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Some ichnological concepts, methodologies, applications and frontiers

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Abstract: Ichnology straddles the boundary between palaeontology and sedimentology, and is becoming an increasingly important tool in both fields. For the palaeontologist, trace fossils allow insight into behaviour and biomechanics of animals that would otherwise be the subject of conjecture. For the sedimentologist, trace fossils have a marked impact on the interpretation of sedimentary rocks in that they destroy primary sedimentary structures, but can also reveal subtle palaeoenvironmental information beyond the resolution attainable by analysis of primary physical sedimentary structures. This contribution aims to review the major developments in the field of ichnology, and to highlight some of the tools and approaches currently used by ichnologists. A personal ethos for the study of trace fossils in core is outlined as a model ichnological protocol, and some of the frontiers of the science as a whole are briefly discussed.

Some landmarks in the history of ichnological research

From nomenclatural chaos to stability (ICZN)

Structures that we now recognize as trace fossils have been recorded and named in the literature for centuries. In the early history of palaeontology, a profusion of names was created for shapes preserved in rocks. In many subdisciplines of palaeontology, resolving these early names was a comparatively simple process. For ichnologists, however, sifting through the plethora of names of taxa commonly misidentified as sponges, seaweeds and plants has been a monumental task. The individual to whom we owe the greatest debt is Häntzschel (1962, 1965, 1975) for his monographic works on the numerous synonymies of many forms that were originally poorly documented and illustrated.

The task of ichnotaxonomy was made even more difficult by the International Zoological Congress (to whom all taxonomists look for guidance in taxonomic procedure), who initially insisted that, to be valid, all trace fossil names erected after 1930 were to be accompanied by a statement identifying the trace-making animal (ICZN 1964). The net effect of this was to render most post-1930 trace fossil names invalid. This is because ichnologists can seldom identify trace-making organisms; indeed a single trace may be made by many different taxa and – in the case of compound trace fossils – a single trace may be the work of several organisms (e.g. Pickerill & Narbonne 1995; Rindsberg & Martin 2003).

The approach taken by most ichnologists in response to the 1964 decision of the ICZN was to continue to apply the rules of the ICZN without the blessing of officialdom. However, in anticipation of a revised version of the ICZN, Sarjeant & Kennedy (1973) published a draft proposal for a separate ichnological code, adapted from the ICZN and its sister publication, the ICBN (International Code for Botanical Nomenclature). A less radical approach was taken by Häntzschel & Kraus (1972) and Sarjeant (1979), who proposed specific amendments to the pre-existing ICZN, which were eventually integrated into the subsequent version (Melville 1979; ICZN 1985) despite some fierce opposition to the inclusion of non-reproducing forms (e.g. Lemeche 1973). The ICZN (1985) therefore overturned the original ruling regarding the identification of trace-making organisms, rendering post-1930 ichnotaxa valid under the code regardless of whether a trace-maker could be identified, and vilifying the personal decision of most ichnotaxonomists to persist with applying the rules of the ICZN despite not being bound by them.

In the most recent edition of the ICZN (1999) ichnology seems to have been largely embraced by the zoological community. Trace fossil genera (ichnogenera) established after 1999 must have a designated type species (ichnospecies) (ICZN 1999, Article 66.1); for earlier established ichnotaxa no type species need be designated but may be assigned at a later date according to the rules (ICZN 1999, Article 69). The status of ichnotaxonomy is thus now firmly established as a subdiscipline of taxonomy and – thanks to the new provisions within the

Table 1. *The archetypal Seilacherian ichnofacies*

Ichnofacies	Predominant trace fossil types	Inferred control (Seilacher)
Skolithos	Vertical traces of suspension feeders	Bathymetry (above fair-weather wavebase, FWWB)
Cruziana	Horizontal and vertical deposit feeders	Bathymetry (between FWWB and storm wavebase, SWB)
Zoophycos	Pervasive deposit feeders	Bathymetry (shelf and slope below SWB)
Nereites	Shallow burrows with complex morphologies showing highly programmed behaviours	Bathymetry (basin-floor with turbidites)
Glossifungites	Traces characteristically preserving scratches, mostly of suspension feeders	Firm surfaces associated with incipient submarine lithification
Scoyenia	Non-marine traces	Freshwater conditions (red-bed deposition)

ICZN (1999) and the sensible taxonomic practices of ichnologists over the last 30–40 years – ichnology can only grow as a rigorous science.

Among the problems that do remain is the exclusion of modern traces by the International Code of Zoological Nomenclature (ICZN 1999, article 1.2.1), which restricts the use of ichnotaxa to fossil and not to modern traces. This regulation complicates the description of modern borings and burrows, but, as such incipient trace fossils may be incomplete, some taxonomic problems may thereby be avoided. The simplest means of making comparisons between modern traces and their ancient counterparts is to use the prefix ‘aff.’ to denote their affinity to a trace fossil while acknowledging that modern traces have no validity under the current ICZN. A grey area also exists in defining when a modern trace becomes a trace fossil: at abandonment of the burrow, at burial, or at lithification? Other issues, particularly the exact definition of what constitutes a trace fossil, are currently under discussion (see Bertling *et al.* 2003). Most modern ichnologists consider rootlets and other plant traces as trace fossils, though the ICZN is reluctant to include non-animal taxa for obvious reasons. It may therefore be that the simplest solution to these issues is for a separate ichnological code to be created and given some form of approval by the ICZN and ICBN. Such issues are as yet unresolved and remain a challenge.

Ichnofacies approach

The observations of Seilacher (1964, 1967) that recurrent associations of trace fossils could be recognized in the rock record represents the first widely applicable use of ichnology. Initially, six recurrent sets of trace fossils (named ichnofacies) were recognized by Seilacher (1967) and named for a characteristic trace fossil. The eponymous trace fossil need not be present for

identification of an ichnofacies, with the types of trace fossils/feeding strategy being diagnostic. These ichnofacies are widely used in palaeo-environmental interpretation (Table 1).

The archetypal Seilacherian ichnofacies (Table 1) were based largely on assemblages of traces in a particular lithofacies and related to a bathymetric gradient from shallow Skolithos to deep Nereites ichnofacies. The Scoyenia ichnofacies was however created differently, being an environment-led definition in contrast to the other behaviourally defined ichnofacies.

The recognition of these basic ichnofacies groupings was of great utility to sedimentologists as an aid to palaeoenvironmental interpretation. This work was immediately grasped by both the palaeontological and sedimentological communities, and was seminal in inspiring refined sedimentary facies models and in stimulating further classification of associations of trace fossils into additional ichnofacies. The subsequent proliferation of ichnofacies has been reviewed recently (Bromley 1996; Pemberton *et al.* 2001), and the most important are listed in Table 2. The controls on the distribution of ichnofacies have been conclusively demonstrated to be more than simply bathymetric (Fürsich 1975; Ekdale *et al.* 1984; Frey *et al.* 1990; Bromley & Asgaard 1991; Gierlowski-Kordesch 1991; Wetzel 1991; Fig. 1), but the ichnofacies themselves retain their usefulness albeit in modified form.

As can be seen from Table 2 there is no consistent ethos behind the creation of ichnofacies. The most anomalous of these are the vertebrate footprint ichnofacies and coprofacies, which are more likely to be trace fossil assemblages related to local palaeoecology and palaeobiology of producers than ichnofacies of inter-regional applicability. In addition, Bromley’s proposed *Fuersichnus* ichnofacies has been demonstrated from a variety of non-marine environments (Buatois & Mángano 2004).

Table 2. History of the development of the ichnofacies concept, highlighting the inferred palaeoenvironments of the later ichnofacies

Ichnofacies	Palaeoenvironment	Author(s)
Paleodictyon and Nereites ichnosubfacies	The deep marine ichnofacies was subdivided into Paleodictyon for sand-rich proximal turbidites and Nereites for mud-rich distal turbidites	Seilacher (1974) recognizes the first subdivision of one of the archetypal ichnofacies. Building on the work of Książkiewicz (1970); Crimes (1973)
Rusophycus	Fluvial/shallow lacustrine	Bromley & Asgaard (1979) as an ichnocoenosis, and as an ichnofacies by Bromley (1996)
Fuersichnus	Originally inferred to be representative of shallow lacustrine settings, below FWWB. Has subsequently been shown to extent to a variety of freshwater settings (Buatois & Mángano 2004)	Bromley & Asgaard (1979) as an ichnocoenosis and as an ichnofacies by Bromley (1996)
Trypanites	Lithic/hardground substrates	Frey & Seilacher (1980)
Teredolites	Woody (xylic) substrates	Bromley <i>et al.</i> (1984)
Redefined Scoyenia	Freshwater shallow lacustrine and fluvial settings	See emendation of original definition by Frey <i>et al.</i> (1984); Buatois & Mángano (1995)
Curvolithus	A subset of the Cruziana ichnofacies, found in settings with high sedimentation rates. Particularly delta and fan delta deposits	Lockley <i>et al.</i> (1987) based on the earlier Curvolithus ichnocoenosis of Heinberg & Birkelund (1984)
Psilonichnus	Coastal dunes	Frey & Pemberton (1987)
Arenicolites	A subset of Cruziana ichnofacies (opportunistic colonization of event beds)	Bromley & Asgaard (1991)
Mermia	Lacustrine turbidites	Buatois & Mángano (1993)
Entobia	Subdivision of Trypanites (boring traces)	Bromley & Asgaard (1993)
Gnathichnus	Subdivision of Trypanites (rasping traces of organisms feeding on the surface of lithic substrates)	Bromley & Asgaard (1993)
Termitichnus	Palaeosol ichnofacies including coprolites, rhizoliths and traces in xylic matter e.g. leaves	Smith <i>et al.</i> (1993), replaced by Coprinisphaera of Genise <i>et al.</i> (2000)
Laoporus Brasilichnium Brontopodus Caririchnium and 'Shorebird ichnofacies'	The variety of footprint assemblages represent a diverse array of palaeoenvironments, though their facies specificity is in doubt, and the separation of Laoporus and Brasilichnium on stratigraphic grounds is not well founded	Lockley <i>et al.</i> 1994
Coprofacies	Based on the distribution of various coprolite types. The facies-specificity of coprolites is in doubt and has not been widely used to date	Hunt <i>et al.</i> (1994)
Coprinisphaera	Palaeosols with insect nests	Genise <i>et al.</i> (2000)
Ophiomorpha rudis ichnosubfacies	Subdivision of Nereites ichnofacies proposed for channel and lobe to lobe fringe environments but is only recognized from Eocene and younger strata	Uchman (2001)

