Figure 4 Model of velocity as a function of time owing to damage from the Landers rupture, the Hector Mine shaking, and the combination of the two compared with observations. Shown is healing as a logarithm of time[10], although details just after each event and extrapolating into the future are not well constrained. The velocity before the Landers earthquake was not measured.

inferred from fault-zone-guided waves on the scale of a few hundred metres[4].

Previously we showed that fault zones heal[5], and here we have shown that the combination of shaking and static stress reduces the modulus of a recently broken fault zone. This probably indicates that the strength of the fault was reduced, which could trigger earthquakes. Our observation thus may provide a direct measurement of the missing connection between shaking and the facilitation of distant aftershocks[20,21]. Regional clustering of earthquakes is another plausible result of one big earthquake weakening the regional set of faults around it, either as an anomalous activation of a region[22] or as the progression of ruptures along a fault, with the shaking modulated by directivity[23].

Another implication of our result is that existing friction laws may need improvement. Currently, friction is modelled simply (or not so simply) as a function of a state variable, which is the history of sliding, and current sliding rate of a point on a fault plane[24]. If shaking can significantly reduce strength, it may also help to explain the puzzle of aftershock occurrence very near the mainshock fault plane, which strikes where the Earth has been strongly shaken but where the regional stress is reduced. Shaking-induced weakening also may be involved in the progression of rupture during earthquakes, because strong shaking is likely to precede the arrival of the rupture front. □

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Head and backbone of the Early Cambrian vertebrate *Haikouichthys*

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Agnathan fish hold a key position in vertebrate evolution, especially regarding the origin of the head and neural-crest-derived tissue[1]. In contrast to amphioxus[2], lampreys and other vertebrates possess a complex brain and placodes that contribute to well-developed eyes, as well as auditory and olfactory systems[3].

These sensory sytems were arguably a trigger to subsequent vertebrate diversifications. However, although they are known from skeletal impressions in younger Palaeozoic agnathans[4], information about the earliest records of these systems has been largely wanting. Here we report numerous specimens of the Lower Cambrian vertebrate *Haikouichthys ercaicunensis*, until now only known from the holotype[5]. *Haikouichthys* shows significant differences from other fossil agnathans: key features include a small lobate extension to the head, with eyes and possible nasal sacs, as well as what may be otic capsules. A notochord with separate vertebral elements is also identifiable. Phylogenetic analysis indicates that this fish lies within the stem-group craniates. Although *Haikouichthys* somewhat resembles the ammocoete larva of modern lampreys, this is because of shared general craniate characters; adult lampreys and hagfishes (the cyclostomes if monophyletic[6,7]) are probably derived in many respects.

The putative Early Cambrian agnathan *Haikouichthys*, from the Chengjiang Lagerstätte[8] near Kunming, Yunnan, was only known from a single, incomplete specimen. Although its vertebrate affinities have been widely accepted[9,10], many of the conclusions about its anatomy and thereby its phylogenetic position are regarded as 'highly provisional'[11]. The discovery of more than 500 specimens, from a locality near Haikou, reveals a series of new and unexpected features that imply a major reconsideration of several features of early agnathan evolution.

Most notable in this respect is the identification in at least 300 specimens of a small (usually less than 1 mm in length) lobate extension at the anterior end of the animal (Fig. 1a–d). It is separated from the rest of the head by a slight constriction. Its most conspicuous feature is a pair of dark oval stains, interpreted as eyes. Although an approximately circular area in some specimens may indicate the lens, this feature is too inconsistent to be reliable. In a few specimens (Fig. 1e, g) the position of an eye is marked as a concave impression, consistent with it having a scleral layer. In life, the eyes may have been relatively flat, although the quality of preservation does not allow inferences on the presence of extra-ocular muscles. The upward direction of the eyes and their position on the anterior lobe suggests, however, that their mobility may have been restricted. Between the eyes is a median structure, often paired and preserved in a similar manner to the eye stains. This may represent part of the olfactory organ, possibly the nasal sacs (Fig. 1a–d). An alternative interpretation, that these structures represent the pineal/parapineal complex[12], is considered less likely. This is because of their relative sizes, position with respect to the eyes, paired nature, and style of preservation suggesting relatively tough tissue. Along the anterior edge of this lobate extension to the head there is a pair of arcuate structures, meeting about a notch that may define the position of a median nostril (Fig. 1a–d). Typically the arcuate structures have relief, and in life were apparently plate-like and possibly composed of cartilage. Other than the plates, no other part of the anterior lobe appears to have been reinforced. More posteriorly, however, the next region of the head is often heavily pervaded by diagenetic mineralization, probably originally sulphides but now oxidized. In the holotype an attempt was made to reconcile this mineralization with the organization of the cranial cartilages seen in the lampreys[5]. The distribution of this mineralization in the new material shows considerable variation and makes this comparison problematical. There is, however, some consistency in the expression of a pair of sub-circular areas, and these may represent the otic capsules (Fig. 1a, b), although no internal structure is evident.

