5-1980

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INVERTEBRATE LEBENSSPUREN OF HOLOCENE FLOODPLAINS: THEIR MORPHOLOGY, ORIGIN AND PALEOECOLOGICAL SIGNIFICANCE

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ABSTRACT—Although rocks of floodplain origin are volumetrically important, they contain relatively few trace fossils; both abundance and diversity are low. Conversely, Holocene floodplain sediments locally contain abundant and diverse lebensspuren mostly produced by insects, spiders, nematodes, annelids and molluscs. At least 8 insect orders and 31 families include species that burrow in floodplain sediments and yet none of their lebensspuren are unique to this environment.

Taxonomically dissimilar insects produce morphologically similar lebensspuren, and the same species, or individual, may produce very dissimilar lebensspuren. Thus, identification of tracemakers for rocks of floodplain origin is as difficult as for marine rocks. Trace fossil form genera morphologically similar to Holocene floodplain lebensspuren include Skolithos, Cylindricum, Sabellaria, Macroopus, Planolites, Palaeophycus, Sinusites, Cochlichnus, Amphorichnus and possibly also Scolicia; many previous authors have regarded these as more typical of marine environments than of floodplains.

INTRODUCTION

Despite the abundance and variety of Holocene floodplain lebensspuren, these biogenic structures are rare in the fossil record and also are virtually unstudied in comparison to those from marine and freshwater (mostly lacustrine) environments. Furthermore, the record of vertebrate produced terrestrial trace fossils, especially tracks, is considerably better documented (Voorhies, 1975) than the record of invertebrate traces.

The purposes of the present paper are two-fold: 1) to describe the morphology and origin of some common Holocene floodplain lebensspuren, especially those produced by insects and 2) to evaluate the paleoecological significance of Holocene lebensspuren for the recognition of ancient floodplain environments. Achievement of these goals will partially fill gaps in the most recent compendia on trace fossils (Frey et al., 1975, p. xi; Hantzschel, 1975). Although the present report is confined to floodplain lebensspuren, many of the same forms are known to occur in sediments and rocks deposited in other environments, both marine and upland dunes (Ahlbrandt et al., 1978).

Except for glacial deposits, rocks of floodplain origin are volumetrically the most important of any nonmarine sedimentary environment. They locally contain an abundant mammalian fossil record, but because bones are more dispersed in floodplains than in stream channel deposits, vertebrate paleontologists have generally expended less effort collecting from ancient floodplains than from channels (pers. commun., R. M. Hunt, Jr. and M. R. Voorhies, 1976). The rigorous of living in the unstable substrates of active channels (both erosional and depositional) virtually precludes discovery of trace fossils in association with body fossils from channel deposits. However, such associations would be expected from deposits of floodplain origin. The fact that trace fossils are usually destroyed during transportation may provide useful evidence for in situ accumulation when found in association with bones and thus aid in the reconstruction of fossil communities (sensu Fagerstrom, 1964).

Published research on Holocene and fossil invertebrate lebensspuren of nonmarine origin is indeed meager. Because a majority of Holocene floodplain lebensspuren are produced by insects, the chief researchers have been entomologists and, not uncommonly, their work on burrow morphology has been incidental to their prime efforts dealing with body morphology, systematics, ecology, or economic aspects of insects. The chief compilation of Holocene nonmarine invertebrate (insects, spiders, crustaceans, "worms," etc.) lebensspuren is Chamberlain (1975), but the major emphasis in this work is on aquatic, rather than flood-
plain environments. The coverage by Chamberlain is, however, remarkably diverse and includes several forms from near-shore terrestrial environments.

Data relating to body morphology that can be inferred from fossil lebensspuren may be severely limited. The disparity between body and burrow morphology becomes even more apparent when one realizes that similar looking burrows are made by an array of different invertebrates, or that differently shaped burrows may be made by a single “maker” or different ontogenetic stage of a single “maker” (Osgood, 1975). Moreover, any given burrow may be occupied by parasites, predators, or even a burrow “thief” which has supplanted the original “maker.” Not uncommonly, organisms may inhabit natural cavities in the substrate which may be incorrectly considered to have been excavated by the occupant (Palmer, 1928).

TERMINOLOGY

Frey (1973) has described and defined a large number of special terms used in ichnology but did not include the following which are essential to the present report and also are not included in Torre-Bueno (1962):

cell—a subterranean cavity, usually at the end of a shaft or tunnel, which is generally ovoid and larger than the diameter of the shaft or tunnel to which it is connected. Used for depositing eggs, pupating, or turning around. (Text-figs. 3c, 4b, 4c, 4e–g, 4j, 4l, 4m; Pl. 1, figs. 2, 3.)

chimney—an above ground structure, made of mud and clay, which is vertical, cylindrical and usually open at the apex. Generally made to keep out rain, predators, or parasites from burrow entrance.

runway—a surface groove or trench used repeatedly as a pathway.

