Notes on the behaviour of *Ummidia* trapdoor spiders (Araneae, Ctenizidae): burrow construction, prey capture, and the functional morphology of the peculiar third tibia

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Summary

Burrow construction behaviour and prey capture behaviour in two populations of the trapdoor spider genus *Ummidia* are described from the direct observation and photography of six individuals collected from Clemson, South Carolina, and Jackson County, North Carolina. From these observations and others it can be concluded that the function of the third tibia, with its unusual saddle-shaped depression, is to press against the burrow wall and generate a force opposing those generated by other legs pressing against other sectors of the burrow wall and to thereby foster effective movement and anchoring in the burrow. Design features which promote this function include the saddle-shaped dorsal half of the tibia, the enlarged distal end of the tibia, the flattened nature of the tibia and metatarsus surfaces which contact the wall, and the stout spines covering these surfaces.

Introduction

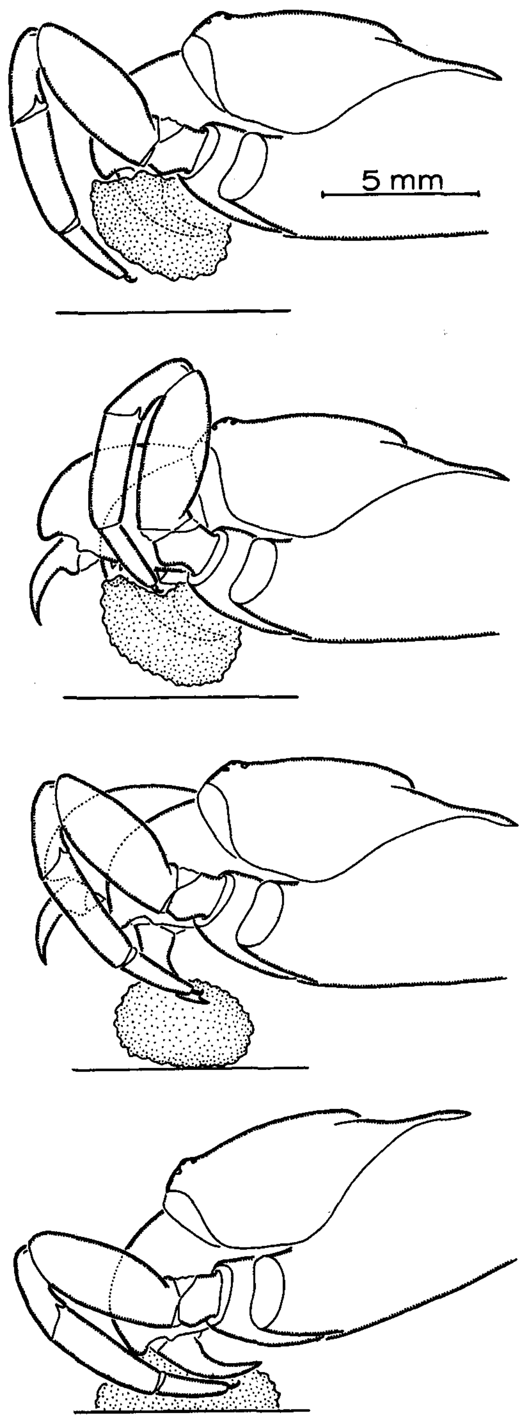
In three papers published in 1886, G. F. Atkinson described in considerable detail the burrow construction behaviour of *Ummidia carabivora* (Atkinson), and possibly *Ummidia audouini* (Lucas), from North Carolina. Otherwise only brief scattered accounts of the behaviour of this interesting and widespread trapdoor spider genus have been published. Moggridge (1873) quoted and summarised observations previously published by P. Browne, P. H. Gosse, W. Sells and J. O. Westwood on the burrow structure of *Ummidia nidulans* (Fabricius) from the Caribbean and *Ummidia aedificatorius* (Westwood) from Spain. Pickard-Cambridge (1908), Bacelar (1927, 1933) and Buchli (1962) contributed to our knowledge of burrow structure, prey capture and mating behaviour in the southern European *Ummidia picea* (Thorell). Baerg (1928) described the pre-ballooning dispersal behaviour of *Ummidia* spiderlings from Arkansas. Additional information on *Ummidia* behaviour can be found in Gertsch (1949, 1979) and Buchli (1969). The purpose of this paper is to clarify and extend our knowledge of burrow construction and prey capture behaviour in *Ummidia* and to consider the function of the distinctively shaped tibia of the third leg.

