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OBSERVATIONS ON THE TUNNEL MORPHOLOGY OF *HETEROCERUS BRUNNEUS* MELSHEIMER (COLEOPTERA: HETEROCERIDAE) AND ITS PALEOECOLOGICAL SIGNIFICANCE

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ABSTRACT—The burrow structures of *Heterocerus brunneus* Melsheimer and its larvae are described from both field (northeastern Kansas) and laboratory habitats. These are further interpreted in light of known North American heterocerid biology. Two important observations are that significant features of any one burrow varied with the consistency (especially the water content) of the substrate, and that different insects were making superficially similar burrows at the same field site. It would require exceptional preservation, or associated body parts, to positively identify fossil traces of these structures as heterocerid burrows, but their general pattern should be readily recognized as foraging traces in even the most degraded preservations.

INTRODUCTION

THE HETEROCERIDAE, or variegated mud-loving beetles (Figure 1), are represented in North America by a single genus (*Heterocerus*) with approximately 16 species (Arnett, 1968). The systematics of the American species were reviewed by Pacheco (1964).

Heterocerid adults and larvae live primarily near ponds, lakes, and rivers. They are found in naturally-occurring cracks and crevices, or, more frequently, in tunnel or burrow systems which they excavate in the moist mud or sand on or near the shore. The adults' tunnels are not dwellings or shelters (sensu Stanley and Fagerstrom, 1974), as they are not used repeatedly like those of crustaceans or mammals. Instead, they appear to be feeding structures, created while the sediment is relatively moist, and abandoned (by flight of the insects) when it becomes too dry for further burrowing.

Ratcliffe and Fagerstrom (1980) reviewed the general types of invertebrate lebensspuren in Holocene floodplains and discussed their potential significance in paleoecology. This report describes one such trace in detail.

OBSERVATIONS

Subsurficial burrows of a number of insects were observed in ephemeral ponds a few hundred meters from the Missouri River in northeastern Kansas. Samples of the burrows were collected, some with the living insects still in place, and taken to the laboratory for study. For one species, *Heterocerus brunneus* Melsheimer, it was possible to induce the formation of new burrow structures and thus confirm the relationship between insect and burrow.

The tunnels of adults are horizontal, just below the surface, meandering, and usually branched or forked (Figure 2.1). Tunnels often parallel or abut each other, but none was observed to actually cross the path of another. In most cases the tunnels end blindly, the beetles apparently having backed some distance down them to begin a new branch tunnel. The tunnels are subcylindrical, depressed-ovate in cross section, and stand in positive relief on the horizontal bedding surface (Figure 2.2). North American adult heterocerids do not make vertical tubes through the bedding planes.

Adult beetles have fossorial legs. The adaptations for digging consist of widening of the tibia and presence of heavy spines on the lateral edge of the tibia (Figure 1). These legs are used to remove sediment from in front of the head, to push the sediment to the side and rear, and, at the same time, push the body forward. Impressions of the lateral spines of the tibia may be seen clearly on the interior of some tunnel walls (Figures 2.3, 2.4, 3.3). Chamberlain (1975) described the interior wall of the tunnel as "striated," but neither this study nor that of Ratcliffe and Fagerstrom (1980) verified this. It is difficult to see how the body morphology and mode of tunneling of these animals could produce a striated tunnel; possibly Chamberlain interpreted the scratch marks of the tibial spines as striations.

Adult heterocerids form tunnels in exposed muddy or sandy areas by pushing the sediment upward a small amount at a time while simultaneously ploughing forward. This upward movement compacts the cohesive surficial sediments into small irregular blocks and simultaneously cements these "compaction units" into a hummocky roof above the beetle. This roof remains after the insect has passed, forming an open tunnel (Figure 2.2, 2.4). The separate compaction units can be seen on the exterior of the tunnel roof (Figure 2.1, 2.5, 2.6). There is no actual removal of soil from the tunnel as is the case with many digging Hymenoptera and Coleoptera. The heterocerid method of compaction tunneling is probably used by other organisms, such as the mole cricket (Gryllotalpidae), inhabiting the same saturated muds and sands near the edges of bodies of water.

The two principal factors limiting the construction of such tunnels (assuming an appropriate habitat) are cohesion of the sediment and maximum grain size. Compaction tunneling cannot be accomplished in dry, loose sand or in wet, soupy muds because there is insufficient cohesion of the grains; dry muds are also unsuitable as they form an essentially incompressible mass. This method of tunneling is also limited to fine-grained sediment, as the insect must be capable of compacting the roof of the tunnel, and sufficient clay must be present to hold the sediment together as it dries.

