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Macroevolution of animal body plans: is there science after the tree?

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Abstract:	<p>A renewed emphasis on the gaps in organization that exist between the crown-group body plans of higher-level animal taxa is a hallmark of the emerging consensus in metazoan phylogenetics. Bridging these gaps is the greatest hurdle that stands in the way of translating our knowledge of phylogeny into a renewed understanding of the macroevolution of animal body plans. Unless a good fossil record is available there is little hope that we will be able to bridge many of these gaps empirically. We have therefore little choice but to resort to our more or less informed imagination to produce the historical narratives that are the ultimate goal of our studies of animal evolution. Only by fully engaging with the challenges of devising testable scenarios will we be able to tell where along the spectrum of science and fiction our understanding of animal body plan evolution will finally come to rest.</p>
<p>Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.</p> <p>Figure 2.svg Figure 1.svg</p>	

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Macroevolution of animal body plans: is there science after the tree?

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Abstract

A renewed emphasis on the gaps in organization that exist between the crown-group body plans of higher-level animal taxa is a hallmark of the emerging consensus in metazoan phylogenetics. Bridging these gaps is the greatest hurdle that stands in the way of translating our knowledge of phylogeny into a renewed understanding of the macroevolution of animal body plans. Unless a good fossil record is available there is little hope that we will be able to bridge many of these gaps empirically. We have therefore little choice but to resort to our more of less informed imagination to produce the historical narratives that are the ultimate goal of our studies of animal evolution. Only by fully engaging with the challenges of devising testable scenarios will we be able to tell where along the spectrum of science and fiction our understanding of animal body plan evolution will finally come to rest.

Keywords Metazoa, phylogeny, body plan, scenario

“Were all the qualities of things apparent to Sense, there would be no longer any mystery. A glance would be Science. But only some of the facts are visible; and it is because we see little, that we have to imagine much” (G. H. Lewes in Carignan 2003: 464)

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3 Peter Holland concluded his foreword to *Animal evolution. Genomes, fossils, and trees*
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5 (Telford and Littlewood 2009: vi) thusly: “A revolution in understanding animal
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7 evolution is upon us.” He is optimistic that we are now finally able to solve a problem
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9 that has plagued studies of deep animal evolution ever since Haeckel’s trees. Holland
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11 (Telford and Littlewood 2009: v) observes that for most of this period progress was
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13 hampered because:
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20 “there was no way to test alternative scenarios, no objective source of data to evaluate putative homology
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22 or proposed relationships. Every scenario was consistent with the available data, although certainly some
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24 theories were more outlandish than others! This was *the* major stumbling block to advance in the study of
25
26 animal evolution, and it persisted through much of the 20th century. The problem is now clearly in focus
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28 and at least part of the solution is at hand.” [italics in original]
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32 Holland believes that the infusion of molecular biology into the study of animal evolution
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34 is a large part of this solution. He singles out molecular phylogenetics and molecular
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36 developmental biology as particularly promising generators of new insights, a view
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38 broadly shared in the community (Edgecombe et al. 2011, Telford 2009). Yet, although
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40 these molecular disciplines are indeed substantial contributors to our understanding of
41
42 metazoan evolution, I will argue that their achievements constitute as much a
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44 sidestepping as a partial solution to Holland’s perceived barrier to progress. Animal
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46 phylogenetics is rapidly approaching a tipping point, but it is far from certain that it will
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48 usher in a new era of revolutionary understanding of animal evolution.
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56 ***Genealogie versus Phylogenie* and chronicle versus historical narrative**
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3 Haeckel's *Generelle Morphologie* (1866a, b) almost single-handedly founded metazoan
4 phylogenetics. Haeckel's main ambition was to reconstruct the macroevolution of body
5 plans, and he named his new science *Phylogenie* (Haeckel 1866a: 30). Haeckel's
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Haeckel's *Generelle Morphologie* (1866a, b) almost single-handedly founded metazoan phylogenetics. Haeckel's main ambition was to reconstruct the macroevolution of body plans, and he named his new science *Phylogenie* (Haeckel 1866a: 30). Haeckel's *Phylogenie* was concerned with investigating "the connected chains of forms of all those organic individuals that have branched off from one and the same shared stemform" (Haeckel 1866a: 30). In other words, *Phylogenie* aimed to trace the evolution of form within evolutionary lineages. Of course, in order to do that one also needs to reconstruct the relationships between those lineages. Haeckel called this science of evolutionary relationships *Genealogie* (Haeckel 1866a: 29), the results of which he thought could be clearly and concisely summarized in his still frequently reproduced *Stammbäume* (Haeckel 1866a: 88). So although Haeckel considered the study of *Genealogie* and *Phylogenie* to be intimately entwined, phylogeny went beyond pure genealogy to reconstruct the evolution of organismal form.

Haeckel's distinction between genealogy and phylogeny is important for appreciating the nature of progress in metazoan phylogenetics. Haeckel's thinking is mirrored by two concepts from the philosophy of history (O'Hara 1988). The evolutionary *chronicle* denotes the branched chronological series of organismal character state changes along lineages. Evolutionary history goes beyond the chronicle, and injects causal statements, explanations, and interpretations to create descriptive and explanatory *historical narratives*. An example illustrates this distinction. Mapping character states on a tree generates the hypothesis that annelids and molluscs are sister taxa, and that annelids evolved their segmented coelom after their lineage diverged from that of molluscs. These

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2
3 are aspects of the evolutionary chronicle. To infer the nature of the last common ancestor
4 of molluscs and annelids, and to use it as the basis for a scenario that attempts to explain
5 the origin of the segmented coelom of annelids as a secondary consequence of the
6 evolutionary expansion of the circulatory system as the annelid lineage evolved
7 parapodia (Westheide 1997) is an instance of historical narrative. In essence narratives or
8 scenarios add 'how' and 'why' questions to the basic 'what' questions of chronicles, and
9 they explicitly consider aspects of the evolutionary process.
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22 Evolutionary morphologists, such as Haeckel, did not sharply separate chronicle and
23 narrative. However, during the 20th century the evolutionary chronicle and narrative
24 became increasingly unwoven into separate scientific strands, and progress on these
25 strands has been strikingly uneven.
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32 33 34 **Completing the chronicle in the age of forensic phylogenomics**

