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THE WORK OF DUNG BEETLES AND ITS FOSSIL RECORD

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The ancient Egyptians saw in the life cycle of the scarab beetle (*Scarabaeus sacer*), hatching from the ground, then maneuvering and burying its ball of dung, a metaphor for divine agency in the rising and setting of the sun, and the promise of immortality and good fortune. The real significance of their activities as a sanitary squad, cleaning up after large herbivores, was dramatically demonstrated following the introduction of cattle into Australia during the 19th century. The production of large cakes of dung

by these Eurasian ruminants, compared to the dung produced by native marsupials, dingos and aboriginals, proved more than could be handled by native decomposers. A cake of cattle dung, which would last only a few weeks in Britain during warm weather, or as little as 20 minutes in Africa, could persist on the ground for up to five years in Australia. A sizable area of agricultural land (estimated as some 300,000 acres in 1966) was thus at best, removed from productive service, and at worst, a breeding ground for flies and unpalatable weeds (Waterhouse, 1974; Bornemissza, 1976).

Kinds of nesting behavior

Dung is a waste material by most human and bovine standards, but for dung beetles it is a precious resource. The beetles use dung mainly for food, either as ordinary fare, as nuptial gifts and feasts, as a larder for surviving harsh seasons or as nourishment for developing larvae. There are several ways of provisioning larvae (Halffter and Matthews, 1966; Halffter, 1977). Some dung beetles oviposit on exposed dung, which serves as a food source for free-living larvae. Other dung beetles take a great deal more effort to ensure the survival of their young. The

burrow-stuffers (Group I of Halffter, 1977) excavate a simple or branched burrow beneath a pile of dung, and pack the end of the burrow or chambers with dung. They may then lay one egg in each mass, or several eggs in a single large mass of dung. The underground ball-makers (Groups II and III) also excavate a burrow beneath the dung, but shape their supply into spherical or pear-shaped masses. In some cases, the brood balls may be covered with a thick coat of clay (Group II). In other cases, the female beetle may remain underground to tend and defend her growing brood (Group III). The overland ball-rollers (Groups IV and V) disperse the dung by

shaping it into balls and rolling it some distance from the source. Nests of some ball-rolling beetles consist of a single, untended brood ball (Group IV), whereas parental care of several brood balls and progeny are found in other dung beetles (Group V). Overland ball-rollers generally bury their brood balls. A final kind of behavior, known only in *Eurystemus*, includes parental care of several brood balls, without either rolling them away or burying them in the soil beneath the dung (Group VI). This behavior is anomalous in the sense that it does not continue the trend of progressively more elaborate parental care seen in Groups I to V.

Most dung beetles are solitary, although some of the burrow-stuffers, underground ball-makers and overland ball-rollers are subsocial (in the sense of Wilson, 1971), providing some parental care for the young. Subsocial behavior in provisioning larvae is most prominent among the diverse populations of dung beetles found in subtropical and tropical grasslands. Both specific diversity and the variety of nesting behavior are less at high latitudes and altitudes and in forests, where dung beetles with free-living larvae predominate (Halffter and Matthews, 1966). The scattered dung beetles in fields and woods of Fårö, a small island in the Baltic Sea north of

Gotland (Landin, 1961), may be contrasted with the assertive hordes of beetles cleaning up after elephants in the savanna of Tsavo National Park, Kenya (Heinrich and Bartholomew, 1979).

Evolution of dung beetles

Correspondence of the nesting behavior of dung beetles and habitat is a striking example of coevolution of vegetation, insects and large vertebrates. Halffter and Matthews (1966) and Halffter (1977) have offered some opinions on the course of this coevolution, drawn from their extensive knowledge of mod-

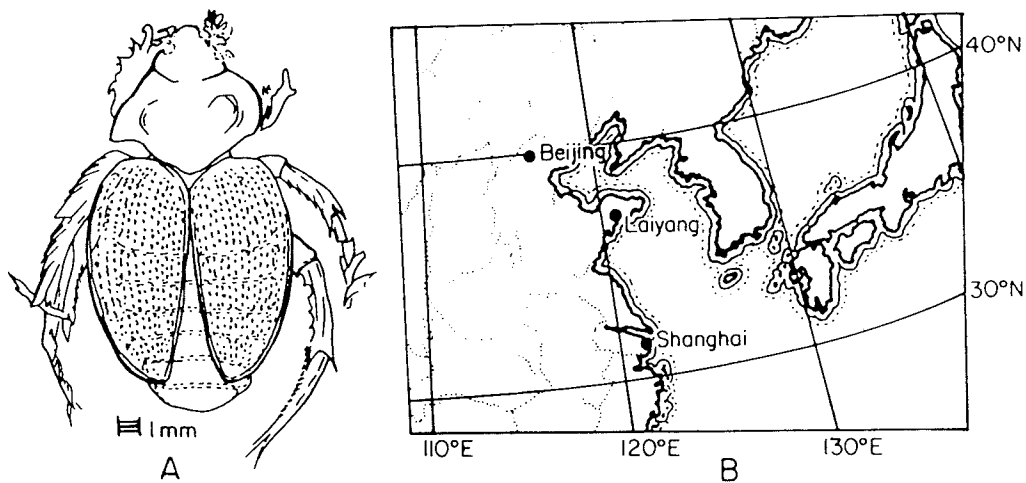


Fig. 199. Fossil scarabaeid beetle, *Proteroscarabaeus yeni* from Early Cretaceous lake deposits near Laiyang, Shandong (Shantung), China. (From Grabau, 1928.)

ern dung beetles and their behavior. But there is also a fossil record of dung beetles, both as remains of the insects themselves and of their larval nests. These latter are much more common as fossils in terrestrial sedimentary rocks than generally realized, and provide a potentially important, although little exploited, source of information concerning the evolution of nesting behavior.

The fossil record of the family Scarabaeidae, which includes the living dung beetles, is very incomplete. The order Coleoptera (beetles), of which they are a part, is known from as far back as Permian times (Crowson, 1981). The most common remains of beetles are isolated wing cases (elytra). Seldom preserved are the lamellate or flabellate segments of the antennal club or the robust limbs characteristic of scarabaeid beetles. According to Crowson (1981), a small fossil beetle (*Aphodiites*) from very Early Jurassic (Hettangian) rocks of Switzerland is superficially similar to modern, free-living, dung-eating, scarabaeid beetles of the subfamily Aphodiinae. A larger beetle (*Opiselleipon*) from late Early Jurassic (Toarcian) rocks of northern West Germany is another fossil similar to scarabaeid beetles. *Geotrupoides* from latest Jurassic (Tithonian) rocks of southern West Germany is regarded by Crowson (1981) as the oldest representative of the subfamily Geotrupinae. A variety of well preserved geotrupine and hybosorine scarabaeids (*Geotrupoides*, *Proteroscarabaeus* and *Holcorobeus*) are known from Early Cretaceous rocks of central Asiatic U.S.S.R. and northeastern China (Grabau, 1928; Arnoldi et al., 1977; Rodendorf and Rasnitsyn, 1980). A Mesozoic origin of scarabs can also be defended on the basis of the abundant niche provided by dung of the first large dinosaurs (Halffter and Matthews, 1966, p. 193), and from the global distribution of scarabaeid beetles, especially the variety of endemic forms in Australia, which has been geographically isolated since the very early Tertiary (Britton, 1970). Fossil scarabaeid beetles have also been found in Tertiary lake deposits of Europe (Balthasar, 1963) and North America (Wilson, 1977b; Grande, 1980); some of these as old as Middle Eocene.

