

**LEAF MINING AND GRAZING IN SPIDER BEETLES
(COLEOPTERA: ANOBIIDAE: PTININAE):
AN UNREPORTED MODE OF LARVAL AND
ADULT FEEDING IN THE BOSTRICHOIDEA**

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Abstract.—The first larval leaf mining and live-leaf feeding by adults is reported in the Anobiidae and the more inclusive superfamily Bostrichoidea. Larvae of *Pitnus antillanus* Bellés bore in leaves of *Tournefortia gnaphalodes* (L.) (Boraginaceae) and adults feed on leaves of the larval host plant. Larvae complete their development and pupation within a single leaf. It is suggested that leaf mining is a recently derived trait in *Pitnus*.

Key Words: leaf mining, Anobiidae, Ptininae, spider beetles, *Pitnus antillanus*, *Tournefortia gnaphalodes*

Compared to the very large number of species in the Coleoptera, relatively few are known to be leaf miners. The families Buprestidae, Chrysomelidae, and the Curculionidae, sensu lato, (i.e. Belidae, Attelabidae, and Curculionidae [Connor and Taverner 1997]) contain the majority of species (Hespenheide 1991) with smaller numbers in the Nitidulidae and Mordellidae (Paulian 1988). Nearly all species in the Anobiidae (including the Ptininae) feed exclusively on plant or fungal materials in their larval stages, with the majority boring in dead wood or bark (White 1962). There is, though, a large range of feeding habits and styles in this family. For example, most species of *Tricorynus* (= *Catorama*) feed in seeds, although a few have been reared from galls (White 1965, 1974). Many species of dorcatomine anobiids feed on fungi (White 1974, 1982) and members of the subfamily Ptininae mainly scavenge dry organic matter of plant or animal origin (Law-

rence and Britton 1991). Specialized habits within the latter general category include species closely associated with human (Howe 1959, Hinton 1941) and bee (Linsley and MacSwain 1942 and references therein) stored products. Many others are ant associates (Lawrence and Reichardt 1969), and one species may be a termitophile (Zayas 1988). *Pitnus exulans* Erichson subsists mainly on the dried remains of insects and spiders and the dry eggs of spiders (Hickman 1974). No ptinines, or any other members of the Bostrichoidea, have ever been recorded to mine or feed on living leaves.

Leaf mines are channels created by insects (or possibly other organisms) within mesophyll or epidermal tissues. An insect must leave both layers of the epidermis or their outer walls intact in order to be considered a true miner (Hering 1951). This paper describes the life history of this type of miner, *Pitnus antillanus* Bellés, based on field and laboratory observations.

The biology of the 12 members of the genus *Pitnus*, *sensu stricto*, is poorly known (Bellés 1992). All published information is limited to data on specimen labels. A perusal of data reported by Bellés indicates that *Pitnus* is associated with succulent plants in beach or xeric habitats. Although single records exist for associations with *Cryptocarpus* sp. (Nyctaginaceae), fish poison tree (*Piscadia piscipula*: Fabaceae), sea grape (*Coccoloba uvifera*: Polygonaceae), *Djaleya* sp. [sic] and green leaf tobacco (*Nicotiana tabacum*: Solanaceae), repeated records exist for cacti (two records and species in southwestern North America) and *Tournefortia* (= *Mallontonia*) *gnaphalodes* (three records for two species in Florida and the West Indies). Several additional records mention shrubs or leaf litter on beaches (three records and species).

Pitnus antillanus is a rarely collected species known from Puerto Rico (including Mona Island and Cayo Solito) and the Virgin Islands (Bellés 1992). Observations to date are limited to label notes indicating specimens were extracted, via berlese funnels, from beach litter and dead leaves of *T. gnaphalodes* (Bellés 1992, Ivie unpublished).

MATERIALS AND METHODS

Pitnus antillanus specimens collected by two staff members of the Virgin Islands Beetle Fauna Project (D. S. Sikes and R. S. Miller) were noticed feeding on leaves of a living Boraginaceae on the east end of St. Croix in January, 1993. Following up on this observation of such a rare species, beetles were observed on two occasions (in August, 1995) by one of us (M.A.I.) on the host plant, *Tournefortia gnaphalodes* (Linnaeus), Boraginaceae, at East Bay, (St. Croix) and Smith Bay, (St. Thomas) U.S. Virgin Islands. Host-plant branches with infested leaves also were collected for examination in the laboratory. These branches were preserved in 95% ethanol and each leaf and stem carefully examined for eggs, larvae, and pupae in the laboratory.