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36 Cladistics achieved the methodological unification of phylogenetics, and declared the
37 epistemological and logical priority of phylogenetic pattern over evolutionary process
38 (Rieppel 2010). As a result phylogenetics contracted to a near exclusive focus on
39 evolution's chronicle. Indeed, O'Hara (1988: 144) defined systematics as the study of just
40 the evolutionary chronicle. Phylogeneticists no longer needed to speculate about the
41 processes by which ancestors were modified into descendants. Indeed, the relegation of
42 intractable 'how' and 'why' questions to the periphery of phylogenetic research was seen
43 as the defining epistemological triumph of cladistics. Evolutionary scenarios became
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3 optional extras, second order derivatives of cladograms that could be appended to the end
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5 of cladistic analyses.
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10 Molecular phylogenetics completed the separation of the phylogenetic chronicle and
11 narrative. Molecular sequence data allows the inference of phylogenetic relationships
12 without any conjectures whatsoever about how and why animal body plans evolve. For
13 metazoan phylogenetics these epistemological advances came around the same time. The
14 first morphological cladistic analyses of metazoan phylogeny were published in the early
15 1990s (Brusca and Brusca 1990, Schram 1991), and the first molecular tree of the animal
16 kingdom appeared in 1988 (Field et al. 1988). Both of these approaches have produced
17 valuable new insights into higher-level animal relationships over the last quarter century,
18 but it is notable that no new phylogenetic analyses have used morphological evidence in
19 recent years. Claus Nielsen's decision to remove the chapter on morphological
20 phylogenetics from the third edition of his important reference work on animal phylogeny
21 (Nielsen 2012) marks this changing tide towards the sole use of molecules in the field.
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41 After the outline of the new molecular view of animal phylogeny was first sketched by
42 analyses of a single very informative gene—18S rRNA (small subunit ribosomal RNA)
43 —progress is now driven primarily by phylogenomic analyses based on transcriptome
44 and genome-level datasets comprising large numbers of loci. Researchers tease apart
45 these large datasets with forensic care to identify and remove sometimes very strong non-
46 phylogenetic signals. Examples of forensic phylogenomics in action are Rota-Stabelli et
47 al. (2013) reanalyzing Regier et al.'s (2010) landmark study of arthropod phylogeny, Pick
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3 et al.'s (2010) reanalysis of Dunn et al.'s (2008) milestone paper on metazoan phylogeny,
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5 and Philippe et al.'s (2011a) reanalysis of Schierwater et al.'s (2009) phylogenomic
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7 analysis of early metazoan divergences.
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12 Metazoan phylogenetics has only recently become phylogenomic, and progress can be
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14 expected to continue apace despite the remaining challenges (Philippe et al. 2011a). This
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16 inspires hope that we will eventually achieve a fully resolved metazoan tree. But the
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18 developing consensus (Edgecombe et al. 2011, Nielsen 2012) already reveals that
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20 connecting the dots may well be substantially more difficult than drafting the tree in the
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22 first place.
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29 **A gappy tree and the demise of intermediate taxa**

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32 Conspicuous gaps in organization separate the crown-group body plans of higher-level
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34 animal taxa. This insight is nothing new, but the emerging phylogenetic consensus brings
35
36 these morphological gaps into sharper focus than ever before. Molecular phylogenies
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38 have fractured many of the smoother phenotypic continua of the past. The dissolution of
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40 Articulata is emblematic. Cuvier initiated two centuries of near universal consensus when
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42 he united annelids and arthropods into a taxon Articulata on the basis of their shared
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44 segmented body plans in the early 19th century. Molecular evidence undid this
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46 phylogenetic Velcro by segregating annelids and arthropods into two large protostome
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48 clades, Lophotrochozoa (=Spiralia) and Ecdysozoa, respectively. This separation was
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50 initially strongly contested by zoologists because it was considered highly unlikely that
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52 the many morphological and developmental similarities of the segmented body plans of
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3 annelids and arthropods had evolved independently (Nielsen 2003, Scholtz 2003). Yet,
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5 this was only one of the first molecular assaults upon our ingrained phylogenetic
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7 intuitions.
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12 The removal of what may informally be called intermediate taxa is a hallmark of
13
14 molecular insights into metazoan phylogeny. Although no extant taxa are truly
15
16 intermediate in a direct phylogenetic (ancestor-descendant) sense, the degree to which
17
18 they can shed light on the stepwise evolution of body plans depends on their position in a
19
20 tree. Sponges (Porifera) provide a clear example (Figure 1). Resolving sponges as a
21
22 paraphyletic grade at the base of Metazoa allows the inference that eumetazoans evolved
23
24 from ancestors with a sponge-like body plan (Sperling et al. 2009). This arrangement
25
26 allows one to trace the stepwise evolution of a series of novelties to the point where a
27
28 motile sponge larva-like animal has been posited as the last common ancestor of
29
30 Eumetazoa (Nielsen 2012). In contrast, if sponges are a sister clade to the rest of Metazoa
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32 we would not be able to infer this sequence of steps, leaving the nature of the last
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34 eumetazoan ancestor much more uncertain.
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44 Other taxa have been similarly deposed from the intermediate positions they had in many
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46 of the older trees (Table 1), disrupting previously inferred phenotypic continua of
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48 evolving body plans. For instance, the analysis of Heimberg et al. (2010) rejected the
49
50 enduring phylogenetic hypothesis, based on morphological data, that hagfish are the
51
52 sister group to a clade of the morphologically more complex lamprey and gnathostomes.
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55 Their results instead support a clade comprising hagfish and lamprey as a sister group to
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3 gnathostomes, which suggests that hagfish are a morphologically simplified offshoot
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5 from a more complex vertebrate ancestor. This removes hagfish from a phylogenetic
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7 position in which it could “provide an experimental model for investigating the
8
9 evolutionary assembly of the vertebrate body plan shared by lampreys and gnathostomes”
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11 (p. 19379), making “attempts to explain mechanistically the distinction between
12
13 vertebrates and invertebrates even more formidable” (p. 19382). Similarly, placing the
14
15 morphologically relative simple acoelomorphs and *Xenoturbella* as sister group to a clade
16
17 of echinoderms and hemichordates rather than as sister group to the remaining more
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19 complex bilaterians “will result in a much bleaker prospect for reconstructing ancestral
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21 bilaterian features” (Lowe and Pani 2011: R153).
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29 This emphasis on the disappearance of intermediate taxa is not meant to imply that the
30
31 emerging consensus on metazoan phylogeny does nothing but obscure the evolution of
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33 body plans. Yet, these examples involve taxa whose value for understanding body plan
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35 evolution has contracted from illuminating the assembly of body plans of other taxa, to
36
37 mostly illustrating how just their own body plans may have evolved, while
38
39 simultaneously revealing unexpected amounts of convergent evolution and character loss.
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41 Before discussing how we can bridge these chasms between the higher-level crown body
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43 plans of animals, we first need to understand the full scale of the challenge of revealing
44
45 the evolutionary assembly of animal body plans.
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53 **Limits to the resolution of hypotheses of body plan evolution**

