A GREGARIOUS, MYCOPHAGOUS, MYRMECOPHILOUS MOTH, *AMYDRIA ANCEPS* WALSINGHAM (LEPIDOPTERA: ACROLOPHIDAE), LIVING IN *ATTA MEXICANA* (F. SMITH) (HYMENOPTERA: FORMICIDAE) SPENT FUNGAL CULTURE ACCUMULATIONS

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Abstract.—The lepidopteran *Amydria anceps* Walsingham (Acrolophidae) is reported for the first time as a myrmecophile. Its gregarious larvae feed on the exhausted fungal substrate accumulations outside mature colonies of the Mexican leaf-cutting ant, *Atta mexicana* (Smith), a fungus-growing ant in Mexico. This constitutes the second report of an acrolophid myrmecophile. Morphology of the principal life stages of *A. anceps* are described, as well as its general natural history. No interactions were observed between *Amydria* larvae and *A. mexicana,* although the larvae of *A. anceps* are attacked by ichneumonid and tachinid parasitoids. Chalcids (primary or secondary parasitoids) also are associated with *A. anceps* larvae. Thus, there are potentially five trophic levels in this system: fresh plant material—*Atta* fungal symbiont—*Amydria anceps*—ichneumonid and tachinid parasitoids—chalcid hyperparasitoids.

Key Words: Acrolophidae, *Amydria, Atta,* biology, Formicidae, leaf-cutting ant, Mexico, mycophagous, myrmecophile

The attine leaf-cutting, fungus-growing ants, *Atta* and *Acromyrmex* spp., utilize large amounts of plant biomass for the subterranean cultivation of the fungal symbionts (Basidiomycetes: Agaricales: Lepiotaceae) they use as food (Waller and Moser 1990, Mueller et al. 1998). The fungal strains cultivated by *Atta* and *Acromyrmex* have been identified as species of the mushroom genus *Leucoagaricus,* principally *Leucoagaricus gongylophorus* (Möller), as well as similar species as *L. weberi* Muchovej, Della Lucia and Muchovej (Bononi et al. 1981, Fisher et al. 1994, Pagnocca et al. 2001). After overgrowth by the fungus and subsequent harvesting of fungal biomass by the ants, the manured, compostlike sub-

strate consists mainly of fungal and plant cell walls and is disposed of by the ants. The different species of attine fungus-growing ants show at least two strategies for disposal of the exhausted fungal substrate: some species (most *Atta* species, such as *Atta texana* (Buckley) and *A. cephalotes* L.) create special subterranean galleries where the used up fungal substrate is stored (Waller and Moser 1990); other species take this substrate to the outside and dump it in "garbage piles" at variable distances from the nest. Species such as *Atta mexicana* (Smith), *Trachymyrmex turrifex* (Wheeler) (S. Sanchez-Pena, personal observation), and *A. colombica* Guérin (Anderson and Ratnieks 2000, Hart and Ratnieks 2001, U.

Fig. 1. A mature colony of *Atta mexicana* in the urban area of Monterrey, Mexico. The substrate accumulations on the street by the curb (a) consist of the spent fungal material (dumps) characteristic of this leaf-cutter ant.

G. Mueller, personal observation) frequently deposit the piles adjacent to the nest. The *Atta* substrate dumps, whether subterranean or exposed, constitute an accumulation of organic matter that attracts an abundant and diverse community of invertebrates (Waller and Moser 1990) and microorganisms (Rogers et al. 1995, Hart and Ratnieks 2001, Sanchez-Pena, unpublished observations).

Atta mexicana (Smith), the Mexican leaf-cutting ant, is a widespread fungus-grower in Mexico and parts of Central America. This species eliminates the exhausted, compostlike, fungal substrate by dumping it on a garbage heap outside the nest (Fig. 1). The exhausted fungal substrate is made up of particles or granules up to a few millimeters in diameter. In both *Atta colombica* and *A. mexicana,* these external dumps can be more than two feet tall and have a volume of several gallons.

