ICHNOTAXONOMY AS A SCIENCE

Andrew K. RINDSBERG

Biological & Environmental Sciences, University of West Alabama, Livingston, AL 35470, USA,
e-mail: arindsberg@uwa.edu

Abstract: If ichnotaxonomy is to be scientific, then its results must be repeatable. While some ichnotaxa are identified consistently, others are not, suggesting that ichnotaxonomy is not a mature science. When researchers disagree on the identification of a specimen, it suggests that closer examination is needed: an intermediate stage in the scientific method. But when ichnologists publish different names for the same trace fossils, multiple trials of classification have yielded different results, suggesting a failure of the hypotheses that led to the names.

The burgeoning of invertebrate ichnology from the 1960s onward was made possible by demonstrating its utility to the petroleum industry; in part, this was accomplished by simplifying the ichnotaxonomy of common trace fossils to the point where a specialist was not required to make use of them in sedimentology and stratigraphy. The biological aspect of trace fossils, albeit of great interest, was downplayed in favour of a severely geometric approach. Ironically, this has had the effect of obscuring basic relationships of trace fossils and their palaeoenvironments that could be of great use to sedimentologists.

Previous researchers have emphasized the value of a uniform approach in ichnotaxonomy. To accomplish this, ichnologists should take inspiration from the taxonomy of body fossils. Making ichnotaxonomy more replicable will take time and effort among investigators. In the long run, this can be accomplished by a holistic approach that includes close observation of trace fossils, standardized procedures of description and diagnosis, reinvestigation of type material, attention to bioprint (morphological traits that reveal the anatomical and ethological characteristics of the tracemakers; Rindsberg and Kopaska-Merkel, 2005), avoidance of taphonomic and human bias, and above all, cooperation.

Key words: Taxonomy, ichnotaxobases, trace fossils, ichnology, standardized classification.

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INTRODUCTION

Ichnotaxonomy – the theory and practice of classifying traces, to paraphrase Mayr's definition of taxonomy (1969) – is currently not a mature science. If science depends on tests of hypotheses capable of yielding the same results on repetition, then ichnotaxonomy is still in flux despite many years of effort by researchers. This lack of reliability limits the utility of the field by hampering comparisons between the work of different individuals.

If ichnotaxonomy were repeatable, the principles behind naming trace fossils would be stable from one decade to the next, and from one worker to the next. Allowing room for differences in interpretation that affect taxonomy, scientists should be able to examine the same specimen independently and give it the same name in most cases. A delightful example of this did occur at the Museu Geológico de Lisboa during the Ichnia 2016 meeting, when several visiting ichnologists converged on the type specimen of *Taenidium lusitanicum* Heer, which had just been reassigned to *Cladichnus* D'Alessandro and Bromley (Neto de Carvalho

et al., 2016), and confidently pronounced it to be an example of *Hillichnus* Bromley, Uchman, Gregory and Martin. I hasten to add that the paper of Neto de Carvalho *et al.* (2016) is in other regards an exemplar of good procedure in ichnotaxonomy, and that *Hillichnus* is still on the way to becoming more broadly known (Knaust, 2017). The point is that everyone who was already familiar with *Hillichnus* recognized it within moments. However, consensus is not always so easily obtained.

Ideas, including recently erected ideas and taxonomic revisions, take time to diffuse through the community of scientists. This is one of the purposes of conferences. Unanimity is not expected, but neither is it expected for taxonomists to disagree on identifications as routinely as is observed in contemporary ichnology. The problem is to make ichnotaxonomy reproducible.

This is not the first time that ichnologists have exhorted themselves to standardize names and procedures. The effort is an ongoing one, with steps on the way includ-

ing those of Krejci-Graf (1932), Seilacher (1953a, b), Häntzschel (1962, 1965, 1975), Frey (1973), Sarjeant (1975), Frey and Seilacher (1980), Pickerill (1994), Bromley (1996), Bertling *et al.* (2006), Bertling (2007), Buatois and Mángano (2011), and Knaust (2012), together with the efforts of monographers of formations, geographic areas, and particular ichnotaxa, a selection of whom were noted by Rindsberg (2012, table 3).

A key aspect of the problem is the lack of a well-defined ichnospecies concept. What *is* an ichnospecies? The concepts behind the term *species* have been debated by biologists for decades, adding clarity to procedures in biological taxonomy. We can say that an ichnospecies is a taxonomic group of traces analogous to a species in Linnaean nomenclature, but the concept of a biological species is not much like that of an ichnospecies. Both consist of populations of individuals (in the statistical sense), but members of biological species are or were living and may contain genetic material useful for constructing a phylogenetic tree, an enormous advantage in taxonomy. In this regard ichnologists are in a similar condition to that of palaeontologists working on moulds and casts; both must rely on morphology rather than genetics to create a classification and deduce relationships. Most ichnologists agree that the diagnostic morphology of an ichnospecies must reflect significant, distinctive behaviour, not merely superficial differences in appearance due to taphonomy (e.g., Fürsich, 1973; Bertling *et al.,* 2006; Rindsberg, 2012) – but behaviour is deduced from the trace fossils, not directly observed.

And what is a unit of behaviour? One might think that ichnologists would pay close attention to the work of ethologists in this regard, but in fact there is little communication between the two fields (Vallon *et al.,* 2015). Should we regard behaviour as basically a function of organisms, or instead of ecological niches? Historically, invertebrate ichnology has emphasized the latter in its role as handmaiden to petroleum geology, particularly characteristics that can be used to deduce salinity, water depth, and other palaeoenvironmental parameters. But vertebrate ichnologists are more interested in footprints in relation to the animals that made them, an organismal approach. It seems likely that, in the long run, the organismal approach will prove to be the more powerful, as it fosters anatomical as well as palaeoenvironmental study. If that is the case, then ichnotaxonomists should distinguish ichnospecies on the burrowing behaviour of different organisms where possible, as deduced from morphology.

Considering the fact that many ichnotaxonomists are trained in organismal taxonomy as well, it is surprising that ichnotaxa are often treated as structures that are divorced from their biological underpinnings. As shall be seen, the procedures of organismal taxonomists can clarify analogous cases in ichnotaxonomy as well.

To illuminate the problem of reproducibility, four case studies are offered, on (1) the perceived ichnodiversity of a large outcrop by different ichnologists, (2) crustacean burrows, (3) bivalve feeding-locomotion burrows, and (4) vertebrate trackways. Following discussion of the case studies, suggestions are offered for improving approaches to ichnotaxonomy.

CASE STUDIES

Case study 1:
Arenigian Ochre Cove Formation,
Bell Island Group of Bell Island,
Newfoundland (Canada)

The time was August 16, 2012; the place, Bell Island. Several dozen ichnologists spent several hours examining the Bell Island Group in outcrops on the north coast of the island, led by Duncan McIlroy during the International Congress on Ichnology, Ichnia 2012. It was a beautiful, sunny day and attendees were thoroughly enjoying themselves. Many had studied the classic monograph on the trace fossils of the Bell Island Group by Fillion and Pickerill (1990), and Seilacher and Crimes' (1969) paper on its trilobite burrows. Yet when Jack Matthews waggishly polled field trip attendees on how many ichnogenera they thought were represented, there was no agreement. Answers ranged from 4 to 20, averaging about 10. Later, in a presentation to the conferred ichnologists, he analyzed these numbers statistically, raising loud laughter among the participants – and lingering questions as to why the range of answers was so broad.

True, not everyone saw the same specimens, but there was a fundamental disagreement among the assembled ichnologists that would not have been present among specialists on molluscs or trilobites. Examples of failure to reach taxonomic agreement on trace fossils are common. One only has to ask a group of ichnologists how best to classify crustacean burrows – or even such common taxa as *Monocraterion* Torell – to realize how different their taxonomic philosophies are. The lack of reproducibility in ichnotaxonomy is alarming because it indicates that whatever we are accomplishing in our endeavours, it is not yet science. Science is reproducible.

Case study 2:
Crustacean burrows
of the *Spongeliomorpha–Ophiomorpha–Thalassinoides* (SOT) group

Presented with a hodgepodge of ichnogenera named from the 1820s onward, Walter Häntzschel (1962, 1965, 1975) and others strove to make sense of the taxonomic tangle by determining which were junior synonyms. Ichnotaxa erected in Europe were often given different names in North America, e.g., *Ophiomorpha* Lundgren, 1891 was commonly termed as *Halymenites* Sternberg, 1833 by Americans until Häntzschel (1952) placed them in synonymy. *Thalassinoides* Ehrenberg, 1944 was not widely appreciated until its revival by Häntzschel (1962) and Kennedy (1967), and *Spongeliomorpha* Saporta, 1887 was obscure before Bromley and Frey (1974) reinvestigated the ichnogenus. Naming and describing the ichnogenera individually was not enough; they had to be described in a uniform terminology with respect to one another – differential diagnoses – before patterns could emerge.

By the 1960s, it was already clear that these burrows were chiefly made by crustaceans and that they could be useful as palaeoenvironmental indicators (Häntzschel, 1952; Weimer and Hoyt, 1964), and they had come to the attention of sed-

imentologists and stratigraphers. There was a strong incentive to create a reproducible classification that was simple enough to be used by petroleum geologists with minimal training. The first such classification was offered by Fürsich (1973), who took a holistic approach to the problem (Fig. 1). Although complete information was not at hand for every ichnospecies, he used what was available to distinguish them on the basis of overall morphology, orientation of burrow elements, and branching. He dismissed the morphology of the uppermost parts of the burrows because they are commonly eroded away, and also sculpture, because it was known that the same burrow system could have knobby and smooth burrow segments depending on adjacent substrate texture. All ichnospecies were grouped within the earliest ichnogenus to be named, *Spongeliomorpha*. This classification had the advantages of using the burrows' most constant morphologic characters. It also had the pragmatic advantage that nonspecialists who were faced with an incomplete or poorly preserved specimen could still identify it accurately as *Spongeliomorpha* isp. A tacit advantage was that the resulting ichnogenus was closely tied to a few clades of crustaceans, though the possibility remained that other groups might make similar structures.
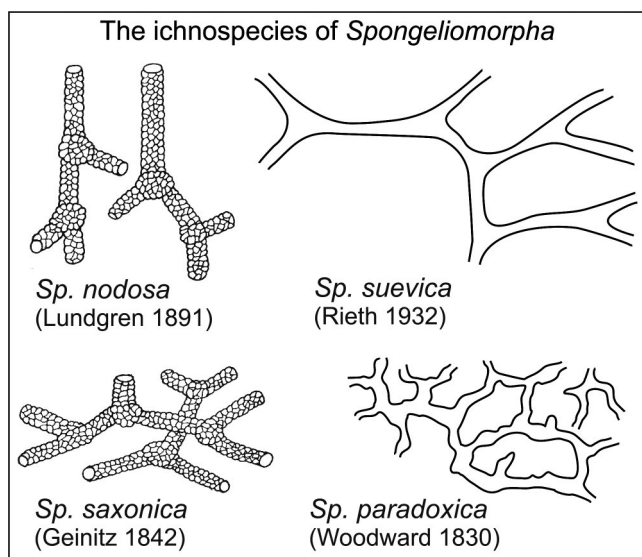

