the nervous system are derived from successive segmental neuromeres. The deutocerebrum innervates the antennae of insects, the anterior antennae of crustaceans and the chelicerae of spiders and scorpions[3]. But the real meat of the endless dispute has always concerned the nature of the appendage-less frontmost part of the brain, the protocerebrum. Is it some sort of non-segmental leftover inherited from the very earliest animal ancestors of the arthropods[6] (a mystical structure called the acron in the literature), or does it represent the neuromere of a once appendage-bearing anterior segment[7]?

Two lines of evidence have been put forward in support of the existence in ancient arthropods of a protocerebrum with an appendage. First, all extant arthropods (except pycnogonids) possess a small, appendage-like outgrowth of the body which lies just in front of the mouth and is called the labrum. Confusingly, the labrum is not innervated by the protocerebrum (fanning the flames of the dispute); however, in the embryo it starts off right at the front of the animal, and migrates backwards during development. If the labrum represents a highly modified appendage, then its anterior position in development might indicate that it is the long-sought limb of a protocerebral segment.

Second, there is the fossil evidence of the earliest arthropods from 530–490 million years ago. Many of these early arthropods possessed a pair of large, grasping or branched appendages, known as the 'great appendage', found at the anterior of the head. Indeed, a phylogenetic reconstruction published a few years ago suggested that the great appendage was innervated from the protocerebrum[7]. We cannot investigate the nervous system of a fossil, however, and this reconstruction has been hotly disputed, with many researchers preferring to see the great appendage as equivalent to the antennae of insects and crustaceans[8].

However, if, for the sake of argument, we accept these two lines of evidence at face value, we could reasonably conclude that the protocerebral appendage started out as a great appendage that has subsequently shrunk to the small nub of tissue we now see in most living arthropods as the labrum.

The wider significance of the conclusions of Maxmen *et al.*[2] now becomes clear. The presence of a bona fide appendage on the pycnogonid protocerebrum (and the absence of a labrum) gives support to the protocerebral origin of the great appendage and to the idea that the labrum is the remnant of this ancient appendage. More excitingly, it implies that the pycnogonids are extraordinary living fossils, retaining an organization of their head that all other living arthropods lost hundreds of millions of years ago.

How, then, might we test these new results[2]? First, we would like a way to verify the association of chelifore with protocerebrum. One way to achieve this would be to use domains of gene expression as segmental markers. Hox genes are especially useful in this regard, as they have relatively stable domains of expression along the anterior–posterior axis of arthropods. This approach has been used successfully to line up the head segments of arachnids and insects, for example[3]. Thus, the anteriormost expression of the Hox gene *Deformed* (*Dfd*) marks the fourth segment in both arachnids (Fig. 1a) and insects. Because the arachnid/insect first segment has no associated appendage, this *Dfd* expression in the fourth segment lines up with the third appendage. If the traditional interpretation of pycnogonid appendage assignment is correct, the anteriormost appendage — the chelifore — will be associated with the second segment and, as in arachnids, the fourth-segment expression of *Dfd* will therefore be seen in the third appendage of the pycnogonid larva (Fig. 1b). But if Maxmen *et al.* are correct, the chelifore comes from the first segment and, counting backwards, *Dfd* expression in the fourth segment will therefore be seen in the fourth appendage rather than the third (Fig. 1c).

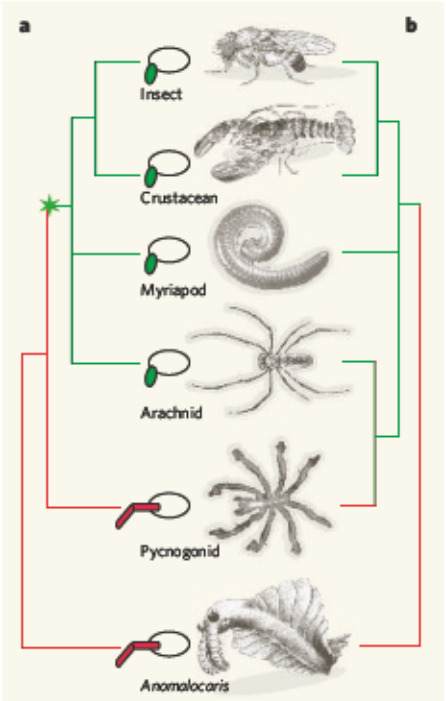

Figure 2 | Possible evolutionary position of pycnogonids and interpretation of Maxmen and colleagues' results[2]. **a**, If pycnogonids branched off before the appearance of insects, crustaceans, myriapods and arachnids, we can interpret their protocerebral chelifores (red) as equivalent to the supposedly anterior great appendage of fossil groups such as *Anomalocaris*. The labrum (green) would have evolved in the common ancestor indicated with a star. **b**, But if pycnogonids are related to arachnids, then either their protocerebral chelifores could be an atavistic re-evolution of the great appendage, or the labrum must have evolved independently in arachnids and the other three taxa. Both of these latter hypotheses are contentious, and could raise doubts about the conclusions of Maxmen and colleagues.

50 YEARS AGO

It is well known that myxomatosis has caused a high mortality among wild rabbit populations in most parts of England and Wales... Where it has been possible to make accurate observations, a mortality-rate of about 99 per cent was found... Only in one part of the country, the Sherwood Forest area of Nottinghamshire, have attenuated strains of the virus been found in rabbits. In this area estate workers and the Ministry's field-officers noted from April 1955 onwards the presence of an unusual number of individuals that appeared to be recovering... It is emphasized that the attenuation of the myxoma virus in part of Sherwood Forest is an isolated case, affects only a relatively small area, and calls for an increase rather than a slackening of efforts to destroy surviving rabbits.

From *Nature* 22 October 1955.

100 YEARS AGO

Field Book of Wild Birds and their Music — This is a very pretty little book, with many charming illustrations of American singing-birds, and numerous attempts to represent their songs in our musical notation. It would seem as if the songs of American birds lent themselves more readily than those of our European species to such notation, for this is by no means the first attempt of this kind which has recently been made on the other side of the water. The present reviewer is under the disadvantage of not having heard these birds in their native land, and is quite ready to believe that Mr. Mathews's musical notations may give an American the vague idea of what his birds sing; at the same time, as one whose knowledge of music is even older than his knowledge of birds, he must emphatically express a hope that British ornithologists will not imitate their American brethren in trying to render our familiar songs on this system... by far the greater number can only be represented in the amusing way in which Mr. Mathews has noted the song of the bobolink — by a cloudy jumble of notes and lines... which suggests a flute-player gone mad.

From *Nature* 19 October 1905.

50 & 100 YEARS AGO