the density of the packing.

But until someone extends Hales's result to higher dimensions, we have no proof that any packing in a dimension greater than three is optimal. ☐

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Evolutionary biology

Origin of the spider's head

Michalis Averof

Comparing the structure of the head between different classes of arthropod has been controversial and often frustrating, yet it can tell us about the origins and relatedness of these different classes. The heads of crustaceans, myriapods and insects contain a characteristic set of at least five segments, which are thought to be homologous among these groups. But the morphology of chelicerates — which include spiders, scorpions, mites and horseshoe crabs — gives no good clues about the relationship of their segments to the head segments of other arthropods. Now, however, studies based on the expression of developmental genes by Damen *et al.*[1] and Telford and Thomas[2], published in *Proceedings of the National Academy of Sciences*, provide convincing evidence for previously unexpected homologies.

Chelicerates do not have a body region that could be obviously characterized as a head. Their bodies are subdivided into two portions — the prosoma (front) and the opisthosoma (back). The prosoma contains segments that bear the chelicerae (spider's fangs), pedipalps and four pairs of walking legs. It carries the main feeding, sensory and locomotor apparatus and, in a functional sense, acts as a head and thorax combined (Fig. 1). But from its morphology, we have so far been unable to find clear evidence for the relationship between this region and the segments of other arthropods.

Damen *et al.*[1] and Telford and Thomas[2] now provide evidence that comes not from the morphology itself, but from the genes that generate that morphology. They studied the Hox (homeotic) genes, which are known to specify the identity of the different types of segment within the body of insects[3]. These genes are particularly attractive for distant evolutionary comparisons of segment specialization[3–5] because their function seems to be widely conserved (in animals as diverse as arthropods, vertebrates and nematodes), and their activity is faithfully reflected by restricted expression in particular regions of the body. Different classes of arthropod have almost identical sets of Hox genes[3,5], but these are expressed differently in animals that have distinct patterns of segmental specialization[4–6]. Similarities in the expression of these genes have been used as evidence for a common origin (homology) of the corresponding specialized types of segment[4].

Damen *et al.* and Telford and Thomas report the identification and expression of Hox genes in two different members of the Chelicerata, a spider[1] and a mite[2]. The results from the two species are congruent and point to the same conclusion — that expression of Hox genes in the prosoma of chelicerates is similar to the expression of homologous genes in the head segments of other arthropods. This suggests that the entire prosoma of chelicerates may correspond to a head (Fig. 2). Indeed, the similarities are so striking that the authors do not hesitate to suggest specific one-to-one homologies between segments of the prosoma and the head segments of other arthropods.

Most convincing are those of the most anterior parts of the body, between the cheliceral segment and the first antennal (deutocerebral) segment, and between the pedipalpal and the second antennal or intercalary (tritocerebral) segment. In more

Figure 1 **The prosoma of a horseshoe crab (ventral view). The mouth is surrounded by legs bearing prominent endites (arrowheads), a characteristic associated with feeding. Damen *et al.*[1] and Telford and Thomas[2] propose that the prosoma corresponds, in evolutionary terms, to the head of other arthropods such as crustaceans and insects.**

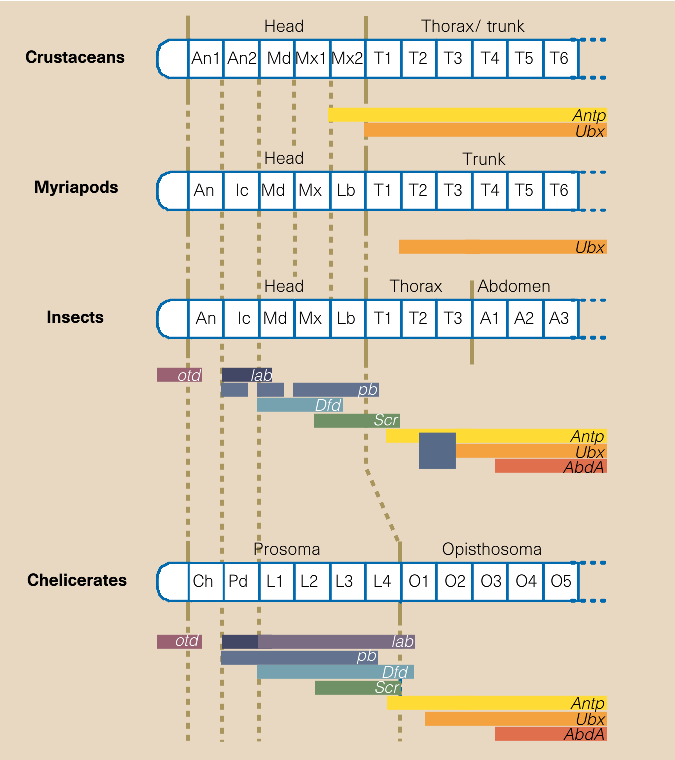

Figure 2 **Expression of Hox genes and inferred relationships among anterior body segments in different arthropods. Arthropods express almost identical sets of Hox genes in different regional domains (colour coded for homologous genes)[1–6,9]. Although there are some variations within arthropod classes, the expression domains shown are those thought to be typical or ancestral for each class. The homologies between insect, crustacean and myriapod segments are based on morphological evidence.**

posterior segments, the assignment of homologies becomes more doubtful, as the patterns of morphological diversification (for example, the distinction between prosomal and opisthosomal segments in chelicerates versus head and trunk/thoracic segments in other arthropods) do not correspond so precisely between different arthropods. Nevertheless, it seems likely that the leg-bearing region of the prosoma is related to the posterior head (gnathal) region of crustaceans, myriapods and insects, and that the limbless opisthosomal region might correspond to the thorax or trunk of the other arthropods.

