A Caterpillar that Eats Tortoise Shells

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ABSTRACT The larva of the tineid moth *Ceratophaga vicinella* is a scavenger that feeds on the keratin plates of dead gopher tortoises (*Gopherus polyphemus*) in south Florida. The larva makes a multilayered silk tube that extends over part of the shell and into the sandy soil beneath. The mature pupa appears to ratchet its way up the tube by using abdominal spines. *Ceratophaga* larvae are the only insects that are able to subsist on a diet of solid, dry keratin. The genus *Ceratophaga* is primarily African; *C. vicinella*, the only New World species, is possibly a remnant of a more widespread lineage. Unless *C. vicinella* has another, unknown dietary resource, it is almost certainly an endangered species.

The gopher tortoise, *Gopherus polyphemus*, is a terrestrial turtle restricted to the Coastal Plain of southeastern North America. It spends much of its time in deep burrows, emerging to feed and look for mates (Ernst et al. 1994). It is subject to various predators and accidents. If overturned in soft sand, a tortoise is usually unable to right itself and dies within a day or two. Recent threats include road mortality and respiratory disease (Berish et al. 2000). Shells of dead gopher tortoises in south Florida may be enveloped in a type of crust that appears to be rooted to the ground (Fig. 1A–C). This crust is the combined feeding tubes of caterpillars, *Ceratophaga vicinella*, belonging to the clothes moth family (Tineidae) (Deyrup and Deyrup 1999). The historical range of *C. vicinella* includes most of peninsular Florida and Mississippi (Heppner et al. 2003), but the current range may be smaller. Here we provide some details of the natural history of this remarkable moth.

Our study was done at the Archbold Biological Station (ABS) in Highlands County, south-central Florida. The ABS habitats where tortoises live are sandhills, disturbed grassy areas, and, to a lesser extent, Florida scrub and scrubby flatwoods. These habitats at the ABS are described in Abrahmson et al. (1984). The tortoise shells that we studied were from animals that had died in the field from unknown causes. We reared the caterpillars on tortoise shells in the laboratory, under ambient temperature and lighting, in plastic containers of sand periodically moistened with water. Close-up photographs were taken with a Wild M400 Photomacroscope or with a scanning electron microscope.

Larva

Each larva constructs an unbranched silk tube that extends over the keratin plates of the tortoise shell and into the sand substrate. During decomposition of tortoise carcasses, individual scutes (plates) often exfoliate from the bone carapace; larvae also feed on these dissociated scutes. Feeding on intact shells begins on the surface that contacts the sand. The tubes eventually extend about 3–10 cm into the sand. It is probable that the underground portion of the tube protects larvae from temperature extremes, moisture loss, and parasitoids. Several parasitoids attack larval Tineidae, including tineid species that live in silk cases (Robinson and Nielsen 1993). At the ABS, a wasp, *Apanteles* sp., attacks a tineid, *Phereoeca dubitatrix*, that lives inside a tough, portable silk case. No parasitoids were reared from *C. vicinella*. The underground portion of the tube may also anchor the shell or scute to the ground, which could be

