Demise of the Atelocerata?

Maximilian J. Telford and Richard H. Thomas

The relationships among the major lineages of that spectacularly successful group of ‘jointed-legged’ animals, the arthropods, have provided morphologists, embryologists and palaeontologists with over 150 years of unresolved controversy. The arthropods comprise the insects, crustaceans (crabs, shrimps and the like), myriapods (centipedes, millipedes and allies) and chelicerates (the horseshoe crabs and arachnids) and are probably close to more enigmatic groups such as the lobopods (velvet worms). The difficulties found in discerning arthropod relationships typify the more general challenge to biologists studying relationships between groups arising early in the history of animals. Principal among these difficulties is that natural selection, acting over hundreds of millions of years, sometimes causes related animal groups to diverge morphologically while unrelated ones may converge to become superficially similar. Two papers appearing on pages 163 and 165 of this issue1,2, using disparate sources of molecular data, claim to have some of the answers to the question of arthropod relations and, gratifyingly, they broadly agree.

Almost every possible phylogeny of the arthropods has had its adherents, but only three hypotheses have received wide support in recent decades.

A polyphyletic view, championed by Sidnie Manton11, derives three distinct groups of living arthropods from different non-arthropod ancestors. These three groups are the crustaceans, the chelicerates and the Uniramia (the lobopods and the myriapods plus insects, all of which have single-branched legs). The polyphyletic view has recently been widely rejected using both morphological evidence and molecular data. The two other commonly accepted views derive all arthropods from a single arthropod-like ancestor. These are the ‘TCC’ theory3,4,5, which has a group containing the extinct trilobites (T), the crustaceans (C) and the chelicerates (C) separate from the insects and myriapods, and the ‘mandibulate’ hypothesis (a in the figure), linking the crustaceans to the myriapods plus insects (the Mandi-

bula)6, leaving the trilobites and cheli-
cerates as outgroups.

Environment-driven convergence, a problem inherent in morphology-based phylogenetic analyses of the arthropods, has been considered. Gene sequence data have been widely seen as a panacea for this problem as changes in gene sequences

a. A phylogenetic tree showing the popular mandibulate hypothesis of arthropod relationships which links the myriapods and insects with the crustaceans as closest sister-group.

b. A phylogenetic tree showing the close relationships between the insects and crustaceans supported by two papers in this issue1,2. Brown bars indicate shared derived morphological traits of the insects and crustaceans which support this link: (1) mandible formed of a fused limb basal; (2) detailed similarities in the ontogeny of the nervous system; (3) detailed similarities in the cellular composition of the eyes and their connections to the brain. Yellow bars indicate characters inferred to be shared by insects and myriapods through convergence due to terrestrial life: (4) urinarian limbs: (5) tracheal breathing; (6) malphigian tubules for nitrogen excretion; (7) lack of appendages corresponding to the second antennae of crustaceans. According to this hypothesis of arthropod relationships, both the myriapods and crustaceans might be saraphyic.
are thought to be largely unaffected by the environment, with the result that similarity of DNA sequence more accurately reflects relationships. The reality of sequence evolution is more complex than this statement suggests, making difficult the retrieval of phylogenetic signals from such ancient divergences. Friedrich and Tautz2 have analysed the largest arthropod DNA sequence data set so far from the small and large subunits ribosomal RNA genes of a carefully selected range of taxa. Importantly, they have also taken pains to test for and control several factors known to bias the recovery of the correct phylogeny.

Boore et al.3 use molecular data in a manner more familiar to traditional systematists. They have looked for gene rearrangements within the small mitochondrial genomes of animals (37 genes, usually) and used gene boundaries as characters to produce a phylogenetic tree. These rearrangements occur only rarely and are considered to be immune to selective pressures. The vast number of potential rearrangements makes identical novel arrangements in unrelated taxa extremely unlikely. Events such as these provide ideal characters for phylogenetic analysis. Both studies provide further strong support for a monophyletic Arthropoda, a concept particularly strengthened by the novelty of the data of Boore et al., who also tentatively include the lobopods in this assembley.

