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# *Actinopus* trapdoor spiders (Araneae, Actinopodidae) killed by the fungus, *Nomuraea atypicola* (Deuteromycotina)

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Seventeen individuals in a dense aggregation of *Actinopus* trapdoor spiders found in northwestern Argentina were killed by a deuteromycete fungus, *Nomuraea atypicola*. The spiders' habitat and burrow structure are described, other host records for *N. atypicola* are listed, and the morphology and probable mode of infection and growth of the fungus are described and discussed. The position of the dead spiders just below the burrow entrance, a location advantageous for aerial conidial dispersal but atypical for dead trapdoor spiders, suggests that the pathogen adaptively alters its host's behaviour.

## 1. Introduction

During a collecting trip to northwestern Argentina in late March 1988, we (Coyle and Goloboff) studied in Salta Province an aggregation of *Actinopus* trapdoor spiders, some of which were victims of a remarkable pathogenic fungus, the hyphomycete *Nomuraea atypicola* (Yasuda) Samson, which one of us (Goloboff) had previously observed killing *Actinopus* in this same locality (May 1983) and in Tucumán Province (January 1985). The observations presented here provide the most complete knowledge to date on the interaction between a mygalomorph spider and a fungal pathogen, and they suggest that this

fungus is an important limiting factor in this and perhaps other populations of *Actinopus*. A recent review by Evans and Samson (1987) on the fungal pathogens of spiders and a paper by Nentwig (1985) indicate that, in spite of the paucity of information on spider-killing fungi in the spider literature, such fungi may play a significant role in the regulation of spider populations.

## 2. Observations

This *Actinopus* population (an undescribed species, Goloboff in prep.) was located on a steep ravine bank along the Bermejo River at La Quena

at an elevation of 300 m, just north of the Tropic of Capricorn in Salta Province. A disturbed forest, transitional between the dryer Chaco woods and the wetter Yunga, was growing near the ravine bank, which was partly covered with herbs, hard bromeliads, cacti, and a low canopy of shrubs and small trees. The soil was humid, firm sandy loam. In an area of about 9 sq. m we observed approximately 50 *Actinopus* burrow entrances and a few burrows of *Idiops clarus* (Mello-Leitão) (Idiopidae), *Chaco obscura* Tullgren, and *Stenoteromatta* sp. (both Nemesiidae). *Neocteniza toba* Goloboff (Idiopidae) and another species of *Actinopus* also occur in this locality, but were not present in the *Actinopus* aggregation we studied. The *Actinopus* entrances were covered with thick rounded trapdoors with a soil-colored, slightly concave outer surface and a white, silk-covered inner surface beveled around the edge to fit snugly into the silk-reinforced rim of the burrow entrance (Figs. 1–4). The burrows extended into the soil at roughly right angles to the bank surface and were lined with a very thin and nearly imperceptible layer of silk (Fig. 5). These features readily distinguish *Actinopus* burrows from those of *Idiops* and *Neocteniza* (Goloboff 1987).

Seventeen *Actinopus* burrows were observed with *N. atypicola* synnemata projecting from the burrow entrance (Figs. 2–5). Close examination of nine of these burrows revealed the following: A white compact mycelial mass filled the upper end of the burrow. Imbedded in this mycelium was the dead spider, invariably facing toward the burrow entrance with its venter against the ventral-most sector of the burrow wall. Extending from the entrance end of the mycelium was a cylindrical synnema consisting of a proximal, smooth, white sterile portion and a distal, pale lavender, sometimes slightly enlarged, fertile portion with a roughened velvety texture and a rounded apex. Invariably the synnema had pushed open the trapdoor so that the fertile portion was partly or entirely exposed above the ground surface. Lengths and diameters (range, mean, and standard deviation in mm) of the four intact alcohol-preserved mycelial masses with enveloped spiders were respectively 8.9–17.7 (15.6±2.12) and 6.9–8.6 (8.12±0.80). Lengths and midpoint diameters of the seven intact alcohol-preserved synnemata were

