

Distinguishing heat from light in debate over controversial fossils

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Fossil organisms offer our only direct insight into how the distinctive body plans of extant organisms were assembled. However, realizing the potential evolutionary significance of fossils can be hampered by controversy over their interpretation. Here, as a guide to evaluating palaeontological debates, we outline the process and pitfalls of fossil interpretation. The physical remains of controversial fossils should be reconstructed before interpreting homologies, and choice of interpretative model should be explicit and justified. Extinct taxa lack characters diagnostic of extant clades because the characters had not yet evolved, because of secondary loss, or because they have rotted away. The latter, if not taken into account, will lead to the spurious assignment of fossils to basally branching clades. Conflicting interpretations of fossils can often be resolved by considering all the steps in the process of anatomical analysis and phylogenetic placement, although we must accept that some fossil organisms are simply too incompletely preserved for their evolutionary significance to be realized.

Keywords: bodyplan; controversy; development; evolution; fossil

Introduction

It seems to be a widespread perception that palaeontologists commonly disagree over the interpretation of fossils—perhaps more than is necessary and, sometimes, more than may be decent. In part, this debate arises because some fossils are very difficult to interpret, and dispute reflects the scientific process of hypothesis testing. But this is not the only cause of conflict, and judging between opposing interpretations of the same fossils can be difficult. Take, for example, the early Cambrian fossils *Yunnanozoon* and *Haikouella* (Fig. 1). The vertebrate affinity of these extinct animals is now so firmly embedded in the literature that they are presented as evidence for evolutionary transitions between major body

plans in critiques of creationism/intelligent design,^(1,2) or as evidence in debates concerning the emergence of neural crest,^(3–5) vertebrate brain and sensory systems,^(6,7) myosepta,⁽⁸⁾ the origin of jaws⁽⁹⁾ and even the evolution of cognition.⁽¹⁰⁾ Yet their phylogenetic placement is, in fact, far from being resolved. In addition to craniates,^(3,11) yunnanozoans have also been interpreted as stem-cephalochordates,⁽¹²⁾ stem-chordates,⁽¹³⁾ crown-hemichordates,^(14,15) neither chordates nor hemichordates,⁽¹⁶⁾ stem-ambulacrarians,⁽¹⁷⁾ stem-deuterostomes^(15,17–19) and even stem-bilaterians.^(18,20) Why the equivocation? Can all of these interpretations really be consistent with the available evidence? Or is the interpretation of fossils so subjective that it is all in the eye of the beholder?

Perhaps because many of us have collected fossils in our formative years, their recognition and interpretation can be perceived as trivial, leading to the pejorative view, like Medawar's, that 'palaeontology is a particularly undemanding branch of science'.⁽²²⁾ However, as has been shown by debate over the fossil record of early life on Earth and other planets,⁽²³⁾ interpreting fossils can be distinctly non-trivial, requiring that we marshal every analytical, observational and epistemological tool in our armoury. And it is surely worth the effort because fossil taxa provide crucial insights into some of the most fundamental questions in evolutionary biology. Fossil taxa uniquely provide a timescale of minimum ages for the establishment of clades and the calibration of molecular clocks, and a geological context for establishing the ecological setting of historical evolutionary events. Fossil taxa amplify information on the geographical distribution of living clades, testing and constraining hypotheses of biogeographic evolution. Fossil taxa also reveal the sequence in which the diagnostic characteristics of extant clades were acquired, exposing the pattern in which body plans were assembled and, thereby, providing a framework for models of organismal developmental evolution. In so doing, fossil taxa yield unsuspected characters or character combinations that challenge decisions on polarity and homology based on extant taxa alone, sometimes leading to radical reinterpretations of the evolutionary relationships of living groups. These roles, codified by Patterson,⁽²⁴⁾ provide the foundation for the integral functions that palaeontology plays in evolutionary developmental biology.⁽²⁵⁾

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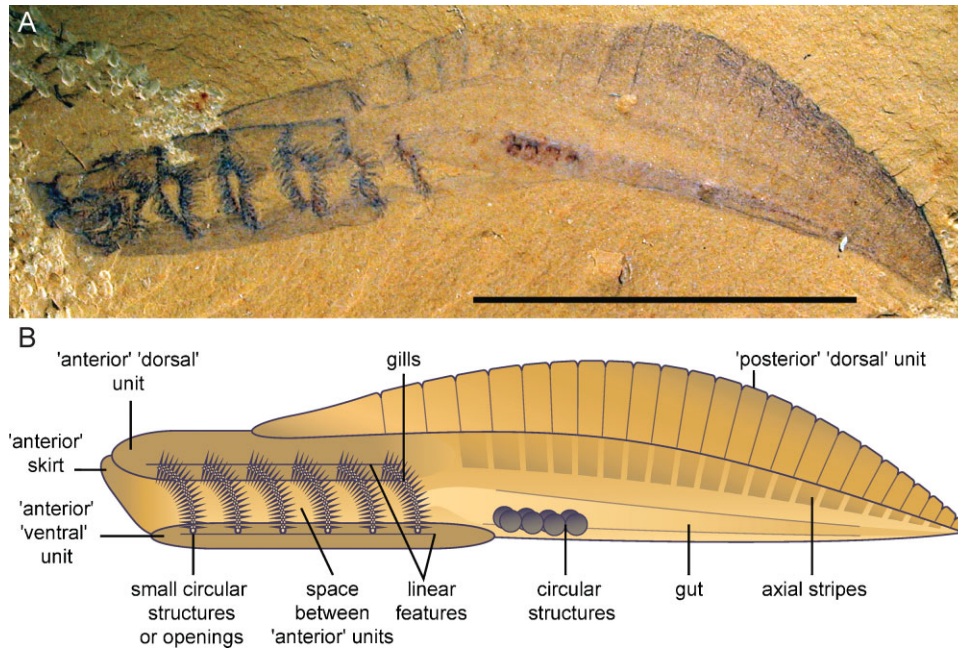