Unfortunately, this fossil record of the Family Scarabaeidae reveals little of the history of dung beetles, because these are found only in a few subfamilies (Geotrupinae and Scarabaeinae of Arnett, 1963). These subfamilies include beetles which feed on carrion, roots, soil organic matter, decaying fruit, leaf litter, wood, fungi, live foliage, and nectar, as well as dung (Richter, 1958; Britton, 1970). Fossilized larval nests of dung beetles are more informative guides to their behavior and diet than fossil beetles.

Fossil nests of dung beetles from South American grasslands

Numerous fossil nests of dung beetles have been found in terrestrial deposits of Tertiary age in Argentina and nearby Uruguay (Fig. 200). The oldest of these are from paleosols of probable Paleocene age formed on Cretaceous rocks near Comallo in the Province of Rio Negro (Volkheimer, 1971). Unfortunately, the fossils themselves have not yet been described. The oldest described fossil nests are from floodplain deposits of Early Eocene age (Casamayoran of the local chronostratigraphic scheme; Marshall et al., 1977) at Punta Casamayor and at Los Leones, in Santa Cruz Province, Argentina (Frenguelli, 1938a, b). The exact geological setting of these fossil nests was not specified, but the drab grayish color of these weakly bedded deposits would be compatible with the presence of partly gleyed, lowland, fossil soils, which

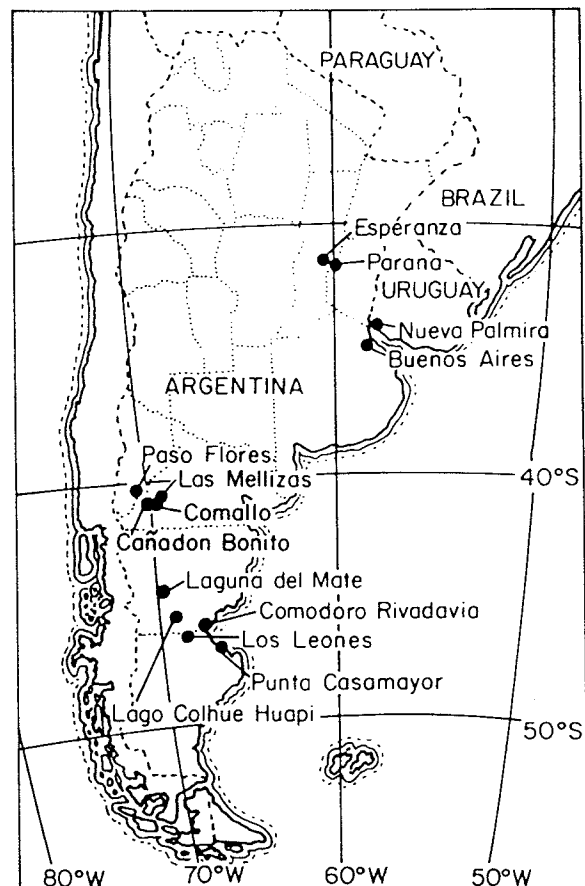


Fig. 200. Localities for likely fossil nests of dung beetles in Tertiary and Quaternary terrestrial deposits of southern South America.

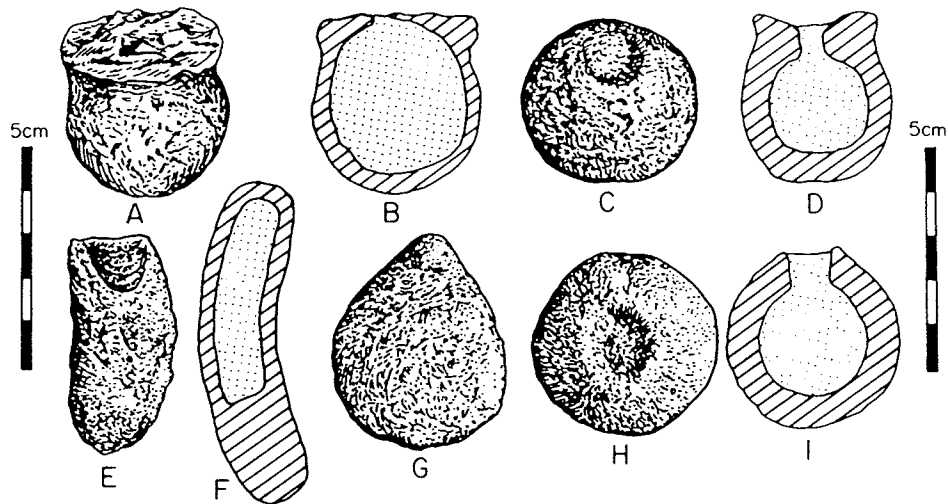


Fig. 201. Likely fossil nests of dung beetles from Miocene Oxisols near Nueva Palmira, Uruguay (A–D), and an Early Oligocene Inceptisol, near Paso Flores, Argentina (E–I): *Fontanaicbnus kraglievichi* from exterior (A), and in cross-section (B); *Devincenzichnus murguiae* from exterior (C) and in cross-section (D); an unnamed elongate nest or filled burrow from exterior (E) and in cross-section (F); *Coprinsphaera* sp. from exterior of an unhatched nest (G); and of a hatched nest (H) and in cross-section (I).

supported mesic woodlands and savannas, a vegetation in evidence from associated fossil plants and mammals (Webb, 1978). The fossil nests are hollow, thick-walled, spherical and pear-shaped shells of clay, similar to those formed around brood balls by living beetles of the genus *Phanaeus*. Sauer (1955, 1956) coined the name *Coprinsphaera ecuadoriensis* for similar trace fossils from Pleistocene ashes in Ecuador. Early Eocene nests from Argentina could be referred to a different species of the same genus, much smaller (29–39 mm in diameter) than the trace fossils from Ecuador.

Similar fossils of *Coprinsphaera* have been found in mid-Eocene (Mustersan) fossil soils near Laguna del Mate, in Chubut Province, Argentina (Andreis, 1972). These paleosols had few recognizable horizons, chestnut color and abundant root traces and clay skins. They may have been Inceptisols or Mollisols (of Soil Survey Staff, 1975) of savanna or other grassland vegetation. Such vegetation may also be inferred from the variety of notoungulates with high-crowned (hypsoodont) teeth, found together with mixed feeders such as megalonychid ground sloths, at this stratigraphic level (Webb, 1978). Even as long ago as the Eocene, dung beetles appear to have buried a food supply for their larvae, coated it thickly with clay (Group II behavior of Halfiter, 1977), and been common in association with large mammals of grassland ecosystems.

By the Early Oligocene (Descadan) there were a variety of nests of dung beetles (Fig. 201E–I) corresponding to diverse nesting behavior. Near Paso Flores (Neuquen Province, Argentina), numerous nests were found from 40 to 70 cm below the surface of a fossil soil (Frenguelli, 1939). This is a massive, brown-colored unit of rock with greenish mottles and reddish nodules of ferric oxyhydrate, and was probably an Inceptisol supporting savanna or woodland vegetation. Again, confirmation of such vegetation can be found in the remains of both browsing and grazing mammals, as well as fossil logs and leaves of palms, elms, and sycamores found at this stratigraphic level (Webb, 1978). Most of the fossil nests were of the *Coprinsphaera*-type (Fig. 201G–I), 35.5–54 mm in diameter. A single large *Coprinsphaera*, 59 mm in diameter, may represent a separate species. As for living beetles of the genus *Phanaeus*, the dung was probably first hidden in a burrow very close to the source. Only rarely do these modern beetles roll an irregular wad of dung a short distance before burying it. In the privacy of their own burrows, these living beetles construct one or more pear-shaped, clay-lined nests, with a large food chamber and a small adjacent egg chamber. The egg chamber is destroyed upon the exit of the young beetle (Halfiter and Matthews, 1966), which breaks up the pear-like shape, leaving hollow, gaping spheres of clay like *Coprinsphaera*. Elongate fossil nests were also found (Fig. 201E, F) in

