EVOLUTION OF TERRESTRIAL BURROWING INVERTEBRATES

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INTRODUCTION

The important role of fauna in modifying the regolith by redistributing particles is now widely acknowledged (e.g., Paton *et al.* 1995). One issue of some importance to regolith studies and the interpretation of paleosols is how the role of terrestrial bioturbation has evolved since life first invaded the land areas of Earth in the Early Paleozoic. This particular issue was raised during a discussion session at an earlier regolith conference (Eggleton 1998) and this paper is an attempt to answer this more fully in respect to invertebrates. In particular this contribution attempts to address the issue of when different kinds of burrowing invertebrates, in which burrowing is demonstrated or may be reasonably assumed, first appeared. In an ideal situation a combination of hard evidence provided by well dated fossils and trace fossils together with less certain but nevertheless important information obtained from habitat reconstruction and phylogenetic relationhips would be employed. However, such a combination is rarely achieved and hence most of the relationships discussed are based on a mixture of available evidence.

MODERN BIOTURBATING INVERTEBRATES

The main bioturbating invertebrates are ants, earthworms and termites though locally other types may be important especially in more extreme conditions (Paton *et al.* 1995). Various crustaceans are prodigious burrowers in swampy sites and the tidal zone. In certain situations high densities of particular taxa occur where habitat conditions are particularly favourable such as occurs with cicada nymphs and trapdoor spiders. Also of interest is the development of purposefully constructed mounds that forms an integrated part of the nest system. Such mounds are a product of eusocial behavior whereby two or more generations ovelap in the nest, and in which parental care and some division of labour occurs especially between the reproductive and non-reproductive castes. This feature is regarded as a special and rare evolutionary event in invertebrates occurring only in the Hymenoptera (ants) and Isoptera (termites). From the viewpoint of pedogenesis and hence regolith studies the significance of eusocial development is in nest construction, the amount of soil moved, the depth of soil affected, the concentration of elements including metals and other minerals, and the fact that nests may permit habitation of a wider range of environments than if these insects were solitary.

Ants (Hymenoptera)

The earliest definite ant fossils appear in the Upper Cretaceous *c.* 80 Ma ago with well preserved specimens reported from New Jersey and Alberta in North America and also in Siberia (Holldobler & Wilson 1990). A disputed find of Lower Cretaceous age in Victoria, Australia is thought to be more wasp-like rather than a true formicid. They also note that Cretaceous specimens are fairly rare representing < 1% of insect impressions in amber. However, Urbani *et al.* (1992) argue that the strong monophyletic association between old world and new word wingless army ants (Dorylinae and Ecitoninae respectively) demand a common ancestor and hence must predate the joining of the American continents c. 106 Ma. An earlier age for ants is consistent with a mid-Mesozoic origin of Hymenoptera (Labandeira & Sepkoski 1993). By the Oligocene (*c.* 35 Ma) and Miocene ants are much more common and in some cases dominate the amber collections. This suggests major adaptive radiation from the Early Tertiary at a time when Laurasia and Gondwana remained separated and the fragmentation of Gondwana was well advanced. For example, the Madagascan ant fauna shows much stronger affinities with Africa rather than India even though it separated from the latter *c.* 90 Ma compared to Africa *c.* 120 Ma (Fisher 1996). Common and widespread genera such as *Aphenogaster*, *Formica*, *Iridomyrmex*, *Lasius*, *Monomorium*, *Ponera* and *Terraponera* date to the Oligocene and one of these, *Iridomyrmex*, to the Eocene. The genera *Aphenogaster*, *Iridomyrmex*, *Monomorium*, and *Ponera* occur in Australia at the present time and an Early Tertiary age in Australia is likely. So far, however, the the oldest definite fossils date from the Early Miocene where they are well preserved in calcareous deposits of the Upper Site at Riversleigh as are millipedes, slaters, flylarvae and cicadas (Archer *et al.* 1991). Furthermore, some of these genera are active mounders such as *Iridomyrmex purpureus* in Australia and several species of *Formica* in Europe and North America. This implies that social organization and hence reasonably sized nests and active mounding may have been widespread before Mid Tertiary. Definitive proof of this resides with fossilized nest systems which until recently have not been described, a point emphasised by Hasiotis and Bown (1992) and Donovan (1994) even though an undated silicified nest of the weaver ant, *Oecophylla*, is known (Boucot 1990). However, this ant constructs arborel nests from leaves and twigs and not soil. The occurrences of the so called "ant-nest silcrete in South Australia (Callen *et al.* 1986, Alley *et al.* 1994,

Benbow *et al.* 1995, Callen *et al.* 1995) may change this perception. At least one of these sites in the Watchie Sandstone, a Miocene unit near Lake Eyre (Paul Rogers *pers. comm.* 2001) was identified by John Greenslade (formerly CSIRO Division of Soils) as closely resembling a meat ant (*Iridomyrmex purpureus)* nest (Neville Alley *pers. comm.* 1996). If this is correct it represents the first known fossil soil nest by ants. However, it is not clear from existing descriptions whether or not other examples are fossil termite or ant mounds. Clearly there is a need for a detailed study of these nests.