The mouth is not clearly visible, but a ventral recessed area immediately behind the anterior lobe may indicate the position of the oral opening. Another newly observed feature is a series of more or less square-shaped structures extending posteriorly within the main dorsal region of the head and anterior trunk. These are sometimes connected by a broad, dark strand. This feature is interpreted as a series of separated vertebral elements (arcualia), associated with the notochord (Fig. 1e–l). The shape of the individual vertebral elements is somewhat variable. They may be bifid or arched, and in some cases appear to have encompassed the entire notochord. Up to ten such vertebral elements have been identified, and it is likely that the series extended further backwards, but it is obscured by the overlying impressions of the trunk myomeres. The original composition was possibly of cartilage, and occasional diagenetic mineralization may reflect some degree of calcification. The last noteworthy feature that is not apparent in the holotype is lamellate regions located between the branchial supports on the lower side of the head region. These most probably represent the gills, and on occasion are delimited by boundaries that suggest an original pouch-like structure (Fig. 1e, g, i–l). The entire branchial area generally has a much rougher texture than the remainder of the head, from which it is clearly delimited.

In other respects the new material of *Haikouichthys* largely confirms the earlier observations[5]. The more complete specimens suggest that the posterior part of the trunk tapered evenly (Fig. 1f, h, j, l). Although preservation of the caudal region is poor, there is no evidence for a caudal fin. The presence of a dorsal fin and what appears to be a ventral fin-fold is confirmed, although unequivocal evidence of the latter being paired is not available (Fig. 1f, h, j, l). In the dorsal fin the associated fin-rays are only occasionally visible, perhaps owing to the original thickness of the dorsal fin, but as in the holotype they appear to be anteriorly tilted. The myosepta are well defined, and at the posteriorly directed flexure of the myomeres some specimens show repeated areas of positive relief. Additional details are not visible, but if these correspond to a set of underlying gonads[5] (Fig. 1j, l) then this may indicate a primitive metameric arrangement reminiscent of amphioxus. A dark strand running posteriorly on the lower side of the trunk may represent the intestine. There is some evidence that the anus was sub-terminal, thus defining a short post-anal region (Fig. 1f, h, j, l). In the head region the branchial arches are confirmed as a series of posteriorly recurved structures, each apparently composed of a single unit (Fig. 1e, g, i, k). The exact total is equivocal because of variable preservation, but it is most probably seven or eight.

Haikouichthys was evidently a swimmer, although its degree of activity is conjectural. We note, however, co-occurrence of this fish with other pelagic taxa such as *Xidazoon*, and the relative scarcity of benthic forms. The specimens may have been buried alive, possibly as a result of storm-induced burial. Most specimens were collected from a series of graded beds consisting of a lower sand/siltstone unit (about 3 mm thick) and an overlying mudstone, up to 50 mm thick. The typical occurrence is close to the boundary between the two units, and 'shoals' of specimens often show a preferred orientation. Specimens tend to occur in bed-parallel orientation, but where buried obliquely the portion in the mudstone is usually much better preserved than that in the adjacent silty unit.

The new material of *Haikouichthys* shows that our knowledge of the earliest agnathans has been incomplete, with the implication that in several respects the cyclostomes, although almost unchanged since the Carboniferous[13], are in fact much derived. In particular, the anterior lobe with its eyes (and possible olfactory organ) has no direct counterpart in the other early craniates. There is, however, a possible similarity in the anterior position of the prominent eyes of conodonts[14] and the Ordovician arandaspids[15], although in the latter group this feature has been interpreted as a specialization[16]. Anteriorly located eyes are also known in some of the 'naked' fossil agnathans, most notably *Jamoytius*[17] and probably also the anaspid-like fish *Euphanerops*[4]. If this condition of anterior eyes is primitive to vertebrates, it may indicate derivation from the frontal eye of an amphioxus-like ancestor[18], although this would entail various changes including their location on a stable platform and the development of a balancing mechanism[19], which in the form of a

correlated vestibulo-ocular system represents a key step in vertebrate evolution[20]. It also suggests that the more usual posterior position of the eyes is a result of rostral growth, perhaps in response to the increase in size of the olfactory organ. The more tenuous identification of the olfactory organ in *Haikouichthys* makes its phylogenetic role more speculative, but if correctly identified its