two sizes, one 17–21 mm and the other 22–23 mm in diameter. Frenguelli (1939) thought that these nests were similar to those of the living dung beetle *Onthophagus*, but these latter are simply elongate burrows stuffed with dung and lack what Frenguelli interpreted as clay walls of the fossils (Halffter and Matthews, 1966). The clay lining could be regarded as a subsequent layer washed in, before final filling of the nest. Alternatively, it could be a fecal tube, like that of the living beetle *Pelotrupes youngi* Howden (1955, p. 18, fig. 2), although the fossil lining appears much more robust. It is also possible that these fossil nests are a record of nesting behavior unknown in living dung beetles. Whatever the resolution of these interpretive difficulties, these nests provide additional evidence for a diversity of nesting behavior in South America during Early Oligocene times. Molds of larval cells of wasps or bees complete the array of trace fossils found in the fossil soil near Paso Flores (Frenguelli, 1939). *Coprinsphaera*-like trace fossils are also common at several other localities of comparable age in Argentina (Frenguelli, 1938a, b, 1939; Spalletti and Mazzoni, 1978): near Cañodon Bonito (Rio Negro Province), Comodoro Rivadavia (Chubut) and Lago Colhue Huapi (Chubut). By Oligocene times, dung beetles were diverse, common, and widespread in southern South America.

Fossil nests of dung beetles from subtropical woodlands of South America

Another diverse assemblage of trace fossils (Fig. 201A–D) is known from fossil soils near Nueva Palmira, in southwestern Uruguay (Roselli, 1939, 1976; Frenguelli, 1939, 1946; Bonino de Langguth, 1978; Schlüter, 1984), probably Miocene in age (Frenguelli, 1939). The trace fossils come from a massive, dark red, weakly calcareous, clayey rock, capping Cretaceous bedrock. This is probably a relict soil of Miocene age, formed under woodland, in a subhumid, seasonally dry, subtropical climate. Many of the fossil nests are similar to *Coprinsphaera*, but for the collar-like rims around the exit hole. This collar is only weakly differentiated in remains referred to the trace fossil species *Devincenzichnus murguiae* (Fig. 201C, D), but forms a prominent platform in *Fontanaichnus kraglievichi* Roselli (Fig. 201A, B). These collared fossil nests may have been formed end to end in a burrow, similar to nests of the living dung beetle *Dichotomius carolinus* (Linnaeus) (Halffter and Matthew, 1966). While Roselli regarded *Devincenzichnus* as the nest of a dung beetle, he thought *Fontanaichnus* was the nest of a wasp because of three small irregularities which he interpreted as egg chambers. These small

chambers are not convincingly described or illustrated, and their interpretation remains uncertain. Also found in the relict soil were spectacular multicellular nests of bees (*Uruguayichnus auroranormae*, Roselli, including "*Prosceliphron*" of Frenguelli, 1946), very similar to the clustered underground chambers of sweat bees (Apoidea, Halictidae), such as *Halictus quadricinctus* F. Also found was another small fragment of a larger hymenopteran nest (*Uruguayichnus castellanosi* Roselli), and some enigmatic, asymmetric, near-ellipsoidal nests with distinctive, lamellar walls (*Teisseirichnus barratini* Roselli), perhaps made by litter feeding beetles.

There are clear differences between this assemblage and these fossil soils, and those of Early Oligocene (Descadan) age from near Paso Flores (already described) and of Miocene (Santacrucian) age from near Las Mellizas, in the province of Rio Negro, Argentina (Frenguelli, 1938a, b). A warmer, wetter climate and more lush vegetation in northern than southern South America can be inferred from the distribution and nature of Miocene fossil plants (Menendez, 1971) and mammals (Webb, 1978) and is compatible with what little is known about fossil soils of this age (Frenguelli, 1939; Roselli, 1939; Spalletti and Mazzoni, 1978; and interpretations offered herein). It could be that the fossil nests reflect this difference in habitat, and that non-grassland assemblages of dung beetles characteristic of subtropical woodlands and forests (as discussed in detail by Halffter and Matthews, 1966) had arisen by Miocene times.

Pleistocene nests of beetles associated with the giant fauna of South America

Fossil nests of clay, like *Coprinsphaera*, have also been found in Pleistocene sediments of Argentina (Frenguelli, 1938a, b) and Ecuador (Sauer, 1955, 1956). Many were preserved within the carapace of a fossil glyptodont in a large burrow (presumably its den) of Early to Middle Pleistocene (Ensenadan) age from near Parana (province of Entre Rios). These nests were 11–27 mm in diameter (Frenguelli, 1938a, b) and, from their geological occurrence, could equally have been stocked with carrion as with dung. The genera of living beetles *Pbanaeus* and *Deltochilium*, which form similar clay-lined nests, include some species which feed on dung and others feeding on carrion (Halffter and Matthews, 1966).

Large (82 and 87 mm diameter) fossil nests were found in Late Pleistocene (Lujanian) deposits near Esperanza (province of Santa Fé), in association with abundant remains of some of the largest mammals

known to have lived in Argentina. There is a direct linear relationship between the size of the nest of dung beetles and the size of the beetle (Halffter and Matthews, 1966, p. 106). It is also possible that large nests evolved in response to gigantism in the mammalian fauna, as Frenguelli (1938a, b) suggested from the occurrence of these fossils. Some of the largest living species of dung beetles [for example, *Heliocopris dilloni* (Guérin)] form huge spheres from the dung of the largest land mammal, the elephant (Heinrich and Bartholomew, 1979).

Fossil nests of dung beetles in open woodlands of North America

Fossil nests of dung beetles have only been recognized recently in North America, although Clark et al. (1967, p. 124) came close to identifying them in referring to "casts of pupa cases or larval burrows" in the early Late Oligocene Scenic Member of the Brule Formation in Badlands National Park and surrounding regions, South Dakota (Fig. 202). In my own studies of this sequence in the Pinnacles area of Badlands National Park, I have found nests of both dung beetles and of bees at two horizons in the Scenic Member (Orellan or early Late Oligocene of Prothero et al., 1982) and at two horizons in the Poleslide Member (Whitneyan or mid-Late Oligocene) of the Brule Formation (at levels 51.8, 61.9, 92.4 and 97.8 m in a measured section in which the non-redeposited top of the Pierre Shale is at 8.3 m; Retallack, 1983, 1984b). Only at the lowest level were they abundant in a calcareous layer up to 20 cm thick. This was the petrocalcic horizon, 110–125 cm below the surface of a fossil soil, which has a clayey, pink, B (illuvial) horizon and a greenish-gray A horizon (Fig. 203). The

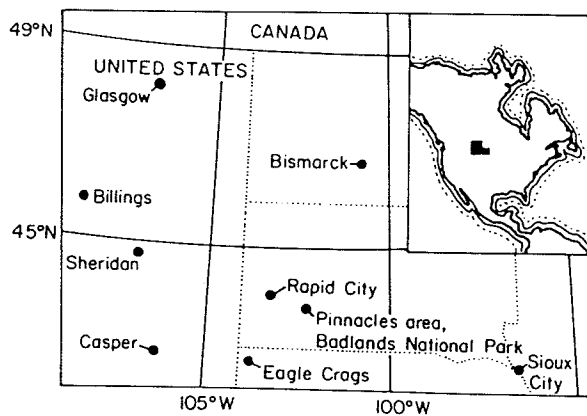


Fig. 202. Localities for likely fossil nests of dung beetles in Tertiary terrestrial deposits of central North America.