Figure 1. Yunnanozoan anatomy. A: Fossil remains of *Yunnanozoon lividum*, lateral view, specimen rcbyu 10310, from the Cambrian Chengjiang Biota, Yunnan Province, China. Scale bar 10 mm. B: Body parts present (diagrammatic, parasagittal view; not all parts are evident in (A)). Fossils preserved in different orientations of collapse indicate that the body is bilaterally symmetrical. This provides good evidence for the sagittal plane of the animal, but anterior and dorsal directions are matters of interpretation. There has been little discussion of this since the first paper on yunnanozoans, with almost all authors agreeing with the orientations indicated in the figure, but in fact determination of anterior is based on the assumption that the more complex end of the animal is its head; dorsal and ventral are completely arbitrary.⁽²¹⁾ We indicate this uncertainty with inverted commas. The different taxa currently accommodated within yunnanozoans could be either distinct species or nothing more than taphonomic variants, but there are few if any differences between the fossils that are significant in determining their affinities. [(A) previously illustrated by Hou *et al.*,⁽²¹⁾ reproduced with the authors' and publisher's permission].

However, the potential of extinct taxa to play these important roles depends entirely on determining where they sit in the Tree of Life (and this applies equally whether that placement is based on a precise phylogenetic hypothesis or is expressed in terms of taxonomic classification). It is unfortunate, therefore, that the fossil taxa that are deemed to be of greatest import, such as entirely soft-bodied organisms from Cambrian and Precambrian Lagerstätten, are among the most hotly debated.

It is our view that much of the disagreement over the interpretation of fossils is unnecessary and emerges from failure to consider fully all the basic elements of fossil interpretation. These are: (i) determination of the intrinsic properties and topological characteristics of the fossil itself; (ii) justification of the choice of interpretative model; (iii) consideration of the impact of decay and fossilization processes and (iv) systematic classification of the fossil taxon. We outline how paying insufficient attention to one or more of these elements can lead to incorrect interpretations of fossils, review the reasons why different palaeontologists reach different conclusions about the affinity of fossil organisms, and indicate the criteria that differentiate testable

scientific hypotheses regarding anatomy and affinity from mere assertions of expert opinion. Armed with these insights it is possible to separate heat from light in debates over the interpretation of controversial fossils.

Interpreting fossils using a comparative model

The evolutionary and palaeobiological significance of a particular fossil organism derives from its phylogenetic position—however that is expressed—with some fossils, especially those branching from the stems of major extant clades, providing greater insight than others. But how is phylogenetic position established, and how can alternative interpretations be evaluated?

One of the fundamental steps in the process of interpretation is to consider with which, of a range of possible organisms or groups of organisms, a fossil should be compared in attempting to identify its anatomical homologies. Obviously, one fossil taxon can be compared with others, but ultimately the chain of comparisons must link to an extant

organism or it is uninformative with regard to homology (see the yunnanozoan saga below). Unfortunately, interpretations of homology run the risk of being biased by the initial choice of comparative model, which can itself be biased by prejudices regarding taxonomic affinities.⁽²⁴⁾ Decisions at this stage inevitably colour any ensuing phylogenetic analysis. This problem, that the identification of anatomical homologies is contingent upon the systematic framework in which they are considered, has vexed comparative anatomists for centuries.⁽²⁶⁾ Much has been written about how this inductive approach to identifying homologies must be both explicit and testable and how, if it is not, the search for a systematic home for any organism is reduced to a circular argument based on nothing more than general similarity.⁽²⁷⁾ The problem is not peculiar to fossil organisms. Tunicates have long been known to be chordates on the basis of a series of detailed, universally accepted homologies, including a nerve cord overlying a notochord. However, neither these homologies nor this hypothesis of affinity have always been agreed upon. Kowalevsky's proposal for the origin of vertebrates from ascidian larvae, based primarily on the identification of a nerve cord lying dorsal to a notochord in ascidian larvae,⁽²⁸⁾ was rejected by von Baer,⁽²⁹⁾ not because von Baer opposed evolutionary theory, but because his preconceived frame of reference, that tunicates should be grouped with molluscs, precluded orienting the body of the ascidian larva such that the nerve cord lay dorsal to the putative notochord.⁽²⁶⁾ Debate over the affinity of chaetognaths,^(30,31) sea spiders,⁽³²⁾ *Xenoturbella*^(33,34) and even familiar organisms such as snakes^(35,36) and turtles,^(37,38) is testament to the endurance of this problem: the identification of homology requires, among other criteria, an a priori hypothesis of grouping at some level before the process of comparative anatomical interpretation can proceed.⁽³⁹⁾

Interpreting the topological and intrinsic properties of fossils

An important distinction must be drawn between characters that derive from comparative anatomical interpretation and attributes that are intrinsic to a fossil. At the most basic level, it is possible to improve the rigour of anatomical (and hence phylogenetic) interpretations by initially relying less on extant organisms as comparative models, and instead placing greater emphasis on topological analysis of structures in the fossils themselves. Even fossil specimens that are preserved as collapsed, near-2D remains preserve some basic geometric and topological information, including the shape, juxtaposition and number of distinctive parts. Robust reconstructions of the original 3D shape and disposition of the parts of the organism can be obtained by taking taphonomy into account (see next section) and by integrating information from a number of specimens preserved in different orientations, a process

analogous to viewing the organism from different directions.^(40,41) These topologically reconstructed organisms, without any interpretation of what the particular parts represent in terms of anatomy and homology, are independent of phylogenetic context and comparative analysis. This independence is fundamental to the testability of hypotheses of homology and consequent phylogenetic placement.