The similarities between some non-marine and marine ichnofacies, as highlighted by Bromley (1996), demonstrates parallel behavioural evolution in the non-marine and marine realms, presumably due to comparable environmental controls. The notable exception is the near-absence of a deepwater mudstone ichnofacies in non-marine settings, which is probably due – at

least in part – to the predominance of anoxia resulting from thermal stratification in lakes (Buatois & Mángano 2004). This increased reliance upon interpretation of sedimentary environment before ichnological characterization (subjective ichnofacies *sensu* Reading 1978) suggests that there is little utility in continuing to create archetypal ichnofacies – a stance

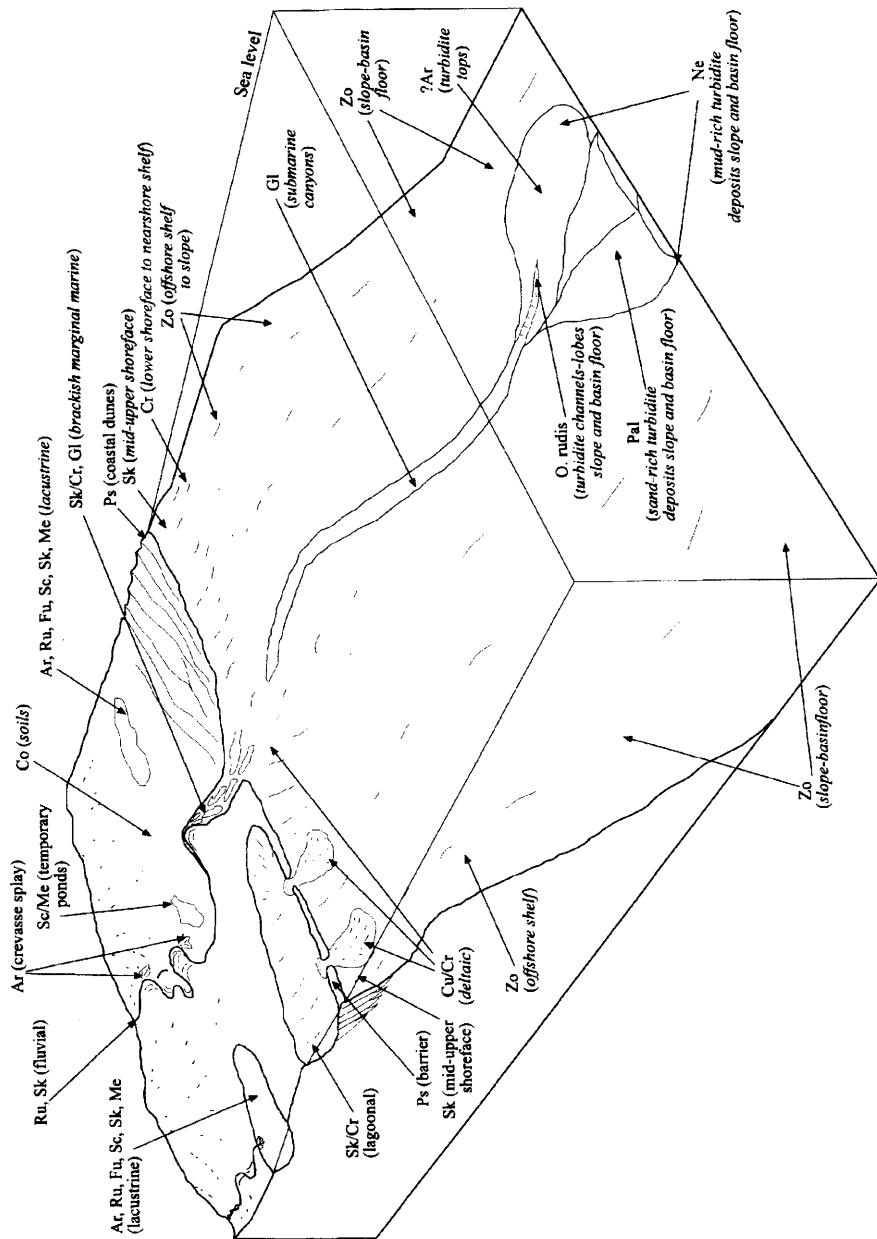


Fig. 1. Summary diagram showing current thinking on the likely distribution of the main soft/loose and firmground ichnofacies (based on Bromley 1996) and based on condition of still-stand of sea-level. Ar, *Arenicolites* ichnofacies; Cu, *Curvulithos* ichnofacies; Co, *Coprinites* ichnofacies; Cr, *Cruziana* ichnofacies; Fu, *Fuersichnus* ichnofacies; Gl, *Glossifungites* ichnofacies; Ne, *Nereites* ichnofacies; Ru, *Rusophycus* ichnofacies; Ps, *Psilonichnus* ichnofacies; Sc, *Scoecenia* ichnofacies; Sk, *Skolithos* ichnofacies; Zo, *Zoophycos* ichnofacies. During marine flooding events and sea-level fall some ichnofacies become more widespread (e.g. *Glossifungites* ichnofacies).

Table 3. Characteristics that make fossils good zone fossils; the ideal zone fossil would fulfil all criteria

Characteristic	Rationale
Rapidly evolving, i.e. narrow stratigraphic range	Improves resolution of biozone
Widespread distribution	Eases interregional correlation
Good preservation potential	Improves chances of occurrence in a given rock unit
Abundance	Improves chances of occurrence in a given unit
Facies independence	Allows correlation independent of palaeoenvironment
Easy identification	Allows use by non-experts

supported by Goldring (1993, 1995) and discussed further below in terms of ichnofabric analysis and ichnocoenoses.

Ichnostratigraphy

Biostratigraphy is the methodology by which stratigraphers can subdivide the rock record, and correlate from region to region using the record of evolution and extinction of fossil taxa. The basic subdivision of stratigraphic time is the zone, and the fossils that define those zones are known as zone fossils.

In accordance with the criteria in Table 3, the best zone fossils are likely to be rapidly evolving organisms with a pelagic portion to their lifecycle (improves distribution), and should comprise distinctive hard body parts. Thus trace fossils generally make poor zone fossils – due largely to the benthic lifestyle of trace-making organisms – except during intervals where benthic organisms that produce distinctive burrows evolve rapidly. Convergent behavioural evolution is the norm in ichnology, which accounts for the longevity of most ichnotaxa; convergent evolution of burrowing organisms has also been demonstrated (cf. Seilacher 1994). Bio-events that have the potential to include trace fossils of biostratigraphic significance include radiation events, and the evolution of distinct trace-making groups.

Radiation events

Neoproterozoic-Cambrian. The Cambrian Radiation is perhaps the most dramatic of all the radiation events in the stratigraphic record, being the period of time in which most anatomical design becomes established. Many of the taxa represented by this diversification of body form were benthic in nature, and ‘experimentation’ in body form and behaviour are to be expected. It is thus unsurprising that this period has been identified by a number of authors as having excellent potential for ichnostratigraphy (Crimes 1975, 1987, 1992; Alpert 1977; Fedonkin *et al.* 1983; Narbonne *et al.* 1987). The most

robust of these have been the schemes of Crimes (1975, 1987, 1992), which included a vast dataset of Neoproterozoic to Cambrian occurrences but rely on unpublished stratigraphic inferences. The most widely used ichnozones are those based on the Neoproterozoic-Cambrian type section in southeastern Newfoundland erected by Narbonne *et al.* (1987). Indeed the boundary itself was defined at the junction between the *Harlaniella podolica* and *Phycodes pedum* ichnozones (Brasier *et al.* 1994).

