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Rolled-Leaf Hispine Beetles (Chrysomelidae) and their Zingiberales Host Plants in Middle America

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ABSTRACT

The Arescini and Cephaloliini are two closely related tribes of hispine chrysomelid beetles, parasitic upon Zingiberales in the New World tropics. These "rolled-leaf hispinæ" live in and feed from the scroll-like immature leaves of Zingiberales. Adults are flat and less spiny or sculptured than most other Hispinæ, tropical or temperate. Larvae are grossly flattened and morphologically suited for life between the appressed host plant surfaces. Larvae do not burrow into the plant tissues but live and feed from the surface of host organs, as do adults, by reciprocal scraping with the mandibles. Host species specificity varies from monophagous to polyphagous within Zingiberales families for both larvae and adults. Some species change host species geographically. It is rare for one beetle species to attack plants in more than one Zingiberales family. Species richness of beetles is correlated with host-species range, size, and diversity.

EXTRACTO

Dos tribus con afinidades cercanas de coleópteros hispinos chrysomélidos, la Arescini y la Cephaloliini están limitadas a vivir sobre plantas de la orden monocotiledonia tropical Zingiberales. Estos son coleópteros de los trópicos del Nuevo Mundo pero tienen familiares en los trópicos del Viejo Mundo, que son similares lo mismo morfológicamente que funcionalmente.

Yo llamo e estos coleópteros los hispinos de hoja enrollada pues en América Media siempre estan asociados con las hojas inmaduras producidas por los Zingiberales. Aunque durante la etapa larval algunas especies se especializan en comer otras partes de las plantas, los adultos de la mayoría de las especies se congregan y alimentan en los embudos formados por las hojas enrolladas. Estos coleópteros son planos y de superficie tersa. Tienen menos espinas, crestas, y punciones que los demás miembros de la sub-familia Hispinæ, sean tropicales o de partes más templadas. La forma plana y tersa del cuerpo adulto les permite vivir en las estrechas cavidades formadas por las superficies de las hojas enrolladas de la Zingiberaceae. Las larvas están aun más modificadas para este tipo de vida. Son éstas completamente aplastadas y muy parecidas a los insectos escamas (hembras adultas de la familia Coccidae, Homóptera), o a las larvas de miembros de la familia Psephenidae (Coleóptera). Las larvas y también los adultos se alimentan raspando la superficie de las hojas, el pecíolo o el tallo. Las larvas no penetran en los tejidos de la planta.

El nivel taxonómico de especie de estos coleópteros en la América Media no está bien definido. Hay gran cantidad de grupos aun sin describir, y otros han sido, taxonómicamente, divididos demasiado. Estudios de los patrones de uso de las plantas hospederas de estos coleópteros prometen tener gran valor en la clasificación de estos coleópteros, los cuales son extremadamente polimórficos. Existe entre éstos una extensión de especies expresamente asociadas con diferentes plantas. Algunas especies son monófagas otras se encuentran asociadas con series de especies de Zingiberales y algunas especies atacan diferentes especies de plantas en diferentes áreas geográficas. Muy pocas especies atacan plantas en diferentes familias de Zingiberales. La riqueza de especies de estos coleópteros está relacionada con algunas características de sus plantas hospederas. Estas características son parecidas a las usadas para predecir el número de especies en otros sistemas de artrópodos/plantas que son taxonómicamente mas generalizados. Por ejemplo: la extensión geográfica de la especie de planta hospedera, el tamaño de la planta y la diversidad de familias de las plantas en que estos coleópteros se encuentran parecen influenciar el número de especies de hispinos de hoja enrollada que diferentes especies de Zingiberales mantienen.

THE ROLLED-LEAF HISPANAE are two closely related tribes of chrysomelid beetles parasitic upon Zingiberales in the New World tropics. They spend their entire life cycle upon species of this monocotyledonous order and occur virtually nowhere else. This allows populations to be easily found and facilitates ecological experimentation under natural conditions. The various families within the Zingiberales tend to maintain distinct species-groups of these beetles. Although beetle species change host species geographically they are generally restricted to only one Zingiberales family throughout their range. This paper is a general description of rolled-leaf hispine life history, taxonomy, and host affiliation in Middle America. Biogeographic and ecological patterns are sug-

gested for this area with the intention that these be compared with those of the rolled-leaf hispines of other areas. This insect/plant association is elaborately represented in South America (Maulik 1937) but is poorly known. The Old World tropics have hispine beetles closely related to those discussed here (Gressitt 1957) and their hosts include species within the Zingiberales (Gressitt 1963).

ZINGIBERALES HOSTS

The Zingiberales is a tropical group of eight distinct families, the Costaceae, Zingiberaceae, Marantaceae, Cannaceae, Heliconiaceae, Sterilitziaceae, Lowiaceae, and the Musaceae (Tomlinson 1969). All but the

last three of these families are native to Middle America (Hutchinson 1959). The Zingiberales is recognized as distinct from other monocot groups, and as being composed of closely related families. In the words of Tomlinson (1969) it is an "isolated but closely knit assemblage." Species of this order are terrestrial, rhizomatous herbs that are branched usually only at the base. Only a few species are woody or arborescent even though many grow to 15 m in height. There are many shoots per individual rhizome and these are produced both sequentially and simultaneously. The aerial axis in most families is largely encased by overlapping leaf sheaths (Cannaceae, Heliconiaceae, some Marantaceae, Musaceae, and Zingiberaceae), whereas species in other families have nude, elongated internodes (Costaceae, and some Marantaceae). Two of the families have aerially branched vegetative axes (most Costaceae and some Marantaceae). The predominant situation is a terminal inflorescence that is the last growth of the shoot. However, some species of Costaceae, Marantaceae, and Zingiberaceae bear the inflorescence on a short, separate, basal shoot that does not carry foliage. In Middle America the Zingiberales is a mesophytic order; drier regions have fewer species. Even so, species occur in a full range of habitats, from undisturbed forest through regenerating second growth vegetation to open, recently disturbed areas such as road sides and pasture edges. Each species is fairly restricted to a narrow range of situations. For a good discussion of the spectrum of habitat types of sympatric *Heliconia* species see Stiles (1975).

Unfortunately, the taxonomy of the Zingiberales is incomplete at the species level. The Middle American Heliconiaceae are presently being revised (e.g. Stiles 1975), and the Marantaceae have recently been

revised (Kennedy 1974). The New World Costaceae were also recently revised (Maas 1972), but although Middle America appears to be the center of diversity, this family is poorly investigated there because the field work supporting Maas' reorganization was done in Surinam. The Cannaceae is comprised of only few species in Middle America relative to the other native Zingiberales families (Segeren and Maas 1971). The taxonomy of Middle American Musaceae is not complex as there are only several agricultural and a few ornamental cultivars in the region (Simmonds 1959). The Zingiberaceae has recently been revised (Maas, in press).

ROLLED-LEAF HISPINAE

The alpha taxonomy of Middle American rolled-leaf hispinae is well developed and is based upon specimens collected since the mid-19th century and classified at that time in Europe. The Champion Expedition, summarized in *Biologia Centrali-Americana* (Baly 1885-1894), resulted in the classification of many of the forms one finds presently associated with Middle American Zingiberales. Although the taxonomy of rolled-leaf hispinae has been based upon adults only (Uhmann 1957, 1964), the species of the tribe Arescini (*Arescus*, *Xenarescus*, *Nympharescus* and *Chelobasis*) and the taxonomically adjacent *Cephaloleia* (of the tribe Cephaloliini) have larvae with a strange "water-penny"-like morphology, and virtually all are associated with hosts in families of the Zingiberales. The distinctness and homogeneity of both adult and larval morphology, and the consistent host affinity suggests the group to be an autochthonously radiated phylogenetic assemblage rather than a heterogeneous group. Table 1 gives a synopsis of the gen-

TABLE 1. *Species richness, geographic range, and host affiliations of the rolled-leaf hispine genera of Tropical America. The number of described species is taken from Uhmann (1957, 1964). Other information is from original field and museum experience.*

Rolled-leaf hispine tribes and genera	Described species ^a	Known hosts	Known geographic range
<i>Cephaloliini</i> <i>Cephaloleia</i>	182 (65)	All families of Middle American Zingiberales except Cannaceae and Musaceae	All Tropical America
<i>Arescini</i> <i>Arescus</i>	6 (0)	<i>Heliconia</i>	All Tropical America
<i>Xenarescus</i>	1 (0)	<i>Heliconia</i>	Trinidad, Tobago, and northeastern South America
<i>Chelobasis</i>	4 (2)	<i>Heliconia</i>	All Tropical America
<i>Nympharescus</i>	6 (0)	<i>Heliconia</i>	Colombia, Ecuador, and Peru

^a The figure outside parentheses for all tropical America, in parentheses the number of species known by Uhmann (1957, 1964) from Middle America.

era of rolled-leaf hispinae, their known species richness, host plants, and geographic range. Several other closely related groups which have a similar adult and larval morphology are not included, as they do not attack Zingiberales in Middle America, for example *Demotispa* and *Euxema* (in the Cephaloliini) and *Alurnus* (of the taxonomically close tribe Alurini) are associated with palms in Middle America. However the larvae and adults of these genera live and feed in the folds of the immature fronds in a fashion reminiscent of the rolled-leaf hispinae on Zingiberales and the larvae have the distinct "water-penny"-like appearance of the rolled-leaf hispinae.

LIFE CYCLES

Eggs of the rolled-leaf hispinae are very flat, elliptical in outline, and transparent with a white or brown tint (fig. 2, upper left). The egg membrane is thin and delicate, and eggs are fragile and subject to rapid desiccation. In nature, the eggs are usually laid singly but sometimes in groups of up to 10, but always laid on the surface of damp, live host tissue, and are often hidden under overlying plant parts. Eggs do not diapause, but begin to differentiate soon after laying and hatch within 10 to 30 days. Egg size is positively correlated with the size of the adult beetle. The smallest eggs (of *Cephaloleia lata* Baly) are approximately 1 x 1.5 mm, and the largest (of *Arescus*, *Nympharescus* and *Xenarescus* species) are approximately 3 x 5 mm.

The progress of differentiation is visible through the transparent egg membrane. At hatching, the larva exits from the egg membrane by crawling out from under its anterior lip, and the flat ellipsoidal membrane remains tenaciously attached to the leaf. Empty egg membranes can easily be distinguished from unhatched ones, for eggs that do not produce a larva do not have the characteristic exit tear. There are three apparent sources of egg mortality. The first is desiccation which occurs when eggs are laid on a plant part that dries before the eggs hatch. The second is cannibalism by conspecific larvae and predation by the adults of different rolled-leaf hispine species. Both larvae and adults graze along the leaf, bract, or stem in a linear fashion and chew through encountered eggs. This cannibalism-predation could be density dependent, but only in a stochastic fashion because the proportion of the host leaf grazed by hispine larvae is almost always small, even at the highest naturally occurring densities. The third source of egg mortality is hymenopterous parasitoids. In fig. 2, upper left, each dark, cigar-shaped body in the eggs is an immature trichogrammatid wasp; notice the larval grazing marks which barely miss

the egg. Eggs of rolled-leaf hispinae that have been parasitized are distinguishable from nonparasitized eggs, even after the adult wasps have emerged, by the presence of the pupal wasp exuviae or larval carcass fragments.

At emergence, the larva is the same shape as the egg and just slightly larger in outline area than the egg membrane. The larvae are flat and reminiscent of adult female scale insects (Coccoidea: Homoptera) or water pennies (larval Psephenidae: Coleoptera). Broad extensions of the margins of the thoracic and abdominal tergites extend laterally and forward to completely cover the legs and head, and the ventral margins extend down at the edges. In some species the margin bears many tiny, outwardly pointing hairs, but in others it is entire and may be pressed against the leaf surface as protection against desiccation.

Larvae of the two tribes are slightly different in shape (fig. 2). The larvae of Arescini (see section on systematics) tend to be elongated and more than twice as long as wide (fig. 2, middle left). However, though the larvae of some species of Cephaloliini are almost as wide as long (fig. 2, lower right), others are elongate (fig. 2, upper right), less flat, and live and feed on young leaf petioles rather than on mature leaves or on rolled leaves. *Cephaloleia* species that are small as adults molt only once during development (fig. 2, lower right), whereas species that are large as adults (most Arescini and few Cephaloliini), molt up to eight times before pupation (fig. 2, middle left, and Strong and Wang, in press). As molting time approaches, the larva ceases to move, becomes opaque, then splits along the dorsal midline. Skins cast off at molting usually stick to the leaf, bract, or stem (fig. 2, lower right). The just-emerged larva (from egg or molt) is transparent white to brown, is very soft and fragile, and feeding movements of the head and the pigmentation of the eyes can sometimes be seen through the semi-transparent body of the larva. As the larva approaches molting the skin becomes much more tough and brown. Growth in size is rapid just after molting but slows as the next molt approaches. Larvae begin feeding within hours of hatching or molting and feed by scraping the ventrally-directed, scoopshaped, toothed, mouth parts reciprocally across the plant surface (fig. 2). The larva crawls forward with each scoop, leaving a linear trail which is often littered with cylindrical fecal pellets (fig. 2 middle left). Though feeding movements of larvae are similar to those of adults, the feeding scars left by adults have a more even border than those left by larvae (fig. 1, 2, 3 and 4), and the tarsal claws of the adults of



FIGURE 1. Atlantic lowlands, C.R.; Upper left: A rolled leaf approximately 2 m long of a single *Heliconia imbricata* shoot. Note the funnel shape with the upper end open allowing access to animals. Upper right: *Costus* sp. damaged by adults of the rolled-leaf hispine *Cephaloleia bistrionica*. The leaf was eaten when still rolled though no rolled leaves remained on the plant at the time the photograph was taken. The leaves are approximately 30 cm long. Lower left: Damage to *Heliconia imbricata* by larvae of *Chelobasis perplexa*. Feeding marks are long and narrow and do not usually penetrate the leaf. Lower right: *Calathea leucostachys* in flower. The leaf scars are caused by larvae of the rolled-leaf hispine *Cephaloleia* c.f. *erichsoni* which also eat the wet inside edge of the mature petiole (see table 2, and fig. 2, upper right).

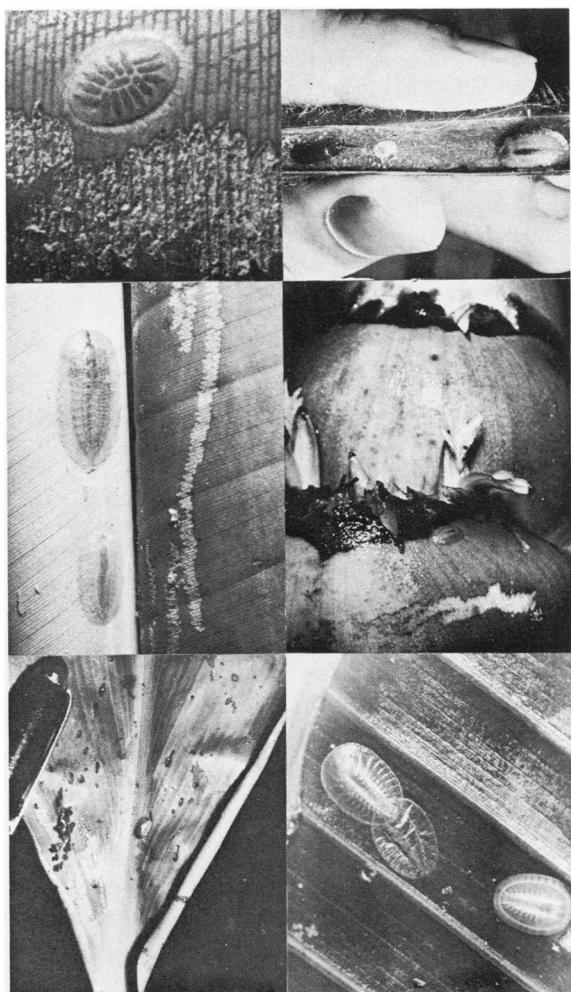


FIGURE 2. Atlantic lowlands, C. R.; Upper left: Egg of *Chelobasis perplexa* parasitized by hymenoptera (Trichogrammatidae, Chalcidoidea). Each spindle-shaped object in the egg is a developing wasp. Notice the leaf damage trail passing by the egg, caused by a larva of the same species. Larvae destroy eggs by grazing through them. The egg is approximately 4.5 mm long. Upper right: Adult, egg, and larva of *Cephaloleia c.f. erichsoni* on the petiole of *Calathea leucostachys* (see fig. 1, lower right, and table 1.) Middle left: Larvae of *Chelobasis perplexa* on the rachis of a rolled leaf of *Heliconia imbricata*. The anterior end of the larva is uppermost. Note scar on right side of leaf made by upper larva. Also note larval feces in lower left of photo and between the two larvae. The upper larva is 16 mm in length. Middle right: Larva of *Cephaloleia puncticollis* on inflorescence of *Heliconia imbricata*. Note grazing marks across bottom of photo. The larva will crawl to progressively higher bracts as the inflorescence matures. This larva is approximately 6 mm long. Notice the ant in the lower corner of photo though there is little, if any, interaction between ants and these larvae. Lower left: Larva of *Cephaloleia histrionica* and its damage on a leaf of *Costus* sp. Contrast this damage with that done by the adults of this beetle in figure 1, top right. Lower right: Larvae of *Cephaloleia consanguinea*. The individual on the right will soon molt, whereas the larva on the left is in the process of molting, and has already cast its skin.

some species leave a parallel row of punctures on each side of the feeding scar. I term this mode of feeding "strip mining." For many rolled-leaf hispine species the larval lifespan is longer than that of the rolled leaf, so larvae must periodically seek a new feeding location. When the leaf unfurls, the larva must crawl to another rolled leaf on a different plant because each host plant produces only one leaf at a time, and there is substantial delay between the sequential rolled leaves of a single plant. Larvae move between host plants by night, and hide beneath petiole bases during the day. Upon finding a rolled leaf, they remain and feed until it unfurls. When one of these larvae is experimentally placed within a few centimeters of a rolled leaf it shows no directed movement toward the leaf, and often as not crawls in the opposite direction. Experimentally marked larvae released on a row of host plants, connected by having had their leaves tied together, randomly reassort themselves on the various plants within a few days, even if one of the plants in the connected row bears a rolled leaf. Only when a larva crawls onto a rolled leaf does it stop and feed (Strong and Wang, in press). Similarly, the larvae of *Cephaloleia consanguinea* Baly (and *Cephaloleia ornatrix* Donck. on mature leaves of *H. pogonantha*), feed beneath litter and debris on top of mature, unfurled leaves of *Heliconia imbricata* (fig. 3); the paths of larvae isolated from debris indicate no directed movement toward it, even though it may be only a few centimeters away. The movement of larvae has not been observed to exceed 15 cm per minute along an unobstructed plant surface.

There are four areas of host-plant utilization for the larvae (table 2): inside the scroll of the rolled leaf (fig. 1, upper left), on inflorescence bracts (fig. 2, middle right), on the wet petioles of immature leaves (fig. 2, upper right), and on the surface of mature, unrolled leaves (fig. 3). Larvae utilizing the immature scroll feed from the surface that will be the lower side of the leaf (*Chelobasis* on *Heliconia latifolia*, and *H. imbricata*; *Xenarescus monocerus* on *H. bibai*; *Nympharescus separatus* on *H. pogonantha*). These larvae scrape long scars along the rolled leaf (fig. 2, middle left), sometimes including the leaf rachis, and leave substantial amounts of frass alongside the scars. Species that live and feed on the inflorescence bracts, like *Cephaloleia puncticollis* (fig. 2, middle right) strip mine the surface of the younger, wetter bracts on the inflorescence and move sequentially to younger bracts as the older ones dry and harden. They may also feed on the bases of the flowers themselves in the semi-aquatic environment inside the bracts, but they are not responsible for as

much damage to the flowers as are the larvae of syrphid Diptera (Seifert 1975). There are several species with petiole-feeding larvae among the hispines that attack Marantaceae (table 1). These larvae live at the base of the petioles when not feeding, and ascend with new leaves as these grow out of the axil. They often feed from the rolled leaf as well as the petiole.

The larval habitat on the mature leaf surface is usually created by another leaf falling on top of the unfurled Zingiberales leaf. Rain water collects beneath the fallen leaf, and this area remains wet while the rest of the leaf dries between showers. The larvae feed from the host leaf epidermis. Adults of species that live as larvae beneath fallen leaves feed from

rolled leaves, and eggs are laid both in the rolled leaf and beneath fallen leaves on unrolled leaf surfaces. The first three larval lifestyles listed in table 1 have been found in host species in the Heliconiaceae, Costaceae, Marantaceae, and Zingiberaceae. The fourth, "leaf top-fallen leaf" lifestyle has been found only in species associated with Heliconiaceae.

Pupation (fig. 5) follows a period of decreasing larval mobility, but in most species occurs with little modification of the shape of the last instar larva. Superficially the pupa looks like a large, dark, immobile larva. The most modified pupae are in *Xenarescus*, from Venezuela and the Lesser Antilles. In this genus the pupae have two flukes protruding forward from the anterior end which lie flat against the

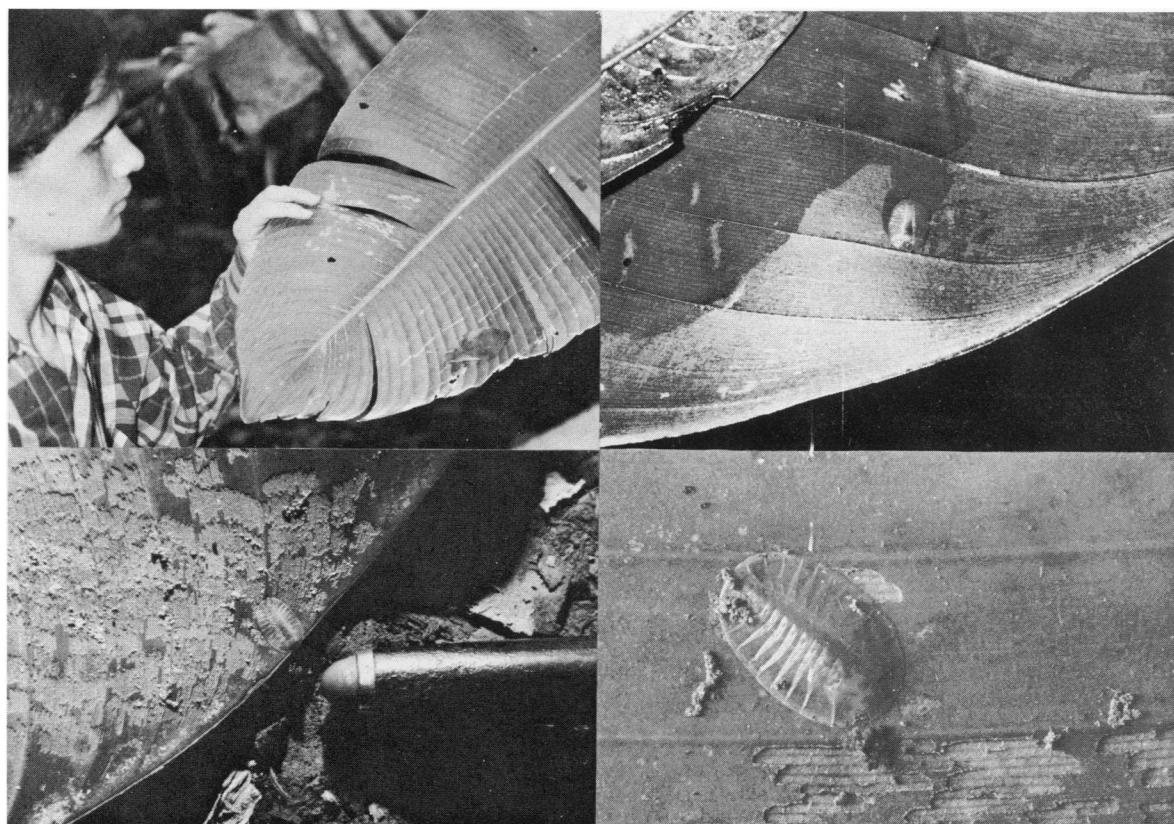


FIGURE 3. Atlantic lowlands, C.R.; Upper left: Tip of *Heliconia imbricata* leaf showing larval damage of *Cephaloleia consanguinea* (near finger tips of T. S. Ray), and fallen dicot leaf in lower right section of this photo. The leaf damage occurred when this part of the *Heliconia* leaf was protected beneath a fallen leaf. When the fallen leaf slips from the *Heliconia* leaf the *Cephaloleia* larva haphazardly wanders in search of another fallen leaf. The linear leaf scar in the upper right hand section of this photo was made by larvae of *Chelobasis perplexa* when the leaf was rolled. Upper right: *Cephaloleia consanguinea* larva moving away from fallen leaf. Note the moisture maintained beneath the fallen leaf, even though the rest of the *H. imbricata* host leaf is dry. Lower left: Patch of damage on edge of *Heliconia imbricata* leaf which was done by *Cephaloleia consanguinea* while the damaged area was beneath a fallen dicot leaf. *C. consanguinea* pupates beneath fallen leaves and detritus on the host leaf rachis. Lower right: Closeup of *C. consanguinea* larva, its host leaf damage, and its feces, which are in linear piles. This larva is approximately 8 mm in length and its anterior end is pointing down to the right.

plant substrate (fig. 5, top). Ventrally, the developing legs, abdomen, pronotum and head are visible.

All rolled-leaf hispine species I have studied pupate above ground on the host plant. Pupation site varies

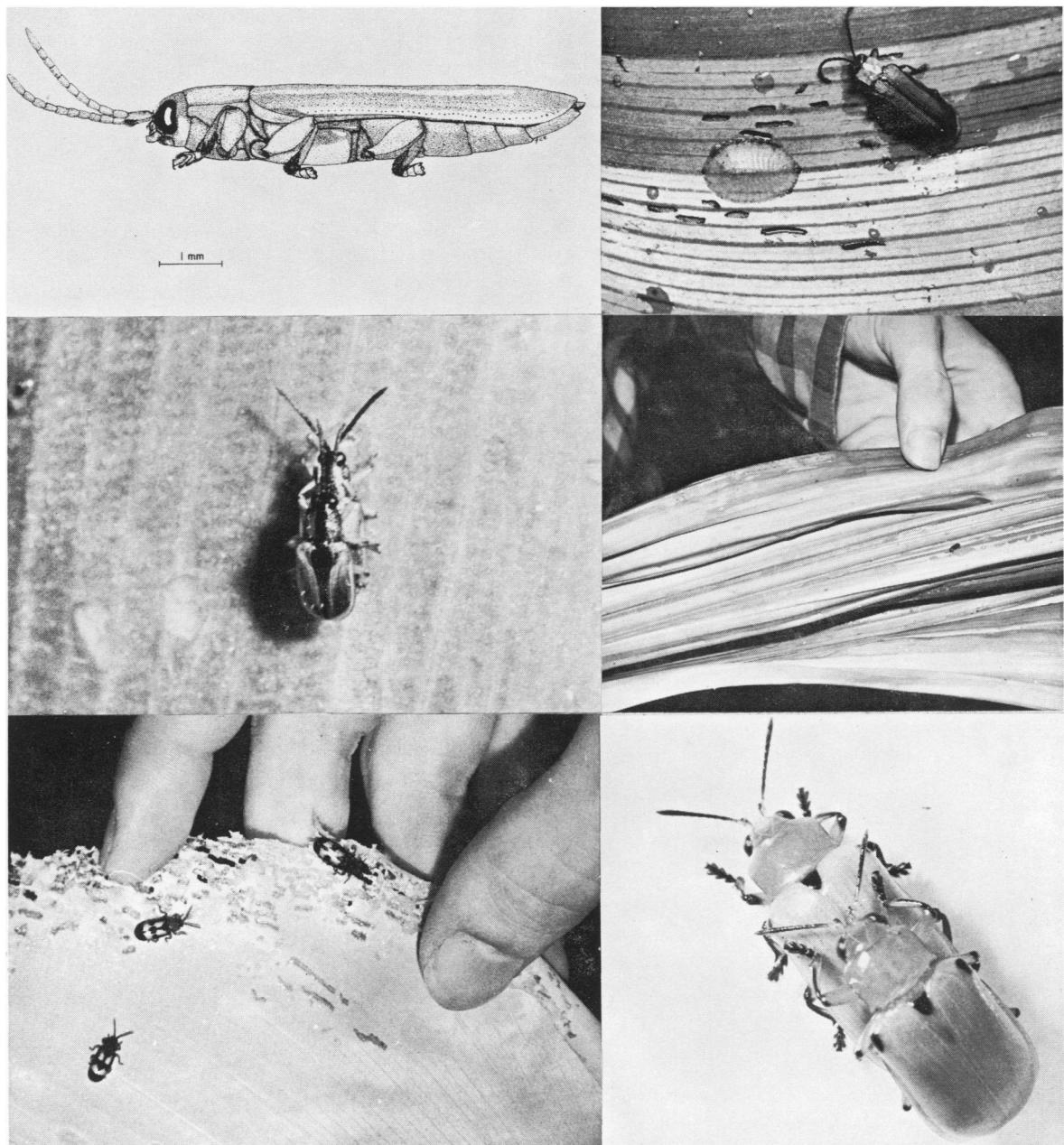


FIGURE 4. Upper left: Drawing of adult *Cephaloleia vicina*, side view. Note flat shape that facilitates life between tightly appressed leaf and stem surfaces of host Zingiberales. Upper right: Larva and adult of *Cephaloleia* sp. from Monte Verde, Puntarenas Prov., Costa Rica. This species is restricted to high elevations and to *Heliconia tortuosa*. Leaf damage is attributable to the larva. Middle left: Amplexed pair of *Cephaloleia bistrionica* on *Costus* sp. from Atlantic lowlands, C.R. Male is superior with his antennae touching the insides of the female antennae. (see also fig. 1, top right, and fig. 2, lower left). Middle right: Leaf of *Cyclanthea bipartita* (Cyclanthaceae) with adult of *Cephaloleia* sp. nov. from Canal Zone, Panama, which is the only known non-Zingiberales rolled-leaf hispine. Lower left: *Cephaloleia* sp. adults and their damage on an inside corner of a rolled-leaf of *Ischnosiphon* cf. *cerotus* from Atlantic lowlands, C.R. Lower right: Amplexed pair of *Chelobasis bicolor* from Atlantic lowlands, C.R.

among hispine and host species, and even among populations of hispine species on the same host. Most species of *Arescus* and *Chelobasis* on *Heliconia* pupate near the ground beneath the petiole bases of the lowest, oldest leaves on the stalk. However, pupae of one *Chelobasis bicolor* population near Canas,

in Guanacaste Province, Costa Rica, were found in the dead inflorescences of *H. latispatha*; and on Trinidad and Tobago *Xenarescus monoceros* pupates high on the plant axis of *Heliconia bihai*, at the base of the erect inflorescence stalk. *Cephaloleia* sp. nov. pupates close to the ground in the concavity of petiole

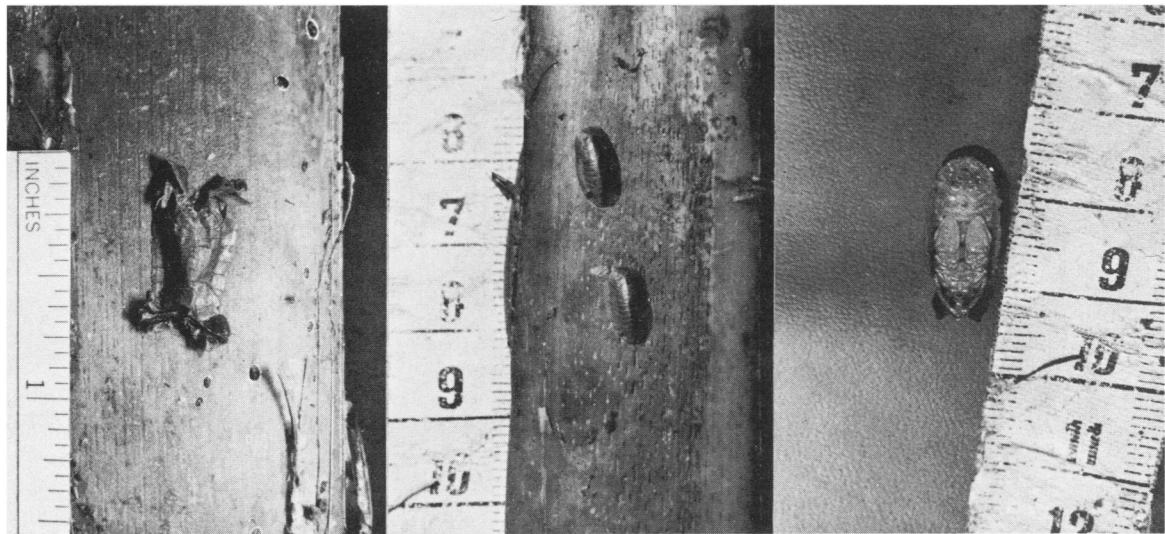


FIGURE 5. Left: Remains of pupal case of *Xenarescus monoceros* on stalk of *Heliconia bihai*, from Tobago, W.I., the adult having emerged less than an hour before this photo was taken. The anterior of the beetle was at the top. Cast pupal cases disintegrate with the first rain or mechanical damage following eclosion. Middle: Pupae of *Cephaloleia puncticollis* on stalk of *Heliconia latispatha* at Tilaran, Costa Rica. This hispine species lives only in the inflorescence of *Heliconia* species as a larva. The individuals shown moved almost a meter down the stalk before pupating. Anterior of the beetles is up, the scale is in cms. Right: Ventral view of pupa of *Xenarescus monoceros* from Trinidad. Note the anterior projections from the head and the eye spots. Anterior end is toward the bottom, the scale is in cms.

TABLE 2. Larval feeding area and oviposition sites of some rolled-leaf hispine species.

Host species	Species of rolled-leaf Hispinae	Plant part on which larvae feed and eggs are laid
<i>Calathea leucostachys</i>	<i>Cephaloleia</i> c.f. <i>ericsoni</i>	
<i>Calathea inocephala</i>	<i>C. ericsoni</i> Baly	
<i>Ischnosiphon</i> c.f. <i>cerotus</i>	<i>C. sp. nov.</i>	
<i>Heliconia tortuosa</i>	<i>Chelobasis bicolor</i> Gray	
<i>Costus laevis</i>		
<i>Heliconia latispatha</i>	<i>Cephaloleia histrionica</i> Baly	
<i>Heliconia pogonantha</i>	<i>Chelobasis perplexa</i> Baly	
<i>Renealmia strobilifera</i>	<i>Nympharescus separatus</i> Baly	Scroll of immature rolled leaf.
<i>Heliconia bihai</i>	<i>Cephaloleia sallaei</i> Baly	
	<i>Xenarescus monoceros</i> Ol.	
<i>Calathea warscewiczia</i>	<i>Cephaloleia</i> sp. nov.	
<i>Heliconia latispatha</i>	<i>C. puncticollis</i> Baly	Upon young bracts of inflorescence, exclusively.
<i>Heliconia imbricata</i>		
<i>Heliconia pogonantha</i>	<i>Cephaloleia consanguinea</i> Baly	Eggs laid both in rolled-leaf and on upper sur-
<i>Heliconia marea</i>	<i>C. ornatrix</i> Donck.	face of unrolled, mature leaf, beneath other
	<i>C. sp. nov.</i>	leaves that have fallen on top of the host plant
		leaf. Larvae feed on the wet surface of the
		mature host leaf, exclusively.

bases on *Ischnosiphon cerotus* populations throughout Middle America, as does *Cephaloleia championi* Baly on *Calathea inocephala* in Costa Rica. *Cephaloleia histrio* Baly pupates in the short internode several nodes down from the apical meristem of Costa Rican *Costus laevis* and *Costus malortearia*. In regions that are continually wet, with host plants growing year round, the pupal development is direct, without diapause.

In areas with long dry seasons like coastal Guanacaste Province in Costa Rica, the Northern Pacific regions of Panama, the Bayano region of Panama, the Chiriquí region of Panama, or parts of Trinidad and Tobago, host plants do not produce foliage year-round that is edible by rolled-leaf hispines. Where the dry season is severe, as in parts of Guanacaste Province or Chiriquí Province, host plants may even wither and die back to root stock. In these situations the pupae may diapause (Strong 1977). Diapausing pupae are hidden beneath overlapping petiole-base tissues on the stalk of the plant near ground level, and are often found together with live but very slow-moving adults. It is not clear whether these adults emerged from pupae subsequent to the beginning of the dry season or whether they are over-summering, having emerged during the previous wet season. Pupae collected during the dry season will eclose into live adults after storage in a moist atmosphere for several days.

The adult crawls out of the pupa from under the anterior edge, leaving a very fragile pupal case (fig. 5, left) which soon collapses. It is difficult to census eclosed pupal cases because the host tissue to which they are attached is often wet, and decomposition is so rapid that within hours even known pupal skins are unrecognizable against the brown host stalk. Immediately after eclosing, the teneral adult is soft with dull colors, for the vivid reds and yellows do not gain luster until several days after having emerged. Within several hours of emergence, the hardened adults fly to a rolled leaf and copulate immediately upon encountering a mate (fig. 4, lower right). Egg laying can follow eclosion by less than a week. Adults begin to feed from the rolled leaf within a day of eclosion.

Adults of all rolled-leaf hispine species spend much of their lives in rolled leaves, and feed from them (fig. 1), even adults of species whose eggs are laid in inflorescences. For example adult *Cephaloleia puncticollis* are common in inflorescences of *Heliconia imbricata* where they copulate, oviposit, and feed (fig. 2, middle right), but adults of these populations may also be found feeding in the rolled leaves of *H. imbricata*. As is true of other herbi-

vorous insects (Opler 1973) it is possible to distinguish the leaf damage of different rolled-leaf hispine species. The position on the leaf, width, length, and shape of the grazing mark are all useful in this regard. For example, *Cephaloleia* species generally feed near the edges of the leaf whereas Arescini tend to feed away from the edges (Strong 1977). Adult feeding of the larger species can penetrate the leaf, especially when the leaf is young and tender. Adults of smaller species and larval feeding do not penetrate the leaf (fig. 1, lower left). Rolled leaves of larger Zingiberales, such as species of *Heliconia*, (which are the largest Zingiberales) often contain feeding adults of several hispine species. The larger species of Marantaceae in the genera *Calathea* and *Ischnosiphon* can also contain more than one feeding species.

When the rolled leaf unfurls, adults leave in search of another. In the case of adult *Cephaloleia histrio* Baly and *C. suturalis* Baly (fig. 4, middle left) the search is short, for the host genus *Costus* simultaneously produces a series of leaves rolled inside of each other and the insect merely crawls around the edge of the outside unfurling leaf into the next one. However most Zingiberales extrude rolled leaves singly and sequentially from the axil, with a sufficiently long period between extrusion of rolled leaves that the adult must leave and fly to another rolled leaf on a different plant. Most flying is done at night. The dispersing rolled-leaf hispine flies to another host plant and after landing, pounds with its antennae and walks around the plant stalk; if no rolled leaf is encountered it flies to another plant. When a rolled leaf is found, it crawls up and into the scroll through the loosely rolled open edge. Persistent amplexus among male-female pairs is common (fig. 4), copulation being accomplished when the aedeagus circles down from the tip of the pygidium of the superior male into the oviducal aperture of the female. Several seconds elapse before disturbed males withdraw the aedeagus, and, as it is withdrawn, the final stages of the deflation and involution of the elaborate penis tip can be seen. Amplexus does not occur during flight.

HOST PLANT AFFINITIES

In my experience, all Middle American Zingiberales families support breeding populations of rolled-leaf Hispinae except the Musaceae (which are not native) and the Cannaceae. *Cephaloleia* occurs on all of the four attacked host families, and the four genera of Arescini are restricted to the monogeneric Heloniaceae (table 2).

Cephaloleia contains the only rolled-hispine spe-

cies that I have found with host affiliations outside the Zingiberales. Based on experience gained in over 300 days in Middle America working with rolled-leaf hispine since 1970, this apparently undescribed species is monophagous on *Cyclanthea bipartata* (Cyclanthaceae) in Costa Rica and Panama (fig. 4, middle right). Adults of this beetle live in the convoluted folds of immature leaves, eat the epidermis and oviposit on the petioles of immature leaves near ground level, where these petioles are soft and wet. The larvae feed on young petioles and sometimes upon the unfurled leaf. The Cyclanthaceae are so commonly found in the same habitat with Zingiberales in Middle America that one phytogeographer has named the association "Scitamineen-Ufergesellschaft" (Knapp 1965), Scitaminales being the old name for the Zingiberales (Tomlinson 1969). Species of these two orders characteristically occur together in the naturally disturbed areas of river and creek banks, within primary forest. It may be that the ecological proximity of the host species potentiated the evolutionary host plant shift onto *Cyclanthea bipartata*. Alternatively it is possible that I found this shift only because the hosts co-occur, and that other, as yet undiscovered, *Cephaloleia* have shifted to hosts unrelated and ecologically unassociated with Zingiberales.

Adults and larvae of rolled-leaf hispine species are generally associated with host species of a single Zingiberales family. For example, there are eight rolled-leaf hispine taxa associated with *Heliconia* at the La Selva field station of the Organization for Tropical Studies, near Puerto Viejo, Heredia Province, Costa Rica. Six of these are found as both adults and larvae only on *Heliconia* (*Nymphaescus separatus* Baly, *Chelobasis perplexa* Baly, *Chelobasis bicolor* Gray, *Cephaloleia puncticollis* Baly, *C. consanguinea* Baly, *C. ornatrix* Donck.). *Cephaloleia vicina* Baly, is found on *Heliconia* in the larval stage and usually in the adult stage too, but occasionally adults are found in and feed on the rolled leaves of several species of *Calathea* and in a species of *Ischnosiphon* (Marantaceae). The last species, *Cephaloleia nigripicta* Baly, is sometimes found feeding on species of Marantaceae both in the larval and adult stages at La Selva, but usually is associated with *Heliconia*.

Another example of species of rolled-leaf hispinae attacking hosts in more than one family involves *Cephaloleia lata* Baly. Since 1970 I have observed 45 different populations of *Calathea* (Marantaceae) from Mexico to Panama; in all cases the adults were feeding from rolled leaves and the larvae were feeding from immature petioles and rolled leaves. No

C. lata were ever found on any other host plant, yet in June and July of 1976, at Finca La Selva, Heredia Province, Costa Rica, I collected 73 *Cephaloleia lata* adults (but no larvae) from 113 rolled leaves of *Alpinnia coronarium* (Zingiberaceae). This ginger species is a common roadside weed in Middle America, having been introduced from Asia (H. Kennedy, pers. comm.). I have examined over 60 Middle American populations of *Alpinnia coronarium* for insects since 1970 and have found no other instance of it being attacked by rolled-leaf hispines.

The hispine species regularly attacking the greatest number of host species within families also tend to attack hosts in other Zingiberales families. *Cephaloleia nigripicta* and *C. vicina* have the most catholic host tastes of the heliconian hispine species, both within and between sites. At Finca La Selva, for example, three of the eight *Heliconia* hispine species attack only one host species (*Nymphaescus separatus* on *H. pogonantha*; *Cephaloleia consanguinea* on *H. imbricata*; *Cephaloleia ornatrix* on *H. pogonantha*), two of the eight attack host species (*Chelobasis perplexa* on *H. imbricata* and *H. latispatha*; *Chelobasis bicolor* on *H. crenulata* and *H. "17"* (Stiles 1975)), one of the eight attack five host species (*Cephaloleia puncticollis* on *H. imbricata*, *H. latispatha*, *H. crenulata*, *H. wagneriana*, and *H. "17"*); *Cephaloleia vicina* and *C. nigripicta* attack all of the heliconias at La Selva. *Cephaloleia lata*, that is described above attacking *Alpinnia coronarium* in the Zingiberaceae, attacks a larger proportion of *Calathea* species than any other Marantaceae hispine.

Rolled-leaf hispine species attacking the larger number of *Heliconia* species within sites tend also to have greater geographic ranges. *Cephaloleia vicina*, *C. nigripicta* and *C. puncticollis* occur from southern Mexico through the Darien of Panama into South America. *Chelobasis bicolor* is geographically similar but is restricted to wetter sites within that range (Strong, in press). *Nymphaescus separatus*, *Cephaloleia consanguinea* and *C. ornatrix*, occur only in the Atlantic lowlands of Costa Rica. Notice that there is no apparent correlation between breadth of utilization of host species and the tribe of rolled-leaf hispinae, for both tribes have monophagous and polyphagous species.

The general restriction of these hispine species to hosts within a single family of the Zingiberales is well shown by the fact that they virtually ignore bananas. Reports in the agricultural entomology literature of rolled-leaf hispines attacking this crop are scarce, sometimes inaccurate, and do not indicate that larvae, and therefore reproduction, occur on bananas. For example, *Cephaloleia "nigricornis"* (*C.*

puncticollis) has been recorded infrequently as a minor pest of bananas in Costa Rica, where it is sometimes found in the rolled leaves or, more importantly, scarring the skin of the fruit (Lara E. 1970). No larvae have been reported, nor have I ever found larvae on the many banana plants or fruits I have examined. Leaves infrequently show slight damage attributable to rolled-leaf hispines, and very rarely an individual of *Cephaloleia puncticollis* or *C. vicina* is in the rolled leaves. In my experience, larvae of *C. puncticollis* are restricted to *Heliconia* species with erect (as opposed to pendant) inflorescences, and the adults also frequent both inflorescences and rolled leaves of these *Heliconias*. *Cephaloleia puncticollis* does not usually associate with the rolled leaves or inflorescences of other Middle American Zingiberales families. It would be instructive to isolate the chemical attractant(s) of these hispines from bananas and investigate its (their) distribution among *Heliconia* species and plant parts.

Cephaloleia puncticollis has been collected from bananas several times through the years. For example tray 51 in the drawer "Hispinae; Amplipalpini, Cephaloliini (*Oediopalpa* to *Demotispa*) of the United States National Museum of Natural History, contains 40 specimens of *Cephaloleia puncticollis* which bear the remark "on bananas in Panama." In box 52, *C. puncticollis* from Guatemala in 1936 is recorded as "at light on banana ship." In box 61 of the same drawer, *Cephaloleia c.f. suturalis* Baly is recorded as *Cephaloleia semivittata* "on Musaceae" from Porto Bello, Panama, 1911. In my experience *C. suturalis* is a very specific parasite of *Costus* spp., so this last example, and one from Maulik (1937) reporting "*Chelobasis bicolor*" from "Banana (Platanillos Musaceae)" are probably in error. It is noteworthy that *Heliconias* were not taxonomically separated from the Old World Musaceae until more recently than these early papers and records (Hutchinson 1959), and that "platanillos" often refers to *Heliconia* in Middle American Spanish, as differentiated from "platanos" (bananas). In summary there are only a few recorded examples of rolled-leaf hispines attacking bananas in Middle America even though there has been over 50 years of intense entomological work (Simmonds 1959). These recorded examples do not describe serious pestiferous behavior, and they probably refer only to *Cephaloleia puncticollis*, adults of which are apparently attracted to the fruit. I have found no rolled-leaf hispine larvae on bananas, nor are there any known instances of rolled-leaf hispine reproduction on bananas.

SPECIES RICHNESS OF ROLLED-LEAF HISPINAE

In general, the number of species of plant-associated insects is a function of host species range (Strong 1974a, 1974b; Strong, McCoy and Rey 1977), host species size (Strong and Levin, in prep), and local abundance or density of the host plant (Root 1973, Cromartie 1975, Atsatt and O'Dowd 1976). These principles operate in the rolled-leaf hispine/Zingiberales system in Middle America. For example: 1) Zingiberales host species with greater ranges have more associated rolled-leaf hispine taxa. The hispines affiliated with *Heliconia latispatha*, the most widely distributed and locally abundant Middle American Zingiberales species, illustrate how this species/area effect works. Some of the rolled-leaf hispine taxa associated with this host species are restricted to a fraction of its range. In areas of comparable climate the number of these beetle species associated with *H. latispatha* is relatively constant, even though there is geographical replacement of species (Strong, in press). I suspect, based upon field work, that there is geographical replacement of rolled-leaf hispine species for all of the Zingiberales families, though it is not as obvious as in *Heliconia* because there are fewer species associated with these other families. Because of this geographical replacement and the general uniformity of hispine species richness among populations of the host species, broadly distributed Zingiberales have more associated hispine species than do narrowly restricted ones.

2) Zingiberales species with physically larger individuals tend to have more associated hispines than do species with physically smaller individuals. For example, the giant *Heliconia* species such as *H. mariae*, *H. imbricata*, or *H. pogonantha* can have up to five associated hispine taxa, while co-occurring smaller species like "H-3" (Stiles 1975), equally abundant in the immediate area, have only two. In the Marantaceae the same principle applies, but the smallest locally abundant species will often have no associated hispines. For example, the rolled leaves of *Calathea microcephala* are less than 30 mm long, even the smallest rolled-leaf hispine species (*Cephaloleia* sp. nov.) could not fit inside the scroll. The largest Marantaceae (eg. *Calathea lutea* and *C. similis* in Middle America) can have up to three associated rolled-leaf hispine species (*Cephaloleia championi* Baly, *C. erichsoni* Baly, and *C. lata* Baly). The few species associated with the Zingiberaceae and Costaceae render it difficult to see this principle operating in these families.

3) Zingiberales species with greater local abundance

or density tend to be attacked by more rolled-leaf hispine species; locally rare host species are attacked only by the host-generalist species of these beetles. The host-specific hispines (for example *Nymphaescus separatus*, *Chelobasis perplexa*, *C. bicolor*, *Cephaloleia consanguina* and *C. ornatrix*) are locally adapted to particular Zingiberales species within the families, and do not associate with others that may even be the primary host at another geographic location. Populations of *Chelobasis* are especially host specific in this way, and their associations with *Heliconia mariae* populations illustrate how local host plant abundance influences the probability of attack by rolled-leaf hispines. *Chelobasis bicolor* and *Chelobasis cf. perplexa* are associated with *H. mariae* at a few known localities over its range through Costa Rica and Panama. This *Heliconia* is found on the Atlantic coast in this region, or along rivers that empty into the Atlantic. There are breeding populations of *Chelobasis cf. perplexa* attacking *H. mariae* in the Pipeline Road area of the Canal Zone, and in the La Pina area just southwest of the Gatun locks of the Panama Canal. These are the only breeding populations on *H. mariae* I have found in Middle America, even though *H. mariae* occurs sympatrically with *Chelobasis* throughout this region. Interestingly, La Pina and Pipeline Road support the only dense, extensive populations of *H. mariae* with which I am familiar. There are populations of this host species at La Selva and Rio Frio (Heredia Province, