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OBSERVATIONS ON THE NATURAL HISTORY OF AN *UMMIDIA* TRAPDOOR SPIDER FROM COSTA RICA (ARANEAE, CTENIZIDAE)

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ABSTRACT. An *Ummidia* trapdoor spider species near San Vito, Costa Rica, prefers steep slopes and open, sparsely wooded, early successional stage habitats. This habitat preference and the paucity of small juvenile burrows near adult burrows are consistent with spiderling dispersal by ballooning, known to occur in other *Ummidia* species. The entrance and burrow architecture and prey capture and defensive behavior of this species are similar to those of the few other observed *Ummidia* species. *Ummidia*'s door-holding defensive behavior is described in detail for the first time. Two enigmatic phenomena were observed: door hinges were often tilted well away from the horizontal plane, and one spider was found on two successive afternoons with the anterior half of its body fully exposed as it held onto the inner surface of its fully open trapdoor.

The trapdoor spider genus *Ummidia*, which is distributed widely across the southern United States and south through Mexico, the Caribbean, and Central America (Raven 1985), may contain as many as 100 species (N. Platnick pers. comm.). Scattered accounts of burrow structure and construction behavior (Moggridge 1873; Atkinson 1886a, b, c; Coyle 1981), ballooning (Baerg 1928; Coyle 1985; Coyle et al. 1985), prey capture (Coyle 1981), and other facets of *Ummidia* natural history (Gertsch 1979; Coyle 1981) have been published. We report here the first observations of the biology of a Central American species, probably *Ummidia rugosa* (Karsch 1880).

METHODS

Spiders were studied on the grounds of the Las Cruces Field Station of the Organization for Tropical Studies near San Vito, Puntarenas Province, in southwestern Costa Rica near the Panama border. The station is located at an elevation of 1095 m, receives an average of 3600 mm of rain per year, and includes a remnant (about 100 ha) of old-growth premontane rain forest, the once widespread climax ecosystem of the region. Our observations were made on 2–3 March 1992, 3–6 March 1993, and 5–7 March 1995 during the dry season, which lasts from January through March. Four burrow entrances were observed by Coyle in 1992, 16 by Bond in 1993, and 31 by Coyle in 1995. Most entrances studied in 1992 and 1993 were observed and measured again in the subsequent studies. One adult female burrow was excavated, measured, and photographed in each year. Drawings of the body and spermathecae of the adult female collected in 1993 (Figs. 1, 2) and the following description of this and a second (gravid) female collected in 1995 will help identify the species. Both specimens are deposited in the American Museum of Natural History. All measurements are given in millimeters. Values for the gravid female are in parentheses.

Body length (not including chelicerae) 20.7 (21.4). Carapace 10.02 (9.21) long, 8.52 (7.89) wide. Abdomen 11.52 (12.69) long, 8.02 (8.71) wide. Deep procurved thoracic groove, 1.84 (1.72) wide and 6.72 (5.98) from anterior margin of carapace. Carapace uniform chestnut brown, pars cephalica with median longitudinal row of strong setae flanked by two longitudinal clusters of setae. Eye diameters: AME 0.28 (0.20), ALE 0.62 (0.57), PME 0.26 (0.22), PLE 0.28 (0.22). Eye interdistances: ALE-ALE 0.90 (0.86), AME-AME 0.24 (0.17), AME-ALE 0.44 (0.31), AME-PME 0.20 (0.18), ALE-PLE 0.18 (0.20), PLE-PLE 1.34 (1.14), PME-PME 0.68 (0.60), PME-PLE 0.10 (0.08). Endites, labium, and sternum light brown. Sternum 5.56 (4.90) long, 5.23 (4.73) wide. With 5–8 slit sensilla scattered on each side of sternum. Legs dark brown, no distinct markings. Pro- and retromargins of chelicerae each with 8–10 teeth.

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Leg formula IV-I-II-III, with leg II only slightly longer than leg III. Leg I article lengths: coxa 3.24 (2.68), trochanter 1.41 (1.04), femur 5.98 (5.40), patella 3.74 (3.20), tibia 3.98 (3.56), metatarsus 2.49 (2.02), tarsus 1.58 (1.30). Many trichobothria and 2–8 club-shaped bothria dorsally on tarsus of each leg. Three to five club-shaped bothria on dorsal surface of palpal tarsi.