In May–September 2000, samples of associated biota found on *A. mexicana* dumps

were collected at several localities in Mexico. During June and September 2000, gregarious larvae of *Amydria anceps* Walsingham were discovered living in these external dumps in Monterrey, Santiago, and Guadalupe, in the State of Nuevo Leon, as well as in Queretaro, in the State of Queretaro. Queretaro is approximately 800 km from the other localities. Beutelspacher (1977) previously had reared *Amydria anceps* (which he redescribed as a new species, *Acrolophus socialis*) without noting its association with leaf cutting ants. Larvae of this species were reported by Beutelspacher as living in tubes within a compact mass or "colony," resembling a termite nest. Beutelspacher's specimens were collected at the Estación de Biologia Chamela, Jalisco, Mexico.

Walter et al. (1938) reported another, but not congeneric acrolophid, "*Amydria*" *confusella* Dietz, from the subterranean chambers where the Texas leaf-cutting ant, *Atta texana* (Buckley), accumulates the spent

fungal substrate. This appears be the only previous record of an acrolophid myrmecophile. Walter et al. (1938) collected larvae and adults from these subterranean waste chambers. The utilization of the subterranean chambers of *A. texana* (some of which are more than 2 m below ground surface) probably requires adaptations, behaviors, and cues different from those required to exploit the exposed heaps of *A. mexicana.* The present deposition of Walter's specimens is unknown and, consequently, the identification of the moth could not be verified. Larvae of both *Amydria* and *Ptilopsaltis,* the allied genus which includes *confusella,* are known to be scavengers on plant debris as well as guanophiles in caves (Davis 2000, Davis et al. 1986, Davis and Robinson 1998).

Amydria anceps Walsingham

Amydria anceps Walsingham *Amydria anceps* Walsingham 1914: 363.—Davis 1984: 20; 2000: 481.

Acrolophus socialis Beutelspacher 1977: 145.—Davis 1984: 20 (synonym of *Amydria anceps*).

Adult (Figs. 2–3).—*Head:* Pale buff with darker brown scales concentrated near vertex and lateral over occipital tufts, to almost entirely dark brown. Vertex and occipital areas rough with semi-erect scales; frons usually less rough; scales slender with mostly bidentate, sometimes tridentate apices. Antenna filiform, ~0.4 length of forewing; scape smooth, buff to dark brown; flagellum buff to brown, with a single annulus of slender scales per segment. Haustellum and maxillary palpus vestigial, normally not visible on uncleared head. Labial palpus slightly upcurved, with a strong ventral scale brush, especially prominent on segment II; palpus buff, variably marked with dark brown, especially laterally; 2–3 dark bristles arising laterally from III, and up to 7 bristles from II; segment III elongate, slender, smooth, sometimes with a dark median ring of dark brown scales.

Thorax: Light brown dorsally and ventrally, heavily irrorated with dark brown dorsally. Forewing length: ♂, 4.5–11.0 mm; ♀, 6.5–13.0 mm. Forewing light brown, variably irrorated with dark brown scales until often appearing generally dark brown; a more or less distinct pattern of dark brown markings along costa, with largest forming an irregular, broadly U-shaped band from basal third of costa to apical third; base of wing with an oblique, dark basal band; another large band extending ⅓–½ across distal ⅕ of wing; fringe light brown, irrorated with dark brown. Hindwing uniformly light grayish brown to dark brown; ♂ frenulum a simple, stout spine; ♀ usually with 4 smaller spines. Foreleg without epiphysis; light brown, heavily irrorated with dark brown over coxa and femur; tibia mostly dark brown with two light brown rings at middle and apex; tarsomeres dark brown, with basal and apical light brown rings; midleg similar to foreleg in color; spurs light brown; hindleg uniformly light brown except for suffusion of darker scales dorsally. *Abdomen:* Varying from uniformly light brown in paler specimens to dark brown dorsally and light brown ventrally in darker forms.

Male genitalia (Figs. 4–8): Uncus deeply bifid. Tegumen an elongate narrow dorsal ring. Vinculum short, broadly U-shaped, with a slight median indentation (Fig. 4). Gnathos fused apically into a narrow U-shaped sclerite. Valva simple, nearly as long as genital capsule, slender, tapering to even more slender cucullus (Fig. 6). Aedoeagus ~0.8 the length of valva, moderately broad and flat to apex; apical third laterally separated into a larger, more membranous dorsal half and a sclerotized, acute ventral half (Fig. 8); cornuti absent.