Fig. 2. Ichnospecies of *Ophiomorpha* according to Frey *et al.* (1978). In their view, *Ophiomorpha* is determined by its nodose wall. Ichnospecies are distinguished by details of the nodose structure, other characteristics being rejected as ichnotaxobases. **A.** Single node: most ichnospecies. **B.** Double nodes: *O. borneensis.* **C.** Rounded single nodes: *O. nodosa.* **D.** Meniscate fill, not considered as diagnostic. **E.** Scratched wall, no nodes: *Thalassinoides* or *Spongeliomorpha,* not *Ophiomorpha.* **F.** Spiky single nodes: *O. irregulaire.* Reprinted from Frey *et al.* (1978, fig. 1) by permission of *Palaeogeography, Palaeoclimatology, Palaeoecology.*

Fig. 1. Ichnospecies of *Spongeliomorpha* according to Fürsich (1973), recognizing burrow orientation, branching, and constancy of diameter as morphological traits, but downplaying sculpture. Reprinted from Fürsich (1973, fig. 6) by permission of *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte.*

This classification was soon supplanted by Frey *et al.* (1978), who took a very different approach to the SOT group (Fig. 2). As to their impact on other researchers, it is worth noting that Frey and his colleagues were among the most knowledgeable researchers on crustacean burrows in the world; Frey in particular had made many resin casts of modern burrows and had a firm grasp of the morphology of burrows made by different species on the Georgia coast (Basan and Frey, 1977). In contrast, Fürsich was then a graduate student. Frey *et al.* (1978) argued that because these burrow systems were rarely observable in complete
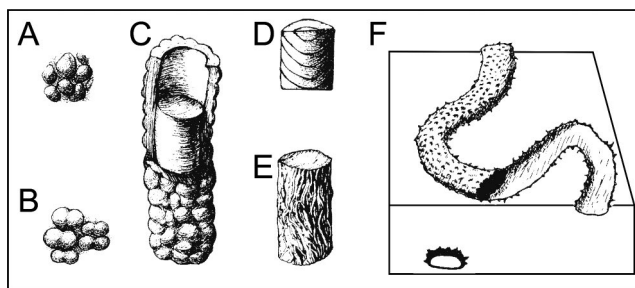
form as fossils, the classification should be adapted to use with very incomplete specimens such as burrow segments. These were distinguished on the basis of sculpture – a feature that Fürsich (1973) had rejected as inconstant. This analysis resulted in the three ichnogenera that are commonly employed today (knobby *Ophiomorpha,* striate *Spongeliomorpha,* smooth *Thalassinoides*), with ichnospecific diagnoses revised to be brief and eliminate most of the morphologic information on these trace fossils. Frey *et al.* (1978) did not ignore these extra features, and even recommended that researchers pay close attention to them, but the simpler system did make it possible to ignore morphology other than sculpture, particularly when workers referred to names like *Thalassinoides* without detailed description. Sedimentologists and petroleum geologists found the system easy to use even in cores, and Fürsich's (1973) classification fell rapidly into disuse, despite a later attempt to revive it (Schlirf, 2000).

Compare the differing schemes to those for the classification of plants. Early botanists placed great emphasis on the structure of flowers, leaves, or other parts before Ray (1682) established a stable system based on all available morphological information. Similarly, the SOT group was approached by reference first to holistic morphology and then to sculpture, which achieved general usage. But was the consensus correct in this case?

Evidently it was not. During the 1980s and 90s, more and more resin casts were taken of various species of crustaceans, to the point where Bromley (1996) was able to devote an entire chapter of his *Trace Fossils* to the immense diversity of crustacean burrows. Basan and Frey (1977) had not only illustrated the morphology of Georgia coastal crustacean burrows, but also described them in morphologically consistent terms, including, in some cases, their characteristic changes through time (*ichnogeny,* to use the term coined by Belaústegui *et al.,* 2016). It became obvious that the SOT group did not cover the full range of burrow systems

produced by modern crustaceans, let alone ancient forms. Moreover, lumping them together in a few ichnogenera would render them difficult to use as palaeoenvironmental indicators. Accordingly, Frey *et al.* (1984) not only had no objection when Fürsich (1981) named *Psilonichnus* (arguably a form of *Thalassinoides* by the classification of Frey *et al.,* 1978), but even extended his work. At least some *Pholeus* Fiege, 1944, *Macanopsis* Macsotay, 1967, *Gyrolithes* Saporta, 1884, and *Keckia* Glocker, 1841 were eventually recognized as other crustacean burrows, with others being added to the list at an increasing rate, e.g., *Camborygma* Hasiotis and Mitchell, 1993, *Sinusichnus* Gibert, 1996, and *Lepeichnus* Belaústegui *et al.,* 2016. If this trend continues, the SOT problem will cure itself as the most distinctive burrow systems are split away from the indigestible lump of "thalassinoidean burrows" (Table 1). What remains will be the trace fossils that are most similar to the type material, and which are commonly held to be the work of thalassinidean shrimp.

Table 1

Characteristics of contrasting taxonomic philosophies
of classifying crustacean burrows based on
short segments of burrows *versus*
complete burrow systems.

Short segments of burrows	Complete burrow systems
Pragmatic	Holistic
Uses only selected information	Uses entire morphology
Easy to identify incomplete material	Hard to identify incomplete material
Easy to learn	Difficult to learn
Does not encourage careful observation	Encourages careful observation
Few ichnogenera and ichnospecies	Many ichnogenera and ichnospecies
Does not support detailed palaeoenvironmental analysis	Supports detailed palaeoenvironmental analysis
Consensus since 1978	Gradually supplanting the consensus

Again, a comparison with more seasoned taxonomy is apt. Two genera, *Nautilus* Blainville and *Ammonites* Bruguière, once covered almost the full range of planispiral fossils, including many foraminifera as well as cephalopods. At one time, these genera each contained hundreds of species, but over the next two centuries, nearly all of these species were transferred to new genera (Spath, 1945), and it is now recognized that the cephalopods are included in two subclasses, the Nautiloidea and Ammonoidea. The SOT group merit a similar fate. Nothing will be lost, because the group can be given a formal ichnofamily name, or an informal one such as "ophiomorphids". Fragments of burrows can be called ophiomorphids as fragments of cephalopods are called nautiloids or ammonoids.

In the nineteenth century, burrow genera were created using whatever material was at hand. Today, the new ichnogenera split off from the SOT group are routinely based on relatively complete and well preserved material (Rindsberg, 2012), supporting the holistic approach encouraged by Fürsich in the 1970s. As Seilacher (1975, p. vii) exhorted, "we should not let the weeds grow again!" This can be accomplished best by reference to modern analogues, where they are available, and consideration of tracemakers should not be ignored in ichnotaxonomy.

Case study 3:
***Protovirgularia* M'Coy,**
1850 and similar burrows

The great majority of vertebrate trackways were never mistaken for anything else and the makers of crustacean burrows began to be recognized with the advent of modern invertebrate ichnology. But the makers of the common trace fossil *Protovirgularia,* which was originally interpreted as an octocoral, remained obscure long into the twentieth century. Nathorst (1881) recognized that it was a "trail", i.e., a locomotion burrow, and Richter (1941) noted that it was one of a group that he called *Ichnia spicea.* As is by now a familiar story, other workers continued to name taxa that would later be recognized as synonyms of *Protovirgularia.* Miller and Dyer (1878) erected *Walcottia;* Hallam (1970), *Imbrichnus;* Hakes (1976), *Chevronichnus.* The corrective process of taxonomic collapse was slow and episodic. Häntzschel (1975) recognized that two species of "graptolites" named by Richter (1853, 1871) were forms of *Protovirgularia,* but distinguished *Imbrichnus* as separate and relegated *Walcottia* to the "unrecognized and unrecognizable" trace fossils. Rindsberg (1994) placed *Imbrichnus, Biformites* Linck, and *Chevronichnus* in synonymy with *Walcottia,* as well as some material that had previously been assigned to *Biformites, Crossopodia* M'Coy, *Gyrochorte*? Heer, *Pelecypodichnus* Seilacher, and *Uchirites* Macsotay in North American studies, and recognized bivalves as the most probable tracemakers. He emphasized the significance that sediment cohesion has on the preservation of these burrows, giving them a great diversity of forms that do not reflect fundamental differences in behaviour. In a paper published within a few days of Rindsberg (1994), Seilacher and Seilacher (1994) independently placed all of the following ichnogenera in synonymy with *Protovirgularia: Crossopodia* (in part), *Walcottia, Pennatulites* Stefani, *Paleosceptron* Stefani, *Uchirites, Imbrichnus, Sustergichnus* Chamberlain, and perhaps *Biformites.* They also placed the study of these trace fossils on a firm basis by relating them to the life activity of modern bivalves. The similarity of results between two papers written at the same time is heartening: Maybe ichnotaxonomy is a science after all, when it is based on biological considerations and taphonomic variation is disregarded.

Subsequent workers have continued to puzzle over the interrelationships of these ichnogenera. In particular, it would be interesting to know more about *Pennatulites,* which has many narrow branches emanating from a broader master burrow, and how its behaviour may differ from that of the

more recently named *Hillichnus;* the presence of these narrow branches suggests that these forms should remain separate from *Protovirgularia,* though their behaviour is related. *Biformites* has been reinterpreted as an ophiuran trace fossil based on examination of type and other material (Schlirf, 2012; Knaust and Neumann, 2016). However, these are details; thanks to the work of ichnotaxonomists, *Protovirgularia* is now one of the most commonly recognized trace fossils.

Synonymization of several relatively obscure trace fossils into a few useful ichnogenera was enabled by observation of their morphology *as related to* interpretation of analogous modern traces and their function. It would have been possible to classify the specimens into taxa based on morphology alone, but taphonomic differences would have interfered with the process. Thus, where biological affinities can be recognized, they should be weighted strongly in choosing among morphologic ichnotaxobases.

