Shcheprova et al. [4], who found that bud6Δ daughters born to older mothers had a shorter lifespan. It would also imply that asymmetric inheritance does not exist for mothers to retain accumulated damage as a means of making their daughters young, since the daughters are better off (at least with regard to lifespan) without it. Instead, it may be that retention of damaged molecules into the mother cells benefits the longterm fitness of the colony.

Together, the findings of Gehlen et al. [9] and Khmelinskii et al. [8] put forth a new model for asymmetric inheritance of ERCs that is both elegant and simple. What are the broader contexts of these findings? To our mind, there is good news and (potentially) bad news. The good news is that the simple diffusion models need not apply solely to plasmids without centromeric elements. Thomas Nystrom and colleagues have shown in an elegant series of studies that mother cells preferentially retain a range of damaged cellular molecules, including oxidized and aggregated proteins [11,12]. Geometry could also play a role in the restriction of these and other molecules to mothers, whether they be nuclear or cytoplasmic components. It should be noted that recent studies have proposed active mechanisms as well for the maintenance of damaged proteins in mothers [13]. Nevertheless, the influence of geometry should be considered.

The potential bad news is that yeast are different from mammalian cells in at least two important contexts. The first is that yeast divide by budding. The second is that they have a 'closed' mitosis; that is, the nuclear envelope does not breakdown as it does in mammals . It is unclear whether models based on geometry will be sufficient to explain the asymmetric segregation of molecules in mammals without these peculiarities. As Gehlen et al. [9] point out, however, a default system for retention of cellular components is something worth considering, whether it might apply to asymmetric accumulation of damaged components or factors important for the differential behavior of the two cells that arise from a common division, as in the case of stem cells dividing to produce another stem cell and a cell committed to a differentiated lineage. Passive diffusion as a controlling factor may indeed be the shape of things to come.

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Animal Evolution: A Soap Opera of Unremarkable Worms

Recent phylogenies have suggested that acoelomorph flatworms might provide insights into the nature of the ancestor of bilaterian animals. However, according to new data acoelomorphs might instead be degenerate deuterostomes closely related to Xenoturbella, muddying the waters of early animal evolution.

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The past few decades of phylogenetic research have resulted in a major reorganisation in the relationships between animal phyla, but by now phylogenetic trees based on molecular studies are quite congruent for many of the major phyla. As increasing amounts of sequence data can be generated ever more cheaply, many of the more obscure phyla, whose placement in the tree of life has puzzled biologists for decades and often led to heated debates, are now being sequenced for inclusion in large phylogenomic datasets. However, many of these phyla turn out to be just as problematic for molecular phylogeneticists as they were for morphologists [1]. As a result, these obscure phyla have been placed at various changing positions in the tree. Some of these groups, such as the chaetognaths (also called 'arrow worms'), are pelagic with quite complex body plans, whereas others, like gastrotrichs, are small, ciliated, simple animals that glide between particles in the substrate. A recent paper [2] now has proposed a radical new grouping of two of these problematic taxa: Xenoturbella and acoel flatworms. Why all the attention for such simple creatures? Part of the answer lies in the possibility that they may represent an early branch off the lineage leading to the bilaterians [3–5].
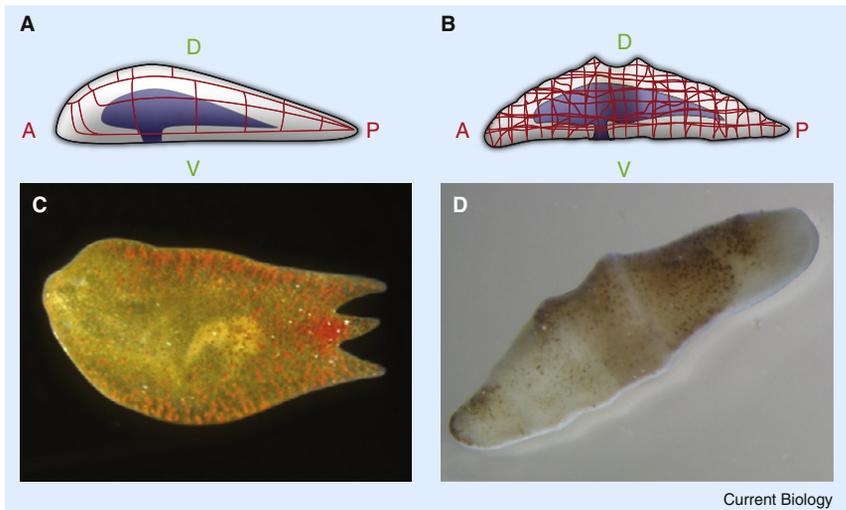
Figure 1. Morphology and basic body plans of acoel flatworms and *Xenoturbella*.
Diagram of a lateral view of the body plan of acoel flatworms (A) and *Xenoturbella* (B). The diffusely organized nervous systems are marked in red and the ventral mouth and blind gut are marked in blue. The dorso/ventral axes are indicated by D/V and the anteroposterior axis by A/P. (C) Photomicrograph of an acoel flatworm, dorsal view, courtesy of James Sikes. (D) Photomicrograph of *Xenoturbella bockii* courtesy of Max Telford.