Within the range of suitable conditions for such burrowing, the same activity can produce differences in the finished product. Figure 2.6 illustrates a burrow system in which the early phase was excavated in relatively wet mud and the later phase (the blind-ended branches) under much drier conditions. As can readily be seen, the separate compaction units are much better defined in the latter.

To emerge from one of these tunnels, the adult heterocerid simply angles upward until the surface is reached. The beetle then either walks or flies to another site. Such tunnel terminations, one with spine marks demonstrating activity outside the tunnel, can be seen in Figures 2.1 (arrow) and 3.1. To begin a tunnel, an adult heterocerid would simply angle downward slightly and begin digging into the substrate.

Adult heterocerids forage in these subsurface galleries. This is probably done during the burrowing process, as the tunnel interiors show little evidence of modification following their initial formation. The extensive and repetitive pattern of the burrows is characteristic of foraging behavior.

Along shorelines, the primary source of food for adult heterocerids is plankton washed on shore; further from the shoreline it appears to be the algae and microscopic organisms that inhabit the interstitial spaces near the surface of wet sediment. The feces that litter many of the galleries (Figure 3.2, 3.3, 3.6) seem to be mostly mud, indicating that discrimination during feeding is low.

Heterocerid oviposition occurs within the tunnels. Claycomb (1919) observed small masses of eggs in tunnels, and Silvey (1935) reported, for *Heterocerus auromicans* Kiesenwetter, small clusters of eggs left in abandoned burrows about one inch below the surface. He noted that such tunnels were usually lined with feces, and that the eggs were embedded in the mat of excretia. Oviposition was not observed in this study, although feces were common enough; it seems likely that Silvey's observations would apply to this species also.

The larvae of heterocerids also make use of tunnels. They certainly use the burrows constructed by their parents because they hatch there, but they also form a very different tunnel of their own. Silvey (1935) reported the larval tunnels to be smaller in diameter and frequently different in form from those of adults. In this study, the larval tunnels were found to be much smaller than the adult tunnels, with smooth sides and a circular cross section (Figure 3.4, 3.5); they also differed by extending into a third dimension, descending to depths of a few centimeters below the subsurficial adult burrows. It was sometimes possible to trace the larval burrows to their intersection with adult burrows (Figure 3.5, 3.6); in most such cases the entry to the larval burrows had been partially or fully blocked by later activity of the adult.

SIGNIFICANCE TO SYSTEMATIC PALEONTOLOGY

Bryson (1939) unequivocally suggested that characteristics of excavated insect burrows are so definite that an investigator can learn to identify the species of insect responsible for the work by the manner in which the soil has been excavated. Unfortunately, Bryson's efforts to support this are not overly convincing, with most examples identified to order or genus rather than species. The authors regard his conclusions as simplistic and erroneous. Insect feeding on organic matter between or on grains of sand, for example, may be conducted successfully in a wide variety of ways, and not all the different patterns need be unique to, or even characteristic of, particular species. Under different conditions the same species and even the same individuals may proceed in different ways, with resultant differences in burrow characteristics (Ratcliffe and Fagerstrom, 1980). Certainly larval and adult tunnels differ considerably, as seen in this study and as reported by Silvey (1935). (Although if larval and adult tunnel systems can be shown to be connected, with a tenable assumption that a single species is involved, a much stronger case can be made for an identification.) Conversely, there is a remarkable convergence in burrow morphology among taxonomically dissimilar insects.