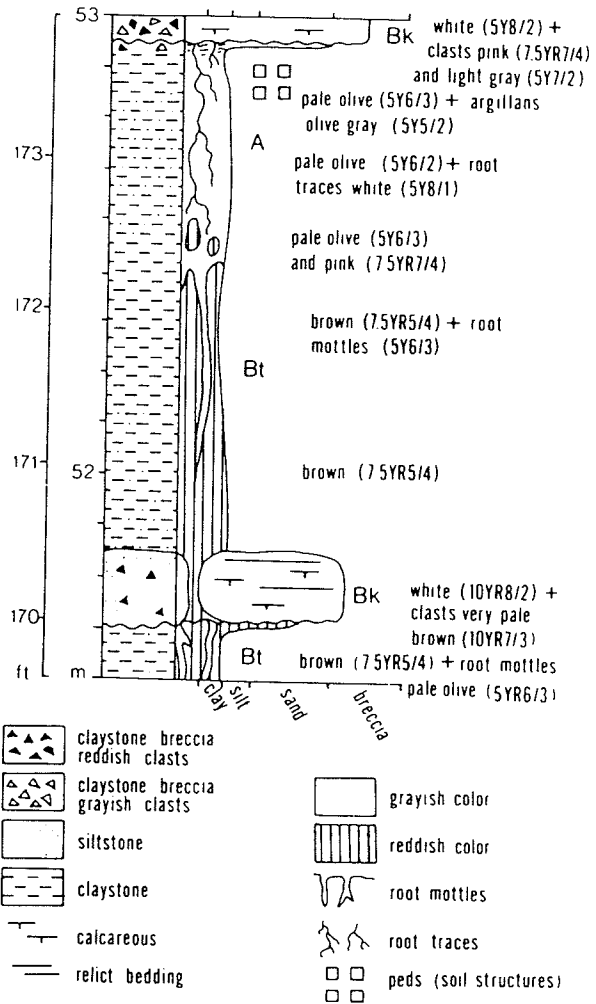


Fig. 203. Paleosol with a petrocalcic horizon (Bk) containing nests of solitary wasps or bees and of dung beetles. Scenic Member of the Brule Formation, Badlands National Park, South Dakota (51.8–53 m in measured section of Retallack, 1984b).

fossil nests may once have been present in the upper portions of the fossil soil, but are only recognized where preserved in three dimensions in the petrocalcic horizon. The fossil soil was mapped in the field as an unnamed Gleska Series paleosol, #30, and was probably once a Petrocalcic Paleualf in the classification of the U.S. Department of Agriculture (Soil Survey Staff, 1975) or a Red Brown Earth of the Australian C.S.I.R.O. (Stace et al., 1968). Considering these identifications, its well developed soil horizons, large fossil root traces and relationships with channel deposits and with other paleosols, this paleosol probably supported open woodland which formed a

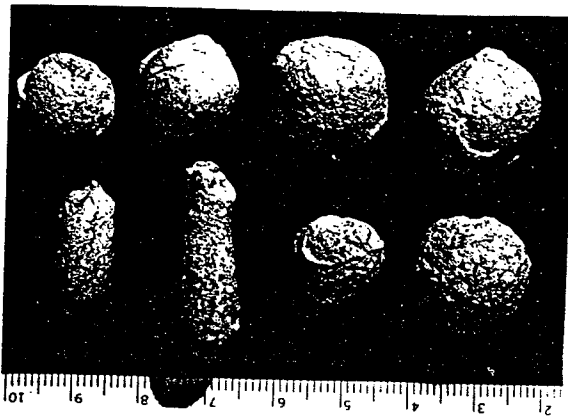


Fig. 204. Casts of likely nests of bees (two lower left) and of dung beetles (others) from the mid-Oligocene, Scenic Member, Brule Formation, Badlands National Park, South Dakota. Clockwise from the top right, these are Indiana University, Department of Geology, specimens 15690E, 15690B, 15694A, 15690D, 15690H, 15690F, 15690A, 15690G. Scale is in centimeters.

streamside gallery dissecting extensive interstream savanna (Retallack, 1981, 1982, 1983). Such vegetation is also in evidence from the mammalian fauna of these fossil soils, which consists largely of browsing woodland forms (Clark et al., 1967; Webb, 1977; Retallack, 1983). This woodland was considerably more open than that supported by better developed paleosols of a similar kind formed in this area earlier in the Oligocene. Similar fossil nests were also found in a paleosol (at 92.4 m in the measured section in the Poleside Member) identified as an Andic Ustochrept (of the U.S.D.A.) or Solonized Brown Soil (of the C.S.I.R.O.) formed under savanna. The beetles which excavated these nests lived in open grassy

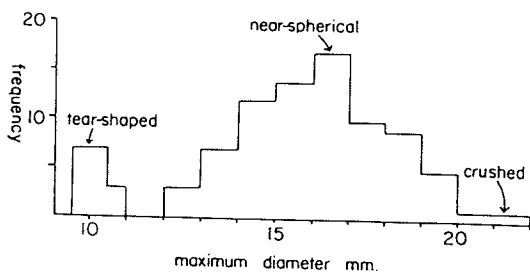


Fig. 205. Size distribution of maximum diameters of casts of 17 nests of wasps or bees and 79 nests of dung beetles from a single block at the 51.8 m level of a measured section of the mid-Oligocene, Scenic Member, Brule Formation, Badlands National Park, South Dakota. Indiana University, Department of Geology, specimen 15923.

woodlands and savannas in a warm temperate, seasonally dry, subhumid to semi-arid climate.

As collected in the field, the remains include both near-spherical (scarabacid) and elongate, tear-shaped (bee) molds of cells (Fig. 204). The tear-shaped nests are similar to those from Argentina already mentioned (Frenguelli, 1938a, b, 1939) and also to those described and named *Celliforma spirifer* by Brown (1934, 1935) from the Eocene of Wyoming, although the Oligocene fossils have not yet been found with the diagnostic spirally grooved plug of the Eocene nests. These Oligocene hymenopteran nests (*Celliforma ficoides* Retallack, 1984b) will not be considered further here. A collection of 79 of the near spherical molds collected from a single block of matrix varied from 12.2 to 21.3 mm in maximum diameter, with a mean size of 16.2 and standard deviation of 1.9 mm (Fig. 205). Some of this variation is due to compaction, presumably during late diagenesis of these deposits, because some of the casts are noticeably flattened and distorted. Even considering this, there is a wide range of diameters of the near-spherical nests. They may have been constructed by several species of beetle, but are treated as a single taxon of trace fossil (*Pallichnus dakotensis* Retallack, 1984b). Unlike those attributed to the work of wasps or bees, the near spherical molds have a thin (1-2 mm) rind of clay which is fibrous in texture and darker in color (Munsell, very pale brown, 10YR 7/3) than the surrounding matrix (white 10R 8/2). This rind has a characteristically sharp, inner boundary, along which the casts can easily be extracted from their matrix. The outer boundary of this dark rim is diffuse and irregular. In vertically oriented, sawed slabs of matrix (Fig. 206), casts of nests can be seen at the ends of burrows filled with clay darker than the surrounding matrix, but like that of the overlying B horizon of the fossil soil (these burrows are meta-tubules in the non-genetic terminology of Brewer, 1964). The burrows appear to be lateral chambers (at least three of them) 1-3 cm long, off a near vertical shaft. These relationships are disrupted by other crosscutting tubular roots of various sizes. These include fine (1-2 mm) calcite crystal tubes, and large (3-7 mm) meta-isotubules (containing prominent skeleton grains and papules).

