Figure 4 a. Domain-averaged ratio of stress to yield strength $\tau/\alpha$ for $n = (3-8) \times 10^5$ for the last three characteristic cycles illustrated in Fig. 1. This plot clearly shows the stages within model quake cycles. Large events are indicated by sharp peaks in $\tau/\alpha$. Also shown are the size–frequency statistics for the early stages of quake cycles ($\tau/\alpha < 0.47$); b, and the later stages ($\tau/\alpha > 0.47$). c, Immediately following large events, $\tau/\alpha$ decreases rapidly as the weakest faults from a new population fail. The stress and strength continue to self-organize as fluctuations increase; the emergence of a critical state is marked by a levelling off or decrease of $\tau/\alpha$ at a value above $0.47$ (indicated by the dashed line). Qualitatively, this occurs when high-strength asperities begin to fail. b, c, Plots of quake size (measured as $M$) versus $\tau/\alpha$ for every 1/10 log $M$ unit (diamonds). The size–frequency statistics for the subcritical state (defined as $\tau/\alpha < 0.47$) and the critical state ($\tau/\alpha > 0.47$) are shown in b and c respectively. The dashed lines in b and c show the negative slope $B = 2/3$ (corresponding to a Gutenberg–Richter $b$-value equal to one). Comparing the slopes, it is apparent the Gutenberg–Richter scaling is more closely approximated during the critical than the subcritical state. This shows that self-similarity is violated in the early stages of a quake cycle and emerges during the transition to the critical state.

(asperities) continues, stress and strength increase. (3) Criticality. Here, large stress/strength fluctuations occur as stronger asperities fail, initiating four-stage quake cycles on increasing spatial and temporal scales within the characteristic cycle. (4) Extinction. The characteristic cycle ends with failure of major asperities and a main-shock sequence that spans nearly the entire domain. This is accompanied by a rapid stress and strength drop as the yield-strength distribution is reinitialized with the mean population strength.

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The Late Precambrian fossil Kimberella is a mollusc-like bilaterian organism

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The fossil *Kimberella quadrata* was originally described from late Precambrian rocks of southern Australia. Reconstructed as a jellyfish, it was later assigned to the cubozoa ("box jellies"). It has been cited as a clear instance of an extant animal lineage present before the Cambrian. Until recently, *Kimberella* was known only from Australia, with the exception of some questionable north Indian specimens. We now have over thirty-five specimens of this fossil from the Winter Coast of the White Sea in northern Russia. Our study of the new material does not support a cnidarian affinity. We reconstruct *Kimberella* as a bilaterally symmetrical, benthic animal with a non-mineralized, univalved shell, resembling a mollusc in many respects. This is important evidence for the existence of large triploblastic metazoans in the Precambrian and indicates that the origin of the higher groups of protostomes lies well back in the Precambrian.

The Winter Coast outcrops (Ust'-Pinega Formation) contain a rich 'Ediacara-type' biota. *Kimberella* occurs in several facies all through the section, but most specimens have come from the undersides of fine-grained sandstone gutter casts, in member 9 of the local stratigraphic section. Channels in a clay substrate were colonized by a rich biota; when the channels were rapidly infilled with sand, the biota was preserved in situ. Associated with *Kimberella* in member 9 are large round 'medusoids', the distinctive fossils *Trichladium* and *Dickinsonia*, and some undescribed forms.
Small round fecal pellets, meandering trace fossils, and small pyritized algae also occur. Kimberella is an oval-to-pear-shaped, bilaterally symmetrical fossil, with several zones arranged concentrically. Fossils range from 3 to 105 mm in length; the largest specimen is incomplete (Fig. 1c) and may have been 130–140 mm long in life. The size range is continuous; no discontinuities exist in size or structure that would suggest sexual dimorphism or a size-structured population. Nor is there striking ontogenetic change over the observed size range; the smallest specimens are near-miniatures of the large ones. Films of frambooidal pyrite on some specimens resulted from anaerobic bacterial activity after burial.

The distal portions of the fossils demonstrate a relatively inflexible outer margin, and an inner zone that is often distorted or folded.