Topological relations are crucial in establishing structural correspondence and putative homology between parts in two or more organisms.⁽²⁷⁾ Without the criterion of topology as a potential falsifier of character hypotheses, all methodological constraints on the search for morphological similarity are removed, because any anatomical part becomes comparable to any other.⁽²⁷⁾ It is also true, however, that topological data in fossils are sometimes equivocal or unobtainable. In such cases other criteria, normally subordinate to topology, assume greater importance. These include the intrinsic properties of parts (referred to as 'special qualities',⁽²⁷⁾ or 'correspondence of composition'⁽⁴²⁾), which might include shape or original histological composition. They also include the criterion of linkage by intermediate forms, allowing putative homologues to be recognized through a transformational sequence, which could include other fossils.

Unfortunately, many interpretations of fossil anatomy, especially those dealing with exceptionally preserved, non-biomineralized fossils, do not clearly articulate the criteria upon which homologies are founded, or distinguish primary topological data from anatomical and phylogenetic interpretation. Where interpretations differ, determining which is the more robust is not simply a matter of opinion. Rather, it is the evidence and the methods used to define and delineate anatomical characters that should be the focus of debate, and it is these that must be rejected and replaced with new evidence or methods if new character interpretations are proposed.⁽²⁷⁾ Clearly, this is difficult if evidence and methods are not articulated, and there are too many instances in which disagreement over characters revolves around claim and counterclaim regarding resemblance between putative homologues (Box 1: Carpoids). In such cases, character identity is contested, but remains untested, and this is the source of some of the problems and perceived lack of objectivity in the interpretation of fossils.

Taphonomic transformation and loss of phylogenetic characters

Previous discussions of the problems associated with anatomical interpretation and homologies of fossils have focused on the characters of biomineralized skeletons. This is not altogether unsurprising, given that such hard parts are generally all that is preserved in the fossils. However, where fossils preserve the remains of soft tissues, and especially

when a fossil organism was entirely soft-bodied, additional complicating factors come into play.

No organism avoids the rigors of decay on its path from death to fossilization and so no fossil should be interpreted as though it were a living, freshly killed, or histologically fixed organism. Thus, an understanding of the patterns and processes of decay, the effects of environmental conditions and the mode of death, as well as the processes of fossil preservation are integral to the interpretation of any fossil. This is the often gruesome science of taphonomy whose stock-in-trade is the study of everything that can happen to an organism after it dies.⁽⁵²⁾

Much taphonomic work has focused on patterns of post-mortem decay in modern organisms, and entire atlases of such gore have been published,^(53,54) serving as guides to the interpretation of the fossil remains of organisms that have undergone varying degrees of decay. Briggs and Kear's taphonomic study of the polychaete *Nereis*⁽⁵⁵⁾ is a classic example (Fig. 2), showing how anatomical components that differ in their intrinsic compositional properties are lost at different stages of decay, and how body parts change their topological relations and shape as their supporting tissues rot. Unchecked, polychaete decay proceeds until only the cuticle remains, which duly collapses to two dimensions and is eventually disaggregated. Clearly, studies of this kind are integral to interpreting the anatomy of fossil organisms.



Figure 2. The pattern of polychaete decay, illustrating progressive loss and distortion of anatomy, from fresh worm (top left) through flaccidity and flattening (top right and bottom left), to ruptured cuticle with body and gut contents flowing out. In the latest stages of experimental decay only jaws and setae remain (centre). See⁽⁵⁵⁾ for details; dishes are ca. 9.5 cm across.

Generally, of course, taphonomy records the gradual loss of anatomy until, under what might be considered routine conditions, nothing remains. More rarely, the recalcitrant, decay-resistant tissues, such as bones, teeth, scales and shells in animals, or stable polymers such as sporopollenin in plants, will survive to be transformed into fossils. However, even in instances of exceptional preservation, where soft tissues are fossilized, it would be a mistake to think that there has been no, or very little decay. This is because decay is a prerequisite for the bacterially mediated rapid mineral replication by which the most labile of soft tissues are preserved.⁽⁵⁶⁾ Moreover, exceptional fossilization does not necessarily represent a curtailment of decay, but can represent a different decay pathway in which preservation probabilities are reversed, such that skin and muscle are preserved, while mineralized tissues are not (e.g. bog bodies⁽⁵⁷⁾). Because of the unusual circumstances of soft-tissue preservation, new 'pseudoanatomical' structures can be introduced that bear no relation to the anatomical structures of the original organism, leading to spurious interpretations of anatomy. Similar issues are at the centre of debate over the interpretation of the oldest putative bilaterian fossil, *Vernani-malcula* from the 580 million year old Doushantuo Formation. The original authors^(58,59) describe small but perfectly preserved fossils, with phosphate replication of cellular level structures otherwise unseen in the fossil record, including coeloms, and three distinct, intact primary cell layers. Bengtson and Budd,⁽⁶⁰⁾ on the other hand, point out that these phosphatized structures exhibit fabrics characteristic of the geological process of diagenetic crystal growth, and present a compelling argument that the 'anatomical' details can be explained equally well, if not better, as layers of diagenetic mineral encrustation lining small cavities—a geologically ubiquitous and unremarkable phenomenon—and that there is thus no evidential basis upon which to interpret these pieces of rock as bilaterian fossils.