ECOLOGY OF BURROWING BY INSECTS AND SPIDERS

Insects and spiders burrow in the soil for a number of reasons. A complete or partial subterranean existence has adaptive value because the sediment is an environment where temperature is fairly constant, moisture is higher, light is absent, predaceous and parasitic pressures are often reduced, and food resources may be more abundant. Many arthro-pods are found in the substrate either ovipositing, pupating, resting, feeding, constructing dwelling or brood chambers, or seeking temporary refuge from the weather and natural enemies.

Some species burrow into sediment of variable texture that may be saturated or dry, loose or compacted; others have been reported burrowing into solid rock (Stephen et al., 1969). The terrain may be flat to vertical; burrows in vertical banks normally remain open longer than those on horizontal surfaces because they are less likely to be filled with debris by wind or rain. Plant cover varies, and large, dense roots may inhibit some digging forms. Species that forage in the substrate prefer organically rich soil whereas nesting species prefer soils of low organic content. Burrow depths range from horizontal tunnels just beneath the surface of the soil (semi-endostatal) to shafts 2.7 m deep in some Scarabaeidae (Howden, 1955).

Osgood (1972) found that the amount of organic matter in the O₂ horizon was the most important soil characteristic in determining whether or not a particular area may be expected to have solitary bee nests. Areas with high levels of organic matter in the O₂ horizon had significantly fewer nests. He also noted that nesting sites for these bees have sparse to moderate plant growth on soils that are well drained and with good surface flow. Rau (1925) suggested that the most important factor for burrowing by an andrenid bee was the amount of rainfall and the resulting level of the water table. Smith and Hein (1971) noticed that the concentration of staphylinid beetle tunneling activity varied depending on grain size and cohesion of the sediment while Willis and Roth (1962) demonstrated that soil moisture determined whether or not burrowing would occur by a species of Cydnidae (Hemiptera). According to Sakagami and Michener (1962), the shafts of halictid bees usually extend below the level of the cells, possibly serving as a drain for excess rainwater or to provide communication with more humid soil levels in times of drought.

Silvey (1936), in his study of burrowing freshwater beach insects, found that wind often influenced the distribution of burrowing insects, especially if it was prolonged or strong which resulted in forcible scattering. He noted that wind may also influence food supply, sta-
bility of the beaches, and water content of the surface sand. Moreover, wave action caused occupancy of the narrow inner beach to be more hazardous than other areas of the shore.

Stephen et al. (1969) mentioned that the presence of available water often influences the selection of a site by chimney forming anthophorid bees nesting in hard, dry soils. These species transport drops of water which are used to moisten and soften hard, dry surfaces so that excavation of the shaft and construction of the chimney can proceed.

Evans and Eberhard (1970) noted that comparisons of the gross features of the nests and nesting behavior of various wasps is related to the evolution of wasps and the origin of various aspects of their complex behavior as well as that of their relatives, the ants and the bees. They concluded that one of the major adaptations achieved by wasps in relatively recent geologic time was the making of deep, complex nests in the soil which permitted survival during adverse environmental conditions or heavy parasite pressure. In a similar case, Sakagami and Michener (1962) concluded that primitive halictid bees made nests with the cells dispersed in the sediment around the shaft. They believe the evolution of cell arrangement has proceeded toward increased concentration of the cells, and that this clustering permits greater economy of labor which may have selective advantages resulting in reduction and disappearance of the lateral tunnels leading to the cells. Stephen et al. (1969), in discussing bees, noted that although nest architecture is a direct expression of behavior, it is probably impossible at this time to construct a phylogenetically significant outline of architectural types; various groups of bees (and other insects) have evolved structural patterns for their nests along parallel lines, but "progress" has not always proceeded towards increasing complexity.

DIVERSITY OF BURROWING SPIDERS AND INSECTS

Spiders and insects that burrow in Holocene floodplain sediments are locally very abundant (Stanley and Fagerstrom, 1974, Fig. 13B) and diverse and are capable of producing Lebensspuren of considerable variety. Of lesser importance are crustaceans, annelids, nematodes and molluscs.

The following is a summary of the 8 orders and 31 families of extant spiders and insects that contain burrowing species in floodplain sediments. Their burrows are potentially capable of preservation as trace fossils. Selected examples of insects, spiders and their burrows are illustrated in Text-figs. 1–4. For further information, Borror, DeLong and Triplehorn (1976) give a general survey of the Class Insecta and their relatives.