Materials and Methods

All observations were made in the laboratory on four adult and two nearly adult *Ummidia* females collected near Clemson, South Carolina and Sylva and Cullowhee, North Carolina. According to W. J. Gertsch (pers. comm.), these are all probably *U. carabivora.* The burrows were constructed in humid sandy loam soil in terraria. Burrow construction data are derived from approximately 55 observation hours of eight burrows in the process of construction. A 16 mm movie camera running at 32 frames per second and a 35 mm camera with an electronic flash were used to record portions of the behaviours. Three complete prey capture sequences were recorded on movie film; 43 other capture attempts were observed but not recorded on film. *Tenebrio* larvae were used as prey. All figures were drawn from movie film frames or slides.

Burrow construction behaviour

Burrow construction can be conveniently divided into three phases: (1) the initial excavation phase during which a burrow one and one-half to two times the spider's length is formed, (2) the door construction phase during which the trapdoor is formed, and (3) a subsequent excavation phase during which the burrow is lengthened under cover of the trapdoor. The duration of each of these construction phases varies considerably and probably depends upon many factors. The duration of the first phase varied from 90 to 300 minutes (N=5, mean = 220 minutes), the door construction phase ranged from 75 to 210 minutes in duration (N=7, mean = 145 minutes), and the final phase is an open ended process which was not closely monitored. It is worth noting that Atkinson (1886b) found wide variation in the duration of phase 1 (30-180 minutes, N=14) and phase 2



1
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Figs. 1-4: Lateral views of *Ummidia* female showing position of fangs, chelicerae, pedipalps and soil load during carrying (1) and three stages of soil release (2-4).

(15-240 minutes, N=15) even though he was observing a sample of spiderlings belonging to the same brood and placed in identical containers with the same soil conditions.

First the specific behaviour patterns which are performed during burrow construction will be described. Then the arrangement of these patterns in each phase of burrow construction will be discussed.

Specific behaviour patterns

Digging. Simultaneously the chelicerae are raised and spread apart and the fangs extended. Then, as the cephalothorax moves toward the substrate, the fangs are flexed and the chelicerae lowered. The fangs cut into the soil and press a load of soil up against and between the chelicerae. The first legs, contrary to a statement by Gertsch (1979), do not act as digging tools.

Carrying (Fig. 1). The soil is held between the chelicerae and the flexed fangs. The pedipalps are held in a flexed state in front of and somewhat below the soil load. They cradle the soil load, seldom actually touching it, and seem to prevent the soil load from rubbing against the burrow wall during transport.

Pivoting. Whenever the spider reverses its direction in the burrow, such as after digging or after releasing soil, it does so by flexing its body laterally at the pedicel and pivoting around its own dorsoventral axis.

Releasing (Figs. 2-4). The tips of the pedipalps are held against the top of the soil load on each side of the chelicerae. One chelicera is lifted as its fang is extended (Fig. 2). Then this fang is flexed. Next, as this chelicera is lowered and its fang extended to push down against the soil load, the second chelicera is lifted as its fang is first extended (Fig. 3) and then flexed. Finally, this chelicera is lowered and its fang is extended against the soil load. The pedipalps are extended slightly during the process of release to help push the soil from the chelicerae. This process may be repeated but is sooner or later followed by a joint pushing of both chelicerae against the released soil as the cephalothorax moves forwards and down (Fig. 4).

Silk application. First one posterior spinneret extends to apply silk to the substrate, then it retracts as the other extends in the same manner. One such complete cycle of spinneret movement lasts about 2/3 second and the cycles follow one another without pause. As this rhythmic pattern continues, the spider controls the placement of the silk by shifting its abdomen and entire body. The silk issues from the spigot population as a multitude of minute sticky threads which, when applied, usually have the collective appearance of a very thin sheet or band.