Taphonomic processes can disrupt the phylogenetic placement of fossils in two ways. Not only do they result in artefacts that can be misinterpreted as phylogenetically informative homologies, they also reduce the amount of data available for comparative analysis, thus diminishing phylogenetic resolution. The fossilized rotten carcasses of acanthodians (an extinct group of stem-osteichthyans) from the late Devonian Miguasha Lagerstätte provide an example of how the interplay of these two factors leads to erroneous phylogenetic placement (Box 2: *Scaumenella*). At worst, there may be such extensive loss of anatomy that precious few characters remain and attempts to find an appropriate phylogenetic milieu for identifying homologies are entirely futile. This may be exemplified by fossil problematica, such as *Tullimonstrum*⁽⁶¹⁾ and *Typhloesus*,⁽⁶²⁾ which have resolutely defied systematic classification beyond stem-Bilateria—but this does not indicate that they are stem-bilaterians in the phylogenetic sense. We draw out this distinction later.

Box 1: Carpoids – Problems with the living, not the dead.

Most of our examples illustrate the difficulties and potential pitfalls of the description of fossils, but they are not representative of all palaeontological practice. Carpoids possess an exoskeleton of calcitic stereom and have traditionally been allied with echinoderms, but stereom is among the very few characteristics that they share with this phylum, and other characters, such as gill slits, have led to suggestions of chordate affinity.⁽⁴³⁾ In fact, there are at least three mutually exclusive schemes that provide point-for-point alternative interpretations of carpoid anatomy.^(44–46) In each case, interpretations of homology are based on different anatomical models, and this has become a paradigmatic example of how debate over anatomy and affinity can become polarized into apparently irreconcilable hypotheses.

The carpoids are lifted from phylogenetic purgatory, however, because their topological and intrinsic characteristics have been reconstructed independently of anatomical interpretations,⁽⁴⁷⁾ laying bare the underlying assumptions and explanatory power of the competing hypotheses. Advocates of all the alternatives remain, but a degree of reconciliation has been found because part of the blame for character conflict lay with our view of the relations between deuterostome phyla. With the recognition that hemichordates are the sister clade of echinoderms and not chordates, expectations of the nature of the last ancestor shared by living deuterostomes have changed fundamentally (Fig. 3). Surprisingly, because many anatomical features previously thought to be characteristic of chordates turn out to be primitive to all living deuterostomes,⁽⁴⁸⁾ chordates, and not echinoderms, provide a better model for interpreting carpoid anatomy. Considered in this phylogenetic context, carpoids are a paraphyletic ensemble of stem-echinoderms,⁽⁴⁹⁾ with the acquisition of stereom preceding the loss of gill slits in the assembly of the crown-echinoderm body plan.⁽⁵⁰⁾ We could infer from extant deuterostomes that the absence of gill slits from echinoderms results from secondary loss, but carpoids provide literally rock-solid evidence to corroborate this inference, and further reveal the order of assembly of crown-echinoderm characters.^(50,51)

The example of carpoids demonstrates that fossil organisms can be difficult to interpret because no simple comparative model exists; consensus over carpoids remained out of reach because an organism that shared chordate- and echinoderm-like characters did not fit deuterostome phylogeny. Metazoan phylogeny remains poorly resolved and we have no idea of the homologies shared by most clades of phyla. It should come as no surprise that interpretations of fossil organisms such as *Odontogriffus*, the halkieriids, wiwaxiids, and other halwaxiids, remain so hotly debated.

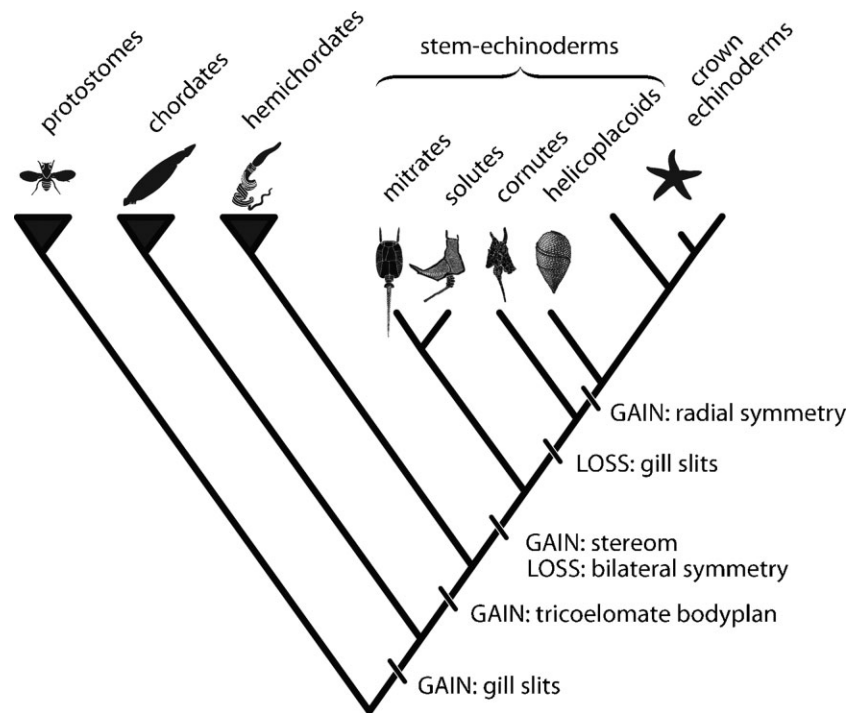


Figure 3. Deuterostome relationships and patterns of acquisition and loss of characters discussed in the text. Relationships are based on molecular data but with mitrates and solutes (carpoids) added on the basis of observable shared derived morphological traits. After Smith.⁽⁴⁹⁾

Box 2: ‘Scaumenella’ snakes and ladders: A rotten fish slides down then back up the vertebrate tree.

