TRACE FOSSILS OF BURROWING BEETLES AND BEES IN AN OLIGOCENE PALEOSOL, BADLANDS NATIONAL PARK, SOUTH DAKOTA

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ABSTRACT—Trace fossils of beetles and bees are preserved in the petrocalcic horizon of a paleosol of early late Oligocene age within the upper Scenic Member of the Brule Formation in the Pinnacles area, Badlands National Park, South Dakota. The paleosol has a greenish-gray A horizon over a reddish-brown B horizon, and it has been identified as a Petrocalcic Paleustalf. It formed under streamside, gallery woodland. This and an extensive savanna of interfluves grew in a warm temperate and subhumid climate.

Near-spherical internal molds of chambers which terminated short subhorizontal branches from deep vertical burrows have been interpreted as pupal cells of beetles, most like those of dung beetles (Coleoptera, Scarabaeidae, subfamilies Geotrupinae and Scarabaeinae). These trace fossils (*Pallichnus dakotensis* ichnogen. et ichnosp. nov.) are indications of a greater degree of brood care than in some Geotrupinae but less than in most Scarabaeinae.

Tear-shaped internal molds of subhorizontal cells clustered along deep vertical shafts, are interpreted as larval cells of bees, most like those of sweat bees (Hymenoptera, Halictidae, Halictinae). These trace fossils (*Celliforma ficoides* ichnosp. nov.) are uncertain indicators of the degree of social behavior, which was certainly much less than that seen in modern paper wasps and honey bees.

The presence of both these kinds of trace fossils supports previous hypotheses indicating the importance of dry, warm grasslands and grassy woodlands for the adaptive radiation of both dung beetles and bees during Tertiary time. These Oligocene fossils are evidence that some aspects of the continuing coevolution of these and other elements of grassland ecosystems had been initiated, but this Oligocene ecosystem was still far short of modern levels of sophistication and interdependence.

The following new taxa are proposed: *Pallichnus dakotensis* ichnogen. et ichnosp. nov. and *Celliforma ficoides* ichnosp. nov.

INTRODUCTION

CHARLES DARWIN (1859) clearly appreciated the interrelationships of living things and the soil in his invitation "to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing in the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and so dependent upon each other in so complex a manner, have all been produced by laws acting around us." As Darwin also understood, the fossil record of such an ecosystem would be meager indeed; at best a few bones or phytoliths, or perhaps some leaves and pollen in deposits of a nearby bog or stream. Another source of information about the coevolution of different parts of an ecosystem is the nature of the soil on which it developed and of burrows and other traces of soil organisms.

Fossil soils (paleosols) may be evidence of former climate, plants and other organisms, topography, parent material and time for formation (Retallack, 1981). Paleosols, like trace fossils, have an additional advantage. They are in place, where they formed, and can be directly related to sedimentary facies and paleoenvironments. They are also evidence of ancient environments independent of associated fossil bones or leaves, and can be used to check or enlarge interpretations of past life based on such remains. In this paper, a single fossil soil, and its trace and body fossils, are interpreted to reconstruct a few parts of an ancient ecosystem.

The classifications used in this paper include those of Arnett (1963) for beetles, and Krombein et al. (1979) and Michener (1974) for wasps and bees. The specimens described are in the collections of the Geology Department, Indiana University, Bloomington. Chemical analyses were obtained on an ARL EMX-SM Electron Microprobe in the Department of Geology, University of Oregon.
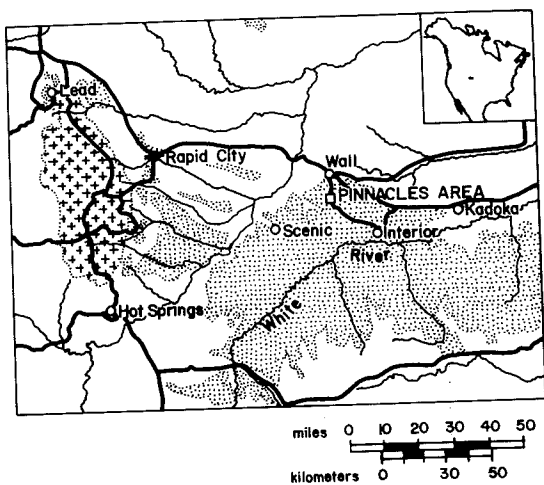
FIGURE 1—Location of the Pinnacles area in southwestern South Dakota showing rivers (fine lines), U.S. highways (thick lines), crystalline and metamorphic core of the Black Hills (crosses) and outcrop area of late Eocene to Oligocene, White River Group (stipple).

A FOSSILIFEROUS PALEOSOL

Many paleosols have been found in the late Eocene and Oligocene, White River and lower Arikaree groups of Badlands National Park, South Dakota (Figure 1). Eighty-seven paleosols of ten different kinds (series) have been recognized in a detailed measured section (Figure 2) in the Pinnacles area of the park (Retallack, 1983). The paleosol described here (Figures 3, 4) contains abundant tear-shaped and near-spherical trace fossils in its lower part. Similar trace fossils also occur in other paleosols of the sequence, but are not so well preserved or abundant in them. The Badlands of South Dakota are better known for other kinds of fossils: a variety of root traces (Retallack, 1983), endocarps ("pits") of hackberry (Chaney, 1925), aquatic invertebrates (Cook and Mansfield, 1933; Gries and Bish-
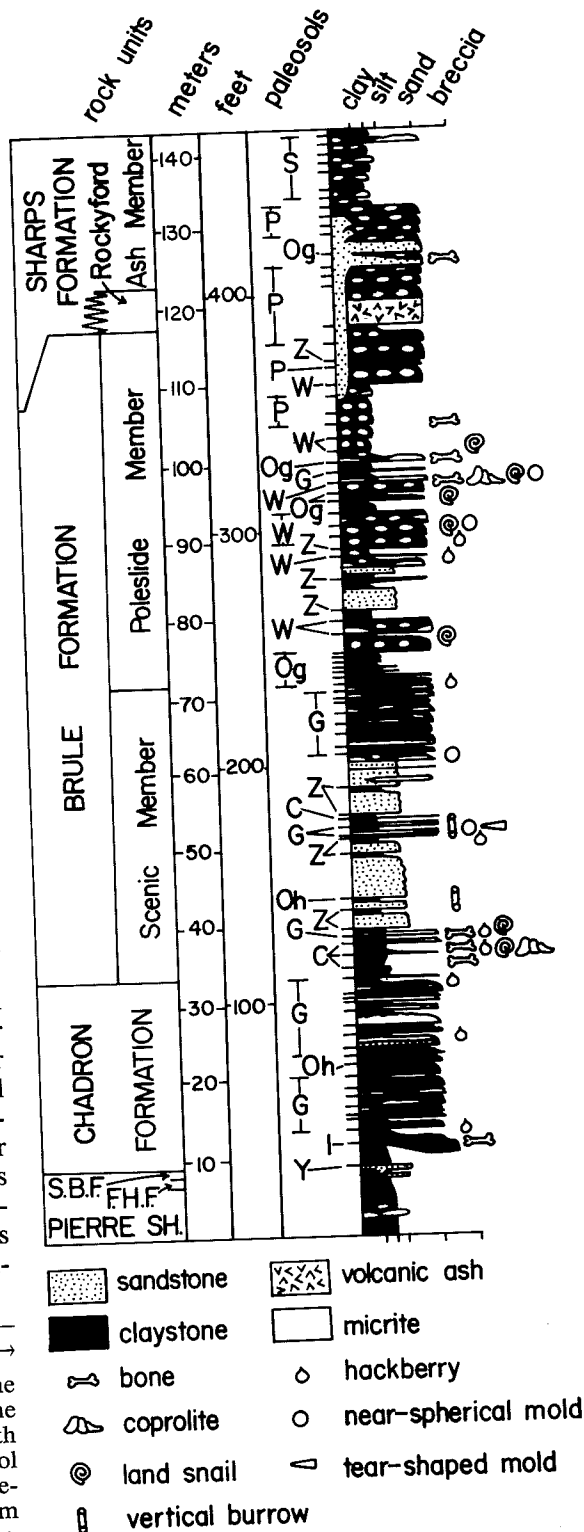
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FIGURE 2—Simplified stratigraphic section of the White River and lower Arikaree groups in the Pinnacles area, Badlands National Park, South Dakota. Section and abbreviations for paleosol series are based on more detailed work of Retallack (1983). Other abbreviations are for Slim Buttes Formation (S.B.F.) and Fox Hills Formation (F.H.F.).
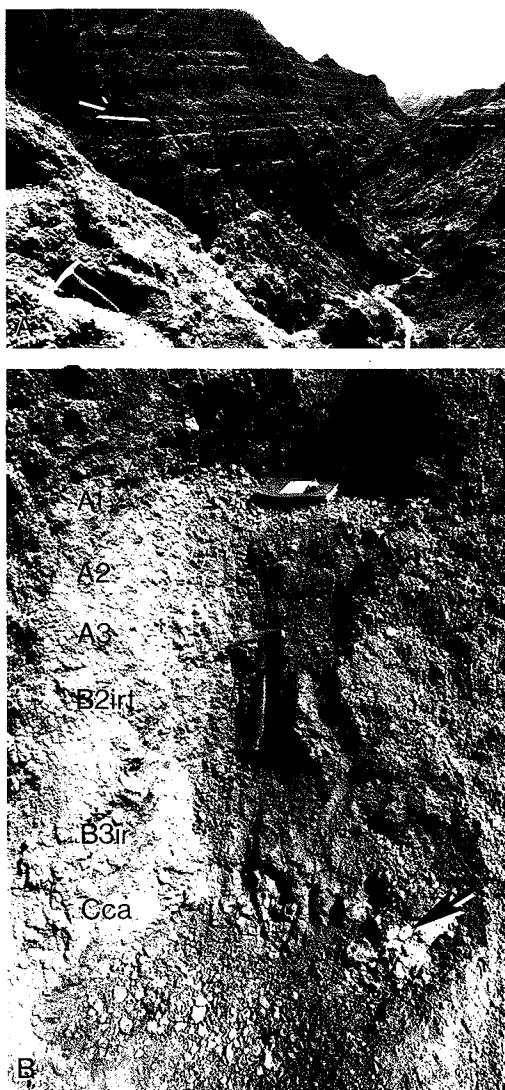
FIGURE 3—Unnamed Gleska paleosol 30. *A,* excavated at hammer (lower left) and visible in cliff (petrocalcic horizon arrowed). *B,* excavated and labelled with interpreted soil horizons, showing natural popcorn-weathered surface (right hand side) and petrocalcic horizon with *Pallichnus dakotensis* ichnogen. et ichnosp. nov. (at arrow) and *Celliforma ficoides* ichnosp. nov. This paleosol is in the upper Scenic Member, 1.3 km southeast of Pinnacles Lookout, Badlands National Park.