CLASS ARACHNIDA: ORDER ARANEIDA (spiders)

CTENIZIDAE (trap door spiders), ANTRODIAETIDAE (antrodiaetids), THERAPHOSIDAE (tarantulas), and LYCOSIDAE (wolf spiders) (Text-fig. 1a). Spider tunnels (Text-fig. 1b) may be simple or branched, and some have side chambers which are separated from the main burrow by hinged doors. Most spider burrows are lined with silk which may help to inhibit collapse of the walls.

CLASS INSECTA

ORDER ORTHOPTERA (grasshoppers, crickets, roaches, etc.)

GRYLLOTALPIDAE (mole crickets) (Text-fig. 1d): burrow in moist sand or mud, frequently near bodies of water. The generally horizontal burrow (Text-fig. 1e–f) is usually just beneath the surface and may branch repeatedly. Frey and Howard (1969) and Hanley, Steidtmann and Toots (1971) illustrated probable mole burrows.
cricket (not mole beetle) burrows, and Chamberlain (1975) discussed and illustrated their tunnels near water. The forelegs of mole crickets are adapted for scraping and pushing aside moist sand or soil as the insect moves forward as it feeds.

**Tridactylidae** (pygmy mole crickets) (Text-fig. 1g): burrow in the loose, saturated sand or mud near streams and lakes. Burrows (Text-figs. 1h–i) are of varying depths and configurations. Chamberlain (1975) presented a good account of the pygmy mole crickets and illustrated their burrows.

**Order Dermaptera** (earwigs)

Forficulidae, Labiidae, Labidiuridae, Chelisochidae: many species frequently lay their eggs in a burrow in the soil; the female guards the eggs in the burrow. The method of burrow construction is probably undescribed.

**Order Hemiptera** (true bugs)

Saldidae (shore bugs) (Text-fig. 2a): most species inhabit the damp soils adjacent to bodies of water. Many species burrow, but the burrows (Text-figs. 2b–c) have been poorly described.

Gelastocoridae (toad bugs): some species dig burrows in the sand, loose soil, or mud near rivers, lakes and ponds (Hungerford, 1919).

Cydnidae (burrower bugs) (Text-fig. 2d): usually found under stones or logs, in sand, or in mud near the roots of grass tufts. Willis and Roth (1962) discussed the characteristics of the cells (Text-fig. 2e), burrowing, and environmental factors influencing cydnid behavior. Cydnid cells seem to normally lack an access shaft.

**Order Homoptera** (cicadas, leafhoppers, and their kin)

Cicadidae (cicadas): mature nymphs (Text-fig. 1c) construct a vertical emergence shaft (25–50 cm long) (Text-fig. 1b) from their subterranean root feeding areas just prior to adult transformation. The shafts are made by preliminary scraping of soil from within the burrow followed by compacting (also from within the burrow).

**Order Coleoptera** (beetles)

Cicindelidae (tiger beetles) (Text-fig. 2f): the adults dig burrows in which to spend the night, escape inclement or hot weather, and to overwinter. The predatory larvae are morphologically adapted for burrow life; larval burrows (Text-figs. 2g–h) may be vertical to right-angled, straight or curved, and from a few cm to 1.25 m in depth. Balduf (1935) compiled data from several sources on habits and burrows, and Cridde (1907) provided data on burrow depths in different soils and described the construction of hibernating burrows of several species. Wallis (1961) described the mode of burrowing, and Shelford (1908) discussed tiger beetles and their burrows.

Carabidae (ground beetles) (Text-fig. 3a): both the larvae and adults of many species of this large family burrow in floodplain habitats creating a great variety of burrow configurations (Text-figs. 3b–e). Kirk (1972–1975b) and Silvey (1936) provided detailed observations on carabid burrows.

Limnebiidae (minute moss beetles): many of these very small beetles tunnel in the damp sand at the water's edge or make use of tunnels excavated by carabids, staphylinids, and other shore-dwelling insects (Leech and Chandler, 1956).

Staphylinidae (rove beetles) (Text-fig. 3f): the larvae and adults of many species burrow on beaches and sand bars; the burrows vary greatly in configuration (Text-figs. 3g–i). Smith and Hein (1971) discussed and illustrated the burrows of *Bledius* spp. Zur Strassen (1975) indicated that some *Bledius* spp. feed on algae growing on single sand grains in the damp layer just beneath the surface, and that these algae are collected by the adults and...
stored along the walls of galleries or in special chambers where the larvae will find them.