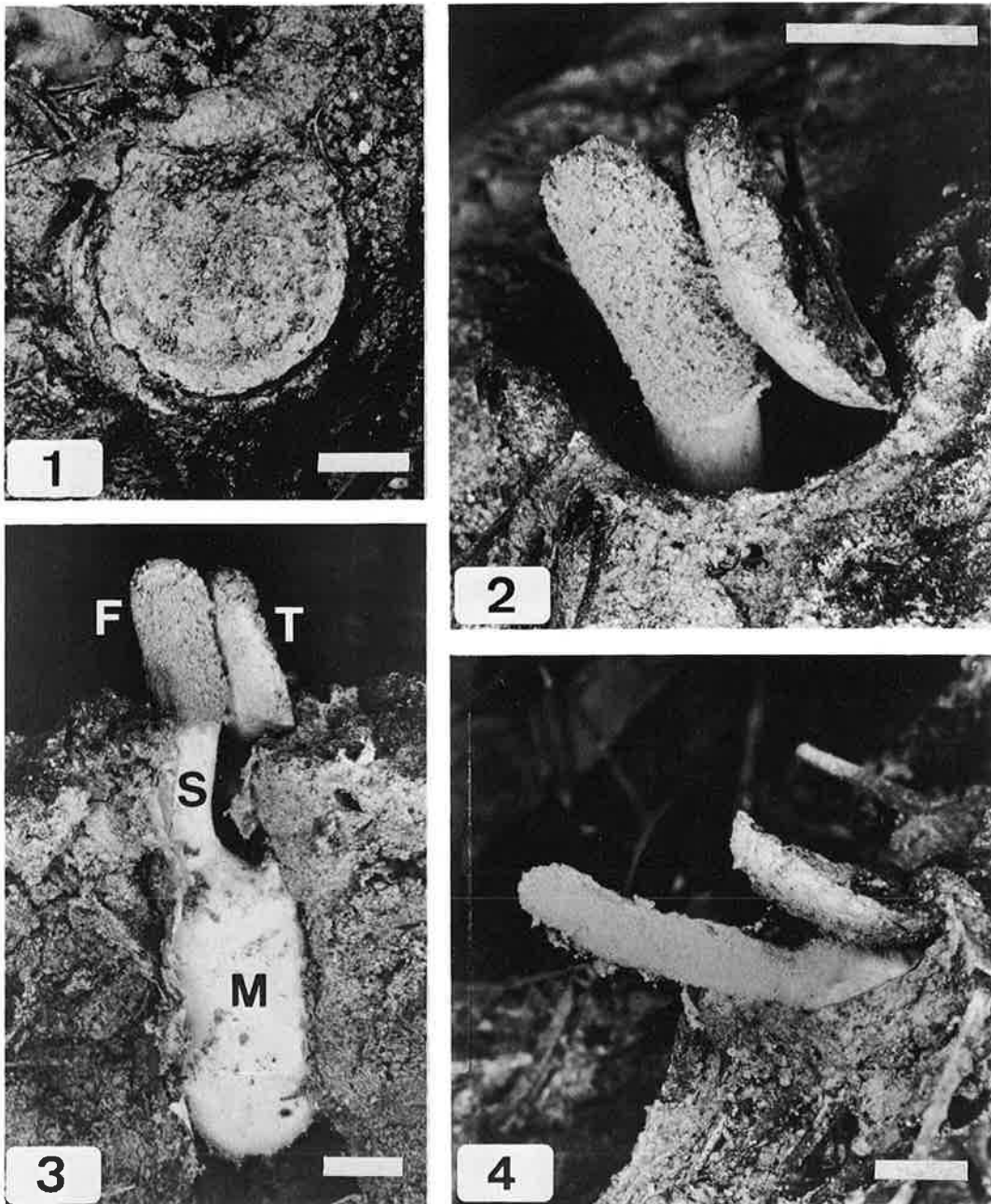
respectively 10.0–33.1 (21.6±9.87) and 2.3–4.0 (3.03±0.53).