**Figure 1** Specimens of Kimberella from Ust'-Pinea Formation, Winter Coast of White Sea, all coated with NH₄Cl. All specimens are curated at the Paleontological Institute (PIN), Russian Academy of Sciences, Moscow. All are preserved on undersides of sandstone channel casts in member 9 unless otherwise noted. All scale bars are 1 cm. a. Large, well preserved specimen, with deep central depression. Note folding of soft tissues away from shell edge, which has buckled (arrow) (PIN 3993/4003). b. Specimen partially folded over, demonstrating deformation of soft parts and bilateral symmetry of organism (PIN 3993/4026). c. Largest specimen known; note lateral displacement of shell with crenellations extending out from under shell edge at right (PIN 3993/4004). d. Specimen from thinly interbedded argillite and siltstone, member 1 of local section; arrow indicates position of anterior bulge (PIN 3993/4001). e. One of two specimens showing series of pits (spicules?) along proximal ridge (PIN 3993/4026). f. Small but well preserved specimen showing primary features (PIN 3993/4033). g. Specimen showing rotation and displacement of shell from the main axis (PIN 3993/4027). h. Poorly preserved specimen from talus, probably from sandstones of member 10 of local section; note continuation of zones around posterior (pointed) end, as well as possible buccal mass indicated by arrow (PIN 3993/4009).
over but never cracked (for example, see Fig. 1a, b, e). Within the inner zone is a row of crenellated structures, typically about 30 in number. These usually form a U-shaped band, but extend completely around the fossil in a few specimens. A thin linear structure, the proximal ridge, separates the crenellated zone from the interior; this ridge seems to be an overprint of a higher anatomical structure onto the imprint of the ventral surface of the organism. Rare specimens show a band of resistant point-like structures associated with the proximal ridge (Fig. 1e). The central part of the organism is preserved in negative relief. Its position and depth vary, depending on how much the organism was compacted and deformed; it may extend up to 20 mm into the host rock in large specimens. It may be deformed to be almost flat (Fig. 1f) or displaced with respect to the softer parts (Fig. 1c), but is rarely found bent laterally. Therefore, its original substance was comparatively firm.13 Numerous fine striae run laterally from the medial depression in many specimens: they are generally clearest in the most flattened specimens. At least three specimens show a small bulge near the broader end, on the midline of the body, inside the proximal ridge (Fig. 1d, h).

Kimberella was first formally described as a cubozoan medusa preserved on its side.1 The crenellated zones were interpreted as gonads or as muscle bands, and the organism was reconstructed as having tetraradial symmetry. However, none of our specimens shows anything other than bilateral symmetry. If Kimberella were tetraradially symmetrical, we would expect to find more than two crenellated zones in at least a few specimens. Even folded specimens show no more than two crenellated zones (see Fig. 1b for example). Nor was Kimberella triradially symmetrical; the lateral zones are not repeated in the central zone. Kimberella, preserved in negative relief, was a 'resistant' organism: extant cubozoans are delicate and, if preserved at all, would form fossils in positive hyporeliefl, like most 'medusoids'.12 We cannot confirm the presence of gonads, tentacles and rhopalial; the best-preserved specimens lack any trace of tentacles or rhopalia. The crenellated structures, formerly interpreted as gonads, formed a continuous band around the body, unlike the discrete gonads of cubozoans. Furthermore, Kimberella is common in member 9, which otherwise includes definitely benthic forms almost exclusively; there is no evidence of subaerial exposure or mass stranding at this level. Ediacaran fossils of planktonic organisms typically appear in different facies from benthic forms.10,11 We conclude that Kimberella was a benthic bilaterian, not a medusa.

The key to interpreting this fossil is the fact that the organism consisted of both firm and soft parts, and that compaction during decay 'overprinted' structures that in life were at different levels in the organism. In one specimen (Fig. 1g), both the central depression and the outermost ridge have been slightly rotated and moved forward together over the softer parts. Another (Fig. 1a) shows the softer 'crenellated structures' pulled away from the outer ridge, and another (Fig. 1c) shows them protruding beyond the outer ridge. Specimens like these show that the firmer parts formed a discrete anatomical unit, partially separable from the soft parts. We therefore interpret the central depression and outermost zone of Kimberella as parts of a thin oval shell, not mineralized but fairly stiff, at least in its central part. This shell lent the animal strength during burial and sediment compaction, at which time softer tissues were deformed and compressed by un lithified sediment entering the shell from below, and finally overprinted on the overlying sand.