**Heteroceridae** (variegated mud-loving beetles) (Text-fig. 3j): the larvae and adults live in tunnels in the sand and mud along the shores of streams and lakes. The galleries (Text-fig. 3k) are horizontal, just below the surface, meandering, and often branched. Chamberlain (1975) noted that the walls of the burrow were "striated", but we have not observed this. Silvey (1936) described and illustrated the burrows of larval and adult heterocerids. Tunnels are made by pushing through the substrate.

**Scarabaeidae** (scarabs) (Text-fig. 4a): the members of several subfamilies of scarabs form feeding burrows and often elaborate breeding burrows (Text-figs. 4b–c) for their young. Halffter and Matthews (1966) compiled a detailed account of these structures for the dung beetles of the subfamily Scarabaeinae.

**Order Mecoptera** (scorpionflies)

**Boreidae** (winter scorpionflies): larvae live in subterranean shafts to depths of about 15 cm (N. D. Penny, pers. commun., 1977) where they are phytophagous on the rhizoids of mosses. Maximum burrow diameters are about 3 mm.

**Order Hymenoptera** (ants, wasps, bees)

**Formicidae** (ants): the ground nests of these familiar insects range from small and simple to very large and complex. Most species have a system of runways, shafts and tunnels, but others may have only a simple burrow and some of these are very near bodies of water.

**Vespidae** (paper wasps): some of these social wasps construct nests of hexagonal paper cells in the ground (e.g. *Paravespula*; Rathmayer, 1975).

**Eumenidae** (mason wasps): some species form cells with access shafts; the walls of the cell may be composed of hard clay containing tiny grains of sand with larger stones encrusting the exterior while the inner surface is smooth (Spradbery, 1973). Spradbery also noted that many mason wasps use excavated soil to build temporary chimneys of variable design and length.

**Pompilidae** (digger wasps) (Text-fig. 4d): the adults of many species excavate and provision ground burrows for their young. The morphology of the burrows (Text-figs. 4e–g) is exceedingly variable among the species, but it is generally a simple, oblique tube with a terminal cell. Evans et al. (1953), Evans and Yoshimoto (1962), Powell (1958), Rau and Rau (1918), and Williams (1956) observed and described the burrowing behavior and burrow morphology of several genera.

**Sphecidae** (solitary wasps) (Text-fig. 4h): members of most of the subfamilies nest in the soil and provision their nests (Text-figs. 4e–g) with various captured insects which serve as food for the larvae. Burrowing by sphecids has been described by Cazier and Mortenson (1964, 1965a–c), Evans (1958, 1965, 1966a, b), Evans and Eberhard (1970), and Rau and Rau (1918).

**Apoidea** (bees): burrowing members of this superfamily belong to the families Colletidae (plasterer bees), Andrenidae (Text-fig. 4i) (mining bees), Halictidae (also mining bees), Melittidae (melittid bees), Megachilidae (leafcutting bees), and Anthophoridae (digger and cuckoo bees). Bohart (1952) and Stephen et al. (1969) gave the following data for the bees in general: the soil nests (Text-figs. 4j–m) of solitary bees are usually branched and contain brood cells; the main burrow may be vertical, meandering, a downward spiral, or oblique, and it is frequently lined with fine particles of soil which are probably tapped into place by the pygidium. Many species line the burrow or cells with a wax-like or varnish-like waterproof secretion while oth-
ers (Megachilidae) line the cells with plant materials brought in from the field. Burrow depths range from 2–90 cm. Most burrowing bees construct lateral tunnels from the main burrow with one to several cells present on each lateral; the generally ovoid cells may be vertical or horizontal, single, in linear sequence, or clustered. The nest (burrow), or portions of it, are plugged after the cells have been provisioned and capped. Some species plug only the area adjacent to the cell while others completely backfill the laterals, and still others plug the nest entrance.

At the supra-generic level, some differences in architectural plans are discernable (i.e., all halictid nests have a wider entrance tunnel than branch tunnels), but in some families (i.e. the Megachilidae) the diversity of nest types defies classification. The burrows and burrowing behavior have been described by many authors; chief among these have been Bohart (1964), LaBerge and Isakson (1963), LaBerge and Ribble (1966a, b), Linsley, MacSwain and Smith (1952, 1955), Sakagami and Michener (1962), Stephen (1966), and Stephen, Bohart and Torchio (1969).