position and size is more comparable to that seen in lampreys, and to some extent hagfish, including fossil representatives[13], than in most other agnathans and the gnathostomes. The branchial arches of *Haikouichthys* are unlike the intricate branchial basket of lampreys. Their apparently simple structure is somewhat reminiscent of the arrangement seen in the gnathostomes, especially regarding
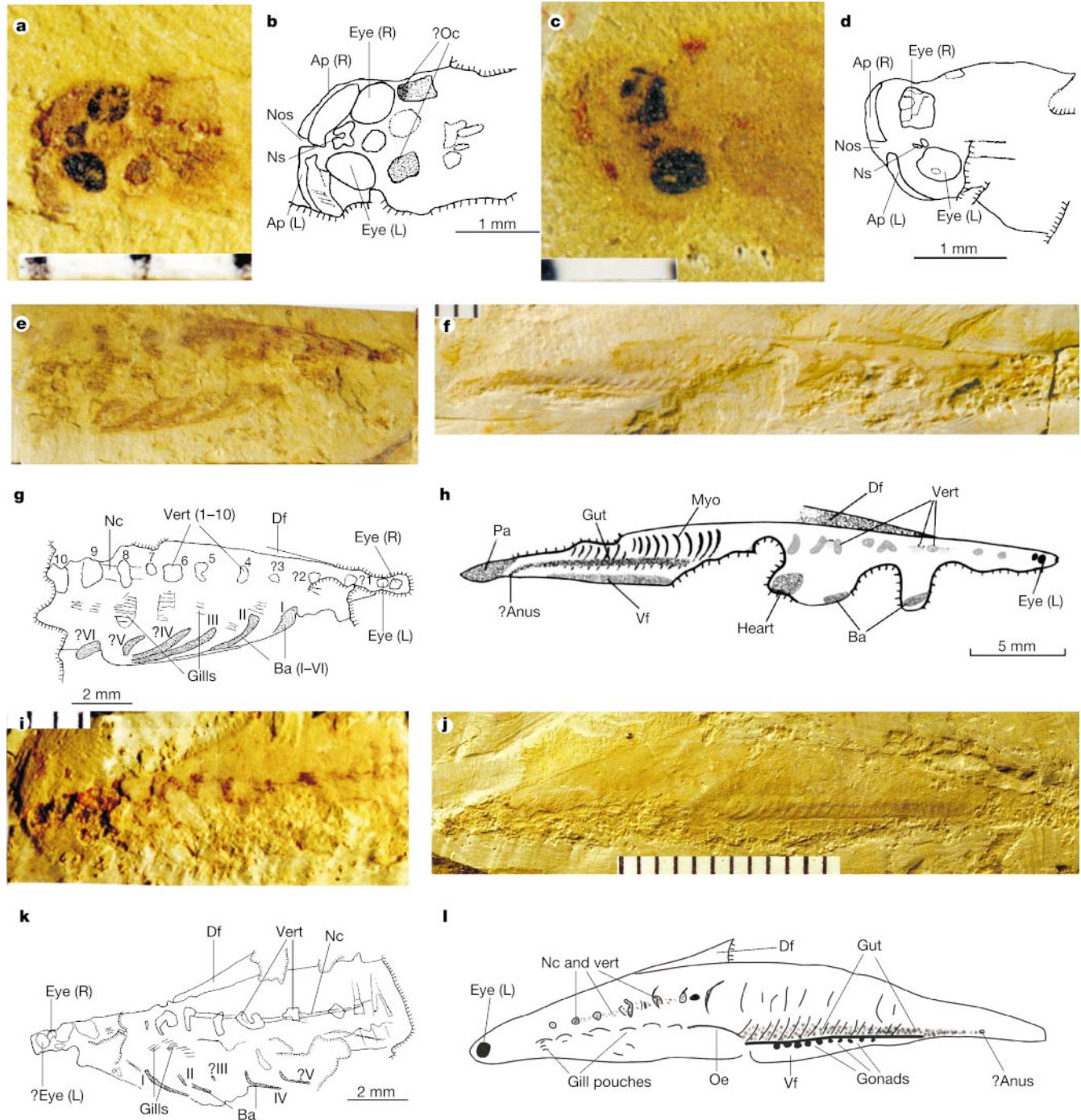
Figure 1 *Haikouichthys ercaicunensis* from Haikou, Kunming, Yunnan. **a–d**, Details of the head, emphasizing its anterior structures; preservation is dorso-ventral. **a**, **b**, ELI-0001003 (273). **c**, **d**, ELI-00010013 (323). **e**, **g**, **i**, **k**, Details of the anterior, emphasizing the notochord with associated vertebral elements and branchial arches. **e**, **g**, ELI-0001015 (12B), anterior to the right. **i**, **k**, ELI-0001020 (8), anterior end to the left. **f**, **h**, **j**, **l**, Nearly complete specimens. **f**, **h**, ELI-0001002 (191), anterior end to the right. **j**, **l**, ELI-0001001 (172), anterior end to the left. Ap, anterior plates; Ba, branchial arches; Df, dorsal fin; Myo, myosepta; Nc, notochord; Nc and vert, notochord with vertebral elements; Nos, nostril; Ns, nasal sacs; ?Oc, otic capsule; Oe, oesophagus; Pa, post-anal tail; Vert, vertebral elements; Vf, ventral fin-fold. L, left; R, right.

