Response to Comment on "A New Species of Yunnanozoan with Implications for Deuterostome Evolution"

The combination of complex taphonomies and bizarre anatomies in Chengjiang fossils can lead to radical divergences of opinion concerning phylogenetic placements. Yunnanozoans exemplify this difficulty, but the proposal by Mallatt *et al*. (*1*) that they represent some sort of protovertebrate is difficult to substantiate. Their arguments revolve around six key claims: The presence of eyes, a large brain, an agnathan-like anterior, a notochord, segmented myomeres with muscle fibers, and a postanal tail—of which the first three would be specifically congruent with vertebrate affinities. None of these arguments is persuasive. Although this discussion centers on our recent description of *Haikouella jianshanensis* (*2*), our interpretations are also based on abundant material from the two related species *Yunnanozoon lividum* and *H. lanceolata*.

Fossilized eyes are well documented in the Chengjiang material, notably in a number of arthropods (*3*) and the undoubted agnathan fish *Haikouichthys* (*4, 5*) and *Zhongjianichthys* (*5*). In contrast, the purported eyes identified by Mallatt *et al*. are remarkably indistinct. Unfortunately, Mallatt *et al.* give no details of how many of their specimens show the supposed eyes. In more than 1000 of our specimens, many of which show a well-preserved anterior division, none show equivalent structures. The radically different shapes of the two so-called eyes in figure 1A in (*1*) should also be noted, as well as our observation that the putative eye in figure 1B in (*1*) is adjacent to the first (unlabeled) gill and is strikingly similar to the gill arch terminations that we documented (*2*). It therefore appears to form the dorsal attachment. We welcome this evidence in support of our conjecture (*2*) that the gills were attached at either end, contrary to earlier suppositions (*6*).

We also question (*7, 8*) the notion that yunnanozoans possessed either myomeres or a notochord. The recognition of muscle fibers would in itself be unremarkable. We note, however, that such "muscle fibers" are also visible in some vetulicolians. This fact, in conjunction with consideration of their size and sinuous disposition as illustrated by Mallatt *et al.*, suggests that they may more likely be compressional folds in a cuticular covering. Even if these structures represented some type of muscle fibers, which are restricted to the dorsal-most region [figure 1C in (*1*)], they have no direct bearing on whether the muscle blocks are arranged in the diagnostic cone-in-cone configuration of myomeres. Thus, the dorsal segments of yunnanozoans show no evidence for the diagnostic "V" or "W" outline of myomeres, and in contrast to vertebrates (and amphioxus), the purported yunnanozoan notochord is in a ventral position where it could not act as an antagonist.

The remaining claims of Mallatt *et al*. can be addressed more cursorily. Although we are pleased that they agree with us about the nature of the anterior skirt, in contradistinction to earlier work (*6*), we fail to see how this compares in any detailed way with the anterior of either *Haikouichthys* (*4*) or the larval lamprey. Concerning the position of the gill arches, we reiterate the evidence for an external position (*2*) based on careful examination of the relative levels of fossil preservation, and note that this is consistent with earlier illustrations (*6*). Mallatt *et al.* identify a large brain [previously interpreted as "tripartite" in (*6*)], but we doubt this identification, for two reasons. First, it finds no counterpart in any of our material and is inconsistent with our identification of possible paired nerve cords (*2*). Second, even if yunnanozoans were protovertebrates, which we emphatically contest, it would be difficult to imagine that they were more derived than amphioxus. The latter animal has a very simple and small brain, and even divisions between hind- and mid-brain are cryptic (*9*). The claim for a postanal tail is based on the questionable identification of the posterior termination of the gut, while the attenuated "tail" is a very inconstant feature and most likely a product of folding and compression.

The conjectures of Mallatt *et al*. are based not only on questionable interpretations of fossil material, but also presuppose a deuterostome phylogeny that fails to take into account the related vetulicolians (*10*). Considering vetulicolians and yunnanozoans as stem-group deuterostomes reopens many questions concerning both their early evolution and the origin of the various apomorphies. Despite reconstructions of vetulicolians being equipped with eyes and antennae (*11*), neither these features nor any other structure (e.g., jointed legs) that would in turn be consistent with an arthropodan affinity, can be identified in the thousands of vetulicolians fossils. We agree with Mallatt *et al*. that the origins of many deuterostome characters need further exploration, but we suggest that treating yunnanozoans (and vetulicolians) as deuterostome stem-groups will reinvigorate various unresolved problems, including the origin of the pharyngeal openings.

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References and Notes

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