There are very few published examples of how taphonomy can influence interpretations of the systematic position of fossil organisms. Perhaps the most explicit is the case of ‘Scaumenella’.⁽⁶³⁾ Initially described and tentatively interpreted as ‘chordate, and probably a vertebrate’,⁽⁶⁴⁾ ‘Scaumenella’ was later considered widely to be an early protochordate of some sort.^(65,66) However, subsequent examination of large numbers of specimens revealed ‘Scaumenella’ to be the rotted remains of one or more species of acanthodian⁽⁶³⁾ (extinct crown-gnathostomes)(Fig. 4). The problem with ‘Scaumenella’ is that taphonomic processes conspired to preserve non-biomineralized anatomical characters that normally do not fossilize (*e.g.* various cranial traces including the remains of eyes) yet destroy phosphatic skeletal characters (scales and spines). Significantly, it is the latter that are diagnostic of acanthodians, and the specimens in which they are lost preserve only characters that, in terms of total group gnathostomes, are symplesiomorphies.

Correct determination of the phylogenetic affinities of ‘Scaumenella’ is possible only because large collections reveal that they lie towards one end of a spectrum of decayed and partially preserved remains,⁽⁶³⁾ but what would be the most reliable interpretation of the rotten ‘Scaumenella’ if we did not have this taphonomic spectrum? Topologically based anatomical interpretation would include a tapering body outline with more complex structure and paired stains at the broader end, connected to a distinct line running along or closer to one side of the body; this side of the body bears the remains of a structure resembling a fin; within the body outline in some specimens is a series of transverse features. There is very little information here to inform a choice of anatomical comparator, but this is clearly an animal, and differences in the juxtaposition of structures in different specimens indicate bilateral symmetry. In this context a complex sub-terminal region with paired structures is reasonably interpreted as an anterior head, which together with a more posterior fin and a tapering body, is suggestive of something fish-like (*i.e.* chordate). An interpretation of the transverse features as the remains of branchial structures, and the anterior-posterior line as a notochord is topologically congruent with a chordate model.

What, then, could we say about the phylogenetic placement of ‘Scaumenella’? A chordate with a head with paired sensory organs would suggest a position within the vertebrate crown group, but placement this far up the tree is not warranted by the possession of these few characters because they must have been acquired somewhere along the vertebrate stem. Thus, in the absence of other evidence, we would interpret ‘Scaumenella’ as a stem-vertebrate in Hennig’s sense (see *stem groups and systematic limbo*), sitting in an unresolved position within total group vertebrates.

There is a further cautionary note to this tale. ‘Scaumenella’ resembles other poorly preserved fish-like fossils, such as *Achanerella*.^(67,68) This comparison might tempt us to interpret ‘Scaumenella,’ like *Achanerella*, as a ‘naked anaspid’ (*i.e.* within crown-vertebrates, between crown-lampreys and thelodonts). Given that we know ‘Scaumenella’ is actually an acanthodian, this level of phylogenetic precision would be both wrong and positively misleading.

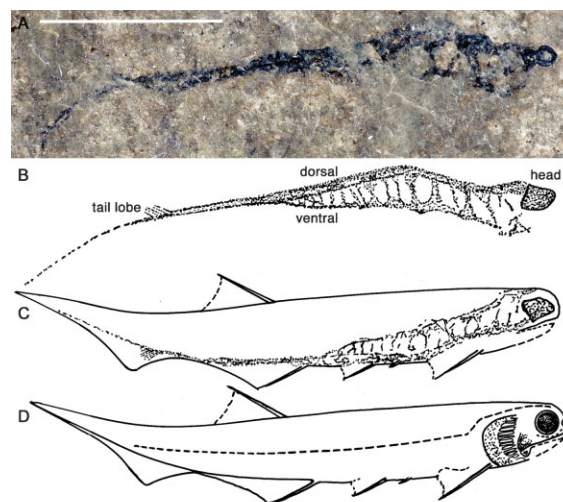


Figure 4. Beland and Arsenault’s explanation of the relationship between ‘Scaumenella’ and the acanthodian *Triazeugacanthus* (from the Devonian Escuminac Formation of Miguasha, Quebec). **A:** Specimen of ‘Scaumenella’ (NHM P19056; scale bar 5 mm). **B:** ‘Scaumenella’ Holotype as drawn by Graham-Smith,⁽⁶⁴⁾ showing his anatomical interpretations. **C, D:** Reconstruction of ‘Scaumenella’ within the body outline of *Triazeugacanthus*, and reconstruction of the pre-decay anatomy. Modified from Beland and Arsenault,⁽⁶³⁾ and Graham-Smith,⁽⁶⁴⁾ (C) and (D) reproduced with the publisher’s permission.

Phylogenetic loss or absence of characters

Clearly, phylogenetic characters can be absent from organisms for biological reasons, too. This can be because of evolutionary loss (snakes and whales lack legs, but retain membership of Tetrapoda, nevertheless) or through evolutionary transformation, such that homologies become unrecognizable. It almost seems too obvious to mention that characters may also be absent from a fossil because it predates their evolution, but the implications of patterns of character acquisition for interpreting the affinity of fossil organisms are far less widely appreciated than they should be. Specifically, as we consider increasingly inclusive clades within the Tree of Life, the inventory of characteristics shared by their members diminishes concomitantly. Furthermore, the nature of those characters also changes, from gross-anatomical structures shared by groups of species, genera, families and orders, to cytological, embryological or molecular characters uniting phyla and their aggregative clades.⁽⁶⁹⁾

Importantly, this does not mean that the extinct organisms that populated deep branches in the Tree of Life, such as the urbilaterian, were necessarily simple. Rather, the perceived simplicity is an artefact of the secondary loss⁽⁷⁰⁾ and the evolutionary transformation⁽⁷¹⁾ of homologues, a corollary of which is that, with increasing phylogenetic depth, the number and nature of characters at ancestral nodes become increasingly difficult to infer. It inevitably follows that assigning fossil (and living⁽³²⁾) organisms to deeper branches becomes increasingly reliant on the absence of characters indicative of more-derived phylogenetic positions. This can be problematic in that the plesiomorphic nature of such organisms is more securely established through the presence of a mélange of characters some of which exhibit primitive, and others, derived states.