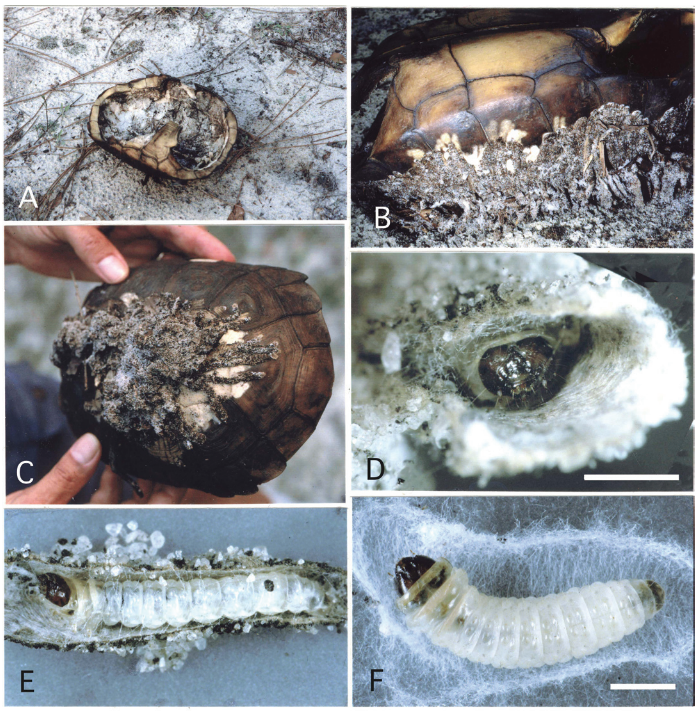

Fig 1A. Shell of dead gopher tortoise on sand. **B**, **C**. Silk tubes of *C. vicinella* on shell suface in contact with sand. **D**. Frontal view of larva, exposed by transection of the silk tube. **E**. Lateral view of larva, exposed by lengthwise bisection of the tube, showing the layered nature of the tube wall. **F**. Dorsal view of larva, in process of reconstructing its silk tube. Bars = 2 mm.

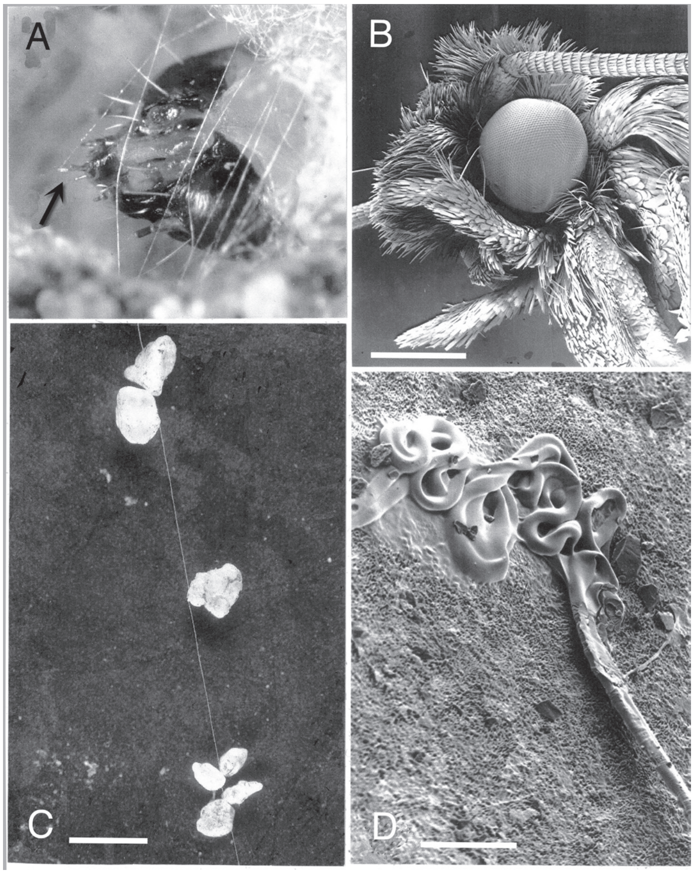

Fig. 2A. Head of larvae *C. vicinella*: a strand of silk is seen extruding from the glandular spout (arrow). **B**. Lateral view of head of adult. **C**. Strand of silk from the silk tube of the larva with attached grains of sand that the larva had incorporated into the wall of the tube. **D**. Site of attachment of silken strand on tortoise shell. Bars: **B** = 0.5 mm; **C** = 1.0 mm; **D** = 0.02 mm.

particularly useful when larvae are feeding on small, dissociated scutes, light enough to be moved about by the wind.

The silk tube is a complex structure, produced by rapid sidewise or lengthwise movements of the head, which bears the single "spigot" from which the silk is extruded (Fig. 2A). The tube is fastened to the keratin substrate by loops of silk that appear to have been deposited in a semiliquid state (Fig. 2D). The anchorage secured by such attachments is extremely strong, which raises questions about the silk's composition and formation. It takes considerable force to pull a tube from the shell, more than usually needed to pull a lepidopteran silken cocoon from its site of attachment. The tube is lined with smooth, white silk, primarily transverse in orientation with respect to the tube (Fig. 1F). A second (middle) layer of silk is composed of multidirectional, pale brown strands. A dark outer layer (Fig. 1D and E) combines feces and sand, held together with silk. The subterranean portion also includes a loose network of sand grains held together with silk (Fig. 2C). The attachment of silk to the sand grains is unusually strong. Before pupation, larvae spin a flattened, liplike exit (Fig. 3D).

Silk tubes are not unique to *C. vicinella*. They are made by some other clothes moths in the subfamilies Tineinae and Scardiinae (Davis 1987). The feeding habits of most *Ceratophaga* spp. have not been described in detail, but there are no reports of extensive tubes extending into the soil. The African *C. vastellus*, which lives in horns and hooves, apparently excavates tunnels or burrows in the keratin substrate (Walsingham 1881, 1898; Gozmány and Vári 1973), with, in at least some cases, an elongated external silk tube (Busck 1910). This kind of excavation is not possible on a gopher tortoise shell because the keratin plates are too thin. Although other larval tineids are not known to produce subterranean tubes, this behavior occurs in the family Acrolophidae, which is closely related to the Tineidae (Davis 1987). At the ABS some acrolophids that feed on dead leaves produce tubes that extend down into the sand, resembling those of *C. vicinella*.

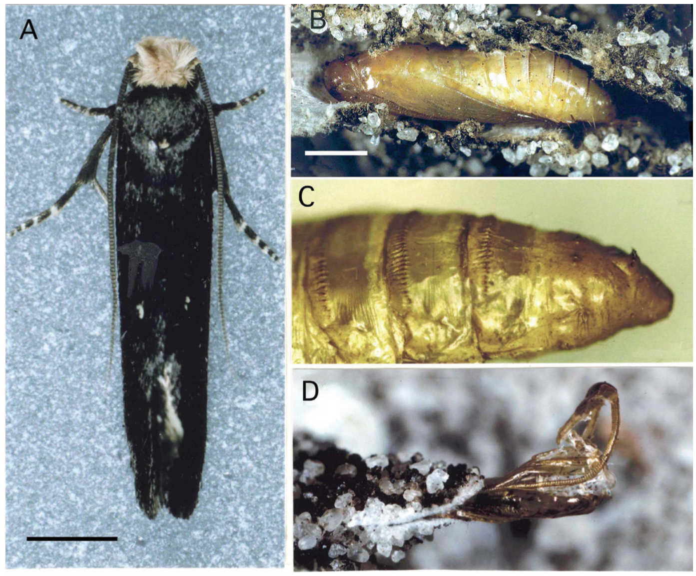

Fig. 3A. Live adult *C. vicinella*. **B**. Pupa. **C**. Detail of pupal abdomen showing rows of transverse spines and the subterminal recurved projection. **D**. Pupal skin, projecting from silken tube after moth emerged. Bars: **A** = 2 mm; **B** = 1 mm.

Pupa

Pupation (Fig. 3B) occurs in the silk tube, probably in the subterranean portion and far from the exit. The pupal abdomen is mobile, and equipped with dorsal transverse rows of rearward-pointing spines on segments 3–9 (Figs. 3C, 4A–C) and a single forward-pointed, subterminal, claw-like projection (Fig. 4D). These structures may enable the pupa to secure the necessary purchase as it moves to and fro within its tube in avoidance of disturbances or unfavorable conditions, and ultimately, as it ratchets its way to the tube exit before emergence of the adult (Davis and Robinson 1999).

Adult

The adult moth (Figs. 2B, 3A) is blackish brown with an inconspicuous white discal spot on each forewing, and a conspicuous tawny brush of hair on the top of the head. This brush of hair is typical of tineids, and the strong color contrast between the head and the rest of the insect is not unusual (Robinson and Nielsen 1993).

