Figure 1 Growth of plant and fungus in the the presence of arsenate and the influence of fungal colonization on arsenate accumulation by the host plant. **a,** Biomass of *H. ericae* mycelia after 17 d in medium containing arsenate ($n=24$) and root-lengths of *C. vulgaris* seedlings grown on agar plates containing arsenate for 3 months ($n=9$). Filled symbols, fungus; open symbols, plants. Triangles, mine populations; circles, heathland populations; dotted lines, fungus; solid lines, plants. **b,** Arsenate uptake (24 h) from a 0.1 mmol m^{-3} arsenate solution by 4-month-old sterile *C. vulgaris* seedlings with or without *H. ericae* from site of origin ($n=3$). Graphs show means ± s.e.

from the mine has enhanced efflux of arsenite (efflux from mine isolates, $14.4 \pm 3.0\%$ h^{-1}; heathland isolates, $6.6 \pm 3.0\%$ h^{-1} ($P < 0.001$)). *H. ericae* has independently evolved the same strategy as one used by bacteria that reduce arsenate intracellularly to arsenite[6] for efflux.

Arsenate resistance in *C. vulgaris* is not achieved by exclusion, as we found no alteration to influx or efflux for either arsenate or phosphate. Higher plants normally resist arsenate through downregulation of arsenate/phosphate transporters[7], but *C. vulgaris* has adopted an alternative mechanism. We suggest that the fungus dominates arsenate/phosphate accumulation, acting as a filter to maintain low plant arsenic levels through arsenite efflux while enhancing plant phosphorus status. When exposed to arsenate for 24 h, heathland *C. vulgaris* inoculated with heathland *H. ericae* accumulated 100% more ($P = 0.01$) arsenate than uninoculated heathland plants or mine plants (with and without mine *H. ericae*), which all had comparable arsenate accumulation (Fig. 1b). Infection of mine *C. vulgaris* with mine *H. ericae* did not place the host under additional arsenate stress.

We found that mine and heathland *H. ericae* were constitutively copper resistant, which confers resistance upon non-resistant *C. vulgaris*[8]. In contrast, *H. ericae* and its host must have adapted to arsenate contamination in parallel, by the fungus selectively

accumulating phosphate over arsenate. Our data show that evolution of host and symbiont is fundamental to the colonization of polluted soils by key plant taxa.

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1. Macnair, M. R. *New Phytol.* **124**, 541–559 (1993).
2. Cairney, J. W. G. & Meharg, A. A. *Environ. Pollut.* **106**, 169–182 (1999).
3. Smith, S. E. & Read, D. J. *Mycorrhizal Symbiosis* (Academic, San Diego, 1996).
4. Lee, R. B. *Ann. Bot.* **50**, 429–449 (1982).
5. Straker, C. J. & Mitchell, D. T. *New Phytol.* **106**, 129–137 (1987).
6. Silver, S. & Phung, L. T. *Annu. Rev. Microbiol.* **50**, 753–789 (1996).
7. Meharg, A. A. & Macnair, M. R. *J. Exp. Bot.* **43**, 519–524 (1992).
8. Bradley, R., Burt, A. J. & Read, D. J. *Nature* **292**, 335–337 (1981).

Pattern recognition

Tunes and templates

A tune is a succession of musical tones that is easily recognizable when repeated. Here we describe an experimental technique and preliminary results that test a simple theoretical idea about tune recognition.

The theory is that the initial experiences of the melody form a template in the plane defined by pitch and time[1]. When the tune is repeated, it is compared with this template, and for the appropriate starting time there will be matches between what is received and what is predicted from the template: the number of these matches is a decision variable determining the detectability of the tune. Detectability can be impaired either by randomly removing some of the notes from the tune, or by adding interfering 'noise' notes to it. The theory predicts how these two types of interference should combine with each other, and we have experimentally tested whether this prediction is correct.

We took a well known melody (the first four bars of *Eine Kleine Nachtmusik* by W. A. Mozart) and mixed random notes with it to find out how many such 'noise' notes could be tolerated while still recognizing the tune. We did the experiment with the whole melody, and also with 1, 2, 4 or 9 notes selected randomly and independently on each trial from the full set of 18, preserving their order and timing. In any one experiment, the number of melody notes was fixed and the task was to identify whether they were present.

It is easiest to understand the experimental design by considering a matrix of 37 rows for the note pitches by 128 columns for their timing. For a given starting time, the melody notes marked 18 elements of the matrix. The masking or noise notes were then scattered randomly within the matrix. The subject's task was to decide whether the stimulus contained part or all of the melody, or alternatively whether it belonged to the set of noise-only notes. For each number of melody notes, Fig. 1 shows the number of masking noise notes that could be tolerated while still allowing 75 per cent correct responses in the single-interval forced-choice trials.