Female genitalia (Fig. 9): Posterior apophysis short, approximately as long as the eighth abdominal segment. Lamella antevaginalis ~ smoothly curved. Ductus bursae thickened, short, less than half the length of posterior apophysis, gradually enlarging to mostly membranous corpus bur-

Figs. 2–3. Adults of *Amydria anceps*. 2, Male, forewing length 5.5 mm. 3, Female, forewing length 12 mm.
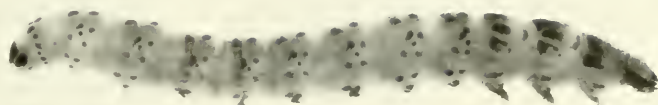
sae which extends about 3× length of apophysis; a small accessory bursa branching off caudal end of corpus bursae at common juncture with ductus bursae; basal, ventral half of accessory bursae wall with an elongate-oval ring of thickened tissue; corpus bursae with an elongate, dense, coarse patch of small, irregularly shaped, short spicules extending a short distance along caudal half of corpus anterior to junction of accessory bursa; anterior margin of spinule patch deeply excavated. Ductus seminalis joined to corpus bursae from caudal end of cornutal excavation.

Egg.—Upright, cylindrical, with 18 longitudinal ridges evenly dispersed and converging toward either pole; length 0.46 mm, diameter 0.3 mm (Beutelspacher 1977).

Figs. 4–9. Genitalia of *Amydria anceps*. 4, Male, ventral view (0.5 mm). 5, Lateral view of fig. 4. 6, Valva, mesal view. 7, Male aedoeagus, ventral view. 8, Lateral view of fig. 7. 9, Female, ventral view (0.5 mm). Scale lengths indicated in parentheses.

Figs. 10–12. Larva and larval tubes of *Amydria anceps.* 10, Larva, lateral view; length 21 mm; maximum diameter 2 mm. 11, Dorsal view of fig. 10. 12, Larval tubes; longest tube 15 cm in length and 5 mm in diameter.

Larva (Figs. 10–11).—Length of largest larva 22 mm; maximum diameter 2 mm. Head width 1.5 mm; dark reddish brown, with a prominent lateral dark brown to black streak through stemmatal area; streak becoming slightly broader toward rear margin of head. Six stemmata present; 3–5 aligned in a contiguous, vertical, anterior series. Integument cream to buff with dark reddish-brown plates and pinacula. Prespiracular pinaculum of prothorax partially fused to pronotum and bearing all three L setae together with spiracle. Thoracic legs well developed; coxal plates well separated. Prolegs on A3–6 and A10; crochets 25–28 in number, arranged in a uniserial ellipse on

A3–6; anal proleg with 17–18 crochets arranged in a slightly curved line; all prolegs with 2–3 scattered rows of spines immediately anterior to crochets.

Larval case (Figs. 12–13).—An elongate silken tube, up to 15 cm in length, 5 mm in diameter, densely covered with small plant fragments.

Pupa (Fig. 14).—Length of largest pupa 10.2 mm. Head smooth. Abdomen with dorsum of A2–6 with an anterior row of numerous minute spines and a smooth posterior ridge which continue nearly ⅔ around each segment; A7–8 with anterior row of dorsal spines more reduced and continuing around each segment as a ventral ridge;

Figs. 13–14.   Larval tubes and pupae of *Amydria anceps*. 13, Dump mound of *Atta mexicana* colonized by *Amydria* larva; tubes (t) with active larvae are visible on dump's surface. Erosion has removed some of the substrate that normally completely covers the tubes. White 35 mm film container included for scale. 14, Five pupal exuviae (arrows) after adult emergence, on dump surface, protruding nearly perpendicular 7–10 mm from substrate. The exuviae remain attached to the buried larval tubes, which open to the surface.

posterior ridge also reduced on 7–8 and completely encircling each segment. Cremaster of A10 consisting of a large, prominent pair of stout dorsal spines and a much shorter pair of stout ventral spines.