Other radiation events. The early terrestrialization event has the potential to yield biostratigraphic data, but such sections do not yield abundant ichnological data and there is a potential problem with likely endemicity and diachroneity of early non-marine faunas/ichnofaunas. Rapid radiation is also recorded after major extinction events (see Twitchett & Barras 2004), such as the Permo-Triassic extinction event, which is estimated to have eradicated 96% of all family-level diversity (Jablonski 1991). Importantly, however, no phylum is known to have become extinct at that particular stratigraphic level so – although there was rapid radiation – no fundamentally new body plans evolved or died out, which limits the potential usefulness of ichnostratigraphy, but the stepwise reappearance of ichnotaxa can be of stratigraphic utility (Twitchett & Barras 2004).

Evolution of distinct trace-making groups

Palaeozoic arthropods. One of the first direct applications of ichnology to petroleum geology was the development of an ichnostratigraphic scheme for the correlation of peri-Gondwanan shallow marine ‘unfossiliferous’ quartzites (Seilacher 1970, 1985, 1992, 1993; Fig. 2), which are important reservoir intervals throughout the Middle East and North Africa. The main trace fossils involved in this ichnostratigraphic scheme are ichnospecies of *Cruziana* and related arthropod trace fossils. Such traces are abundant both in core and in outcrop, but body fossils are notoriously rare. The concept of basing an ichnostratigraphic scheme on Lower Palaeozoic arthropod traces is thus well founded in that

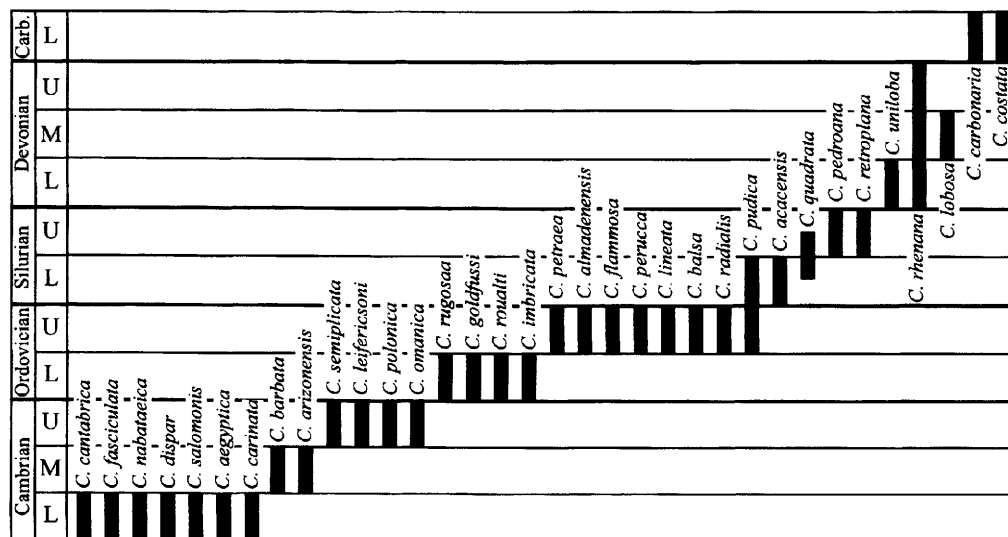


Fig. 2. The *Cruziana* ichnostratigraphy of Gondwana (redrawn from Seilacher 1992).

they are abundant and widely distributed, and the trace-makers (trilobites and other arthropods) were rapidly evolving during this phase in their history. The drawback with the use of the scheme is that the trace-making arthropods are benthic and thus prone to provincialism (cf. Magwood & Pemberton 1988). In addition, many of the characters used to define the ichnospecies upon which the scheme relies are only rarely seen in material other than the exquisitely preserved type material. The majority of material examined in the field can thus be difficult to identify by the non-expert.

Triassic–Jurassic. During the Permian through to the Jurassic footprints of the archosaurs are comparatively common, particularly in Europe (Haubold 1984), North America (e.g. Olsen 1980) and South Africa (Ellenberger *et al.* 1970). The rapid evolution of the archosaur faunas is reflected in their changing footprint morphologies from early (Triassic) *Cheirotherium*-type footprints to later (Jurassic) tridactyl footprints such as the ichnogenus *Grallator*. Such schemes are reliant upon an abundance of well-preserved surface tracks, and have been well calibrated by accessory biostratigraphic data (e.g. Cornet & Traverse 1975). The difficulties of recognizing surface tracks make an awareness of possible under-track artefacts an invaluable skill (Manning 2004). In particular, features such as detached heel-like structures and ‘spurs’ in some ichnospecies of *Brachycheirotherium* may be related to transmitted heel structures (see Manning 2004, figs 17c, 21b,

22c). Vertebrate footprint ichnotaxonomy is a particularly difficult field, and much work needs to be done to fully appreciate which characters are useful for ichnotaxonomy.

Tertiary. The radiation of terrestrial insects is well reflected in the fossil record of their burrow chambers, which is a taxonomic character widely used to identify modern insect taxa. The radiation of insects in the Tertiary was extremely rapid, and their distribution is highly sensitive to regional climatic shifts (Genise 2004). The Insecta are widely dispersed owing to their commonly airborne adult phase, presence in a range of non-marine environments, and their easily characterized egg chambers that have a high preservation potential. The Insecta with their staggered first occurrence datums thus fit the optimal characteristics of a zone fossil (see Table 3).

Seafloor and sediment oxygenation

One of the most fundamental controls on the distribution of benthic animals and their trace fossils in aqueous environments is the availability of dissolved oxygen. This may be present either in bottom waters or in porewaters, but is essential for all metazoan life. The links between ichnological/benthic macrofossil distributions and bottom water oxygenation are well established (Bromley & Ekdale 1984; Savrda & Bottjer 1987; Ekdale & Mason 1988), though recent work (Schieber 2003) has demonstrated the need for

careful assessment of apparently unbioturbated sediments through work with image analysis. Appreciation of the role of sediment anoxia in ancient successions is immature, though the impact of sediment anoxia on modern shallow marine taxa is well known (e.g. Pike *et al.* 2001 and references therein). Likewise, Wignall (1993) has correctly highlighted the fact that changing substrate conditions can favour depauperate ichnofaunas similar to those that typify anoxic bottom-water conditions.

Sediments deposited in low-oxygen settings results are generally rich in organic carbon and thus have a high source rock potential to petroleum systems (e.g. Oschmann 1991a, b; Wignall 1994). Determination of the palaeo-oxygenation of such sediments can be approached by geochemical means as well as through ichnology and palaeoecology (Wignall & Myers 1988; Wilkins *et al.* 1996; Wignall & Newton 2001). The organically rich nature of these facies also means that they are a potential treasure-trove of nutrients for deposit-feeding organisms (Diego & Douglas 1999). Colonization during amelioration of low-oxygen conditions by an opportunistic fauna is a common phenomenon that is documented in both modern and ancient sediments (e.g. Sagemann *et al.* 1991; Savrda & Bottjer 1991; Wignall & Pickering 1993; Bromley *et al.* 1995; Smith *et al.* 2000; Martin 2004; Fig. 9). Indeed, the ecology of deep-sea sites in general is now becoming much better known (e.g. Kaufmann & Smith 1997). Recent work has also highlighted the role of chemosymbiosis as a feeding strategy in such settings (Paull *et al.* 1984; Hovland & Thomsen 1989) and has led to the reinterpretation of some trace fossils as being the result of such behaviour (Seilacher 1990; Fu 1991).

Sequence stratigraphy

Perhaps the most significant predictive stratigraphic tool developed in recent years is that of sequence (seismic) stratigraphy, which was developed by Exxon Production Research Co. in the late 1970s (Vail *et al.* 1977), and has since been further refined and debated (see the excellent review of Nystuen 1998). The basic model involves the recognition of unconformity-bound packages of sediment (sequences), which can be related to cycles of relative sea-level change. Within these sequences higher frequency increases in relative sea-level can be recognized (flooding surfaces), which (envelope) progradational sedimentary packages known as parasequences. The study and correlation of

these parasequences is known as high-resolution sequence stratigraphy (Howell & Aitken 1996).

The majority of integrated ichnological/sequence stratigraphic approaches have employed the use of trace fossils, either in the recognition of key stratigraphic surfaces (e.g. Bromley & Goldring 1992; Taylor & Gawthorpe 1993; Ghibaudo *et al.* 1996; Olóriz & Rodríguez-Tovar 1999; MacEachern *et al.* 1999; Malpas 2000; Pemberton *et al.* 2000; Uchman *et al.* 2000) or for improved broad-scale facies interpretations based on a refined ichnofacies-based approach (e.g. Vossler & Pemberton 1988; Frey & Howard 1990; Savrda 1991; Brett 1998; Siggerud & Steel 1999; Pemberton *et al.* 2001).

Despite the firm establishment of the ichnofabric/ichnocoenosis approach to improved facies and stratigraphic analysis (Bockelie 1991; Taylor & Gawthorpe 1993; Taylor & Goldring 1993; Taylor *et al.* 2003; Schlirf 2003), this methodology has been underused (but see Bockelie 1991; Martin & Pollard 1996; Schlirf 2003; McIlroy 2004). The advantage of the ichnofabric/ichnocoenosis approach is that its focus is improved characterization of facies – the fundamental building block of sequence stratigraphy – through improved understanding of trace fossil fabrics and seafloor ecology with respect to the host sediments. Once established, an ichnofabric scheme can be used to assess stacking patterns, while simultaneously enhancing ichnological characterization of key stratigraphic surfaces (McIlroy 2004).

