revision des Ichnotaxon *Tomaculum* Groom, 1902. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 221*, 325–358.

Ekdale, A.A. 1980: Graphoglyptid burrows in modern deep-sea sediments. *Science 207*, 304–306.

Ekdale, A.A. & Bromley, R.G. 2001: A day and a night in the life of a cleft-foot clam: *Protovirgularia-Lockeia-Lophoctenium*. *Lethaia 34*, 119–124.

Ekdale, A.A. & Lewis, D.W. 1993: Sabellariid reefs in Ruby Bay, New Zealand: a modern analogue of *Skolithos* 'piperock' that is not produced by burrowing activity. *Palaios 8*, 614–620.

Fornos, J.J., Bromley, R.G., Clemmensen, L.B. & Rodriguez-Perea, A. 2002: Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Capriae) in Pleistocene aeolinites from Mallorca. (Balearic Islands, western Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology 180*, 277–313.

Foster, J.R. 2001: Salamander tracks (*Ambystomichnus*?) from the Cathedral Bluffs tongue of the Wasatch Formation (Eocene), northeastern Green River Basin, Wyoming. *Journal of Paleontology 75*, 901–904.

Frey, R.W. 1973: Concepts in the study of biogenic sedimentary structures. *Journal of Sedimentary Petrology 43*, 6–19.

Frey, R.W. & Cowles, J.G. 1972: The trace fossil *Tisoa* in Washington and Oregon. *The Ore Bin 34*, 113–119.

Fu, S. & Werner, F. 2000: Distribution, ecology and taphonomy of the organism trace, *Scolicia*, in northeast Atlantic deep-sea sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology 156*, 289–300.

Fürsich, F.T. 1973: A revision of the trace fossils *Spongeliomorpha, Ophiomorpha* and *Thalassinoides*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1973*, 719–735.

Fürsich, F.T. 1974: On *Diplocraterion* Torell 1870 and the significance of morphological features in vertical, spreiten-bearing, U-shaped trace fossils. *Journal of Paleontology 48*, 952–962.

Gaillard, C. 1991: Recent organism traces and ichnofacies on the deep-sea floor off New Caledonia, southwestern Pacific. *Palaios 6*, 302–315.

Genise, J.F. 1995: Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. *Ichnos 3*, 287–299.

Genise, J F. 1999: Paleoicnología de Insectos. *Revista de la Sociedad Entomológica Argentina 58*, 104–116.

Genise, J.F. 2000: The ichnofamily Celliformidae for *Celliforma* and allied ichnogenera. *Ichnos 7*, 26–28.

Genise, J.F. 2004: Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, termites and ants. *In* McIlroy, D. (ed.): The application of ichnology to palaeoenvironmental and stratigraphic analysis. *Geological Society of London, Special Publications 228*, 419–455.

Genise, J.F., Bertling, M., Braddy, S.J., Bromley, R.G., Mikuláš, R., Nielsen, J.K., Nielsen, K.S.S, Rindsberg, A.K., Schlirf, M. & Uchman, A. 2004: Comments on the draft proposal to emend the Code with respect to trace fossils. *Bulletin of Zoological Nomenclature 61*, 35–37.

Genise, J.F. & Bown, T.M. 1994: New trace fossils of termites (Insecta: Isoptera) from the late Eocene-early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior. *Ichnos 3*, 155–183.

Genise, J.F. & Hazeldine, P.L. 1998: The ichnogenus *Palmiraichnus* Roselli for fossil bee cells. *Ichnos 6*, 151–166.

Glaub, I. 2004: Recent and sub-recent microborings from the upwelling area off Mauritania (West Africa) and their implications for palaeoecology. *In* McIlroy, D. (ed.): The application of ichnology to palaeoenvironmental and stratigraphic analysis. *Geological Society of London, Special Publications 228*, 63–76.

Goldring, R. & Seilacher, A. 1971: Limulid undertracks and their sedimentological implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 137*, 422–442.