Case study 4:
Vertebrate ichnotaxa
from the Pennsylvanian of Alabama (USA)

The coal mines of northwestern Alabama have yielded a bonanza of amphibian and early reptile trackways, particularly since the discovery of trackways at the Steven Minkin Paleozoic Footprint Site (Haubold *et al.,* 2005). The original taxonomic work, however, was done by a conchologist, T. H. Aldrich (1930); his paper was well illustrated, but it was his only incursion into ichnology and his diagnoses have since proved to be unsatisfactory. As was common at the time in North America (Haubold *et al.,* 2005), Aldrich diagnosed his ichnogenera largely on the number of preserved digits on pes and manus prints. Unfortunately for his classification, the muds on which the vertebrates walked were plastic and the footprints of the heavier animals were impressed deeply and unevenly, with some toes being deeply imprinted in undertraces and other toes only shallowly imprinted. The result was that the number of digit imprints tended to be greater in the shallower laminae of the prints. Many of Aldrich's names had to be placed into synonymy as a result when Haubold *et al.* (2005) compared new and old collections. In the meantime, the diversity of animals living on the Carboniferous tidal flats of Alabama was grossly overestimated, an example of poor taxonomy leading to poor science.

If Aldrich had been aware of the influence of taphonomy on footprints, as was Hitchcock (1841, figs. 104, 105), then he might have avoided this error, but he would still have been handicapped by a relatively small sample size. Many of his ichnospecies were represented by single specimens. Haubold *et al.* (2005) were able to avoid Aldrich's mistake by observing hundreds of specimens, including transitional forms. The ability to see the full range of variation is as important in ichnology as it is in the study of brachiopods or trilobites.

Despite these advances, stability of nomenclature has still not been reached with the Alabama material. Haubold *et al.* (2005) described five "main" ichnogenera, each with a single ichnospecies. In the same volume, based on the same material, Hunt *et al.* (2005) described seven ichnogenera, each with one ichnospecies, while Martin and Pyenson (2005) puckishly opted for a single highly variable ichnotaxon for the purpose of discussion. Along with the work of later researchers, these represent alternative working hypotheses.

DISCUSSION
The roots of our problem

Some ichnogenera are more consistently recognized than others by different researchers. Ichnologists rarely disagree on the identification of well-exposed examples of the common trace fossils *Arenicolites* Salter, *Arthrophycus* Hall, *Diplocraterion* Torell, *Chondrites* Sternberg, *Cruziana* Orbigny, or *Phycosiphon* Fischer-Ooster. In part, this is a result of hard work. Where original diagnoses were unclear, later workers have examined type material in museums, revisited type localities, compared material from other places, and revised the diagnoses accordingly. The identifications of other common trace fossils, including *Asterosoma* Otto, *Palaeophycus* Hall, *Phycodes* Richter, *Planolites* Nicholson, and *Treptichnus* Miller and Dyer have historically been unstable despite revision. It is worth asking why. Among the reasons are the inherent simplicity of most trace fossils compared to body fossils; the fact that humans, not tracemakers, choose ichnotaxobases; the difficulty of deciding on a consistent, uniform methodology for choosing ichnotaxobases; and the fact we usually deal with incomplete (or incompletely seen) material. These topics are addressed in turn.

Complexity of trace fossils

There is no one factor that makes one ichnogenus more unstable in taxonomy than another, but a few are evident. One factor is the amount of useful information that can be drawn from a specimen of the ichnogenus. A burrow system of complex form such as *Chondrites* is more reliably distinguished than a simple burrow like *Planolites*. Moreover, the names for simpler burrows have frequently been extended to superficially similar burrows, leaving the names in a taxonomic muddle. (If any unbranched segment of a vertical burrow can be *Skolithos* Haldeman, or any unbranched horizontal segment, *Planolites,* then the names do not mean very much.) Another factor is transition; ichnotaxa that have no distinct boundaries from other ichnotaxa are inherently difficult to define.

Most trace fossils are much simpler than body fossils. Compare *Cruziana* – a relatively complex trace fossil – with its presumed trilobite maker, having many distinctly shaped skeletal parts (Fig. 3). The trilobite specialist has far more criteria on which to distinguish taxa than any ichnologist does. When examined under a microscope, a trilobite reveals even more detail; a trace fossil, only mineral grains.

Human choice of ichnotaxobases

If we weight different features as being the most important, then it is easy to create incompatible systems of classi-
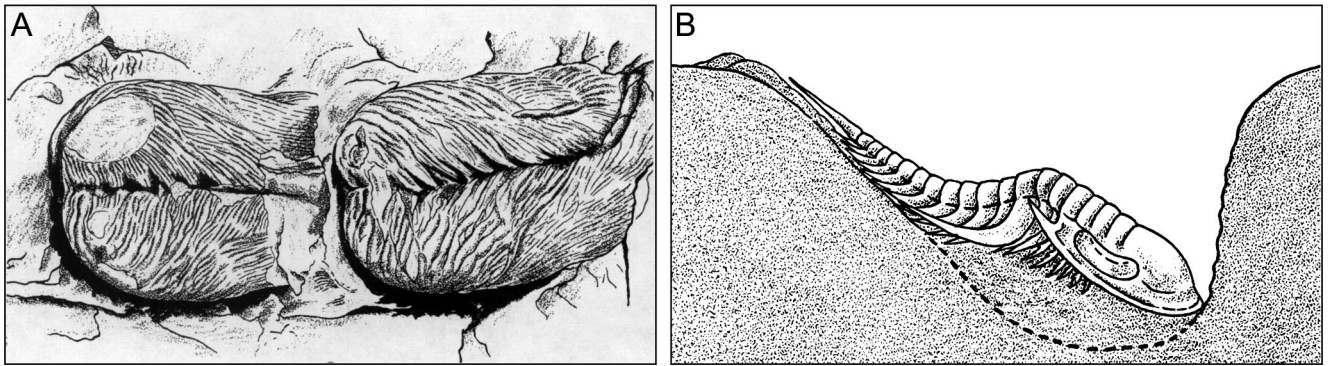
Fig. 3. Body fossils are generally far more complex than trace fossils, and therefore yield more information of taxonomic value. *Cruziana jenningsi* (**A**) and its reconstructed maker (**B**). Reprinted from Fenton and Fenton (1937a, figs. 2, 3) by permission of the *American Midland Naturalist*.

fication. Different researchers choose to weight distinguishing criteria differently. A striate, subhorizontal burrow with a shallow basal spreite was recently compared on the Ichnology Facebook page to *Teichichnus* Seilacher by one reputable researcher (citing the spreite and orientation), to *Palaeophycus* by another (on the basis of the striae and orientation), and to *Trichophycus* Miller and Dyer and *Thalassinoides* by a third (using the striae, spreite, and orientation). This situation is reminiscent of the story of the Six Blind Men and the Elephant, in which six men touch different parts of the elephant and end up comparing the beast's trunk to a snake, its ear to a rug, its tusk to a spear, its flank to a wall, its leg to a tree, and its tail to a rope. Specialists in other biological fields learned long ago (botanists, as early as Ray, 1682) to use *all* morphologic features in taxonomy. Even so, one has to select which features to consider as most important.

Practiced ichnotaxonomists have, or should have, had some education in trace fossils through training and personal observation. But we have not all seen the same trace fossils, nor of the same ages and palaeoenvironments, and this alone probably accounts for some of the differences in named ichnotaxa. Until the middle of the twentieth century, the name *Arthrophycus* Hall, 1852 was commonly applied to specimens in the Americas that were virtually identical to specimens called *Harlania* Goeppert, 1852 in Europe (Rindsberg and Martin, 2005). *Ophiomorpha* Lundgren, 1891 in Europe was equivalent to *Halymenites* Sternberg, 1833 in North America (Häntzschel, 1952). *Asterosoma* Otto, 1854 in Europe was *Asterophycus* Lesquereux, 1876 in North America, even as late as the *Treatise* (Häntzschel, 1975). And so on. The disparity was far more complex between Europe and countries speaking non-Indo-European languages, e.g., Japan (Noda, 1982).

Another factor is social; when an expert calls a fossil by a particular name, other researchers tend to follow (Plotnick and Wagner, 2006). Thus, for example, when Seilacher (1955) first called the zigzag burrows at the base of the Cambrian *Phycodes pedum,* it took forty years before others disagreed and called them by other names (*Trichophycus pedum, Treptichnus pedum,* and *Manykodes pedum,* respectively by Geyer and Uchman, 1995; Jensen, 1997; and Dzik, 2005); the name has still not been stabilized.

Even with modern electronic communications, it is possible for an ichnotaxon newly published in a well-circulated journal to remain obscure until ichnologists from widely separated countries examine specimens in the field or museums. For example, *Ptychoplasma* Fenton and Fenton, 1937b was published in the *American Midland Naturalist,* a major biological journal, but Häntzschel (1975) listed it in the *Treatise on Invertebrate Paleontology* among the "Unrecognized and Unrecognizable 'Genera'" – perhaps for no other reason than his untimely death before this work could be completed. When ichnologists met in person over trays of obscure fossils during the Third Workshop on Ichnotaxonomy, it became possible at last to piece together its synonyms described in three languages in as many different countries (Uchman *et al.,* 2011). *Ptychoplasma* is now being found at an ever increasing number of localities. Ichnology is still in many ways a youthful science, and its practitioners are scattered across the globe. It behooves ichnotaxonomists to attend international conferences to present and absorb information, to see modern and ancient traces in context, and to discuss new approaches.

The difficulty of creating uniform morphological ichnotaxobases

In 1998 and 2002, the first two Workshops on Ichnotaxonomy were conducted in order to establish greater uniformity in the criteria used to distinguish ichnotaxa. The minutes of the first meeting were typed up and distributed, and converted into a draft manuscript by Markus Bertling. During the second conference, the attendees listened to Bertling read the manuscript and debated over every paragraph. Ichnotaxonomists who were unable to attend the meetings were invited to submit comments; the much revised manuscript underwent a lengthy review before publication in *Lethaia* (Bertling *et al.,* 2006) and represents a consensus of many researchers, though not every ichnologist who contributed to the article would agree with every word of it today. According to Google Scholar in 2016, this was the most cited paper of 2006 in palaeontology (325 times by 14 October 2018); it has been used as the basis of further treatments

of ichnotaxonomy (e.g., Bertling, 2007; Knaust, 2012) as well as a convenient guide to procedure in papers that only incidentally touch on trace-fossil classification.