It is regrettable that most sedimentology textbooks focus on Seilacherian ichnofacies (e.g. Frey & Pemberton 1984; Pemberton *et al.* 1992, 2001), rather than also encompassing the more flexible ichnofabric/ichnocoenosis approach outlined below (the notable exception being Goldring 1999).

An ichnological ethos

What follows is a personal approach to the study of trace fossils and ichnofabric, which is designed largely for the study of marine clastic depositional systems (the author's own main focus of research). The basic methodology is of wider application, but should be adapted to the needs of the particular ichnological/sedimentological problem addressed, e.g. non-marine terrestrial systems (see Genise *et al.* 2004) and carbonate systems (e.g. Curran 1994).

The reader should be aware that there are many ways to approach ichnological studies, and that no single approach is correct. All have their strengths.

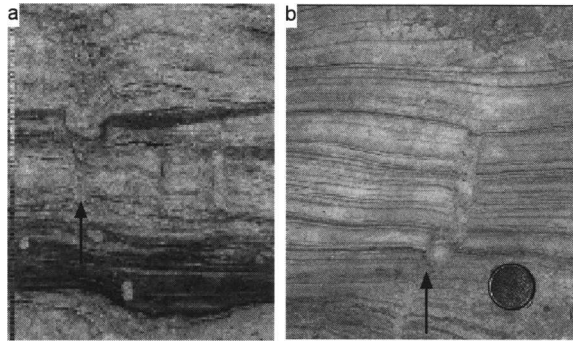


Fig. 3. Comparison of two cross-bedded sandstones with the bivalve escape burrow aff. *Lockeia* (arrowed): (a) represents a non-marine crevasse splay sandstone from the Carboniferous of Northumberland, England (scale bar in mm); and (b) a tidally deposited sandstone Jurassic, Neuquén Basin, Argentina. Ichnotaxonomically, the two specimens are ichnologically similar but sedimentological observations allow recognition of a tidal depositional environment through tidal bundling.

Scale of observation

As with most sedimentological studies, the ultimate aim of an ichnological study commonly determines the resolution at which data are recorded. For example, when looking for long timescale changes in bioturbation, in a thick, sedimentologically homogeneous Neoproterozoic-Cambrian succession, McIlroy & Logan (1999) used decimetre-scale observations of ichnofabric index (*sensu* Droser & Bottjer 1986, 1989, 1991). In contrast, when studying the highly heterogeneous tidal deposits of a tide-dominated deltaic system, the same author made ichnological and sedimentological observations on a centimetre scale (McIlroy 2004).

The key to producing scientifically valid, usable, data is thus to choose an appropriate scale at which to collect ichnological and sedimentological data. The constraints are commonly time available (often a problem when working to industry deadlines), volume of data required/desired, and the inherent variability of the sedimentary succession. Observations should of course always be made in close detail if possible, but if nothing is found in a thick package of homogeneous sand there is little advantage in making numerous statements describing the lack of sedimentological/ichnological features. A conspicuous lack of trace fossils is in itself revealing though, and an important observation in need of explanation.

Sedimentological context

In getting the maximum amount of information from a sedimentary rock it is imperative that

no information is disregarded. In the same way that many sedimentologists record trace fossils as 'bioturbation', so many palaeontologists/ichnologists record the host sediment as sandstone/shale etc. without due regard to the physical sedimentary structures contained therein (Fig. 3). The sedimentologist should look to ichnology to help understand sedimentologically homogeneous rocks (e.g. Gowland 1996; Martin & Pollard 1996; McIlroy 2004). Likewise, the ichnologist may learn about the likely spatio-temporal distribution of ichnofabrics by full consideration of likely sandstone body geometries and stacking based on sedimentological information. Although ideally we should all be transdisciplinary geoscientists, the reality is that for most geologists collaboration and open discussion is the way forward; this is especially so between sedimentologists and ichnologists.

Quantification of bioturbation

The need to quantify the extent to which animals modify sedimentary fabrics has been recognized since the early days of modern ichnology. Many attempts to produce an easy-to-use scheme for the documentation of this bioturbation have been proposed (e.g. Moore & Scrutton 1957; Reineck 1963; Howard & Frey 1975; Frey & Pemberton 1984; Droser & Bottjer 1986, 1989, 1991; Taylor & Goldring 1993). Most of these rely upon estimating the proportion of sedimentary fabric/laminations destroyed by the burrowing activity of animals (i.e. bioturbation). These need to quantify the fabric as seen in vertical cross-section is a bias introduced by the predominance of studies of shallow box

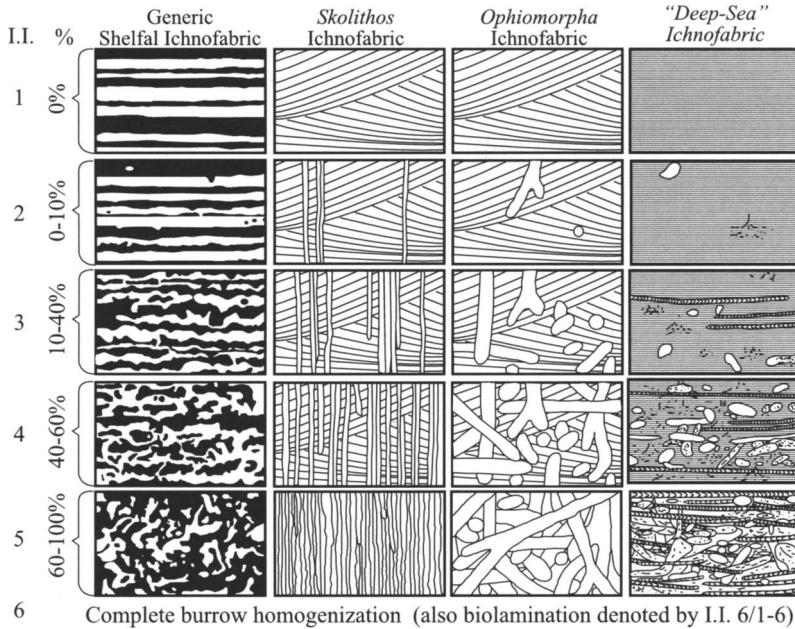


Fig. 4. Ichnofabric indices exemplified by flashcards according to the scheme of Droser & Bottjer (1989); redrawn with permission. Shows the proportions of sediment reworked by bioturbation as seen in vertical cross-section.

cores (modern sediments) and sediment/rock cores (e.g. in oil field studies).

The most usable of these schemes is the semi-quantitative flashcards of Droser & Bottjer (1986, 1989, 1991; Fig. 4), which have been used with success by a number of authors (e.g. Droser & O’Connell 1992; McIlroy & Logan 1999). This approach has recently been extended to include a flashcard methodology for quantification of the extent of bioturbation on bedding planes (Miller & Smail 1997; Fig. 5). A similar, but more sophisticated, means of graphically representing quantitative and semi-quantitative aspects of trace fossil fabrics in vertical section has been proposed by Taylor & Goldring (1993), and is discussed in detail below (Fig. 6).

Ichnofabric analysis

The component of a sediments texture created by the action of animals is known as its ichnofabric. Ichnofabric may be created either by bioturbation (in loose sediment) or by bioerosion (in lithified sediment) by a diverse array of organisms from microbes (e.g. Glaub 2004; Fig. 7a) to dinosaurs (e.g. Manning 2004; Fig. 7b). One of the features of trace-making organisms is that they are commonly highly sensitive to their environment and can thus provide a record of

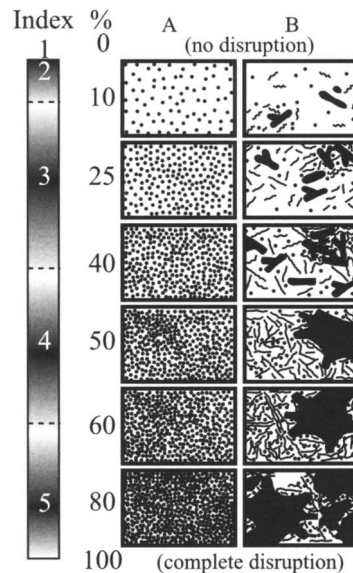


Fig. 5. Flashcards showing the proportion of bedding planes covered by trace fossils from Miller & Smail (1997), as classified into ‘bedding plane bioturbation indices’. Column A represents example bedding planes covered by trace fossils of even size and shape with even distribution; Column B represents example bedding planes covered by trace fossils of different sizes and shapes and with uneven distributions (redrawn with permission).