Termites (Isoptera)
Termites are closely related to cockroaches and not ants as implied in the commonly used term white-ants. Several examples of Cretaceous termites are known from Europe, Asia and North America (Emerson 1967, Jarzembowski 1989). The first of these, *Cretatermes carpenteri*, comes from the mid Cretaceous in Labrador (Emerson 1967). Similarly, an Early Cretaceous form, *Valditermes*, is regarded as a primitive member of Hodotermitidae in England, Spain and Mongolia (Jarzembowski 1989). In addition termite borings and associated coprolites are known from fossilized wood from the Upper Cretaceous (Boucot 1990). Previously, a Permian fossil, *Uralotermes*, was regarded as the oldest Isopteran fossil (Snyder 1949), though this interpretation was subsequently rejected by Emerson (1965). All other termite fossils are Tertiary though none are older than the Eocene (Table 1). Nevertheless, most major termite families are widespread across Eurasia, Africa, North America, South America and Australia. This, together with various phylogenic and distributional trends, was used to suggest that the main termite families were established during the Early Mesozoic (e.g., Krishna 1970) though the general consensus is for Late Mesozoic (Labandeira & Sepkoski 1993). Subsequent research based on gut anatomy and DNA sequencing confirmed that Mastotermitidae is the most primitive family (Noirot 1995, Kambhampati *et al.* 1996) and therefore must be at least Cretaceous.

Table 1: Fossil ages of termite families (modified from Krishna 1970, Snyder 1960, Jarzembowski 1989).

Family	Fossil age and distribution
Mastotermitidae	Eocene (USA, Europe, Australia?), Oligocene (Europe, Asia, Miocene (Germany, Yugoslavia), Pliocene (Brazil)
Termopsidae	Cretaceous* (Labrador), Eocene (Hungary, Baltic), Oligocene (France, Colorado), Miocene (Hungary)
Hodotermitidae	Early Cretaceous (England, Spain, Mongolia), Oligocene (Germany, Siberia, Colorado), Miocene (Germany, USA), Pliocence (Germany)
Kalotermitidae	Eocene (Baltic), Oligocene (Germany, Colorado), Miocene (Europe), Pleistocene (Africa)
Rhinotermitidae	Eocene (Europe), Oligocene (USA, Egypt?), Olig-Miocene (Mexico)
Serriterrmitidae	na
Termitidae	Miocene (Europe), Pleistocene (Africa)

* NB The Labrador specimen, *Cretotermes*, was originally classified in the Hodotermitidae but subsequently placed in the Termopsidae (Emerson 1967).

Large termitaria (termite mounds) are often portrayed as conspicuous feature of termites but this is far from a diagnostic trait. Apart from constructing substantial mounds, which form an integral part of the nest, termites may also create substantial subterranean and/or arborial nests. In addition arborial species often transport considerable soil material to pack out tunnels in living and dead shrub stems and tree trunks. Surface feeders may also construct covered pathways which may enlarge to sheath-like forms. These behaviour traits are confined to two families only: Rhinotermitidae and Termitidae (Table 2) both of which are well represented in Australia. Good examples of fossil nests are however rare. Bown (1982) describes a termite (*Termitichnus quatranii*) nest in Oligocene fluviatile deposits (Jebel Qatrani Formation) in Egypt with a subterranean nest and gallery system that is similar to modern examples especially in (Boucot 1990) which is also consistent with the known fossil age of this family (Table 1). A similar soil-nest is also described from the Miocene in Argentina (Bown & Laza 1990). Also, some of the so called "ant-nest silcrete" of Miocene age in South Australia (see section on ants) are also referred to as termite nests (e.g., Simon-Coinçon *et al.* 1996). These data indicate that termite soil nests and mounds are a Cenozoic feature. However, the reporting of an Upper Triassic termite soil nest in fluviatile sediments (Hasiotis & Dubiel 1995) indicates a much older origin.