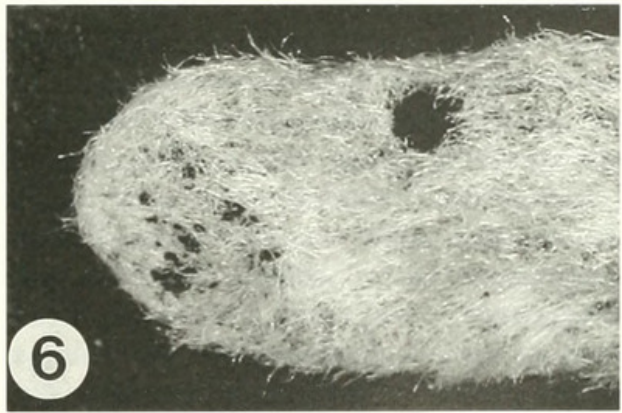
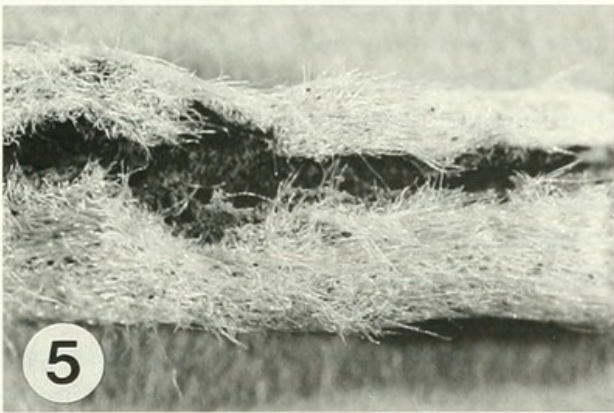
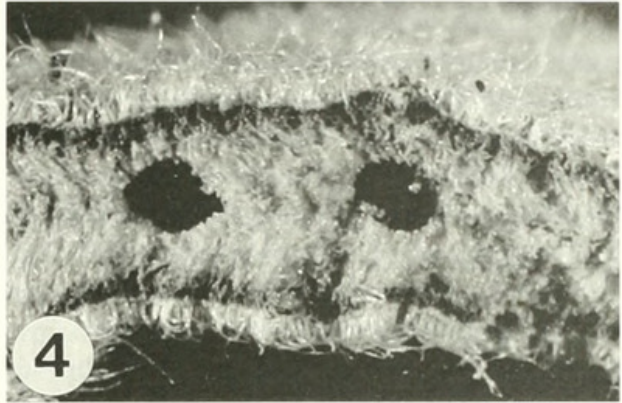
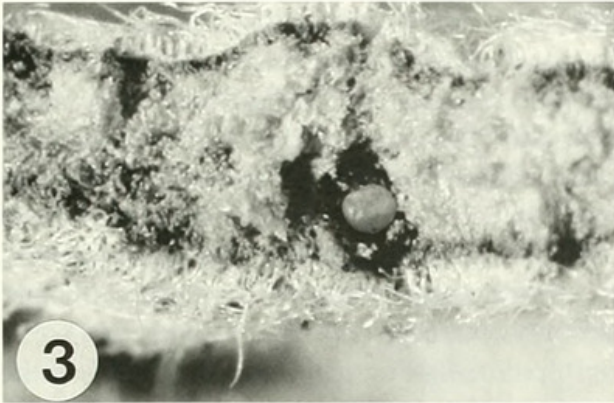
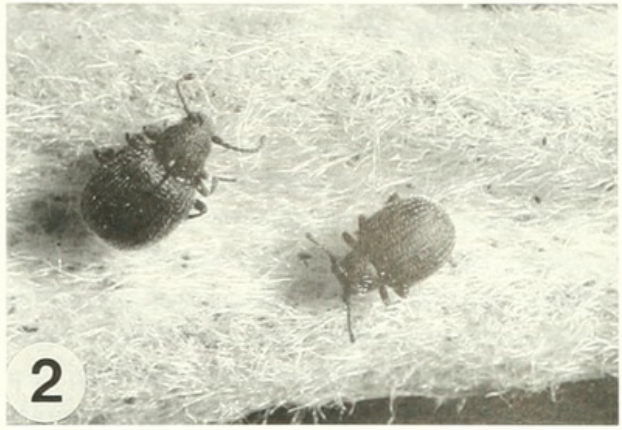
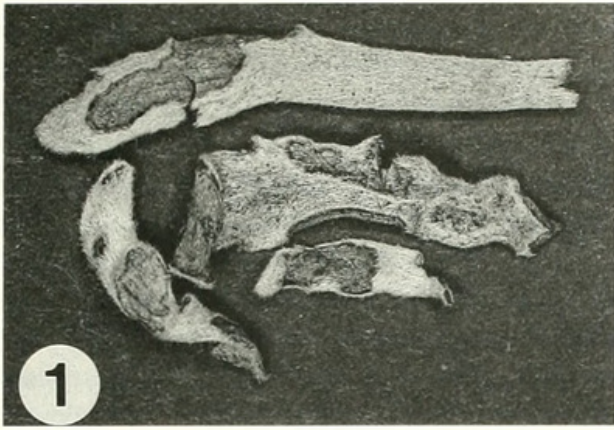
Fifty-eight individuals were collected on