The Bertling *et al.* (2006) consensus emphasized that morphology was the chief, and ultimately the only practical, basis of ichnotaxonomy. Trace fossils rarely contain the tracemaker and never its genetic material, instead consisting usually of inorganic material. However, it was also pointed out that morphology must be interpreted for use in taxonomy. Different researchers can and have emphasized different aspects of morphology, as seen with the SOT group.

Rejection of a purely geometric approach

A purely geometric approach to ichnotaxonomy is tempting because of its claim to objectivity. But even this approach involves human interpretation; what we observe depends on our human senses and how we process sensory information depends on our human brains (Sacks, 2010). For example, neurologists inform us that we see and remember visual information to a greater degree as edges and lines rather than as areas; human beings can even interpret a line drawing as representing an object in three dimensions. Our minds, then, tend to focus on linear aspects of trace fossils – burrow orientation, curving, branching – more than spatial aspects such as the structure of fill. Although there have always been workers who recognized the three-dimensional aspects of trace fossils, historically there have been more who favoured a two-dimensional approach. For example, Hitchcock (1858) was well aware that vertebrate footprints have differences corresponding to their depth, but Aldrich (1930) was not. Indeed, there have been many vertebrate ichnologists who were content to trace an outline of a track without considering its vertical dimension, as Sarjeant (1975, p. 285) complained. Falkingham *et al.* (2018) have recently published an important proposal for a standard method of describing vertebrate footprints in three dimensions. Invertebrate ichnologists have had similar problems, e.g., naming the top and bottom surfaces of the same kind of trace fossils as different ichnogenera (e.g., the echinoid burrows *Scolicia* Quatrefages and *Subphyllochorda* Götzinger and Becker, whose many synonyms were disentangled by Uchman, 1995).

Allow me to erect a strawman. A computer could be programmed to distinguish trace fossils by a rigorously geometric approach with no reference to other factors, but depending on the manner that humans perceive objects. To give a simple example, how would the reader categorize the letters of the alphabet by reference to pure geometry? One reader might differentiate letters according to whether they had no closed loops (e.g., K, L, M), one closed loop (A, D, O), or two (B). Another reader could propose that a distinction between letters composed of straight elements (A, E, F), curved elements (C, O), or both (B, P). A third might support a system based on the number of strokes required to produce the letter: one (C, J, O), two (L, P, V), or more (A, B, M). There is no particular reason to choose one set of categories over another based on pure geometry of trace fossils, any more than there is of letters of the alphabet.

If this is how ichnotaxonomy is supposed to proceed, then it is hard to see how a stable classification can be achieved. And yet an individual fiddler crab can produce burrows shaped like I, J, U, and W during its lifetime on a Georgia tidal flat (Basan and Frey, 1977). Why should we impose a human order that does not exist in nature, but only in our heads? A stable taxonomy of fiddler crab burrows requires consideration of characteristics that are significant to the crustaceans, not just to us. When we create that computer program, we will have to do our best to "think like a crustacean."

Although a purely geometric approach should be rejected in ichnotaxonomy, geometric aspects are useful in conjunction with other information in ichnotaxonomy, and the method can also be applied to other aspects of the study of traces. For example, the architectural typology of Buatois *et al.* (2017) shows great promise in application to palaeoenvironmental analysis.

Information chosen in morphological ichnotaxobases

To be useful, the taxonomy of trace fossils must be *informed* by interpretation based on knowledge of modern traces. The *information* that is most often gathered about modern traces includes *form, function, process, environmental context, maker*. Less routinely, workers collect information on water chemistry, symbionts, water and nutrient flux, and many other parameters, but so infrequently that these are insufficient for basing a classification upon. If form alone is insufficient, however indispensable, for a classification, then the inferred environmental context and tracemaker must be used to inform a morphologically based system.

Form

Pure *form* is insufficient for the comparison of modern and ancient traces. Workers on modern traces usually take note only of the open parts of burrows, and the superficial aspects of locomotion traces. This makes modern and ancient traces difficult to compare, especially in the case of spreite burrows. It is a commonplace that ichnologists have not been able to certainly identify the makers of such common trace fossils as *Chondrites, Nereites* MacLeay, *Zoophycos* Massalongo, and *Phycosiphon* despite the fact that they also occur in Holocene sediments. Taxonomists of body fossils have similar problems, e.g., modern organisms may be distinguished on the basis of body parts that are not fossilized; DNA is lacking in most fossils. Accordingly, the classification of organisms and their traces can have a different basis in particular modern and ancient groups.

Still, the form of a trace fossil is necessarily related to the anatomy of its producer. Trackways preserve, if not an exact mould of the underside of an appendage, a dynamic representation of its movement. Resting traces often preserve the outline of their makers' body, and even dwelling burrows must conform to the size and width of their makers. Even feeding and locomotion burrows may embody temporary resting traces, or features that relate directly to the anatomy of their makers. Form, therefore, can inform ichnotaxonomy.

Function

Function has long been used to inform ichnotaxonomy. In a series of influential papers, Fürsich (1973, 1974a, b) emphasized the importance of behavioural function in classifying trace fossils, including the SOT group and U-shaped burrows. He distinguished between *significant* and *accessory features,* i.e., those of relatively high and low significance, for use as taxobases in ichnogenera and ichnospecies respectively. As Seilacher (1963, 1964) had shown that relationships exist between behavioural function and environmental parameters such as water depth and salinity, such a classification would automatically be useful in sedimentology and stratigraphy.

Unfortunately, this approach has also generated problems. For example, R. K. Pickerill applied the name *Phycodes* to any largely horizontal burrow system having palmate branching, without regard to maker or environment, but noting its function, namely, that this form is most common in deposit-feeding burrows (Fillion and Pickerill, 1990; Han and Pickerill, 1994). Although the type ichnospecies, *Phycodes circinnatum* Richter, 1850, was well described and figured from the start, the ichnogenus was extended to include widely disparate forms including extensions of *Thalassinoides* systems (Fig. 4). In this case, Pickerill tacitly employed function (a particular kind of feeding) to inform the morphological diagnosis of *Phycodes,* to the extent of discarding all other morphological information about these trace fossils. Again, a very human geometrical concept was allowed to override other considerations, making *Phycodes* an easily identified ichnogenus, but one that was virtually meaningless in stratigraphy. Ease of identification should not be the primary factor in ichnotaxonomy; *Phycodes* will have to be revised and several species assigned to other ichnogenera in order to make it useful for palaeoenvironmental analysis and other studies.

Process

Investigators of ancient traces usually have not discussed the *process* by which an organism created a trace fossil as a criterion for classification, but this is not the case for neoichnologists, who are able to witness how animals move and burrow. Perhaps surprisingly, this kind of information has been sought at least since trace fossils have been studied. Caster's (1938) study of modern and ancient limuline trackways is a sterling example of the way that this should be done, with close observation and reasoning (Rindsberg and Martin, 2015) (Fig. 5). Even where close modern analogues are unavailable, deduction of process from morphology is still possible (e.g., Rindsberg and Martin, 2003; Bromley *et al.,* 2003; Martin and Rindsberg, 2007; Knaust, 2010; Belaústegui *et al.,* 2016; Neto de Carvalho *et al.,* 2016).

Ichnologists should pay more attention to the biological literature in this regard. For example, Schäfer (1972) grouped modern processes of marine locomotion, some of which create traces: amoeboid locomotion (flowing of the body), motions of beating cilia, undulatory movement, peristaltic movement, glide-crawling, push and pull-crawling, multiple, circular shovelling, bolting, pacing, drilling, chimney climbing, jump-swimming, etc. Similarly, Ratcliffe and Fagerstrom (1980) listed the processes of formation that occur in modern terrestrial burrows made by insects: raking, pushing, pulling, carrying. Each of these processes is closely linked to the anatomy of the producer; some require the use of appendages, others do not. Careful attention to the details that reveal these processes well repays the effort.

Environmental context

The *environmental context* of trace fossils is indeed of high interest to sedimentologists and stratigraphers, who are generally less concerned about exact identifications of ichnotaxa than about ichnofacies and ichnofabric, and this approach has distorted the classification of some groups of trace fossils. For example, they adopted the simplified, geometrically based classification for the SOT group (Frey *et al.,* 1978), which requires little effort of observation and description. Unfortunately for them, in so doing they slowed down the progress of science with regard to understanding the palaeoenvironmental significance of more specific kinds of crustacean burrows. As these burrow systems are relatively diverse and complex, and their modern equivalents occur within relatively narrow environmental parameters, they have the potential to allow the inference of narrow environmental ranges in ancient strata as well. R. G. Netto (oral comm., 2017) noted that most modern marine substrates are dominated by only one kind of burrow system-producing crustacean, as also in ancient substrates.

Tracemaker

The *tracemaker* was once the *sine qua non* of ichnotaxonomy. In the nineteenth and early twentieth centuries, it was routine to base a new *organismal* taxon on a trace fossil. In many cases, the trace fossil was misidentified as a fossil plant or worm, as discussed by Osgood (1975) and Baucon *et al.* (2012), but in others the trace fossil was used as a proxy for an animal that left no other evidence of its existence (e.g., Hitchcock, 1858; Aldrich, 1930). Thus, Aldrich (1930) could say that the amphibian *Cincosaurus* had five digits on each foot. With experience, ichnologists realized that an exact correspondence between trace fossils and their makers could never be achieved, and they rejected the inclusion of phrases like "trilobite burrow" and "dinosaur trackway" in diagnoses. Some invertebrate ichnologists went to the extreme of considering the makers of trace fossils to be virtually irrelevant to their study.

