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Phylogenetic position of *Diania* challenged

Liu *et al.*[1] describe a new and remarkable fossil, *Diania cactiformis*. This animal apparently combined the soft trunk of lobopodians (a group including the extant velvet worms in addition to many Palaeozoic genera) with the jointed limbs that typify arthropods. They go on to promote *Diania* as the immediate sister group to the arthropods, and conjecture that sclerotized and jointed limbs may therefore have evolved before articulated trunk tergites in the immediate arthropod stem. The data published by Liu et al.1 do not unambiguously support these conclusions; rather, we believe that *Diania* probably belongs within an unresolved clade or paraphyletic grade of lobopodians.

Without taking issue with the interpretation of *Diania* offered by Liu *et al.*[1], or of the manner in which they coded their characters, we were nonetheless unable to derive their cladogram optimally from the data published. Moreover, we could not replicate their results using any other plausible optimality criteria, or by varying additional parameters not specified by the authors.

Liu *et al.*[1] report analysing their data in PAUP*[2] under maximum parsimony and with implied weights[3] using $k = 2$ (a rather arbitrary choice), but do not mention any other assumptions (for example, the imposition of character order). They obtained three most parsimonious trees, each of 130 steps. Straightforward replication of their stated settings yields 13 trees of just 90 steps each, the strict consensus of which is illustrated (Fig. 1). Why such a difference?

Several of their characters contained inapplicable or gap codings. These appear where a 'daughter' character is logically contingent upon the state of a 'parent', and cannot be coded when the parent is absent. For example, character 6 (position of frontal appendage) can only be coded in taxa that possess a frontal appendage (character 5) in the first instance (such that a "0" for character 5 necessitates a "-" for character 6). In morphological analyses such as this, inapplicable states are usually assumed to have no bearing on the analysis, being reconstructed passively in the light of known states. In analyses of nucleotide data, by contrast, gaps may alternatively be construed as a fifth and novel state, because shared deletions from some ancestral sequence may actually be informative. If this assumption is made with morphological data, however, all the logically uncodable states in a character are initially assumed to be homologous, and a legitimate basis for recognizing clades. At best, this assigns double weight a priori to absences in the 'parent' character (because the daughter is always contingent), and at worst is positively misleading. This is the approach that we believe Liu *et al.*[1] may have taken. Reanalysis of their data using 'gapmode = newstate' combined with 'collapse = MinBrlen' settings in PAUP*[2] produced some optimal trees of 130 steps. However, we were still unable to replicate the relationships shown in their Fig. 4, even when varying k between 0 and 10. Rather we either resolved *Diania* in a basal polytomy, or slightly higher in the tree but separated from the arthropods by at least five nodes.

At best, therefore, the position of *Diania* is highly labile and extremely sensitive to the precise methods used. We certainly feel that it is premature to draw conclusions regarding its supposedly pivotal position in the evolution of arthropods. However, our reanalyses do not challenge the more general conclusions of Liu *et al.*[1]: namely that the full complement of arthropod characters were probably acquired piecemeal and possibly convergently. Many closely allied groups exploited successfully some but not all of the characters that typify the arthropod crown group. Only in retrospect do we discern a single, ladder-like trajectory through what was really a much more eccentrically branching bush.
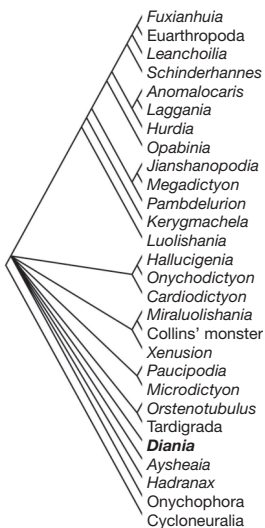

Figure 1 | The strict consensus of 13 most parsimonious trees ($L = 90$) obtained from the published data and settings specified by the authors.

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