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3 Imagine that you wanted to trace the body plan of the bilaterian ancestor from the last
4 common ancestor of Choanoflagellata + Metazoa, but you had to do that in only four
5 steps. Or imagine that you had to reconstruct the evolution of the morphologically
6 intricate body plan of the last common ancestor of living chordates all the way from the
7 urmetazoan in just six steps. Or imagine that you had to describe and explain the totality
8 of evolutionary change associated with the origins of all the three dozen or so taxa
9 traditionally known as phyla in no more than three dozen steps. You might think that
10 these are unimaginable challenges, and you may well be right, but they are not imagined.
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24 The study of animal body plan evolution is inescapably confined within these unforgiving
25 parameters. Each terminal taxon in a tree is placed at the tip of a phylogenetic lineage
26 composed of a series of ancestors stretching back in time. In reality, the phylogenetic
27 lineage of each higher-level taxon comprises a near innumerable and indeterminable
28 number of ancestors, the reconstruction of which would allow one to infer the countless
29 steps involved in the evolutionary divergence of animal body plans. Unfortunately, most
30 of these ancestral body plans are epistemically inaccessible. Generally, the only places
31 along a phylogenetic lineage where we can gain insight into hypothetical ancestral body
32 plans is at the branching points, or nodes, in the tree where lineages diverge. Hence, the
33 number of nodes along a lineage determines how many times that lineage can be sampled
34 to detect evolutionary change by comparing the inferred character states on the sister
35 branches emerging from each node. Thus the number of nodes along a lineage limits the
36 number of steps that are available for reconstructing evolutionary change along that
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3 lineage, and the more steps are available, the higher the resolution that can be achieved in
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5 inferring the evolution of body plans (Figure 2).
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10 Tree topology determines the exact number of nodes that lie along each phylogenetic
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12 lineage (Figure 1). In a fully pectinate (comb-like) metazoan phylogeny with, say, 36
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14 phylum-level taxa as terminals, the longest phylogenetic lineage stretches back 36 nodes,
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16 leaving 35 steps to infer body plan evolution from Urmetazoa. Unfortunately the
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18 metazoan tree is not pectinate. The nodal lengths of the phylogenetic lineages of most
19
20 higher-level taxa are much shorter. The longest phylogenetic lineage of a traditional
21
22 metazoan phylum is likely to stretch no more than 11 or 12 steps from Urmetazoa.
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26 Although a final estimate requires a fully resolved tree, the sizes of the major clades
27
28 allow us to infer that the longest phylogenetic lineages are likely to be concentrated in
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30 Lophotrochozoa (about 8-11 steps) and Ecdysozoa (about 8-10 steps), with shorter
31
32 lineages in Deuterostomia (about 5-7 steps), and the shortest for the non-bilaterians (1-4
33
34 steps). The number of steps along the internal branches of the metazoan tree that are
35
36 available for tracing the evolution of the body plans of the various hypothetical common
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38 ancestors are equally limited. Just five steps separate Urmetazoa from the ancestral
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40 deuterostome or ancestral protostome, and only seven or so steps separate it from the
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42 morphologically complex ancestor of vertebrates.
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51 Clearly, the resolution with which we can hope to reconstruct the evolution of the major
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53 animal body plans is severely limited. How severe these limitations are becomes evident
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55 when we compare the phylogenetic space available for inferring body plan evolution
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3 between the extant animal phyla with that available for tracing evolution within the two
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5 genera that house the king and queen of model organisms. The 30-40 species of *Mus*
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7 provide about the same amount of phylogenetic space to detect evolutionary change as
8
9 the three dozen animal phyla, while the genus *Drosophila*, with over 1,500 species, offers
10
11 a phylogenetic space more than 40 times larger (Markow and O'Grady 2006, Tucker et al.
12
13 2005)! Add to that the vastly greater evolutionary depth of the divergences between the
14
15 animal phyla, and the exciting challenge of trying to understand the details of animal
16
17 body plan evolution attains more than a tinge of intractability. But this sobering
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19 realization has, as we shall see, scarcely detracted researchers from attempting to clothe
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21 the naked branches of their trees with a fragile evolutionary fabric that at times is little
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23 more than a flimsy fantasy.
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32 **Bridging gaps with fossils**

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34 If we take higher-level phylogenies of extant taxa at face value evolution appears to
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36 proceed in a series of Big Bangs, with successive lineage splitting events bracketing
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38 enormous amounts of body plan evolution. Indeed, we infer that large amounts of
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40 evolutionary change have occurred—both phenotypically and genomically (Erwin and
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42 Valentine 2013, Erwin et al. 2011)—along many internodal segments of the metazoan
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44 tree. The standard view, however, does not see this as evidence that body plans evolve in
45
46 series of dramatic jumps. Instead, the organizational gaps in the tree of life are generally
47
48 thought to have been left behind in the wake of the extinction of stem taxa. This
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50 interpretation is borne out by taxa with a good fossil record. For instance, onychophorans
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52 (velvet worms) and arthropods are extant sister taxa, so that their respective ancestors are
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3 separated by only a single step from their joint last common ancestor on a phylogeny.
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6 Clearly, this offers no scope for reconstructing the stepwise assembly of their body plans.
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9 However, the nodal length of their phylogenetic lineages can be greatly extended by
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11 including fossils. A recent study (Legg et al. 2012) managed to add ten extra steps to the
12
13 arthropod stem lineage by including Cambrian fossils. This is the equivalent of adding
14
15 twice the total number of steps available for tracing the origin of the body plan of crown-
16
17 group chordates from the last common ancestor of all animals on a tree of extant taxa!
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22 Similar dramatic improvements in the resolution of hypotheses tracing body plan
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24 evolution are being achieved for other taxa with good fossil records as well, including
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26 echinoderms, many vertebrate groups, molluscs, and brachiopods. The paleontological
27
28 literature makes it abundantly clear that without fossils we are unlikely to ever know the
29
30 nature, sequence and amount of evolutionary change that has occurred along life's many
31
32 lineages. Unfortunately, a sufficiently detailed fossil record to aid in tracing body plan
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34 evolution is not available for many groups, while even in groups with good fossil records
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36 preservation is biased towards more durable tissues, especially skeletons. Worryingly,
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38 recent research has shown that even where informative fossils are available
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40 preservational biases can lead to systematic distortions of the phylogenetic position of
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42 fossils (Sansom and Wills 2013), often resulting in slippage of fossil taxa to positions
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44 lower in the tree, which erroneously suggests they are more primitive than they really are.
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51 52 53 **Bridging gaps with extant taxa** 54 55 56 57 58 59 60