Study of Holocene floodplain lebensspuren in Nebraska indicates that the sampling of burrow morphologies in Text-figs. 1–4 (based primarily on the entomological literature) is very incomplete. The burrows and trails shown in Pl. 1, figs. 1–3, made by unknown animals, are morphologically quite different from those in Text-figs. 1–4 and none can be confidently related to any of the burrowing spiders or insects described above. Thus, it is clearly evident that the same general frustrations experienced by marine ichnologists in attempting to ascribe most trace fossils to particular Holocene and ancient trace makers will also plague ichnologists studying floodplain lebensspuren, i.e. similar burrow or trail forms may be produced by taxonomically dissimilar organisms (Text-figs. 1a–c; 4c–e) and morphologically dissimilar burrows and trails may be produced by the same individual organism (Text-figs. 1f–g; 2a; 2g; 2e–f; 3a–d; 4a–b; 4f–g). Furthermore, none of the Holocene lebensspuren with which we are familiar is unique to floodplain environments.

BIOTURBATION

The above discussion has emphasized the making of discrete burrows (shafts, tunnels, cells, etc.) having moderately firm walls and a discernable relationship to the layering of the enclosing sediment. However, the activities of numerous floodplain invertebrates (especially insects) displace the sediment in ways that destroy or greatly modify the original layering (bioturbation) over extensive areas in some cases (Smith and Hein, 1971).

Insects may push, pull, lick or otherwise manipulate the sediment, either at or below the surface, as they move over or through the sediment. Much of this activity involves feeding on organic matter between or on the grains; however, unlike numerous types of “worms”, insects do not actually ingest the sediment nor do they secrete a mucus lining in their burrows. Thus, the walls of insect burrows are commonly less distinct (lack an alteration “halo”) than those of “worms” and other arthropods. Insect feeding may be conducted in a random manner resulting in varied degrees of sediment disruption (Text-fig. 2; Pl. 1, figs. 1, 4) which produces a gradation of structures from discreet trails and burrows to moderate bioturbation in discontinuous layers to almost complete homogenization of thin sedimentary units (Pl. 1, fig. 5; see also Stanley and Fagerstrom, 1974, fig. 4).

HOW INSECTS BURROW

Knowledge of the manner in which crawling and burrowing Holocene organisms produce

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**TEXT-FIG. 4**—Habitus views of burrowing insects with examples of associated burrows; total range of burrow morphology not shown. Measurement of insects is _approximate_ body length. _a_, Canthon sp. (Coleoptera:Scarabaeidae), 4–15 mm. _b,c_, dung beetle burrows. _d_, Anoplius sp. (Hymenoptera:Pompilidae), 5–15 mm (other pompilids to 30 mm). _e–g_, burrow patterns common to pompilid spider wasps and sphecid solitary wasps. _h_, Sphecius sp. (Hymenoptera:Sphecidae), 20–40 mm. _i_, Andrena sp. (Hymenoptera:Andrenidae), 5–10 mm (other bees to 15 mm). _j–m_, burrows of solitary bees (Apoidea).
preservable structures in soft sediments is vital to a proper understanding of their possible trace fossil analogs (Hallam, 1975). Evans (1966a) stated that behavior is what an animal does with its structure and structure is what an animal uses to behave. The structure (body morphology) of most burrowing insects is, in some way, adapted for digging. The mandibles are often used for scraping, breaking up the sediment and for dragging pebbles, etc., and are usually more robust than in non-digging forms; species nesting in compacted clays tend to have broader mandibles than those nesting in sand. The forelegs of digging insects (Text-figs. 1d, 1g, 3f, 4a) frequently have shovel-like, expanded areas or more spines and hairs for handling excavated materials. Lastly, the pygidium is usually well developed and flat in those species using it for pushing or tapping the sediment.

Numerous insects (e.g. heterocerid beetles) form tunnels by simply pushing through the soil and compacting it so that a tunnel remains after they have passed; there is no actual excavation or removal of soil from a chamber. This method of tunneling is readily seen in the saturated sand near the edges of lakes and rivers. Most of the burrowing Hymenoptera and some of the Coleoptera actually remove the sediment from their nests or burrows and pile it near the entrance.

Olberg (1956; see also Evans, 1966b and Evans and Eberhard, 1970) provided the following widely accepted terms to typify the major modes of digging by wasps; with little modification, these terms could be expanded to include most other insects:

**Rakers** scrape the soil beneath the body using the front legs which are curved toward the midline so that the spines comprising the tarsal comb are directed downward. The front legs move alternately (Pompilidae) or synchronously (most Sphecidae), and the sediment is ejected backwards under the abdomen and out of the nest. Nests are generally oblique as this method does not work for vertical burrows. The observations by Moore (1906), von Lengerken (1916), and one of us (J.A.F.) would place the Cicindelidae in this category also.