FIGURE 4—Columnar section of unnamed Gleska paleosol 30, 1.3 km southeast of Pinnacles Lookout, Badlands National Park, South Dakota.

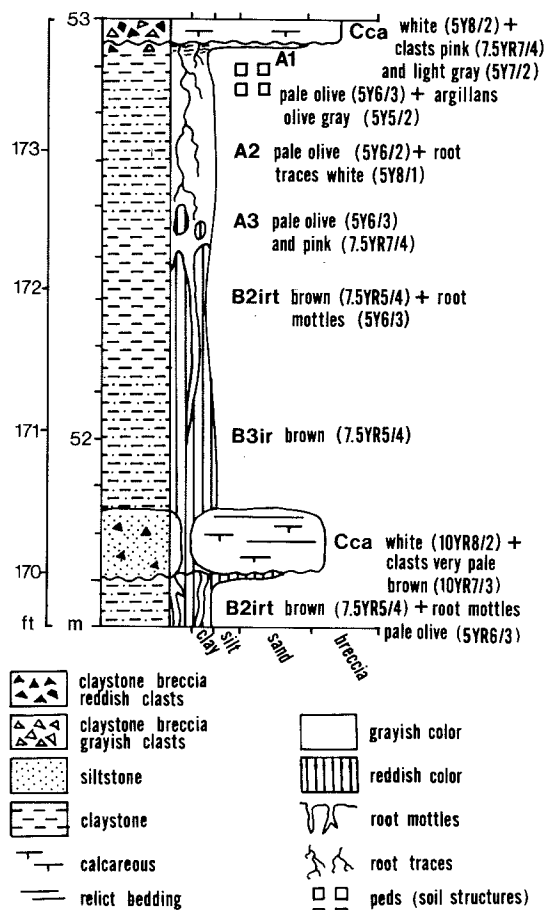op, 1966), shells of land snails (Wenz, 1923), coprolites (Edwards, 1973; Edwards and Yatkola, 1974), animal tracks (Lemley, 1971; Bjork, 1976) and bones of fish, tortoises, lizards, alligators, birds, and mammals (Clark, Beerbower and Kietzke, 1967; Wilson, 1975; Webb, 1977; Bjork and MacDonald, 1981).

The paleosol with especially well-preserved trace fossils is in the upper part of the Scenic Member of the Brule Formation (paleosol no. 30, at 51.8 m (170 ft) in the measured section of Retallack, 1983). Judging from paleomagnetic and biostratigraphic correlations (Prothero, 1982; Prothero, Denham and Farmer, 1982), this paleosol falls within the late Orellan North American Land-Mammal Age, the early part of the late Oligocene, the early part of Chron 10, and is approximately 31 million years old.

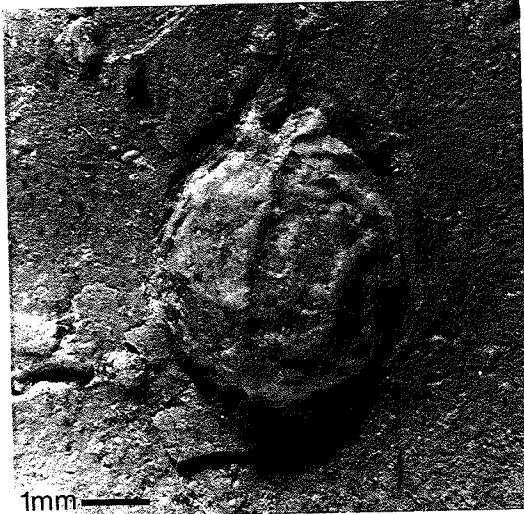The fossiliferous paleosol (Figures 3 and 4)

FIGURE 5—Fossil endocarp ("pit") of hackberry, *Celtis hatcheri* Chaney 1925, in matrix (specimen IU15907A), from unnamed Gleska Series paleosol 29 in the measured section of Retallack (1983), Scenic Member, Pinnacles area, Badlands National Park.

is a thick (115 cm), massive bed of claystone. The uppermost 5 cm of the paleosol (horizon A1) is partly brecciated and cracked, and immediately underlies the erosional surface at the base of the overlying bed. Below this dark, brecciated layer is 25 cm of pale olive, silty claystone (horizon A2), containing calcite-filled root traces and olive gray, clay skins (argillans). This layer passes gradationally into the underlying 35 cm of brown claystone (B2irt) through a mottled layer (A3) some 15 cm thick. Drab, grayish-green mottles forming haloes around root traces penetrate deeply into the brown B horizon. These drab mottles are abundant in the transitional layer (A3), but they are sparse in the underlying brown claystone (B2irt). Down to this level in the paleosol (80 cm to the base of horizon B2irt) the claystone has a hackly appearance, from subangular blocky clods (peds), defined by clayey and slickensided surfaces (cutans). Below this level for another 20 cm (horizon B3ir) the claystone is more massive and there are slight variations in grainsize, suggestive of relict bedding. Below this again is a nodular, nearly continuous horizon of micritic limestone, about 15 cm thick (a petrocalcic or Cca horizon).

This paleosol is here termed unnamed Gleska paleosol 30, within the local system of nomenclature for these Oligocene paleosols (Retallack, 1983). Like other Gleska-Series paleosols in the same area it probably had a sparse moder humus, a silty gray A horizon of neutral pH, a clayey illuviated B horizon of alkaline pH, and a hard petrocalcic horizon at depth. It has been identified as a Petrocalcic Paleustalf (of Soil Survey Staff, 1975) and a Red Brown Earth (of Stace et al., 1968). Such soils form in seasonally dry or cool, semiarid to subhumid, and subtropical to warm temperate, climates.

The size and distribution of root traces in this paleosol, as well as comparisons with modern soils of the same kind, are indications that it formed under open woodland (Retallack, 1983). The only direct remains of this vegetation are endocarps of hackberries (*Celtis hatcheri* Chaney 1925; Figure 5), which were not found in this paleosol, but are known from other Gleska-Series paleosols of this area. The endocarps were probably favored for preservation by an original stony composition like that of living hackberries (*Celtis occidentalis*; Yanovsky et al., 1932; Lanning, 1961). Presumably there were also other species of trees. Like Oligocene vegetation in the Rocky Mountains (Leopold and MacGinitie, 1972) and the Gulf Coast (Daghlian, Crepet and Delevoryas, 1980), as well as vegetation of the Great Plains during the early Eocene (Hickey, 1977) and early Miocene (MacGinitie, 1962), it is likely that trees growing in this paleosol were mainly dicotyledonous angiosperms. There is no direct evidence for the nature of the herbaceous ground cover, responsible for fine root traces near the surface of the paleosol. It may have included grasses, which had certainly evolved earlier during the Tertiary (Stebbins, 1981; Retallack, 1982), as well as other angiospermous herbs and small shrubs. Grasses of the tribe Stipeae and forbs of the family Boraginaceae are represented by fossil fruits in Miocene and younger sediments of the Great Plains (Thomasson, 1979). Paleosols of the Gleska Series are found overlying or underlying sandstone paleochannels, and separate paleochannels from other kinds of paleosols (Conata Series), which appear to have supported savanna vegetation (Retallack, 1983). The open woodlands of Gleska-Series paleo-

sols thus appear to have formed broad galleries along streams.