In the arrangement of the nests in the burrow and in the nature of the nest walls, the fossil nests are similar to pupal cells of living *Geotrupes stercorarius* Linnaeus (Teichert, 1955), *G. horni* Blanchard (Howden, 1955), *Onthophagus nuchicornus* (Linnaeus) (Burmeister, 1930) and *O. landolti* Harold (Howden, 1957; Howden and Cartwright, 1963). These species

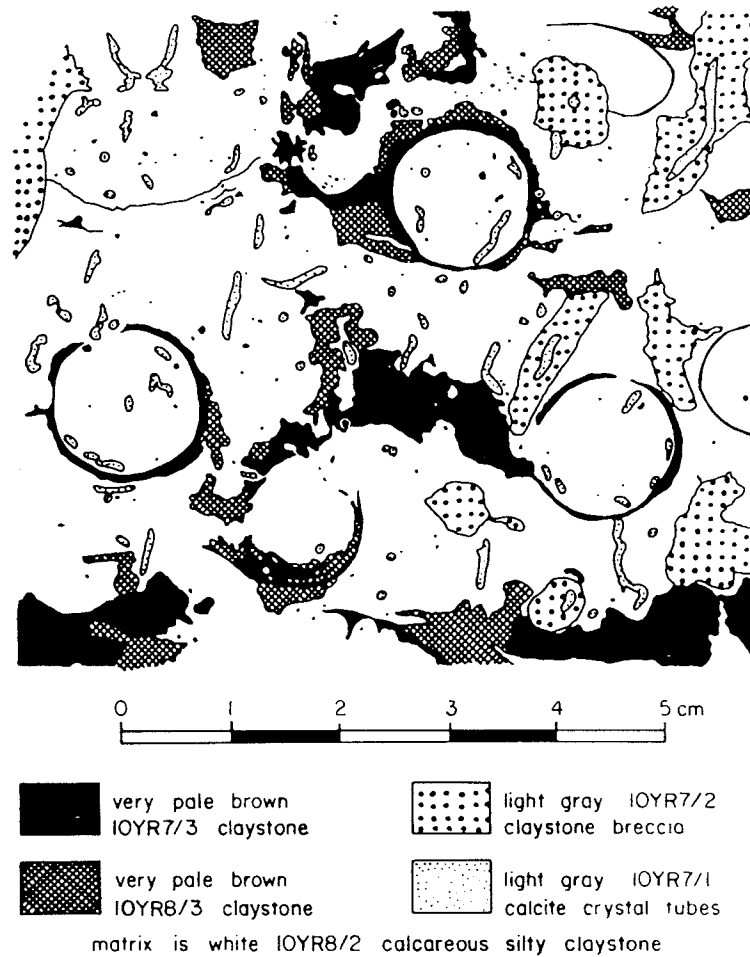


Fig. 206. Diagram of a sawed slab of the petrocalcic horizon cut perpendicular to bedding, from the 51.8 m level in a measured section of the mid-Oligocene, Scenic Member, Brule Formation, Badlands National Park, South Dakota, showing calcite crystal tubes after fine roots (fine stipple), para-isotubules after large roots (coarse stipple), meta-isotubules after burrows (black and cross-hatched), clay clasts (small and black), and hollow nests of dung beetles (large black-rimmed circle), and of wasps or bees (elliptical form at upper right only). Indiana University, Department of Geology specimen 15921B.

do not roll balls of dung, nor do they form clay-lined nests in underground chambers. They merely pack the end of chambers with dung derived from directly overhead (Group I of Halffter, 1977). This method of nesting (Group I) is thought to have been the earliest to evolve in dung beetles, and to have been inherited from similar use of plant litter by pre-existing beetles (Halffter and Matthews, 1966; Halffter, 1977). Even less elaborate behavior (a more primitive Group I behavior) is found in living beetles such as *Liatongus monstrosus* Bates which arrange eggs and masses of dung alternately within long burrows.

From these various observations and comparisons, it appears that this Oligocene species of dung beetle

made nests at the end of chambers on several (at least three) short (1–3 cm) lateral passages from a main shaft, which was near vertical to depths of up to 125 cm. The food supply for the larva was not lined with a thick coat of clay, although there may have been a thin outer layer of soil or a mixture of soil and larval and original dung. After hatching of the egg, the larva grew by consuming dung in the brood chamber. When this was nearly exhausted, the larva constructed a pupal cell from remaining uneaten dung, and larval feces. During pupation the brood chamber and associated burrows were filled with brown soil material from the overlying horizon of the soil. After emergence of the young beetle, the near spherical

pupal cell was filled with calcareous siltstone from the surrounding matrix.

Many living species of geotrupid beetle use plant litter instead of dung (Richter, 1958; Halfster and Matthews, 1966), but this is unlikely for these Oligocene beetles, considering the finely fibrous texture of the walls of the nest as examined in petrographic thin sections and under the scanning electron microscope (Retallack, 1984b), the open vegetation and subhumid to semi-arid climate likely to have created the paleosols (Retallack, 1983) and the unusually abundant fossil mammals at this stratigraphic level (Clark et al., 1967; Webb, 1977).

The fossil nests are unusually deeply buried in the paleosol, but this is not exceptional for living geotrupid beetles, such as *Lebrus apterus* Laxmann and *Ceratophyus typhoeus* Linnaeus (Burmeister, 1930; Crowson, 1981). The pupal cells of living geotrupine beetles differ in one important respect from the fossils: they are ellipsoidal. The near spherical shape of the fossil nests is most like those of modern scarabaeine beetles, such as *Ontophagus nuchicornus* Linnaeus (Burmeister, 1930) and *O. landolti* Harold (Howden, 1957; Howden and Cartwright, 1963).

The low diversity and probable Group I kind of nesting behavior for these Late Oligocene fossils, may be contrasted with the assemblage of Early Oligocene age from near Paso Flores, Argentina, already discussed. It has long been recognized that grassland ecosystems evolved earlier and further in South than in North America during the Early and Mid-Tertiary. This can especially be seen from the early and widespread appearance of high-crowned teeth (hypodonty) and of elongate, slender limbs (cursoriality) in South American fossil mammals (Webb, 1978). By Oligocene time, diverse and elaborate nesting behavior was already widespread and of considerable antiquity in savannas and open grasslands in South America, whereas from what little is known of nesting behavior in savannas and open woodlands of North America, it appears to have been only like that of living woodland beetles.

Fossil nests of dung beetles from desert shrublands of North America

It is also possible that some other North American trace fossils were produced by dung beetles. These are from the Early Miocene (Arikarean; Hunt, 1978), Harrison Formation at Eagle Crags, near Harrison, in northwestern Nebraska. This locality is best known for the large, helical burrows (*Daemonelix*) of beaver-like rodents (*Palaeocastor*) whose paleoecology has been masterfully elucidated by Martin and Bennett

(1977). As these authors correctly maintain (Häntzschel, 1975), the trace fossil, generic name, *Daemonelix*, should be restricted to the spectacular large, helical burrows (Fig. 207A-D). These are only some of the various fossils with the same characteristic silicified, white, fibrous, exterior texture, which Barbour (1897a, b) included in the genus. Under this name were included at least four different kinds of burrows, as well as fossil roots, and remains superficially similar to dung pellets and cakes and the brood chambers of burrow-stuffing, dung beetles.

The most common burrows of *Daemonelix circumaxilis* Barbour 1892 (Fig. 207A-D) are 11-14 cm in diameter and are thought to have been excavated by beaver-like rodents, *Palaeocastor fossor* (Peterson). Martin and Bennett (1977) also found a single large helical burrow of *Daemonelix*, 21 cm in diameter, which they thought was constructed by *Palaeocastor magnus* Romer and McCormack. Burrows of a third size (5-7 cm diameter) are not, or less regularly coiled (Fig. 207E; "Daemonelix irregular" of Barbour, 1897a, b). These are best removed from the genus *Daemonelix*. They are thought to have been the work of the extinct endoptychine gopher *Gregorymys* by Martin and Bennett (1977).