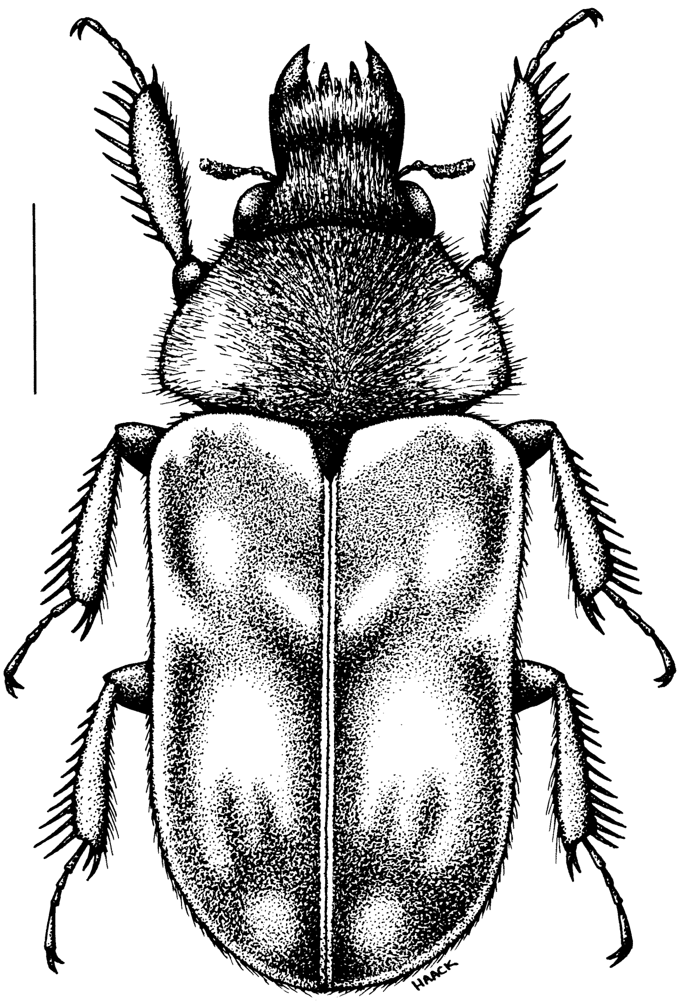

FIGURE *1*—Dorsal view of *Heterocerus brunneus* Melsheimer. Scale bar 1 mm.

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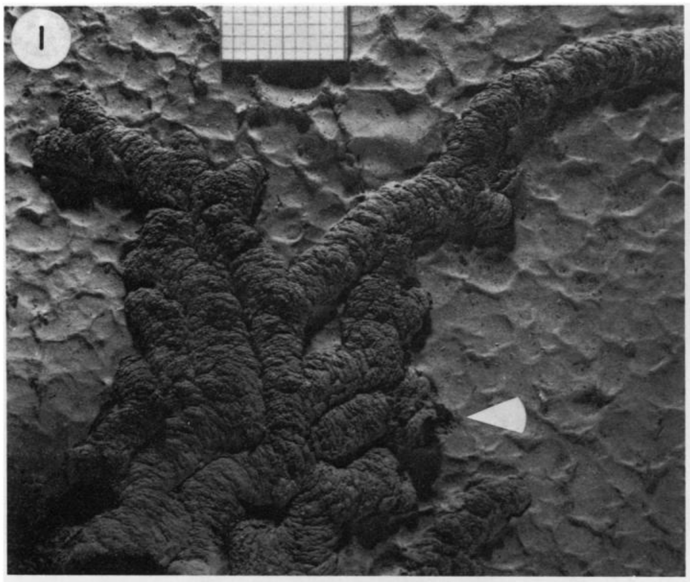
FIGURE *2*—Various views of *Heterocerus brunneus* Melsheimer burrows. *1,* surface expression of burrow complex, note characteristic foraging pattern, burrow exit noted by arrow, scale is 10 mm; *2,* cross section of tunnel, note ridged inner surface, scale bar is 0.1 mm; *3,* impressions of tibial spines on inner tunnel wall, scale bar is 0.1 mm; *4,* partially unroofed tunnel, showing construction of roof from separately compacted units of mud, note impressions of tibial spines on tunnel floor, scale bar is 0.1 mm; *5,* detail of outer surface of tunnel roof, showing compaction units, scale bar is 0.1 mm; *6,* burrow complex illustrating differences in tunnel surface detail related to drying of mud surface during construction, area at center of photo was earliest part of complex, scale bar is 10 mm.