Goldring, R., Pollard, J.E. & Taylor, A.M. 1997: Naming trace fossils. *Geological Magazine 134*, 265–268.

Handley, S.J. & Bergquist, P.R. 1997: Spionid polychaete infestations of intertidal Pacific oyster *Crassostrea gigas* (Thunberg), Mahurangi Harbour, northern New Zealand. *Aquaculture 153*, 191–205.

Hänztschel, W. 1975: Part W, Miscellanea, supplement 1. Trace fossils and problematica, 2nd ed. (revised and enlarged). *In* Moore, R.C. & Teichert, C. (eds.): *Treatise on invertebrate paleontology*. Geological Society of America and University of Kansas Press, Boulder-Lawrence.

Haubold, H. 1971: Ichnia Amphibiorum et Reptiliorum fossilium. *In* Kuhn, O. (ed.): *Handbuch der Paläoherpetologie*, Teil 18, 124 pp. G. Fischer, Stuttgart.

Haubold, H. 1996: Ichnotaxonomie und Klassifikation von Tetrapodenfährten aus dem Perm. *Hallesches Jahrbuch für Geowissenschaften B 18*, 28−86.

Hering, E.M. 1951: *Biology of the leaf miners*, 420 pp. Junk's, Gravenhage.

Hirsch, K.F. 1994: The fossil record of vertebrate eggs. *In* Donovan, S.K. (ed.): *The palaeobiology of trace fossils*, 269−294. Johns Hopkins, Baltimore.

ICZN (International Commission for Zoological Nomenclature) 1999: *International Code of Zoological Nomenclature, adopted by the International Union of Biological Sciences, 4th ed*. 232 pp. International Trust for Zoological Nomenclature, London.

James, J.F. 1884−85: The fucoids of the Cincinnatian group. *Journal of the Cincinnati Society of Natural History 7*, 124−132, 151−166.

Książkiewicz, M. 1977: Trace fossils in the flysch of the Polish Carpathians. *Palaeontologia Polonica 36*, 1−208.

Labandeira, C.C. 2000: Timing the radiations of leaf beetles: hispines on gingers from Latest Cretaceous to Recent. *Science 289*, 291−294.

Lockley, M. 1998: Philosophical perspectives on theropod track morphology: blending qualities and quantities in the science of ichnology. *Gaia 15*, 279−300.

Löwemark, L. & Schäfer, P. 2003: Ethological implications from a detailed X-ray radiograph and ^{14}C study of the modern deep-sea *Zoophycos*. *Palaeogeography, Palaeoclimatology, Palaeoecology 192*, 101−121.

Magwood, J.P.A. 1992: Ichnotaxonomy: a burrow by any other name? *In* Maples, C.G. & West, R.R. (eds.): Trace fossils. *Paleontological Society Short Courses in Palaeontology 5*, 15−33.

Manning, P. L. 2004: A new approach to the analysis and interpretation of dinosaur tracks. *In* McIlroy, D. (ed.): The application of ichnology to palaeoenvironmental and stratigraphic analysis. *Geological Society of London, Special Publications 228*, 93−123.

Mikuláš, R. 1999: Notes on the concept of plant trace fossils related to plant-generated sedimentary structures. *Vestník Českého geologického ústavu 74*, 39−42.

Mikuláš, R. 2000: Trace fossils from the Middle Cambrian of the Barrandian area. *Práce Českého geologického ústavu 12*, 1−29.

Nielsen, K.S.S. & Nielsen, J.K. 2001: Bioerosion in Pliocene to late Holocene tests of benthic and planktonic foraminiferans, with a revision of the ichnogenera *Oichnus* and *Tremichnus*. *Ichnos 8*, 99−116.

d'Orbigny, A. 1847: Zoophytes. Voyages dans l'Amérique méridionale, 5 (4), 7−28. Paris.

Pabst, W. 1896: Thierfährten aus dem Oberrothliegenden von Tambach in Thüringen. *Zeitschrift der Deutschen Geologischen Gesellschaft 48*, 638−643.