MICROHABITAT, HABITAT, AND DEMOGRAPHY

Burrows were found only on steeply sloping (60–90°) earthen trail banks, not on gently sloping or level ground. No burrows were found during a careful 30 min search on hands and knees for entrances in the level lawn immediately above the bank where most burrows occurred. The apparent preference of these spiders for steep banks, a preference not exhibited by western North Carolina *Ummidia* (which are typically found on level and gently sloping ground), may be the result of the heavy rains experienced by the Costa Rica population selecting against any proclivity to construct burrows in flood-prone ground. All but five of the burrows were situated in stable soil partly covered with moss and sheltered from rain and runoff by overhanging roots or other materials. The entrances of burrows found in less sheltered microhabitats showed evidence of erosion damage; two of these projected nearly 20 mm above the surrounding soil.

Most burrows were located on the non-forested grounds of the Station along the end of the trail leading to the "Mirador." The rest were located in very young second growth forest within 20 m ("Jungle Trail") and 200 m (trail to Rio Jaba) of the Station grounds. Searches along stable trail and stream banks in older second growth and primary forest failed to locate any burrows. The apparent preference of these spiders for disturbed, sparsely wooded habitats is shared by *Ummidia* populations in western North Carolina (F. Coyle pers. obs.) and Arizona and Mexico (Gertsch 1979) and may be linked to a reliance on aerial dispersal by ballooning, a trait observed in populations in North Carolina (Coyle 1985; pers. obs.) and Arkansas (Baerg 1928). Such a relationship would fit Greenstone's hypothesis that less predictable habitats select for higher rates of ballooning (Greenstone 1982; Coyle et al. 1985). The type of ballooning characteristic of *Ummidia* and other mygalomorphs, ballooning which apparently requires air currents stronger than gentle updrafts (Coyle 1983, 1985), might

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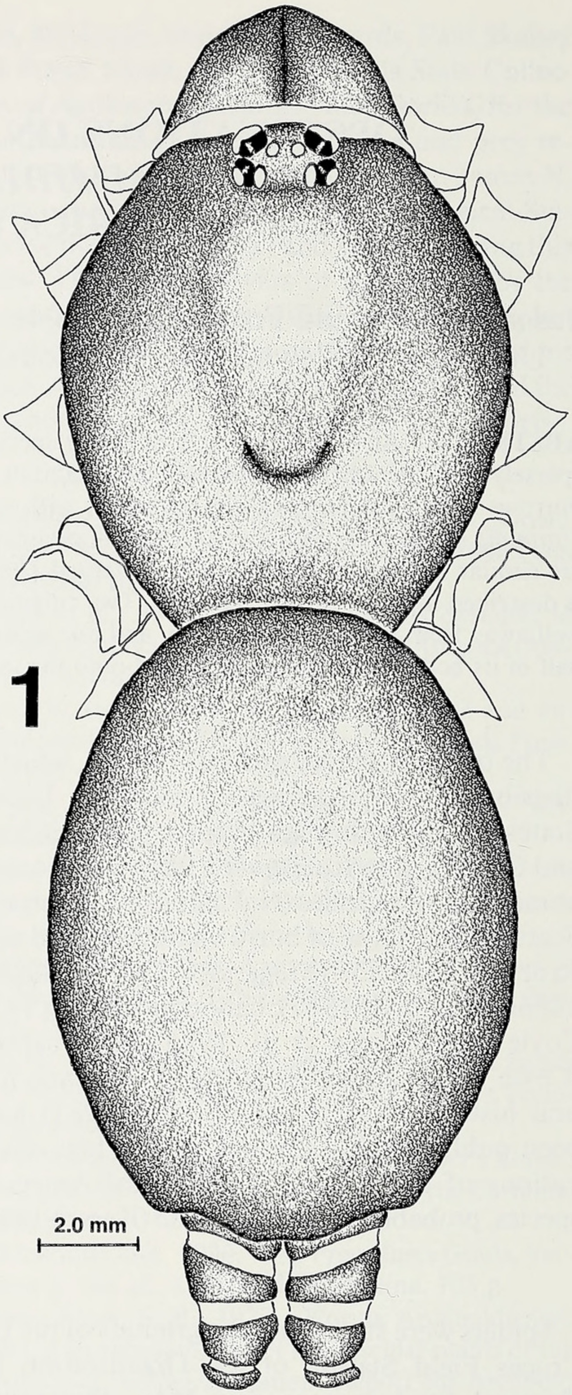

