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Leonard Finkelman
Linfield College

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Crossed Tracks

Mesolimulus, Archaeopteryx, and the Nature of Fossils

Leonard Finkelman
Linfield College
dinosaurphilosophy@linfield.edu

Abstract

Organisms leave a variety of traces in the fossil record. Among these traces, vertebrate and invertebrate paleontologists conventionally recognize a distinction between the remains of an organism's phenotype (body fossils) and the remains of an organism's life activities (trace fossils). The same convention recognizes body fossils as biological structures and trace fossils as geological objects. This convention explains some curious practices in the classification, as with the distinction between taxa for trace fossils and for tracemakers. I consider the distinction between "parallel taxonomies," or parataxonomies, which privileges some kinds of fossil taxa as "natural" and others as "artificial." The motivations for and consequences of this practice are inconsistent. By comparison, I examine an alternative system of classification used by paleobotanists that regards all fossil taxa as "artificially" split. While this system has the potential to inflate the number of taxa with which paleontologists work, the system offers greater consistency than conventional practices. Weighing the strengths and weaknesses of each system, I recommend that paleontologists should adopt the paleobotanical system more broadly.

1. Introduction: A Day on the (Jurassic) Beach

One hundred and fifty million years ago, the detritus of animal life accumulated on the shoreline of a Jurassic sea. A horseshoe crab took its last journey, literally stopping dead in its tracks. Beside the dead body, molted theropod feathers—carried by a soft Jurassic breeze—settled on the sand. Body and feathers both became part of a daily routine: each day's tide would carry in mineral-rich sediments as it rose and carry out organic molecules from the animals' remains as it fell. Consequently the remains hardened into rock and disappeared beneath developing limestone beds.

The shoreline eventually became the German town of Solnhofen. Through two centuries of excavation from the town's limestone quarries, paleontologists found a fossil bounty. Included among these fossils are the horseshoe crab's shell, its tracks, and imprints of the theropod feathers.

Lomax & Racay (2012) named the horseshoe crab *Mesolimulus walchi*, but one would be incorrect to say that the tracks are *M. walchi* tracks. *M. walchi* is a name that applies to *body fossils*, or the fossilized remains of organism. By contrast, the horseshoe crab's tracks are fossilized evidence of the organism's 'life activities' and so qualify as *trace fossils* (Ride, *et al.* 2012, article 23.7; Pemberton & Frey 1982). Lomax & Racay therefore classify the tracks in the trace fossil species *Kouphichnium walchi*. By convention, vertebrate and invertebrate paleontologists classify body fossils in taxa associated with biological kinds. This system excludes trace fossil taxa, which paleontologists regard as geological features (Carney, *et al.* 2012). The International Code of Zoological

Nomenclature (ICZN) therefore proscribes different taxonomies for body fossils and trace fossils. This distinction is clearly exemplified by the horseshoe crab's shell and its associated trackway.

By contrast, the feather imprints are a borderline case in the body fossil-trace fossil distinction. Herbert von Meyer named the first feather imprint found at Solnhofen *Archaeopteryx lithographica* (1861); when paleontologists recovered skeletal remains of feathered theropods from the same limestones, they applied the same name to those body fossils. However, in a 2011 review of the species *A. lithographica* the ICZN committee ruled that the species name should not apply to von Meyer's feather impressions because each are the result of different historical processes. Impressions and body fossils preserve different kinds of information; consequently, the two kinds of fossil could not be definitively correlated with one another. So the committee argued; to the contrary, structural similarities between feather impressions and body fossils sometimes allows paleontologists to draw inferences about body fossil taxa from feather impressions (Carney, *et al.* 2012; Foth & Rauhut 2017; Rauhut, *et al.* 2018). The status of feather impressions as trace fossils therefore remains in dispute.

The purpose of this essay is to dissolve the debate: recent paleontological work undermines traditional justifications for the body fossil-trace fossil distinction. Taxonomic practices based on that distinction might therefore be revised. I argue in favor of one potential revision.

In the following section I explore different reasons given for distinguishing between body fossils and trace fossils. As we will see, these reasons highlight either historical or structural differences between fossil kinds. My goal in the third section is to refer to the

examples raised above to show how neither historical nor structural differences yield consistent distinctions between body fossils and trace fossils. *Mesolimulus*, *Kouphichnium*, and *Archaeopteryx* offer illustrative examples of the difficulties in distinguishing fossil kinds. These difficulties can be generalized to all vertebrate and invertebrate fossils. Following that, I show in the fourth section how paleobotanists offer a practical system that integrates fossil taxonomies by classifying all fossils as “artificial” morphological taxa. In the fifth section, I consider the advantages and disadvantages of adopting a similar strategy more broadly. The consequence would be a system that treats body fossils and trace fossils as equally “artificial” with respect to biological taxa. I endorse that view and conclude with recommendations for future work.