No bones were found in the paleosol described here, although other Gleska Series paleosols contain a distinctive fossil fauna. Fossil land snails [*Pseudolisinoe leidyi* (Hall and Meek) Wenz 1923; Figure 6] are found in both Gleska and Conata Series paleosols of the Scenic Member. Mammalian fossils of Gleska-Series paleosols include largely tortoises (*Stylemys*), oreodons (*Merycoidodon*) and horses (*Mesohippus*), with common squirrel-like rodents (*Ischyromys*) and rabbits (*Palaeolagus*). Some of these paleosols also have yielded concentrations of duck-like (anatine) eggs and pig-like entelodonts (*Archaeotherium*). There are many other, rarer elements of the fossil fauna of the Scenic Member, which also may have roamed Gleska-Series soils (Harksen and MacDonald, 1969; Retallack, 1983). This fauna of stream-side woodlands consisted of animals generally larger than those in adjacent savanna soils (Conata Series), where there were largely rabbits (*Palaeolagus*), squirrel-like rodents (*Ischyromys*) and small deer-like ruminants (*Leptomeryx* and *Hypertragulus*).

During deposition of the upper Scenic Member, Badlands National Park was a broad, low-gradient floodplain flanking the Black Hills to the west. Streams were low to moderate in sinuosity and braided in some reaches (Clark, Beerbower and Kietzke, 1967). Judging from their sandstone paleochannels, these streams were not deeply incised into their floodplain and were flanked by levees of low relief. Gleska-Series paleosols appear to have formed in positions flanking these streams, and are commonly truncated by the steep, cut banks of paleochannels. Other kinds of soils formed on swales and mounds of point bars (Zisa Series) and on dry floodplains, away from streams (Conata Series). The water table was usually deeper than the petrocalcic horizon of the fossiliferous paleosol described here. Since there are few drab mottles or other indications of waterlogging in the underlying paleosol, the permanent water table may have been deeper than 1.5 m.

Like other Gleska-Series paleosols, the example described here formed on a mixture of re-sorted soil material, airfall volcanic ash and alluvium from the Black Hills (Retallack, 1983). Claystone breccia is not as prominent
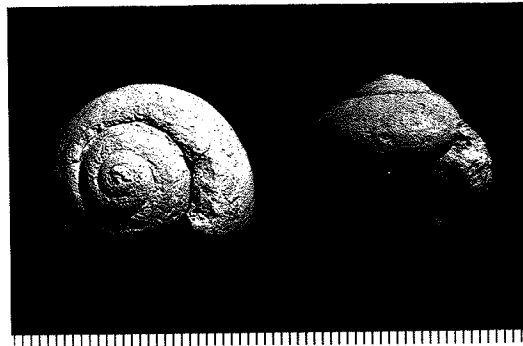

FIGURE 6—Fossil land snail, *Pseudolisinoe leidyi* (Hall and Meek) Wenz 1923. Specimens IU15912A (left) and IU15788A (right), from A horizons of unnamed Ogi Series paleosol 59 and Wisangie Series paleosol 60 (respectively), in measured section of Retallack (1983), Poleslide Member, Pinnacles area, Badlands National Park.

a feature of this paleosol as of other Gleska Series paleosols. Clasts re-sorted from other soils may have been a less important component of its parent material.

On the basis of comparison with modern soils with calcareous horizons developed to a similar degree (Gile, Peterson and Grossman, 1966; Williams and Polach, 1971; Birkeland, 1974), a very conservative estimate of the time elapsed during the formation of this paleosol is 6,000 years (Retallack, 1983). Within Birkeland's (1974) scale as modified by Retallack (1983), the paleosol is strongly developed. I have been able to analyze this paleosol in relation to work on the time for soil development in central California (Harden, 1982; Dembroff et al., 1982). Although the California soils formed in a different climate (Mediterranean) and parent materials (granitic), it is likely that the actual time for formation of the Gleska-Series paleosols was much greater than previously estimated.

PUPAL CELLS AND BROOD BURROWS OF DUNG BEETLES

The most common kind of trace fossil in the petrocalcic horizon of unnamed Gleska paleosol 30 is near-spherical internal molds of silty micrite, which are easily separated from their matrix (Figure 7). Some of these are irregular in shape. Some are slightly ellipsoidal. Many have been slightly flattened,
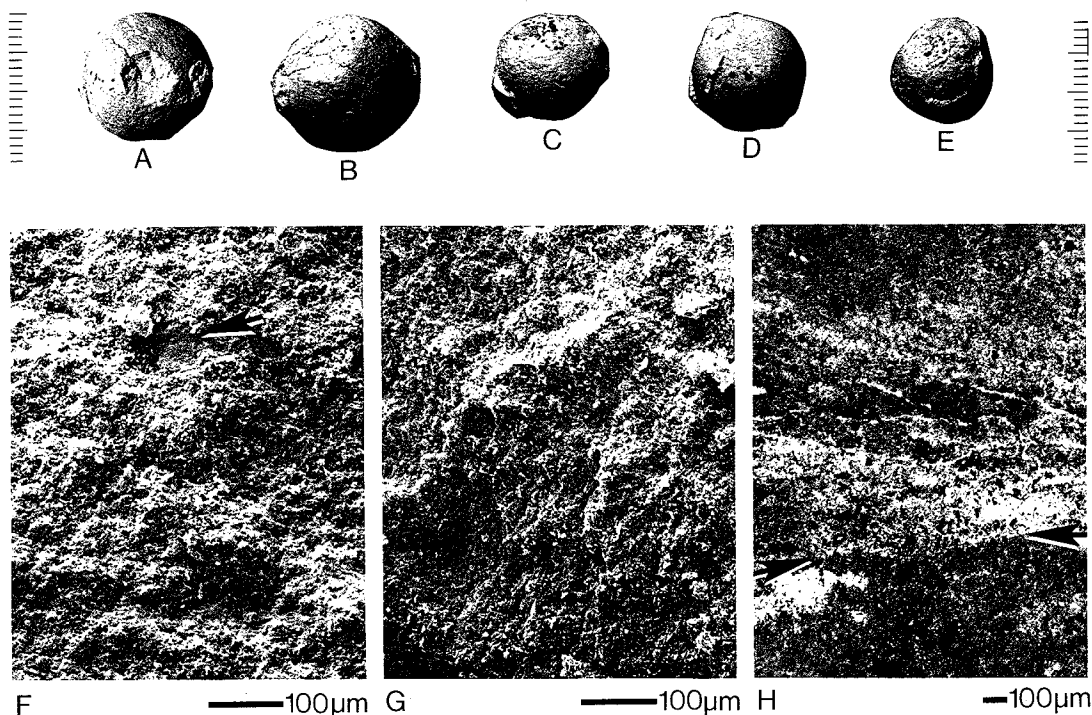
FIGURE 7—Trace fossils attributed to dung beetles, *Pallichnus dakotensis* ichnogen. et ichnosp. nov. *A–E*, internal molds at same scale as millimeter scales on extreme left and right, showing irregular exit area (*A, B*), adhering clay rind (*C*), distorted outline (*D*) and molds of scratches (*E*); *F–G*, scanning electron micrographs of fabric in naturally fractured surface of fibrous clay rind (*G*) and of internal mold (*F*) with claystone clast (arrow); (*H*), photomicrograph of petrographic thin section across clay rind, showing sharp inner boundary of rind (between arrows), fibrous, diffuse outer boundary of rind (above), and calcite crystal tubes after roots (below left hand arrow). One specimen (*E*) is from unnamed Gleska series paleosol 34 and others are from unnamed Gleska paleosol 30, both in upper Scenic Member, Pinnacles area, Badlands National Park. Specimen numbers are IU15790G (*A, B*), IU15790F (*C*), IU15790E (*D*), IU15794 (*E*), IU15923 (*F, G*) and IU15925 (*H*).

presumably by burial. Some are lumpy and bulbous. In a collection of 79 of these from a single block of matrix the maximum diameter varied from 12.2 to 21.3 mm, with a mean of 16.2 mm and a standard deviation of 1.9 mm (Figure 8). The distribution of sizes is unimodal, and very slightly skewed toward larger sizes. The largest mold was noticeably crushed, as were several others larger than the mean. Thus the skewness toward larger sizes and range of sizes may be partly an artifact of slight compaction during burial. Even so, the range in size of spherical molds is considerable. Although they may have been made by several different species with similar nesting behavior, the fossils are treated as a single taxon of trace fossil.

Many of the molds have an irregular area, usually a cavity, disrupting the smooth curve of the outer surface (Figure 7A, B). Some also have curved ridges near this irregular region (Figure 7E), fiber-like ridges and small (1 mm-diameter), raised bumps which are stained with iron-manganese.

