A termite tale of climate change

Once upon a time the Namib was wooded savanna. What turned it into desert, when, and how? Fossil termite hives offer clues, writes **Martin Pickford**.

Throughout sub-Saharan Africa and other parts of the world, termites play a huge ecological and geological role. Evidence of their activity is widespread, but geologists seldom appreciate the work that these social insects do because most of it lies hidden beneath their feet and because it is often difficult to identify the species responsible. The discovery of fossilized harvester termite hives in the arid coastal regions of Nambia, however, is now helping palaeontologists to piece together the story of massive climate change that occurred millions of years ago.

Signs of activity

Buried stone lines in the soils and palaeosols of the tropics, which are frequently seen in roadcuts, are normally caused by the busy work of termites. For millennia they have been carrying clay, silt, and sand upwards in the soil, then dumping it at the surface as small earth-lined foraging tunnels or as larger mounds and chimneys. As a result, over long periods of time, stones tend to 'drift' downwards in the soil profile, accumulating at or near the local water table, which termites cannot penetrate.

Termite activity in ancient sand dunes of the Namib Sand Sea near Awasib, Namib-Naukluft Park, Namibia. The lack of a termite mound above the disturbed sediment indicates that this complex may have been made by Hodotermes, although no hive is exposed in the deposits to confirm the identification.

Under normal circumstances, termites are almost never preserved as fossils – their bodies are too soft and they decay rapidly[1]. Above ground termite mounds are seldom preserved as fossils because they tend to erode away before being buried. If they are buried rapidly enough, however, the mounds and tunnel systems that these insects make can be fossilized, as happened in East Africa when lava flows and volcanic ashes blanketed the countryside, and in the Namib Desert when sand dunes over-rode and buried these structures.

Fossil termite mounds have been recorded in South Africa, Namibia, Tanzania, Kenya, and West Africa. But published records are rare, and the makers of the mounds are seldom, if ever, precisely identified. Termite foraging tunnels (called *Termitichnus*, originally described from indurated [hardened] sand dunes in Namibia)

Termite earth-movers

A vast biomass of termites inhabits the continent of Africa. Many species spend most of their lives underground or hidden in the depths of trees, so it's easy to underestimate just how many there are and what they do.

They use a wide range of plant material, often to make subterranean fungus gardens, where they grow the small mushrooms that are their food. Taken together, African termites consume more vegetation than all the mammalian herbivores put together.

Many termite species build mounds that poke up above ground as low hillocks or tall, chimney-like constructions. Most of us have seen and been impressed by these mounds, but few people realize that, taken together, termites do more geological work than any other living creatures except perhaps for the humble earthworm. Termites in Africa collectively move millions of tons of earth every year, which makes them important geological agents.

To find out more, consult Vivienne Uys's *A Guide to the Termite Genera of Southern Africa* (see page 29).

1. Although termite fossils are extremely rare, some have been recorded in amber (or, fossilized tree resin) and in shales in various parts of the world. In Kenya, for example, there is a shale deposit at Waril in the Tugen Hills aged 10 million years, which preserves imprints of the wings and bodies of alate termites that fell onto damp silts exposed along an ancient lake shore.

Opposite (left): Harvester termites, Hodotermes mossambicus *(Hagen), in a circle of grass that has been harvested for food.*

Photograph: ARC-Plant Protection Research Institute

*Opposite (right):*Termitichnus *is the scientific name for fossilized foraging tunnels made by termites at Rooilepel, Namibia. Here the tunnels have been filled with sand, and the surrounding dune sediment has been blasted away by the wind, exposing the ancient tunnel system in three dimensions in the position in which it was formed.*

Above left: An almost complete hive of the harvester termite Hodotermes, *exposed at Grillental, northern Sperrgebiet, Namibia. This specimen has the polar (top) part preserved. The presence of a hard sandstone deposit behind the fossil protected the upper part from destruction by wind-blown sand.*

Above right: Ball-shaped structure now preserved in sand, originally constructed at Rooilepel, Namibia, by the sand termite Psammotermes *some 16 million years ago.*

are often preserved, but on their own they're difficult to tell apart from tunnels made by ants or other insects. It's easier to identify the maker if the termite mound is preserved. If the fungus garden is preserved (as happened in East Africa), it is sometimes even possible to determine the family of termites responsible.