FIGURE *3*—Various views of *Heterocerus brunneus* burrows; all scale bars are 0.1 mm. *1,* thin, uplifted tunnel roof at burrow exit, note tibial spine marks outside tunnel; *2,* interior of tunnel with scattered fecal pellets; *3,* tunnel floor with fecal pellets and tibial spine marks, note some spine marks on fecal pellets, demonstrating more than one passage of the beetle; *4,* oblique section through larval tunnel, note rounded shape and smooth surface; *5,* section through both larval and adult tunnels of smaller individual, with intersection visible inside adult tunnel (arrow); *6,* opening of larval tunnel (arrow) in floor of adult tunnel; opening is partially obscured by blob of mud, apparently moved into opening by later passage of adult.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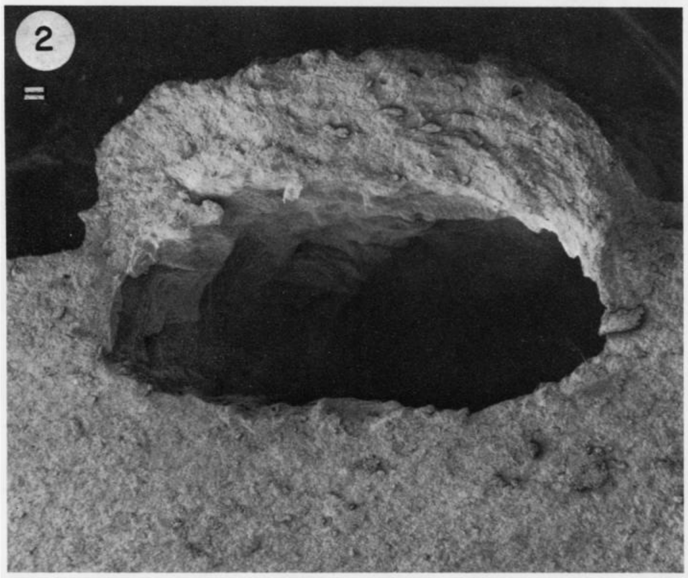
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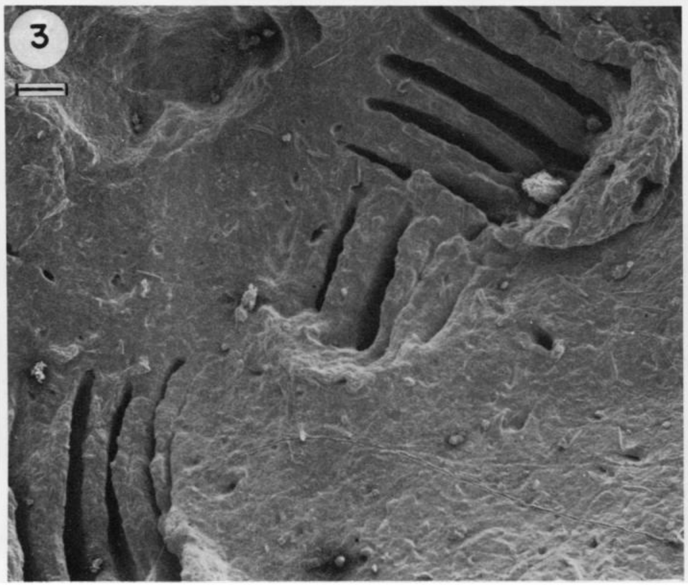
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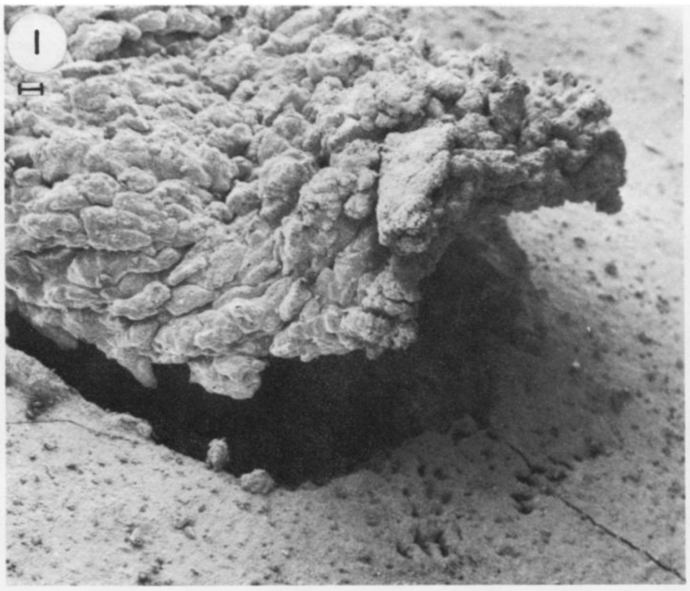
