

The western United States and Mexico showing where *Sporormiella* spores were found in ●, historic and ▲, late-glacial sediments. Scale bar, 450 km. Top right: a, *Sporormiella intermedia* spore; b, fossil spores from mammoth dung, Bechan Cave; c, fossil spores from DSDP core 480; d, modern *Sporormiella minima* spores. Scale bar, 10 µm. (Modified from ref. 1.)

considerably less abundant after about 11,000 years ago, corresponding to the time when Clovis hunting communities were active there. Davis<sup>1</sup> has now gone one step further than the dung hunters and has studied the dung-inhabiting fungus *Sporormiella*, whose spores he found preserved in the sediments of lakes in the western United States (see figure). These spores are abundant only in lakes around which there is a high local density of large herbivores. In fossil sediments they became very prominent following the introduction in historic times of domesticated herbivores, but Davis also finds them to be frequent in the sediments of late-glacial times, before 11,000 years before present (BP). They decline markedly at about this date, providing further evidence about the date of megafaunal extinction. So, even in the absence of skeletal evidence, the decline of the megafauna can be observed and dated.

Dating, of course, is critical in the debate concerning the causes of megafaunal extinction. Grayson has examined<sup>2</sup> the available dates and finds some important gaps in our knowledge of the time periods during which some members of the megafauna were present in North America. Only 7 of the 35 extinct genera considered had firm dates from the terminal Wisconsin (12,000–10,000 BP). Many of the megafauna, Grayson contends, may not have survived until 12,000 years ago, thus complicating any explanation of the mechanisms involved in their extinction.

If the human predation was the cause of

extinction, one would expect a correlation between archaeological and extinction dates, which seems to occur in the case of the Shasta ground sloth. But even when such correlation exists, it still provides only circumstantial evidence and does not demonstrate a causative relationship. Further information concerning the contemporaneous environment could be useful, especially if signs of human activity can be detected over wide areas. Take the case of Madagascar, for example. Seventeen megafaunal species disappeared from this island in relatively recent times, in the latter part of the Holocene (the past 10,000 years). The association between such extinctions and human settlement (dating around 2,000–1,500 BP) is compelling, and explanations of the precise nature of these events have often been linked with the increasing frequency of fires and consequent habitat changes on the island.

Burney has examined<sup>3</sup> this hypothesis by analysing the charcoal content of lake cores from the centre of Madagascar. He finds that in the past 10,000 years the highest levels of charcoal abundance occurred between approximately 10,000 and 4,000 BP. Charcoal then declined very strongly and remained low for more than 2,000 years, only rising steeply at about 1,200 years ago. From these data he

concludes that fire was important in the ecology of Madagascar through the early part of the Holocene. Although fire had become less frequent and/or extensive before human occupation of the island, it is unlikely that the animals and plants of Madagascar would have been particularly fire-sensitive. It is possible, of course, that the human-induced fires of more recent times differ from the old fires in their timing, duration, extent or intensity, but their overall impact on lake charcoal influx is considerably less than the fires of the early Holocene. The simple explanation of megafaunal extinction as a result of habitat modification by human-induced fires is not, therefore, supported by the charcoal data. Direct predation, of course, is still a possibility.

So, if human agencies were involved in the death of the megafauna, they covered their tracks pretty well. Proving human involvement is likely to be an arduous task, but establishing a climatic link is undoubtedly even more difficult. □

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## Evolution of behaviour

# Burrowing by vertebrates

M.J. Benton

TODAY, many vertebrates form burrows for living, feeding or protection — familiar examples include rabbits, moles, certain snakes, lizards and amphibians, and lungfish. The burrows can be well-formed semi-permanent underground systems, often of considerable complexity, but most are temporary passages forced into surface layers of the soil. The evolution of burrowing habits can be studied by analysing the behaviour and ecology of modern burrowers, or by examining the functional morphology of their digging organs — the paddle-like forelimbs of moles, or the strengthened snout of burrowing lizards which can be used to batter a tunnel into soil. Another approach, which has now yielded much new information, is to examine fossil burrow systems.