Probably the most confidently identified termite constructions are the hives of the harvester termite *Hodotermes*, which are not fungus gardens but the nests where young and adult termites congregate.

Detail of the cell structure of a Hodotermes *hive from Grillental, Namibia, showing the large cells connected to each other and arranged into horizontal shelves.*

Namibia's *Hodotermes* fossil hives

The coastal area of Namibia is exceptional because evidence of ancient termite activity abounds, and at least two kinds of termites can be identified from the traces that they left. In the fossil sand dunes of the Namib Sand Sea are the ubiquitous (and often well preserved) hives, foraging tunnels, and networks of the sand termite *Psammotermes*. But perhaps the most unexpected fossils are the calcified hives of the harvester termite *Hodotermes*, which occur in the Early Miocene (20 million years old) deposits of the Sperrgebiet and elsewhere in the Namib.

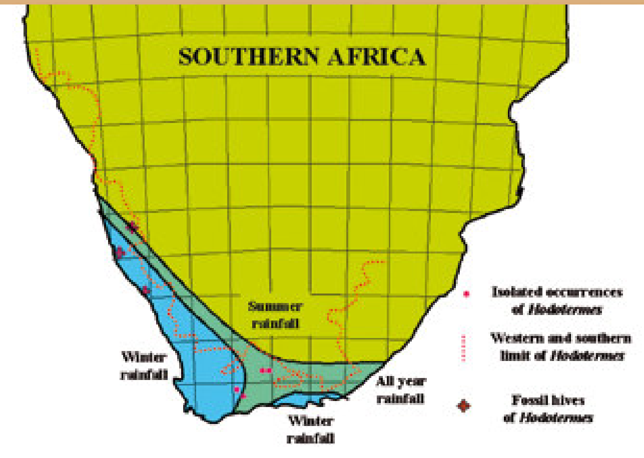
Harvester termites do not construct surface mounds. Instead, they build spherical underground hives up to half a metre in diameter from 'carton' (a mixture of organic and inorganic material with the consistency of brittle cardboard), consisting of masses of large cells arranged roughly into horizontal layers or 'shelves', with each cell having open connections or ramps to its neighbours above and below. There is often a vertical tube running through the hive from top to bottom, providing a sort of 'highway' for rapid access to various parts of the hive.

Hodotermes is one of the few 'polycalate' termites. This means that one group builds several hives, up to a metre beneath the surface, which are connected by underground tunnels. The hives of these termites normally decay when the insects abandon the complex but, in the right conditions, such as those in the Namib, the cell walls can become impregnated by calcite, and this preserves them as fossils. Not only can individual hives become fossilized but, on occasion, so can entire polycalate complexes.

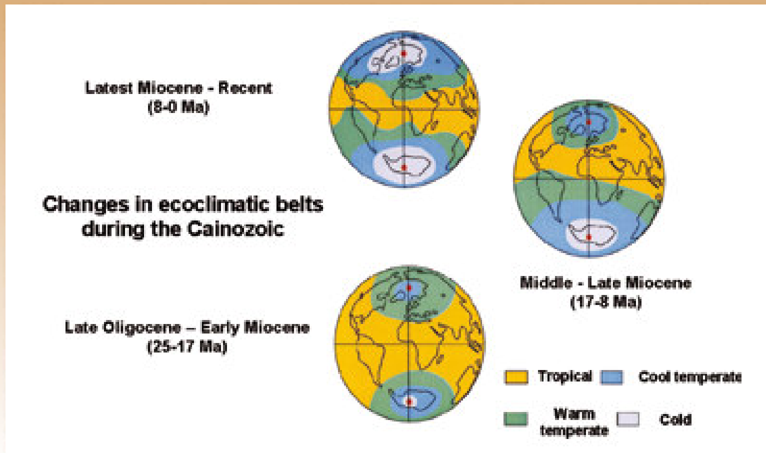
Usually however, only the outer parts of the hives get calcified: the centres are left unaltered and decay away to leave hollow, ball-shaped fossils. As erosion makes them weather out of the ground, they often form ring-shaped structures, almost like an inflated inner tube lying on the ground. This is because the upper 'polar' part of the sphere, being the first bit exposed, erodes away or breaks into small pieces, leaving the lower 'equatorial' part of the hive intact. This section resembles a ring. Many such termite rings have been recognized in the Sperrgebiet and the Namib-Naukluft Park in sediments ranging in age from 20 million years to Recent times.