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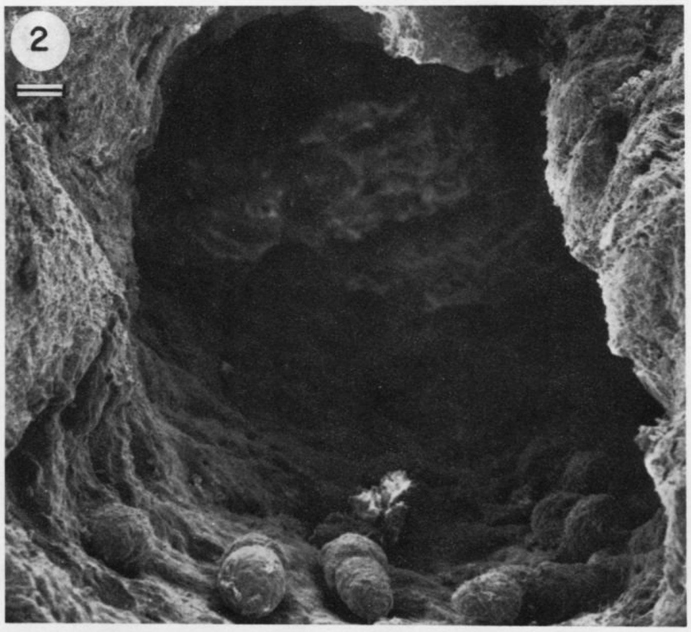
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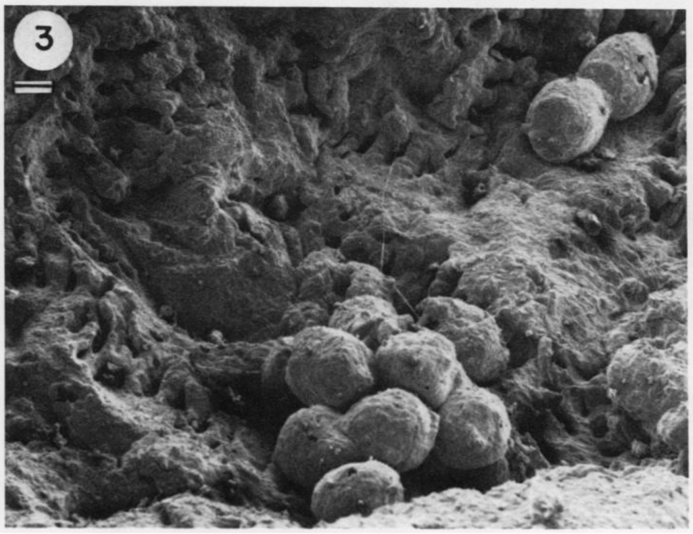
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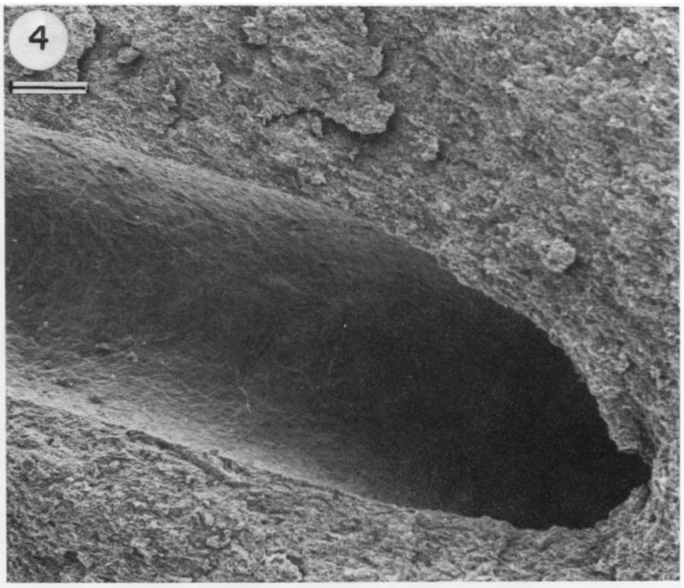
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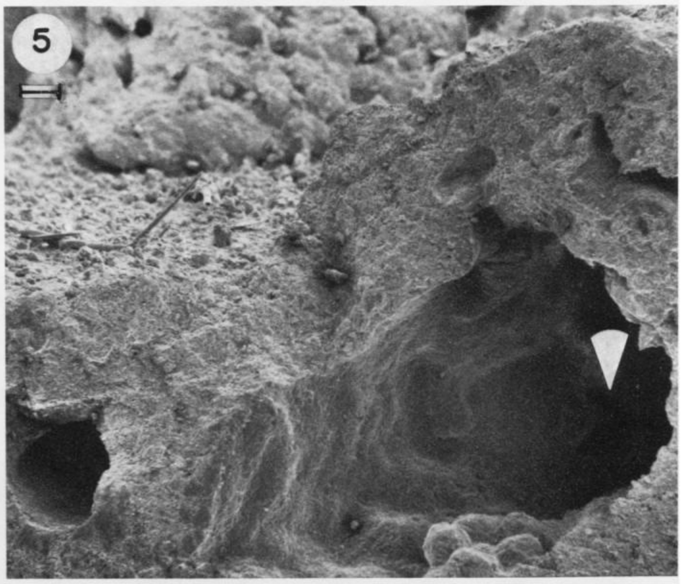
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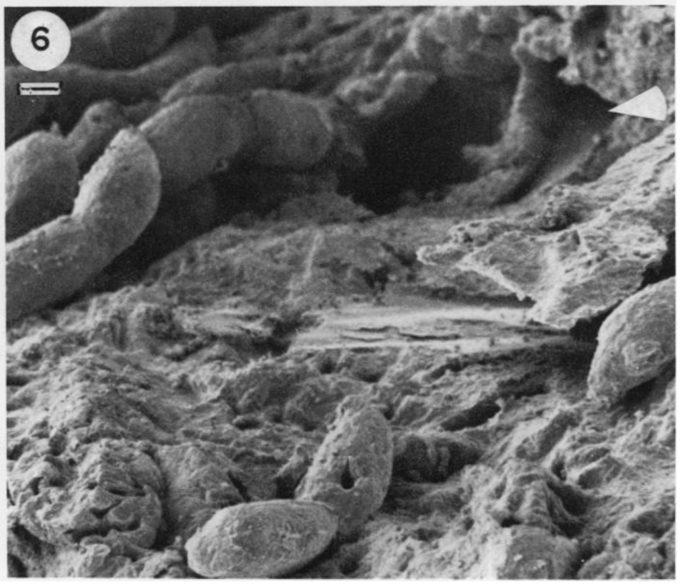
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The taxonomic diversity of burrowing insects is very high. Ratcliffe and Fagerstrom (1980) recognized insects in seven orders and 29 principal families that produce terrestrial lebensspuren capable of fossilization. Only two of these families (Heteroceridae and Gryllotalpidae) include species that form subsurficial compaction burrows, but these are in different orders. This indicates that adaptation to this lifestyle has some selection advantage, and suggests that members of additional taxa could have built these sorts of tunnels in the past.