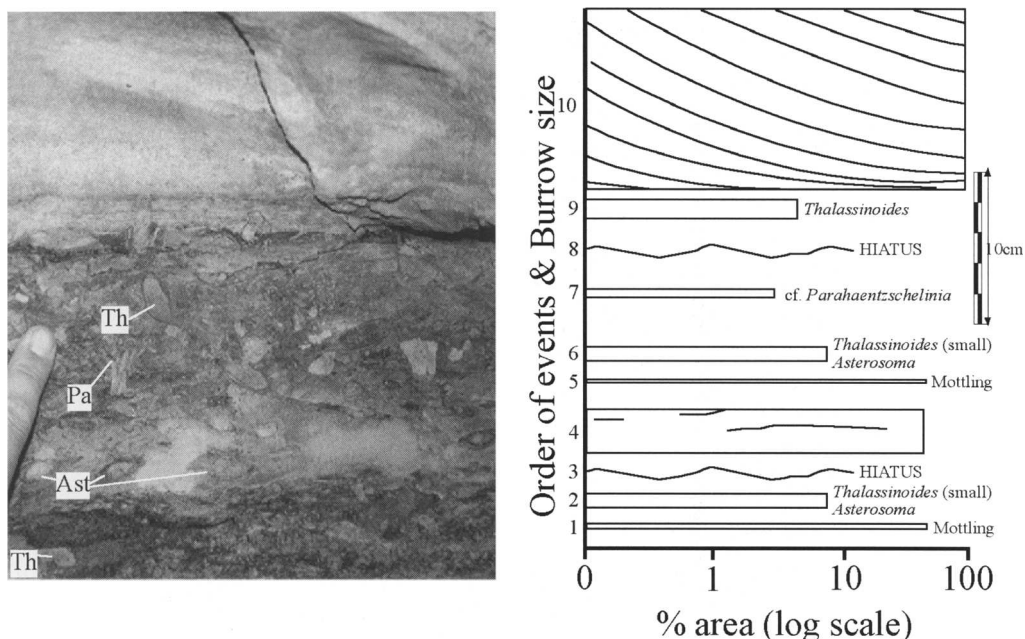


Fig. 6. Example of a modified ichnofabric constituent diagram adapted from Taylor & Goldring (1993) expressing the ichnofabric of an outcrop from the Lajas Formation, Neuquén Basin, Argentina. Ast, *Asterosoma*; Pa, cf. *Parahaentzschelima*; Th, *Thalassinoides*. Note that the horizontal scale is used at the base of the diagram, which is the author's personal preference.

palaeoenvironmental conditions before, during and after deposition of a bed (Fig. 8). When considering physical sedimentary structures alone, information can be gleaned only about conditions at the time of deposition, which in many cases (e.g. hurricane-deposited sandstone beds on the normally quiescent proximal shelf) can be anomalous. The modern sedimentologist should therefore not only be able to record the presence of bioturbation but also be able to combine information from sedimentary structures and other macro/micropalaeontological data in

order to fully characterize their facies and understand their palaeoenvironment of deposition. As discussed above, ichnofabrics are best investigated on a bed-by-bed scale, which normally requires sedimentary logging at a scale of at least 1:50. The features of ichnofabric that should be recorded during routine investigation of sedimentary rocks include:

- intensity of bioturbation;
- diversity;
- relative abundance;

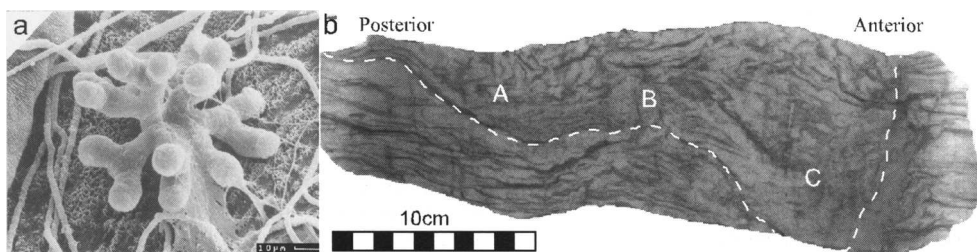


Fig. 7. Different scales of ichnofabric development: (a) artificial casts of microborings similar to *Fasciculus* in a shell clast (Recent of Mauritania courtesy of I. Glaub); (b) vertical cross-section through a dinosaur track showing bioturbation by a large bipedal dinosaur from the Jurassic Scalby Formation of Yorkshire, UK ('dinoturbation' of some authors) (courtesy of P. Manning).

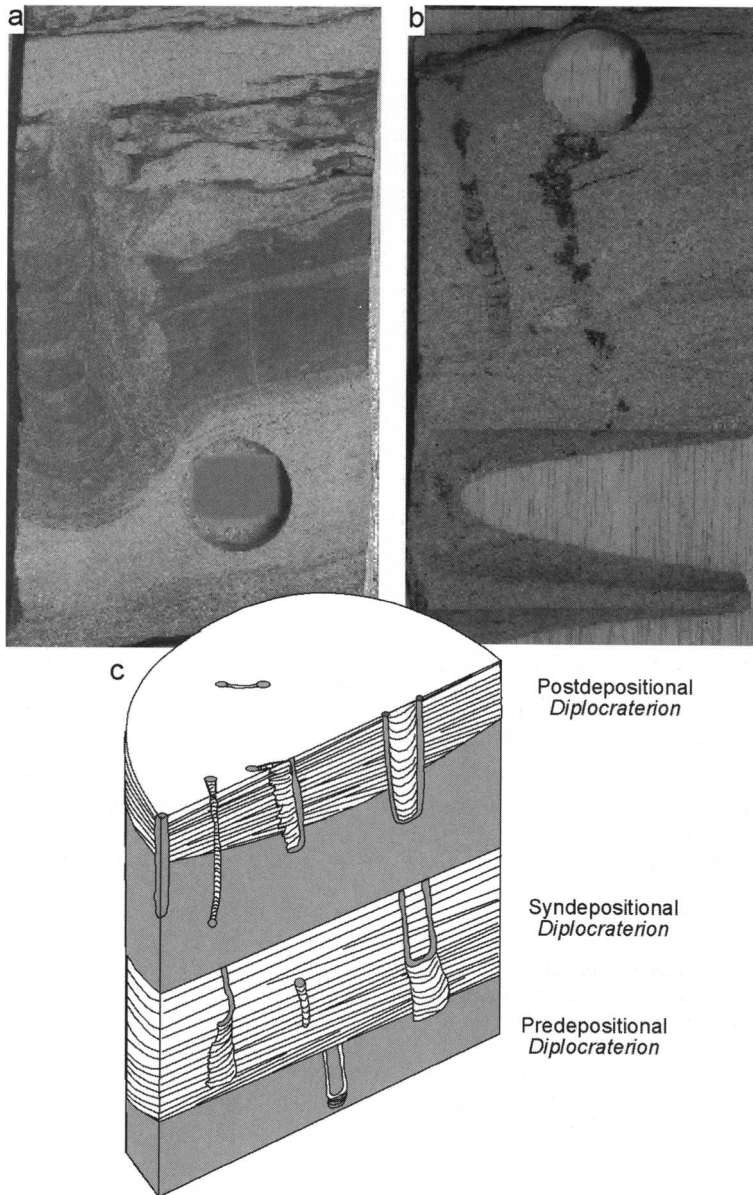


Fig. 8. Cored section with *Diplocraterion parallelum* seen in (a) longitudinal and (b) transverse cross-sections. The greatly different proportions of the cut surface covered by traces is dependent on the section taken. The percentage by volume of core bioturbated is in both cases c. 40%.

- ichnometry;
- infaunal tiering;
- succession of bioturbation;
- colonization styles.

Intensity of bioturbation

Sedimentologists should approach this using one of the many 'bioturbation index' schemes as

described in the section above. The present author recommends either the ichnofabric index schemes of Droser & Bottjer (1986, 1989, 1991), or bed-by-bed estimation of bioturbation as a percentage. It is emphasized, however, that the parameters outlined below should also be investigated in order to make the most of the available ichnological data. It must also be remembered

Environmental Conditions	Simple colonization & Simple tiering	Simple colonization & Complex tiering	Compound colonization	Characteristic effect on ichnofabric
Sudden inundation preserving frozen tier profile				Sudden inundation of an infaunal community can cause the complete preservation of the tiering profile of a sediment. With slow burial however escape burrows may be formed. Frozen tiers allow us to confidently assess the normal community structure of the sediment.
Rapid continuous sedimentation				Rapid continuous sedimentation can improve the preservation potential of shallow tiers and early rapidly formed components of the ichnofabric e.g. pioneer ichnocoenoses. It generally discourages large semi-permanent burrows like <i>Thalassinoides</i> . Traces showing escape (equilibration) behaviour may also be common components
Rapid episodic sedimentation				Rapid discontinuous sedimentation improves the preservation potential of early components of the ichnofabric e.g. pioneer ichnocoenoses. But may result in erosion of shallow tiers. Traces showing panic escape behaviour (rather than equilibration) may also be common components of the ichnofabric.
Slow continuous sedimentation				Slow continuous sedimentation tends to result in ichnofabrics dominated by elite (usually deep tier) trace fossils at the expense of the shallow tiers and can thus give a highly biased impression of the original ichnocoenoses.
Softground hiatus				Ichnofabrics deposited at a hiatal surface are commonly visually complex due to multiple phases of re-burrowing. Tiering profile tends to be retained, with elite trace fossils dominant. In some cases a succession of ichnocoenoses may be elucidated recording a deepening event. Early seafloor diagenesis is also common.
Environmental amelioration				With palaeoenvironmental amelioration ichnodiversity and intensity of bioturbation tend to increase rapidly. In some cases a pioneer ichnocoenosis may be recognised composed of trophic generalists tolerant of harsh environmental conditions e.g. <i>Planolites</i> and <i>Chondrites</i> and components of the Arenicolites ichnofacies.
Environmental deterioration				With palaeoenvironmental deterioration ichnodiversity, intensity of bioturbation and trace size tend to decrease rapidly, eventually resulting in unbioturbated sediments. Typical environmental changes include salinity change, palaeo-oxygenation and increasing current strength.