Apart from these similarities, some differences in the expression of Hox genes can be found in the transitional region around the posterior part of the head/prosoma and the anterior part of the trunk/opisthosoma. The significance of these differences is not yet clear. Shifts in the expression of Hox genes have been associated with evolutionary changes in the morphology and function of particular types of segment[6], but this is not easy to assess in animals with widely divergent morphology. Cambrian fossils show that there were different patterns of segmental specialization in that region of the body[7,8], suggesting that segmental identities in that region have not stayed unchanged.

Comparing patterns of gene expression provides a new way to study morphology. Although there is no reason to assume that data from gene expression will be superior to anatomical data — they both reflect different aspects of the same reality, the evolution of genetically encoded morphological features — these comparisons are attracting much interest today. The hope is that this so-far-unexploited source of information might help us to resolve some of the tricky or unexpected relationships that remain concealed by the external appearance. Chelicerates and the other arthropods are separated by about 550 million years of evolution. During that time, crustaceans, myriapods and insects have incorporated a number of anterior segments into their head and modified some of the corresponding appendages to function as jaws. The new data indicate that spiders make surprisingly different use of these appendages — they use them for walking. □

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Oceanography

Vents at higher frequency

Cindy Lee Van Dover

The deep-ocean research community is a small one, but the rate at which central dogmas are toppled must be one of the highest in science. Because of the relative inaccessibility of the abyssal environment, general ideas about deep-ocean processes are often advanced on the basis of only a few local or regional observations. As access to the sea floor increases with developing technologies and oceanographic infrastructures, the science becomes ever more volatile and exciting. An example of work that causes us to think again comes in the paper by German *et al.* on page 490 of this issue[1] — there the authors provide remote-sensing data that challenge the current model correlating frequency of hydrothermal vents with the spreading rate of mid-ocean ridges.

When hydrothermal vents were first discovered along submarine mountain ranges in the eastern Pacific, geologists pointed to the obvious link between these hot springs and volcanism. The ensuing searches for vents concentrated on thermally swollen crust of local topographic highs along the mid-ocean ridge axes. The first vents were found on fast-spreading centres — the East Pacific Rise and Galapagos rift — where the ocean plates move apart at spreading rates of 50–80 mm yr^{-1}. At the time, many scientists expressed doubt that hydrothermal activity could be supported on the Mid-Atlantic Ridge, where spreading is much slower (20–40 mm yr^{-1}) and the thermal and volcanic budget is considerably lower. Peter Rona and his colleagues proved this idea wrong in the mid-1980s with the discovery of the so-called TAG site[2], which still ranks as one of the largest and most persistent hydrothermal sites yet discovered on the sea floor.

Ten years later, Baker *et al.*[3] reported the results of sampling hundreds of kilometres of spreading centres moving at various rates — slow, intermediate, fast and ultrafast (>80 mm yr^{-1}). They used vent-prospecting techniques based on two- and three-dimensional mapping of the thermal, optical and chemical anomalies in the water column that are associated with near-bottom, black smoker plumes, and concluded that plume incidence increases linearly with spreading rate (Fig. 1). This model predicts that the ultraslow end-member exemplified by the southwest Indian ridge (14 mm yr^{-1}) should have no more than one vent site every 200–300 km. German *et al.*[1] have now tested this prediction with extensive plume surveys and find it to be off by more than a factor of three.

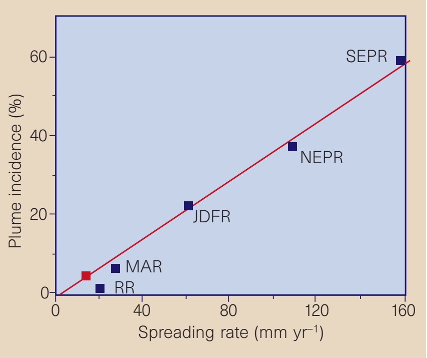

Figure 1 **Incidence of hydrothermal plumes plotted against spreading rate of ocean ridges, where plume incidence is the percentage of ridge-axis length that is overlain by significant plume anomalies in the water column. The red square is the predicted value for extremely slow-spreading ridges (<15 mm yr^{-1}) such as the southwest Indian ridge. This model, based on spreading rate alone, underestimates the frequency of hydrothermal venting on the southwest Indian ridge by three times, as German *et al.*[1] now show. RR, Reykjanes ridge; MAR, Mid-Atlantic Ridge; JDFR, Juan de Fuca ridge; NEPR, northern East Pacific Rise; SEPR, southern East Pacific Rise. (Modified from ref. 4.)**

In explaining the higher-than-expected incidence of hydrothermal vents on extremely slow-spreading ridges, German *et al.* implicate tectonism as the process that allows sea water to penetrate to deep heat sources and sustain hydrothermal activity at spatial frequencies that are higher than those predicted from spreading rate alone. To an observer in a submersible, hydrothermal activity at fast-spreading centres is patently influenced by volcanism: basalt lavas at the spreading axis are barely fractured and fissured by tectonics before the next incidence of combined tectonism and volcanism refreshes the surface and incrementally spreads the plates apart. On slow-spreading centres, it is the deep ravages of tectonism that are most obvious, while spreading increments involving volcanic eruptions are infrequent.

The discovery of numerous vents on the southwest Indian ridge opens the door for site visits by geologists who wish to understand controls on hydrothermal activity, and by geochemists intent on parsing and integrating estimates of thermal and chemical fluxes through hydrothermal systems. Biologists, too, will jump at a chance to visit these vents, with the prospect of discovering new