Thus, should fossil burrows of this general type be found, it would not only require good preservation to distinguish between the heterocerids and gryllotalpids as the builders, but there would always remain the nagging possibility that some completely different, extinct organism might be involved. Apart from exceptional preservation, or association with body parts, it seems likely that heterocerid burrows would fare no better than most trace fossils in systematic paleontology.

In fact, modern heterocerid burrows most closely resemble the trace fossil genera *Paleophycus* (when branched, as in this study) and *Planolites* (when unbranched, a less common situation). Both *Paleophycus* and *Planolites* are shallow, endostratal to semi-endostratal (endichnia or exichnia), cylindrical to ellipsoidal, unpacked tunnels (Häntzschel, 1975). The diameter in both these genera varies considerably, but overlaps the 1–3 mm typical for heterocerid burrows. No occurrence of either of these genera has been reported in association with heterocerid body parts, but then the heterocerids, like many insects, have yet to be reported in the fossil record under any circumstances.

PALEOECOLOGICAL SIGNIFICANCE

Although a fossil trace of a heterocerid burrow may not readily serve to identify its builder, it can still provide information on its builder's behavior. The general pattern is characteristic of foraging, and if it can be determined that the trace represents an unpacked shallow burrow rather than a surface trail or deep tunnel, the interpretation becomes restricted enough to be useful.

An understanding of the relationship between such traces and behavior patterns is best when based upon direct observations of living organisms. As Hallam (1975) pointed out, the study of the manner in which modern organisms produce preservable structures in soft sediments is vital to a proper understanding of their possible trace fossil analogs. Such an understanding can, in turn, make a major contribution to the reconstruction of the paleoenvironment, and paleoecology, of a specific site.

The real value of terrestrial insect lebensspuren is likely to be their contributions to such larger analyses. Rhoads (1975) pointed out that any efforts at environmental reconstruction are strengthened when more than one line of "complementary independent evidence," such as trace fossils, body fossils, sedimentary features, and stratigraphy, can be used. In the study of ancient floodplain deposits, where few body fossils are found that can provide much evidence on local environmental conditions, heterocerid fossil traces could be useful indeed.

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