The smallest burrows (2-3 cm in diameter) also have abrupt, rounded ends, and often branch from the larger burrows, including both *Daemonelix* (Fig. 207C, D) and those attributed to *Gregorymys* (Fig. 207E). These are especially similar to feeding burrows of living dung beetles (Halfster and Matthews, 1966, figs. 14-19). Of comparable diameter are short lengths of burrows, sometimes with both ends rounded (Fig. 207I-K; "Daemonelix cigars or fingers" of Barbour, 1897a, b). These are similar to brood chambers of a dung beetle such as *Ontophagus*. This living genus of scarabaeine has a burrow-stuffing or Group I nesting behavior. Its larvae develop in a mass of dung stuffed into the end of a burrow or chamber, and sealed off from the outside by a plug of earth. Also compatible with this kind of nesting behavior are flattened masses superficially similar to dung cakes, with connected portions of burrows, also about 2 to 3 cm in diameter (Fig. 207F; "Daemonelix cakes" of Barbour, 1897a, b). Perhaps these Miocene beetles, like *Ontophagus*, provisioned their brood chambers with dung derived from directly overhead rather than rolling it overland. Since the likely dung beetle burrows are associated with several kinds of vertebrate burrows and appear at stratigraphic levels below the oldest vertebrate burrows, then it is unlikely that they were obligate inhabitants of vertebrate burrows like some modern species of *Ontophagus* (Halfster and Matthews, 1966, p. 205).

Also found at Eagle Crags were balls of similar fibrous material (Fig. 207G, H; "Daemonelix balls" of Barbour, 1897a, b). Only some of these (Fig. 207H) are of a size compatible with the likely beetle burrows, and these are just as likely to have been dung pellets as brood or food balls of dung beetles.

Finally, there are abundant root traces (Fig. 207L; "great tubes of *Daemonelix*" and "Daemonelix fibers"

of Barbour, 1897a, b). In some cases their cellular, internal structure is preserved in chert (Fig. 207M). Root traces of this kind were found isolated in the matrix and closely adpressed to bones and to the surface of all the burrows (Fig. 207B), cakes, balls and fingers (Barbour, 1887a, b; Marsland, 1897), thus bestowing their characteristic white, fibrous appearance. As Martin and Bennett (1977) have discussed at

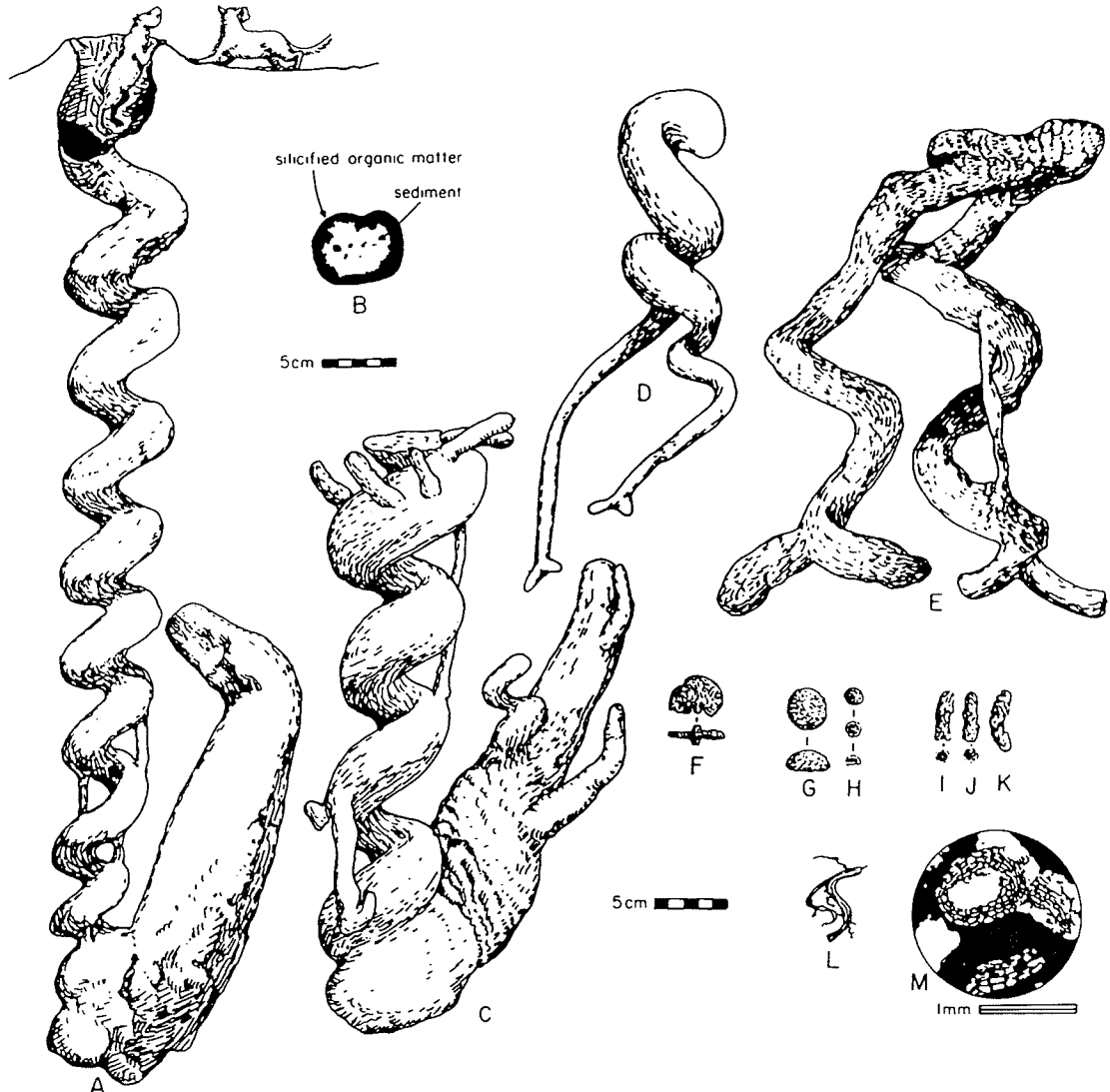


Fig. 207. Trace fossils from the Early Miocene, upper Harrison Formation, of northwest Nebraska, all drawn to the same scale, except M ($\times 4$). A. Reconstructed helical burrow of *Daemonelix circumaxilis* and its constructor, the beaver *Palaeocastor fossor*. B. Cross-section of a *Daemonelix* burrow, showing silicified roots and other organic matter (black) and sedimentary fill (stipple). C, D. Additional *Daemonelix* burrows with smaller burrows, possibly of dung beetles. E. Burrow of a size attributed to the extinct endoptychine gopher *Gregorymys*, with a smaller burrow, possibly of a dung beetle. F. Possible dung cake and small burrow, possibly of a dung beetle. G, H. Possible pellets of dung. I-K. Possible brood-chambers of a dung beetle with geotrupine nesting behavior. L. Fossil root trace. M. Preserved cellular structure of silicified roots. (Rescaled and redrawn from Barbour, 1897a, b; Marsland, 1897; and Martin and Bennett, 1977.)

length, any weakness in these ashy, sandy soils, such as pre-existing burrows, would have been a favored location for root growth.