As we have seen, taphonomy compounds this problem. A complete anatomy is never preserved and so it can be extremely difficult to know whether characters are absent because they have rotted away, or because they were not present to begin with.⁽⁷²⁾

Stem groups and systematic Limbo

Uncertainty over primitive absence, secondary loss or taphonomic non-preservation of phylogenetically informative characters in fossil organisms can, however, be accommodated in hypotheses of phylogenetic placement and affinity. Hennig devised a means of controlling for these errors by developing the 'stem-group' and an allied suite of concepts for integrating fossils into a systematic framework of their living relatives.⁽⁷²⁾ Rather than continually redefining a given clade from a list of characters that diminishes every time a more

plesiomorphic fossil member is discovered, lacking one or two more characters from the expected inventory, Hennig argued that groups should be defined on the basis of their living members, allowing stable diagnoses to be obtained from those organisms that are best known. Fossils are then allocated, at different levels in the phylogenetic hierarchy, to the stems of groups so-defined. Thus, a stem is a paraphyletic assemblage of extinct sister taxa to an extant clade. The latter is known as a crown group; together the stem and crown comprise the total group.^(72,73) Hennig recognized that some fossils would be wrongly placed in the stem rather than the crown of a clade because they lack some of the diagnostic characters for taphonomic rather than evolutionary reasons, in which case the stem also represented a form of systematic Limbo from which some taxa may be promoted to the crown with the discovery of additional anatomical data. However, he also foresaw that the order in which stem taxa that primitively lack some crown-group characters branch off from the stem can reveal the phylogenetic order in which the characters of the crown group were acquired.

Hennig's prophecy regarding the informativeness of stem taxa has been realized in spades, especially in revealing the incremental origin of major groups of organisms. Reconstructing the stems of birds,⁽⁷⁴⁾ mammals,⁽⁷⁵⁾ tetrapods,⁽⁷⁶⁾ gnathostomes,⁽⁶⁹⁾ echinoderms⁽⁵⁰⁾ and arthropods,⁽⁷⁷⁾ among many others, has revealed the order in which 'body plan' characters were acquired, and allowed homologies and homoplasies, that would otherwise remain indistinguishable in extant groups of organisms, to be differentiated.⁽²³⁾

So the *expectation* of stem classification has changed, from representing a state of systematic Limbo, to a statement of precise phylogenetic placement with evolutionary implications.⁽⁷⁸⁾ Nevertheless, in practice, the underlying meaning of stem membership has not changed, because it will always remain difficult to differentiate stem members that lack crown-group characters for taphonomic reasons from those that never had them. This problem is especially acute at deeper levels within a stem because, by definition, these organisms will share fewest characters with their respective crown groups and, at increasingly deeper levels in phylogenies, where homologies between component crown groups become increasingly obscure and less likely to be preserved^(79,80) (see previous section). Thus, although evolutionary biology has sought to address ever more fundamental events in animal evolution, and the stem members of increasingly inclusive taxa have been identified—including the stems to animal phyla,^(77,49,81,82) combinations of phyla,^(19,83–87) and even sub-kingdoms^(19,88)—some of these assignments are inevitably tenuous. For instance, hypotheses of the affinity of the vetulicolians range widely (Box 3: Vetulicolians), from tunicates to kinorhynchs, with the view that they are stem deuterostomes^(15,19) conforming to the expectation that ancestral deuterostomes would have been

Box 3: Vetulicolians: simple animals or just simple fossils?

Vetulicolian fossils (Fig. 5) are difficult to compare with anything alive today, but is that because they are fossils or was their anatomy as distinct in life as it now seems? Although the intrinsic geometry and topological structure of the fossils is clear, there is not a lot of anatomy upon which to base comparative analysis. Vetulicolians are bilaterally symmetrical and bipartite, composed of an anterior carapace and segmented 'tail'. They possess a medially positioned through-gut, the anus located in the posterior-most segment, if not also terminally positioned. Anteriorly, there is an opening and within the carapace is a paired series of five pouch-like structures containing filamentous traces; it is not clear whether these pouches open anteriorly and/or to the exterior through openings in the bodywall. There might also be evidence for short, longitudinally aligned filaments associated with the base of the bodywall.

Aldridge *et al.*⁽⁹⁰⁾ have recently reviewed vetulicolians, and examined a broad range of possible phylogenetic interpretations, including arthropods, stem-arthropods, stem-panarthropods, stem-kinorhynchs, stem-bilaterians, stem-deuterostomes, stem-ambulacrarians, tunicates, stem-echinoderms, stem-chordates, stem-tunicates and stem-vertebrates. Uncertainty in interpretations arises partly because of the limited amount of anatomy that these fossils preserve, but also because the phylogenetic indications of what is preserved are contradictory. Characters that seem to suggest one hypothesis are difficult to reconcile with other characters. Indeed, although there may be consensus over how certain structures are interpreted (for example, that the paired series of pouch-like structures represent gills) ensuing interpretations of affinity remain polarized between deuterostomes and arthropods.

Clearly, there is *prima facie* evidence for the assignment of these organisms to the bilaterian total group, but as Aldridge *et al.*⁽⁹⁰⁾ note there is currently insufficient anatomical evidence on which to resolve their affinity with any greater precision. They will remain in this state of systematic Limbo unless additional and compelling evidence of their position within the bilaterian total group is uncovered.