The simplest theory assumes that the starting time of the melody is known. The template acts as a sieve and performance depends on the total number of notes that passed through the holes corresponding to the expected positions of the melody notes. For the 'melody' trials, these numbers exceed those on the 'noise-only' trials by $\Delta\mu$, which is the average number of melody notes in those trials, namely 1, 2, 4, 9 or 18. If σ is the standard deviation of the number that occur in the noise-only trials, then $d' = \Delta\mu/\sigma$ (ref. 2). The statistics of the number of melody-matching notes from the masking noise is binomial; hence σ is equal to $\sqrt{(npq)}$. In our case, p and q are constant, so σ is proportional to $\sqrt{n}$, the
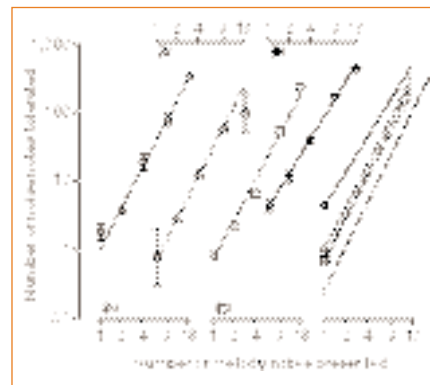
Figure 1 The subjects' task was to distinguish between a 'noise' sequence of notes and a 'melody' sequence. The melody sequence differed from the noise sequence by containing 1, 2, 4, 9 or 18 notes drawn from a melody in addition to noise. The number of noise notes that could be tolerated for 75% correct answers was estimated from 200 trials. The four sets of data points on the left show these results plotted on logarithmic scales; the results for each subject are separated by horizontal shifts. Straight lines were fitted, and these lines with their appropriate symbols are replotted at the right with a single horizontal scale, together with the theoretically predicted line of slope 2 (broken line). Three of the subjects (open symbols) were musically untrained or amateur musicians, and for them the fitted values of the slopes lie reasonably close to the predicted value of 2 (circle, 2.02 ± 0.054; triangle, 2.04 ± 0.067; square, 1.94 ± 0.12). The fourth subject (filled circles) is a professional musician and was the only subject with absolute pitch. She tolerated more noise notes, her results have less variability and lie on a shallower slope (1.63 ± 0.067) than the others.

square root of the number of noise notes. Thus, for constant d', n varies as the square of the number of melody notes. On log–log plots we would expect the data values to fall on lines of slope 2.

Figure 1 shows that for three of the subjects this tentative prediction was quite well borne out. The fourth subject was a professional musician: she could tolerate more noise notes, her results were less variable, and they lay on a line of lower slope. This indicates that she had the greatest advantage when only a small number of melody notes were presented, possibly as a result of her well-developed sense of absolute pitch.

Our experiment represents a highly constrained situation because a correct answer can hardly imply recognition of the melody, particularly from only a few melody notes. But it does answer some elementary questions about the basis of musical recognition, and the technique can be developed to test whether it is absolute pitch, the occurrence of particular intervals, or other features of the melody that matter.

These experiments were prompted by results on the detection of biological motion[3] and other visual tasks[4]. We believe that they point to another field where the effects of masking noise can help to elucidate the mechanisms of pattern recognition.

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1. Warren, R. M. *Auditory Perception*, 126–130 (Cambridge Univ. Press, 1999).
2. Swets, J. A., Tanner, W. P. & Birdsall, T. G. in *Signal Detection and Recognition by Human Observers* (ed. Swets, J. A.) 3–57 (Wiley, New York, 1964).
3. Neri, P., Morrone, M. C. & Burr, D. C. *Nature* **395**, 894–896 (1998).
4. Tripathy, S. P., Mussap, A. J. & Barlow, H. B. *Vision Res.* **39**, 4161–4171 (1999).

Palaeontology

A refugium for relicts?

Luo[1] suggests that the vertebrate fauna from the Yixian Formation (Liaoning Province, China) shows that this region of eastern Asia was a refugium, in which several typically Late Jurassic lineages (compsognathid theropod dinosaurs, 'rhamphorhynchoid' pterosaurs, primitive mammals) survived into the Early Cretaceous[1] (Fig. 1). Data from slightly older sediments in the Japanese Early Cretaceous, however, suggest that the faunal composition of this region can only be partly explained by the concept of a refugium.

The Kuwajima Formation of Ishikawa Prefecture, central Japan, is yielding an important Early Cretaceous vertebrate fauna. This unit is a lateral equivalent of the
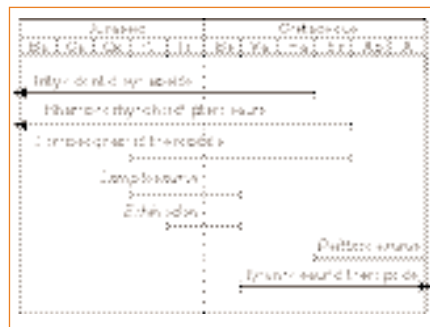
Figure 1 Stratigraphic ranges of clades that include taxa recovered from the Yixian Formation, China, and the Kuwajima and Itsuki Formations, Japan[1,4,9]. Data on *Camptosaurus* and *Echinodon* are from ref. 13. Arrows, lineage extends beyond the time range shown here; solid bars, first and last occurrences. Al, Albian; Ap, Aptian; Ba, Bathonian; Be, Berriasian; Br, Barremian; Ca, Callovian; Ha, Hauterivian; Ki, Kimmeridgian; Ox, Oxfordian; Ti, Tithonian; Va, Valanginian.