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3 Although adding fossils is the only way to significantly lengthen the phylogenetic
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5 lineages of the major metazoan taxa, gaps in body plan organization can also be bridged
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7 to some extent by the more detailed study of extant taxa. For instance, light was recently
8
9 shed on the enigmatic evolutionary origin of the peculiar worm-shaped aplacophoran
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11 molluscs by the discovery of several sets of muscles in the larvae of an aplacophoran that
12
13 until then were only known from polyplacophorans (chitons), suggesting that
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15 aplacophorans evolved from an ancestor with a complex polyplacophoran-like
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17 musculature (Scherholz et al. 2013).
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24 A popular way in which researchers attempt to bridge the chasms between disparate
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26 phenotypes is to inform comparisons with data on the genetic components underpinning
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28 morphologies and developmental processes. The discovery that widely conserved and
29
30 homologous genetic regulatory circuitry is involved in the development of
31
32 morphologically dissimilar structures opened up an entirely new comparative vista.
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34 Previously seemingly incomparable phenotypes can be connected via the so-called ‘deep
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36 homology’ of their genetic regulatory machinery (box 1), which has led to some
37
38 spectacular insights into the construction of body plans (Shubin et al. 2009). For instance,
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40 the finding that the bulk of post-synaptic scaffold proteins expressed in metazoan nervous
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42 systems are also expressed in the flask cells of a larval demosponge (Sakarya et al.
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44 2007)—a group of animals devoid of nerve cells—provides tantalizing clues for
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51 connecting disparate body plans.
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3 Other intriguing proposals, for instance, that the central complex of arthropod brains and
4 the basal ganglia of vertebrates are homologous structures directing similar behaviors
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6 (Strausfeld and Hirth 2013), and that the mushroom bodies of annelids are homologous to
7
8 the vertebrate pallium (Tomer et al. 2010), also derive much of their support from finding
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10 that homologous genes are expressed in the neural tissues of these distantly related
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12 groups. However, results such as these should be interpreted with great caution because
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14 the conclusions are often precariously placed on the slippery slope of pairwise
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16 comparisons between very distantly related taxa. Comprehensively sampled comparisons
17
18 are needed to decide if the deep homology of the underlying genetics is matched by
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20 homology of the dependent phenotypes, or whether conserved genetic regulatory
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22 machinery has been co-opted independently into the development of non-homologous
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24 phenotypes.
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34 **Unbridgeable gaps?**

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36 While the nodal lengths of phylogenetic lineages place ultimate constraints upon the
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38 resolution of our hypotheses for animal body plan evolution, our ability to trace what has
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40 happened might be further limited by peculiarities of the evolutionary process. Some
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42 have taken the absence of evidence for finely graded series of intermediates between
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44 complex animal body plans to suggest that extraordinary evolutionary mechanisms may
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46 be at work that are able to produce complex morphologies without producing identifiable
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48 intermediates. For instance, Conway Morris (2010: 141) posits the possibility of “baffling
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50 series of self-organizations” to help explain the early evolution of complex body plans,
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52 thereby obviating the need for “conveniently cryptic prior stages”. Alternatively, Koonin
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3 (Koonin 2007) thinks that metazoan body plans could have emerged in what he calls a
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5 Biological Big Bang, which is defined as a period of extremely rapid evolutionary change
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7 driven by exceptional levels of genetic information exchange between lineages that
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9 establish new types of organization without detectable “intermediate ‘grades’ or
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11 intermediate forms”. If there turns out to be any truth to these unorthodox ideas it will be
12
13 futile to try to reconstruct the early evolutionary assembly of animal body plans. Luckily
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15 these ideas are for the moment ‘based’ only on the absence of evidence. However, the
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17 issue of evolutionary step sizes is relevant here.
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24 Although the distinction is largely intuitive and qualitative, the prevailing consensus is
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26 that morphological step sizes during evolution are generally small, but that larger steps
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28 are not theoretically impossible. Several workers have recently argued that saltational
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30 evolution—defined as phenotypically large evolutionary steps, irrespective of the size of
31
32 the associated genetic steps—may be more pervasive than generally thought (Frazzetta
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34 2012, Theißen 2009). But even if saltational evolution of phenotypes is possible,
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36 determining exactly where in the metazoan tree this may have happened is no trivial
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38 challenge, if only because it is impossible to be certain that intermediate body plans have
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40 never existed. But what does seem clear is that during the history of clades evolutionary
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42 step sizes need not remain constant. Hughes et al. (2013) conducted a quantitative
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44 analysis of the evolution of morphology across 98 metazoan clades, and they found that
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46 the predominant pattern across the Phanerozoic is one of clades reaching high
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48 morphological disparity early in their history. These results suggest that the pace of
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50 phenotypic evolution was generally highest early in the history of clades. This could be
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3 due either to the concentration of large morphological step sizes or unusually high rates
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5 of cladogenesis early in the history of clades. Lee et al. (2013) recently showed that such
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7 elevated evolutionary rates early in the history of arthropods are true both for molecular
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9 and phenotypic evolution, with molecular and morphological evolutionary rates being 5.5
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11 and 4 times faster, respectively, in the Cambrian than the average rates later in the history
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13 of the clade. These findings suggest that accurately reconstructing the early evolutionary
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15 assembly of body plans is a particularly formidable task.
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22 **Bridging gaps with imagination**