Figure 5. *Vetulicola cuneata* Hou, 1987, lateral view, specimen YKLP 10901, scale bar 5 mm, and close-up of lateral groove structure, specimen YKLP 10902, scale bar 1 mm. Specimens from the Chengjiang biota, Yunnan Province, China. Previously illustrated by Aldridge *et al.*⁽⁹⁰⁾ and reproduced with the permission of the authors and The Palaeontological Association.

anatomically simple.⁽⁸⁹⁾ However, there can be no doubt that vetulicolian fossils provide an incomplete record of their original anatomy. Thus, vetulicolians may be considered stem deuterostomes only in the sense that they fail to exhibit any characteristics that can be interpreted unequivocally to ally them with a more exclusive clade, or else confirm their plesiomorphic nature. The deuterostome stem may be the most fully resolved position to which vetulicolians can be assigned on the basis of available evidence, but it represents nothing more than a qualified statement of phylogenetic uncertainty, not a precise phylogenetic hypothesis (Box 3: Vetulicolians).

The yunnanozoan saga—how and why things go wrong

To return to where we started, the history of research into yunnanozoans illustrates the full spectrum of problems that hamper robust analysis of affinities, with disagreement over what component body parts are actually present in the fossils (irrespective of how they are interpreted anatomically), over the topological relations between body parts, over the intrinsic properties of body parts, and over choice of anatomical comparator and the criteria used to support interpretations of homology (and little explicit justification or discussion of the

importance of this). Even for the few body parts that everyone agrees are present in the fossils (summarized in Fig. 1), there is disagreement over how they are interpreted as anatomical homologies.

Among the most critical points of disagreement are whether there is distinct axial structure between the gut and the 'posterior' 'dorsal' unit, and whether the gills are external, or enclosed within the outmost body wall. These features are of particular significance because, based on them, different authors make different choices of comparative anatomical model. Dzik⁽¹³⁾ and Mallatt and Chen,⁽¹¹⁾ for example, unlike most authors, explicitly justify their choice of chordates as an interpretative model using a small number of characters they find in the fossils, including a distinct axial structure between gut and 'dorsal' unit, identified by them as notochord. Shu *et al.*,⁽¹⁴⁾ however, identified only one structure between the 'ventral' circular structures (their gonads) and the 'posterior' 'dorsal' unit, and interpreted this as a gut, while Shu *et al.*⁽⁴⁴⁾ did not identify a distinct axial structure. Consequently neither interpretation includes a notochord among their anatomical characters, nor do they consider chordates to be an appropriate comparative model. The issue of gill position determines whether the anterior portion of yunnanozoans is interpreted as, for example, a cephalochordate like pharynx within an atrium,^(3,11,45) or as a juxtaposition of structures unknown among extant animals but consistent with a combination of characters theoretically possible in a stem deuterostome.⁽⁴⁴⁾ The latter hypothesis draws heavily on comparisons between yunnanozoans and vetulicolians, but, as should be evident from Box 3, this does little to increase the data upon which to base phylogenetic placement.

A number of other structures fall into a different category of disagreement, linked more to comparative anatomical interpretation than to physical preservation: the presence of eyes and brain, for example. In the anatomical context provided by having chordates or basal vertebrates as a model, the presence of eyes and a brain is expected, and there are indistinct darker patches present in a very few fossil specimens that can be interpreted in this way. In a different anatomical context, however, these stains are just artefacts of decay and fossilization, not distinct body parts, and thus fall outside the scope of anatomical interpretation and homology.

Many of the differences in hypotheses of yunnanozoan affinity are a simple consequence of the comparative model chosen, but there is considerable variation in the degree to which model choice is justified (and therefore explicitly testable). As noted above, Dzik⁽¹³⁾ and Mallatt and Chen⁽¹¹⁾ justify anatomical comparisons with chordates based on their recognition in the fossils of a set of structures including key chordate characters widely acknowledged as diagnostic of the phylum (such as notochord and branchial arches). Dzik goes on to articulate the evidence for each of the characters

he identifies, drawing on topological data, intrinsic properties of structures, and taphonomic arguments, and acknowledges explicitly that his other anatomical interpretations follow from this chordate model. In terms of testability, this approach allows both the physical evidence for the presence of these structures in the fossils, and the evidence for their interpretation to be evaluated independently. Rejection of the key chordate characters would lead to rejection of the chordate comparative model, all anatomical interpretation contingent on model choice, and thus the hypothesis of affinity. Where model choice is not explicitly justified, and is based more on general similarity, there is no route to falsification other than to deny the validity of the comparator, with arguments resting on little more than relative plausibility and expert opinion (see Rieppel and Kearney⁽²⁷⁾ for a discussion of this in a slightly different context). Interpretations of yunnanozoans as hemichordates may fall into this category because, although Shu *et al.*⁽¹⁴⁾ state (p. 428) that 'pairs of gill pores and tubes in *Yunnanozoon* are a significant synapomorph [sic] so it must be closely related to the hemichordate–chordate group' they go on to narrow down this very broad placement by noting that 'the tripartite body plan of *Yunnanozoon* is reminiscent of that of the extant hemichordate *Balanoglossus*' with a collar and proboscis '*similar to the collar and proboscis of *Balanoglossus**' (our emphasis). At least one of these characters (the proboscis) is no longer a feature of yunnanozoan reconstructions produced by these authors.⁽⁴⁴⁾ It is also worth noting that several authors have explained the differences between their anatomical interpretations and those of others by claiming that they have better material.^(14,46) Obviously, such qualitative statements are difficult to test rigorously, and carry limited weight in any case: a new set of specimens might preserve body parts that earlier material did not, but that does not invalidate the topological data preserved in the existing dataset.