Fig. 9. Example ichnofabrics as developed under a range of palaeoenvironmental and sedimentological conditions.

that ichnofabric is a 3D phenomenon, and that examination of a 2D surface (e.g. a cut surface of a core) can be misleading; if possible, an impression of ichnofabric in the opposite plane should be sought in order to estimate the percentage bioturbation as a volume (see Fig. 8).

Diversity

Ichnological diversity is comparatively simple to measure from both core and outcrop sections, with experience. The number of trace fossils

present within a rock unit can be simply quantified, though care must be taken (especially in core) to ensure that a single trace in different orientations (e.g. different cross-sections of the same trace) is not counted twice. Although trace fossil diversity cannot be directly related to biological diversity it is usually considered as a reasonable proxy. For example, a diverse fauna of shallow infaunal bivalves may only produce two trace fossils (*Lockeia* as the resting trace and *Protovirgularia* as the locomotory

trace). In most cases, however, high ichnological diversity corresponds to amenable palaeoenvironmental conditions, and low diversity or lack of bioturbation to harsh palaeoenvironments. The exact causes of environmental stress are diverse and must be assessed on a case-by case basis using ichnological, palaeontological, sedimentological and sometimes geochemical/palynological means. It is also observed that ichnological diversity is more difficult to assess in core materials where identification below the level of ichnogenus is seldom possible and the morphology of complex branching forms is difficult if not impossible to recognize (except on the limited number of bedding surfaces).

Relative abundance

Merely presenting the number of different trace fossils present within a rock unit can be a misleading piece of information where the assemblage is dominated by a single ichnotaxon with minor accessory components. Documentation of the relative volumetric proportions of all traces within an ichnofabric and their relative chronology is the fundamental procedure behind good ichnofabric analysis. This can be particularly instructive if combined with simple

(but tentative) interpretation of the likely trophic niche of the trace-maker.

Ichnometry

In addition to documenting the diversity and abundance of traces, the dimensions of the burrows themselves can be of great importance. The parameter that is most easily recorded is burrow diameter. Studies have shown that trace fossils become narrower with increased salinity stress (Hakes 1976; Gingras *et al.* 1999) and decreasing dissolved oxygen in porewaters/bottom waters (e.g. Bromley & Ekdale 1984). This reflects well-known biological trends in such settings (e.g. Milne 1940; Remane & Schlieper 1971). In addition, during some periods of rapid evolution there is a stratigraphic component, in which burrow size increases with time, e.g. the Cambrian explosion (McIlroy & Logan 1999).

Infaunal tiering

The distribution of organisms (and their traces) below the sediment is known as tiering. The preservation of a tiering profile is reliant upon rapid killing off of the community (e.g. burial under an event bed or death of the community

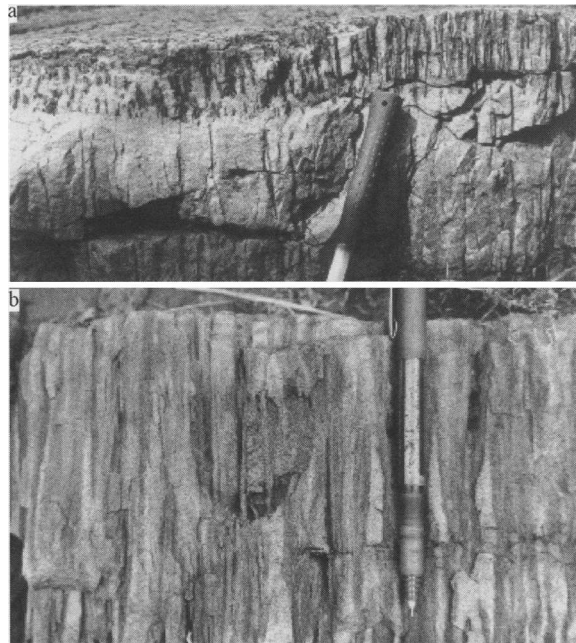


Fig. 10. Ichnofabrics in outcrops of the Pacoota Sandstone, Amadeus Basin, central Australia showing: (a) environmental deterioration represented by a decrease in burrow size of *Skolithos*; (b) development of an early *Arenicolites*-dominated ichnocoenosis (*Arenicolites* ichnofacies) cross-cut by a later, *Skolithos*-dominated, ichnocoenosis (*Skolithos* ichnofacies). The upper bed probably represents a single spatfall as all burrows are the same (small) size. The small size of traces may represent burrows of juveniles buried during a phase of gradually increasing bioturbation.

due to an anoxic event), because – with continuing deposition – deeper burrows tend to overprint shallower ones (Fig. 10b). This tiering of the infaunal community is typically considered to be a response to partitioning of the infaunal realm into different niches occupied by organisms with different feeding strategies (Bottjer & Ausich 1982; Bromley 1990, 1996; Wetzel & Uchman 1998). The occupants of these different niches, which share similar feeding strategies, have been grouped into ‘ichnoguilds’ by Bromley (1990), though these rely to a large degree on interpretation of behaviour, which is notoriously difficult to determine with accuracy for most trace fossils. Diagrammatic representation of tiering may be done using either the tiering diagrams of Bromley (1996, p. 295, fig. 12.11) and Wetzel & Uchman (2001) or the more integrated ichnofabric constituent diagrams (ICD) of Taylor & Goldring (1993; see the modified ICD in Fig. 6). More importantly however, several authors appear to use ‘complex tiering’ for all visually complex ichnofabrics (Taylor & Goldring 1993; Taylor *et al.* 2003). Complex ichnological tiering is defined herein as being formed

in a sediment in which the trace-making organisms are vertically partitioned into tiers containing more than one trace fossil (see Fig. 9). Multiple occupancy of a given tier should be demonstrable by mutual cross-cutting of the tier’s occupant traces (see below).

Succession of bioturbation

Understanding the order of emplacement of burrows and tracks is a fundamental skill that all modern ichnologists should incorporate into studies aimed at palaeoenvironmental analysis. The recognition of successive cross-cutting palaeocommunities (ichnocoenoses, see below) associated with the same sedimentary unit can lead to an improved understanding of the colonization history and/or changing palaeoenvironmental conditions subsequent to the deposition of a given bed (cf. Wetzel & Uchman 2001). One of the features of such cross-cutting relationships is that later burrows or tracks tend to obscure earlier burrows, and deeper burrows tend to overprint shallower ones with continuing sedimentation (see Figs 9, 10b). In many cases one or a few trace fossils (termed elite trace

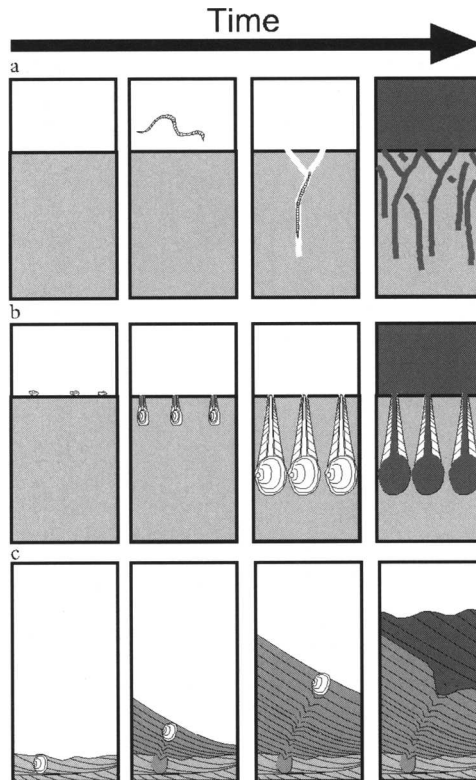


Fig. 11. Styles of colonization of sedimentary surfaces: (a) transport of adult and colonization from above; (b) spatfall; (c) equilibration and colonization from below.

fossils by Bromley 1996) visually dominate an ichnofabric. The elite trace fossil is often produced by a late-stage bioturbator(s), or may be visually striking due to a prominent fill/burrow lining.

Colonization styles

The colonization of sedimentary surfaces may be achieved in a variety of ways, which can be basically summarized as being from:

- (a) a depositional surface;
- (b) an eroded surface;
- (c) beneath the sediment surface (usually of a migrating bedform);
- (d) a higher stratigraphic level (Fig. 11).

Options (a) and (b) can be difficult to distinguish if the eroded sediment is unlithified and thus not a classical '*Glossifungites* surface' (cf. MacEachern *et al.* 1992; Fig. 6). Option (c) represents the behaviour of a fauna well adapted to conditions with high sedimentation rates (cf. the mouth-bar facies of McIlroy 2004). Colonization of sediments from a higher stratigraphic level is a common feature of turbidites (e.g. Kern 1980; Buatois & Mángano 2004), though colonization can be from below (e.g. Uchman 1995).