The crenellated structures are often deformed and were clearly soft; we interpret them as lateral folds of the body, usually retracted under the shell but occasionally seen protruding (Fig. 1c). The frequent U-shape of the crenellated zone may be explained by the asymmetry of the anterior—posterior outline of the shell (the highest point of the shell was closer to the anterior). The crenellations may have had a respiratory function. Although their number does not increase significantly with organism size, except in the largest specimens, the folds are small or even absent in small specimens, and longer and deeper in larger specimens. Assessing the respiratory function of the crenellations is difficult, because compaction makes it hard to estimate the volume of the organisms. However, our estimates of the total surface area of the crenellations scale isometrically with the product of body length and width. Kimberella may also have hosted microbial symbionts within the crenellations, as with the cera or paraophoria of symbiont-bearing gastropods;15 symbiosis has often been proposed as a lifestyle for Ediacaran organisms.13,15 Some specimens show a broad flat region between the crenellated zones, which we interpret as a creeping foot. There is no sign of true segmentation of the body, but fine lines running from the midline to the foot in some specimens may be strands of dorsoventral musculature. The anterior bulge, identified in the Australian material as the 'stomach', may be the mouth and its associated muscles forming a buccal mass. There is no sign of a true radula, but radulae are very rarely preserved in any fossil molluscs.

Figure 2 shows our reconstruction of Kimberella. The basic architecture of the fossil, showing metamereism without observable segmentation, a shell and a broad flattened foot, is closely comparable to that of primitive molluscs. The arrangement and inferred function of the crenellations is like that of the ctenidia of chiton and the 'ventilatory flaps' of monoplacophorans, although as similar structures have evolved independently at least three times in the Mollusca;14, the question of homology is not straightforward. The anatomy of Kimberella is also comparable to the soft anatomy of the Cambrian halkieriids, which appear to be relatives of molluscs and possibly other protostomes. Halkieria has a similar shape and division of the body into central and axial zones. It also has a zone of faint striae around the sole of its creeping foot, similar to the crenellated zone of Kimberella and plausibly having a respiratory function.17,18 It is even possible that the resistant pointlike structures

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**Figure 2** Reconstructions of Kimberella. a. Dorsal view. c. Crenellated zone; I. lobe; s. stripe; dr. distal ridge; pr. proximal ridge; m. medial depression; a. anterior knob. b. View of living organism, with folds of 'crenellated zone' extended beyond margin of shell; the folds would usually have been retracted under the shell at the time of burial.
A neuronal population code for sound localization

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The accuracy with which listeners can locate sounds is much greater than the spatial sensitivity of single neurons1-3. The broad spatial tuning of auditory neurons indicates that a code based on the responses of ensembles of neurons, a population code, can be used to determine the position of a sound in space. Here we show that the tuning of neurons to the most potent localization cue, the interaural time difference in low-frequency signals (<~2 kHz; refs 4, 5), becomes sharper as the information ascends through the auditory system. We also show that this sharper tuning increases the efficiency of the population code, in the sense that fewer neurons are required to achieve a given acuity.

Sensitivity to interaural time differences (ITDs) first occurs in the main nuclei of the superior olivary complex (SOC). The information is then transmitted to the inferior colliculus, and from there to the auditory thalamus, which in turn projects to the auditory cortex. We examined ITD sensitivity at its point of creation (the SOC) and at two higher levels (inferior colliculus and auditory thalamus) through neural recordings in unanaesthetized rabbits. Examples of the ITD tuning in the SOC and thalamus are shown in Fig. 1a. These 'composite' ITD curves represent the averaged responses to tones of different frequencies as a function of ITD. In both nuclei, the curves are overlapping and broad in relation to the total range represented. Note, however, that the ITD tuning widths in the thalamus are much narrower than in the SOC.

The sharpening of ITD tuning as the information ascends the auditory system is also shown in Fig. 1b. c. The mean width of the composite curves showed a large decrease for the SOC to the inferior colliculus (730 to 430 μs), and a smaller decrease from there to the thalamus (430 to 350 μs) (Fig. 1b). The sharpening was not due to differences in the frequency content to which the samples of neurons in each structure responded, because it also occurred on a frequency-by-frequency basis (Fig. 1c). Much of the sharpening must therefore be due to neural processing. Possible mechanisms for the sharpening include inhibitory processes4 and convergence of temporally coincident activity5.

To determine how the sharpening of ITD tuning affects performance at each level, we used a model similar to that described in refs 9, 10. This model is similar to the 'position-variable' model of ITD sensitivity derived from behavioural data and responses from the auditory nerve1. Such models begin by aligning all the neurons according to their preferred sensitivity, in this case the best ITD, to form a 'neural axis'. To the extent that the spatial field is not mapped

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