The conidiogenous structures (Figs. 6, 7) covered the apical fertile part of the synnema. Conidiophores were densely crowded and formed a hymenium-like layer consisting of verticillate clusters of metulae and phialides. Metulae were adpressed and more or less cylindrical with the apical part swollen (5–7 × 3–5 µm). Phialides were in groups of 3 to 4 and were cylindrical with a very short neck (4–5 × 2.0–2.5 µm). Conidia were typically cylindrical (sometimes slightly curved), smooth, and hyaline to faintly purple (4.0–5.5 × 1.4–1.7 µm).

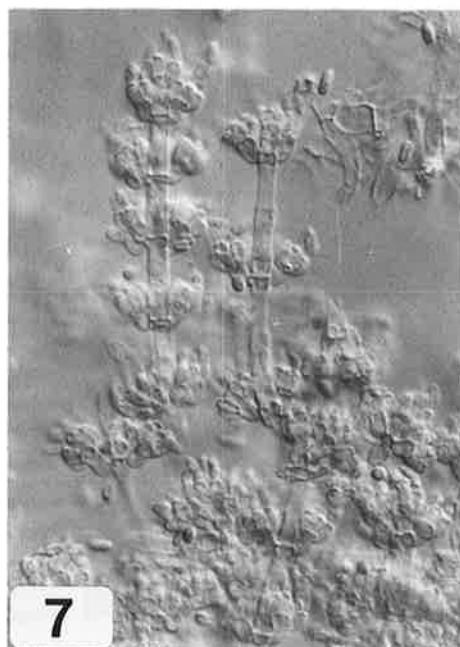
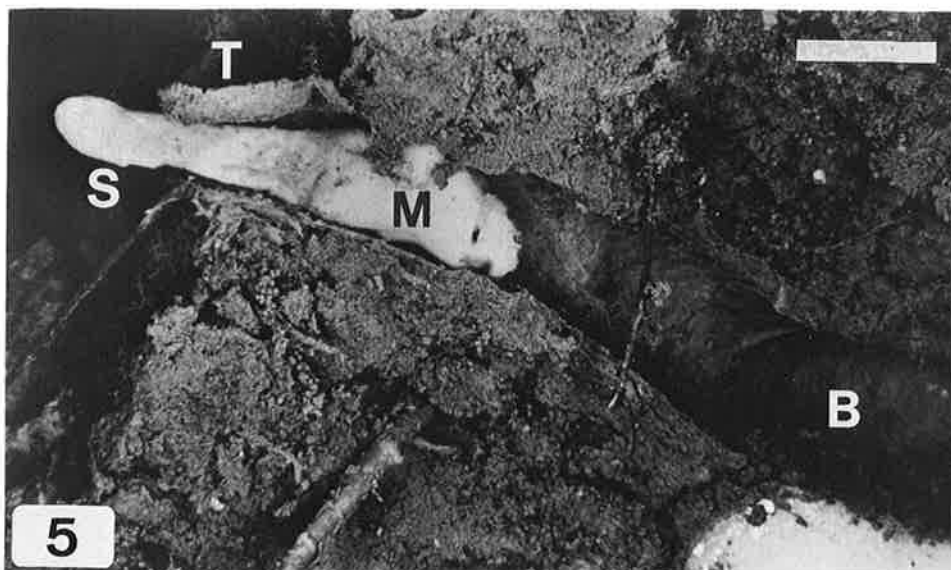
### 3. Discussion

*N. atypicola* has been observed killing a wide variety of spiders in many parts of the world. In Japan it has been found on several burrowing mygalomorph taxa: the purse web spider, *Atypus karschi* Dönitz (Atypidae) (Yasuda 1915), and the trapdoor spiders (Ctenizidae), *Pachylomerus fragarius* Dönitz (= *Latouchia*?) (Kawamura 1929), *Latouchia typica* (Kishida) (Petch 1939), and *Latouchia japonica* Strand (Kobayasi 1941). It has been found on an unidentified trapdoor spider in Brazil (Greenstone et al. 1987). Nentwig (1985) found this fungus on araneids (two species of *Argiope* and one of *Nephila*) in Panama. Unidentified spiders have been killed by *N. atypicola* in Sri Lanka (Petch 1932), Ghana (Samson 1974), and Florida (Samson 1974). Greenstone et al. (1987) demonstrated that under laboratory conditions *N. atypicola* is able to infect and kill a wide variety of hunting and web building araneomorph spiders.

