Development and the radiation of animal phyla[1,2]

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Problematic taxa are taxa which fall outside received classifications. The book itself is devoted to many of those which can't easily be placed into phyla now alive, or which have ambiguous affinities at the phylum level, or for which an affinity has only recently been well established. There are quite a lot of them, and there is no overall survey either here or anywhere else I know.

There are, perhaps, three levels of problems with such beasts (well, some are algae and such). One is just that many of them aren't well known yet, either from inadequate specimens or inadequate study. Oddly, there actually seems to be, or at least to have been, a bias against studying strange phyletic orphans. Babcock notes the trouble caused by biases in descriptions as a result of too-hasty inferences on affinities. The second level concerns phyletic affinities and the nature of the organism when alive. The third level is less obvious and deserves a little discussion.

Say one has a beast like <u>Anomalocaris</u>, the largest animal of the Cambrian and a predator at that. It is morphologically quite isolated and no affinities are apparent for it below Metazoa. Different parts of it were indeed originally placed in three mutually unrelated phyla, by the principle of the blind men and the elephant, before their association was recognized. It is now often regarded as belonging to a phylum of its own because of its great difference in body plan from everything else we know. Well, maybe it was. Then again, it is quite as plausible that the differences we see don't reflect such a real distinction. This is partly because the concepts we have for phyla are based on what is alive now and on their obvious relatives. Within a phylum there can be quite enormous diversity in body plan. Nobody complains that the Coleoptera (or at least the Decapoda) are placed in the same phylum as the puffball-like adult Rhizocephala, or the asymmetric Carpoidea in the same phylum as the Asteroidea (or, by a few, in the same phylum as the Mammalia). The recently established affinities of the Pentastomida as a subgroup of the Crustacea weren't recognized earlier only because, as terrestrial parasites, they lack larvae. We recognize higher taxa by major adaptive changes about the time the taxa originate, and subsequent divergence may be insufficient to cancel or supersede the adaptive heritage of that history. So maybe <u>Anomalocaris</u> is just part of some known phylum's radiation, even if at the base. (Don't ask me which phylum! I do, though, make a perhaps new suggestion below with respect to another case.)

There is another possibility, distinct from the preceding under a surficial similarity, as a slime mold is distinct from a fungus. Development, as it evolves

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[1] Contribution 96, Lothlorien Laboratory of Evolutionary Biology

[2] **Problematic Fossil Taxa.**
Edited by **Antoni Hoffman and Matthew H. Nitecki.** 1986 (4 December). Oxford Univ. Press. xi + 267 pp. Acid-free paper. ISBN 0-19-503992-0. Hardbound. $69.00.

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within an adaptive zone, tends to inhibit major divergence. This is because evolution builds on what is there before, with aspects of both an inverted pyramid and a network in the development of all multicellular organisms. Drastically changing one part of an even loosely integrated system is difficult. (There are well-known side-steps to this difficulty, miniaturization is another that is less well known, and Raff may be finding a new one in sea urchins, but that doesn't matter here. The difficulty provides an ecodevelopmental explanation for the observed fact of little major divergence in most of the Phanerozoic.) Similarly, adaptation itself is integrated and selects for fine tuning of what is already there. Adaptive changes then have a large inertial base to overcome, so major changes aren't common.

These restrictions, though, are themselves a result of evolution and presumably were much less stringent very early in the radiation of metazoans. If so, what we see as large differences in body plan may represent comparatively minor differences in development itself. That doesn't mean that the differences in adaptation would be correspondingly moderate, but it does raise the possibility that this was sometimes the case. If our classifications are to reflect what is important to the animals rather than to us, we must consider the possibility that there were fewer real phyla in the middle Cambrian (to a Cambrian taxonomist) than there are today and that developmental and adaptive entrenchment, in addition to adaptive diversification, have raised the effective hierarchical level of some groups since that time.

I mean to raise this general alternative as a real possibility rather than to advocate it. We nevertheless have the practical problem of what to do with the various phyletic orphans which appear in the Vendian and the Paleozoic. The usual practice has been until recently to leave them incertae sedis at the phylum level, at least, and this would seem to be the least objectionable alternative now. Placing them as orphan phyla, with or without formal names, makes a positive claim which is more than we can really substantiate. The same is true for attaching most of them to existing phyla. I do find it a bit amusing that the first three extinct orphans to gain wide recognition as separate phyla have all later been incorporated into existing phyla: Archaeocyatha into Porifera, Graptolithina into Hemichordata, perhaps even with two extant orders, and Conodonta into Chordata, probably even into Agnatha. We will presumably have better knowledge of both adaptation and phyletic interrelations of extinct orphans (and their internal phylogeny, to infer the ancestral phenotypes) in the dueness of the course, and at such times we will be in a better position to evaluate how adaptively distinct they were from their known relatives.

The book itself contains papers, not always accurately cross-referenced, on a good sample of phyletic orphans. The papers range from detailed revisions (even with new taxa) to discursive discussions, but all have some consideration of possible affinities. Fedonkin gives a bottom-up view of the Vendian fauna by concentrating on the diversity of coelenterates, some resembling the hypothetical gastraea and others showing grades of advancement which are not discussed clearly in relation to extant coelenterate groups. He reasonably proposes that some bilateral genera are coelenterate derivatives without further issue, but he also wants to derive the Annelida and Arthropoda directly from the Coelenterata, having metamerism originating with bilateral symmetry. This can hardly be taken seriously without discussion of the Turbellaria. Perhaps the paper was written before Seilacher's radical reinterpretation of the Vendian fauna, but in most (not all) ways the views of these authors are rather orthogonal to each other, not as much in conflict as one might expect.

Other highlights of the book are Rozanov's account of some of the basal Cambrian mesofauna and two papers by Dzik, one arguing persuasively for agnathan affinities of the Conodonta (but without reference to earlier work by Gross with the same conclusion from partly similar evidence) and the other making a speculative but reasonable case for an expanded Machaeridia (plated wormlike animals) to include even forms like Wiwaxia of Burgess Shale fame.

Briggs and Conway Morris have a better discussion of the phylum-level affinities of Wiwaxia, but that doesn't affect Dzik's case for a broad Machaeridia. I suspect that the group is real and even molluscan (Wiwaxia, at least, has a radula), although if so they had a separate origin of armor from the other armored mollusks. Paleontologists tend to forget that the ancestral mollusks lacked a shell. I don't mean that the Aplacophora (Caudofoveata and Solenogastres) are primitive; they usually even have calcareous elements which may well be vestigial armor. (Are the Aplacophora demetamerized descendants of the Machaeridia rather than of primitive Polyplacophora or the like?) A derivation of the Machaeridia from a metameric ancestral mollusk (note Neopilina, where the residual metamery is unlike that in any turbellarian) removes the supposed difficulties of a molluscan affinity and accounts in a direct way for all the evidence I know. In this way the origin of the Mollusca can reasonably be equated with the origin of the radula, a major adaptive innovation which may have opened up a new adaptive zone, despite its later loss by the Pelecypoda and probably most Rostroconchia.

Literature cited

Gross, W. 1960. Ueber die Basis bei den Gattungen Pelmatolepis und Polygnathus (Conodontida). Paläontologische Zeitschrift, 34: 40-58.