

ed from the pinnule surface. These characteristically show a ring of papillate epidermal cells surrounding the sunken stomatal complex, which is out of sight below the surface (Fig. 1b). We prepared material for the scanning electron microscope (Fig. 1, a and b) by mounting a portion of a pinnule to the specimen stub, etching the specimen surface, rinsing, coating with gold-palladium, and observing the surface directly.

Barthel (7), working with compression fossils, illustrated the lower surface of *Alethopteris davreaxi* and *A. cf. grandini*, both of which have a similar ring of papillae surrounding sunken stomata. Cuticles from compression fossils when viewed from the outside may not reveal all the stomatal features when they are sunken below the surface. Therefore, it is probable that paracytic stomata and other stomatal types are more prevalent among seed ferns than has been reported.

Paracytic stomata are present in a variety of extant plants (1). Several taxonomists now accept the paracytic and not the anomocytic stomatal type as primitive in the angiosperms (8, 9). Bar-

anova (8) cites the Bennettitales (Mesozoic) as the oldest fossil group to show clearly the paracytic type. The occurrence of paracytic stomata in Carboniferous seed ferns is of interest in this context since seed ferns, if only by default, are widely conceived of as ancestors of angiosperms.

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References and Notes

1. For a review, see E. Fyris-Claessens and W. Van Cotthem, *Bot. Rev.* **39**, 71 (1973).
2. R. Florin, K. Sven. *Vetenskapsakad. Handl.* **10** (1931).
3. D. L. Dilcher, *Bot. Rev.* **40**, 1 (1974).
4. D. D. Pant, *Plant Sci. Ser. (Alahabad)* **1**, 1 (1965).
5. G. A. Leisman, *Am. J. Bot.* **47**, 281 (1960).
6. M. A. Faulwell and J. T. Schabillon, paper presented at the annual meeting, Botanical Society of America, Corvallis, Ore., 17 to 22 August 1975.
7. M. Barthel, *Beih. Geol.* **33**, 1 (1962).
8. M. Baranova, *Taxon* **21**, 447 (1972).
9. W. W. Payne, *Am. J. Bot.* **57**, 140 (1970).
10. Supported in part by NSF grant BMS 74-12647. We are grateful for the use of facilities of the Center for Electron Microscopy, University of Illinois.

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Cryptoses choloepi: A Coprophagous Moth That Lives on a Sloth

Abstract. *The larvae of the sloth moth, Cryptoses choloepi, live in the dung of the three-toed sloth, Bradypus infulscatus. Adult female moths apparently leave the fur of the sloth to oviposit when the sloth descends, once a week, to the forest floor to defecate. Newly emerged moths fly from the dung pile into the forest canopy to find a sloth.*

The story of the moth that lives in the fur of tree sloths has long enjoyed the status of an entomological anecdote, and has been mentioned in many texts of entomology and parasitology (1). The various life cycles proposed for this insect differ in detail but support the belief that all stages of the moth live continuously in the dense coat of the host, where the larvae presumably feed on sloth hair or on the algae peculiar to sloth hair, or both. While this life cycle has been generally accepted, no investigation of the fur of a living sloth has revealed any life stage but the imago (2). We have recently elucidated the life cycle of the Panamanian sloth moth, *Cryptoses choloepi* Dyar (Pyrilidae: Chrysauginae), and find that it differs from the one generally proposed.

Adults of *C. choloepi* were taken from sloths captured on Barro Colorado Island (BCI) and surrounding mainland areas in the Panama Canal Zone (3). On the three-toed sloth, *Bradypus infulscatus*, populations of moths per sloth ranged

from 19 to 132 individuals (mean = 49; $N = 7$). On the two-toed sloth, *Choloepus hoffmanni*, moths were less abundant; no more than 12 moths were collected from a single sloth (mean = 8; $N = 3$). Careful examination of the sloths revealed no signs of eggs, larvae, or pupae of *C. choloepi*. The sex ratio of male to female moths in populations from three-toed sloths was roughly 3:1 (177 to 61), while that from two-toed sloths was 7:1 (21 to 3).

Gravid female moths removed from the host to screen cages readily oviposited on any hard substrate. We offered larvae newly hatched from these eggs a variety of diets, including the hair and dung of three-toed sloths and the leaves of *Cecropia eximia*, *Poulsenia armata*, and *Lacmellea panamensis*—the three tree species which these sloths most often frequent (4). The larvae did not feed on the sloth hair or leaves, but commenced feeding as soon as they were placed on sloth dung.