From slabs of their matrix, cut vertically to the former land surface (Figure 9), the internal molds can be seen to have separated along the sharp boundary between silty micrite of the mold and a thin (1–2 mm) rind of brown claystone, which fades outward into silty micritic matrix like that of the mold. This clayey rind may have a crude lamellar structure near its inner margin. Occasionally pieces of this clayey rind were found adhering to molds otherwise free of matrix (Figure 7C). Under the light (Figure 7H) and scanning
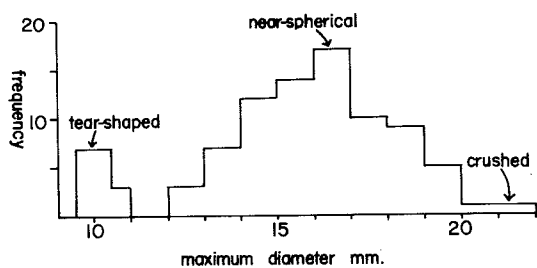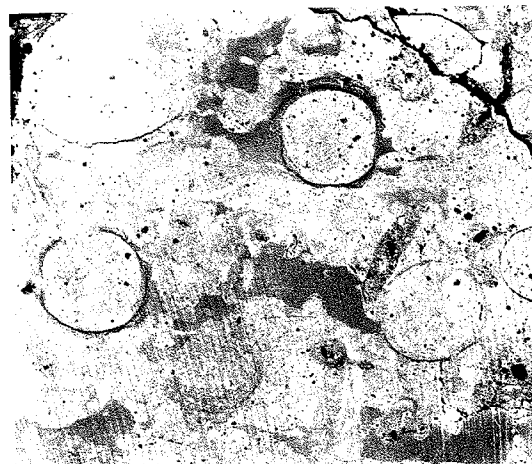
FIGURE 8—Frequency distribution of maximum diameters of tear-shaped and near-spherical internal molds from the petrocalcic horizon of unnamed Gleska paleosol 30, Pinnacles area, Badlands National Park (measured from bulk samples IU15923 and IU15924).

electron microscopes (Figure 7G), this clayey rind has a fibrous appearance, of diffuse, irregular, filaments in roughly parallel orientation. This contrasts with the unoriented appearance of the micrite within the chambers, which also contain some claystone clasts (Figure 7F). Chemical analysis of the clay rind with the electron microprobe (Figure 10) showed it to be much richer in total iron than the adjacent silty micrite, significantly enriched in phosphorus but not perceptibly different from surrounding micrite in manganese. Organic matter was not analyzed, because it is known to be poorly preserved in paleosols compared to original, well-drained soils (Stevenson, 1969) and because carbonaceous fossils are especially rare in the White River and lower Arikaree groups of Badlands National Park (Retallack, 1983). From these observations, the clay rind is interpreted to be composed of a mixture of iron oxyhydrate, clay and calcified organic fiber.

In some of the sawn slabs, brown clay extends away from the near-spherical internal molds, filling short, lateral branches from a near-vertical main shaft (Figure 9). This clay and that of the clay rim, is like that of the overlying B horizon of the paleosol; thus these structures are meta-isotubules in the terminology of Brewer (1976). The burrow branches are each 1–3 cm long and extend to that part of the near-spherical molds where the clay rind was disrupted. In some cases (Figure 9) short streaks of clay extend 4 to 5 mm out from the opposite side of the near-spherical mold.

The meta-isotubules are extensively cut by

■	very pale brown 10YR7/3 claystone	▨	light gray 10YR7/2 claystone breccia
▧	very pale brown 10YR8/3 claystone	▦	light gray 10YR7/1 calcite crystal tubes

matrix is white 10YR8/2 calcareous silty claystone
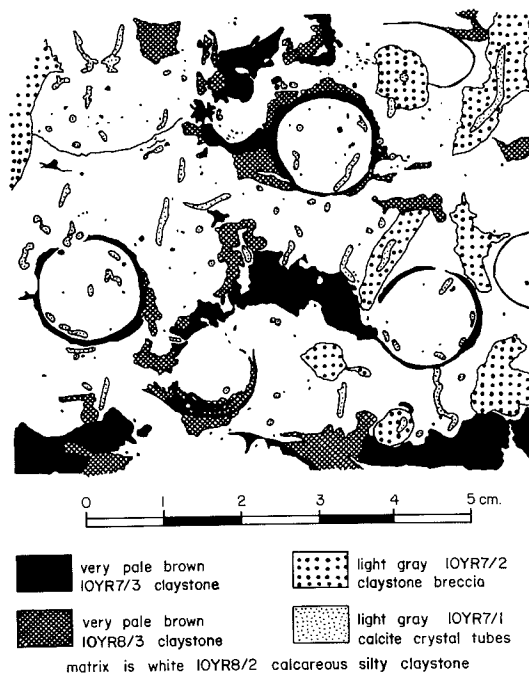
FIGURE 9—Vertically oriented slab (IU15921B), photographed under kerosene and sketched, from petrocalcic horizon of unnamed Gleska paleosol 30, Pinnacles area, Badlands National Park, showing *Pallichnus dakotensis* ichnogen. et ichnosp. nov. (dark circles) and associated burrows and root traces.

narrow (less than 1 mm diameter) calcite crystal tubes, which are sometimes surrounded by drab, greenish gray haloes (para-isotubules of Brewer, 1976). Some of these crystal tubes also follow the inside of the clay rind, and appear as elongate streaks of calcite

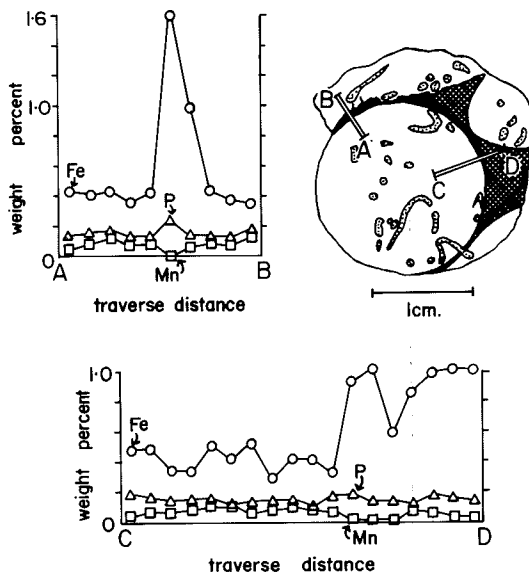FIGURE 10—Weight percent Fe, P and Mn from electron microprobe analyses along traverses indicated on sketch of *Pallichnus dakotensis* ichnogen. et ichnosp. nov. (IU15921A), drawn with same conventions as for Figure 9. Each analysis is from a 100 µm spot and has an experimental error approximately equivalent to the height of the symbols.

on the outside of the near-spherical internal molds.

The calcite-crystal tubes and para-isotubules are interpreted as fossil root traces, and they are abundant within paleosols of Badlands National Park (Retallack, 1983). The near-spherical internal molds and meta-isotubules are interpreted as trace fossils of insects. They could be regarded as endichnial burrows in the terminology of Martinsson (1970) and as full-reliefs (Vollformen) and dwelling burrows (domichnia) in the terminology of Seilacher (1964). Material filling the burrow probably fell in from a higher level in the soil rather than from an overlying deposit and burrow branches were probably sites of both feeding and pupation, as well as "dwelling."

Some aspects of the behavior of the makers of these trace fossils can be reconstructed without comparison with living organisms. They made deep (100–125 cm) vertical shafts, with short (1–3 cm) subhorizontal side passages. The burrows discovered may be only a small part of a more extensive system. Each side passage ended in a near-spherical chamber with walls of ferruginized clay and fibrous organic matter. The burrow system was filled with brown silty claystone from the overlying B horizon of the soil, but the abandoned near-spherical chambers were filled largely with silty micrite like that of the matrix of the petrocalcic horizon.

These trace fossils are very similar to brood burrows of scarabaeid beetles, particularly of the dung beetle subfamilies Geotrupinae and Scarabaeinae, which provision an underground nest with food for their developing larvae. Despite the name "dung beetles," some species of both subfamilies provision burrows with carrion or leaf litter (Ritcher, 1958; Halffter and Matthews, 1966; Wilson, 1971). Evidence that dung was used in these trace fossils is slim and circumstantial: the irregularly fibrous nature of the wall material, its high phosphorus content, and the unusually abundant associated remains of large mammals. Considered as traces of dung beetles, the near-spherical chambers could be interpreted either as the remains of a brood ball or as a pupal cell. Interpretation as a brood ball seems unlikely by comparison with those of modern scarabaeid beetles (Halffter and Matthews, 1966; Halffter, 1977). None of the fossils have thick clayey shells, nor do they show any evidence of a former air-space around them. Nor is more than one near-spherical mold found at the end of each branch of the burrow. It is more likely that the near-spherical fossils were pupal cells, formed at the end of the branch of the burrow, when most of the food filling it was consumed. This explanation also has the advantage of accounting for some minor features of the fossils. Irregular bumps on some molds may be impressions of feces of the larva. Irregular extensions of brown silty claystone on the side of the molds opposite the burrow (Figure 9), may be collapsed egg chambers, like those made by living beetles, *Ceratophyus typhoeus* Linnaeus and *Lethrus apterus* Laxmann (illustrated by Burmeister, 1930; Lengerken, 1954).