The ecology of colonization of disturbed/defaunated sediment has been a focus of marine ecological research for many years, and has many applications in understanding the palaeoecology of marine event beds. The colonization of marine hardgrounds is generally considered by ecologists to be largely by larval settling (Roughgarden *et al.* 1985). In soft marine sediments, however, colonization by larval stages is also supplemented by passive (currents) or active (locomotion) relocation of adults (Hall 1994; Snelgrove & Butman 1994; Cummings *et al.* 1995; Shull 1997). The potential contribution to the sediments ichnofabric of relocated adults is much greater than larval settling (spatfall; see Fig. 11b), and is best developed in regions with high flow strengths where hydraulic transport of adults is common. In addition, spatfall may be seasonal in nature, in which case the colonization window (*sensu* Pollard *et al.* 1993) may be controlled by biological rather than physical phenomena.

A sedimentological/ichnological description that encompasses all the points above should correspond to an excellent basis for further interpretation. The process of interpreting ichnofabrics and bioturbated sediments is an important step, which should involve careful appraisal of the succession studied. Caution should be exercised when assessing such detailed datasets, so that over-interpretation is avoided.

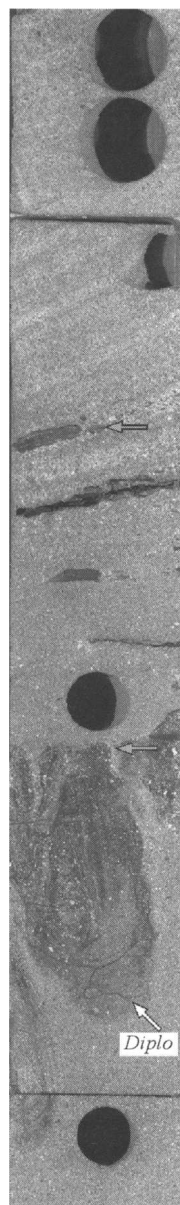


Fig. 12. Coarse-grained multi-storey tidal channel sandstones with rip-up clasts (upper arrow) with anomalously intense bioturbation (from arrowed surface) by *Diplocraterion* with a well-developed teardrop shape reflecting ontogenetic growth. From the Tilje Formation, Norwegian Shelf. Core is 10 cm wide.

For example, it is well known that modern marine communities are highly patchy in distribution and not predictable relative to prevailing currents etc. This is demonstrated in the few studies of spatial distributions of ichnofaunas

and ichnofabrics that have been performed thus far (Palmer & Palmer 1977; Goldring *et al.* 1998; Uchman 2001)

Ichnocoenoses

The term 'ichnocoenose' was originally introduced by Davitashvili (1945) to mean the traces of a biological community or biocoenose (*vide* Radwański & Roniewicz 1970); ichnocoenose in its original sense thus means the ichnological equivalent of standing crop. Terms for the buried and fossilized ichnocoenose – taphocoenose and orictocoenose respectively – were also introduced by Davitashvili (1945), but have fallen into disuse. The term 'ichnocoenosis' was subsequently independently introduced by Lessertisseur (1955) to encompass fossil assemblages of ichnotaxa equivalent to biocoenose, and was adopted in the latter sense by several authors (Häntzschel 1962; Radwański & Roniewicz 1970).

As noted by Pickerill (1992), communities can rarely, if ever, be recognized in the fossil record, owing to the effects of time averaging. Trace fossils – though study of their cross-cutting relationships (ichnofabric analysis) – can give a detailed impression of the work of several successive communities within a bed. It is useful, therefore, to retain ichnocoenosis as an approximation of its original meaning of the traces of a biological community. Ichnocoenoses should therefore ideally be considered as comprising a group of trace fossils that can be demonstrated – by ichnofabric analysis – to have been formed by the action of what approximates to a single benthic community or a succession of similar communities (based on Ekdale *et al.* 1984).

The normal condition in the stratigraphic record is that beds are colonized by a succession of different communities, and that several superimposed ichnocoenoses can be recognized. Such time-averaged trace fossil fabrics are probably best known as assemblages. An ichnological assemblage is thus made up of all the trace fossils found within a given rock unit (usually a bed), regardless of their relative chronology, and may be composed of one or more ichnocoenoses.

Ichnocoenoses and Seilacherian ichnofacies

As highlighted by Bromley (1990, 1996), the use of ichnocoenosis as being synonymous with Seilacherian ichnofacies (Dörjes & Hertweck 1975; Frey & Pemberton 1987) is erroneous and problematic. Seilacherian ichnofacies were founded on the recognition of ichnological

assemblages, not ichnocoenoses, and it is important that the two are not confused. An element of ichnofabric analysis is needed to recognize the presence of the Arenicolites ichnofacies (Bromley & Asgaard 1991), which is commonly overprinted by the Cruziana or Skolithos ichnofacies (Fig. 11a). A number of marine ichnofacies rely upon ichnofabric analysis to distinguish palimpsest fabrics representing different ichnofacies. Some authors, however, do not generally use these more subtle ichnofacies (e.g. Pemberton *et al.* 1992, 2001, who do not discuss the Arenicolites and Curvolithus ichnofacies). In addition, the use of the prefixes proximal/distal/depauperate is increasingly common (e.g. Pemberton *et al.* 2001; Bann & Fielding 2004; Buatois & Mángano 2004). It would seem therefore that – although ichnofacies are useful as a starting point for ichnological studies – ichnologists working on shallow marine systems have outgrown ichnofacies, and indeed some ichnofacies actually hide important palaeoenvironmental information (cf. Frey & Goldring 1992). The future direction of ichnological work in the shallow marine and ultimately the non-marine is probably through the creation of bespoke ichnological models on a basin-by-basin scale, incorporating description of assemblages (cf. Fürsich 1976 for discussion of assemblages) and ichnocoenoses (as resolved by ichnofabric analysis) rather than a reliance on the creation and application of ever more Seilacherian ichnofacies. The study of the non-marine is, however, still in its comparative infancy, and there is still much merit in using an ichnofacies-type approach (cf. Buatois & Mángano 2004; Genise 2004).

Ichnofabric stacking patterns as a correlative tool

Having used some variety of the protocol outlined above to describe and understand the ichnology of the stratigraphic succession in question, the next challenge is to use these data in a meaningful manner. As described above, ichnocoenoses are the building block of applied ichnological studies, in both outcrop and core. In many cases beds may contain more than one ichnocoenosis – i.e. comprise an assemblage or association that makes up the sediment's ichnofabric. In core studies, ichnofabric is the most usable stratigraphic unit. In outcrop, however, where good vertical sections are not always available, associations/assemblages of interface traces and the more prominent of the pervasive traces should suffice; quantification of the ichnology is nonetheless still important.

By integrating ichnological and sedimentological data, a sedimentologist should be able to produce a refined facies model, which may then form the basis for stacking pattern analysis at a variety of scales. Through application of Walther's law (Walther 1894), trends in relative sea-level within a given sedimentary package can be established, progradational trends being recorded by deeper water facies/ichnofabrics/associations being overlain by shallower water facies/ichnofabrics/associations (as resolved in the integrated conceptual facies/ichnofabric model). Analysis of ichnofabric stacking patterns in such a way has been used to great effect to understand complex or difficult bioturbated successions (Bockelie 1991; Taylor & Gawthorpe 1993; Martin & Pollard 1996; McIlroy 2004) at either the sequence or parasequence scale. The methodology is identical to that used by sedimentologists in routine stratigraphic studies, but incorporates both palaeontological and sedimentological data for improved facies characterization. The above approach may also be used at a coarser scale with ichnofacies as the building blocks.

Departures from the expected succession of facies predicted by applying Walther's law (Walther 1894) to the conceptual facies model need to be explained by either autocyclic or allocyclic means. The surfaces thus identified are known as key stratigraphic surfaces and are discussed below.

Recognition of key stratigraphic surfaces

The recognition of key stratigraphic surfaces lies at the heart of the sequence stratigraphic approach to understanding and predicting sedimentological phenomena. The classification of such surfaces has been gradually refined, partly through the recognition of the Glossifungites ichnofacies (e.g. MacEachern *et al.* 1992; Pemberton *et al.* 2004), but also through other styles of facies dislocation (Taylor & Gawthorpe 1993; Taylor & Goldring 1993; Goldring 1999; Schlirf 2003; Taylor *et al.* 2003).

Noteworthy phenomena are generally changes to the normal ichnological patterns of a given sedimentological succession, such as:

- horizons with anomalously intense bioturbation (Fig. 13);
- horizons with anomalously low or high ichnodiversity (Fig. 13);
- horizons with anomalous ichnofauna, e.g. a horizon with marine trace fossils in an otherwise non-marine succession (Fig. 13);

- horizons that, by ichnofabric/ichnofacies analysis, can be demonstrated to be host to a succession of ichnofaunas recording gradual deepening or shallowing events (Fig. 13);
- horizons showing anomalously large burrows that evince growth to adult size while living at a single horizon, e.g. loop-shaped *Diplocraterion* (Fig. 12);
- horizons across which there is a dislocation of facies as evinced by ichnological and/or sedimentological analysis (Fig. 6).

Hypothetical model examples of the ichnological expression of key stratigraphic surfaces are by no means intended to be exhaustive. Each depositional system has its own unique character, and models such as that of Taylor *et al.* (2003) should be used for guidance, but departures from such idealized cases are to be expected.