Okurodani Formation that outcrops in neighbouring Gifu Prefecture[2]. Stratigraphic, biostratigraphic and radiometric data show that the Okurodani Formation is basal Cretaceous (Valanginian or Hauterivian) in age[3]. The Kuwajima Formation has yielded more than one hundred isolated teeth of a new genus of tritylodontid synapsid[4]. Before these discoveries, tritylodontids were thought to have become extinct sometime in the Middle or early Late Jurassic, as the youngest-known tritylodontid (*Bienotheroides*) was recovered from late Middle Jurassic deposits. This discovery supports the concept of an East Asian refugium, but other evidence suggests that different factors may have had an equally strong influence on faunal composition.

A theropod dinosaur referable to the unnamed clade Oviraptorosauria + Therizinosauroidea[5] has also been found in the tritylodontid locality. This clade is best known from the Late Cretaceous of mainland Asia, although several taxa referable to this clade are known from the late Early Cretaceous of Liaoning (*Beipiaosaurus*[6] and *Caudipteryx*[7]), and possibly from the Early Jurassic of Yunnan Province, China[8]. The Japanese material, consisting of a single manual ungual (Fig. 2) with a pronounced posterodorsal lip (a feature synapomorphic of this group of theropods[5]), is one of the earliest representatives of this group. The Itsuki Formation of Fukui Prefecture, a lateral equivalent of the Okurodani and Kuwajima Formations[2], has produced an isolated tyrannosaurid tooth, identifiable by its D-shaped cross-section — a synapomorphy of tyrannosaurids[9].

These Japanese discoveries, combined with the presence of late Early Cretaceous taxa in the Yixian Formation (such as the ornithischian dinosaur *Psittacosaurus*[10]), suggest that several dinosaur clades (such as tyrannosaurids and psittacosaurids) may have originated and diversified in eastern

Figure 2 Manual ungual of a theropod dinosaur from the Kuwajima Formation (Valanginian or Hauterivian) of Shiramine, Ishikawa Prefecture, Japan. Note the prominent lip posterodorsal to the articular surface of the ungual, a synapomorphy of the clade Oviraptorosauria + Therizinosauroidea[5]. Scale bar, 5 mm.

Asia while a number of other lineages (tritylodontid synapsids, compsognathid dinosaurs and 'rhamphorhynchoid' pterosaurs) persisted in this region. Moreover, the presence of hypsilophodontid and iguanodontid ornithopod dinosaurs in the Japanese Early Cretaceous[11] suggests faunal connections with western Asia and Europe. The historical biogeography of this region appears to be much more complex than was thought previously.

Alternatively, the so-called relict taxa in eastern Asia may indicate that faunal turnover at the Jurassic–Cretaceous boundary was not as marked as has been suggested[12]. The presence of camptosaurid (*Camptosaurus*) and heterodontosaurid (*Echinodon*) ornithopods in European Early Cretaceous faunas[13] indicates faunal similarities to the Late Jurassic Morrison Formation of North America. The presence of 'Late Jurassic' taxa in eastern Asia may simply represent another example of this more gradual Jurassic–Cretaceous faunal transition (Fig. 1), although more evidence is needed to distinguish between these alternatives.

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1. Luo, Z. *Nature* **400**, 23–25 (1999).
2. Maeda, S. *J. Collect. Arts Sci. Chiba Univ.* **3**, 369–426 (1961).
3. Evans, S. E. *et al. New Mexico Mus. Nat. Hist. Sci. Bull.* **14**, 183–186 (1998).
4. Setoguchi, T., Matsuoka, H. & Matsuda, M. in *Proc. 7th Annu. Meet. Chinese Soc. Vert. Paleontol.* (eds Wang, Y.-Q. & Deng, T.) 117–124 (China Ocean, Beijing, 1999).
5. Makovicky, P. J. & Sues, H.-D. *Am. Mus. Novitates* **3240**, 1–27 (1998).
6. Xu, X., Tang, Z.-L. & Wang, X.-L. *Nature* **399**, 350–354 (1999).
7. Sereno, P. C. *Science* **284**, 2137–2147 (1999).
8. Zhao, X.-J. & Xu, X. *Nature* **394**, 234–235 (1998).
9. Manabe, M. *J. Paleontol.* **73**, 1176–1178 (1999).
10. Xu, X. & Wang, X.-L. *Vertebrata PalAsiatica* **36**, 147–158 (1998).
11. Manabe, M. & Hasegawa, Y. in *6th Symp. Mesozoic Terrest. Ecosyst. Biotas* (eds Sun, A.-L. & Wang, Y.-Q.) 179 (China Ocean, 1995).
12. Bakker, R. T. *Nature* **274**, 661–663 (1978).
13. Norman, D. B. & Barrett, P. M. *Spec. Pap. Palaeontol.* (in the press).