Burrow packing. While the distal ends of the chelicerae press against the wall at the bottom of the burrow, the legs flex over the dorsum of the cephalothorax and press against the opposite wall sector further up the burrow. Usually the fourth legs do not press against the burrow wall, but hang onto the entrance rim. Burrow packing probably both enlarges the burrow and strengthens its walls.

Rim moulding. With the spider facing up and out of the burrow opening, the pedipalps and first legs extend forward, reach beyond the entrance rim, and then are flexed to pull soil to the rim. The soil is then pressed between the ventral surfaces of the distal articles of these appendages and the chelicerae. This activity helps strengthen the entrance rim, which must support considerable weight whenever the spider holds its door shut.

Door shape testing. This pattern proceeds and guides the placement of the soil load onto the edge of the developing trapdoor. With its venter against the underside of the door and hinge, the spider touches the door edge with the tips of its pedipalps, first legs and, sometimes, second legs. Each tarsal tip touches and withdraws and touches again in rapid succession. Usually the cephalothorax turns from one side to another so that a large sector of the door edge is tested each time. If any notch is present in the door edge, the testing soon concentrates there, with the pedipalps performing the final touch tests before the soil is applied.

Door moulding (Fig. 5). The anterior and ventral surfaces of the chelicerae press against the under surface of the soil load just released on the edge of the trapdoor while the distal articles of the pedipalps and first legs simultaneously press against the upper surface. The pedipalps and legs lift and shift laterally and press down in unison again. This cycle of shifting and pressing is performed from three to ten (usually three to five) times before other activities commence. Door moulding compacts the soil released on the door edge and causes it to adhere more firmly to the developing door.

Door fit testing. This pattern, which occurs when the trapdoor is nearly finished, serves to determine whether the door fits the entrance properly. The spider attaches the claws of the first legs and perhaps the pedipalps to the under surface of the door, pulls the door down tightly against the entrance rim, and holds it in that position for several seconds. If more soil is to be added to the door, it is pushed open before the spider releases its hold.

Soil ejection (Fig. 6). The spider faces up and out the burrow and holds onto the entrance rim with the second legs. The first legs are raised and hold the door open at an angle of 45° or more. The pedipalps are moved from the carrying position and are flexed strongly at the patella so that the tarsi are positioned behind the soil load on each side of the chelicerae. The pedipalps are suddenly extended, snapping forward at the same time as the chelicerae are lifted and the fangs extended. Thus the pedipalps catapult the released soil pellet up and away from the burrow entrance. Clayey soil pellets are flipped further than sandy soil which tends to fly apart. The horizontal distance that soil is catapulted ranges from 5 to 80 cm.

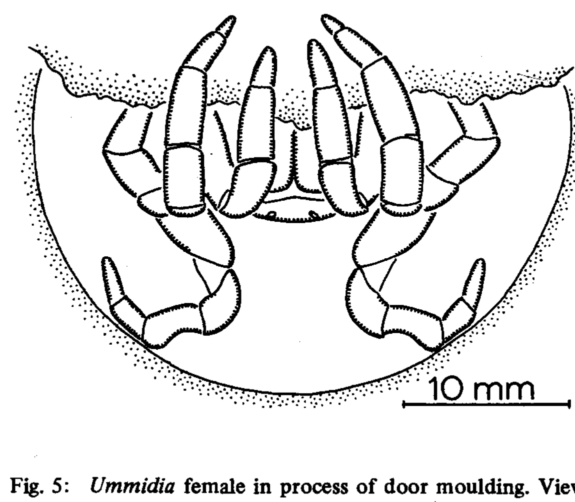

Fig. 5: *Ummidia* female in process of door moulding. View from directly above burrow entrance.

Phases of burrow construction

Phase 1: The initial excavation

Digging, pivoting, carrying and release of the soil are the first and most frequent patterns performed during burrow construction. At first most soil is released outside the developing entrance rim, but toward the end of phase 1 the soil is usually released on the entrance rim and sometimes on the burrow wall below the rim. Burrow packing is performed sporadically during this phase.

The frequency and duration of silk application increase during the later part of phase 1. At times, as many as six soil loads may be dug and released in succession before silk is applied. Although it is not normally performed synchronously with other patterns, silk application sometimes occurs during digging and during soil release. Although silk is applied primarily to the entrance rim, it is also applied outside the burrow on newly deposited soil and to the walls and even bottom of the burrow. Usually, silk is applied where the last load of soil was placed. The primary function of silk application is probably to strengthen the burrow walls and entrance rim.