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24 Even with a fully resolved tree in hand, buttressed by a rich fossil record, gaps remain
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26 between body plans. Our imagination is the only tool that can braid the fragmentary
27
28 evidence into a seamless historical narrative that relates the what, how and why of the
29
30 evolution of body plans. Since such descriptive and explanatory historical narratives are
31
32 the ultimate goal of macroevolutionary research (Ghiselin 1997), it is important to
33
34 understand the background knowledge, intuitions, and rules of thumb that we bring to
35
36 articulating evolutionary scenarios.
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43 The role of the imagination—more or less informed—has always played a central role in
44
45 the study of the macroevolution of animal body plans. Anton Dohrn, the founder of the
46
47 Naples Zoological Station, wrote in a letter to Edmund B. Wilson in 1900 that
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49 “[p]hylogeny is a subtle thing, it wants not only the analytical powers of the “Forscher”
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51 [researcher], but also the constructive imagination of the “Künstler” [artist],—and both
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53 must balance each other, which they rarely do,—otherwise the thing does not succeed”
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3 (in Groeben 1985: 16). Yet, although only the imagination can take us beyond the bare
4 branches of the tree, Peter Holland's quote at the beginning of this paper reminds us that
5 the long history of metazoan phylogenetics bears the indelible stigma of a science that
6 has long been overly fond of speculation. And it is not difficult to see why this is. The
7 19th and 20th century literature is replete with imaginative evolutionary scenarios that are
8 often barely tethered to any empirical substrate.
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20 For instance, it has long been a strategy to boost the believability of scenarios of body
21 plan evolution by claiming that they are consistent with general evolutionary principles.
22 But even if evolutionary principles are sound in theory, there may be preciously little
23 evidence that they operate in particular situations. In his popular book *Embryos and*
24 *ancestors*, for example, De Beer promoted Garstang's idea that the dorsal nerve cord of
25 chordates originated through the dorsal confluence of two lateral ciliary bands in an
26 animal akin to an echinoderm larva. The only 'evidence' De Beer adduced for this
27 hypothesis was his claim that it agreed with "the principle of neurobiotaxis, according to
28 which a concentration of nervous tissue takes place in the region of greatest stimulation"
29 (De Beer 1940: 53). Assuming, without evidence, that the echinoderm-larva like chordate
30 ancestors swam with their backs to the surface De Beer concluded that their ciliary bands
31 migrated dorsally in response to "the rays of light penetrating through from the surface"
32 (p. 53). He then concluded that "all that is required to turn the Echinoderm larva into a
33 chordate is the formation of the notochord and the piercing of the gill-slits" (p. 54).
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Clearly, the ease with which de Beer envisaged these evolutionary transformations in
body plan scarcely satisfied the burden of proof associated with the hypothesis.

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6 Despite the immense improvements in our ability to infer evolution's chronicle we have
7
8 made far less progress in restraining our imagination when devising evolutionary
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10 scenarios. Not all researchers are inclined to constrain their scenarios within the confines
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12 of strongly supported trees. And even for those who do stay within the boundaries
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14 suggested by the tree, the challenge of devising testable scenarios is as great now as it
15
16 was in the times of Haeckel and Dohrn. To show how far, or how little, some of our
17
18 scenarios of animal body plan evolution have progressed since the time of Haeckel, I will
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20 present three examples to illustrate some approaches adopted by modern workers.
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27 **Creating scenarios: the imagination unleashed**

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29 Cavalier-Smith (1998) proposed a most creative scenario, hypothesizing that the tiny
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31 ciliated feeding tentacles of entoprocts are the evolutionary precursors of arthropod
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33 limbs. The sole 'support' for this remarkable hypothesis is that some solitary entoprocts
34
35 can use their tentacles to assist in a peculiar form of somersaulting locomotion. Without
36
37 addressing Cavalier-Smith's claim that his scenario "involves much less change than the
38
39 view that arthropods evolved from a coelomate legless worm", the Achilles heel of this
40
41 idea is that entoprocts and arthropods are distantly related phyla positioned in two
42
43 different clades—a result explicitly accepted by Cavalier-Smith. Connecting the dots
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45 between these two phyla is therefore a futile exercise.
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53 Theißen (2009: 48) proposed a saltational origin of barnacles. Citing the absence of an
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55 abdomen in barnacles, as well as the seeming absence of the Hox gene *abdominal-A*—a
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3 gene expressed in the abdomens of other arthropods—Theißen concluded that it “thus
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5 appears likely that the deletion (or substitution) of a homeotic gene resulted in the
6
7 saltational origin of an organism without an abdomen that established a new evolutionary
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9 lineage.” This inference seems boosted by the fact that ascothoracidans, the sister group
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11 of barnacles, do have abdomens and *abdominal-A*. Yet, a significant obstacle to a
12
13 saltational scenario that derives barnacles from an ascothoracid-like ancestor is this: the
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15 penis of male ascothoracids is located on the abdomen. A hopeful beginning of a new
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17 lineage this is not.
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24 Perhaps it is unfair to single out these two scenarios because they were created by a
25
26 microbiologist and a botanist, but similarly imaginative attempts to bridge the gaps
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28 between body plans created by zoologists are not hard to find. Schierwater et al.’s (2009)
29
30 hypothesis for the origin of the bilaterian body plan is presented as similarly self-evident
31
32 as De Beer’s theory for the origin of the chordate nervous system: “[o]ne of the easiest
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34 models for adopting a bilateral symmetry suggests that the “urbilaterian” kept the benthic
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36 life style of the placula [a placozoan-like ancestor] but adopted directional movement.
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38 The latter almost automatically leads to an anterior-posterior and ventral-dorsal
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40 differentiation. The pole moving forward develops a head and becomes anterior, the body
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42 side facing the ground carries the mouth and thus by definition becomes ventral” (p.
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44 0041). Although this might well be true—ignoring for the moment how well the chosen
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46 phylogeny supports this hypothesis—this scenario, like De Beers’s, contains precious
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48 little detail about the actual evolutionary transformations involved. Yet, researchers
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50 cannot always avoid erecting minimalist scenarios. A central message of this paper is that
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3 available evidence for fleshing out the macroevolutionary steps of body plan evolution is
4 often very scanty indeed. However, despite the minimum of evidence presented, this
5 particular scenario can be seen to fray at the edges. The asymmetric placozoans, upon
6 which the placula ancestor is modeled, do not show directional movement, yet they have
7 already acquired a differentiated dorso-ventral axis. The evidence is therefore compatible
8 with an alternative scenario in which dorso-ventral differentiation precedes antero-
9 posterior differentiation.
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22 **Using evolutionary intuitions to judge trees and scenarios**