Ichnological frontiers

Progress

As outlined above, the field of ichnology has progressed apace, especially since the early 1970s when the seminal compilations of Crimes & Harper (1970, 1977) exemplify the state of rapid advancement of the subject and the burgeoning interest in its applicability. Since the early 1970s ichnology has become increasingly relevant to a variety of related disciplines, including zoology, ecology, archaeology, geochemistry, diagenesis, sedimentology, sequence stratigraphy, petroleum reservoir characterization and petroleum exploration.

In recent years the ichnological understanding of non-marine depositional systems has improved enormously, largely through the work of South American ichnological research groups (e.g. Buatois & Mángano 1993, 2004; Genise *et al.* 2000, 2004). There is, however, still much to do by way of integrating this improved understanding with sedimentological and sequence stratigraphic work, as outlined by Buatois & Mángano (2004).

Ichnology and the petroleum industry

The most applied aspect of ichnological work involves studies that are of relevance to the petroleum industry. The utility of trace fossils stems from the comparatively simple study of ichnofabrics in core, and the excellent palaeo-environmental information that they hold (cf.

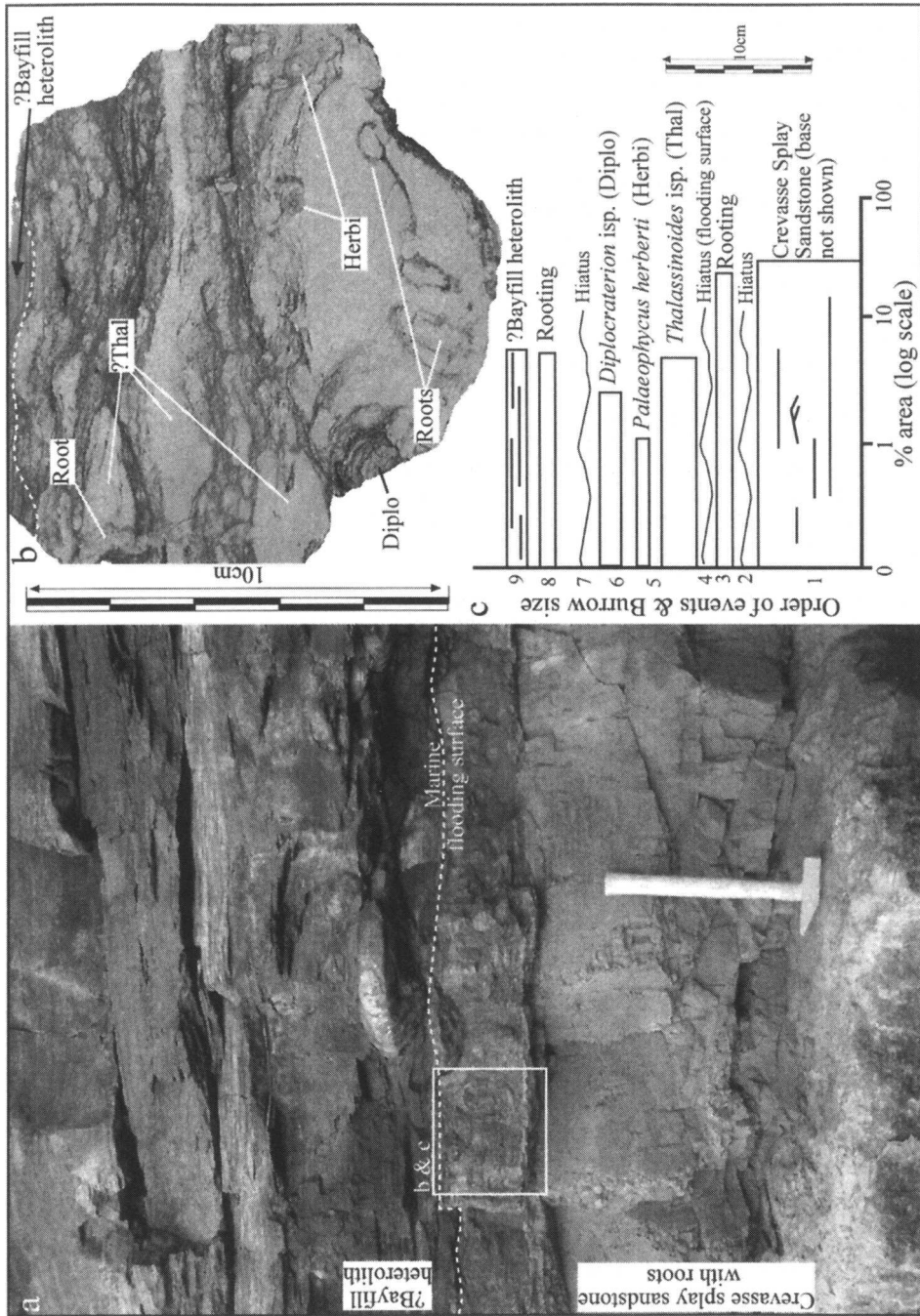


Fig. 13. Intercalation of marine and non-marine ichnofabrics from the Cloughton Formation, Jurassic, Yorkshire Coast, UK: (a) field photograph of the interval with marine flooding and bioturbation; (b) ichnofabrics associated with the marine flooding surface; (c) ichnofabric constituent diagram of the ichnofabric in (b) above.

Chamberlain 1978 and many authors since) is thus invaluable to industry. The demands of the modern petroleum industry on accurate characterization of facies are highly exacting. With the increased use of reservoir modelling of sedimentary facies and highly detailed petrophysical studies of reservoir units, the need for high-quality interpretation of sedimentary facies is greater than ever. If facies are misidentified, the foundation stone of most other elements of the reservoir characterization process falls down, and nasty surprises may lie in store during field development. By using all information available to interpret sedimentary facies, such risks are minimised.

Facies characterization

The use of ichnology to characterize sedimentary facies is well developed in shallow and marginal marine depositional systems (e.g. Bockelie 1991; McIlroy 2004) but is much less so in the non-marine (see the recent inroads made by Genise 2004; Buatois & Mángano 2004), where depositional systems are much more variable and prone to the variable effects of climate and the preservation potential of many trace fossils is comparatively low. Future work on non-marine ichnology should work towards incorporating animal and plant trace fossils (Bockelie 1994) in sedimentological and sequence stratigraphic models.

In recent years much exploration effort has been directed toward deepwater turbidite plays, e.g. Gulf of Mexico, west of Shetland, west of Africa. This trend has been reflected in the increased research into characterization of turbidite architectural elements. These data have not, however, been well integrated with ichnological studies despite there being many ichnologists specializing in the ichnology of deep marine facies. The potential for combination studies involving sedimentology and ichnology alongside data from provenance techniques, palynological techniques (biostratigraphic and palynofacies; see MacEachern *et al.* 1999) and geochemical techniques (especially in carbonates) is massively underused at present, and provides yet another rich source of potential information for petroleum geologists to use.

Reservoir quality

Parameters of interest to the petroleum geologist are the porosity and permeability of potential reservoir intervals. These two parameters are to a large extent controlled by sedimentological heterogeneity but also by diagenesis. One feature of bioturbated sandstones is that clay-grade material is commonly mixed into the matrix of

the sediment, which can be involved in diagenetic reactions that may reduce porosity and permeability after diagenesis (Worden & Morad 2003). Trace fossils may also connect sand layers separated by impermeable mudstones, thereby improving reservoir characteristics (Gingras *et al.* 1999; Pemberton *et al.* 2001, 2004) and systematically clean sandstones of clay (Frey & Wheatcroft 1989; Prosser *et al.* 1993). Recent experimental ichnology has also demonstrated that clay mineral authigenesis can occur in the guts of organisms, making the clay mineral assemblage of sediments metastable, and thereby influencing the of creation of clay mineral cements upon burial (McIlroy *et al.* 2003).

New technologies

Of the burgeoning technologies being developed by the petroleum industry perhaps the most exciting for the ichnologist is that downhole imaging (FMI) is now just bordering on a resolution whereby ichnology may become useful (e.g. Bourke 1992; Salimullah & Stow 1995), and can only get better. Advantages include the potential for recovery of image data down the full length of the well, which means that the sedimentologist/ichnologist need not work exclusively on cored intervals. The image data are challenging to interpret, but ichnologists have been working with difficult sections of trace fossils in core for many years, and should be adaptable enough to exploit this potentially rich data source.

Experimental and neoichnological studies

Experimental and neoichnological studies have a rich history, including the classical studies of modern sediments of both intertidal and subtidal settings using box-coring and serial sectioning or X-ray analysis (e.g. Reineck 1958; Howard & Reineck 1972). Such techniques need to be improved and more closely related to depositional events in modern settings to facilitate more informed interpretation of ancient environments. Facilities for visualizing such data, including tomography of serial sections (e.g. Fu *et al.* 1994; Sutton *et al.* 2001), X-ray and NMR imaging techniques, have improved. In addition, time-series X-rays of ichnofabrics in laboratory experiments has never been fully exploited and should be very revealing.

In addition, ecological information concerning infauna of many modern environments is well established and ideal for incorporation into models of ancient depositional environments (e.g. Reed 2002 on deep marine traces; McIlroy 2004 on tidal depositional environments).

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