2. Traces and Fossils

Cleal & Thomas (2010) offer a useful distinction between *organism fossils* and *fossil organisms*. Organism fossils are geological objects (such as limestone slabs or permineralized skeletal elements) that preserve some trace of an organism or its activities. Fossil organisms are the once-living things from which organism fossils come (262). A single fossil organism may yield a variety of organism fossils. Lomax & Racay (2012), for example, describe two organism fossils (i.e., a shell and a trackway) that trace to the same fossil organism (i.e., a Jurassic horseshoe crab). Following Darwin (1859), vertebrate and invertebrate paleontologists (collectively, *paleozoologists*) collect evidence from organism fossils to reconstruct the evolutionary history of fossil organisms (Plavcan & Cope 2001; Bertling 2007; Bell 2012).

Paleozoologists traditionally distinguish organism fossils either as *body fossils* or as *trace fossils* (Pemberton & Frey 1982; Sarjeant 1990; Crimes & Droser 1992; Bromley 1996; Bertling, *et al.* 2006; Falkingham, *et al.* 2016). While this distinction is widely accepted among researchers, paleozoologists offer many and varied reasons for recognizing and upholding it. Reasons for distinguishing body fossils from trace fossils (or “*ichnofossils*”) are generally either historical or structural. In this section I will recount both historical and structural arguments for distinguishing organism fossil kinds.

Historical reasons for distinguishing body fossils from ichnofossils focus on how organism fossils relate to fossil organisms. In the horseshoe crab’s case, Lomax & Racay treat the shell as a direct representation of the fossil organism. The shell, after all, was once a part of the horseshoe crab’s body, hence the term “body fossil.” The trackway, by contrast, is an organism fossil that does not directly represent the fossil organism. Turner (2005) argues that the correlation between a trackway and its maker is underdetermined at fine taxonomic resolutions (220-221). Consequently, the trackway is less direct evidence of the fossil organism. It is one among many traces of the horseshoe crab, hence the term “trace fossil.”

Paleozoologists who agree on this point nevertheless recognize that the distinction must be rendered in more precise terms. An organism fossil such as the feather impression described by von Meyer (1861) may not have been part of a fossil organism’s body *per se*, but the evidence it gives of the fossil organism is more “direct” than a trackway. More precise definitions of “body fossil” and “ichnofossil” would be necessary to determine what kind of fossil is the feather impression.

A common first step towards greater precision is to define “body fossils” as the fossilized remains of a fossil organism’s phenotype. This is meant to provide contrast with ichnofossils, defined as the fossilized remains of an organism’s ‘life activities’ (Pemberton & Frey 1982, 844), the fossilized ‘works of an organism’ (Ride, *et al.* 2012, article 10.5; *cf.* Bertling, *et al.* 2006), or structures ‘left in or on a soft sediment or in a hard substrate by a living organism’ (Crimes & Droser 1992, 340).

Pemberton & Frey (1982) argue that this formulation of the historical distinction is also objectionably vague. For example, shells and their molds in surrounding substrate are equally well considered the remains of an organism’s phenotype and its “works” or “life activities” (845). Indeed, all organism fossils propagate information about a fossil organism’s life processes. If an ichnofossil is simply any object whose provenance yields information about past life processes, then all fossils should be ichnofossils (*cf.* Currie 2018, 63-84).

Frey (1973) argues that the distinction between body fossils and ichnofossils is better drawn in terms of structural differences between the two. He defines such structures as

...tangible evidence of activity by an organism, fossil or recent, other than the production of body parts...[including] the entire spectrum of substrate traces or structures that reflect a behavioral function...[excluding] molds of body fossils that result from passive contact between body parts and the host substrate, but not imprints made by the body parts of active organisms. (quoted in Simpson 1975, 41)

Bertling, *et al.* (2006) offer a refinement of the concept:

Generally, a trace fossil is defined as follows: a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate...[which] may be rock, soft to firm sediment, dead organic matter (peat, wood, shell, bone) or (then) living organic tissue. (266)

These definitions both highlight important structural features of ichnofossils that are not true of body fossils. Ichnofossils 'exist only by virtue of the soft or hard substrate on or in which they formed... They are an integral part of the substrate' (Crimes & Droser 1992, 340). Since ichnofossils are 'close to primary sedimentary structures,' paleozoologists diagnose ichnofossils by geological features, rather than the biological traits with which they diagnose body fossils (Raup & Stanley 1971, 16-17; Bertling 2007, 82; Carney, *et al.* 2012). Relevant structural differences therefore imply disciplinary and methodological differences in the study of body fossils and ichnofossils.