The commonest fossil vertebrate burrows are those ascribed to lungfish. Dozens of examples have now been reported in rocks dating from the Devonian (360–408 million years ago) to the present day. The modern African lungfish, *Protopterus*, burrows into the mud of drying lakes in summer to aestivate — the metabolic rate slows down, and the

animal survives until the rains fall. The aestivation burrow is up to 1 m deep, and the lungfish curls itself up into a ball and surrounds itself with a mucus envelope to prevent the loss of body water. There is only a small opening at its mouth to allow breathing. Only a few fossil lungfish burrows contain the bones of lungfish<sup>1–3</sup>, but the shape of the burrows and their relationship to the sediment indicate their origin (Fig. 1).

Cylindrical upright pipe-like structures, 3–25 cm in diameter and up to 2 m deep, cutting through several layers of sandstone and mudstone, are typical of burrows from the early Devonian<sup>4,5</sup>. The burrows taper downwards to a rounded base. It is not certain that these burrows were made by lungfish, but if they were, aestivation behaviour must have arisen very early, as the earliest skeletal fossils date from the same time. Postulated lungfish burrows have often been reported from rocks younger than the Devonian<sup>1–3,6</sup>. There have been changes in size over time — post-Devonian specimens rarely exceed 15 cm in diameter and 1.7 m in depth (typical sizes are 5–10 cm diameter, 25–50 cm depth). They frequently occur in

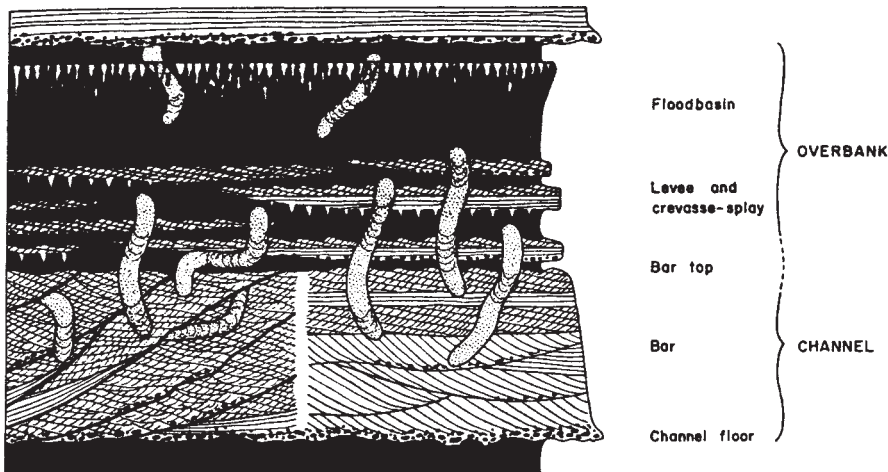


Fig. 1 Postulated lungfish burrows from the early Devonian of South Wales. The surrounding sediments (black, mudstones; cross-hatching, sandstones; white, calcareous soil horizons) indicate warm-flood plain conditions. (From ref. 4.)

large assemblages, and generally in sediments that indicate warm conditions and occasional arid periods.

Smith has recently reported<sup>7</sup> the surprising discovery of well-preserved burrow systems made by dicynodonts, an extinct vertebrate group (Fig. 2). He found large burrows in the late Permian (240-million-year-old) Beaufort Group of South Africa. The burrows are helical in shape, starting with a modest spiral about 6 cm in diameter at the top, expanding to about 16 cm at the base and then straightening out into a 25-cm-broad section. In all 50 or so specimens, the helix is dextral (similar finds from the Northern Hemisphere are awaited with interest!). The burrows are clearly set off from the surrounding sandstones, being generally filled with mudstone or siltstone that would have entered from above after the burrow went out of use.