**Pushers** back out of the burrow pushing soil behind them with the aid of the well-developed pygidium which acts like a ram. Some Carabidae and Scarabaeidae do this.

**Pullers** gathered the loosened soil into a ball-like lump between the head and front legs and is pulled out as the insect backs out of the nest. The pile of soil may be deposited immediately at the surface or dragged a few cm from the nest. Most burrows are oblique as in the rakers.

**Carriers** excavate in much the same way as do pullers except that the removed soil is actually taken some distance from the nest either by walking or flying, thus leaving no evidence of digging at the nest site.

"It should not be assumed that the four types of digging are mutually exclusive; for example, *Tachytes mergus* starts the nest as a 'raker,' then becomes a 'puller' when it reaches damper sand; *Bembix* spp. may be pullers

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**EXPLANATION OF PLATE 1**

**FIG. 1**—Holocene surficial trails (grooves) and semi-endostral tunnels in mud; potential *Sinusites* and *Planolites* respectively. "Makers" unknown. Length of bar scale 10 cm. Vertical view. Santa Paula Creek near Santa Paula, California.

**2**—Unbranched, inclined endostral shafts and possible insect cell (arrow) in recently collapsed vertical face of floodplain sand. "Makers" unknown. Length of scale 11 cm. Middle Loup River near Mullen, Nebraska.

**3**—Inclined and vertical endostral shafts and solitary (a) and clustered (b) insect (?) cells in recently collapsed vertical face of floodplain sand; open entrance to one shaft near upper right corner; cf. Text-figs. 4j-m. Length of bar scale 4 cm. Middle Loup River near Mullen, Nebraska.

**4**—Partial bioturbation (by insects?) of ripple-marked Holocene floodplain sand. Diameter of coin 24 mm. Vertical view. Elkhorn River near West Point, Nebraska.

**5**—Complete bioturbation by insects of loose, damp, surficial Holocene floodplain sand. Length of bar scale 2 cm. Vertical view. Elkhorn River near Scribner, Nebraska.

**6**—Shallow (barely endostral) tunnel system; same area as Pl. 1, fig. 5 except that loose surficial sand has been removed to reveal tunnels; cf. Text-figs. 1e, 3d, 3k. Length of bar scale 2 cm. Vertical view.
Table 1—Broad categories of Holocene floodplain lebensspuren as possible analogs of ancient trace fossil genera.

<table>
<thead>
<tr>
<th>Abbreviated description of Holocene lebensspuren</th>
<th>Selected Holocene examples</th>
<th>Potential trace fossil genus* (and examples)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Endostratal (exichnia) unbranched, cylindrical, vertical shafts (dwellings; shelters) up to at least 20 cm. deep and lacking terminal cell.</td>
<td>Text-figs. 1b, 4k; Stanley and Fagerstrom, 1974, fig. 13B.</td>
<td>Skolithos, Cylindricum, Sabellarifex; Stanley and Fagerstrom, 1974, figs. 3, 9B, 13A.</td>
</tr>
<tr>
<td>2. Endostratal (exichnia) unbranched, cylindrical, vertical to steeply inclined shafts (dwellings; shelters) up to at least 20 cm. deep and with terminal cell.</td>
<td>Text-figs. 1b, 2b, 3c, 3b, 4c, 4g.</td>
<td>Macanopsis, Amphorichnus</td>
</tr>
<tr>
<td>3. Endostratal (exichnia) cylindrical shafts (dwellings; shelters) with variously complex side passages and cells.</td>
<td>Text-figs. 4b, 4e, 4f, 4i, 4l, 4m.</td>
<td>Undescribed and unnamed.</td>
</tr>
<tr>
<td>4. Shallow endostratal to semi-endostratal (endichnia or exichnia) unbranched, cylindrical to ellipsoidal, unpacked tunnels.</td>
<td>Text-figs. 1i, 2c, 3k.</td>
<td>Planolites; Stanley and Fagerstrom, 1974, Fig. 8 (center). Hanley et al., 1971, fig. 3.</td>
</tr>
<tr>
<td>5. Shallow endostratal to semi-endostratal (endichnia or exichnia) branched, cylindrical to ellipsoidal, unpacked tunnels.</td>
<td>Text-figs. 1e, 1f, 3d; Hanley et al., 1971, fig. 5.</td>
<td>Palaeophycus; Stanley and Fagerstrom, 1974, fig. 8 (upper left).</td>
</tr>
</tbody>
</table>

* For generic descriptions see Hantzschel, 1975, p. 57–W108.

when handling small stones, although typically rakers par excellence; *Ammophilia* spp., although carriers, often do a certain amount of raking when opening or clearing the nest. Nor should it be assumed that all examples of one type behave identically. For example, although most rakers build up a pile of soil at the nest entrance, others dig in such a way that the soil particles are sprayed over a wide area” (Evans, 1966b). According to Evans and Eberhard (1970), combinations of scraping and pushing are characteristic of more generalized digger wasps while pulling probably evolved as a mechanism for handling more compacted soil, and carrying as a modification involving total removal of soil particles which resulted in greater concealment of the nest.