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24 Because many macroevolutionary scenarios are rooted in only a thin layer of evidence
25 one's intuitions about what is and is not possible in evolution is often the only 'tool' in
26 one's arsenal for judging scenarios. Given that one's background knowledge and one's
27 implicit instincts about the limits of evolutionary change are highly personal, this
28 introduces a degree of subjective speculation and authoritarianism into both the creation
29 and the evaluation of macroevolutionary scenarios that is in marked contrast to the
30 epistemological rigour of tree building. An exchange between Simon Conway Morris and
31 Stephen Jay Gould in the popular magazine *Natural History* some years ago illustrates
32 this with respect to ideas about the origin of brachiopods (lampshells). Drawing on his
33 own scientific work Conway Morris (1999: 50) proposed that for a "functionally
34 plausible and historically believable" scenario for the origin of the bivalved brachiopods
35 "all that was needed" was for a slug-like halkieriid ancestor to shrink so as to bring the
36 two shells at the opposite ends of the animal into close apposition, so that it could fold
37 over to produce a brachiopod. Although some brachiopod larvae go through a folding
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3 process upon settlement Gould (1999: 54) remained thoroughly unconvinced by this
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5 scenario, labelling Conway Morris's linking of halkieriids and brachiopods "fanciful".
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10 Similar clashes of evolutionary intuitions litter the literature. Irreconcilable views are
11
12 especially common on the subject of the origin and the evolutionary significance of
13
14 ciliated larvae. For instance, recent attempts to modify Garstang's theory for the origin of
15
16 the chordate central nervous system from ciliary bands of larva-like organisms are
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18 considered "inconceivable" by some zoologists (Salvini-Plawen 1998: 129), but the best
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20 synthesis of available evidence by others (Nielsen 1999). The hypothesis that ciliated
21
22 larvae have evolved convergently in different clades of the animal kingdom was
23
24 considered "the epitome of hand waving" by some (Peterson et al. 1997: 626), while
25
26 others see the alternative as an unsupported remnant of "the now disregarded Haeckelian
27
28 paradigm" (Rouse 2000: 232). And with respect to the question of whether ciliated
29
30 planktotrophic larvae recapitulate the adult body plan of a distant animal ancestor, or
31
32 whether they represent a new life cycle stage inserted into a primitively direct developing
33
34 ontogeny, authors may see their hypothesis labelled "pure speculation" (Nielsen 2013:
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36 12) for precisely the same reason—presumed incompatibility with the operation of
37
38 natural selection—that these authors themselves used to reject the alternative scenario
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40 (Sly et al. 2003).
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50 In many such situations of a stalemate in the battle of phylogenetic scenarios trees
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52 provide the only opportunity to re-assess unexamined intuitions about body plan
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54 evolution, particularly when a robustly supported molecular tree suggests a previously
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3 unexpected phenotypic transformation. Yet, researchers are often surprisingly reluctant to
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6 revise their evolutionary intuitions on the basis of new trees. We are often willing to
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9 wield our barely articulated instincts to cast doubt on, or even dismiss, relationships
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11 derived from carefully conducted phylogenetic analyses. The reaction of an expert on
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13 crustacean morphology to a recent molecular phylogeny of arthropods is emblematic of
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15 this attitude. Ferrari (2010) expressed his incredulity at the new results by quoting Chico
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17 Marx: “Well, who you gonna believe, me or your own eyes?”. Ferrari could simply not
18
19 imagine the evolutionary transformations implied by the molecular tree, but nowhere in
20
21 the article did he articulate any cogent foundation for his intuitions (Jenner 2011).
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27 When one’s evolutionary intuitions are not well founded there is a real risk that one is
28
29 unwilling to accept a new topology that might be correct, and that might afford novel
30
31 insights into evolution. The optimal result of a phylogenetic analysis of microRNAs
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33 performed by Philippe et al. (2011b: 257) “rather implausibly” suggested the paraphyly
34
35 of acoels, and the authors therefore accepted a less parsimonious solution. Although their
36
37 suspicion that the evidence is misleading may well be correct, rejecting an optimal tree
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39 on the basis of an unarticulated gut feeling places the study of body plan evolution on an
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41 epistemologically slippery slope.
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48 In their benchmark molecular phylogenetic analysis of metazoan phylogeny Peterson and
49
50 Eernisse (2001) found that brachiopods and phoronids were nested within a clade of
51
52 spiralian. They considered this result “dubious” (p. 189) because they thought it
53
54 implausible that these groups had lost or strongly modified spiral cleavage and
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3 trochophore larvae. However, these authors surely knew that other spiralian, such as
4
5 cephalopods and several groups of platyhelminths, have also modified or lost both spiral
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7 cleavage and trochophore larvae.
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12 Similarly, in their comprehensive review of metazoan phylogeny Edgecombe et al.
13
14 (2011: 158) concluded that morphological data do not support the recently proposed
15
16 affinity of acoelomorphs and *Xenoturbella* to deuterostomes, in part because these worms
17
18 “do not show any traces of deuterostome characters, such as gill slits, that one would
19
20 expect to be present even in highly derived lineages.” Yet, as they acknowledge on the
21
22 next page, gill slits were lost without a trace along the lineage leading to crown-group
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24 echinoderms. This example is significant also because this paper was written by nine
25
26 experts in metazoan phylogeny, morphology and embryology. It shows that even
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28 evolutionary intuitions held by the most knowledgeable authorities may unravel with
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30 surprising ease.
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39 These examples illustrate the nebulous nature of many of our evolutionary intuitions. We
40
41 remain profoundly ignorant about many aspects of body plan evolution, and given the
42
43 scanty evidence upon which we base many of our scenarios, our imagination inevitably
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45 plays a decisive role in devising and judging scenarios. But if scenarios can be so easily
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47 created and defended, sometimes with only the loosest ties to a deliberately selective
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49 body of evidence, we are forced to ask how scientific our attempts to narrate body plan
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51 evolution actually are.
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Turning evolutionary séances into scientific scenarios

Our success in producing detailed descriptive and explanatory narratives of the macroevolution of animal body plans trails far behind the progress we have made in tracing the chronicle of metazoan phylogeny. This lag is inevitable insofar as robust phylogenetic trees are needed to set the boundaries for any evolutionary scenario. The emerging consensus on metazoan phylogeny, however, also highlights deep gaps in our knowledge, many of which we are as poorly equipped to bridge now as were the 19th century evolutionary morphologists. The major stumbling block to a better understanding of animal evolution identified by Peter Holland therefore remains stubbornly in place.

The phylogenetic lineages of the major metazoan crown-groups are discouragingly short in terms of the number of nodes available along each lineage for resolving the assembly of body plans. This seriously limits the resolution achievable by scenarios, especially in the absence of fossils. But before any evolutionary transformations between body plans can be traced we must infer hypothetical ancestors. In their new book on the Cambrian explosion Erwin and Valentine (2013: 317) liken our attempts to infer the body plans of ancient animal ancestors to séances. The older the nodes in question, the more apt this analogy is. The divergences between most pairs of higher-level crown-group sister taxa are so significant that the inferences of hypothetical ancestral body plans are generally accompanied by substantial error bars. These become compounded as one integrates the inferences of increasing numbers of hypothetical ancestors to reach deeper and older nodes in the tree. Add to this matrix of uncertainty the potentially limitless play of our

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3 imagination, and our attempted explanatory historical narratives may end up being little
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5 more than untestable fiction.
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10 Although large empirical gaps are an inescapable reality for students of animal
11 macroevolution, there are nevertheless guidelines to help avoid flimsy fantasies and to
12 create more scientific scenarios. First, scenarios must stay within the constraints set by
13 well-supported trees. One incurs a substantial burden of proof by proposing a scenario
14 that is at odds with our understanding of phylogenetic relationships. Second, potentially
15 incompatible evidence and obvious difficulties associated with proposed scenarios should
16 be explicitly considered. Scenarios rooted in the proposed existence of obviously non-
17 functional organisms are unconvincing. Third, alternative scenarios that can explain the
18 data equally well or better require explicit consideration. Hence, the reasons for
19 preferring one scenario to another need to be explicated. Fourth, it is worth critically
20 examining the empirical or logical basis of one's evolutionary intuitions, especially if one
21 is tempted to reject a phylogenetic hypothesis or a scenario because one finds the
22 evolutionary changes involved implausible or unlikely. Similar evolutionary
23 transformations may have already been documented in other taxa, which should inspire
24 one to revise or sharpen one's intuitions. Fifth, scenarios should be based on as broad an
25 empirical basis as possible. This will enhance both their testability and their explanatory
26 value, and thereby increase their heuristic scientific value. For instance, Conway Morris'
27 scenario for the origin of brachiopods from a halkieriid-like ancestor was elaborated by
28 Cohen et al. (2003) into what they called the brachiopod fold hypothesis. Although
29 inevitably speculative, this scenario attempts to integrate data from both living
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3 brachiopods and the fossil record, and it has been found useful enough by other
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5 researchers for them to use it to inform the construction of new phylogenetic data
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7 matrices (Conway Morris and Caron 2007, Sigwart and Sutton 2007, Vendrasco et al.
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9 2004).

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15 For many of us research begins and ends with scenarios. We are driven to understand not
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17 just the ‘what’ questions revealed by character state changes mapped onto trees, but also
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19 the ‘how’ and ‘why’ questions that lie beyond the trees. We perform phylogenetic
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21 analyses to weed out scenarios not supported by our trees, and to improve upon our
22
23 tentative sketches of what may actually have happened to body plans in deep time.
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26 However, the poverty of the available empirical record relevant to most questions of body
27
28 plan transformation makes connecting the dots immensely challenging. Some have
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30 attempted to formulate general principles thought to govern macroevolutionary change
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32 that could help us understand how phenotypes evolve (Budd 2006, Kemp 2007). Such
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34 general principles, however, are of limited value for revealing the many unique details of
35
36 particular evolutionary transformations. Even the most densely documented scenarios
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38 still need to be animated by our imagination.
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46 Because we cannot avoid the matrix of subjectivity and more or less informed
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48 speculation and intuition within which we create and debate scenarios some have
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50 dismissed thinking about scenarios as being entirely pointless, even undesirable. Gee
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52 (2000: 114) encapsulates this sentiment by writing that “Deep Time cannot sustain
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54 scenarios based on narrative.” If so, we will never be able to proceed beyond an acausal
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3 chronology of character state changes, and we will never be able to really understand the
4 evolution of body plans. In the end Gee may well be right. Yet, before we feel compelled
5 to draw such a dispiriting conclusion, I think that at the moment we are very far from the
6 point where we will have pushed the building of scientific scenarios to its limits.
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12 13 14 15 **Two conditions for future progress**

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17 If we want to transform our growing understanding of metazoan relationships into a
18 better understanding of animal evolution, we will need two things above all else: (1)
19 sufficient and properly targeted research funding, and (2) sufficient numbers of broadly
20 trained organismal biologists.
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27 (1) Progress in metazoan phylogenetics was boosted by several major funding initiatives,
28 such as the *Assembling the Tree of Life* initiative funded by the National Science
29 Foundation of the United States, and the *Deep Metazoan Phylogeny* priority program
30 financed by the Deutsche Forschungsgemeinschaft of Germany. Lest we are content with
31 a wintry forest of many bare-branched phylogenies planting these trees was only the first
32 step towards a fuller understanding of animal evolution. However, I think it is very
33 unlikely that funding bodies would be willing to ringfence money for dressing up our
34 trees on a level comparable to that made available to built the trees. Luckily, animal body
35 plan evolution is already a core topic for two multidisciplinary sciences: evolutionary
36 developmental biology and molecular paleobiology (Peterson et al. 2007, Raff 2000). I
37 therefore think that the responsibility for developing the emerging metazoan chronicle
38 into a proper narrative will mostly fall on the shoulders of these two disciplines.
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3 (2) Much of the expertise that has recently driven progress in metazoan phylogenetics is
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5 wholly insufficient to drive progress in understanding animal evolution. In addition to
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7 skilled bioinformaticians and molecular evolutionists, we desperately need broadly
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9 trained organismal biologists with the ability to understand and work with different types
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11 of data, from embryology to ecology. We therefore need to train more organismal
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13 biologists, including taxon specialists, whose combined expertise will be our best guide
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15 to explore the immense universe of remaining questions.
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22 If we fail to satisfy these two criteria I fear that many of the trees produced in the last
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24 several decades and in the future will be stillborn. But if we do capitalize on the recent
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26 revival of interest in the kinds of questions that first occupied the minds of Haeckel and
27
28 his contemporaries, we will have a real opportunity to explore the limits of what we can
29
30 ever hope to know about animal evolution.
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36 **Acknowledgments**