Pemberton, S.G. & Frey, R.W. 1982: Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. *Journal of Paleontology 56*, 843−881.

Pemberton, S.G. & Frey, R.W. 1985: The *Glossifungites* ichnofacies: modern examples from the Georgia coast, U.S.A. *In* Curran, H.A. (ed.): Biogenic structures: their use in interpreting depositional environments. *Society of Economic Paleontologists and Mineralogists, Special Publication 35*, 237−259.

Pickerill, R.K. 1994: Nomenclature and taxonomy of invertebrate trace fossils. *In* Donovan, S.K. (ed.): *The palaeobiology of trace fossils*, 3−42. Johns Hopkins, Baltimore.

Pickerill, R.K. & Donovan, S.K. 1998: Ichnology of the Pliocene Bowden shell bed, southeast Jamaica. *Contributions to Tertiary and Quaternary Geology 35*, 161−175.

Pickerill, R.K. & Narbonne, G.M. 1995: Composite and compound ichnotaxa: a case example from the Ordovician of Quebec, eastern Canada. *Ichnos 4*, 53−69.

Pickford, M. & Dauphin, Y. 1993: *Diamantornis wardi* nov. gen, nov. sp., giant extinct bird from Roilepel, lower Miocene, Namibia. *Comptes rendus de l'Academie des Sciences Paris, série II 316*, 1643−1650.

Plaziat, J.C. & Mahmoudi, M. 1988: Trace fossils attributed to burrowing echinoids: a revision, including new ichnogenus and ichnospecies. *Géobios 21*, 209−233.

Pohowsky, R.A. 1978: The boring ctenostomate Bryozoa: taxonomy and paleobiology based on cavities in calcareous substrata. *Bulletin of American Paleontology 73*, 1−192.

Radwański, A. 1977: Present-day types of traces in the Neogene sequence; their problems of nomenclature and preservation. *In* Crimes, T. P. & Harper, J. C. (eds.): *Trace fossils 2*. Geological Journal, special issue 3, 227−264. Seelhouse, London.

Reineck, H.-E. & Flemming, B.W. 1997: Unusual tracks, traces and other oddities. *Courier Forschungsinstitut Senckenberg 201*, 349−360.

Rice, M.E. 1969: Possible boring structures of Sipunculida. *American Zoologist 9*, 803−812.

Richter, R. 1948: *Einführung in die zoologische Nomenklatur* (2nd ed.), 252 pp. Kramer, Frankfurt/M.

Rindsberg, A.K. 1990: Ichnological consequences of the 1985 International Code of Zoological Nomenclature. *Ichnos 1*, 59−63.

Rindsberg, A.K. 1994: Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations. *Geological Survey of Alabama, Bulletin 158*, 1−107.

Rindsberg, A.K. 1999: Workshop on ichnotaxonomy (WIT), Bornholm, Denmark, August 4−7, 1998. *Ichnology Newsletter 21*, 48−50.

Röder, H. 1977: Zur Beziehung zwischen Konstruktion und Substrat bei mechanisch bohrenden Bohrmuscheln (Pholadidae, Teredinidae). *Senckenbergiana Maritima 9*, 105−213.

Sadler, C.J. 1993: Arthropod trace fossils from the Permian De Chelly Sandstone, northeastern Arizona. *Journal of Paleontology 67*, 240−249.

Sarjeant, W.A.S. 1975: Plant trace fossils. *In* Frey, R.W. (ed.): *The study of trace fossils: a synthesis of principles, problems, and procedures in ichnology*, 283−324. Springer, New York.

Sarjeant, W.A.S. & Kennedy, W.J. 1973: Proposal of a code for the nomenclature of trace fossils. *Canadian Journal of Earth Sciences 10*, 460−475.

Schlirf, M. 2000: Upper Jurassic trace fossils from the Boulonnais (northern France). *Geologica et Palaeontologica 34*, 145−213.