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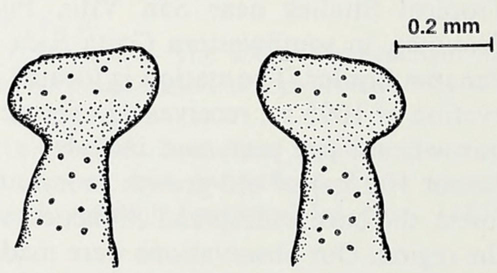


Figures 1, 2.—Adult female *Ummidia* collected in 1993 from Las Cruces, Costa Rica. 1, Dorsal view without pedipalps and legs; 2, Spermathecae.

be especially ineffective and risky for a fossorial spider living in an old growth forest, where the necessary breezes are probably rare to nonexistent except at the top of the canopy.

Despite much effort in 1993 and 1995 to find smaller burrow entrances, the great majority (94% in 1993 and 65% in 1995) were large (with door widths of 15–29 mm) and belonged to near adult or adult spiders, judging from the door widths (20–23 mm) of the three excavated burrows, all of which contained adult females. About half of these burrows were loosely clustered in groups of 2–4 burrows per m^2; others were more isolated. The only smaller entrances found were one with a 10 mm wide door (1993), two with 13 mm wide doors (1995), and nine much smaller entrances of very young individuals (1995). These latter entrances were 1.5–3.5 mm wide, and all but two of these burrows were unoccupied, as evidenced by severely damaged or missing doors. Two of these very small burrows were each about 50 mm from one adult burrow, another two were 10 mm and 15 mm from another adult burrow, and the other five were between 35 mm and 180 mm from a third adult burrow. This paucity of young burrows in locations where adults are common provides additional support for the hypothesis that spiderling ballooning is the primary dispersal mode of this species. Adult female burrows of non-ballooning fossorial spiders like the antrodiaetids are often surrounded by numerous burrows of early instars (Coyle 1971; Coyle & Icenogle 1994), whereas juveniles of a North Carolina *Ummidia* population known to balloon are almost never found near an adult burrow. The higher ratio of unoccupied/occupied very small burrows (0.78) than unoccupied/occupied large burrows (0.13) found in 1995 is consistent with the expectation that young juveniles experience particularly high mortality rates because their high surface to volume ratio and shallow burrows make them especially vulnerable to environmental crises like drought and erosion.