Discussion

The cosmopolitan family Tineidae includes about 3,000 species, the great majority of which breed in unusual materials by lepidopteran standards (Robinson and Nielsen 1993). These include various sorts of detritus (usually permeated with fungi), woody fruiting bodies of fungi, and keratin in the form of hair, feathers, and horn (Robinson 2004a). The Tineidae are the most primitive of the higher Lepidoptera (Ditrysia) (Robinson and Nielsen 1993). Their persistence might well be due to entrenched trophic specializa-

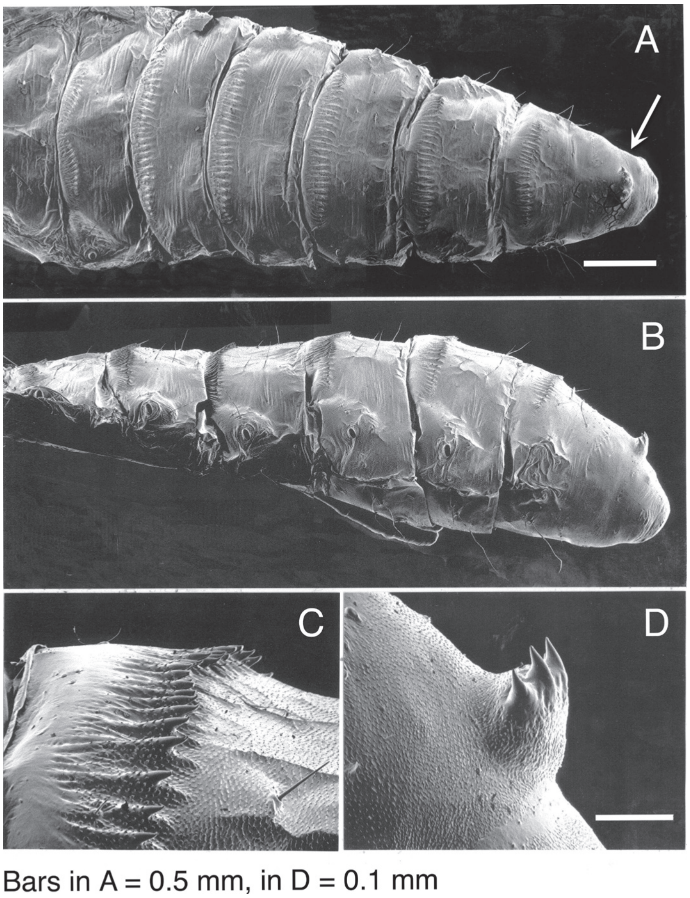

Fig. 4A. Dorsal view of pupal abdominal skin showing transverse rows of spines and median subterminal projections (arrow). **B**. Same in lateral view. **C**. Close-up of one of the rows of spines. **D.** Close-up of subterminal projection. Bars: **A** = 0.5 mm; **D** = 0.1 mm.

tions, analogous to those found in some specialized basal lineages of parasitic Hymenoptera, such as the Vanhorniidae, Heloridae, Roprioniidae, Pelecinidae, Evaniidae, and Aulacidae (Deyrup 1985), as well as some families of Neuroptera such as the Sisyridae, Mantispidae, and Myrmeleontidae. The keratin feeders represent a dietary extreme among detritivores because they are able to break down highly stable disulphide linkages between cystine residues. This is accomplished, at least in the clothes moth *Tineola*, by a large array of proteolytic enzymes under virtually anaerobic conditions, at a high pH, in a strongly reducing milieu (Robinson 2004a).

There seems to be a progression from a fungal diet, to detritus (including keratin) permeated and partially digested by fungi, to an unmodified keratin diet (Robinson 2004a). A diet of solid, unmodified keratin in the form of dry horn or hooves is the culmination of this progression and occurs only in *Ceratophaga* (Robinson 2004a).