This major clade of animals is divided into two lineages, the protostomes and deuterostomes, and is characterized by a significant jump in organismal complexity: an anteroposterior and dorsoventral axis, the innovations of mesoderm and a central nervous system, and a through gut. These characters distinguish bilaterians from more basal groups, such as cnidarians, with simpler body plans. Acoel flatworms and *Xenoturbella* have been proposed to represent a 'missing link' between the simple cnidarians and more complex bilaterian phyla [4]. However, the new phylogenetic analysis by Philippe *et al.* [2] pulls the acoelomorphs and *Xenoturbella* from a previously supported position as basal bilaterians [4–6] and places them within the deuterostomes as a sister group to echinoderms and hemichordates, thus undermining their importance for understanding the early evolution of bilaterians.

Resolving phylogenetic relationships at the base of the bilaterians has been a very hard nut to crack. It seems likely that the early bilaterians rapidly diversified into their major lineages, which is reflected in short branch lengths at the base of the bilaterian tree, making it challenging to resolve their relationships [4]. The large disparity in body plans between bilaterians and cnidarians, and the lack of intervening branches between the two groups, give the impression that the bilaterian innovations appeared all at once, without any clues to the timing and order by which each of the bilaterian characters appeared. Only a few animal groups have body plans that could be plausible intermediates between cnidarians and bilaterians, so resolving the phylogenetic positions of these groups will be crucial for testing hypotheses of bilaterian evolution [3]. One such intermediate group are the Acoelomorphs, a group of small animals with anteroposterior polarity, bilateral symmetry but no through gut, no coeloms and a diffusely organised nervous system (Figure 1A,C). They have slithered their way around the base of the tree in recent years, but have been difficult to pin down robustly to any one position [1,7]. Tantalisingly, a growing consensus over the past decade has placed acoelomorphs at the base of the bilaterians, outside of protostomes and deuterostomes. This topology would suggest that acoelomorphs are the only group to have emerged from the branch leading to the bilaterians, after the split from cnidarians, and consequently represent a key group for understanding the early emergence of bilaterian body plan innovations [4–6,8].

Philippe *et al.* [2] focussed their analysis on recently reported affinities between acoelomorphs and another obscure worm, *Xenoturbella* [4], which shows significant morphological similarities with acoels, such as a ventral mouth, blind gut, no coeloms and a diffusely organized nervous system [9] (Figure 1B,D). Previously, a series of phylogenomic studies robustly supported a position of *Xenoturbella* within the deuterostomes, closely related to echinoderms and hemichordates (Figure 2A) [10,11]. Nonetheless, a recent study [4] using ever-expanding data sets found support for a topology linking *Xenoturbella* to acoels, which sent *Xenoturbella* on a journey to the base of the bilaterians (Figure 2B). Now, Philippe *et al.* [2] have used three independent datasets to revisit this important issue; mitochondrial DNA, ESTs and miRNA complements. They too find support for a clade comprising Acoelomorpha and *Xenoturbella* (Xenacoelomorpha), but instead place these groups within the deuterostomes as the sister group to echinoderms and hemichordates (Figure 2C).

If the topology proposed by Philippe *et al.* [2] is correct (Figure 2C), then rather than a story of gain of phylogenetically informative characters, we must entertain the possibility that much of deuterostome evolution is instead a tale of loss of morphological and molecular complexity. However, assessing the extent of loss in these animals depends on our ability to reconstruct ancestral deuterostome characters. Deuterostomes include echinoderms, hemichordates, amphioxus, urochordates and vertebrates, which possess a broad range of body plans, and life-histories. The marked morphological disparity in deuterostome body plans has resulted in only a handful of characters that can be confidently attributed to a deuterostome ancestor: gill pouches and an associated pharynx that are suggestive of a muco-ciliary mechanism of feeding, as well as a tricoelomic organization that arises by enterocoely, a pouching of mesendoderm [12]. As acoelomorphs and *Xenoturbella* appear to lack these traits, all of them would have been lost in the Xenacoelomorpha, along with the through gut and coeloms.

Despite the paucity of shared morphological characters, researchers have inferred a minimal set of developmental genetic features that must have been present in the deuterostome ancestor. In particular,
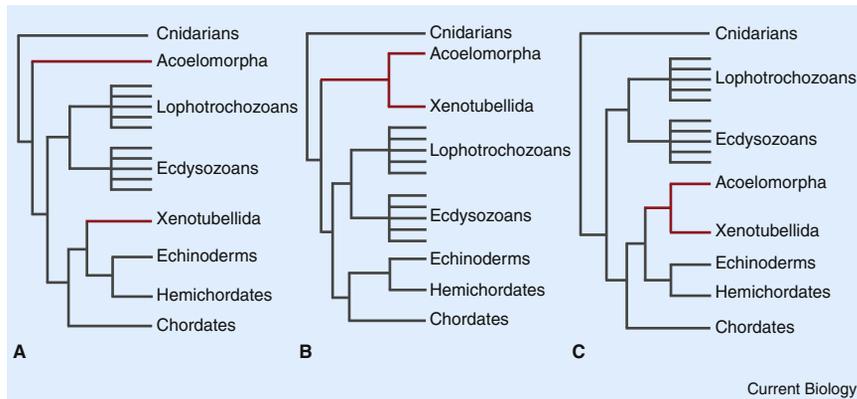
Figure 2. Alternative hypotheses for the phylogenetic position of acoelomorphs and Xenoturbellida within metazoans.

(A) Basal position of Acoelomorpha within bilaterians, but *Xenoturbella* located within the deuterostomes [10]. (B) Grouping of Acoelomorpha with *Xenoturbella* at the base of the bilaterians [6]. (C) New hypothesis of Xenacoelomorpha as sister group to echinoderms and hemichordates within the deuterostomes [2].

comparative developmental studies between chordates and hemichordates have revealed a conserved network of regulatory genes involved in patterning ancient deuterostome axes [13]. Some of these, such as Hox genes, have been investigated in acoels [14] and *Xenoturbella* [15], and both their presence or absence and expression patterns again would suggest some secondary loss of complexity in these animals. Further studies will be required to assess the extent of these losses. From the revised placement of Xenacoelomorpha within the deuterostomes, it follows that at least three major deuterostome clades (Xenacoelomopha, Echinodermata, and Urochordata) must have independently altered their body plans in radical ways. This extensive character loss and divergence make it difficult to reconstruct early deuterostome evolution.

Although significant for our understanding of deuterostome evolution, the impact of these new findings on early bilaterian evolution is more profound: if this new topology is true, and acoelomorphs are not basal bilaterians, it has serious implications for our understanding of the early evolution of bilaterians. Acoelomorphs would lose their promise as an early lineage that captured a snapshot of evolution along the stem leading to bilaterians. Rather than representing a compelling series of transitional character states, acoelomorph features such as a blind gut and lack of coeloms would instead represent secondary losses or simplifications.

Likewise, molecular genetic features of acoels considered ancestral and transitional, such as a limited Hox cluster, would also represent secondary loss [3,14]. If it stands the test of time this revised topology will result in a much bleaker prospect for reconstructing ancestral bilaterian features.

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Object Vision: A Matter of Principle

A new study shows that sparse coding — a principle which elegantly explains neural selectivity in the early visual system — may also explain selectivity in V4, an intermediate visual area implicated in object vision.

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Our brains recognise visual objects almost instantaneously and without noticeable effort. Objects can often be identified from any angle, even

when they are partially covered by other objects, and, remarkably, we can usually identify objects that we have never seen before. Such flexible, robust object recognition is an impressive feat, which even the most