All these difficulties are further compounded by the different approaches that have been used to translate the information derived from interpretations of anatomical homology into hypotheses of phylogenetic relationship and affinities. Some incorporate yunnanozoans into the author's own evolutionary scenario,^(13,44) whereas others employ what, on the face of it, seem to be more robust cladistic approaches, some even supported by formal, parsimony-based analysis.^(3,11) What none of these authors discuss, however, is that their phylogenetic conclusions cannot escape the constraints imposed by their choice of comparator; in a cladistic sense, they will almost always fall out in the stem to the crown taxon to which they are being compared (and this applies whether the author subscribes to cladistic methods or not) because, inevitably, they lack some of the characters of the crown group. The problem is determining whether those characters are absent because they had not yet evolved, or because of their failure to fossilize. Without taphonomic

constraints, the phylogenetic placement of yunnanozoans cannot be fully resolved. Comparing yunnanozoans with *Branchiostoma*, *Balanoglossus* or a basal vertebrate will lead to their interpretation as a stem cephalochordate,⁽¹²⁾ a stem enteropneust⁽¹⁴⁾ or a stem vertebrate,^(3,11) respectively.

Ultimately, much of the confusion arises because different anatomical interpretations lead to mutually exclusive hypotheses of affinity, but one hypothesis does not provide a test of another. It is the testing that is difficult. Parsimony analysis may be one way forward, but as we have seen, it may give a false sense of confidence in the results. At present, the best way to determine relative robustness of interpretations is to consider all the factors influencing them, including taphonomy, and to put more weight in those analyses that justify explicitly their comparator choice, articulate clearly the fossil evidence for the characters that led them to that choice, and which acknowledge that at least some of the characters that are crown group synapomorphies must have been acquired through the stem lineage. 'Our specimens are better than yours' is not in itself an adequate argument.

Realizing the evolutionary significance of fossils is difficult, but worth it

Much of what we have discussed to this point might be thought of by some as elementary palaeontology, yet if all the factors that influence the description and interpretation of fossils were considered in every case, there would be much less room for controversy. Why is it, then, that a few fossils generate so much debate, while most do not? The principal reason is that the majority of fossils, from trilobites to *Triceratops*, are preserved as skeletal remains, the intrinsic and topological characteristics of which require little or no reconstruction, and for which the process of choosing a model for anatomical interpretation is much more straightforward. Fossil organisms that are outside the crown of phyla, or even the crown of clades comprising multiple phyla, are inherently more controversial. This is partly because such fossils, potentially, have more to tell us about evolution and the relationships of major groups of organisms. However, controversy also arises because the diagnostic characteristics of such clades are poorly resolved, the fossils possess few fossilizable characters, and still fewer characters will be phylogenetically informative. For such fossils, the process of interpretation should be explicit in (i) analysing the topological characteristics and intrinsic properties of the fossil organism, (ii) providing justification for the interpretative model employed in the comparative anatomical analysis, (iii) considering the primitive, secondary or taphonomic absence of characters and, in consequence, (iv) evaluating whether a fossil taxon is referred to a particular stem group for taphonomic, rather than phylogenetic reasons.

Anatomical interpretations need not, and perhaps should not, leap directly to a particular clade of living organisms (*e.g.* a phylum) as an interpretative model, but follow instead from a comparison with a broad grouping of organisms (*e.g.* Deuterostomia, Bilateria or Metazoa) and our understanding of the phylogenetic distribution of synapomorphies within such a clade. More detailed anatomical interpretations should then follow from more specific comparisons with particular taxa. Comparative model choice should be explicit and, in cases where there is more than one possible model, the tests and reasoning used to exclude alternatives should be presented. However, where the relationships of living taxa remain poorly resolved, such as among lophotrochozoans, identifying the phylogenetic affinity and significance of plesiomorphic fossil taxa will remain problematic because the distribution of homologies remains equally poorly resolved (Box 1: Carpoids).

Where fossil organisms are known only from fragmentary remains yet preserve what seem to be good crown-group synapomorphies there may be no recourse except to jump directly to a specific interpretative model (*e.g.* acanthodian fin spines in *Scaumenella*—Box 2). However, interpretations of affinity based on such criteria run the risk of being overturned by future discoveries that: (i) further elucidate skeletal anatomy, testing character congruence, revealing putative synapomorphies as mere homoplasies; or (ii) overturn hypotheses of character distribution (Box 1: Carpoids).

Taxa exhibiting plesiomorphies alone will do so, in almost all cases, because of taphonomic artefact, and ignorance over their classification should be qualified by assigning them to the more inclusive clade for which those characters are synapomorphies. Thus, it is imperative that a distinction is drawn between the assignment of a fossil to a particular stem as a statement of phylogenetic precision, and the use of stem classification as a qualification of systematic ignorance. Such a distinction may be achieved by simply referring fossil taxa of the latter kind to the total group, rather than to the stem, of the least inclusive clade indicated by the anatomical evidence. In terms of formal systematic classification, the incertae sedis qualifier could be used, as suggested by Patterson and Rosen⁽⁹¹⁾ and Nelson.⁽⁹²⁾

Finally, we emphasize that fossil remains cannot be interpreted as though they are living organisms. This is especially true of fossils exhibiting exceptional preservation: decay is required to promote rapid fossilization of labile tissues, and taphonomic processes invariably introduce topological artefacts related to decay and later diagenetic mineralization. All interpretations of fossils should take this into account. We urge great caution over the descriptions and interpretations of fossils purported to show no evidence of decay and interpretations that fail to consider the mechanism of fossilization.

To conclude, the interpretation of fossils is distinctly non-trivial, but as many examples bear out, it is certainly worth the

effort. Fossil organisms allow us to see their living relatives in a new light, and to understand better their pattern of evolutionary emergence.

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