28 August, 1995 at East Bay and used to establish colonies. Cultures were set up in plastic Petri dishes of two different sizes using dead leaves. A single large colony was kept in a 90 × 15 mm dish and smaller subcultures were maintained in 55 × 15 mm dishes. Leaves were scattered throughout the bottom of the large culture dish, one to two layers deep. Groups or individual leaves were used in the small Petri dishes. With isolated leaves, the development of individual larvae could be more carefully studied. Small pieces of apple were added periodically as a food and moisture source, and a 1-cm square piece of paper towel was moistened daily with distilled water to humidify the cultures.

Voucher specimens have been placed in the Virgin Islands Beetle Fauna Project Collection (Montana State University), The Ohio State University Insect Collection, and the collection of TKP.

RESULTS

Field observations.—Returning to the site of the Sikes and Miller collections on August 28, 1995, plants were examined for adult beetles. Visual searching was not productive as the beetles are tiny (1.0–1.4 mm) and are exceedingly difficult to see on the grey-green foliage covered with silvery trichomes. A sharp tap over a beating sheet, however, yielded *P. antillanus* in abundance. Closer examination showed a progression from healthy, firm, fleshy leaves at the top of each stem, down through wilted, shriveled ones, to dried hard brown obviously dead leaves at the bottom of the whorl. Bare stem, with leaf scars, occupied the remainder of the stem. Dead leaves laid in piles under the plant. Splitting open the woody stem (the expected larval habitat) showed no evidence of larval feeding. The leaves, however, showed evidence of leaf mining. Ptinine larvae were observed in several leaves with the leaf condition ranging from turgid to flaccid. Newly eclosed adults were found in dry leaves. A general progression of leaves with less-to-more ma-



Figs. 1–6. Host plant damage, egg, and adults of *Pitnus antillanus*. 1, Adult feeding damage on the host plant, *Tournefortia gnaphalodes*. 2, Adults on leaves of the host plant. 3, Exposed egg which had been oviposited through a split in the leaf surface. 4, Cross-section through a leaf exposing two mines in leaf mesophyll tissue. 5, Exposed mine of late instar on a section of leaf. 6, Emergence hole of adult.

ture larvae seemed to go from terminal to basal positions respectively, with adults in the lowest leaves. Examination of more *T. gnaphalodes* on St. Thomas yielded concurring observations. No larval mortality from either parasites or pathogens was observed in field collected leaves.

Adult behavior.—Adult beetles were repeatedly observed feeding on living leaves of

the host plant, *T. gnaphalodes* in the Virgin Islands. Microscopic examination showed that beetles chewed leaf trichomes or hairs to gain access to the leaf surface and mesophyll tissue. Feeding damage was usually not so deep as to completely perforate leaves (Fig. 1). In culture, adults were observed to feed on dead leaves (and pieces of apple). Although the leaves are thickly covered with

fine overlapping trichomes, they did not seem to impose any difficulties in feeding. Beetles consumed the trichomes as readily as epidermal or mesophyll plant tissue. The hairs did not create any difficulties for movement, as numerous individuals were observed walking quickly over leaf surfaces (Fig. 2). Adult feeding damage created discolored areas that were used as hiding places. Adults survived in colonies for as long as three months.