Virtually all burrows are of a simple tubular morphology due to the twisting and spiraling movements of the “maker.” In those insects that plow through the substrate, burrows are more apt to be slightly wider than high; rarely there may be scrape marks on the inside of the tunnel but these cannot generally be attributed to any particular body part.

The entrance to many burrows is characterized by a small to moderate conical pile of excavated soil variously described as a tumultus, push-up, or mound. In active or freshly worked nests a tumulus is evident, but it is often rapidly destroyed by wind or rain. Conspicuous tumuli often provide recognition landmarks for parasites and predators, especially bombyliid flies which flick their eggs into the entrance (Linsley, 1958). Kirk (1974) observed that adult carabids extrude excavated soil from their burrows by “pushing” and that if the soil was moist, the extruded soil occasionally formed masses 1–2 cm long that retained the shape of the burrow entrance. Other burrowers (notably Eumenidae, some Masarinae [Vespidae], some Anthophoridae) construct an earthen chimney at the nest entrance which is thought to keep out water or parasites and predators.

Silvey (1936) provided a key to the burrows of eight species of adults and five species of larvae in two families of beetles (carabids and heterocerids) based on branching, depth, diameter, and orientation. Minkiewicz (1933) proposed names for 11 types of terrestrial nests in the Sphecidae, and Malychev (1921, 1935) suggested a complete classification of the nest types of bees; other classifications of bee nests were given by Iwata (1942) and Stephen et al. (1969). These nest classifications are largely
descriptive and seem to be little used in the current literature, possibly because the architectural plans of nests are almost endless in their variety and do not lend themselves to convenient classification.

PALEOECOLOGICAL SIGNIFICANCE

The lebensspuren produced by the various activities of insects, spiders and other invertebrates described above can be grouped into six broad categories (Table 1) for the purpose of interpreting them as possible Holocene analogs for trace fossil form genera. Selection of the potential trace fossil genera in Table 1 was guided by the following three assumptions: 1) the host sediment (matrix) is sufficiently different from the cast sediment that the wall of the fossil is clearly recognizable so it can be inferred that the original trail or burrow was open and then passively filled by sediment from above rather than by collapse of the trail or burrow wall, 2) the lebensspuren have been formed with minimal disruption of lamination in the matrix and therefore lack spreiten and 3) the walls of the lebensspuren are smooth and lack “scratch marks.”

Most of the genera listed in Table 1 are widely assumed to be characteristic of, or even confined to, rocks of marine origin. However, our research clearly indicates that for rocks of Pennsylvanian age (when the body fossil record of large insects begins) or younger, this assumption may be invalid. Thus, future interpretations of both water depth and salinity based on these taxa should give strong consideration to the possibility that the rocks containing them are of floodplain or even upland origin.

Seilacher (1963) has discussed the problems of using trace fossils produced by invertebrates for the recognition of marine vs. nonmarine depositional environments. He summarized selected assemblages of nonmarine trace fossils from the Lower Cambrian to the Upper Triassic and concluded that the morphology of many trace fossils is “independent of salinity,” i.e. some of the same taxa could “occur in both marine and freshwater environments.” The present authors would also extend this conclusion to terrestrial floodplains. For example, the surface of soft floodplain muds and sands commonly contains large numbers of long, shallow simple grooves (trails) with smoothly rounded transverse sections 1–20 mm across that may be made by insects, nematodes (Wallace, 1968), annelids, molluscs (Pryor, 1967), etc. (Category 5, Table 1). Although the probability of such trails becoming trace fossils is low, they do occur as hypichnal and epichnal grooves and ridges (Moussa, 1970). In the Holocene examples we have seen, the trails have no regular pattern or arrangement (they wander aimlessly), are generally unbranched and are good analogs for such trace fossils as Sinusites (Seilacher, 1963, p. 82–83) or possibly Scolicia.