From my own examination of Eagle Crags (made with the generous assistance of Dr. R.M. Hunt during the summer of 1981), the distribution of these various trace fossils within the sequence is just as depicted in Barbour's sketch (1897a, fig. 19; 1897b, plate 20) except that each kind of trace fossil can be found to the top of the exposed sequence from its lowest appearance. From the various interpretations offered here, this short (about 70 m) sequence appears to record an amelioration of conditions and increasing community diversity with time. Coprolites became more diverse as a variety of fecal pellets supplemented cake-like piles of dung, which occur at lower stratigraphic levels. At these lower levels likely burrows of insects were shallow and sparse. Possible brood chambers of dung beetles became prominent in a higher part of the sequence. To these burrows were later added those thought to be made by gophers (*Gregorymys*) and finally the large *Daemonelix* burrows of *Palaeocastor*. Fossil soils in the sequence are evidence of concurrent changes towards greater stability of the land surface with time. No fossil soils can be seen at the base of the sequence, a few weakly developed fossil soils appear at the level where the possible brood chambers of dung beetles first appear, and there is a thick, well developed paleosol near the top of Eagle Crags. These were all calcareous soils, with a prominent caliche horizon when well developed. They were probably Aridisols, Inceptisols, or Mollisols, supporting savanna or open shrublands in a semiarid to arid climate. The little weathered, ashy, loess-like nature of these sediments is also an indication of a semiarid, desert like climate (Schultz, 1942; Martin and Bennett, 1977; Hunt, 1978). From the presence of numerous *Daemonelix* burrows extending to depths of up to 3 m (Martin and Bennett, 1977), it can be assumed that permanent water table was at least that deep. It may have retreated to even deeper levels seasonally because fossils other than vertebrates found in a nearby channel deposit included only diatoms, charophytes and ostracodes, all aquatic organisms which can withstand periodic severe desiccation (Hunt, 1978). Fossil mammals in this assemblage were mostly chalicotheres, rhinoceroses, horses and bear-like amphicyonids, a mixture of browsers, grazers and carnivores, which also provide evidence of savanna or shrubland vegetation (Hunt, 1978).

In such an habitat, the abundant organic material associated with the large helical burrows would have been a conspicuous resource for dung beetles. Some

of this organic matter was clearly living roots of plants, now beautifully preserved, but there is so much unorganized fibrous and amorphous silicified material in these large burrows that it is likely that dung, plant litter, decaying roots, humus and fungi were also present. Many comparable modern burrows of vertebrates also house scarabaeoid beetles. In some cases the beetles and their vertebrate hosts are probably indifferent to each other (commensal), but for some species of beetles which are associated strictly with particular species of vertebrates, the relationship may be mutually beneficial (mutualistic). The dung beetle *Outbopbagus cynomysi* Brown for example, is only found in the burrows of the prairie dog (really a rodent), *Cynomys ludovicianus* (Ord) (Halffter and Matthews, 1966, p. 48). The use of vertebrate burrows is common and characteristic of scarabaeoid beetles living in arid climates where deep, large burrows provide a refuge from extremes of temperature and dryness (Halffter and Matthews, 1966, p. 205). Although the evidence of trace fossils is necessarily circumstantial, this fossil assemblage of Early Miocene age from northwestern Nebraska may be a record of the association of burrowing vertebrates and dung beetles in a semiarid climate.

Conclusions

The fossil record of nests of dung beetles described here extends back to the first appearance of savanna and other open grassland vegetation in both North and South America, as assessed from the evidence of fossil mammals (Webb, 1977, 1978) and soils (Retallack, 1982, 1983). This adds credence to the view of Halffter and Matthews (1966) that dung beetles arose in and evolved along with grasslands, where they remain most diverse today. They probably arose independently on each continent from pre-existing phytophagous, saprophagous or necrophagous scarabaeid beetles because from their very first appearance in the fossil record they were provincial in their nesting behavior. Group I nesting behavior is still characteristic of dung beetles in North America, and Group II behavior in South America, even where dung beetle assemblages of northern and southern affinities now mix in Mexico (Halffter and Matthews, 1966; Halffter, 1974, 1976). This limited mixing of assemblages of dung beetles in Central America is surprising compared to the extensive interchange of mammals since the Late Pliocene (Marshall et al., 1982) when a continuous land bridge between North and South America was established. Halffter and Matthews (1966) also envisage the evolution of assemblages of dung beetles characteristic of wood-

lands and of arid lands as secondary radiations from those of grasslands. From what little is now known, this is also supported by the fossil record of dung beetles. Scarabeid nests are only known in woodland and arid land paleosols as old as Oligocene, post-dating their appearance in savanna and other grassy vegetation in both North and South America.

Given the limited occurrences of likely fossil nests of dung beetles known, these agreements between evolutionary scenarios based on study of modern dung beetles and on the fossil record must be regarded with suspicion. They clearly need to be tested against a greater number of cases. The fossil record of nests of dung beetles in the Americas is still inadequate. What were they like in the rest of the world? Did scarab beetles use the dung of dinosaurs, and in what ways? These questions remain unanswered, probably because few suspect the nature of these problematic, nodule-like, trace fossils. To those in pursuit of fossil land vertebrates in alluvial sequences, consider the sacred scarab; it may bring good luck!

REFERENCES

- Andreis, R. R. 1972. Paleosuelos de la formación Musters (Eoceno medio), Laguna del Mate, Prov. de Chubut, Rep. Argentina. Revista de la Asociación Argentina de Mineralogía, Petrología y Sedimentología, v. 3, p. 91-97.
- Arnett, R. H. 1963. The Beetles of the United States. Catholic University of America Press, Washington, 1112 p.
- Arnoldi, L. V. and others 1977. Mesozoiskie Zhestkokrilie (Mesozoic Coleoptera). Paleontologicheskogo Instituta Nauk S.S.S.R., Moskva, Trudy, 161: 204 p.
- Balthasar, V. 1963. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region. Tschechoslowakische Akademie der Wissenschaften, v. 1, 391 p.
- Barbour, E. H. 1892. Notice of new gigantic fossils. Science, v. 19, p.99-100.
- Barbour, E. H. 1897a. Nature, structure and phylogeny of Daemonelix. Bulletin of the Geological Society of America, v. 8, p. 305-314.
- Barbour, E. H. 1897b. History of the discovery and report of progress in the study of Daemonelix. University of Nebraska University Studies, v. 2(2), p. 81-124.
- Bonino de Langguth, V. 1978. Nidos de insectos fosiles del Cretacico Superior del Uruguay. Revista del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia" Paleontología, v. 2(4), p. 65-75.
- Bornemissza, G. E. 1976. The Australian dung beetle project, 1965-1975. Australian Meat Research Committee Review, v. 30, p. 1-30.
- Brewer, R. 1964. Fabric and Mineral Analysis of Soils. Wiley, New York, 470 p.
- Britton, E. B. 1970. Coleoptera. In C.S.I.R.O., Insects of Australia. Melbourne University Press, Melbourne, p. 495-621.
- Brown, R. W. 1934. Celliforma spirifer, the fossil larval chambers of mining bees. Journal of the Washington Academy of Science, v. 24, p. 532-539.

- Brown, R. W. 1935. Further notes on fossil larval chambers of mining bees. ibid., v. 25, p. 526-528.
- Burmeister, F. 1930. Die Brutfürsorge und das Bauprinzip der Gattung Onthophagus Latreille. Zeitschrift für Morphologie und Ökologie der Tiere, v. 16, p. 559-647.
- Clark, J., J. R. Beerbower and K. K. Kietzke 1967. Oligocene sedimentation in the Big Badlands of South Dakota. Fieldiana Geology Memoirs, v. 5, 158 p.
- Frenguelli, J. 1938. Nidi fossili di Scarabeidi e Vespidi. Bolletino della Societa Geologica Italiana, v. 57, p. 77-96.
- Frenguelli, J. 1939. Nidos fósiles de insectos en el Terciario del Neuquén y Río Negro. Notas del Museo de La Plata, v. 4, Paleontologia, no. 18, p. 379-402.
- Frenguelli, J. 1946. Un nido de esfégido del Cretáceo superior del Uruguay. Notas del Museo de La Plata, v. 11, Paleontologia no. 90, p. 259-267.
- Grabau, A. W. 1928. Stratigraphy of China. Part II. Mesozoic. Geological Survey of China, Peking, 774 p.
- Grande, L. 1980. Paleontology of the Green River Formation, with a review of the fish fauna. Bulletin of the Geological Survey of Wyoming, v. 63, 333 p.
- Halffter, G. 1974. Elements anciens de l'entomofaune neotropicale: ses implications biogeographiques. Quaestiones Entomologicae, v. 10, p. 223-262.
- Halffter, G. 1976. Distribucion de los insectos en la zona de transicion Mexican. Relaciones con la entomofauna de Norteamerica. Folia Entomologica Mexicana, v. 35, 64 p.
- Halffter, G. 1977. Evolution of nidification in the Scarabaeinae (Coleoptera, Scarabaeidae). Quaestiones Entomologicae, v. 13, p. 231-253.
- Halffter, G. and E. G. Matthews 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomologica Mexicana, v. 12-14, 281 p.
- Häntzschel, W. 1975. Treatise on invertebrate paleontology. Part W, Miscellanea.

