An arthropod sphinx

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The Sphinx is an enigmatic monster in Greek mythology that had the body of a lion, wings of a bird, and head and bust of a woman. As the myth goes, the Sphinx guarded the gate to Thebes and would kill anyone unable to answer her riddle. The Sphinx riddle was eventually correctly solved by Oedipus who later became the king of Thebes.

The new fossil—*Miraluolishania haikouensis*—described by Liu et al.^[1] from the Lower Cambrian Chengjiang Lagerstätte qualifies for an arthropod sphinx. *M. haikouensis* not only has a chimera of features that apparently belong to different animals, but also is a frustrating riddle to those who are interested in the early evolution of arthropods. This new trophy from Chengjiang has an annulated, worm-like trunk with a pair of possible antennae and fourteen pairs of clawed, nonjointed appendages. Its basic body plan is thus broadly similar to **onychophorans** (velvet worms). In addition, *M. haikouensis* also bears dorsal spines. These paired dorsal spines are probably homologous to dorsal plates or spines of such legendary fossils as *Hallucigenia*, *Microdictyon*, and *Onychodictyon*, which are informally referred to as **Cambrian lobopods**. Liu et al.^[1] reconstruct *M. haikouensis* as a lobopod animal with uniramous antennae, dorsal eyes, and some degree of tagma differentiation. They also propose that *M. haikouensis* represents a transitional form between more primitive lobopods and **euarthropods** (= pycnogonids + myriapods + crustaceans + insects + chelicerates + pentastomids^[2]). More specifically, they unite euarthropods, *Anomalocaris*, *Opabinia*, *Miraluolishania*, and extant onychophorans in a clade that is characterized by preliminary cephalization and the presence of eyes.

It is clear that living euarthropods, onychophorans, and tardigrades (water bears) form a closely related group—the broadly defined arthropods (or panarthropods)^[3,4], and that Cambrian lobopods are phylogenetically related to the arthropods in the broad sense^[5–9]. But the exact nature of this relationship has been controversial. To illustrate this controversy, we need to introduce the concepts of crown group, stem group, and total group in phylogenetic interpretation^[10]. A **crown group** is the minimal clade that includes all extant members of a group. Thus, crown group arthropods refer to the minimum clade that includes all living euarthropods, onychophorans, and tardigrades

(Fig. 1(a)). A **stem group** is an extinct member that is outside the crown clade in question but has a closer phylogenetic relationship to the crown than to any other crowns. Hence, stem group arthropods are any fossils that are basal to the crown arthropod clade but are more closely related to the crown arthropod clade than to its sister group—the cycloneuralians^[11]. A **total group** is the sum of the crown and stem groups. With regard to the phylogenetic relationship between Cambrian lobopods and euarthropods, the only consensus is that they all belong to the total-group arthropods.

But where is the exact phylogenetic home of Cambrian lobopods within the arthropod tree? Traditional wisdom holds that they are either crown- or stem-group onychophorans (Fig. 1(a))^[5,7]. Recent analyses, however, suggest that Cambrian lobopods are phylogenetically diverse and likely paraphyletic or polyphyletic (Fig. 1(b)); many of them have been interpreted as stem-group euarthropods or stem-group arthropods^[6,8,9]. The interpretation of *Miraluolishania haikouensis* as a transitional form bridging the morphological gap between more primitive lobopods and euarthropods^[1] appears to support the latter scenario (Fig. 1(b)). If so, more detailed morphological study of Cambrian lobopods will certainly help us to improve the phylogeny of arthropods and euarthropod (by providing appropriate out-group control).

Liu et al.'s phylogenetic interpretation of *Miraluolishania haikouensis*^[1] also raises several important questions. First, the grouping of euarthropods, onychophorans, and eyed lobopods would indicate that their eyes are homologous. Recent study of the development of onychophoran eyes shows that this may not be the case^[12]. It remains to see whether genetic regulation of eye development in onychophorans and euarthropods is homologous. Second, if the arthropod tree is littered with paraphyletic lobopods, one should carefully look for lobopodian features or otherwise explain the lack of such features in tardigrades as consequences of miniaturization or phylogenetic distance^[7,9]. The exact phylogenetic relationship of tardigrades, onychophorans, and euarthropods remains to be clarified^[3,13]. But if tardigrades were included in Liu et al.'s analysis^[1], they could place some constraints on the phylogenetic interpretations of Cambrian lobopods as well.

Obviously, more work needs to be done on *Miraluolishania haikouensis* and other Cambrian lobopods. The cladogram presented in Liu et al.^[1] is useful, but it is assembled by visual inspection rather than computerized cladistic algorithm. This makes it difficult to estimate the robustness of the cladogram, to optimize character evolution along the branches, and to evaluate potential homoplasies and secondary losses in the cladogram. For example, it is unclear how well the clade (euarthropods + *Anomalocaris* + *Opabinia* + *Miraluolishania* + extant onychophorans) is supported. The unresolved trichotomy

Fig. 1. (a) A cladogram showing the possible phylogenetic relationship among euarthropods, tardigrades, onychophorans, and cycloneuralians^[3,4,11,13], and illustrating the concepts of crown group, stem group, and total group. Traditionally, Cambrian lobopods (dotted branches) are interpreted as stem- or crown-group onychophorans. † indicates extinct members. (b) Cladogram modified from Liu et al.^[1]. In this cladogram, most Cambrian lobopods (dotted branches) are interpreted as stem-group euarthropods or stem-group arthropods. † indicates extinct members.

at the base of this clade makes an ambiguous statement about the relationship between *Miraluolishania* and onychophorans. However, the limited number of available characters preserved in Cambrian lobopods does not allow a rigorous cladistic analysis. Clearly, there is a need to carefully examine other arthropod sphinxes in order to tell a complete story of arthropod evolution. Liu et al.'s contribution^[1] is important, but it also shows that, for Cambrian paleontologists, the journey to knock out all sphinxes and become the king of the Thebes will be a long one.

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