ENTRANCE AND BURROW STRUCTURE

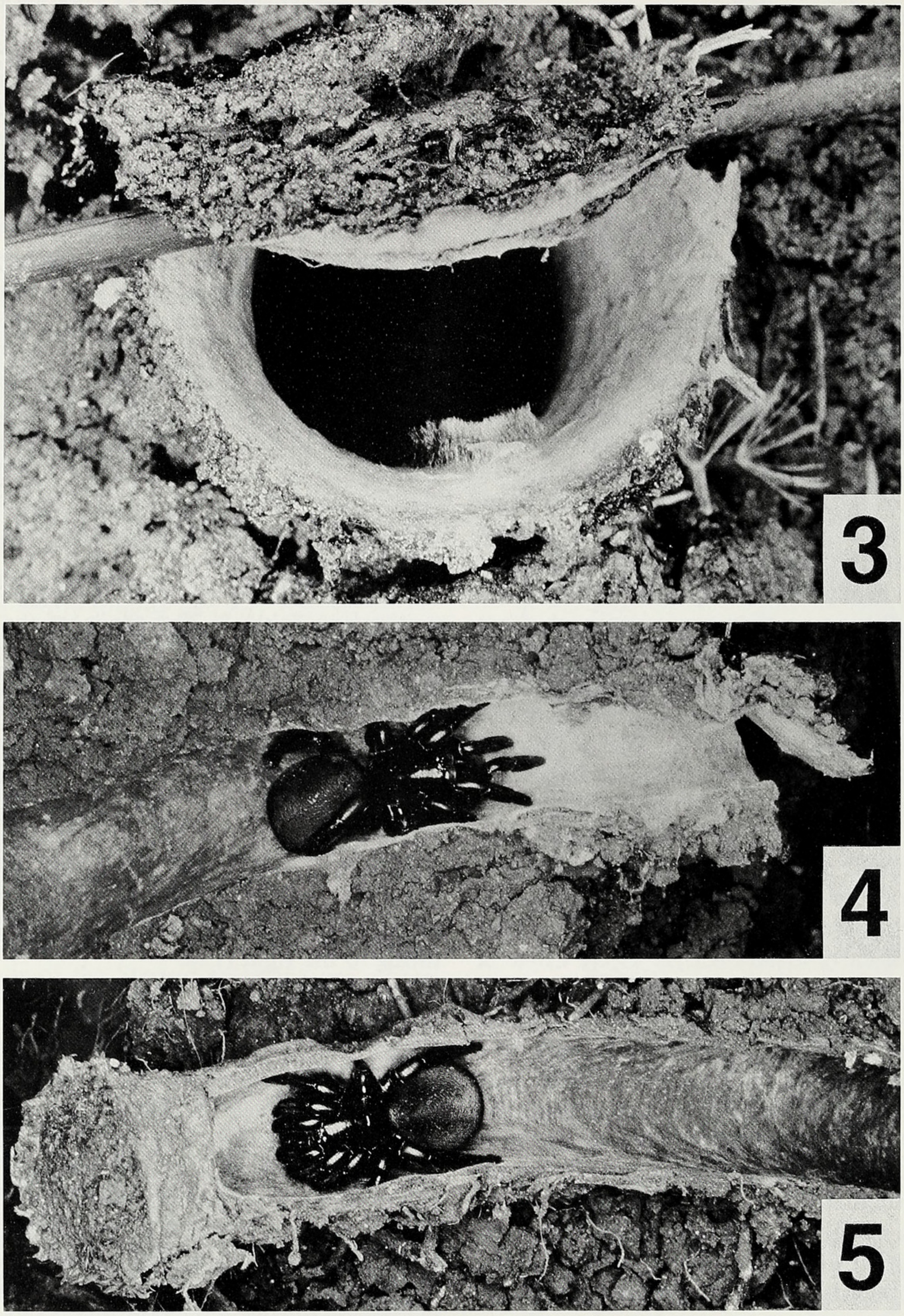
The trapdoor is relatively thick and rigid with beveled edges (Figs. 3, 4, 10, 11; Table 1). When the door is closed, these edges fit snugly into the tough entrance rim which flares outward to form a complementary bevel. The entrance rim is usually nearly flush with the surrounding soil but may extend as much as 5–10 mm above it. The door is composed of soil and silk. Its inner surface is covered with a thick, tough white layer of silk, and its outer surface, which is soil with bits of dead plant material and sometimes moss, resembles the surrounding ground surface (Figs. 3–5, 10–12). The door is connected to the entrance rim by a broad hinge, the bulk of which is thick tough silk continuous with the entrance rim and burrow lining. On the outer surface of some doors are roughly concentric semi-circular ridges or flaps (Figs. 3, 4) which are probably old, smaller doors to which more soil and silk were added as the spider grew. Pieces of plant material and irregular tabs of silk plus soil up to 10 mm long often extend from the entrance rim lips and door edges (Figs. 10, 11) and, like the linear litter and tabs attached to the entrances of other trapdoor spiders (Coyle 1986; Coyle et al. 1992; Coyle & Icenogle 1994), may serve to extend the spider's prey-sensing radius.

Data on burrow entrance structure is summarized in Table 1. The shape of the door is similar to that of many trapdoor taxa (Fig. 9). However, a most peculiar feature of these entrances is their orientation. Contrary to the consistently near-horizontal hinges of most other trapdoor species living on steep slopes (Coyle 1986; Coyle & Icenogle 1994), most of these *Ummidia* doors were oriented with the hinge tilted well away from the horizontal, and some were vertical or nearly so (Figs. 5, 11). In 1995, left tilting hinges (8) were less common than those tilting to the right (12).

Figures 4, 5, and 6–8 illustrate the three excavated burrows. All three extended roughly straight back (100–160 mm) into the trail bank, approximately perpendicular to the surface. As has been observed for other *Ummidia* species (Gertsch 1979), burrow diameter was fairly constant throughout each burrow's length. The full length of each burrow was lined with silk, but the silk was much thicker near the entrance than elsewhere (Figs. 4, 5). The upper third of the longest burrow was lined with an especially thick leathery lining composed of several layers of silk and soil that were probably applied in response to the very loose soil in that spot (Fig. 5).

PREY CAPTURE BEHAVIOR

The foraging posture and prey capture behavior of these spiders are similar in form to those of the North American *Ummidia* studied by Coyle (1981). Approximately 30 min after sunset the Costa Rican spiders assumed the foraging pos-



Figures 3–5.—Photos of burrows of adult females of *Ummidia* at Las Cruces, Costa Rica. 3, Entrance with trapdoor propped open to show small broken silk seal and small old door attached to upper surface of functional trapdoor; 4, Side view of burrow and trapdoor excavated (same as in Fig. 3) in 1992, with female (upper wall of upper end of burrow has collapsed so that door is shifted from its normal position); 5, Side view of burrow excavated in 1993, with female, showing nearly vertical hinge and upper surface of partly open trapdoor.

ture; the trapdoor is opened slightly (1–3 mm) and the spider is positioned just below the door with the tarsi of its pedipalps and first and second legs resting on the lip of the entrance rim (Fig. 10). Several arthropods were placed near entrances to elicit prey capture responses. Only three capture attempts were observed; an opilionid was attacked when it touched the trapdoor with one

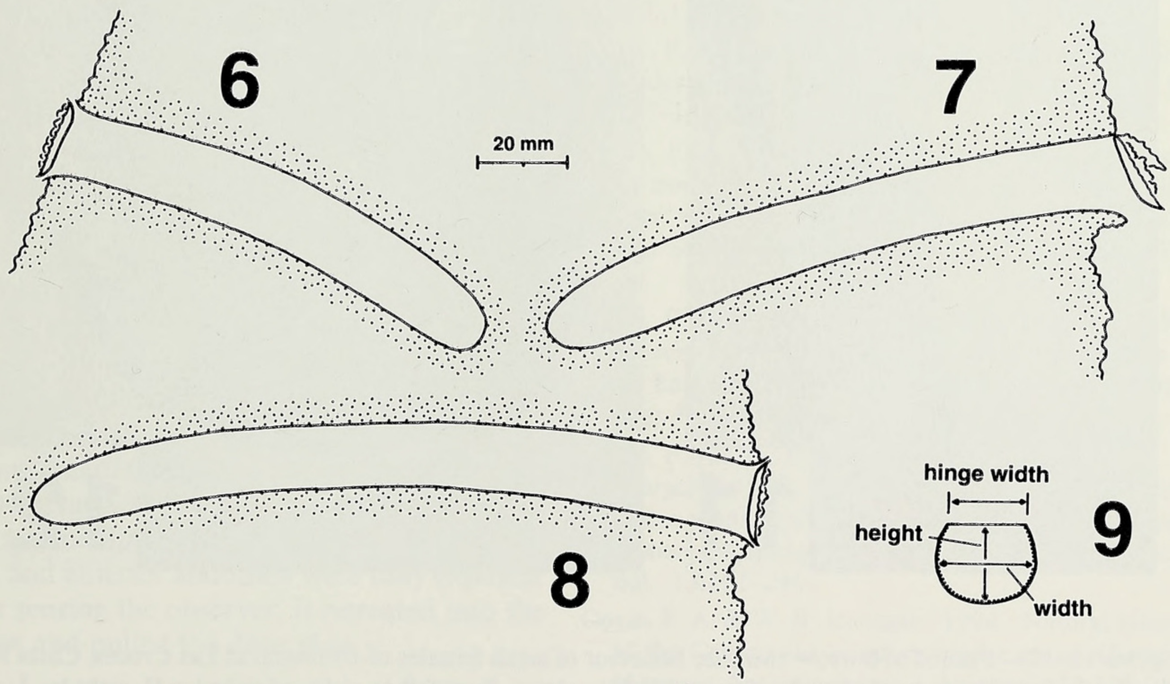
Table 1.—Orientation, dimensions, and shape indices of *Ummidia* trapdoors from Las Cruces Field Station, Costa Rica. Range, mean, and standard deviation given. Only larger entrances (doors over 14 mm wide) included. 1995 sample (n = 20) was measured by Coyle and included many of the entrances in the sample (n = 15) measured by Bond in 1993. Door hinge index = door width/hinge width, and door shape index = door width/door height; see Fig. 9.

	1993 sample	1995 sample
Door thickness (mm)	1.5–3.0, 2.46 ± 0.57	
Hinge angle (degrees)	0–90, 51.0 ± 33.4	0–85, 40.1 ± 24.0
Hinge width (mm)	13–21, 16.9 ± 2.0	14–25, 18.7 ± 3.0
Door width (mm)	15–27, 19.3 ± 3.0	16–29, 21.6 ± 3.0
Door height (mm)		11–22, 16.9 ± 2.6
Door hinge index	1.00–1.29, 1.14 ± 0.10	1.00–1.29, 1.16 ± 0.07
Door shape index		1.13–1.47, 1.29 ± 0.09

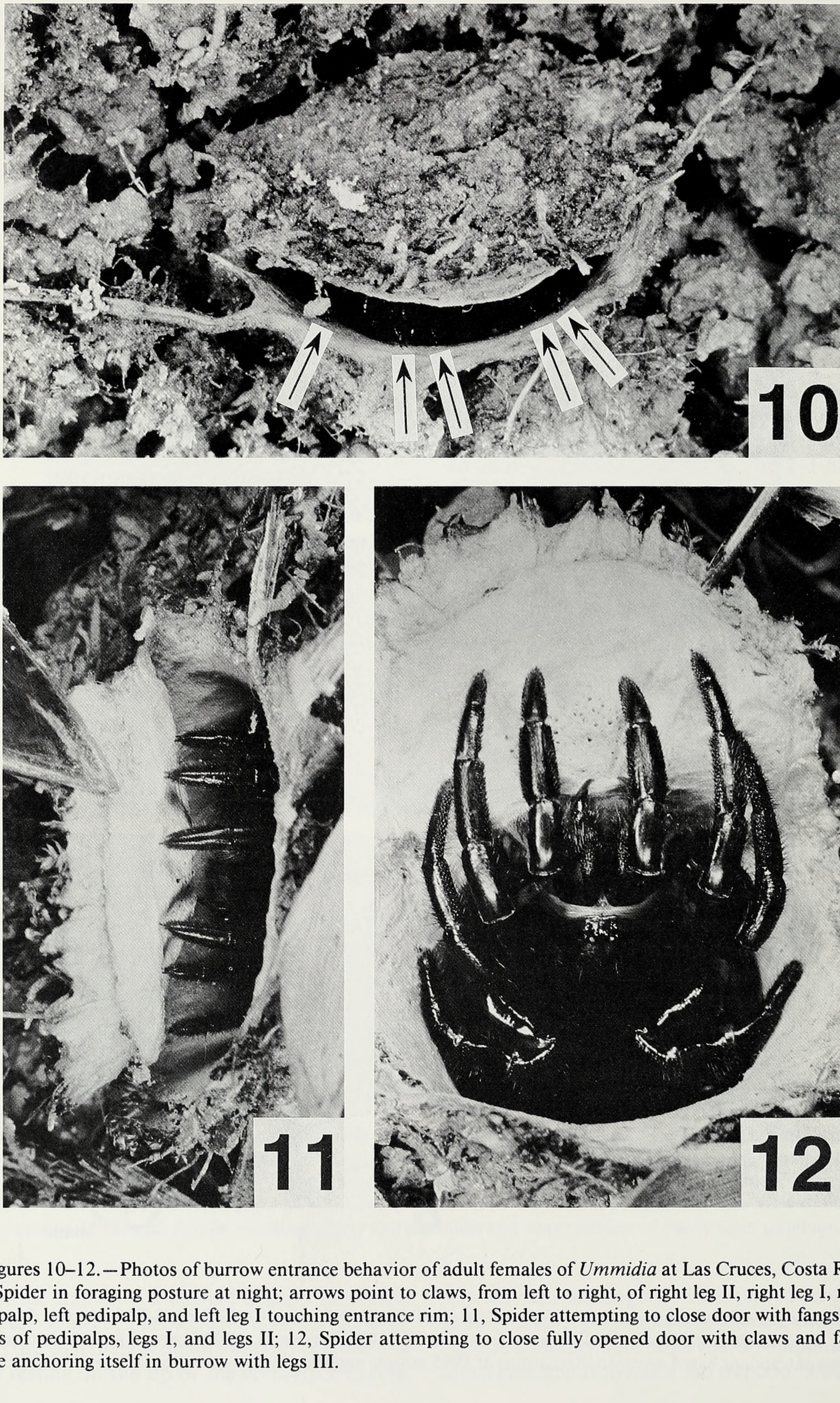
of its tarsi, a broad caterpillar covered with white scalelike hairs was attacked when it crawled within 1–2 mm of the trapdoor, and a small hemipteran was captured when it walked within 3–5 mm of the trapdoor. In all cases the door popped open and the spider lunged from the entrance, exposing all but the posterior half of its abdomen while holding onto the burrow with its fourth and possibly third legs. Prey were grabbed with the pedipalps and first legs. The opilionid and caterpillar were immediately released, but the pedipalps and legs flexed to pull the hemipteran close to the chelicerae for the strike, after which the spider immediately retreated into the burrow with prey.

DEFENSIVE BEHAVIOR

At night spiders were quick to pull their doors shut and hold them tightly closed when the entrances were directly illuminated by a flashlight. During daylight hours, attempts to open (with a knife blade) or measure closed doors often caused the spiders to quickly pull the doors tightly closed; clearly many spiders monitor their entrances rather closely, even in the daytime when doors are closed and substrate vibrations may be the



Figures 6–9.—Drawings of burrows of *Ummidia* females at Las Cruces, Costa Rica. 6–8, Side view drawings of the three adult female burrows that were excavated; 6, 1995 burrow; 7, 1992 burrow; 8, 1993 burrow; 9, Outline of trapdoor based on mean dimensions of 1995 sample and showing the three door shape measurements.



Figures 10–12.—Photos of burrow entrance behavior of adult females of *Ummidia* at Las Cruces, Costa Rica. 10, Spider in foraging posture at night; arrows point to claws, from left to right, of right leg II, right leg I, right pedipalp, left pedipalp, and left leg I touching entrance rim; 11, Spider attempting to close door with fangs and claws of pedipalps, legs I, and legs II; 12, Spider attempting to close fully opened door with claws and fangs while anchoring itself in burrow with legs III.

only sign of danger. As Gertsch (1979) observed in other *Ummidia* species, a great deal of force is required to pry open these secured trapdoors with a knife blade or pair of forceps. Even when the door is forced open the spider continues to maintain its grip, revealing its method (Figs. 11, 12). With its venter facing the hinge, the spider holds the inner surface of the door with its fangs and the claws of its pedipalps and first and second legs, much as described by Gertsch (1979) and Coyle (1981) for North American *Ummidia* species. Claw and fang marks are found on the undersurface of all doors (Fig. 12). The spider anchors itself to the burrow by pressing the enlarged distal end of the saddle-shaped tibia and adjacent dorsal surface of the metatarsus of each third leg against the burrow wall (Fig. 12), as described for North American *Ummidia* populations by Coyle (1981), and by presumably holding onto the wall deeper in the burrow with the tarsal claws of its fourth legs. By opening doors in the daytime when spiders were not in contact with their doors, we could see that a spider usually closes its door with its tarsal claws before inserting its fangs. While this mode of door-holding requires that a spider in foraging position first rotate 180° around its longitudinal axis, an extra maneuver which taxa that hold doors shut only with tarsal claws need not perform (Coyle et al. 1992), the *Ummidia* mode probably produces much more pulling power than if fangs are not used.

Two spiders, one in 1992 and one in 1995, had each lightly sealed its door shut with a thin small patch of silk (Fig. 3) but moved up and closed the door after it was forced open. These seals appeared too weak to prevent predators from forcing the doors open, and instead may serve to hold the door more tightly against the entrance lip during the daytime to reduce the evaporative loss of burrow moisture or ensure crypsis. Another spider exhibited a curious, seemingly vulnerable, posture on two successive afternoons in 1993; it was found motionless and reaching out of the burrow entrance holding onto the undersurface of a fully opened door with its fangs and pedipalp and leg claws so that its prosoma and anterior abdomen were fully exposed. Upon sensing the observer, it retreated into the burrow and pulled the door shut.

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