The trace fossils are similar in many ways to brood burrows of the living scarabaeid beetles *Geotrupes stercorarius* Linnaeus (Teichert, 1955), *G. hornii* Blanchard (both Geotrupinae; Howden, 1955), *Onthophagus nuchicornis* (Linnaeus) (Burmeister, 1930)

and *O. landolti* Harold (Scarabaeinae; Howden and Cartwright, 1963). Compared to the trace fossils, these modern species have more ellipsoidal pupal cells and shallower burrows. Other living beetles, such as *Lethrus apterus* Laxmann and *Ceratophyus typhoeus* Linnaeus (both Geotrupinae), have burrows of comparable depth and deeper (up to 140 cm; Burmeister, 1930). Depth of brood burrows may be related to dryness and other features of the soil, as well as to competition for dung among beetles. It could also be that the petrocalcic horizon of this paleosol has preserved structures formed at a more shallow depth, within a soil which subsequently received several increments of alluvium before reaching its full development. In view of the slight deformation seen in most of the near-spherical fossil molds, it is difficult to place much importance on the slightly elongate shape of modern pupal cells, which are nevertheless often close to spherical (especially in *Onthophagus*; Burmeister, 1930; Howden, 1957). A near-spherical shape can be the result of the concentric feeding of the larva within the brood ball. It can also result from arcuate movements of the larva laying out feces, as its large abdomen shrinks and it assumes the broadly ellipsoidal form of the pupa (Burmeister, 1930; Halffter and Matthews, 1966).

The existence of dung beetles during Oligocene time is indicated by the fossil record of beetles. A small (5 mm long) fossil beetle (*Aphodiites*) from very Early Jurassic rocks of Switzerland (Handlirsch, 1908) is superficially similar to modern, non-burrowing dung-eating, scarabaeid beetles (Crowson, 1981). A larger (15 mm long) beetle (*Opiselleipon*) from slightly younger Early Jurassic rocks of northern West Germany (Bode, 1953) is additional evidence of the Mesozoic evolution of scarabaeid beetles (Crowson, 1981). *Geotrupoides* from latest Jurassic rocks of southern West Germany (Handlirsch, 1908) may be the earliest representative of the Geotrupinae (Crowson, 1981). There were a variety of robust large scarabaeids (*Geotrupoides, Proteroscarabaeus* and *Holcorobeus*) in central Asiatic U.S.S.R. and northeastern China during Early Cretaceous time (Grabau, 1928; Arnoldi et al., 1977; Rodendorf and Raznitzyn, 1980). These probably belong to the subfamilies Geotrupinae and Hybosori-

nae (Crowson, 1981). Among the numerous fossil scarabaeids from Eocene and younger rocks of Europe and North America, the subfamily Scarabaeinae was almost certainly present by the early Oligocene (Halffter, 1959; Balthasar, 1963; Matthews and Halffter, 1968; Wilson, 1977; Grande, 1980; Crowson, 1981). An origin of the subfamilies Geotrupinae and Scarabaeinae before the early Tertiary also may account for their present cosmopolitan distribution. This includes many endemic forms in Australia, which has been geographically isolated since the early Tertiary (Britton, 1970; Matthews, 1972).

The life cycle of living *Geotrupes* (Geotrupinae) and *Onthophagus* (Scarabaeinae) varies in detail from species to species. The following generalized account is based on exceptionally detailed studies of northern European species by Burmeister (1930) and Teichert (1955). Beetles appear on the surface early in the spring after a long, winter hibernation. Following several weeks of feeding in simple burrows crammed with dung, they begin more ambitious burrows for care of the next generation. The female usually constructs a near-vertical burrow beneath a fresh cake of cattle dung, while the male beetle assumes a minor role in excavation and defense at the surface. The female stuffs the ends of branches of the burrow with dung derived from directly overhead. An egg may be laid just beyond the end of the brood chamber, or the egg may be laid in a small chamber within the mass of dung. After closing off the brood burrow, the adults live for a month or more at the surface. Meanwhile the egg hatches into a larva, which steadily consumes the provided dung over the next two or three months. It then pupates for three weeks or so. The young beetles emerge, then excavate shallow feeding burrows for themselves. With the coming of winter, they dig deep burrows and hibernate until the following spring.

By comparison with modern species, the makers of the fossil burrows were probably non-social and solitary, as these terms are defined by Wilson (1971). There may have been some cooperation of male and female beetles in the construction of the nest, but the brood chamber appears to have been too small to allow maternal supervision of the larva. In the classification of scarabaeid behavior presented by Halffter (1977; somewhat mod-

ified from the version of Halffter and Matthews, 1966), the trace fossils correspond to group I, thought to be the most primitive behavior among scarabaeids. Within group I, however, there are nests of a type even more primitive than the fossils, such as nests of living *Liatongus monstrosus* Bates (Scarabaeinae).

These fossil nests and this level of behavior in North America during the Oligocene may be contrasted with an abundant fossil record of group II behavior (of Halffter, 1977) in Argentina and Uruguay. These fossils are clay shells from brood balls like those made by the living genera *Phanaeus, Deltochilum* and *Dichotomius* (all Scarabaeinae). They have been found in Quaternary and Tertiary deposits as old as Paleocene (Frenguelli, 1938a, b, 1939; Roselli, 1939; Halffter, 1959; Halffter and Matthews, 1966; Volkheimer, 1971). It is already known from studies of fossil soils (Andreis, 1972; Spalleti and Mazzoni, 1978; Retallack, 1982, 1983), fossil plant remains (Menendez, 1971; Volkheimer, 1971; Thomasson, 1979; Stebbins, 1981), and fossil mammals (Webb, 1977, 1978) that grassland ecosystems developed earlier in South America (perhaps by the early Eocene) than in North America (probably by the late Oligocene). Compatible with this view is the abundant evidence of advanced nesting behavior of grassland-adapted dung beetles since Eocene time in South America compared with more primitive nesting behavior described here from a North American paleosol formed under woodland, as well as (less commonly) from paleosols of the adjacent savanna.

The fossil record of these nests is also in accord with several hypotheses for the evolution of dung beetles based on studies of modern beetles. In both North and South America, the fossil record of scarab nests now extends back to when grassland ecosystems can first be recognized. These fossils are additional evidence of the importance of grasslands in the evolution of nesting behavior in dung beetles, as proposed by Halffter and Matthews (1966). Fossils from Argentina and Uruguay confirm the South American origin of *Phanaeus, Deltochilum, Dichotomius* and related beetles, as has already been proposed on the basis of their modern distribution by Halffter (1974, 1976). The newly-discovered North American nests are less distinctive, and

represent a primitive and widespread nesting behavior among scarabs. The living beetles *Onthophagus* and *Geotrupes,* whose nests happen to be better known than most and similar to the fossils, are both thought to have been of holarctic origin, to judge from their modern distribution (Halffter, 1974, 1976).

I have been unable to find any published record of trace fossils attributable to dung beetles on any continents other than the Americas. They are similar to nodules and pebbles, and probably they are widely overlooked in the search for associated vertebrates.

SYSTEMATIC ICHNOLOGY OF
BEETLE TRACE FOSSILS

Ichnogenus PALLICHNUS ichnogen. nov.

Diagnosis.—Near-spherical chambers, defined by thin wall of dark clay and organic matter; inner boundary of wall sharp and smooth, so that internal mold is easily separated from rock matrix; outer boundary of wall gradationally passing outward into surrounding matrix; one side of chamber disrupted to form large, irregularly circular, exit cavity, usually about half diameter of main chamber; each near-spherical chamber arranged at end of short branches from vertical burrow, so that exit cavity faces into branch burrow; both vertical and branch burrows of slightly lesser diameter than near-spherical chamber.

Type species.—*Pallichnus dakotensis* ichnosp. nov.

Derivation.—This new name is derived from the Greek words for ball (*palla*) and track (*ichnos*), the latter a conventional suffix for generic names of trace fossils (Basan, 1979).

Comparison.—There are several other ichnogenera of near-spherical trace fossils which are thought to be nests of scarabaeid beetles. These are either hollow spheres with a large circular opening (*Coprinsphaera* Sauer 1955), hollow spheres with thickened walls around the opening (*Devincenzia* Roselli 1939) or cup-shaped objects with a flattened area and flange around the opening (*Fontana* Roselli 1939). The clayey walls of all these ichnogenera are thick (3 mm or more) and equally clearly defined inside and outside. As a result these fossils can be collected as isolated hollow structures, rather than internal

molds as in *Pallichnus*. Although the arrangement of the nests and associated burrows is known in *Pallichnus,* it has not yet been described for any of these other ichnogenera.

PALLICHNUS DAKOTENSIS ichnosp. nov.
Figures 7–10

Diagnosis.—*Pallichnus* with central cavity 12 to 22 mm in diameter, and ferruginized clay and fibrous organic walls 1 to 2 mm thick; central cavity filled with different material (silty micrite) than adjoining burrows (brown silty claystone).

Type specimen.—Sawn slab number 15921B (Figure 10) of Indiana University, Geology Department collections.

Additional material.—Indiana University specimens 15790A–I, 15792B, 15794A, 15920, 15923 (this last a bulk sample of 79 specimens from a single block).

Type locality.—The petrocalcic (Cca) horizon of an unnamed Gleska paleosol (number 30 at 51.8 m in measured section of Retallack, 1983), in a small ridge in the SW¼ NE¼ Sec. 20, T2S, R16E, Pennington County, South Dakota. This is about 1.3 km southeast of Pinnacles Lookout in Badlands National Park, and is in the upper Scenic Member, Brule Formation, White River Group, of early late Oligocene age.

Additional localities.—Additional remains were found in the same paleosol as far east as the road cut along South Dakota Highway 240, and presumably extend farther afield. More were found in another Gleska Series paleosol (the Gleska silty clay loam thick petrocalcic variant, number 34 at 61.8 m in the measured section of Retallack, 1983) in the same ridge as the type locality, also in the upper Scenic Member, as well as closer to Pinnacles Lookout (only 0.8 km southeast, in the NW¼, NE¼ Sec. 20, T2S, R16E, Pennington County) at two stratigraphic intervals (in the C horizon of an unnamed Gleska Series paleosol 61 at 97.8 m and of an unnamed Wisangie Series paleosol 57 at 92.4 m) within the mid-late Oligocene, Poleslide Member of the Brule Formation.

Derivation.—The specific epithet indicates the origin of the trace fossils from South Dakota.

Remarks.—The fossils are described and interpreted here as pupal cells within brood burrows. A precisely similar modern beetle
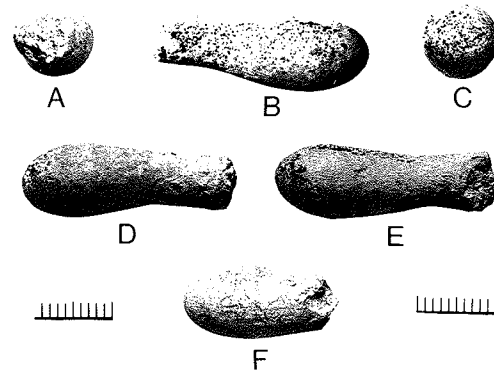

FIGURE *11*—Trace fossils attributed to sweat bees, *Celliforma ficoides* ichnosp. nov.: Different views of an especially well-preserved internal mold (IU15790D), showing truncated outer end (*A*), rounded inner end (*C*), smooth, polished walls (*B, D, E*) except for area with scratches and pits on bottom near entrance (*D*), and also showing convex-down curve of long axis in side view (*B*) and straighter long axis as viewed from above (*E*) and below (*D*); *F,* less complete internal mold, with surficial linear features after roots or fungal hyphae (IU15790H). Both from petrocalcic horizon of unnamed Gleska paleosol 30, Pinnacles area, Badlands National Park.

burrow has not yet been described. The fossils combine features of cell morphology, burrow arrangement, burrow depth and likely placement of the egg cell found in several modern species of the scarabaeid subfamilies Geotrupinae and Scarabaeinae.

Presumably these fossils are in part the objects described by Clark, Beerbower and Kietzke (1967, p. 124) as "casts of pupa cases or larval burrows."

LARVAL CELLS OF BEES

Also found in the petrocalcic horizon of unnamed Gleska paleosol 30 were tear-shaped internal molds of silty micrite (Figure 11). Like the near-spherical remains of *Pallichnus,* these also separate easily from their matrix. The maximum diameters of 17 of these extracted from a single block averaged 10.1 mm, and varied from 9.7 to 10.8 mm (Figure 8). This diameter is reached about a third of the way along the length of the mold from the rounded (distal) end. From there to the proximal end the diameter tapers gradually and the mold is usually broken off irregularly at its narrowest point. In one specimen
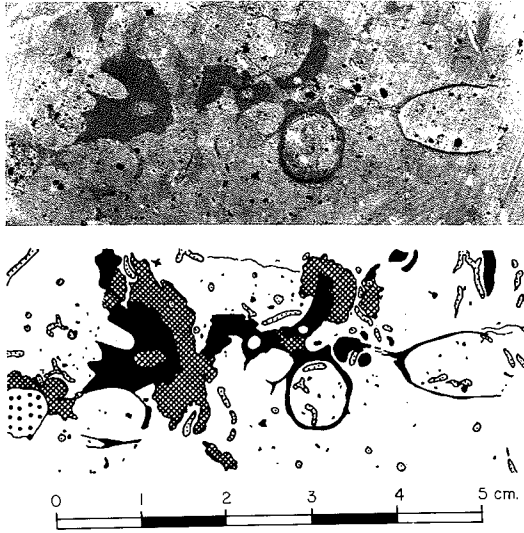
FIGURE *12*—Vertically oriented slab (IU15922), photographed under kerosene and sketched, from petrocalcic horizon of unnamed Gleska paleosol 30, Pinnacles area, Badlands National Park, showing *Celliforma ficoides* ichnosp. nov. (circular and elliptical outlines) and associated burrows and root traces.

(15790D) the diameter tapers from 10.3 mm (maximum) to 7.1 mm (minimum) 21 mm from the rounded end, and then expands a little (to 7.5 mm) before it is broken (Figure 11B–E). In this and other specimens, the long axis of the mold is not completely straight, but bends slightly. The constricted part of the mold on the outside of the bend has a scratched and pitted appearance (Figure 11D), quite unlike the smooth to slightly lumpy surface of the rest of the internal mold (Figure 11B–E).

In the field, the tear-shaped internal molds are noticeably less common and more clumped than the associated near-spherical ones. From the study of sawn slabs of large blocks of matrix whose orientation was marked in the field (Figure 12), it appears that the tear-shaped molds have short (2–5 mm) entrance burrows filled with brown silty claystone. The cells appear clustered around vertical shafts, also filled with brown silty claystone. Most of the cells are horizontal, but some isolated cells also were found at slight (less than 15°) angles from horizontal. The slight curvature of the long axis of the cells in these slabs is convex down. Scratches

and pits on the proximal outer surface of the convex side of the internal molds thus represent impressions of the floor near the entrance of the cell. Only three cells were found attached to the most complete cluster (Figure 12). If associated burrows led to other cells, this cluster may have included as many as six cells. Complete nest systems may have included many of the associated cells whose physical attachment could not be proven. Individual cells are filled with a material (silty micrite) different from the burrows (brown silty claystone), as in associated remains of *Pallichnus*. The cells are defined by a thin (less than 0.5 mm) dark wall which often has a polished appearance on the inside surface. Both the cells and burrows are also much disrupted by narrow crystal tubes and drab para-isotubules, interpreted as later-penetrating root traces (Retallack, 1983).

Like *Pallichnus,* the tear-shaped internal molds appear to have been deep portions of burrow systems with clayey and organic walls. The cells were filled with silty micrite from the surrounding matrix and the associated burrows were filled with brown silty claystone from the overlying B horizon. These trace fossils are most like brood cells of wasps or bees (Hymenoptera). Many of these creatures provision subterranean cells with spiders, insects, pollen or nectar, which serve as food for their developing larvae (Stephen, Bohart and Torchio, 1969; Evans and Eberhard, 1970).

The nature of the lining material of these internal molds is not definitely known. Many have a smooth, waxy appearance, as if some secretion had been applied to the wall of the cell. Local bumpy areas may represent larval feces. Fine lineations may be impressions of silk or fungal hyphae. Organic coatings of cells have not been reported among wasps (Evans, 1966; Evans and Eberhard, 1970; Michener, 1964), but they are found in many groups of bees (Apoidea; families Halictidae, Andrenidae, Melittidae, Anthophoridae and Apidae; Linsley, McSwain and Smith, 1952, 1955, 1956; Linsley, McSwain and Michener, 1980; Sakagami and Michener, 1962; Stephen and Torchio, 1961; Stephen, Bohart and Torchio, 1969; Rust, 1980). There is no indication in the fossils of especially thick cell linings, such as leaves used by living *Megachile* (Apoidea, Megachilidae; Stephen, Bohart and Torchio,

1969; Eickwort, Matthews and Carpenter, 1981) or polythene linings of *Colletes* (Apoidea, Colletidae; Michener, 1974; Batra, 1980).

It is difficult to determine whether or how these fossil cells were closed during larval development. Evidence of closure would not normally be preserved, because the young wasp or bee would destroy it on emergence. The silty micrite fill of the main part of the mold may have been separated from the brown silty claystone of associated burrows by the remains of a cocoon or by a cap of soil or clay. A cocoon seems unlikely, because all of the internal molds have irregularly broken ends, lacking any trace of a wall-like partition or flap. Even if preserved, a plug of loose soil, like that commonly constructed by sweat bees (Apoidea, Halictidae; Sakagami and Michener, 1962), would be difficult to recognize. Some modern bees close brood cells with spirally grooved caps of clay (Linsley, McSwain and Michener, 1980; Stephen, Bohart and Torchio, 1969), and these also have been found in fossil hymenopteran nests (Brown, 1934; Roselli, 1939). However, none were found in or associated with the trace fossils from Badlands National Park.

Considering the depth of these fossils within the paleosol, their clustering and horizontal orientation, very short entrance passages, degree of organic coating and the absence of spiral caps, they are most like the nests of sweat bees (Apoidea, Halictidae, Halictinae; Sakagami and Michener, 1962; Michener, 1974). In branching pattern, they are most like the lower portions of nests of living sweat bees, *Lasioglossum* (*Evylaeus*) *malachurum* (Kirby), *L.* (*Evylaeus*) *marginatum* Brullé and *Augochlora* (*Oxystoglosella*) *semiramis* (Schrottky). In the size of the cells, and probably also of the bees which made them, the fossils are exceptionally large for sweat bees, as measured by Sakagami and Michener (1962). Only the larval cells of the living sweat bee *Halictus* (*Halictus*) *sexcinctus* Fabricius are as large as the fossils. A flat area of the floor near the entrance of the cell is a distinctive feature of many halictine larval cells. When preserved (Figure 11D), this area of the fossils is scratched and pitted and only a little less curved than the roof of the entrance.