Habitat for harvesters

As their name implies, harvester termites eat grass, so they occur most often in places where grass is plentiful, such as steppe, savanna, and wooded savanna. They are rare or absent in forested areas where the rainfall is greater than 750 mm per year, and they cannot survive where there is less than 125 mm annual rainfall. In ▷▷



Winter and summer rainfall belts of southern Africa, and the distribution of the harvester termite, Hodotermes. *It occurs mainly in the summer-rainfall belt, but encroaches into the margins of the winter-rainfall belt in some areas (usually where intermittent rainfall sometimes occurs in summer). But fossil hives of* Hodotermes *occur deep inside what is today the winter-rainfall belt, attesting to climatic change in the past.*



Changes in global climate brought about by growth of the polar ice caps, first the Antarctic one (17–16 million years ago) and, second, the Arctic one (about 8–7 million years ago). The ecoclimatic belts were pushed northwards by growth of the Antarctic ice cap and then squeezed back equatorwards by growth of the Arctic ice cap. This explains why the southern Namib enjoyed summer rainfall 20 million years ago but, since 16 million years ago, has lain mainly in the winter-rainfall belt.

▹ addition, they are found naturally only at the edges of winter-rainfall areas, because the reproductive season, when alates leave the nest, is timed to occur during the summer rains when the climate is warm. When a fossilized hive of *Hodotermes* is found, therefore, it indicates that, at the time it was constructed, the region most likely enjoyed summer rainfall of between 125 and 750 mm per year.

Abundant fossilized *Hodotermes* hives have been discovered in Early Miocene deposits in many parts of Namibia's coastal region, ranging from the Orange River Valley at Arrisdrift and Gypsum-Plate Pan near Oranjemund in the south, to Grillental nearer Lüderitz in the north, and even further north in the Namib-Naukluft Park at Awasib, and elsewhere. The finds are a sign that this zone once enjoyed the summer rainfall in which *Hodotermes* flourishes – in strong contrast with today's winter-rainfall pattern of the Sperrgebiet, with far less rain (less than 100 mm a year) than fell there during the Early Miocene.

In the Sperrgebiet, the fossil hives of *Hodotermes* are associated with other animal remains, notably the bones and teeth of various mammals, birds, reptiles, and amphibians. Many of these confirm the region's summer rainfall palaeoclimate[2].

In the same deposits, for instance, there are fossils of mammals such as pigs, water chevrotains, dassies, and proboscideans, whose teeth indicate that they consumed leaves and fruit, so there must have been substantial stands of trees in the region 20 million years ago. All the indications together yield a picture of a wooded savanna with about 750 mm annual rainfall.

Harvester termites at the entrance to the nest, to which they take food that they have collected. Photograph: ARC-Plant Protection Research Institute

This palaeoenvironmental reconstruction is confirmed by a study of the palaeosols (fossil soils) that yield the fossils and in which *Hodotermes* built its hives. These soils are rich in calcrete nodules and even calcrete sheets. Today, similar calcretes form in areas such as Grootfontein and Etosha in northern Namibia, where the rainfall is up to 750 mm per year, but where evaporation rates are high (over 2 000 mm per year).

What made the climate change

How can one account for the presence of fossil constructions made by summer-rainfall termites such as *Hodotermes* in regions which today experience winter rainfall? How could the climate have been so different in the past, with the coast of southern Namibia located in the summer-rainfall belt?

Before the onset of the Namib Desert 17–16 million years ago, the Antarctic ice cap was considerably smaller than it is today. Indeed, ice was initially confined to mountain tops. But about 17 million years ago, towards the end of the Early Miocene epoch, global atmospheric cooling brought a cover of ice to much larger areas until, by about 16 million years ago, the continent was entirely buried beneath a vast ice cap.