As noted in Häntzschel (1975, p. W108, 117), the precise morphological differences between several trace fossil genera characterized as cylindrical, vertical tubes of various sizes have been debated by ichnologists for over a century. Our purpose here is to point out that floodplain sediments also contain varied burrows of this general form (Category 1, Table 1) and, if preserved in the fossil record, could be included in the genera Skolithos, Cylindricum and Sabellariifex. Previous authors (e.g. Seilacher, 1963, 1967; Alpert, 1974) have regarded these genera as the dwelling structures of suspension feeders (e.g. phoronids, annelids, atremates) that lived in intertidal to shallow subtidal environments. However, the vertical tubes in floodplains are made by spiders and insects as shelters (sensu Stanley and Fagerstrom, 1974, p. 75) for preying, resting, pupating, etc. and thus clearly indicate that both the environmental and ethological interpretation of these genera in Pennsylvanian and younger rocks must be modified to include floodplains and uplands inhabited by a great variety of terrestrial organisms. We know of no pre-Pennsylvanian terrestrial life that built open, tubular shafts like these.

In contrast to the simple cylindrical tubes included in Category 1, Table 1, floodplain-dwelling insects also produce burrows with terminal cells (Category 2, Table 1) which, if fossilized, would belong to the trace fossil genus Macanopsis. It is hazardous, so far as insects are concerned, to infer that there is any ethological significance to the difference between Categories 1 and 2, Table 1; i.e. insect eggs are not always laid in cells and not all cells are used to deposit eggs.

Ichnologists also differ considerably with regard to the morphologic differences between Planolites and Palaeophycus (Osgood, 1970, p. 375; Häntzschel, 1975, p. W95–W97; Frey
and Chown, 1972). The present authors have used the criteria described by Alpert (1975) as the basis for our distinction (Categories 3 and 4, Table 1). In our experience with Holocene floodplain lebensspuren, both unbranched (potential Planolites) and branched (potential Palaeophycus) horizontal, shallow, unpacked tunnels commonly are found together. Both Planolites and Palaeophycus are much better known from marine than from nonmarine environments.

Variation in burrow size for Holocene and ancient shafts (Skolithos) and tunnels (Planolites; Palaeophycus) in sediments and rocks of both marine and nonmarine origin may be the result of different species of burrow trace-makers or of individuals at different ontogenetic stages of the same species (Stanley and Fagerstrom, 1974, p. 71, 80–81).

CONCLUSIONS

On the basis of our studies we conclude as follows:

1. Holocene floodplain lebensspuren are very abundant locally and of great morphologic diversity. However, relatively few of the forms have actually been reported in the fossil record. Insects may produce significant bioturbation of both surficial and shallow intrastratal sediments.

2. The taxonomic diversity of burrowing spiders and insects inhabiting floodplains is exceedingly high. We recognize burrowing species included in 8 orders and 31 families that produce lebensspuren capable of fossilization. Insects and spiders do not ingest sediment nor do they line their trails and burrows with mucus; trace fossils produced by these organisms should have rather poorly defined walls that lack alteration "halos." Therefore, where the trails and burrows of these organisms intersect, disruption of the earlier formed trace is sharply confined to the crossing point and does not extend into the sediment adjacent to the burrow.

3. There is a remarkable convergence in burrow morphology among taxonomically dissimilar insects. Conversely, there may be considerable dissimilarity among burrows made by the same species (or even individual) due to differences in ontogenetic stage, texture and dampness of the substrate, weather, etc. (The observations of Howard, 1976, lend additional support to this conclusion). None of the spider and insect produced lebensspuren with which we are familiar is unique to floodplains.

4. Among the floodplain lebensspuren we have studied are forms which, if preserved in the sedimentary record, would include the trace fossil genera Skolithos, Cylindricurn, Sabellavifex, Macanopsis, Amophorichnus, Planolites, Palaeophycus and Sinusites. Thus, none of these genera in Pennsylvanian (when the body fossil record of megascopic insects begins) or younger rocks may be indicative of marine vs. nonmarine environments.

ACKNOWLEDGMENTS

We would like to thank Lyle Klostermeyer and Gerald Konsler (both formerly graduate students at the University of Nebraska) for their interest and suggestions, and Martha J. Haack, Scientific Illustrator, University of Nebraska State Museum, for her illustrations in Text-figures 1–4. C. Kent Chamberlain shared his ideas on the origin of nonmarine lebensspuren with the junior author on several occasions and also read the final draft of the manuscript. Robert Frey and George Pemberton (Department of Geology, University of Georgia) reviewed the paper and offered valuable criticisms and suggestions. We are grateful to Gail Littrell for typing the manuscript.

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MANUSCRIPT RECEIVED JULY 18, 1979
REVISED MANUSCRIPT RECEIVED SEPTEMBER 24, 1979

The University of Nebraska contributed $500 in support of this article.