Geological features by which researchers classify ichnofossils include weathering, strength, and density (Williamson 1984; Bertling, *et al.* 2006). Fossil tracks, also called ichnites, form one ichnofossil taxonomy (Alcalá, *et al.* 2016). Paleontologists diagnose ichnite ichnotaxa not only by overall track morphology, but also by physical properties such as substrate density and depth (Falkingham, *et al.* 2016, 6-8; *cf.* Bertling, *et al.* 2006). Fossil burrows or dwellings, also called dominichids, form another ichnofossil taxonomy (Seilacher 1967). Paleontologists diagnose dominichid ichnotaxa by orientation, internal structure, and substrate (*ibid*; *cf.* Bertling, *et al.* 2006, 274-280). By contrast with these examples, body fossils preserve phenotypic traits shared with living or fossil organisms and so can be diagnosed with tools and methodologies shared with biologists (Crimes & Droser 1992, 340). To wit: *Mesolimulus* fossils preserve traits easily compared with those of living horseshoe crabs, but *Kouphichnium* fossils do not.

These historical and structural distinctions between body fossils from ichnofossils explain how paleontologists do or don't identify body fossils and trace fossils with fossil organisms. When classified, fossil organisms (like living organisms) would sort into

biological taxa (or “*biotaxa*”). Biotaxa may be coextensive with body fossil taxa because researchers diagnose body fossil taxa by reference to biological traits. By contrast, ichnofossil taxa (or “*ichnotaxa*”) do not correlate with biotaxa because researchers classify ichnofossils by reference to geological properties. In attributing the fossil shell to the species *M. walchi*, then, Lomax & Racay tacitly name both a body fossil taxon and a putative biotaxon. The name *K. walchi*, however, denotes an ichnotaxon uncorrelated with a particular biotaxon.

It is for these reasons that the ICZN asserts that an ichnotaxon name ‘does not compete’ with a body fossil taxon name. Names applying to geological kinds should not be applied to biological kinds, even when the rules of nomenclature (such as rules of priority) might dictate otherwise (Ride, *et al.* 2012, article 23.7). Ichnotaxon names and biotaxon names therefore designate entities in non-overlapping taxonomic systems. These systems run “parallel” to one another, hence the term *parataxonomy* (Pemberton & Frey 1982; Serjeant 1990; Bromley 1996; McNeill, *et al.* 2012).

3. The Problems with Parataxonomy

One significant borderline case in the body fossil-trace fossil distinction is von Meyer’s feather impression. Impressions preserve biological traits useful in the classification and analysis of biotaxa (Carney, *et al.* 2012). For this reason, paleozoologists recognize the taxon upon which the fossil was built, *A. lithographica*, as a biotaxon (von Meyer 1861; Senter & Robins 2003; Foth & Rahut 2017; Rahut, *et al.* 2018). *A. lithographica* is a biotaxon and the first *A. lithographica* specimen was a feather impression; logically, then, feather impressions ought to qualify as body fossils.

As philosophers say, one theorist's *modus ponens* is another's *modus tollens*. In 2011, the ICZN ruled that another specimen should replace von Meyer's feather impression as a neotype for the species because feather impressions are not body fossils:

The name *Archaeopteryx lithographica* von Meyer, 1861 is...a nomen dubium because it is not possible to determine whether the type specimen (the original feather impression) belongs to any of the generic or specific taxa of fossil bird recognized from the Solnhofen limestones. ...The number of [fossil bird] species recognized is not relevant to the question of whether the feather impression can be assigned to a known specific taxon...[the name] cannot be used for any of the avian fossils from the Solnhofen limestones except for the feather impression. (2011, 183)

To summarize the reasoning given here: no feather impression taxon could be coextensive with a biotaxon since disparate kinds of fossil organism could yield morphologically similar feather impressions. *A. lithographica* is a biotaxon and feather impressions do not belong in biotaxa; logically, then, the feather impression initially named as an *A. lithographica* specimen ought to be reclassified.

The implication of the ICZN's ruling must be that feather impressions are ichnofossils. While it is necessary that body fossils preserve biological traits, the preservation of biological traits is not sufficient for an organism fossil to qualify as a body fossil (Bertling, *et al.* 2006, 266). The fossil must also preserve by means of some historical process that permits correlation of the organism fossil with some fossil organism. In particular, body fossils form by direct replacement of organic body elements with minerals, i.e., permineralization. Feather impressions (and other organism fossils such as feeding traces, nests, coprolites, and eggs) may form through permineralization of organic material, but rarely in direct association with the fossil organism's body. The consequent lack of direct association is a feature shared with the geological processes that yield other ichnofossils such as feeding traces, nests, coprolites, and eggs. Paleozoologists classify

these fossils in parataxonomies (Pemberton & Frey 1982; Sarjeant 1990; Mikhailov, *et al.* 1996; Falkingham, *et al.* 2016; Gatesy & Falkingham 2017). None of these parataxonomies correlate with biotaxa (Ride, *et al.* 2012, article 23.7). Since feather impressions share salient features of preservation with other paradigmatic trace fossils, it should follow that feather impressions do not correlate with biotaxa, either.