Earthworms (Oligochaeta)
Eusocial behaviour is not a feature of earthworms but high densities can occur in favourable situations to give the impression of communities. Constant burrowing and production of fecal material can result in an upper soil layer with a distinct fabric. The fecal pellets are an intimate mixture of mineral grains and finely

comminuted organic matter at various stages of decomposition as the binding agents derived from the earthworm gut ages and decays. Fossil evidence of soft bodied organisms such as earthworms (i.e. modern oligochaeta) is very poor. However, a variety of worm forms (polychaetes) are recorded as far back to at least the Ordovician. Some of these such as *Protoscolex* and *Paleoscolex* have been interpreted as early oligochaetes, the ancestors of earthworms, but this interpretation has not met with complete acceptance with others suggesting they are polychaetes (e.g., Edwards & Lofty 1977, Morris *et al.* 1982). Regardless, of exact affinities the Early Paleozoic forms appear to have occupied marine habitats and it has been suggested that the evolution of oligochaetes was from marine to fresh water to swampy to terrestial habitats with the first stage to fresh water occurring possibly in the Silurian (Sawyer 1986). It is not until the Tertiary that reasonably good evidence of modern oligochaetes is forth coming (Morris *et al.* 1982) and it has been suggested that they appeared with angiosperms in the Cretaceous (Edwards & Lofty 1977). Apart from soft body remains evidence of earthworms may be sought indirectly such as from burrow traces, casts (earthworm fecal pellets) and perhaps paleosols with a crumb ped structure. Retallack (1976) records reddish tubules (para-aggrotubules) 7 mm in diameter set in a grayish clay matrix in Triassic paleosols near Sydney. Particular importance is attached to a cross-section through one tubule. It is very convoluted and infilled with elliptical fecal pellets up to 1 mm long composed of material no larger than silt. This is interpreted as a collapsed partly infilled earthworm burrow and becomes the oldest fossil record of earthworms (Retallack 1997). The description and interpretation of this example certainly fits polychaetes but it does not distinguish between oligchaetes and other polychaetes. The situation is also complicated as there is uncertainty over the degree of marine influence in the Narrabeen paleosol sequence (e.g., Naing 1993). Nevertheless, it is reasonable to suggest that the cool temperate forest ecosystem of these paleosols would be a suitable habitat for true earthworms.

Table 2: Distribution of termite families and bioturbation activity.

Biogeographic region	Termite Families								Ref.
	Mast	Hodo	Kalo	Rhin	Termitidae				
					Armi	Term	Macr	Nasu	
Australian	y	y	y	I,M,S	I,M,S	M,S	-	M,S	1
Ethiopian	-	y	y	M	M	M	M	M?	2,3
Madagascar	-	-	y	y	-	M	M	M,S	4
Neotropical	-	1 sp	y	I,S	A,M	y	m?	A,G,MS	5
Oriental	-	m	y	i,G,s	G,m	m,S	M,S	m	6
Neoartic	-	wood	wood	g,M,S	S,M	-	-	S	8
Nth Asia	-	y	y	S	-	m?	m?	m?	7
Nth Afr-Arabia	-	m	dry-wd	S	m	-	-	-	7
Europe	-	-	dry-wd	1 sp S	-	-	-	-	7

Termite families: Mast, Mastotermitidae; Kalo, Kalotermitidae; Hodo, Hodotermitidae; Rhin, Rhinotermitidae. Termitidae sub-families: Armi, Armitermitinae; Term, Termitinae; Macr, Macrotermitinae, Nasu, Nasutitermitinae.
Code: y, species present but no soil movement identified or undescribed; A - arboreal species present; G - subterranean; I - infilling of trunks/stems; M - mounding; S - sheathing . (A,G,I,M,S in capitals indicates a major importance but lower case represents minor importance); - no representives of this family present.
References: 1 Gay & Gallaby 1970, 2 Noirot 1970, 3 Bouillon 1970, 4 Paulion 1970, 5 Araujo 1970, 6 Roonwall 1970, 7 Harris 1970, 8 Weesner 1970 (in Krishna & Weesner 1970).