Hymenopteran nests similar to the fossils but with slightly longer lateral burrows, are made by living *Andrena* (*Leucandrena*) *ery-*thronii* Robertson (Apoidea, Andrenidae; Michener and Rettenmeyer, 1956; Stephen, Bohart and Torchio, 1969). Other hymenopteran nests are even less similar, for the following reasons. The brood cells of the bee-family Fideliidae are unlined, shallow and have long lateral burrows, and those of the Megachilidae are lined with leaves, or other foreign material, and laid out end to end in burrows (Stephen, Bohart and Torchio, 1969; Rozen, 1977). Burrows of sand wasps (Nyssonidae) and spider wasps (Pompilidae) are especially well known (Evans and Yoshimoto, 1962; Evans, 1966; Kimsey, Kimsey and Toft, 1981). Compared to the fossils, these do not extend to such depth within the soil and have oblique, gently sloping entrance tunnels. Burrowing wasps in general (Families Scoliidae, Masaridae, Eumenidae, Pompilidae, Sphecidae) have unlined brood cells. Their burrows are either like those of sand and spider wasps, or are vertical burrows in which the brood cells are at the end of long lateral passages (Michener, 1964; Evans, 1966; Evans and Eberhard, 1970; Spradbery, 1973).

Both wasps and bees were present in considerable variety during late Oligocene time. The earliest Hymenoptera known as body fossils have been found in Triassic rocks of central Asia and eastern Australia (Burnham, 1978) and are very similar to living sawflies (Suborder Symphyta, Family Xyelidae). By the Cretaceous, there was already a variety of wasps, including representatives of the families Scoliidae, Pompilidae, Masaridae and Sphecidae. By the Eocene, the Eumenidae also appear to have evolved. Remains of possible social wasps (Family Vespidae) from Eocene rocks are not very convincing, but they certainly were present by the early Oligocene deposition of the Florissant Lake Beds (Epis and Chapin, 1975; Burnham, 1978). By this time, most major groups of wasps, and presumably most kinds of wasp behavior, were in existence. The fossil record of bees definitely starts with the late Eocene (Berry, 1927; Pomerol, 1982) Baltic amber, which has yielded representatives of the families Halictidae, Andrenidae, Melittidae, Megachilidae, Anthophoridae and Apidae (Zeuner and Manning, 1976; Burnham, 1978). Some scientists (Wilson, 1978, 1982) have argued from the conspicuous absence of bees in sev-

eral Middle Eocene and older localities which have yielded abundant insect fossils, that bees are unlikely to be much older than late Eocene. Others (Michener, 1944; Burnham, 1978) have been more impressed with the diversity of forms in Baltic amber and at Oligocene localities, and they have speculated that bees had a long prior ancestry, perhaps extending back to the mid-Cretaceous rise of angiosperms. Only rarely do other kinds of plants, such as the conifer *Juniperus,* supply bees with their preferred food of pollen or nectar (Burnham, 1978). Analyses of the diversity of angiosperms through geological time (Tiffney, 1981; Muller, 1981) have revealed that the most dramatic increases in variety were during the Eocene and Oligocene, a time of widespread appearance of grasslands in subhumid to semiarid climatic zones of continental interiors (Retallack, 1982). The oldest flowers similar to those pollinated by bees have been discovered in Eocene rocks (Crepet, 1979a, b, 1981; see also Grande, 1980, figure V.23). Although bees may have existed during the Late Cretaceous, the most rapid phase of their adaptive radiation, like that of the angiosperms, was probably during the Eocene and Oligocene.

The following account of the life cycle of the sweat bee, *Lasioglossum* (*Evylaeus*) *malachurum* (Kirby) (Apoidea, Halictidae, Halictinae) from West Germany, is summarized from Michener (1974). Only potential queens (gynes) overwinter in specially constructed cells (hibernacula). In the spring they emerge to lay eggs in newly-constructed brood cells within the nest in which they spent the winter. Each egg is provided with a mass of pollen which serves as food for the developing larva. Within a month the original female (or females) of the nest has a brood of worker females. By the middle or late summer some male bees and gynes also are reared and then mate. Both males and old females die off with the approach of winter. Some fertilized gynes remain in the nest, but most leave to make new nests in which to hibernate.

One conclusion from the monumental study of halictine bee nests by Sakagami and Michener (1962) was that "there is no obvious correlation between the development of social organization and the nest structure." Some highly social species construct more simple nests than less social species (Knerer and Atwood, 1966). In the modified descriptive classification of Iwata (Stephen, Bohart and Torchio, 1969) the fossil nests were probably OsLCh′, more complex than the most simple kind of nest (OCv) and less complex than nests with clusters of brood cells in large chambers [such as $Op(HCv''^n)^m$]. In the classification of halictine nests by Sakagami and Michener (1962), in which they recognize eight groups (I to VIII) from simple to complex, the fossil nests correspond to subtype IIIc. In the ten-rung "social ladder" of nesting behavior of wasps proposed by Evans and Eberhard (1970), the fossil nests correspond to rungs 4 to 7. The fossil nests are thus intermediate in their complexity, compared to those of living wasps and bees. The insects which made these burrows may have been solitary, but they were probably not as highly social (eusocial in the sense of Wilson, 1971) as modern paper wasps (Vespoidea, Vespidae) or honey bees (Apoidea, Apidae). Some degree of cooperation of individuals in constructing and defending these deep and clustered brood cells is likely. The exact degree of sociality of these former bees cannot be determined.

Bees are most common and diverse in subhumid to semiarid regions of the world in dry, hard soils, which support abundant flowering trees, shrubs and herbs. Wasps also are favored by such habitats, together with the availability of small spiders and insects, with which they feed their larvae (Evans and Eberhard, 1970). All these features are compatible with the paleoenvironment of unnamed Gleska paleosol 30, already interpreted on the basis of fossil plants and mammals, the paleosol itself and traces of burrowing dung beetles.

Fossil bee nests have been found in middle Eocene rocks of Wyoming (Brown, 1934, 1935), late Oligocene rocks of Germany (Schütze, 1907), late Oligocene or early Miocene rocks of Florida (Brown, 1935; age disputed by King and Wright, 1979; Scott and MacGill, 1981), and Pleistocene or Holocene rocks of South Australia (Zeuner and Manning, 1976). These have polished walls and spirally grooved caps, which are distinctive of bee cells. None of their associated burrows have been studied in detail. Multicellular nests

in chambers, like those of living sweat bees (Apoidea, Halictidae) appeared by the late Miocene in Uruguay (Roselli, 1939; Frenguelli, 1939; Goñi and Hoffstetter, 1964; Bonino de Langguth, 1978), and wax combs of honey bees (Apoidea, Apidae) by the Pleistocene in Malaysia (Stauffer, 1979). Other nesting traces from the Late Cretaceous of Utah (Brown, 1941a,b; Bequaert and Carpenter, 1941), late Oligocene of West Germany (Handlirsch, 1910) and Oligocene of Egypt (Bown, 1982) are more likely nests of wasps than bees. The evidence of these fossil nests is compatible with the following hypotheses for the evolution of wasps and bees, previously proposed on the basis of their direct fossil record (Zeuner and Manning, 1976; Burnham, 1978; Wilson, 1978) and the comparative morphology and distribution of living forms (Evans and Eberhard, 1970; Wilson, 1971; Michener, 1974). Wasps are known from much older (Cretaceous) fossils than are bees (late Eocene). Judging from their modern distribution, the various lineages of eusocial paper wasps evolved in forests and woodlands of humid to subhumid, and tropical to subtropical climates. On the basis of fossil evidence of wasps and nests, it appears that this probably occurred during the early Tertiary and Late Cretaceous, when such vegetation and climates were much more widespread and extended to higher latitudes than at present. Bees "are a group of flower-visiting wasps that has abandoned the wasp habit of provisioning nests with insect or spider prey and instead feeds its larvae with pollen and nectar collected from flowers or with glandular secretions ultimately derived from the same sources" (Michener, 1974, p. 3). Bees may have evolved during the latest Cretaceous or Early Tertiary, but were such rare or geographically restricted animals that none are found as fossils in rocks older than late Eocene. Fossil bees, bee nests and bee flowers all appear at a time of pronounced evolutionary diversification during the Eocene and Oligocene spread of grasslands in subhumid to semiarid, and subtropical to warm temperate climatic zones of continental interiors. Eusocial behavior developed later in bees than in wasps and within more evolutionary lineages. Judging from the fossil record of bee workers and of communal nests, eusocial behavior in bees is probably not much older than late Eocene.

Like the trace fossils of dung beetles already described, fossil nests of wasps and bees probably have been widely overlooked. They are a potentially important and copious source of information on the evolution of bees and wasps.