Schlirf, M. 2002: Taxonomic reassessment of *Bolonia* Meunier, 1886 (trace fossil) based on new material from the type area in Boulonnais, northern France. *Paläontologische Zeitschrift 76*, 331−338.

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

Seilacher, A. 1964: Biogenic sedimentary structures. *In* Imbrie, J. & Newell, N.D. (eds.): *Approaches to paleoecology,* 299−316. John Wiley & Sons, New York.

Soot-Ryen, T. 1969: Superfamily Mytilacea Rafinesque, 1815. *In* Moore, R.C. (ed.): *Treatise on Invertebrate Paleontology, part N, 1 (Mollusca) 6 (Bivalvia)*: N271−280. Geological Society of America and University of Kansas Press, Lawrence.

Soule, J.D. & Soule, D.F. 1969: Systematics and biogeography of burrowing bryozoans. *American Zoologist 9*, 791−802.

Stoll, N.R., Dollfuss, R.P., Forest, J., Riley, N.D., Sabrosky, C.W., Wright, C.W. & Melville, R.V. (eds.) 1964: *International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology 1961*, 2nd ed. (2nd altered edition). 176 pp. International Trust for Zoological Nomenclature, London.

Sukacheva, I. D. 1982: The historical development of the order Trichoptera. *Proceedings of the Palaeontological Institute of the Russian Academy of Sciences 197*, 1−111. Moskva.

Tapanila, L. 2005: Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: Trace fossil evidence. *Lethaia 38*, 89−99.

Tasnádi-Kubacska, A. 1962: *Paläopathologie, Pathologie der vorzeitlichen Tiere*, 269 pp. Fischer, Jena.

Tassel, R. van 1965: Concrétions tubulées du Merkesmien (Pléistocène inférieur), à Anvers. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie 73*, 469−498.

Taylor, P.D. 1990: Preservation of soft-bodied and other organisms by bioimmuration − a review. *Palaeontology 33*, 1−17.

Trewin, N.H. 1994: A draft system for identification and description of arthropod trackways. *Palaeontology 37*, 811–823.

Tubbs, P.K. 2003: Comment on the draft proposal to emend the Code with respect to trace fossils. *Bulletin of Zoological Nomenclature 60*, 215–216.

Uchman, A. 1995: Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, northern Appenines, Italy). *Beringeria 15*, 1–115.

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

Uchman, A. 1999: Ichnology of the Rhenodanubian flysch (Lower Cretaceous – Eocene) in Austria and Germany. *Beringeria 25*, 67–173.

Vité, J.P. 1952: *Die holzzerstörenden Insekten Mitteleuropas*, 155 pp. Musterschmidt, Göttingen.

Vogel, K., Gektidis, M., Golubic, S., Kiene, W.E. & Radtke, G. 2000: Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: implications for paleoecological reconstructions. *Lethaia 33*, 190–204.

Voigt, E. 1972: *Amathia immurata* n.sp., ein durch Biomuration erhaltenes ctenostomes Bryozoon aus der Maastrichter Tuffkreide. *Paläontologische Zeitschrift 46*, 87–97.

Vyalov, O.S. 1966: *Sledy zhiznedeyatel'nosti organizmov i ikh paleontologicheskoe znachenie*, 219 pp. Naukova Dumka, Kiev.

Vyalov, O.S. 1972. The classification of the fossil traces of life. *Proceedings of the 24th International Geological Congress, section 7 (palaeontology)*, 639–644; Montreal.

Vyalov, O. S. 1973: Classification of the fossil caddis cases. *Dopovidi Akademii Nauk Ukrayinskoy SSR 7*, 585–588.

Wells, C. 1964: *Bones, bodies and disease: evidence of disease and abnormality in early Man*, 288 pp. Thames and Hudson, London.

Wetzel, A. 1991: Ecologic interpretation of deep-sea trace fossil communities. *Palaeogeography, Palaeoclimatology, Palaeoecology 85*, 47–69.