- Supplement 1. Geological Society of America and University of Kansas, Boulder and Lawrence, 269 p.
- Heinrich, B. and G. A. Bartholomew 1979. The ecology of the African dung beetle. *Scientific American*, v. 241, p. 146-156.
- Howden, H. F. 1955. Biology and taxonomy of North American beetles of the subfamily Geotrupinae, with revisions of the genera Bolbocerosoma, Eucanthus, Geotrupes and Peltotrupes (Coleoptera). *Proceedings of the United States National Museum*, v. 104, p. 151-319.
- Howden, H. F. 1957. Investigations on sterility and deformities of Onthophagus (Coleoptera: Scarabaeidae) induced by gamma radiation. *Annals of the Entomological Society of America*, v. 50, p. 1-9.
- Howden, H. F. and O. L. Cartwright 1963. Scarab beetles of the genus Onthophagus Latreille, north of Mexico (Coleoptera: Scarabaeid). *Proceedings of the U. S. National Museum*, v. 114, p. 1-113.
- Hunt, R. M. 1978. Depositional setting of a Miocene mammal assemblage, Sioux County, Nebraska, U.S.A. *Palaeogeography, Palaeoclimatology, Paleoecology*, v. 24, p. 1-52.
- Landin, B.-O. 1961. Ecological studies on dung beetles. *Opuscula Entomologica Supplementum*, v. 19, 227 p.
- Marshall, L. G., R. Pascual, G. H. Curtis and R. E. Drake 1977. South American geochronology: radiometric time scale for middle to late Tertiary mammal-bearing horizons in Patagonia. *Science*, v. 195, p. 1325-1328.
- Marshall, L. G., S. D. Webb, J. J. Sepkoski and D. R. Raup 1982. Mammalian evolution and the Great American Interchange. *Science*, v. 215, p. 1351-1357.
- Marsland, T. H. 1897. Notes on the chemical composition of the siliceous tubes of the Devil's Corkscrew, *Daemonelix*. *University of Nebraska University Studies*, v. 2(2), p. 125-129.

- Martin, L. D. and D. K. Bennett 1977. The burrows of the Miocene beaver Palaeocastor, western Nebraska, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 22, p. 173-193.
- Menendez, C. A. 1971. Floras terciarias de la Argentina. *Ameghiniana*, v. 8, p. 357-371.
- Prothero, D. R., Denham, C. R. and Farmer, H. G. 1982. Oligocene calibration of the magnetic polarity time scale. *Geology*, v. 10, p. 650-653.
- Retallack, G. J. 1981. Fossil soils: indicators of ancient terrestrial environments. In K. J. Niklas (ed.), *Paleobotany, Paleocology and Evolution*. Praeger, New York, p. 55-102.
- Retallack, G. J. 1982. Paleopedological perspectives on the development of grasslands during the Tertiary. *Proceedings of the Third North American Paleontological Convention*, v. 2, p. 417-421.
- Retallack, G. J. 1983. Late Eocene and Oligocene paleosols of Badlands National Park, South Dakota. *Special Paper of the Geological Society of America* 193:82 p.
- Retallack, G. J. 1984. Trace fossils of burrowing beetles and bees in an Oligocene paleosol, Badlands National Park, South Dakota. *Journal of Paleontology*, v.58, p. 571-592.
- Richter, P. O. 1958. Biology of Scarabaeidae. *Annual Review of Entomology*, v. 3, p. 311-334.
- Rodendorf, B. B. and A. P. Rasnitsyn 1980. *Istoricheskoe razvitie klassa nasekomikh (Historical development of the class Insecta)*. Akademiya Nauk S.S.S.R., Paleontologicheskogo Instituta, Trudy, v. 175, 269 p.
- Roselli, F.L. 1939. Apuntes de geología y paleontología uruguayas y sobre insectos del Cretáceo del Uruguay o descubrimientos de admirables instantos constructivos de esa época. *Boletín de la Sociedad de los Amigos de las Ciencias Naturales "Kraglievich-Fontana"*, Nueva Palmira, v. 1(2), p. 29-102.
- Roselli, F.L. 1976. *Contribución al estudio de la Geo Paleontología*. Depts Colonia y Soriano, Montevideo, 176 pp.

- Sauer, W. 1955. *Coprinsphaera Ecuadoriensis*, un fósil singular del Pleistógeno. Boletín del Instituto de Ciencias Naturales de la Universidad Central, Quito, v. 1(2), p. 123-129.
- Sauer, W. 1956. *Coprinsphaera ecuadoriensis* (bola de cangahua) y las esferas elaboradas actualmente por escarabajos de la familia Scarabaeidae. Boletín de Informaciones Científicas Nacionales, Quito, v. 8, p. 550-555.
- Schlüter, T. 1984. Kretazische Lebenssuren von solitären Hymenopteren und ihr Nomenklatur. Aufschluss, Heidleberg, v.35, p.423-430.
- Schultz, C. B. 1942. A review of the Daimonelix problem. University of Nebraska Studies in Science and Technology, v. 2, p. 5-30.
- Soil Survey Staff 1975. Soil Taxonomy. United States Department of Agriculture Handbook, v. 436, 754 p.
- Spalletti, L. A. and M. M. Mazzoni 1978. Sedimentología del Grupo Sarmiento en el perfil ubicado al sudeste del Lago Colhué Huapi, Provincia de Chubut. Obra del Centenario del Museo de La Plata, v. 4, p. 261-283.
- Stace, H.C.T., G. D. Hubble, R. Brewer, K. H. Northcote, J. R. Sleeman, M. J. Mulcahy and E. G. Hallsworth 1968. A Handbook of Australian Soils. Rellim, Adelaide, 435 p.
- Teichert, M. 1955. Biologie und Brutfürsorgemassnahmen von Geotrupes mutator Marsh. und Geotrupes stercorarius L. (Col. Scarab.). Wissenschaftliche Zeitschrift der Martin-Luther-Universität Halle-Wittenberg, v. 5(2), p. 187-218.
- Volkheimer, W. 1971. Aspectos paleoclimatológicos del Terciaria Argentino. Revista del Museo Argentino de las Ciencias Naturales "Bernadino Rivadavia," Paleontologia, v. 1, p. 243-262.
- Waterhouse, D. F. 1974. The biological control of dung. Scientific American, v. 230, p. 101-109.
- Webb, S. D. 1977. A history of savanna vertebrates in the New World. Part I. North America. Annual Review of Ecology and Systematics, v. 8, p. 355-380.

Webb, S. D. 1978. A history of savanna vertebrates in the New World. Part II.

South America and the Great Interchange. ibid., v. 9, p. 393-426.

Wilson, E. O. 1971. Insect Societies. Harvard University Press, Cambridge,

548 p.

Wilson, M.V.H. 1977. New records of insect families from the freshwater Middle

Eocene of British Columbia. Canadian Journal of Earth Sciences, v. 14, p.

1139-1155.