Of the 16 known species of *Ceratophaga*, *C. vicinella* is the only one known to feed on the shell of a turtle, but the habits of several *Ceratophaga* species are unknown (Gozmány and Vári 1973). Most dietary records, primarily associated with *C. vastellus* and *orientalis*, are of horn, hooves, or skin (Walsingham 1881, 1898; Busck 1910; Gozmány and Vári 1973; Robinson 1978). There is a report of *C. vastellus* feeding on the horns of a living animal (Walsingham 1881, 1898), but this is apparently highly unusual, if not erroneous. *C. vicinella* apparently does not attack living tortoises, as hundreds of living tortoises have been observed at the ABS without a single report of suspicious shell damage; in addition, the soil-dwelling habits of *C. vicinella* seem to restrict it to a scavenging role.

C. vicinella is the only known species of its genus in the New World. The group is primarily African (12 species), with 2 species described from India and Sri Lanka, and 1 from China (Robinson 2004b). Some species are known from specimens intercepted in commerce, so natural distributions are not completely clear, but Africa is unquestionably the center of diversity of *Ceratophaga*. The occurrence of a species in southeastern North America is an anomaly, unless it is an introduced species that has not yet been found in its native region. The relationship of *C. vicinella* to its congeners is unknown, as phylogeny within the genus has not been studied, so it cannot be placed phylogeographically. It is possible that *Ceratophaga* formerly had a much more extensive and continuous range. Species might have been associated with the North American savannah ungulates in the Miocene, and with antelopes, horses, bison, and giant tortoises that persisted in southern North America into the Late Pleistocene (Webb 1990). The gopher tortoise, protected by its subterranean habits and by its preference for barren sandy uplands that could not support large populations of human hunter–gatherers or early agriculturalists, may be a last resource for *Ceratophaga* in the New World.

There have been no recent surveys of the range of *C. vicinella*, but historical records are few and disjunct (Heppner et al. 2003). Aside from the first report of its habits in a popular article (Deyrup and Deyrup 1999), it has not appeared in the large body of literature dealing with gopher tortoises. A series of 80 turtle and tortoise shells set out in an open sandhill in northern Florida produced no reports of decomposition of scutes by larvae of *C. vicinella* or other insects (Dodd 1995). Unless *C. vicinella* has an alternative source of larval food, its long-term survival is unlikely. The gopher tortoise is in decline throughout its range, threatened by a combination of habitat loss, proliferating roadways, predators, poaching, and disease (Auffenberg and Franz 1982, Berish et al.2000). A surprisingly large number of insects appear to depend on the gopher tortoise, including beetles (*Onthophagus polyphemi*, *Copris gopheri*, *Aphodius troglodytes*, *Cheloxenus xerobates*) (Woodruff 1982), moths (*Idia gopheri*, *Acrolophus pholetor*) (Davis and Milstrey 1988), and flies (*Machimus polyphemi*, *Eutrichota gopheri*) (Bullington and Beck 1991, Griffiths 1984). Although all of these species share the uncertain future of the gopher tortoise, they are all inhabitants of the tortoise burrow. They do not have the requirement for a long-term, annual supply of dead tortoises distributed within the flying range of a small moth.

On Being Endangered: An Afterthought

Realizing that a species is imperiled has broad connotations, given that it tells us something about the plight of nature itself. It reminds us of the need to implement conservation measures and to protect the region of which the species is a part. But aside from the broader picture, species have intrinsic worth and are deserving of preservation. Surely an oddity such as *C. vicinella* cannot simply be allowed to vanish.

We should speak up on behalf of this little moth, not only because by so doing we would bolster conservation efforts now underway in Florida, but because we would be calling attention to the existence of a species that is so infinitely worth knowing.

But is quaintness all that can be said on behalf of this moth? Does this insect not have hidden value beyond its overt appeal? Does not its silk and glue add, potentially, to its worth? Could these products not be unique in ways that could ultimately prove applicable?

Human creativity, in the commercial world, is increasingly deriving its inspiration from nature. Biomimicry and inventiveness are inexorably linked. The industrial establishment has not, so far, acknowledged its indebtedness to nature, let alone its responsibility to help preserve wilderness. Perhaps naturalists should make it a habit to point out the hidden value of nature wherever they encounter it. This may require a refinement of their sense of alertness, but the effort could prove worthwhile, inasmuch as it could persuade an important segment of the previously uncommitted to join the ranks of the conservationists.

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