SYSTEMATIC ICHNOLOGY OF BEE TRACE FOSSILS
Ichnogenus CELLIFORMA Brown, 1934

Emended diagnosis. — Vasiform, globular or subcylindrical chambers or internal molds of chambers; distal or inner end rounded; proximal or outer end either truncated irregularly, or capped by a flat or conical closure, bearing spiral or concentric grooves on its inner surface; walls polished and smooth so that internal mold is easily separated from rock matrix.

Type species. — *Celliforma spirifer* Brown, 1934.

Remarks. — Although spiral caps have been found in the type species, this feature is not taken to be diagnostic of the genus. Preservation of spiral caps is dependent on the failure of the young bee to emerge; therefore, they are rare in fossil nests. All the named species have internally polished cells. Only in *Celliforma ficoides* has the degree of clustering been established.

CELLIFORMA FICOIDES ichnosp. nov.
Figures 11, 12

Diagnosis. — *Celliforma* with brood cells 20 mm long, and 9 to 11 mm in maximum diameter at a point about one-third the distance from the rounded end, tapering to 7 mm in diameter near a short (3 mm) flaring entrance; cell linings thin (less than 0.5 mm), smooth and slightly lumpy in appearance except near the entrance floor, where the surface is granular and pitted; cells oriented subhorizontally, their long axes slightly curved and convex down; cells arranged in flat-lying, radial clusters, connected through short lateral burrows to a central vertical burrow; cells filled with different material (silty micrite) than associated burrows (brown silty claystone).

Type specimen. — Sawn slab 15922 (Figure

12) of Indiana University, Geology Department collection.

Additional material.—15790D, H, I and 15924 (this last a bulk sample of 17 specimens from a single block).

Type locality.—As for *Pallichnus dakotensis* ichnogen. et ichnosp. nov.

Derivation.—The specific epithet is from a Latin word for fig-like. My first impression on collecting these curious fossils was that they were fossil fruits. This interpretation is incompatible with details of their structure and the nature of preserved fossil plants in Badlands National Park (Retallack, 1983).

Comparison.—Other named species of *Celliforma* differ substantially from *C. ficoides. Celliforma bedfordi* Zeuner and Manning 1976 and *C. septata* Zeuner and Manning 1976 are both preserved as hollow cells with a thick (1 to 2 mm) wall of calcareous sand, in some ways similar to the earthen linings of nests made by living *Melitoma* (Apoidea, Anthophoridae; Michener, 1964). *Celliforma septata* has three separate closures, like those observed by Rau (1930) in nests of living *Ptilothrix bombiformis* (Cresson) (Apoidea, Anthophoridae; formerly in the genus *Emphor*, Krombein et al., 1979). Also hollow are burrows in the chalk roof of a Bronze Age tomb at Megiddo, Israel (Buxton, 1932), which have been referred to the genus *Celliforma* by Zeuner and Manning (1976). It is questionable whether these burrows should be regarded as fossils. They should not be included within *Celliforma* until adequately illustrated and described.

"*Celliforma*" *favosites* Brown 1941a (Brown, 1941b; Bequaert and Carpenter, 1941) is also very different from *C. ficoides.* Like the hymenopteran trace fossils referred to "*Uruguay*" by Roselli (1939), "*C.*" *favosites* is a planar aggregate of laterally linked cells. Both "*Celliforma*" *favosites* and "*Uruguay*" should be placed in separate new genera.

The remaining named species of *Celliforma* are preserved as internal molds like *C. ficoides,* but they differ in the following features. *Celliforma germanica* Brown 1935 shows a broad constriction just inside the entrance of the cell, as in modern nests of *Sphecodogastra texana* (Cresson) (Apoidea, Halictidae, Halictinae; Kerfoot, 1967; Stephen, Bohart and Torchio 1969). *Celliforma nuda* (Dall) Brown 1935 is subcylindrical in shape. The widest part of the internal molds of *Celliforma spirifer* Brown 1934 is near the center of their length, so that they appear less tear shaped and more stout than *C. ficoides.* Both *C. spirifer* and *C. nuda* have been found with spirally grooved closures, and are similar to larval cells of several kinds of living bees (families Andrenidae, Melittidae, Halictidae and Anthophoridae; Stephen, Bohart and Torchio, 1969).

Material similar to *Celliforma* has also been found from an early Oligocene paleosol near Paso Flores, Argentina (Frenguelli, 1939; age after Marshall and others, 1977) and in the Oligocene or Miocene Calizas de Queguay, near Migues, Uruguay (Frenguelli, 1938a; Góni and Hoffstetter, 1964). It is not certain whether these remains have the internal polish usual in *Celliforma.* They equally could be larval cells of wasps or bees.

Remarks.—*Celliforma ficoides* does not appear to be identical in all respects with any modern burrow yet described. The fossils have features found in nests of several species of sweat bees (Apoidea, Halictidae, Halictinae).

RECONSTRUCTION OF AN OLIGOCENE SOIL AND ITS BIOTA

The described trace fossils and paleosol add several new lines of evidence for reconstructing paleoenvironments of Badlands National Park. The painted reconstruction by Jay Matternes (p. 54–55 in MacDonald and MacDonald, 1980) is close to my conception of the paleoenvironment and fauna of Gleska Series paleosols of the early late Oligocene, Scenic Member. His additional reconstruction of the same work (p. 56–57) is a good approximation of the paleoenvironment of Conata-Series paleosols of the same stratigraphic level, as well as Wisangie-Series paleosols of the mid-late Oligocene, Poleslide Member. Less accurate is Matternes' well-known mural in the U.S. National Museum (reproduced by Farb, 1966), which is a composite of ages and subenvironments. My own attempt at reconstructing some aspects of the unnamed Gleska paleosol 30 is shown in Figure 13. The following account summarizes conclusions from preceding sections for a time during the early late Oligocene deposition of the Scenic Member of the Brule Formation.

Unnamed Gleska paleosol 30 formed under gallery woodland flanking loosely sinuous streams. Other parts of the floodplain were vegetated by savanna. The trees of this woodland were moderately sized and well spaced, allowing growth of an herbaceous understory. Some of the trees were hackberries (*Celtis hatcheri*), but the biological affinities of most of the plants remain unknown. Presumably they were mainly angiosperms, and were a source of pollen for bees. Deep and clustered brood cells of bees, probably sweat bees (Apoidea, Halictidae, Halictinae) are preserved in the petrocalcic horizon of the paleosol. There is also evidence for burrowing beetles, in the form of deep, branched, brood burrows. These were probably dung beetles (Coleoptera, Scarabaeidae, subfamilies Geotrupinae or Scarabaeinae). Important providers of dung may have included large amphibious (*Metamynodon*) or cursorial (*Hyracodon*) rhinoceroses, or the more common oreodons (*Merycoidodon*) or horses (*Mesohippus*). Land snails (*Pseudolisinoe leidyi*) also browsed on herbaceous and shrubby plants of these calcareous soils. Climate was seasonal, with pronounced dry, and perhaps cool periods. Temperature regime was warm temperate and mean annual rainfall within the subhumid range.

Although the evidence is circumstantial, there are hints of interaction between elements of this ancient ecosystem. The fossil nests of bees show a degree of complexity found in living bees that are solitary or have a limited amount of social behavior. Bees are dependent on pollen, for which plants, especially herbaceous angiosperms, are compensated by more effective pollination. Trace fossils of beetles are similar to those made by modern dung beetles with a limited degree of behavioral complexity. They are also evidence of considerable effort in sequestering dung away from competitors. From this activity, the productivity of the soil, and consequently both plants and animals may have profited. Although paleosols are evidence of woodland and nearby savanna, only the propagules of hackberry were mineralized with calcite and silica, like those of living hackberries. This adaptation for withstanding passage through the guts of herbivores (Stebbins, 1981) was not yet found in other plants here. Mineralized fruits of grasses and

FIGURE *13*—Reconstruction of the flora and fauna of unnamed Gleska paleosol 30 during early late Oligocene time. The species of plants, pelt of oreodons, form of the burrows beyond the petrocalcic horizon and of the dung beetle burrows at the time of egg laying (black) are all educated guesses.

forbs have not yet been reported from Badlands National Park, despite deliberate searches and their abundance in Miocene and

younger rocks of the Great Plains (Thomasson, 1979 and personal commun.,1983). The Oligocene mammalian fauna of Badlands National Park is commonly regarded as savanna adapted (Clark, Beerbower and Kietzke, 1967). None of the fossil teeth are as high crowned or have as complexly folded enamel as teeth of some modern mammals of grasslands (Webb, 1977). Nor were the limbs of these fossil mammals as suited to rapid movement in open spaces as those of modern savanna fauna, as far as can be judged from comparisons of metatarsal to femur ratios (Bakker, 1983). The Oligocene paleosol and its associated fossils can be considered evidence that several of these aspects of the coevolution of plants, insects and mammals had been initiated. Those parts of the Oligocene ecosystem preserved, however, fall far short of the degree of sophistication and interdependence seen in modern savannas and open woodlands.

Trace fossils in paleosols are undoubtedly far more abundant and diverse than is apparent from the existing literature. They may eventually provide more satisfactory evidence for some of the broad questions of coevolution within terrestrial ecosystems, which I have attempted to outline.

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