Cicadas (Homoptera)
Burrow traces thought to be created by cicada nymphs have been noted in Triassic paleosols in Antartica and in Eastern Australia (Retallack 1997). They are particularly abundant in the Avalon paleosol of the upper Narrabeen Group (Retallack 1997). The tubules (metagranotubules) have circular to elliptical cross-sections about 5 mm across and occur as a dense network of mostly vertical tubes that sometimes appear to taper with depth and branch. Cicada-like insects are known from the Triassic in eastern Australia (Evans 1956)

Spiders (Arachnida)
Spiders, scorpians, ticks and mites form part of the extensive Arachnida order. Scorpians first appear in the Silurian and spiders by at least the Carboniferous with an uncertain Devonian example though good fossil evidence is only available from the Cretaceous and especially the Oligocene (Petrunkevitch 1955). The paucity of fossil spiders in the Mesozoic is a trend also shared by all Arachnid orders and this raises doubts about phylogenetic relationships as well as behavioural trends. Nevertheless, the Early Paleozoic spiders were bulky and hairy and closely resemble modern trapdoor spiders (Orthognatha), which possess special tooth-

like spines on the front of the chelicerae (mandibles) which are used to pick and breakdown soil into transportable lumps. Hence, it is thought that the earliest spiders were ground dwellers of swamp forests that probably excavated shallow burrows and/or even spun flimsy silken tubes (Main 1984). However, there is no fossil evidence to support this conjecture. Spider web, a characteristic of the true spiders (Labidognatha) is well represented in Oliogocene Baltic amber (Boucot 1990).

Crayfish (Decapoda)
Burrows attributed to fresh water crayfish are reported from continental sediments dating back to the Upper Triassic and fossil remains date to Upper Jurassic in North America (Hasiotis *et al*. 1998). The burrows and fossils are very similar to modern crayfish and occupy the same types of habiats viz. along waterways and swampy ground, which implies little change in this taxa over 200 my.

Table 3: Fossil record of some fossorial insects (based on Boucot 1990 and refs in text).

Ants	Termites	Wasps & Bees
Hymenoptera (Jurassic)	*Isoptera (Cretaceous)*	*Hymenoptera (Jurassic)*
social ants (Cretaceous)	social termites (Lower Cretaceous)	social wasps & bees (Oligocene)
leaf ant nest (Miocene)	dry wood termites (Upper Cretaceous)	wasp mud nests (Eocene)
soil nest (Miocene?)	soil termites (Eocene, poss U. Triassic?)	**Cicadas**
mounding ants (?)	mounding termites (Miocene)	Homoptera (Permian)
		nymph burrows (Triassic)

DISCUSSION
The fossil evidence for burrowing invertebrates is very incomplete and it has proved difficult to establish when various taxa engaged in burrowing and even more difficult to establish when it became commonplace Table 3). Thus ants and termites were present in the Cretaceous but it is only in the mid-Tertiary that soil transporting termite taxa are established and ants became commonplace. The ants are regarded as the first group of predatory and eusocial insects that lived and foraged in the soil and ground litter though it is possible that either or both wasps and bees achieved this status. In this regard ants appear to have preempted other insect groups. Why was this niche left untouched for so long? There is no compelling answer. One explanation may be due to the unsuitability of the soil habitat prior to the Cretaceous /mid- Tertiary though there is no obvious reason for this unless it is also related to suitability of food resources. The emergence of the angiosperms at this time, especially the grasses, may be important but this type of explanation is discounted by Labandeira & Sepkoski (1993) in relation to insects as a whole. A similar picture emerges for earthworms in which definite evidence only exists from the Tertiary though an earlier appearance is possible given the close affinity between oligochaetes and the older polychaetes. Earlier Mesozoic evidence for cicadas and possible Late Paleozoic age for spiders imply the existence of earlier burrowing invertebrates but direct evidence for this is lacking. Nevertheless, burrow structures are a feature of many Mesosoic and Paleozoic paleosols and there recognition has been used as evidence for the appearance of terrestial fauna by the Late Ordovician (Retallack & Feakes 1987).

Thus, any explanation of soil formation that attributes a significant role bioturbating invertebrates can only be applied realistically back to the Mid-Tertiary. This tentative conclusion is likely to be reinforced when the impact of angiosperms (especially grasses) and fossorial vertebrates (especially mammals) is embraced. Prior to this the relative importance of burrowing taxa is expected to have been different and its net effect on soil formation is uncertain. Furthermore, it seems that the pre-Cenozoic burrowing fauna were restricted to moister sites though this conclusion may be a function of habitat preservation potential. In this case circularity of argument is difficult to avoid. Nevertheless, the recognized diversity of insects and other invertebrate taxa in the Mesozoic and earlier and the suitability of the soil environment for many animals (Labandeira & Sepkoski 1993, Hasiotis 2000) indicates considerable potential for bioturbation of the regolith

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