37
38 I thank Bjoern von Reumont and Lahcen Campbell for useful comments on the
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40 manuscript.
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45 **Text boxes**

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50 **Box 1.** Many of the molecular components involved in the developmental processes and
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52 complex phenotypes of animals can be traced back to ancestries that lie deep within the
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54 tree of eukaryotes or even prokaryotes. The idea that the evolutionary origin of many
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3 genetic components involved in complex phenotypes predate these phenotypes is
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5 captured in the concept of deep homology. This concept covers a wide range of cases.
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8 These range from examples in which homologous genes are expressed in structures that
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10 are not homologous, such as the *Distal-less* gene that is expressed in the horns of scarab
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12 beetles and vertebrate limbs, to examples in which homologous genes are expressed in
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14 homologous cell types that are themselves part of independently elaborated more
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16 complex organs, such as the *Pax6* gene expressed in photoreceptor cells found in the very
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18 different compound eyes of arthropods and camera eyes of vertebrates. For further
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20 discussion see Shubin et al. (2009) and Scotland (2010).
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27 **Figure legends**

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32 Figure 1. Two alternative topologies for the relationships between the sponge lineages
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34 and Eumetazoa. (a) This tree optimizes the silicious sponges, calcareans, and
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36 homoscleromorphs as a paraphyletic grade. This topology allows the reconstruction of
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38 the body plan of the last eumetazoan ancestor in three steps from Urmetazoa. Nielsen
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40 (2012: 17) reconstructs these steps as the evolution of larval ciliated cells with striated
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42 rootlets (step 1), the evolution of a basal membrane with collagen IV and an outer larval
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44 cell layer with adherens-like cell junctions (step 2), and loss of the sessile adult stage,
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46 which establishes Eumetazoa as a paedomorphic lineage. (b) This tree optimizes the
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48 sponge lineage as a clade Porifera, which only provides a single step for reconstructing
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50 the origin of the eumetazoan body plan from the ancestral animal.
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3 Figure 2. A tree of extant phylum-level taxa highlighting the phylogenetic lineages of
4 Arthropoda and Ctenophora. Only taxa directly branching off from the arthropod lineage
5 are shown, collapsing into single branches several supraphyletic taxa. Ten steps separate
6 the common ancestor of all animals (Urmetazoa) and the last common ancestor of
7 arthropods. Note that the phylogenetic lineage of arthropods is ten times longer than that
8 of ctenophores, and therefore allows a ten times higher resolution of hypotheses tracing
9 body plan evolution because ctenophores diverged much earlier from the remaining taxa.
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Table 1. Examples of formerly intermediate taxa that were often placed in positions that allowed them to shed light on the stepwise evolution of other body plans, and which are now placed in positions where their value for illuminating body plan evolution is greatly reduced.

Taxon	Previous status	Current status
Acoelomorpha (acoels and nemertodermatids)	Intermediate between non-bilaterians and more complex bilaterians, showing that bilateral symmetry and a degree of	Group with the worm <i>Xenoturbella</i> in a sister clade to Ambulacraria (Echinodermata + Hemichordata), implying

	nervous system	that these worms are
	centralisation evolved	probably very much
	before the origin of a	simplified.
	through-gut and nephridia.	
Pogonophora (beard worms)	Intermediate between protostomes and deuterostomes, suggesting that pogonophorans reduced their body segmentation on the evolutionary road to a trimeric body organization (three coeloms or pairs of coeloms arranged along the antero-posterior axis) that was thought to be primitive for deuterostomes.	Within polychaetes. Their similarity in coelomic organization with trimeric hemichordates and echinoderms is convergent.
Brachiopoda (lamp shells) + Phoronida	Intermediates between protostomes and deuterostomes, illustrating the trimeric organization, as well as the feeding mode with ciliated tentacles thought to be primitive for	Within Lophotrochozoa. Feeding with ciliated tentacles evolved independently from that in pterobranchs.

	deuterostomes.	
Sipuncula (peanut worms) + Echiura (spoon worms)	Intermediates between non-annelid spiralian and annelids, illustrating steps in the evolution from non-segmented coelomate protostomes to annelids.	Within polychaetes, indicating that they have lost the segmented body plan of the annelid ancestor.
Pterobranchia	Early branching deuterostomes, exemplifying a body plan intermediate between those of earlier branching sessile animals feeding with ciliated tentacles (brachiopods and phoronids) on the one hand and enteropneusts, echinoderms and chordates with pharyngeal gill slits on the other hand.	Sister group to enteropneusts or within enteropneusts, suggesting that pterobranchs have evolved their sessile filter feeding habits independently from brachiopods and phoronids.
Cephalochordata (lancelet, amphioxus)	Sister group to vertebrates, indicating that the morphological complexity	Sister group to urochordates + vertebrates, suggesting that the chordate ancestor

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4 shared uniquely between may have been much more
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6 cephalochordates and complex than previously
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8 vertebrates, such as a thought, with urochordates
9
10 complex blood vessel being drastically simplified.
11
12 system, a liver caecum and
13
14 a notochord extending
15
16 along the length of the
17
18 body, are primitively absent
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20 in urochordates.
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25 Lampreys Sister group to Sister group to hagfish,
26
27 gnathostomes, implying that implying that the last
28
29 a lot of body plan common vertebrate ancestor
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31 complexity evolved along had a much more complex
32
33 the lineage leading to body plan than that of
34
35 lampreys and gnathostomes, hagfish, suggesting that
36
37 including a cartilagenous hagfish have become
38
39 braincase, dorsal fin rays simplified.
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41 and extrinsic eye
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43 musculature.
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49 Ctenophora Sister groups to bilaterians, Possible sister group to all
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51 implying that the relative other animals, implying
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53 morphological simplicity of either that ctenophores
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55 sponges and placozoans is evolved their body plan
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3 primitive, and that the complexity independently
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Uncorrected version