The upper shaft of the burrow slopes down at an angle of about 30–35°, and the overall depth of the lower chamber is 0.5–0.75 m from the former land surface. The

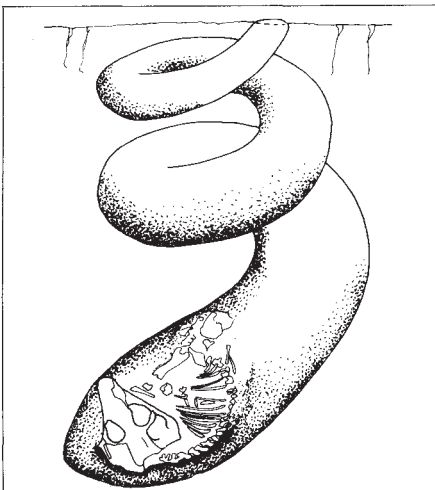


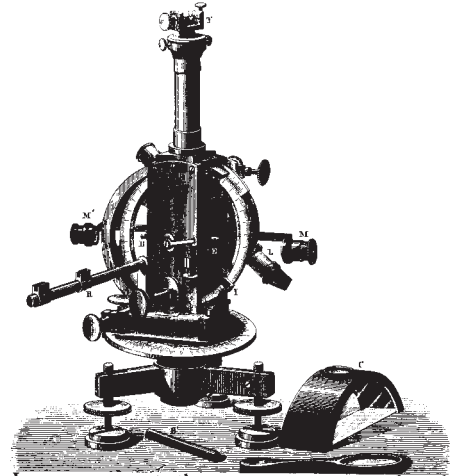
Fig. 2 The dicynodont *Diictodon* preserved curled-up in the terminal chamber of its spiral living burrow, from the late Permian of South Africa. (Based on information in ref. 7.)

walls of the burrows, particularly those of the lower chamber, are marked by irregular scratch marks. The sediments in which the burrows occur are thought to be from an ancient flood plain in which large meandering rivers deposited sandstones, and periodic floods swept finer sediments over the area.

What animals produced these burrows? Large burrows of this kind had hitherto been ascribed only to mammals, which had not evolved by the late Permian. But some remarkable specimens contain skeletons of small mammal-like reptiles, identified as the dicynodont *Diictodon*, which was common at that time. The skeletons are complete, and were found in a curled-up attitude in the terminal chamber of the burrows, which is where *Diictodon* may have sheltered from the heat. The animals excavated the burrows by scratching with the feet and possibly the beak, and the depth was probably limited by the level of the water table.

Similar helical burrows are well known in much younger sediments, generally of Miocene age (5–24 million years ago). *Daimonelix*<sup>8–10</sup> burrows, on the basis of fossil evidence and comparisons with modern burrows, are thought to have been produced by rodents. Typical *Daimonelix* burrows occur in many parts of the world, ranging in age from the Lower Eocene to the Miocene (55 million years ago), but the best examples come from the late Oligocene to early Miocene Harrison Formation of Nebraska<sup>11</sup>. Here, the burrows have an upper entrance pit, a middle vertical spiral and a lower living chamber. However, these later forms may have as many as 20 whorls and they can coil dextrally and sinistrally in the same locality. Further, the tube diameter remains constant and does not increase with depth. The Miocene burrows have been confidently ascribed to *Palaeocastor*, a primitive beaver, on the basis of complete and incomplete skeletons found in the living chamber, which is thought to

## 100 years ago A NEW MAGNETIC SURVEY OF FRANCE



In some respects the magnetometer employed by M. Moureaux possesses advantages over the Kew pattern. In the matter of weight alone there is a considerable difference. A Kew magnetometer weighs nearly 50 pounds, whereas that of the French observers weighs only about 9 pounds. A further advantage possessed by the French model is that it is also an altazimuth instrument, and hence the observer is less dependent upon the knowledge of true time.

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have been made for breeding<sup>11</sup>.

The recent discoveries show that burrowing activities of vertebrates have a long history. Analogy with living forms, together with palaeoenvironmental interpretations, suggest why the burrows were made. Fossils provide evidence for the existence of previously unsuspected, complex burrowing behaviours in completely extinct groups, such as the small dicynodonts, long before the first appearance of rodents in the fossil record. The fossils can also elucidate aspects of behavioural evolution in vertebrates. The Eocene and Oligocene *Daimonelix* burrows, for example, are much simpler than those from the Miocene, and are more like the Permian *Diictodon* burrows, suggesting that the burrow-forming behaviour of rodents has changed through time. The burrow morphology gives hints of how this happened. The fossil lungfish burrows also show that the overall size of this species decreased through time. □

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