The growth of this continental ice cap forced the warm ecoclimatic belts of the world northwards. Southern Namibia, which lay in the summer-rainfall belt prior to Antarctic ice cap expansion, now came to lie within the winter-rainfall belt as the summer-rainfall belt was pushed towards the equator. It also experienced far less rainfall and became hyper-arid, leading to the onset of desert conditions by 16 million years ago, and resulting in the Namib Desert.

At that time, there was no land near the north pole on which ice could accumulate, so there was no counterbalancing ice-cap in the north. Only about 8–7 million years ago did the global climate cool sufficiently for a northern ice cap to form, first on land masses such as Greenland and then on the sea itself, culminating 5–4 million years ago in the Arctic ice cap. The growth of the Arctic ice cap forced the ecoclimatic belts of the world back towards the south, thus squeezing them towards the equator.

2. Bones and skulls of clawed toads (Pipidae, *Xenopus*) are common at Langental and Grillental. Today, these toads occur widely in sub-equatorial Africa where there is permanent fresh water in open countryside, but they generally avoid winter-rainfall areas and forest. The diminutive extinct ostrich *Struthio coppensi*, the earliest known in the world, occurs at several sites, notably at Elisabethfeld, near Lüderitz. It is likely that this species included grass in its diet, just as extant ostriches do. Several of the small mammals, notably some of the rodents and elephant shrews, have hypsodont (high crowned) cheek teeth, indicating that their diets consisted mainly of grass. The early antelope *Namibiomeryx* probably also included grass in its diet, as did the rhinos, and other ruminants such as *Sperrgebietomeryx*, a peculiar creature distantly related to giraffes and antelopes.

More on termites

Termites, writes Vivienne Uys (in her excellent, easy-to-read, illustrated *Guide* to the termites in our region) are secretive, discreet, elusive; dull in colour; and not easy to identify. Feared by farmers and builders as pests that destroy crops and structural timber, they benefit soil quality in tropical ecosystems through processes such as the decomposition of organic material, and they're a valuable food source for predators (including humans). In southern Africa, there are on record 54 genera, in five families. This *Guide* summarizes current knowledge, and is used by people in fields such as termite systematics, natural resource management, ecology, and pest control.

Vivienne Uys, *A Guide to the Termite Genera of Southern Africa*. Plant Protection Research Institute Handbook No. 15. (Pretoria: Agricultural Research Council, 2002). To order, phone Eunice Mudzusi on (012) 808 8222 or e-mail KewaneE@arc.agric.za

The combined geological and palaeontological evidence underscores the hints provided by the fossil termite hives – that, 20 million years ago, the Sperrgebiet was not a desert but was covered in wooded savanna with permanent bodies of fresh water.

Not only have termites played a major role in Africa for the last 20 million years, but their fossilized underground constructions can be studied by palaeontologists to throw light on past climates.

So don't fly into a rage the next time termites eat your books or the wooden floors in your house. Instead, ponder on the fact that they have been around a lot longer than humans have, and consider the possibility that they may well still be here long after we've disappeared. □

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For general information, see A. Emerson, "The Biogeography of Termites" in the *Bulletin of the American Museum of Natural History*, vol. 99(1952), pp. 217–225. For more on *Hodotermes*, read W. Coaton's "Fossilized nests of Hodotermitidae (Isoptera) from the Clanwilliam District, Cape Province" in the *Journal of the Entomological Society of South Africa*, vol. 44(1981), pp. 79–81. Also read W.G.H. Coaton and J.L. Sheasby, "National survey of the Isoptera of southern Africa. 10. The genus *Hodotermes* Hagan (Hodotermitidae)" in the Namibian Entomological Journal *Cimbebasia*, Ser. A, vol. 3(1975), pp. 105–138. For details about ancient termite nests, consult J.M. Moore and M.D. Picker, "Heuweltjies (earth mounds) in the Clanwilliam district, Cape Province, South Africa: 4,000 year old termite nests" in *Oecologia*, vol. 86 (1991), pp. 424–432.