Sloth dung consists of hard, ovoid pel-

lets about 8 mm in diameter. Sloths descend from the forest canopy to its floor at about weekly intervals to defecate, where, hanging to a vine by their forelegs, they dig a depression with their hind claws, deposit about a cupful of these pellets, and then cover the dung loosely with leaf litter (4). Early larval stages of *Cryptoses* spin silken threads between two or three pellets, forming "nets" in which they feed. Later stages spin silken, frass-encrusted tubes which are extended by the larvae as they grow. Mature larvae seal off a section of their feeding tube in which to pupate. Three to 4 weeks are required for development from egg to adult, at ambient temperatures of the forest floor.

We collected and examined sloth dung piles from the floor of rain forest on BCI and from a second area on Cerro Azul, Panama. Of 19 dung piles on BCI, four bore definite signs of infestation by *Cryptoses*. One or more sloth moths emerged from each of 16 of 31 sloth dung piles collected on Cerro Azul. This probably represents a minimum estimate of infestation (5).

In contrast to the sex ratio skewed toward males among moths on sloths, moths that emerged from a dung pile in the laboratory showed a 1:1 sex ratio (16 males to 17 females), while the sex ratio among 52 sloth moths attracted to a light trap at Las Cumbres, Panama, was approximately 1:1.4 (22 males to 30 females) (6).

Three-toed sloths on BCI were captured, cleaned of moths, and released with radio collars (7), which enabled us to locate them. They were recaptured at intervals to measure rates of reinfestation with sloth moths. Three sloths recaptured after 11 days yielded one, two, and nine moths each (totals of three males and nine females), while a sloth recaptured after 39 days had 40 moths (27 males and 13 females).

The following life cycle, which we propose for *C. choloepi* on *B. infulscatus*, may also apply to other sloth moths, including those that live on *Choloepus*. When a sloth descends to the rain-forest floor to defecate, gravid female moths leave the sloth and oviposit on fresh dung. The differential loss of female moths from sloths, resulting in a skewed sex ratio, may be caused by the failure of some females to return to the host after oviposition. Alternatively, the females may simply have a shorter life-span than the males. Mortality of female moths may occur through exposure to predation during oviposition. Larvae develop and pupate in the dung pile. Several weeks after oviposition, adults emerge and fly



Fig. 1. (A) The three-toed sloth, *Bradypus infuscatus*, host of *Cryptoses cholepei*. There is a moth on the sloth's right foot (arrow). (B) A population of moths on the back of a sloth.

into the forest canopy where they find a sloth, mate, and continue the life cycle.

Sloths are common in the rain forests of Panama; they occur at population densities of about ten sloths per hectare on BCI (4) and at about six per hectare on Cerro Azul (5). Thus there would be an ample opportunity for a newly emerged moth to find a sloth by flying a short distance up and through the forest canopy. It is unlikely that newly emerged moths colonize the sloths which their parents infested, as sloths regularly move from tree to tree. Most two-toed sloths studied on BCI changed trees on successive days, while three-toed sloths were in the same tree on successive days about 40 percent of the time (8).

To study the behavior of adult *Cryptoses* on their hosts, we observed the movements of moths on captive and wild sloths. Particular attention was paid to possible feeding at nasal and lachrymal secretions, a behavior that is known for many species of tropical "eye moths" (9). The proboscis of *Cryptoses* is very short, but moths readily imbibed water in the laboratory, and this increased their longevity. While moths were active on the surface of the sloth, especially when the latter was moving, no instances of feeding at the eyes or nose were seen. Adult moths may feed on secretions of the sebaceous glands at the base of the host's hairs, or perhaps on rainwater trapped in the dense coat of the sloth. This water might be enriched by dissolved skin secretions and algal by-products.

As the presence of *Cryptoses* does not appear to have a detrimental effect on three-toed sloths, the relation between the moth and the sloth is most properly described as a phoretic rather than a parasitic one. *Cryptoses* benefits from this association through (i) the enhancement of oviposition-site location (that is, being carried by the sloth to the next fresh dung pile), (ii) the use of the sloth as a refuge from avian predators, and, perhaps, (iii) the enhancement of its diet with secretions of the host or associated algae. Similar phoretic associations be-

tween coprophagous insects and dung-producing mammals have been found in the Coleoptera (10) and Diptera (11), and may represent an incipient stage in the evolution of ectoparasitism.