However, vertebrate ichnologists never rejected inferences regarding tracemakers as informing their classification schemes. Hitchcock (e.g., 1841, 1858) erected several complex systems, though they were not subsequently adopted, perhaps because he himself did not persist long with any one of them. Sarjeant (1975, p. 299) nodded approvingly at Vialov's (1966) tracemaker-based hierarchical system (Table 2), noting that Vialov based his generic (and higher) names on "morphological compatibility" while not being "so precise as to occasion taxonomic embarrassment." From the point of view of vertebrate ichnologists, trace fossils are not a means of deducing ancient environ-

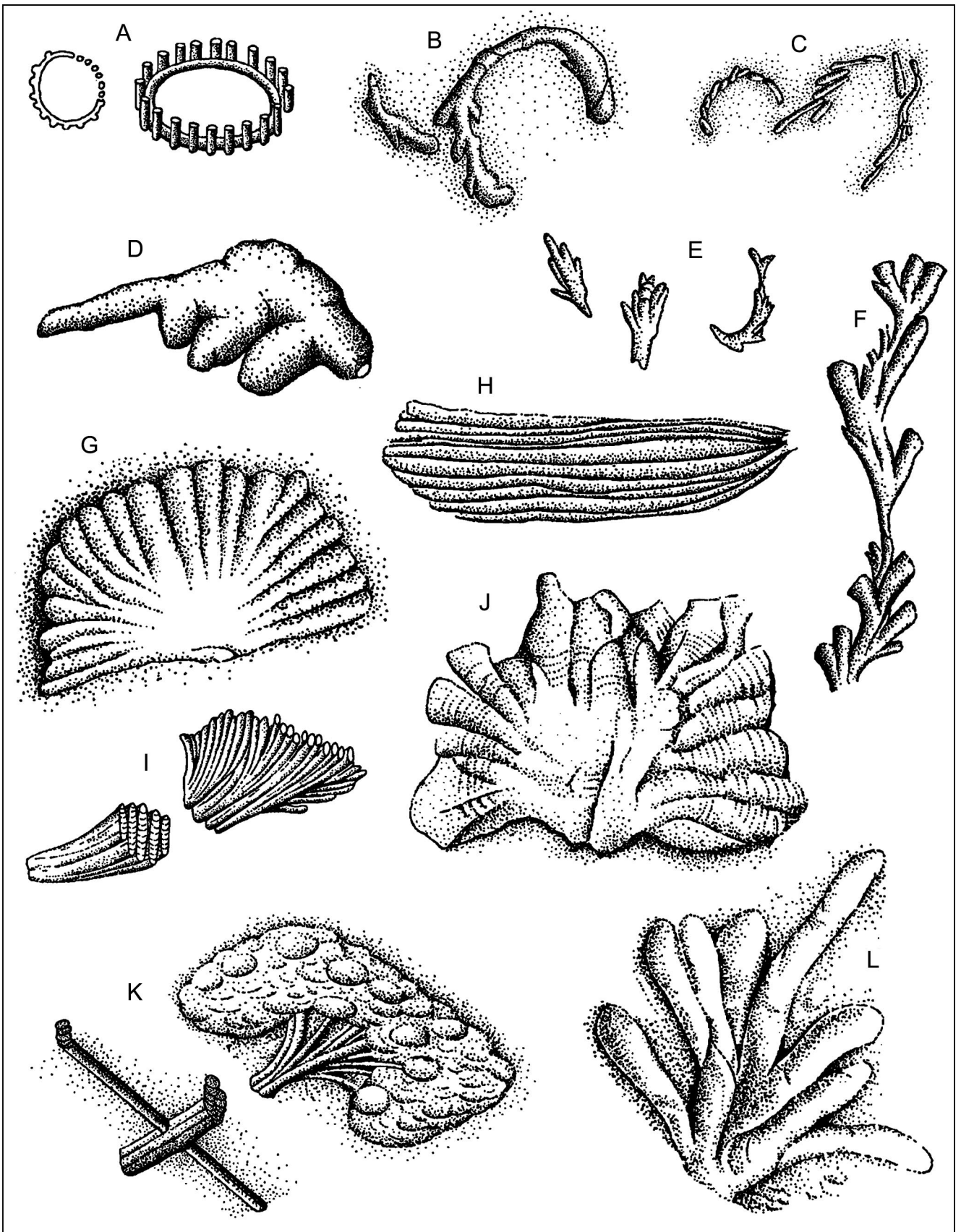**Fig. 4.** Disparate forms attributed to *Phycodes*. **A**. *P. coronatum*. **B**. *P.? antecedens*. **C**. *P. pedum*. **D.** *P. ungulatum*. **E.** *P. curvipalmatum*. **F.** *P. templus*. **G.** *P. auduni*. **H.** *P. wabanaensis*. **I.** *P. circinnatum*. **J.** *P. bromleyi*. **K.** *P. reniforme*. **L.** *P. palmatum*. Reprinted from Han and Pickerill (1994, fig. 5) by permission of *Atlantic Geology*.

Ventral view of an immature specimen of *Limulus polyphemus*, from Woods Hole, Mass.; right side shows chief external anatomical characters of *Limulus* that leave an impression in the trails; left side shows by solid lines those parts of *Limulus* that seem to have homologues in *Paramphibius* as inferred from the tracks and trails. Symbols: A, anus; Ac, anterior doublure-carina or burrowing-carina; As, abdominal or lateral buckler spines; Ch, chelae; D, doublure; En, endognaths; Gb, gill books; Gs, genal spine; Hb, holding border or carina; O, operculum; Pa, prostomial angle; Pbs, posterior buckler spine; Pr, prostomial region; Sf, simple feet of *Paramphibius*; Sr, "sleigh-runner" arc of cephalothorax; I, antennule or chelicera; II, antenna; III, mandible; IV, anterior maxilla; V, posterior maxilla (III, IV, V, endognaths); b, basos; c, coxa or coxognath; cp, carpus (cp+ may be cp plus p); d, dactylus; m, meros; p, propodos; b–d or un, palpus; ch, chelae; VI, maxilliped or ectognath; fl, pusher; ff, fifth pusher blade in *Paramphibius*; ms, maxillipedal spine; fc, false chela; u, unguis. Drawing by A. S. Caster.

Schematic diagram of the walking trail of *Paramphibius*. Trail synthesized from specimens in University of Cincinnati Museum. Interpretation based in part on observed locomotor habits of *Limulus polyphemus* when walking on wet mud. Stages in locomotion: I—Cephalothorax uplifted, front first and highest; genal spines (Gsp) touch mud. II—Maxillipeds extended and anterior feet (1–5) dislodged from front to rear; cephalothorax and appendages carried forward, genal spines usually grooving the mud on either side of trail (Sg); grooves deepest when cephalothorax held highest anteriorly at outset of stage I. III—Cephalothorax lowered; walking legs (1–5) placed essentially peristaltically opposite each other by pairs from front to rear, chelae spread; antennules apparently imprinted only by accident. IV—Maxillipeds (6) freed from mud, flexed, with pusher blades extended and terminal segment bent backward; pusher imprinted in mud usually as a surcharge upon the immediately preceding tracks of the anterior maxillae. V—Extension of maxillipeds, pushing with imbedded pusher, and brace of simple feet. Head raised (I), tail dragging (Tg) the while to make a more or less continuous furrow; "sleigh-runner" (Srg) made if head not lifted high enough to clear surface; "holding-border" (H) bracket may also be occasionally impressed in the track series, if head sinks unusually low in mud; gill books and operculum (o) may also leave faint tangential record. (VI—When needed, telson may be used as a pushing organ and also the buckler by inflection; these are auxiliary to the operations of the circumoral appendages, however, in walking on the surface.) C—Position of the cephalothorax at most forward position indicated here; Gsp—Position of genal spine; 1, antennules; 2, antennae; 3, mandibles; 4, 5, maxillae; 6, maxillipeds. Drawing by A. S. Caster.
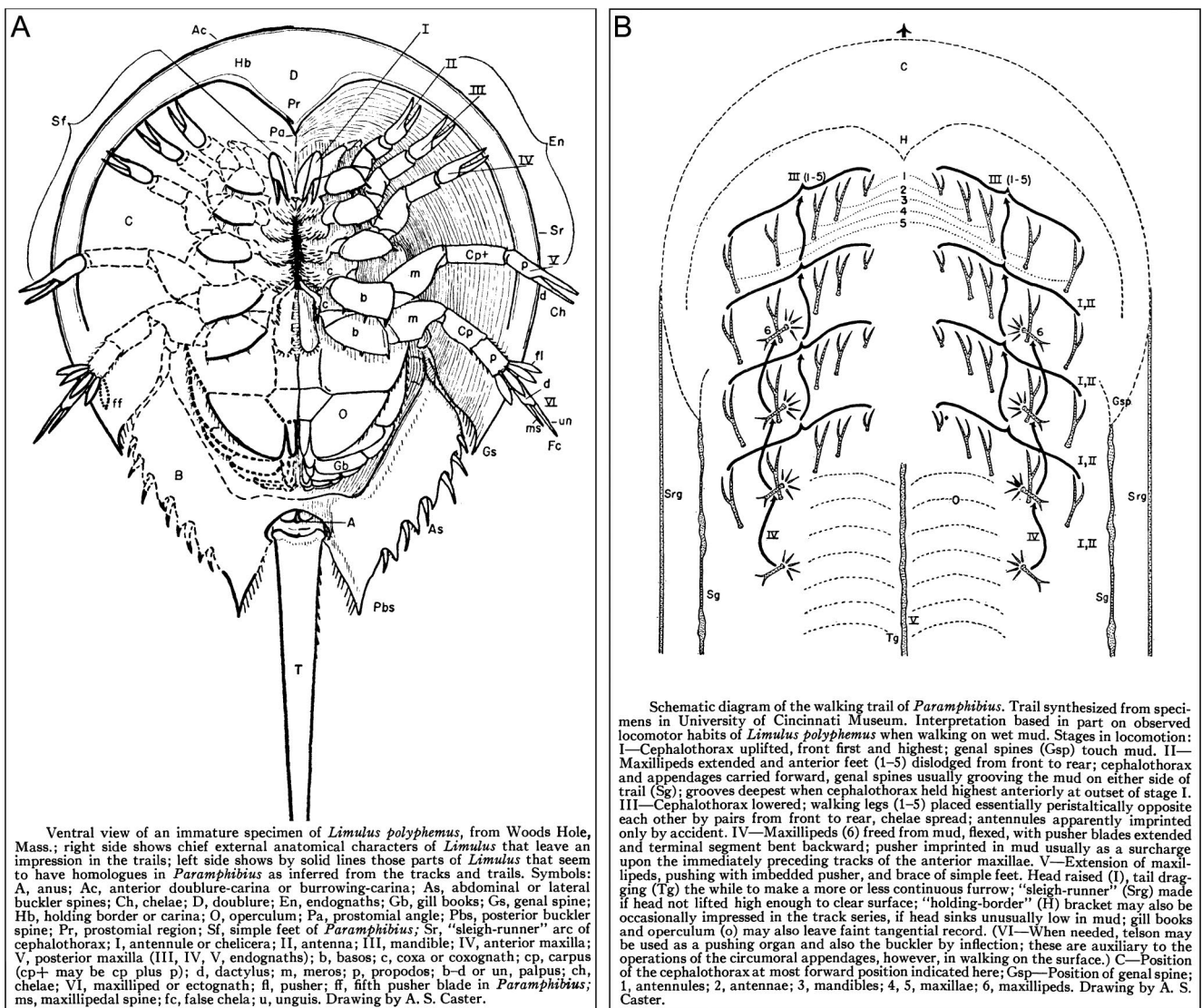
Fig. 5. Comparison of the anatomy of a modern horseshoe crab (**A**) with characteristics of a Devonian limuline trackway (**B**), *Kouphichnium* Nopcsa ("*Paramphibius*" Willard). Reprinted from Caster (1938, figs. 2, 5) by permission of SEPM, the Society for Society for Sedimentary Geology.

ments in order to find petroleum, but chiefly evidence of the behaviour of ancient creatures. One might point out here that vertebrate trace fossils also represent the behaviour of the organisms most similar to human beings, and therefore are not only relatively easy to decipher but also to understand and appreciate. Or perhaps it would be best simply to point out that vertebrate trace fossils tend to have more complex, yet repeatable morphology than most invertebrate trace fossils, at least so far as humans have been able to perceive.

The anatomy of the tracemaker is equally relevant in the case of invertebrates having appendages. In general, the number of paired tracks per set indicates the number of walking appendages in traces made by arthropods: three pairs for insects, four pairs for spiders and some decapod crustaceans (e.g., crabs, whose pincers are not used for locomotion), five pairs for limulines and some decapods, many pairs for myriapods. It makes sense to use the number of inferred appendages per set as an ichnotaxonomic criterion at a high level, even though locomotory trackways of insects and spiders have their basic behaviour in common.

So far, only a few of the most complex invertebrate trace-fossil groups have been suitable for this approach. An early example was given, as usual, by Seilacher (1970) in his brilliant "Cruziana Stratigraphy", which related the details of trilobite anatomy to the details of burrows, and which he continued to develop through his lifetime (Seilacher, 1992, 1994, 2007). Kopaska-Merkel and Rindsberg (2015) followed his approach and found, to their surprise, that *Alph hartselleanus* Rindsberg was not a trilobite trace despite "first impressions," but instead was the work of a crustacean. The number of inferred body divisions and appendages did not match those of trilobites, and this had implications for the palaeoenvironmental interpretation of the containing strata (brackish rather than marine). The most complex invertebrate traces so far known are those of social insects, as well described by Genise (2017).

Table 2

A hierarchical classification of vertebrate traces proposed by Vialov (1966), as cited by Sarjeant (1975, p. 299).

Amphibipedia
Order Labyrinthopedida
Order Caudipedida
Suborder Salamandripedoidei
Reptilipedia
Superorder Theromorphipedii
Order Therapsipedida
Superorder Cotylosauripedii
Order Procolophonipedida
Superorder Chelonomorphipedii
Order Testudipedida
Superorder Lepidosauripedii
Order Rhynchocephalipedida
Order Lacertipedida
Order Sauropterygipedida
Order Pterosauripedida
Order Saurischipedida
Suborder Coelurosauripedoidei
Order Ornithischipedida
Suborder Ornithopedoidei
Order Thecodontipedida
Suborder Pseudosuchipedoidei
Suborder Parasuchipedoidei
Mammalipedia
Order Carnivoripedida
Order Perissodactipedida
Order Artiodactypedida
Suborder Pecoripedoidei
Avipedia

However, we may look to a future in which more such relationships become clear. The taxonomic history of *Protovirgularia* shows what becomes possible when the tracemaker is identified and new hypotheses can be based on anatomical relationships (Seilacher and Seilacher, 1994). Similarly, Seilacher (2000) showed that elements of classic *Phycodes* tend to share a squarish cross-section with *Arthrophycus* and *Daedalus* – an insight that was by no means obvious from the literature, and which encouraged subsequent investigators to examine their own specimens for this feature. The benefits include a better understanding of the tracemakers, their evolution, and their stratigraphic and palaeoenvironmental distribution.

The rejection in ichnotaxonomy of such biological aspects of trace fossils as the anatomy of their makers and their behavioural functions seems absurd in light of the fact that trace fossils are biogenic structures. It should be emphasized that the diagnoses of trace fossils should remain strictly morphological in nature. Observation must be kept separate from inference in ichnology as in any other science. Thus, diagnoses must not include requirements or inferences that an ichnotaxon is the work of a particular group of organisms, nor its function, nor anything else but morphology and original substrate (Bertling *et al.,* 2006). However, for these morphologic diagnoses to be useful, they should be informed by inferences concerning function and tracemaker.

Incomplete material

Historically, the effort to place ichnotaxonomy on a firm basis has often led to oversimplification or emphasis on only a few features. This is natural, especially considering the fact that so many ichnotaxa were only briefly described, and often based on incomplete material. It is difficult to compare a corpus of hundreds of well-preserved trackways with a single, poorly preserved footprint, but ichnotaxa based on single tracks are common in Carboniferous vertebrate ichnology, as discussed by Haubold *et al*. (2005). Similarly, invertebrate ichnologists who wish to use the name *Skolithos linearis* Haldeman may be dismayed to find that no one can be certain what the top or bottom of this burrow looks like. The burrow has a lining; is the shaft of equal diameter throughout, or can it include a funnel at the top? Even well-trained ichnologists visiting the type locality cannot be sure (Knaust *et al.,* 2018). How tempting it is to synonymize dozens of names and begin afresh!

Excessive complication: splitting

In the absence of a standardized approach, authors have often been tempted to point to slight discrepancies between their own material and previously published ichnotaxa and magnify the differences. Again, in the absence of a uniform approach, it is hard to gainsay these discoveries; perhaps they are more significant than they appear at first. Examples of proliferation are not hard to find; probably more than 200 ichnospecies each of *Cruziana* and *Chondrites* alone have been named. It seems unlikely that every one of these authors checked all the previous literature before setting out to name a new ichnospecies of *Cruziana*. Needless to say, aesthetically attractive trace fossils tend to be the most overnamed, just as ornithologists and lepidopterists have tended historically to recognize too many finely divided taxa of birds and butterflies.

Excessive simplification: lumping

Accordingly, it is unsurprising that many taxonomists have approached the problem of excess ichnotaxa with the enthusiasm that Alexander applied to the Gordian knot. Examples are not hard to find. Alpert (1974) proposed that 35 ichnospecies of *Skolithos* be reduced to only five, and despite subsequent disagreement over details, no one has proposed resurrection of the ichnotaxa that he rendered as junior synonyms (Knaust *et al.,* 2018). Chamberlain (1977) counted more than 170 ichnospecies of *Chondrites* and relegated many of them to the dustbin; Fu (1991) recognized only three. Pemberton and Frey (1982) reduced ninety named ichnospecies of *Planolites* and *Palaeophycus* to eight. It should be emphasized that complete specimens of nearly all these ichnospecies have never been found. Given the extreme lumping of the SOT group in the 1970s and its subsequent expansion, one has to wonder how much information, if any, has been obscured by this procedure.

In such cases, a reviser often claims that the details that earlier authors based new taxa upon are insignificant, or that

these details are only preserved in exceptional material. Für-
sich (1974b) made these principles explicit. For example,
he stated that because the apertures of U-shaped burrows
such as *Diplocraterion* are rarely preserved, they should not
be used as diagnostic features, even though he was aware
that apertures are by no means uniform. As to significance,
this must be established by the individual taxonomist, but
the rejection of criteria based on infrequently seen features
requires further consideration. If we consistently rejected
apertural information, for instance, what would become of
Monocraterion Torell, whose type material includes an ap-
ertural funnel (Jensen, 1997)?

Dealing with poor type material

　　If a specialist on bivalves or trilobites discovered a speci-
men yielding more complete information than any previous
material, the new information would not be ignored taxo-
nomically. The specialist would have the choice of (1) iden-
tifying the new find as a previously named taxon, in which
case the diagnosis of the taxon might have to be redefined,
or (2) basing a new taxon on the more complete material.
As an example, when Sohl (1960) revised the Late Creta-
ceous gastropods of the U.S. Coastal Plains, he noted that
the internal moulds of gastropods having significantly dif-
ferent ornament could not be distinguished from one anoth-
er in the absence of the shell. When a taxon had been based
on a steinkern and Sohl found a corresponding shell, he
gave the shell a new name and restricted the older name to
steinkern material. Thus, although Sohl was presented with
a similar problem to that of Fürsich (1974b) with U-shaped
burrows, he took quite a different approach to solving the
taxonomic problem. If Fürsich had taken the same approach,
we would now have a few ichnospecies historically based
on incomplete U-shaped burrows and used accordingly, and
better-established ichnospecies based on more complete
material for specialized use. Sedimentologists would not
be discommoded by this relaxed approach, but discussion
of complete material would be rendered more convenient.
Palaeontologists have learned much from cases of extraor-
dinary preservation: Ichnologists would be wise to do the
same, and follow Sohl's approach.

Dealing with extraordinary type material

　　In some cases, the original material is more complete
than most subsequent finds. In what is now called the lower
Cambrian Mickwitzia sandstone of Sweden, Torell (1870)
had the good luck to find specimens of trace fossils with
apertures preserved; he named them *Monocraterion ten-
taculatum* and *Diplocraterion parallelum*. Unfortunately,
he did not figure them, which led to some confusion later;
as it turned out, the specimens were extraordinary (Jensen,
1997). *Diplocraterion* is only rarely preserved with aper-
tures and there is no reason to believe that they are always of
the funicular form seen by Torell. Accordingly, most spec-
imens referred to *D. parallelum* can only be considered as
identical to it if one ignores the behavioural significance of
the funnels. The case for *Monocraterion* is more perplexing,
inasmuch as the funnel of *M. tentaculatum* contains many
small tubes whose biological function is unknown (Jensen,
1997). As the early Cambrian biota contains many peculi-

arities by comparison with later forms, we should not be
surprised if their traces are peculiar as well. Ignoring the
special features of early Cambrian *M. tentaculatum* and
D. parallelum is not the best way to advance science; in-
stead, we must pay attention to significant behaviour in ich-
notaxonomy. A partial solution may rest in the use of open
nomenclature (Table 3; Bengtson, 1988).

Table 3

Examples of open nomenclature.

Usage	Meaning
Arenicolites	Certainly *Arenicolites*
"*Arenicolites*"	Not *Arenicolites,* because the name itself is inappropriate here
Arenicolites?	Possibly *Arenicolites,* but doubtful for some reason
cf. *Arenicolites*	Compare *Arenicolites,* but incompletely known
aff. *Arenicolites*	Not *Arenicolites,* but an unnamed form with affinity to it
arenicolitid	Member of the ichnofamily Arenicolitidae, i.e., of U-shaped burrows without a spreite
U-shaped burrow	U-shaped burrow with or without a spreite

Incomplete observation and compound trace fossils

　　How should we treat a pair of named ichnotaxa that turn
out to be parts of one whole – *compound trace fossils* in
the phrase of Pickerill (1994)? Again, let us take a hint
from the more numerous and more experienced taxono-
mists of body fossils: If two parts of a trilobite are called
by different names, the younger name becomes a junior
synonym of the older. We can avoid synonymizing names
where the relationship between two trace fossils is uncer-
tain or ambiguous: *Thalassinoides* and *Gyrolithes* need not
become synonyms even though they are sometimes found
connected, because the type material of each end member
is not associated in this manner. Indeed, we can argue that
where different behaviours are represented, then it is best
to give them separate names. As recommended by Bertling
et al. (2006), the relationship can be expressed by using
a symbol used by botanists for hybrids, e.g., *Thalassi-
noides × Gyrolithes*.

　　The question can be extended from compound traces,
where the parts are distinct but connected, to traces that
are incompletely observed. A classic example of the syn-
onymization of different parts of one structure is given by
Seilacher and Meischner (1964), who demonstrated how the
different toponomic "aspects" of the same trace fossil could
be recognized (Fig. 6). *Nereites* MacLeay, 1839 is com-
monly thought of as a meniscate burrow mantled by lobes
of sediment that may also show a laminated internal struc-
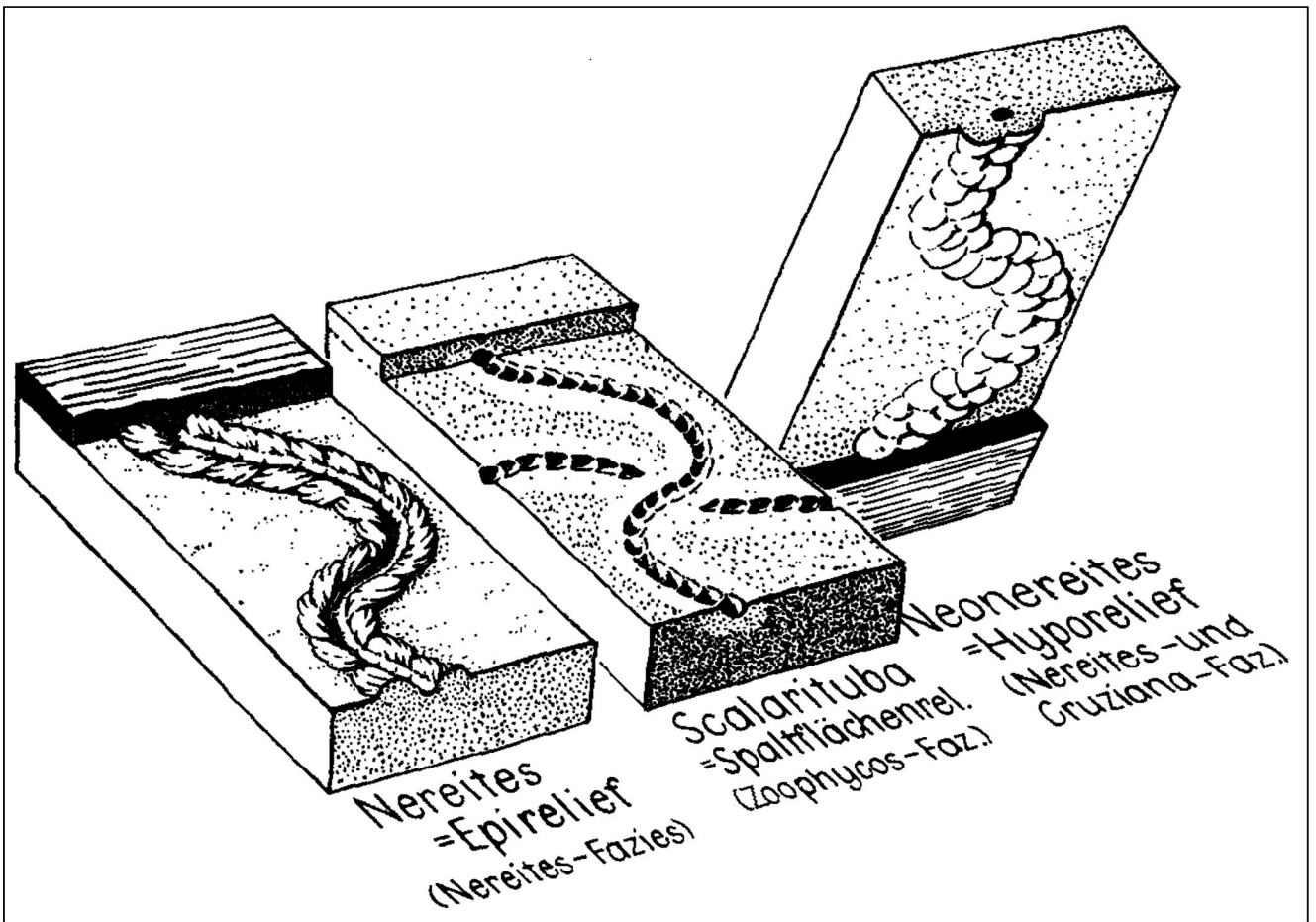ture. Geinitz (1867) later dubbed beautifully well-preserved

Fig. 6. Taphonomy of *Nereites*. Reprinted from Seilacher and Meischner (1964, fig. 12), with the permission of *International Journal of Earth Science* (successor to *Geologische Rundschau*).

epichnial specimens as *Phyllodocites,* and Seilacher (1960) called hypichnia *Neonereites*. The identity of the endichnion *Scalarituba* Weller, 1899, having indistinctly preserved outer lobes, with *Nereites, Phyllodocites,* and *Neonereites* was not obvious until Seilacher and Meischner pointed it out, but has become the consensus view (though some disagree; e.g., Knaust, 2012).

An example of incomplete material is given by *Daedalus* Rouault, 1850, a three-dimensional spreite burrow having a spiralling or scribbling course formed from the shifting of a J-shaped causative burrow. Studying the Ordovician Grès Armoricain of Brittany (France), Rouault (1850) named the three-dimensional spreite as *Daedalus,* the cross section of the spreite exposed on bedding planes as *Humilis,* and pieces of spreite as *Vexillum*. He considered all three to be seaweeds, as many trace fossils were at that time. Lebesconte (1883, p. 468) pointed out that all three fossils were *phases différentes de la vie d'une même plante,* "different phases of the life of a single plant", recognizing that they were taxonomic synonyms.

It is not always easy to determine whether nomenclatural stability is best served by synonymization of parts, or by maintaining their separation in this manner. Returning to the Mickwitzia sandstone, it seems likely that *Halopoa imbricata* Torell (consisting of subhorizontal burrows with a fractured sculpture) represents incomplete branches of

Scotolithus mirabilis Linnarsson (radiating burrow systems that curve downward before levelling outward; these are also incomplete, the presumed intersection of the branches not having been found). Martinsson (1965) argued, probably correctly, that the two ichnogenera were therefore synonyms. Jensen (1997) argued instead for synonymization of *Halopoa* with *Palaeophycus,* based on the similarity of external sculpture in *H. imbricata* and *P. sulcatus* (Miller and Dyer), and pointing out that the sculpture of the few specimens of *Scolithus mirabilis* is not the same as that seen in *H. imbricata,* which is common in the same formation. This is a case where examination of additional material from the type area could resolve the issue.

Expressing doubt

Ichnologists should also make good use of the existing system for expressing doubt about incomplete, poorly preserved, or poorly understood material (Bengtson, 1988). The usage shown here (Table 3) is that recommended by North American taxonomists; details may differ from place to place. The added notations are not considered to be part of the name, but descriptors augmenting it. Incomplete material can thus be given its taxonomic place at the table, but not at its head. It is also possible to leave trace fossils unnamed in published descriptions, however untidy this may appear to the novice.

A holistic approach to incomplete material

In practice, nearly all trace fossil material is incomplete and incompletely known. Ichnologists are in the same state as conodont specialists in this regard. A couple of generations back, some specialists argued that it was impractical to seek out the relationships among conodont elements, even though complete conodont "assemblages" were occasionally discovered. They proposed a parataxonomic system in which elements received names that would not compete in synonymy with those of assemblages (Moore and Sylvester-Bradley, 1957). But holistic thinking prevailed, and as a result conodont specialists invested more effort into discovering assemblages, which corresponded to formerly living organisms (Knell, 2013). The taxonomy of conodonts has not only been placed on a firmer footing as a result, but is also more predictive. Ichnologists should do no less; we should strive to find complete examples instead of contenting ourselves with naming fragments.

Incomplete material can be used to *extrapolate* the complete morphology of a trace fossil. Adolf Seilacher was particularly good at this, and his works contain many striking examples. These constitute *hypotheses* of structural relationships that generated *predictions* of what could be looked for and found by future researchers. While some of them have proved to be unsupported or even *falsified* by further evidence, others have pushed our knowledge forward in remarkable ways. For example, Seilacher (1955; 2007, pl. 35) extrapolated the structure of *Gyrochorte comosa* Heer from the almost two-dimensional views that are commonly all that we see in specimens and field exposures. What seemed in published figures to be merely a shallow trail turned out to be a three-dimensional structure extending deep into individual beds. This had immediate application to the taxonomy of *Gyrochorte* (which could not now include shallow trails that only resembled that aspect of the trace fossil), to the identification of the tracemaker (which had to be a long-bodied, i.e., worm-shaped animal), and to the reconstruction of the tracemaker's ecology (deposit-feeding, or possibly the seeking of prey).

A more important example is the report by Seilacher *et al.* (1998) of trace fossils more than one billion years old in the Vindhyan Supergroup of India. This was a controversial hypothesis, but challenged other scientists to reexamine their own observations and hypotheses. Were the structures really burrows – almost half a billion years earlier than previously attested? What implications would this have for the evolution of life? Were the deposits really one billion years old? These questions and others inspired wide discussion; the original article has been cited 249 times to date.

On a more personal note, I will never forget the impact that Adolf Seilacher had during a field trip arranged by Martin Lockley in 1985 to the Pennsylvanian Minturn Formation of Colorado. Seilacher held the full attention of a dozen students as he noted a pair of large shafts in the outcrop, which, he said, indicated the presence of a U-shaped structure hidden below. In fact, considering the environment of deposition, he predicted that the U was really a Y with a downward extension, analogous to those made today by the bivalve *Solemya* Lamarck in symbiosis with sulphide bacteria (Seilacher, 1990; 2007, pl. 36). He cracked open the rock with vigour before the spellbound audience, expertly breaking it so as to expose the burrow perfectly in vertical section. It was just a U-shaped burrow, not a Y, but the lesson was unforgettable: *Ichnology is a science that generates hypotheses, large and small, with predictions that can be tested – and sometimes falsified*.

Solutions

Several answers to the challenge of making the methods and results of ichnotaxonomy repeatable can be offered. These are organized here as they relate to the standard steps of the scientific method, though it should be emphasized that science takes many different roads toward the truth.

Question

The scientific method classically begins with asking a question or setting a problem. In this regard, it is helpful to be able to converse with one's peers and be understood. Standard terminology for the basic concepts about trace fossils are important: ichnofacies and ichnofabrics, ethological categories, and so on. Here one can point to a continuously improved fabric of ideas within the field (e.g., Seilacher, 1953a, 1964; Frey and Seilacher, 1980; Ekdale *et al.,* 1984; Bromley, 1996; Gérard and Bromley, 2008; Buatois and Mángano, 2011, 2013) – but one that has taken a very different approach from that of modern ethology (Plotnick, 2012). The lack of cross-fertilization with biologists is notable, particularly with ethologists, whose rich history of study of animal behaviour is rarely cited by ichnologists (Plotnick, 2012; Vallon *et al.,* 2015a). Here is an opportunity indeed!

Observation

One solution is to make the *observation* step of the scientific process more effective. Descriptions can be made more comparable by standardizing the terminology of trace-fossil description, an ongoing process (e.g., Seilacher 1953a; Frey, 1973; Ekdale *et al.,* 1984; Bromley, 1996; Buatois and Mángano, 2011; Vallon *et al.,* 2015b). Many of the basic terms for shapes and arrangement already exist in Botanical Latin (Stearns, 1992), with exact equivalents in modern languages. These can easily be found in botanical textbooks, and their use is encouraged.

Collection of large data sets is advised, particularly through photography in the field. The observed range of variation can be usefully incorporated into descriptions of trace fossils, and will inform the diagnoses of ichnospecies and ichnogenera. The investigator should be particularly attuned to variations between small and large traces, and between relatively simple and complex but constructionally similar forms, as these may indicate traces made by juvenile and adult tracemakers of the same species (*ichnogeny,* as in *Lepeichnus* Belaústegui *et al.,* 2016; and earlier demonstrated for modern fiddler crabs by Basan and Frey, 1977).

All relevant information that can be extracted from specimens should be described and considered in an ichnotaxonomic framework. This is a requirement that has been frequently remarked on in the general taxonomic literature

for generations (e.g., Schenk *et al.,* 1948; Simpson, 1961; Blackwelder, 1967; Winston, 1999). Ichnologists are not immune from this necessity; diagnoses need not be terse to be effective.

The researcher should constantly be aware that the features seen first may have little significance for the organisms that make the traces. A viable taxonomy of trace fossils must depend on criteria that are significant to the tracemakers rather than to human beings. The simplest road to understanding trace fossils is, therefore, to study modern tracemakers. Bivalve locomotion burrows would have been far more difficult to understand without the neoichnologic research of Seilacher and Seilacher (1994), for example. As to other researchers, we must expect the unexpected now and then, as happened when a small group of ichnologists strolling a Georgia beach came upon juvenile limulids making trails reminiscent of the *Phyllodocites* aspect of *Nereites* (Martin and Rindsberg, 2007) (Fig. 7).
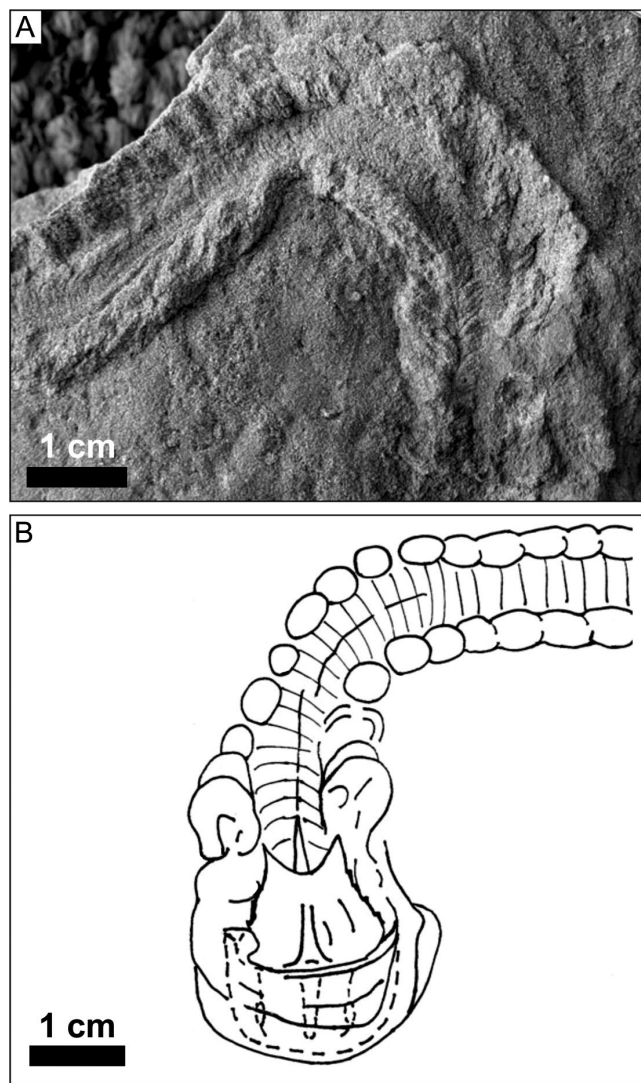
Fig. 7. Comparison of *Nereites* with trace made by juvenile *Limulus*. **A**. *Nereites missouriensis* from the Mississippian Hartselle Sandstone of Alabama (USA). **B.** Trail of juvenile *Limulus polyphemus* on a beach at Sapelo Island, Georgia (USA). Scale bar is 1 cm intervals. Reprinted from Martin and Rindsberg (2007, fig. 29.1) by permission of Elsevier.

Hypothesis and theory

Effective classification is not an end in itself, but a *theory,* that is, a generally held hypothesis, about the relationships of living organisms. Molecular taxonomy has confirmed many organismal relationships that were originally hypothesized on the basis of morphology, and modified many others. Ichnotaxonomists lack this powerful tool, but should recognize that ichnospecies, first of all, ultimately represent *hypotheses* about the interrelationships of individual specimens, and that ichnogenera represent hypotheses about the interrelationships of ichnospecies (cf. Thompson, 2003). While it is desirable for names to be stable, these hypotheses are not set for all time by authority, but must remain *testable,* like any other hypotheses in science. Expect ichnotaxonomy to keep changing, and do not expect the consensus view (or theory) always to be the best one. To be rigid in such matters is to abandon science.

In addition to utilizing the full range of morphology that trace fossils present, the observer should *extrapolate* from known morphology to the unknown, though always with justification from analogous material, and with the extrapolations clearly labelled as hypotheses subject to testing and falsification. Thus, for the dumbbell-shaped burrows *Arthraria* Billings (junior synonym, *Bifungites* Desio), preserved typically as scoured hypichnia, one might speculate that the bulbous tips are merely the visible part of oblique galleries that extended downward, as suggested by Seilacher (2007, pl. 20), or alternatively that the tips end abruptly.

Publication

The last step in the formal scientific method, publication, is a phase that requires the cooperation of the entire community of ichnologists. Successful authors recommend that writers seek out comments on their work while they are still writing, both for clarity and for content. The process becomes more formal on submission of a manuscript to a journal editor, who will solicit reviews from other scientists.

This process clearly works, though it is not trouble-free. Ideally, ichnotaxonomy should be approached in the spirit of cooperation rather than competition. Frey's (1973) revision of trace-fossil terminology was remarkable for the number of colleagues whom he consulted before publication (Table 4) – almost entirely by mailed correspondence. Today, such correspondence often takes place at the speed of light via communications such as email, the SKOLITHOS listserver, and the Ichnology Facebook page.

CONCLUSIONS

The erratic results of ichnotaxonomy show that it is not yet a mature science. Suggestions for improvement include the following.

– Take a holistic approach, in particular by studying the whole trace fossil using as many specimens as possible and in relation to context.
– Make more detailed and biologically informed observations.
– Describe the full range of variation of the ichnotaxon, not merely a platonic ideal.

Table 4

Ichnologists consulted by R. W. Frey
before standardizing ichnologic terms in 1973.

Country	Ichnologists
Canada	Laing Ferguson
Denmark	Richard G. Bromley
France	Jacques Lessertisseur
Germany (FRG)	Jürgen Dörjes Walter Häntzschel Günther Hertweck Karl Krejci-Graf Hans-E. Reineck Adolf Seilacher
Germany (GDR)	Arno H. Müller
Italy	Ardito Desio
Japan	Kotora Hatai
Poland	Andrzej Radwański
Sweden	Anders Martinsson
Union of Soviet Socialist Republics	R. Th. Hecker (Russia) Oleg S. Vialov (Ukraine)
United Kingdom	T. Peter Crimes Anthony Hallam William J. Kennedy Scott Simpson
United States of America	Donald W. Boyd C. Kent Chamberlain Charles D. Hollister James D. Howard Richard G. Osgood Bob F. Perkins Donald C. Rhoads Curt Teichert Heinrich Toots John E. Warme

– Write descriptions in uniform terms.
– Where possible, select ichnotaxobases that relate to the behaviour and anatomy of the tracemakers (*bioprint*).
– Where the data support it, give a single name to all members of an ichnogenic series.
– Filter out taphonomic effects rather than using them as ichnotaxobases.
– Reinvestigate type material; where it is inadequate, seek topotypes.
– Avoid the choice of incomplete or poorly preserved material as types.
– Gradually remove well-defined trace fossils from overly broad ichnogenera.
– Where at all possible, respect the work of other investigators, including the dead.
– Follow the established rules of nomenclature (International Commission on Zoological Nomenclature, 1999).
– This approach should result in a firm basis for the science of ichnotaxonomy.

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