The one grouping common to virtually all previous schemes relating the arthropods is the close relationship of the myriapods and insects; a group united by the common possession of several adult characteristics and often referred to as the aterocerates. The existence of the Ateocerata is disputed by the study by Friedrich and Tautz, who suggest that it is the crustacea and not the myriapods that are the sister group of the insects (incidentally placing the origin of the myriapods earlier than their fossil record suggests) (b in the figure). Boore et al. also present data that support this conclusion. Their interpretation of their data is cautious, however, and they do not separate the traditional aterocerate clades on their summary diagram. The closeness of the insects and crustacea had been supported by some, but not all, previous molecular analyses.3-9

If the close relationship of the crustaceans and insects is accepted, features shared by myriapods and insects, but not the crustaceans, must be shown either to be shared as a result of convergence, most likely because both are terrestrial groups, or to be primitive characteristics secondarily lost in the Crustacea. The following characteristics have traditionally been used to unite the myriapods and insects: unbranched legs, a tracheal system, malphigian tubules, absence of appendages corresponding to the second antennae of crustaceans, and a mandible composed of a whole limb (crustacean mandibles are formed from a limb base). Friedrich and Tautz argue that the first four of these characters are shared through convergence due to both groups being terrestrial; structures similar to the first three are even found in some terrestrial arachnids. Finally, recent gene expression data argues against a whole limb mandible in the insects. The gene Distalless, generally expressed in the tip of insect appendages, is not expressed in the insect mandible.10 This suggests that the appendage tip is modified and that the insect mandible is, in fact, similar to that of the crustaceans. Indeed, Kukalová-Peck7 claims that a limb-base mandible is present in all arthropods.

Other lines of evidence support a sister group relationship between insects and crustaceans11. Nervous system development in the two groups is strikingly similar,12 with no equivalent similarity yet seen in myriapods or chelicerae and, again on a cellular level, crustacean and insect eyes are more similar to each other than either are to those of myriapods or chelicerae.12

Despite their convincing congruence, these results are unlikely to be immediately generally accepted and many questions remain. More needs to be done to pin down the position of the lobopods, as well as the positions of other less well known groups such as the tardigrades and pycnogons (sea spiders). The monophyly or otherwise of both the myriapods and the crustacea also remains uncertain. The position of the chelicerae is still not clear and will determine whether a revised concept of the Mandibulata survives. It seems unlikely that we will have to wait another 150 years for answers to these questions and with them will come a much improved understanding of the evolution of arthropod body form.

**Maximilian J. Telford and Richard H. Thompson are in the Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.**

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12. The sap also rises

All plants are pumps. They take in water through their roots and transpire it as vapour from their leaves. How do they lift the water? Capillary rise is limited to a metre or so, and an atmospheric suction pump cannot lift water above 10 metres; yet trees can grow 100 metres high. Furthermore, aquatic plants cannot use either mechanism, but still thrive; and even land plants survive flooding.

Daedalus reckons that plants move their internal fluids just as we do: by mechanical pumping. Their internal channels form a distributed peristaltic pump, driven by the ceaseless shaking of the wind. On this view, the galvanic wave of a wind-blown field of corn, the ceaseless rustling of forest leaves, even Wordsworth's daffodils "tossing their heads in sprightly dance" have stern biological purpose in their movements.

This theory is supported by a recent finding that many commercial plants, such as tomatoes, aubergines and cucumbers, benefit from the repeated bending of their stems by stroking. They develop a darker green, and grow more compactly, as if the added massage saved them from having to grow extended fronds to catch the wind.

DREADCO gardeners are now testing this notion. They are shaking selected plants in a range of frequencies and vibrational modes to discover the most effective pumping regimes. Control plants are being clamped rigidly immobile to see if their growth is stunted. Once the technique has been optimized, vibro-horticulture should speed the sap through crops of all kinds, boosting their metabolism and growth.

For the smaller plants, a standard laboratory shaker should be ideal. Trays of seedlings could easily be vibrated at whatever frequency and amplitude optimized their growth. Very large single plants, such as trees, might also be driven mechanically by robotic hydraulic rams under programmed control. But for crops such as corn, maize and oats, wind seems the best shaker. A field could be set with big baffle to funnel and direct it, spring-loaded vanes to release a stream of vortices downward, or huge tuned pipes to resonate at the best frequencies. As the crop matured, these could be adjusted to maintain the optimum pattern of vibration.

Aquatic plants would be easier to vibrate. Daedalus is designing special stirrers for watercress beds, and a central wave machine to spread waves out into a rice paddy-field. He also advocates the planting of seaweed on breakwaters and sea defences. The rougher the waves, the more the weede would grow to damp them.