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References and Notes

1. R. Askew, *Parasitic Insects* (American Elsevier, New York, 1971), pp. 93 and 94; J. Baer, *Ecology of Animal Parasites* (Univ. of Illinois Press, Urbana, 1952), p. 90; J. Bourgogne, in *Traite de Zoologie*, P.-P. Grasse, Ed. (Masson et Cie, Paris, 1951), vol. 10, p. 330; T. Cameron, *Parasites and Parasitism* (Methuen, London, 1956), p. 190; M. Hering, *Biologie der Schmetterlinge* (Springer-Verlag, Berlin, 1926), pp. 74 and 130; W. Linsenmaier, *Insects of the World* (McGraw-Hill, New York, 1972), p. 228.
2. R. Casebeer and C. Hogue [*Nat. Hist.* 75, 40 (1966)] examined sloths infested with *Cryptoses* in Costa Rica. The South American sloth moths, *Bradypodcola hahneli* Spuler and *Bradypophila garbei* von Ihering, have not been studied.
3. Tree-climber's spikes were used to climb trees in which sloths were seen. Extendable aluminum poles fitted with either a noose, a saw, or a pruning attachment were used to capture the sloth or drop it to a helper below. After capture, sloths were immediately put in large cloth bags. Few moths were lost during capture. Moths were later removed from sloths with an aspirator under a tent of mosquito netting. Moths came to the surface of the fur when disturbed; and the docility of the sloths permitted a thorough investigation to ensure that no moths were missed.
4. G. G. Montgomery and M. E. Sunquist, in *Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research*, F. B. Golley and E. Medina, Eds. (Springer-Verlag, New York, 1975).
5. Dung was collected on Cerro Azul, Panama, at about 1500-m elevation during a census of sloths taken as a part of a study of sloths as reservoirs of yellow fever (G. Montgomery and C. Seymour, unpublished; C. Seymour *et al.*, in preparation). Dung was incubated in petri dishes placed outdoors in shade on Naos Island, Panama Canal Zone, at sea level. Counts of total numbers of moths that might have emerged and determination of sex ratios were not possible because the dung was inadvertently allowed to dry.
6. Moths were collected by H. Wolda at a light trap in Las Cumbres, Panama, on a year-round basis. The insects were pooled to estimate sex ratios.
7. G. Montgomery, W. Cochran, M. Sunquist, *J. Wildl. Manage.* 37, 33 (1973).
8. M. Sunquist and G. Montgomery, *J. Mammal.* (1973), p. 54.
9. W. Buttiker, *Mitt. Schweiz. Entomol. Ges.* 39, 151 (1967); E. Reid, *Proc. R. Ent. Soc. London Ser. B* 23, 201 (1954).
10. Several dung beetles are known to infest sloths [G. Arrow, *Ann. Mag. Nat. Hist.* 63, 385 (1933)] and kangaroos [E. Mathews, *Aust. J. Zool. Suppl. Ser.* 9, 3 (1972)], but only the beetles that infest kangaroos are known to feed on the host's dung.
11. The adults of certain muscid flies associate with cattle, on which some species actually feed. See O. Hammer, *Biological and Ecological Investigations on Flies Associated with Pasturing Cattle and Their Excrement* (Bianco Lunos Bogtrykkeri A/S, Copenhagen, 1941).
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Restriction Endonuclease Analysis of Mitochondrial DNA from Normal and Texas Cytoplasmic Male-Sterile Maize

Abstract. Mitochondrial DNA from normal and cytoplasmic male-sterile maize was digested with restriction endonucleases *RI* from *Escherichia coli* or *dIII* from *Hemophilus influenzae*. Electrophoresis of resulting fragments revealed distinctions between the two cytoplasmic types. These distinctions suggest that factors responsible for cytoplasmic male sterility are located in the mitochondrial DNA, and that the mitochondrial genome is not inherited paternally.

Although cytoplasmic (extrachromosomally inherited) male sterility of maize was first reported more than 40 years ago (1), the location of the factors conditioning this trait remains unknown. At least five different cytoplasmic male sterility types have been authenticated and a number of others have been reported, although their uniqueness has not been verified (2). The most widely known and studied is the Texas type male-sterile cytoplasm (cms T). Prior to 1970 it was extensively used to avoid de-

tasseling in the production of hybrid seed corn (3). The occurrence of two leaf diseases in epidemic proportions (southern corn leaf blight and yellow leaf blight) on maize lines carrying cms T (4) forced the hybrid seed industry to abandon use of cms T in seed production. Recent studies have shown differences in the response of mitochondria from maize with normal and Texas cytoplasm when challenged by toxins (5) produced by race T of *Bipolaris maydis* (Nisikato) Shoemaker (southern corn leaf blight) and *Phyllos-*