

Acoel flatworms misrepresented?

To see acoel turbellarians raised to such prominence on the pages of *Science* (1) gives us a certain pride. Such a celebrity status for animals we have studied so long ourselves and the recognition of their importance for understanding the origin of the Bilateria are gratifying. However, Ruiz-Trillo *et al.* fall short of establishing the acoels as the earliest bilaterian metazoans. For such a conclusion they have laid all weight on a single set of molecular characters (the 18S rDNA gene) at the expense of a wealth of other characters systematists have discerned in acoels and other platyhelminths in more than a century of study.

Positioning acoels as the basal bilaterians implies some unexpected twists in metazoan evolution. It would mean, for instance, that the epithelial gut of the Bilateria evolved independently of the epithelial gut in the Coelenterates. It would also mean that extracellular matrix (ECM) arose twice, first in sponges and coelenterates and later again in the bilaterian descendants of the acoels. To the contrary, there is ample evidence for a more parsimonious evolution of such characters (2, 3).

A major flaw that leads Ruiz-Trillo *et al.* to make such fantastic claims is their neglect of the sister group of the Acoela, the Nemertodermatida. By their 18S rDNA data this group is placed rather uncertainly at great distance from the Acoela, but there is absolutely no question, by a wealth of rigorous synapomorphies in ultrastructural and other morphological features, that these two groups are sister taxa (4, 5). Phylogenetic analysis of another rDNA gene, for 28S rDNA, seems to support this notion as well (6). Consideration of the Nemertodermatida makes sense of the strange features of the Acoela. For example, the condition of the ECM found in the Nemertodermatida is the very one (2, 7) that makes the reduction of ECM in the body wall of the Acoela understandable (2). Similarly, the peculiar structure of the digestive system of acoel flatworms can only be understood in evolutionary terms as having been derived from a typical epithelial gut like that seen in the Nemertodermatida as well as in the Catenulida and Macrostomorpha (2, 5, 8, 9).

Another critical omission in Ruiz-Trillo *et al.*'s argument is consideration of *Xenoturbella bocki*, an enigmatic worm of uncertain affinities. *Xenoturbella* was recently placed in just the position that Ruiz-Trillo *et al.* propose for the Acoela, as a sister group to all Bilateria (10), yet they make no mention of that placement (11).

Ruiz-Trillo *et al.* (p. 1922) specifically point to characters of the body wall—namely, a network of epidermal ciliary roots, tips of cilia with a distinct step, and lack of extracellular matrix—as phenotypic synapomorphies of the Acoela that are generally accepted (5, 13). But they do not acknowledge that many component characters of the two synapomorphies on ciliary structure extend to the Nemertodermatida and possibly also to the Xenoturbellida (7, 14).

While we agree that the new findings that Ruiz-Trillo *et al.* cite on cell lineage in acoel development may indeed support a very basal position of the Acoelomorpha among the spiralian, judgement of the significance of those findings without comparable knowledge of cleavage in the nemertodermatids is simply premature. Such information on nemertodermatids is sorely needed. After all, nemertodermatids are the only platyhelminths with uniflagellate spermatozoa (15), and their development has the highest likelihood of reflecting an ancestral condition.

Too, the nervous system in acoels, in our opinion, does not differ from that of other platyhelminths so much in the structure of the brain, as Ruiz-Trillo *et al.* stress, as it does in the presence of a single basiepithelial nerve plexus in certain acoels, such as the hofsteniids (7); such a plexus occurs also in the Nemertodermatida and *Xenoturbella* (13).

If the molecular data that are the focus of Ruiz-Trillo *et al.*'s study seem to contradict morphological characters, how do we resolve the discrepancy? Certainly for other taxa the 18S rDNA gene has provided valuable clues to phylogenetic relationships. At the same time, we have to acknowledge that such a single gene as this has inherently limited information (16) and that biases in rate and nucleotide composition in this gene can produce artifacts of “long-branch attraction” and “base skew” that generate seemingly statistically robust but unreal phylogenetic trees. The analysis that Ruiz-Trillo *et al.* apply to the 18S rDNA gene in the lower metazoans is

admirably rigorous, but no amount of analysis will discern meaningful information from a sequence that has been saturated with nucleotide changes as is likely in such an extremely ancient group as the Acoela. Cavalier-Smith (16) cites comparable examples of “just how grossly misleading the rRNA tree can sometimes be” in phylogenetic positioning of the Microsporidia and the Euglenozoa; like the Acoela in Ruiz-Trillo *et al.*'s study, the Euglenozoa is placed “substantially too low” on phylogenetic trees (relative to *Reclinomonas* and Percolozoa) by 18S rDNA analysis. In general, as Abouheif *et al.* (17) have argued, the 18S rRNA gene by itself may be “an unsuitable candidate for reconstructing the evolutionary history of all metazoan phyla,” and the acoels, especially for their ancient roots, appear to be prime examples of such unsuitability.

In the final analysis, we are really not much closer to answering the question we asked some years ago (8): “Is the Turbellaria polyphyletic?” At that time, we showed that no rigorously identified synapomorphies could be found for the Platyhelminthes even though we felt there was little question that all three monophyletic groups were more closely related to each other than to other invertebrates by virtue of shared similarities in their basic body plan. The molecular data simply do not provide any better answers than do the morphological ones. Taking all recent evidence together we would conclude that the earliest branch within the Platyhelminthes is not the Catenulida but the Acoelomorpha. The Acoela itself remains important for hypotheses of metazoan evolution, but any proposal for a new phylogenetic position for it simply must include consideration of the Nemertodermatida and Xenoturbellida and must not neglect the wealth of morphological data we have on lower metazoans.

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11. That *Xenoturbella* was proposed recently by M. Norén, U. Jondelius, and O. Israelsson (*Nature* **390**, 31 [1997]) to be a mollusc (on the basis of molecular markers and on a character of oogenesis) is not reason enough to ignore it. Such a relationship is not supported by the bulk of the data; no known mollusc has a basiepithelial nervous system as does *Xenoturbella* (12). To explain Norén & Jondelius's and Israelsson's unexpected results, we point out that *Xenoturbella* feeds on protobranch molluscs (U. Ehlers, pers. comm.) which may have yielded the data on which their hypothesis of molluscan status is based.
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