A representative sequence of behaviour patterns during a portion of phase 1 is as follows: digging – carrying and pivoting – releasing – pivoting – digging – carrying and pivoting – releasing – pivoting – silk application – digging – carrying and pivoting – releasing – pivoting – packing – silk application – digging – etc. Near the close of phase 1, rim moulding occurs. This pattern usually follows soil release and is usually followed by pivoting and silk application.

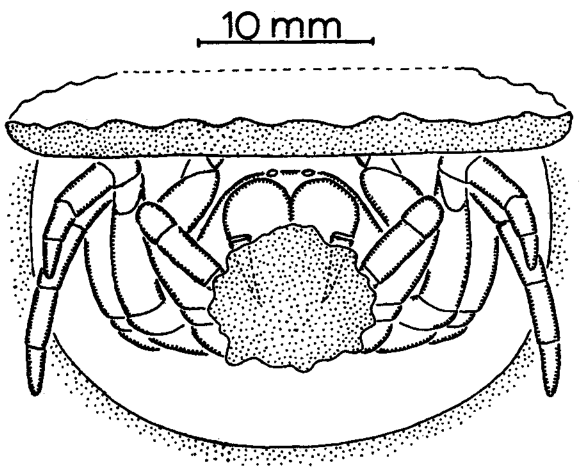

Fig. 6: *Ummidia* female in process of soil ejection. View from above and in front of burrow entrance an instant before the soil is catapulted.

The six spiders observed demonstrated considerable variation in some of the components of this initial excavation phase. One spider performed burrow packing much more frequently than did all the rest, sometimes repeating packing four times in succession. Another spider performed no packing movements at all and applied silk much less frequently than did the others. Another individual ejected soil loads during phase 1; all other spiders ejected soil pellets only after the trapdoor was complete.

Phase 2: Trapdoor construction

Door construction commences when the spider has excavated to a depth of about one and one-half to two times its body length and probably increases protection from both predators and unfavourable climatic fluctuations during subsequent burrow excavation. A typical sequence of behaviour patterns during phase 2 is as follows: digging – carrying and pivoting – ascending ventral sector of burrow wall to entrance rim – moving sideways around burrow wall to dorsal sector (where door hinge is positioned) – ascending to edge of door – door shape testing – soil load released on door edge – door moulding – backing down burrow – pivoting – backing up burrow – silk application to door – descending burrow – repeats entire sequence. Occasionally during this phase soil is deposited on the entrance rim. When the door is nearly complete, door fit testing will sometimes occur after the fifth step (ascending to edge of door) or the final step (descending burrow). What factor(s) the spider monitors when testing door fit is (are) unknown, however the physical resistance of the door to pulling and the passage of light into the burrow are reasonable possibilities.

The spider usually applies silk to the ventral surface of the door proximal or to one side of the newly placed soil load, moves slowly to that new deposit, concentrates its efforts there, moves to adjacent areas and then towards the hinge, finally stopping silk application near the hinge or even lower down the burrow wall. The duration of each silk application bout (N=14) for one spider during door construction ranged from 62 to 172 seconds and averaged 122 seconds.

The door of an adult collected in the field is considerably thicker than the same spider's door newly constructed in captivity. This indicates that a door is normally made thicker by periodic addition of soil and silk, probably to its under surface, after its initial construction. Atkinson (1886a) observed that some of his spiders gathered much of the material used in door construction from the soil surface outside the burrow and that this helped to camouflage the door. Such behaviour was not exibited by the spiders I observed.

Phase 3: Excavation after door construction

Usually the spider becomes inactive after door construction and resumes burrow excavation several hours to a few days later. Additional excavation activity occurs sporadically, successive bouts being separated by several days or weeks. Presumably digging, carrying, and pivoting patterns identical to those of phases 1 and 2 are performed during this phase, although they have not been observed directly. Probably burrow packing and silk application also continue during phase 3.

