for investigating the structure of the mandibles (whole limb versus limb base only). In the millipede Oxidus gracilis (a in the figure), Dil is expressed in the distal part of the mandibles, as predicted in ref. 4, indicating their whole-limb structure.

In light of the recent discovery of the Cambrian fossil whose head and trunk appendages were long and leg-like, the whole-limb mandibles of today's myriapods probably represent an ancestral arthropod state. Thus, we have a testable hypothesis: if myriapods and insects are indeed sister taxa, then Dil should also be expressed in insect mandibles. But Panganiban et al. have shown that Dil is not expressed in mandibles of modern insects. To examine whether the absence of Dil is characteristic of the whole insect lineage, we included in our analysis the primitive wingless insect Thermobia domestica, and found that Dil is not expressed in the mandibles of this species (b in the figure); this further suggests that insect mandibles are formed from the limb base and may be similar to the mandibles of adult crustaceans.

Both O. gracilis and T. domestica undergo direct development, where immature stages differ from the adults mainly in the development of the gonads and genitalia. This allows us to correlate directly embryonic changes in Dil expression with structural changes in adult mandibles. In contrast, only crustaceans that undergo larval development have been studied so far. Consequently, the finding that Dil is expressed throughout the mandibles of crustacean nauplius larvae (c in the figure) is not informative because the larval cells expressing Dil do not contribute to the adult structures (as noted in ref. 6). To infer the origins of the mandibles in adult crustaceans, it is necessary to study species that undergo direct development. We therefore included the terrestrial isopod Armadillidium vulgare, a direct developer, in our analysis. We found that crustacean mandibles are indeed composed of a limb base only, as is evident by the lack of Dil expression in ectoderm (d in the figure).

In summary, our data are consistent with earlier predictions24,25 that the arthropod mandible was originally composed of a whole limb and was similar to the present-day mandibles of the myriapods. Further, our data suggest that during arthropod evolution, the mandible structure changed from a whole limb (c in the figure) to a limb base only, the latter type being a shared feature between insects and crustaceans (b, d). This finding has two important implications. First, it argues against the traditional view that insect and crustacean mandibles are fundamentally different; and second, it directly supports the hypothesis that crustaceans, not myriapods, are the sister group of insects. The overall similarity of nervous and visual systems in both insects and crustaceans provides independent support for this hypothesis10. These findings lessen the case for uniting insects and myriapods into Atelocera.

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References