The following description of the probable mode of transmission, infection, and development of *N. atypicola* on trapdoor spiders has been inferred from our observations and from data pieced together from many species of fungal pathogens of spiders and insects by McEwen (1963), Evans & Samson (1987), and others. Conidia which have come into contact with the surface of the host give rise to germ tubes that penetrate the exoskeleton. Soon after penetration hyphal bodies form and circulate via the hemolymph throughout the host's



Figs. 1–4. *Actinopus* sp. burrow entrances and the pathogenic fungus, *Nomuraea atypicola*, at La Quena, Argentina: 1, Closed trapdoor of uninfected burrow; 2–4, *N. atypicola* synnemata projecting from burrow entrances; 3, Side view of upper end of burrow exposed to reveal mycelium (M) (enveloping the spider), sterile (S) and fertile (F) portions of synnema, and trapdoor (T). Scale lines = 5 mm.



Figs. 5–7. *Nomuraea atypicola* on *Actinopus* sp. at La Quena, Argentina: 5, Side view of upper two-thirds of exposed burrow (B) showing mycelium (M) (enveloping the spider), synnema (S), and trapdoor (T) (white mass at lower right is sectioned plant root) (scale line = 10 mm); 6, 7, Conidiogenous structures on synnema, 660x.

body. The host's death may be the result of toxins produced during this stage of the infection. These hyphal bodies reproduce and form chains that digest and replace host tissue and that form the mycelial mass which eventually engulfs the entire host. The synnema then develops at the end of the mycelial mass nearest the burrow entrance, elongates, pushes the trapdoor open, and eventually produces the conidia which are dispersed aerially.

Literature records and our observations demonstrate that *N. atypicola* forms synnemata only on burrow-dwelling spider hosts, not on hunting or aerial web-building hosts, which instead become covered with a purple layer of mononematous conidiophores (Samson 1974). Apparently, synnema production is triggered by a dark environment and a weak, unidirectional light source, such as the light filtering through the gap between a trapdoor and its entrance rim. Samson & Evans (1977) demonstrated this kind of dark-dependant production of positively phototropic synnemata in another pathogenic hyphomycete, *Paecilomyces fumosoroseus* (Wise) Brown and Smith, which also normally produces mononematous conidiophores on non-hidden arthropod hosts.

*N. atypicola* is considered to be the anamorph of the ascomycete *Cordyceps cylindrica* Petch (Petch 1939, Evans & Samson 1987), which, like the similar species *Cordyceps singeri* Mains, victimizes trapdoor spiders (Mains 1954). The mycelial masses (sclerotia) and cylindrical stromata of these two species are very similar to the mycelium and synnema of *N. atypicola* in both form and growth strategy. These similarities plus the fact that *N. atypicola* was observed (by Goloboff in 1983) killing *Actinopus* spiders in Tucumán Province at Raco (400 km south of La Quena) in the same mountains (the Sierra de San Javier) where the type locality (Tafi, Parque de Aconquija) of *C. singeri* (Mains 1954) is located, support the hypothesis that *C. singeri* is conspecific with *C. cylindrica*.

One especially interesting hypothesis follows from our observation that all nine of the excavated spiders killed by *N. atypicola* were just below the burrow entrance (Figs. 3, 5), while other *Actinopus* (and other trapdoor spiders) that we have found dead in their burrows were usually at or near the bottom end of their burrows. We postulate that the fungus causes the infected spider to position itself

just below the burrow entrance, a location where an emergent synnema can be produced with a minimum of material and energy. Similar cases of pathogenic fungi consistently triggering host behaviors which benefit the pathogen have been observed in some insect host species (Skaife 1925, Steinhaus 1949, Nirula 1957, Madelin 1963).

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