A noteworthy feature of phase 3 is that the excavated soil is not released in the normal manner but is instead catapulted away from the entrance. After the soil pellet is ejected, the spider quickly retreats and the door closes. The time span from the onset of door opening to door closing was 1.5, 2.3, and 2.5 seconds for the three filmed soil ejection sequences. The interval between four successive soil ejections ranged from 80 to 104 seconds.

It seems reasonable to postulate that the primary function of soil ejection is to prevent the build-up of excavated soil around the entrance rim, a situation that might hinder prey capture, result in soil deposition over the door during rains, or advertise the burrow location to predators or parasites. Such a build-up would not occur around an entrance constructed on a strongly sloping surface, but the majority of *Ummidia* entrances that I have discovered are placed on minor, nearly horizontal terraces on ravine banks or are on nearly horizontal ground. *Bothriocyrtum californicum* (O. P.-Cambr.), a ctenizid which commonly builds burrows on nearly horizontal ground, also catapults its soil loads (Passmore, 1933). On the other hand, the antrodiaetid trapdoor spiders of the genus *Aliatypus* which I have observed do not catapult excavated soil and almost invariably construct their burrows on steeply sloping surfaces.

Prey capture behaviour

When kept under a natural light regimen, the spiders assume the prey sensing posture at about nightfall, rarely as much as two hours earlier, and maintain this posture until after daybreak, often until two or three hours hence. The spider is positioned just below the door, facing up the burrow, and is in contact with the under surface of the door, which is cracked open slightly, but the details of the prey sensing posture are unknown. Buchli (1969) suggests that in European *Ummidia* the door may rest upon some of the front tarsi and that the "spoon or racket shaped bothria" on the dorsal surface of the tarsi may be key mechanoreceptors involved in sensing substrate vibrations generated by prey movement. Sensitivity to prey vibrations does not seem to extend much beyond the edges of the trapdoor, for in 43 of the 46 capture attempts observed, the spider responded only after the prey touched the edge of the trapdoor. One strike occurred when the prey was 0.5 mm from the door and two strikes occurred when the prey was 1.0 mm from the door.

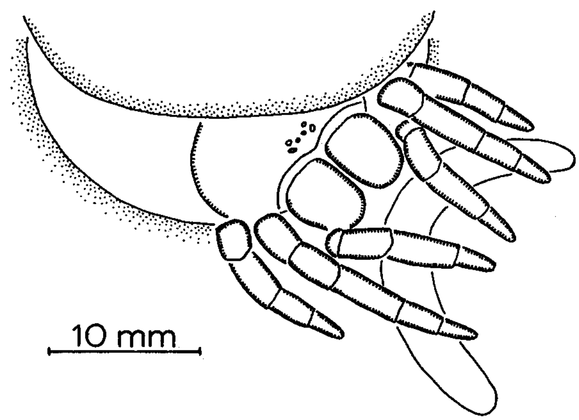

Fig. 7: *Ummidia* female capturing *Tenebrio* larva. Larva is pinned by pedipalps and first legs but fangs have not yet been extended. View from directly above burrow entrance.

The strike begins as the door pops open and the spider lunges out the entrance towards the prey. The cephalothorax extends out over the entrance rim but the abdomen remains in the burrow. The third and fourth legs remain in the burrow and anchor the spider to the burrow walls. The pedipalps and first and second legs reach out of the entrance (Fig. 7). The pedipalps, first legs and occasionally the second legs extend over and pin the prey to the ground. Then these appendages flex to pull the prey towards the chelicerae and usually (although not always!) the fangs are extended and imbedded into the prey. Finally, the spider backs down into the burrow with the prey held primarily by the pedipalps and first legs. The time interval from the first strike movement to contact with the prey was less than 0.03 second for each of the three filmed captures. The interval between the first strike movement and the imbedding of fangs was 0.2 and 0.3 seconds in the two filmed captures where fangs were used. The total duration for each filmed prey capture from the moment of the first strike movement to the disappearance of spider and prey behind the trapdoor was 1.2, 1.4, and 1.8 seconds.

In all 46 prey capture attempts there were only six inaccurate strikes resulting in prey escape. Response flexibility was exhibited when a *Tenebrio* larva that crawled over the top of the trapdoor from the hinge to the free edge was captured while still on the door. The spider rotated so that its venter was against the underside of the door and reached up and over the edge of the door with its pedipalps and first legs to pin and retrieve the prey.

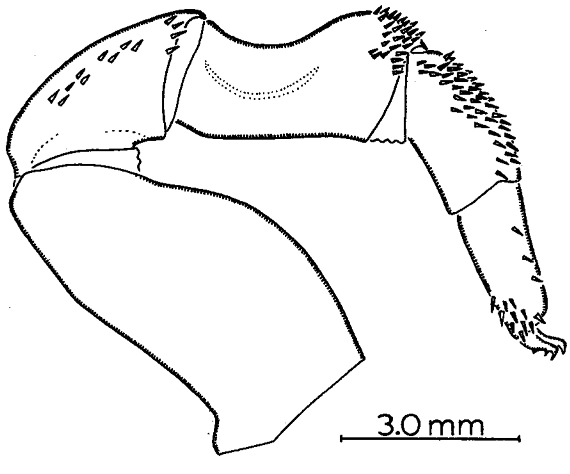

Fig. 8: Prolateral view of the left third leg of *Ummidia* female.

Functional morphology of the third tibia

The unusual saddle-shaped depression on the dorsal surface of the third tibia of *Ummidia* (Fig. 8) has been described by many authors. Three related genera, *Conothele* (Main, 1957), *Hebestatis* (Gertsch, 1979), and *Cyclocosmia* (1 species) Gertsch & Platnick, 1975), also share this characteristic. Simon (1892) mentions two other mygalomorph genera with a similar third tibia design, *Paramigas* (=*Myrtale*) and *Heligomerus*. In spite of frequent reference to this characteristic, only one reference to its possible function could be found. Gertsch (1979) states that the "smooth saddlelike emargination on the third leg . . . presses against the lip or side of the burrow" and helps to anchor the spider within the burrow. My observations show that although this brief description of the mechanism of operation is inaccurate, Gertsch correctly identifies the basic anchoring function of the third tibia.

As illustrated in Figs. 5 and 9, the third legs are normally flexed over the spider's dorsum and press against the burrow wall with the enlarged distal end of the tibia and the dorsal surface of the metatarsus. This generates forces opposing those of other appendages in contact with other wall sectors thereby helping to anchor the spider during most of its activities: digging, moving up and down the burrow, pivoting, soil releasing, silk application, burrow packing, door making and soil ejection. Probably the spider is highly dependent on this third leg anchoring mechanism when holding its door shut after being disturbed. As evidenced by marks left on the under surface of the door, the spider grips the door under surface with fangs, pedipalp claws and leg I claws while anchoring itself in the burrow with its remaining legs. The remarkable force necessary to pry open such a door has been described by Gertsch (1979). Also, the maintenance of the prey sensing posture in a nearly vertical burrow may depend heavily on the bracing function of the third legs.

The shape of the third tibia seems to promote the anchoring function in at least two ways: (1) the

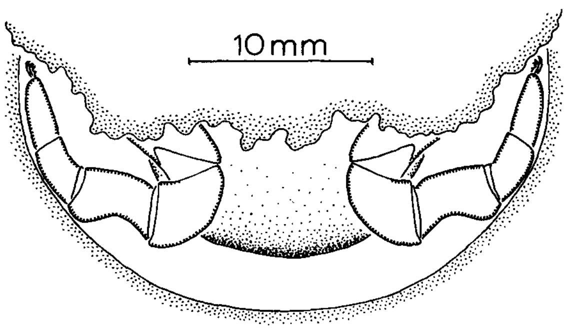

Fig. 9: *Ummidia* female moving up burrow to apply soil to door. View from directly above burrow entrance.

enlarged surface at the distal end of the tibia results in contact with more wall surface area and (2) the U-shaped tibia probably transfers the force applied at the patella-tibia junction more perpendicularly against the wall surface than would a straight tibia. Both of these effects should decrease the chance that the leg would slip laterally along the burrow wall as leg forces are increased. The many stout spines on the distal end of the tibia and on the dorsal surface of the metatarsus and the flattened nature of these surfaces also help increase the friction between the third leg and the burrow wall.

Acknowledgements

I would like to thank Dr William A. Shear for his helpful comments on an early draft of this paper. Heyward Douglass helped obtain two of the spiders used in this study.

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