Oviposition.—Adults laid eggs directly on undamaged plant leaves and generally placed eggs among leaf hairs. They also used damaged areas such as feeding sites, cracks in leaves, or other potential hiding spots (Fig. 3). Only dead leaves were available in the lab, and were readily accepted for oviposition. Eggs are ovoid and white with a pointed tip. Egg length was 0.37 ± 0.03 mm and the width 0.25 ± 0.04 mm ($n = 10$). Eggs were laid singly, although several were found in small groups within approximately 3 mm of each other in particularly good hiding spots. It is not known how many females contributed eggs found in such locations. Eggs were inserted inside leaf tissues only if there was a break in the leaf surface to allow ovipositor access.

Larval development.—Complete larval development appears to take place within a single leaf. Larval mines were found in both mature leaves and smaller, immature leaves attached to within 3 cm of the apical meristems. Larval development can occur entirely within a dead leaf. Eclosion occurred as larvae chewed through their egg shells (egg shells were never completely consumed) and into the leaf epidermis. Larvae then proceeded to hollow out the inner leaf tissues, leaving the outer cells of both the upper and lower epidermal tissues intact. First instar larvae initially develop their mines as a single tract (Fig. 4) but later expand the tunnel as a full depth, blotch mine as they mature (Fig. 5) (terminology from Hering 1951). Blotch mines are formed by tunnel expansion in both a horizontal and vertical direction, with no particular sense of direction. Larvae were con-

strained somewhat by the elongate leaf shape but were not affected by leaf venation. As the leaf gradually narrows to the stem no distinct petiole exists and leaves were mined their entire lengths, but mining was never observed in the stem. No feces are removed or ejected and hence mines always contained a large quantity of frass. Only a single larva per leaf was observed in the field-collected leaves, but on several occasions, more than one larva was found within a leaf in lab colonies. This may be a result of captivity and overcrowding.

Compared to a typical scarabaeiform anobiid larva, *P. antillanus* larvae are very linear and almost eruciform. This modified form enhances their ability to move, as larvae appeared very mobile and can move easily within a mine or over flat surfaces. No carpeting of the mine cavity with silk was observed prior to pupation.

Pupation.—Pupation occurred within the mine created by larval feeding and no particular pupation mine or special burrow was made. No emergence holes or slits were made before larvae pupated, but emerging adults easily chewed small round holes through the leaf tissue to escape pupation chambers (Fig. 6). Thin-walled pupal cocoons were constructed with silk, but the amount of silk used appears to vary a great deal. In most cases the amount seemed to be small, as evidenced by the difficulty we had in locating old pupation sites. Chambers could be detected by the presence of the larval and pupal exuvia. In one case, a relatively large amount of silk was found and formed a thin but tightly woven cocoon. Pupal cocoons were surrounded with debris consisting almost entirely of black fecal pellets.

DISCUSSION

There are now eight families of beetles with known leaf miners (classification of Lawrence and Newton 1995). How these species evolved into leaf miners is unknown, but hypotheses have been presented by several authors. Although buprestids are

mainly cambium borers, it has been noted that cambium tissue is not very different from the thin layer of tissue in a leaf (Needham et al. 1928). Therefore, this ancestral feeding mode may have preadapted species for leaf mining. Curculionoid miners are generally thought to have been derived from stem (Needham et al. 1928) or seed and fruit dwelling ancestors (Connor and Taverner 1997). Later they evolved into petiole borers and other forms that live and feed in the large ribs of leaves and remaining leaf tissue. Chrysomelids contain many species whose larvae and adults feed on leaves. A switch from exposed feeding to feeding within the leaf may have afforded added protection from predators or parasitoids (Needham et al. 1928).