Material examined.—MEXICO: Chia-

pas: El Chorreadero, Chiapa de Corzo: 1 ♀,
11 Aug 1967, O. S. Flint Jr. (USNM). Guer-
rero: Amula, 6,000 ft: 1 ♂ (holotype), 18
Sep. H. H. Smith (BMNH). Tonalapa: 1 ♀
(paratype), Jun, H. H. Smith (USNM). Mo-
relos: Cuernavaca: 1 ♂, 22 May 1949, J.
McKelvey (USNM); 1 ♀, Nov 14, R. Müll-
er (USNM). Nuevo Leon: Anegada Arroyo,
16 mi S. Linares, 1,250 ft: 2 ♂, 2 ♀, D. R.
Davis & W. D. Duckworth, 9 Jul 1963,
slides USNM 32413 (USNM). Monterrey:
4 ♂, 14 ♀, 4 larvae, pupal exuviae, S. R.
Sanchez-Pena, reared from *Atta* mound,
slide USNM 32394 (USNM, UTA); 1 ♂, 3
♀, 20 Jun, 2000, S. R. Sanchez-Pena,
reared from *Atta* mound, slide USNM
32340 (USNM, UTA). Puebla: Tehuacán: 1
♀, Sep 1937, C. Hoffmann, (USNM); 1 ♀,
12 Sep, R. Müller (USNM). Sinaloa: Ven-
adio: 3 ♀, B. Clark (USNM). Tamaulipas:
4 mi S. Ciudad Victoria: 1 ♀, 5 Aug 1963,
D. R. Davis & W. D. Duckworth (USNM).

Distribution.—Known only from sub-
tropical and semiarid areas of northern
Mexico, from Nuevo Leon south to Chia-
pas. Beutelspacher (1977) also reported this
species from Estación de Biologia Chame-
la, Jalisco, Mexico. *Atta mexicana* is known
to occur at every locality reported for *Amy-
dria anceps.*

Biology.—The larvae were found to bur-
row into the fungal substrate heap and to
spin a tough, leathery tube covered with
substrate particles. They live within these
tubes through the larval cycle, probably
protruding only the head outside the tube to
eat while immersed in the substrate. Empty
tubes (Fig. 13) become very visible after
heavy rains that wash away loose particles.
Immediately prior to adult emergence, the
moth pupae force their way ¾ their length
out of the open upper end of the tubes at
the dump surface. Pupae are exposed for
only a brief period after the rains (perhaps
one day). Following a mass emergence, pu-
pal exuviae may be observed in large num-
bers projecting perpendicularly from the
surface of the dump area (Fig. 14). Adult
emergence apparently is triggered by rain.

Two emergence events were observed dur-
ing the summer of 2000, within two days
after heavy precipitation.

Larvae inside cases were collected in the
field and reared to adults. Larvae were in-
cubated at room temperature in plastic con-
tainers, using the spent fungal substrate as
food. Adult moths emerged in these con-
tainers. Hymenopteran (Ichneumonoidea
and Chalcididae) and dipteran (Tachinidae:
Pseudochaeta sp.) parasites also emerged
from some of these field-collected larvae
during rearing. In the field, ichneumonid
and chalcid parasitoids have been observed
engaged in host searching behavior over
Amydria larval cases, on dumps heavily
colonized by *Amydria* larvae. The chalcids
could be either primary parasitoids or hy-
perparasitoids. The trophic levels of this
system are thus potentially five: plant ma-
terial → symbiotic fungus → *Amydria* →
ichneumonids and tachinids → chalcids.

Amydria larvae are the largest colonizers
of the upper layers of the fungal dumps ex-
amined. Further research is warranted to de-
termine the actual nutritional needs of lar-
vae, and their level of dietary specialization
on fungi. No antagonistic interaction was
observed between moth larvae and *Atta
mexicana.* The workers do not dig or tunnel
into the dump material to any significant
extent. The predaceous ponerine ant, *Pa-
chycondyla villosa* (Fabricius), which was
very common at the collection localities,
was observed digging a few millimeters
into the *Atta* dumps in what appeared to be
attempts to reach *Amydria* larvae.

in the following institutions: The Natural History Museum, London, England (BMNH); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); and the University of Texas, Austin, TX, USA (UTA).

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