lower units known as the ceratobranchials and hypobranchials. This suggests that the arrangement of articulated branchial elements in gnathostomes retains some primitive characters, even though it is clear that the origin of the jaw entailed developmental rearrangements[21–23]. The widely spaced vertebral blocks probably acted as supportive structures for the notochord, and as such are reminiscent of the arcualia of adult lampreys. In *Haikouichthys*, however, the vertebral units are larger and more regularly spaced.

The possession of eyes (and probably nasal sacs) is consistent with *Haikouichthys* being a craniate, indicating that vertebrate evolution was well advanced by the Early Cambrian. Although evidently a jawless fish, its precise phylogenetic position is still speculative because this fish shows a puzzling mixture of characters contrary to some previous expectations. Nevertheless, several features of *Haikouichthys*, including what may be metamerically arranged gonads and the anteriorly located eyes, suggest that 'the first fish' may be best regarded as a stem-group craniate (Fig. 2a). Specific connections to other agnathans include the vertebral elements and probable nasal sacs. Despite some similarities to lampreys, in certain respects these living agnathans are probably highly derived.

Until now the other Chengjiang agnathan, *Myllokunmingia*, is only known from a single specimen recovered from a separate locality at a slightly higher stratigraphic level within the Qiongzhusi Formation[5]. Its most obvious differences from *Haikouichthys* are possession of fewer gill pouches (five or six), absence of curved branchial supports, the presence of possible exhalant chambers, and a more anterior extension of the dorsal fin that lacks obvious fin rays. It is clear that the Chengjiang Lagerstätte offers unique insights into early deuterostome diversifications[5,24–26], and continued

excavations are expected to extend further our knowledge of their earliest evolution, including that of the vertebrates. □

Methods

Phylogenetic analysis

The analysis, based on the data of ref. 27, was done by using the phylogenetic package HENNIG86 1.5 (ref. 28) and the matrix and tree editor TREE GARDENER (ref. 29) with a data matrix of 17 taxa (4 extant, 13 fossil, cephalochordates as the outgroup) and 115 morphological and physiological characters (see Supplementary Information). All characters are coded binarily as present/absent. Non-applicable characters are coded as 0 and missing data are coded as '?'. Equally, most parsimonious trees were obtained by using the implicit enumeration* (ie*) command.

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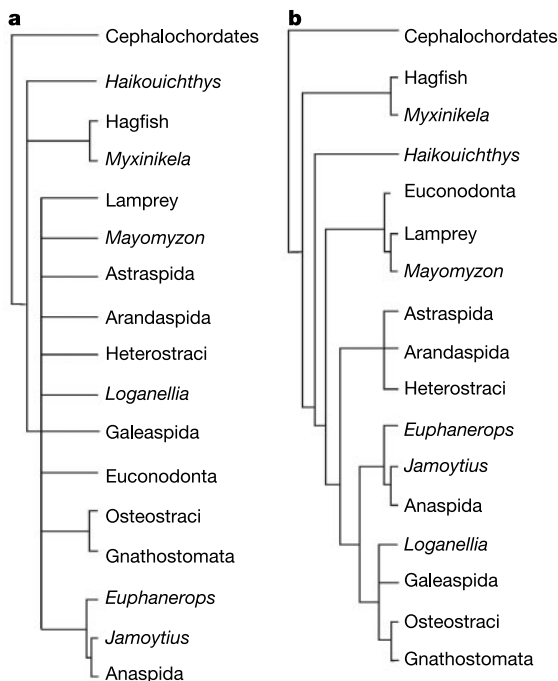
Figure 2 Phylogenetic analysis. **a**, Strict consensus of 23 equally parsimonious trees (length 177 steps; consistency index 0.64, retention index 0.64). *Haikouichthys* appears here in a trichotomy with hagfishes and all other vertebrates (that is, one possibility is that it is a stem craniate), but this is largely because of the inferred presence of metameric gonads. **b**, Strict consensus of four equally parsimonious trees (length 175, consistency index 0.64, retention index 0.64) obtained when the character 'metameric gonads' (114) is inactivated. *Haikouichthys* appears here as the sister-group to all other vertebrates except hagfishes, like *Myllokunmingia* in the analysis of ref. 5.