Most Anobiidae and its sister group, the Bostrichidae, are wood borers. Crowson (1967) proposed that the evolution of the ptnines from within the anobiids may have been due to the switch from wood-boring to scavenging food of both plant and animal origin. He stated that the loss of wood-boring was "a fundamental factor conditioning the divergence of the Ptinidae as a family." Evidence against this hypothesis is that some *Ptinus* spp. are true wood-borers (Howe 1959, Bellés 1980). Unlike *Ptinus*, *Pitnus* is a very derived member of the Ptininae with a characteristic globular body form, fused elytra, and an absence of flight wings. They belong to a lineage of highly derived ptnines (such as *Sphaericus*, *Trigonogenius*, *Gibbium*, etc.) which feed upon accumulations of dead organic matter. Many members of this lineage are known to feed in animal dung, such as rodent pellets (Aalbu and Andrews 1992).

Hering (1951) considered species that do not live in fresh, green leaves but mine dead tissue to be transitional between true miners and saprophytes. *Pitnus antillanus* may represent both forms, as it is a species which may start mining in live tissue but can, if necessary, utilize or complete development in a dying or dead leaf. Adults inside shed leaves are probably the source of reported

beach litter records for the species (Bellés 1992).

Selection for a mining lifestyle may be due to several factors. Mines afford protection from natural enemies and desiccation (Hering 1951) and can allow much higher feeding efficiencies compared to external feeding (Connor and Taverner 1997). The effect from desiccation may be particularly relevant for a small species like *P. antillanus*, which is less than 1.5 mm long (Bellés 1992). Additionally, this species lives in sea beach habitats exposed to high sun (UV radiation) and wind exposure. The succulent leaves of *T. gnaphalodes* provide cover and possibly moisture in a very dry habitat. Further, no parasites or pathogen induced larval mortality were observed in the field-collected leaves. However, we did not find any evidence that larvae are mining to avoid structural or chemical defences of the host plant, or that they are consuming more nutritious parts of the leaf. Indeed, some leaves were almost completely hollowed out by larval feeding.

Pitnus antillanus has a large parental investment in each egg produced. Each egg averages 0.37 mm in length, while adults range in size only from 1.0 up to 1.4 mm (Bellés 1992). Hence, total egg production is probably quite low. Although ptnines vary a great deal in total egg production (e.g. *Ptinus sexpunctatus* Panzer averages only 21 eggs per female while *P. tectus* Boieldieu can lay nearly 1000 [Howe 1959]), low fecundity in *Pitnus* may indicate reduced larval mortality associated with mining. The adults may also be long lived, as evidenced by their abundance when collected with a beating sheet, and the relatively large series (for anobiids) of 20 or 30 specimens used to describe several species (Bellés 1992).

The more linear body form of the larva, rather than the typical "C"-shaped scarabaeiform bostrichoid larva, probably enables *P. antillanus* to move more easily within a mine. In comparison, other ptnine larvae are capable of movement, but are rel-

atively awkward when removed from their feeding site. This is particularly true in the large final instar. The only other bostrichoid larvae known to retain the ability to walk on a substrate are the fungivorous Endecatominae (Kompantsev 1978, Ivie 1985). Although we have no evidence for this, the mobility of the larvae of *P. antillanus* may also be an adaptation for moving from leaf to leaf via the plant exterior. Leaf miners of other families are known to wander on stems to select other leaves during the course of their development (Hering 1951, Ford and Cavey 1985). One general characteristic of mining larvae is a strongly thickened fore body to facilitate penetration into plant tissue (Hering 1951). These modifications were not observed in *P. antillanus*.

Adults are present throughout the year (records in Bellés 1992 and from museum specimens), as is the perennial host plant, so breeding potentially can occur at any time of the year. The host plant for *P. antillanus*, *Tournefortia gnaphalodes*, is a widespread coastal species. It is found at least as far south as Aruba, Bonaire, and Curaçao, throughout the West Indies and Florida, and along the coast of tropical Mexico (Boldingh 1914, Britton and Millspaugh 1920, Long and Lakela 1971). With this broad host distribution, it is likely that many more populations or species of *Pitnus* occur in coastal areas of the Caribbean, in addition to those listed by Bellés (1992).

It is possible that adult or larval feeding affects leaf tissue or causes leaf abscission, which might improve the leaf host as a food source. We suspect that these beetles may be introducing a fungus that affects the larval food source quality. More studies on the beetles and their hosts will need to be done before we can answer these questions.

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