Nevertheless, body fossils share important structural similarities with some ichnofossils. Because of these similarities, ichnofossils such as feather impressions sometimes convey information useful for inferences about fossil organisms (Carney, *et al.* 2012; Foth & Rauhut 2017; Rauhut, *et al.* 2018). While sedimentation processes that account for the preservation of ichnofossils are necessary for the preservation of feather impressions, carbonization of the feathers from which impressions originate may preserve features normally associated with the permineralization of bone (Davis & Briggs 1995, 783). Furthermore, *A. lithographica* body fossils include associated feather impressions that are considered biological structures because of their direct association with uncontroversial body fossils (Carney, *et al.* 2012; Rauhut, *et al.* 2018). Feeding traces, nests, coprolites, and eggs similarly preserve biological traits and may be found in direct association with body fossils (although coprolites directly associated with body fossils are technically known as “cololites”) (Bertling, *et al.* 2006). It is therefore logically possible, if conventionally discouraged, to correlate some ichnofossils with fossil organisms; there is no necessary dissociation between ichnofossil taxa and biotaxa.

Conversely, skepticism of the correlation between body fossil taxa and biotaxa is sometimes warranted. Fossil organisms for which we have incomplete understanding of ontogeny or dimorphism may sort into several distinct body fossil taxa. Poor

understanding of ontogenetic variation in dinosaur groups, for example, may lead paleontologists to split dinosaur fossil organisms into “artificial” body fossil taxa (Lehman 1990; Horner & Goodwin 2009; Rauhut, *et al.* 2018). Sexual dimorphism in fossil organism populations would imply a similar problem: paleontologists’ inability to reconstruct intraspecific interactions from body fossil data problematizes correlation between body fossil taxa and true biotaxa (Lehman 1990; *cf.* Barden & Maidment 2011). Body fossil taxa therefore need not bear a one-to-one correlation with any particular biotaxon.

One might argue that biotaxa correlate more closely with body fossil taxa than they do with ichnotaxa, but this need not be theoretically significant. Instead, the observation may reflect non-theoretical values in taxonomic practice. All taxonomic systems codify some implicit bias by preferentially including information as relevant or excluding information as irrelevant (Schuh & Brower 2009, 124). If paleontologists diagnose body fossil taxa by biological characters and ichnotaxa by geological characters, then the body fossil-trace fossil distinction is less informative of categorical distinctions than it is of differing research interests (*cf.* Kitcher 1984). Commercial, agricultural, and engineering interests tend to motivate selection of characters for geological taxa such as rocks or soils (Ibid; Soil Survey Staff USA 1975; Williamson 1984; DuBois, *et al.* 2007). If geological characters diagnose ichnotaxa, then, the exclusion of biologically significant characters (e.g., size, geographic location, or geological age) implies little about the nature of ichnofossils (*cf.* Bertling, *et al.* 2006). One might be correct in concluding that ichnotaxonomic distinctions are often ‘artificial’ by biotaxonomic standards, but only because biologists are not always interested in geologically relevant distinctions (Ibid, 272).

We may find a more theoretically substantive reason for greater correlation between biotaxa and body fossil taxa rather than between biotaxa and ichnotaxa, but it does not necessarily resolve the foregoing inconsistencies in distinguishing body fossil taxa from ichnotaxa. One reason often given for maintaining that distinction is that theorists are more commonly capable of tracing body fossils to a biotaxon than they are of tracing ichnofossils to biotaxa (see, e.g., ICZN 2011; Lockley, *et al.* 2011; Alcalá, *et al.* 2016; Gatesy & Falkingham 2017). Currie (2018) suggests this is because ‘midrange’ inferences connecting body fossils and fossil organisms are more robust than theories connecting ichnofossils and tracemakers (79-82): our understanding of permineralization and taphonomy consistently allows us to reconstruct a fossil organism from body fossils, but there is no general account that allows us to reconstruct a fossil organism from footprints or feather impressions. If it is the strength of midrange inferences that justifies parataxonomic practices, however, then we should find the same inconsistencies found in other justifications. Paleontology is rife with examples of strong inference from trace fossils to fossil organisms, including tracks (Lockley & Hunt 1994; Lockley, *et al.* 2011), burrows (Crimes & Droser 1992), skin impressions (Bell 2012), and feather impressions (Foth & Rauhut 2017; Rauhut, *et al.* 2018). Again, structural and historical differences between body fossils and ichnofossils—some of which do allow robust inferences from ichnofossils to fossil organisms—do not consistently track with parataxonomic distinctions.

To summarize the points discussed in this section: (1) paleontologists may successfully correlate ichnotaxa with biotaxa; (2) body fossil taxa need not correlate with biotaxa; (3) observations that there are in fact stronger correlations between body fossils and biotaxa do not imply a theoretically significant distinction between ichnofossils and

body fossils. Points (1) and (2) undermine the justification for parataxonomic practices (see Section 2 above). What this discussion should show is that there are no particular structural or historical features that consistently distinguish body fossils from ichnofossils. Hence our difficulty in classifying feather impressions: the distinction between body fossils and ichnofossils is inconsistent.

4. Grafting a Solution

Darwin (1859) argued that taxonomy ought to be informed by evolutionary history (or *phylogeny*). Paleozoologists tend to construct taxonomies with that goal in mind (Gaffney 1979; Benton 2015); however, maintaining parataxonomic systems may be counterproductive towards that end. Ichnofossils yield information that would be lost if body fossils provided our only record of extinct life. Phylogenetic hypotheses therefore benefit from integration of ichnofossil data with body fossil data, but the practice of maintaining parataxonomies has the potential to hinder these efforts. A system that integrates biotaxonomy with ichnotaxonomy is worth some consideration.

Paleobotanists have already adopted such a system. Ironically, the goal of integration is achieved not by correlating ichnofossils with biotaxa, but instead by divorcing “body” fossils from biotaxa. In this sense, paleobotanists deny the paleozoologists’ distinction between body fossils and trace fossils—all kinds of organism fossil are on a categorical par. Although paleobotanists distinguish fossil taxa from biotaxa, the flexibility of their fossil monotaxonomy permits easier integration of fossil taxonomy with biotaxonomy.

A single plant may leave a variety of fossil traces—ranging from fossilized pollen to petrified tissue to leaf imprints—and paleobotanists are rarely in a position to correlate fossils of one kind with another. It is therefore ‘impossible to name taxa of fossils in exactly the same way as taxa of living plants’ (Cleal & Thomas 2010, 261). Paleobotanists have consequently adopted the concept of the “fossil-taxon” as distinct from biotaxa. Article 1.2 of the International Code of Nomenclature for Algae, Fungi, and Plants defines fossil-taxa as: ‘the remains of one or more parts of the parent organism, or one or more of their life history stages, in one or more preservational states, as indicated in the original or any subsequent description or diagnosis of the taxon’ (McNeill, *et al.* 2011). Botanical fossil taxa are what have elsewhere been called “taxonomic species”: groups defined by a variety of ‘purely taxonomic criteria’ and explicitly not by evolutionary descent (Cleal & Thomas 2010, 266; Mayden 1997). Paleobiologists thereby formalize the distinction between fossil plants (sorted by phylogeny) and plant fossils (not necessarily sorted by phylogeny). Since fossil plants ‘no longer exist as realities’ in paleobotanical taxonomy, the goal of sorting plant fossils need not be constrained by standards of identifying biotaxa (Cleal & Thomas 2010, 262).

Cleal & Thomas argue that the strength of this approach is in its flexibility. The paleobotanists’ approach is to let a hundred flowers blossom and a hundred schools contend, as it were. “Fossil-taxa” diagnosed by different characters—e.g., by morphologies from different parts of a plant—are kept distinct, even though the result is an artificially inflated number of taxa. Paleobotanists are therefore forced to take an intentional approach to establishing consistent criteria for correlating fossil-taxa with biotaxa. Paleobotanists may diagnose fossil-taxa by a variety of taxonomic standards, so character

choice for taxon diagnosis need not be constrained by the differing goals or methods of biology or geology; both can be accommodated (Ibid, 266). As a result, some fossil-taxa may be coextensive with biotaxa while others will not. Paleobotanists must take explicit steps to establish independent theoretical criteria for correlating fossil-taxa with biotaxa (*cf.* Plavcan & Cope 2001). Doing so ideally gives paleobotanists consistent criteria for extracting phylogenetic information from fossils (Cleal & Thomas 2010, 266).

The primary difference between the paleobotanical and paleozoological approaches lies in assumptions of “artificiality.” Paleobotanists assume that all fossil-taxa are “artificial,” i.e., not coextensive with biotaxa. In order to demonstrate otherwise, they must apply explicitly stated theoretical criteria for correlating a fossil-taxon with a biotaxon. As we have already seen, paleozoologists’ correlations of fossil taxa with biotaxa are often inconsistent. This inconsistency is a result of the assumption that body fossil taxa are coextensive with biotaxa where ichnotaxa are not necessarily so: since the distinction between body fossils and ichnofossils is often drawn inconsistently, it follows that consequent distinctions between “artificial” and phylogenetically natural taxa should also be inconsistent.

Could paleozoologists adopt the paleobotanical system? There are reasons to think so. Gong, *et al.* (2002) and Jensen, *et al.* (2007) argue that ichnofossils convey enough biological information to be useful in phylogenetic reconstruction; Bell (2012) also argues that skin impressions, which are structurally similar to ichnofossils (see section four above), may nevertheless provide a ‘positive phylogenetic signal’ (1). If these examples can be generalized, then the biological information encoded within ichnotaxon diagnoses may

be sufficient to yield useful biological inferences. That conclusion could justify reconsideration of parataxonomic conventions.

5. Weighing the Options

Theorists have already debated adoption of a monotaxonomic system for paleozoology. Gatesy & Falkingham (2017), for example, argue against a categorical distinction between body fossils and ichnofossils on the grounds that the only valid characters of ichnofossils should be those associated with organisms' phenotypes (*cf.* Bertling, *et al.* 2006). To the contrary, Van Valen (1978) offers strong resistance to the same idea. He argues that ichnotaxon diagnoses must include geological characters to be informative and so any system combining those with body fossil taxa would be objectionably artificial (286-287). These arguments focus on methodologies and practical consequences; the conceptual points raised above may contribute to progress in this ongoing discussion.

One possibility is that “progress” is not necessary. As noted above, paleontologists are already capable of drawing from ichnofossil data for their research goals without resorting to wholesale taxonomic revision (Gong, *et al.* 2002; Jensen, *et al.* 2007; Bell 2012). In fact, paleontologists already have the tools necessary for integrating systems with different taxonomic standards, as evidenced by consideration of “problematic taxa.” Problematic taxa, or *problematica*, are biotaxa that include fossils of uncertain affinity (Häntzschel 1962). These uncertainties may be the result of poor or incomplete preservation, significant phenotypic disparity from known organisms, or artificial taxonomic splitting. *Problematica* are therefore taxonomically isolated from other biotaxa.

Häntzschel notes epistemic similarities in consideration of ichnotaxa and problematica: in particular, phenotypic analysis of each is limited by the informational gap between the described fossil and the organism from which the fossil originated. Conodonts, a collection of taxa that include tooth-like index fossils, provide a clear example of how paleontologists bridge the informational gap (Benton 2015, 52-53). Through careful selection of biologically informative characters, paleontologists determined the phylogenetic affinities of conodonts with early chordates (Donoghue, *et al.* 2000; *cf.* Gatesy & Falkingham 2017). Successful identification of the “conodont animal” shows how paleontologists have developed tools for inference across divisions between taxonomic systems.

On one hand, the conodont example demonstrates how a monotaxonomic system like the one used by paleobotanists may hinder theoretical progress. Paleontologists regarded conodont taxa as problematica until Briggs, *et al.* (1983) described a fossil including specimens from several apparently disparate conodont taxa. The specimens’ association showed that different conodonts were, in fact, different phenotypes from the same animal. The earlier classification of conodonts is therefore an unintentional application of the paleobotanists’ “fossil-taxon” concept. To borrow a distinction from Cleal & Thomas (2010), paleontologists had classified organism fossils rather than fossil organisms. As a result, the true affinities of the “conodont animal” remained obscure for decades longer than they might have otherwise (Donoghue, *et al.* 2000; Benton 2015, 52).

On the other hand, paleontologists resolved the phylogeny of conodonts and chordates precisely because they came to regard conodont taxa as “artificial” and consequently modified their approach to those taxa. The more intentional analyses that followed—those that reframed consideration of characters—yielded the theoretical

progress that remained elusive for so long. By acknowledging that biotaxa and ichnotaxa may be equally artificial (or not), as a monotaxonomy would imply, paleontologists might make similar progress.

Indeed, there are already good reasons to embrace assumptions similar to those made by paleobotanists and regard body fossil taxa as artificial to the same degree as ichnotaxa. Fossil organism taxa for which we have incomplete understanding of ontogeny or dimorphism may have a one-to-many relation with body fossil taxa (see Section 3). In those cases, the informational gap between fossil organism and biotaxon may therefore be as wide as that between fossil organism and ichnotaxon. In other cases, such as *Mesolimulus* and *Kouphichnium*, the gap between fossil organism and ichnotaxon may even be smaller than the gap between other fossil organisms and biotaxa (see also Lockley, *et al.* 2011).

Our initial example might provide an analogous case. Clearly, the *Mesolimulus* organism was the tracemaker of the *Kouphichnium* tracks. Why recognize two organism fossil taxa for one fossil organism? The answer traditionally given by paleozoologists, rooted in their commitment to parataxonomies, would be: because *Mesolimulus* is a body fossil taxon, *Kouphichnium* is an ichnotaxon, and body fossil taxa are natural where ichnotaxa are artificial. As we have already seen, that answer is too quick—body fossil taxa may be artificial or ichnotaxa may be natural. As answer rooted in monotaxonomic practice would be: because each taxon is diagnosed by different characters and we should minimize the number of *a priori* judgments we make about which characters are more significant than others. Such an answer implies the necessity of explicit justifications of significance, which is to the advantage of all researchers.

One might argue against this apparent taxonomic oversplitting. Krell (2004) demonstrates that the kind of sorting that I suggest tends to overestimate biotaxon numbers significantly. If we count both body fossil taxa and ichnotaxa, then, we should expect overstatement of past biodiversity in the fossil record. In other words: it is the nature of ichnotaxa to split biotaxa and so a monotaxonomic reading of the fossil record will artificially inflate biotaxon counts. This may be so, but only if one reads the fossil record with the expectation that organism fossil taxa correlate with fossil organism taxa. My recommendations explicitly reject this assumption. In assuming that all organism fossil taxa are “artificial,” i.e., uncorrelated with particular biotaxa, we would not expect fossil taxon counts to represent biodiversity *per se*. Distinguishing fossil taxon diversity from biodiversity need not imply any inability to estimate past biodiversity: Oliver & Beattie (1996) argue that parataxon counts correlate with biotaxon counts after controlling for taxonomic splitting and lumping. “Control” for splitting and lumping includes use of the tools recommended by Gatesy & Falkingham (2017) for inference across parataxonomies (*cf.* Donoghue, *et al.* 2000; Gong, *et al.* 2002; Jensen, *et al.* 2007; Bell 2012). Since my recommendations include intentional application of these inferential tools, taxonomic splitting may be less a bug than a feature.

In this way, a clear benefit of monotaxonomy would be the greater intentionality with which paleozoologists, like paleobotanists, would have to approach phylogenetic analyses. As with paleobotanists, allowing a hundred flower taxa to bloom puts the onus on researchers to develop more consistent tools for correlating various organism fossils with fossil organisms. High-power phylogenetic analyses require careful and intentional character selection to diagnose relevant taxa (Chippendale & Wiens 1994; Poe & Wiens

2000). Unfortunately, body fossil taxa—the relevant taxa for a majority of phylogenetic history—preserve only low-resolution morphological data (Scotland, *et al.* 2003). Qualitatively similar characters encoded in ichnotaxon diagnoses may provide valuable supplemental information that improves the quality of phylogenetic research (Gatesy & Falkingham 2017). This is the case in paleobotany: since fossil-taxon diagnoses are not biased by assumptions of artificiality, a wide variety of diagnostic characters improve the system’s flexibility (Cleal & Thomas 2010). Similar flexibility would benefit paleozoology: by assuming that *Mesolimulus*, *Koupichnium*, and *Archaeopteryx* are all equally “artificial” taxa, proving otherwise would require paleozoologists to develop explicit standards for privileging a horseshoe crab shell over the tracks upon which it rests (see, e.g., Plavcan & Cope 2001).

This, then, suggests actionable consequences of adopting a monotaxonomy in paleozoology. In a monotaxonomic system wherein *Mesolimulus*, *Koupichnium*, and *Archaeopteryx* are all on an ontological par, all organism fossil taxa are equally “artificial.” Taxa are *prima facie* equally likely (or unlikely, as the case may be) to be coextensive with biotaxa. To intentionally bias diagnostic character selection for or against biological traits would therefore misrepresent the nature of fossil-taxa. Monotaxonomic fossil taxon diagnosis encodes a wider variety of information, potentially including both biological and geological characters in all cases (*cf.* Ibid). Sorting these characters for qualitatively similar information (e.g., biological traits for phylogenetic analysis or geological traits for taphonomic research) requires a more intentional approach to character choice and weighting, forcing researchers to consider more carefully research goals and the relevance of particular structures and features. Careful consideration of character selection and

weighting is among the set of best practices in phylogenetic analysis, to cite one example raised above (Schuh & Brower 2009, 124-130). Consequently, adoption of a monotaxonomy would motivate best practices in at least one important paleontological research domain.

One may be left to wonder, then, why paleontologists haven't already adopted such a system. It is not for lack of trying. The differences in paleontological and paleobotanical approaches to taxonomy can be attributed primarily to historical accident. A variety of paleontologists argued in favor of a monotaxonomy through the development of current taxonomic standards (Pemberton & Frey 1982). Ultimately, those who argued in favor of parataxonomic standards prevailed. They did so because of epistemic limitations: tools for inference from one taxonomy to another were at the time limited and so caution was the watchword in correlating ichnotaxa with biotaxa (Sarjeant 1990). That caution informed the system now encoded in the ICZN (Bertling, *et al.* 2006). Paleobotanists engaged similar debates throughout the twentieth century with proponents of monotaxonomy ultimately winning the day, in part because paleobotanists had already developed tools for stronger inference between different kinds of fossil (Cleal & Thomas 2010). The evolution of attitudes towards parataxonomy seems at least as contingent as evolutionary history itself.

6. Conclusion

The following points summarize the argument given above.

- **Paleozoologists recognize structural and historical differences that distinguish body fossils from ichnofossils.** The structural and historical traits of body fossils mark them as biological entities whereas the structural and historical traits of ichnofossils mark them as geological objects.

- **Because of the nature of these differences, biotaxonomy includes body fossil taxa and excludes ichnotaxa.** Biotaxonomy includes biological kinds and so body fossil taxa may correlate with biotaxa. Ichnotaxa, being geological kinds, cannot.
- **The differences between body fossils and ichnofossils have been overstated.** Some ichnofossils have the structural and historical qualities of body fossils and some body fossils have the historical properties of ichnofossils. **As a result, either biotaxonomy should include ichnotaxa or exclude body fossil taxa.**
- **Paleobotany offers a practical example of biotaxonomy that excludes both body fossil taxa and ichnotaxa.** In constructing a fossil monotonomy, paleobotanists do not distinguish standards of classification for different kinds of fossil. The flexibility of this system allows a wide range of phylogenetic inferences.
- **The differences between taxonomic practices in paleobotany on the one hand and vertebrate and invertebrate paleontology on the other hand are historical rather than theoretical.** Paleozoologists could reasonably adopt a similar system now that inferential tools have developed to improve inference between kinds of taxa.

I therefore recommend the following two revisions to current taxonomic practice:

- **Recognize all fossil taxa as equally “artificial” relative to biotaxa.** Neither body fossil taxa nor ichnotaxa need bear a one-to-one relation with any biotaxon. Body fossil taxa may seem less likely to split or to lump biotaxa, but this is not a consistent consequence of structural or historical features of body fossil taxa.
- **Include a wider variety of character traits in fossil taxon diagnosis.** This would mark an actual shift in practice. The consequences of the shift ought to be salutary given that a less discriminating approach to character selection demands **explicit consideration of research goals and character weighting** when diagnosing fossil taxa.

These recommendations offer some purely philosophical benefits. It is straightforwardly false, after all, to call a body fossil a “bone” or a “shell” or some other part of a fossil organism’s body. Body fossils may preserve phenotypic traits, but the permineralization process fundamentally alters the body element’s chemical structure. The current parataxonomic system diminishes that fundamental change through the implication that body fossils are biological whereas ichnofossils are not. A monotonomic system that unites body fossil taxa and ichnotaxa emphasizes that all organism fossils share a

fundamental similarity and that the differences between them are differences in degree rather than differences in kind (*cf.* Currie 2018, 63-84).

Against this suggestion, one might argue that any such system implies unnecessary vagueness or arbitrariness. For extant biotaxa that have a fossil record, for example, there seems no clear line where the biotaxon should give way to fossil taxa. This is of particular concern for so-called “living fossils,” or biotaxa that seem relatively unchanged from fossil ancestors. In fact, these cases are less a risk than an opportunity on the current account (see also Turner, this volume). I have argued that a monotaxonomic system requires intentional application of tools for inference between different kinds of organism fossil; living fossils may help to develop those tools. Lidgard & Love (2018) argue that living fossils are best understood as suites of characters, or parts of organisms, that remain constant through geological time. The oversplitting concern raised above suggests that fossil taxa would carve biotaxa “between the joints,” so to speak: fossil taxa may represent only part of a biotaxon or part of an organism belonging to a biotaxon. If so, then living fossils offer a kind of Rosetta Stone that gives insight into the relation between fossil taxa and biotaxa. The tools paleontologists require for inference between taxonomic kinds are improved through recognition that the relation between fossil taxa and living fossil biotaxa is less a Sorites paradox and more a part-whole relationship.

To be clear, I do not intend to endorse anything like a “mixed taxon” concept, i.e., one wherein a single taxon includes both body fossils and ichnofossils. Lomax & Racay (2012) are correct to distinguish *Kouphichnium* from *Mesolimulus*, despite the clear association between the fossils, because those taxa are diagnosed by different characters. Furthermore, the 2011 ICZN ruling is correct in its conclusion that a body fossil taxon such

as *Archaeopteryx* should not include feather impressions. Different kinds of organism fossils belong in different fossil taxa. Fossil taxa in this sense are similar to “morphotaxa” distinguished by simple morphological difference (*cf.* Plavcan & Cope 2001); per the suggestions above, however, fossil taxon diagnosis may also include geological characters currently associated with various ichnotaxa. In many cases track fossil taxa will split or lump body fossil taxa; in some cases (as with *Kouphichnium* and *Mesolimulus*) they will not, but that does not diminish differences between the fossil taxa themselves. My point here is that no fossil taxon ought to be treated as coextensive with any biotaxon *ex hypothesi*—again, all are equally “artificial” in this respect. There may be cases wherein a fossil organism taxon correlates with all and only the elements of particular kind of organism fossil, but these cases must be proved even when body fossils are involved.

In the naming and study of animal fossils, the difference between body fossils and ichnofossils is currently considered a distinction with a real difference. To be sure, there are examples wherein that appears to be the case: *Mesolimulus* and *Kouphichnium*, for example. As we have seen, however, there are a variety of issues and other examples—*A. lithographica*, for one—showing that the categorical difference between body fossils and ichnofossils is a distinction without a difference. Paleobotanists have already adopted the latter view and encoded it within their practices. This essay has (hopefully) shown that the ICZN should adopt a similar view. Doing so would offer few difficulties and open new paths for paleozoological research.

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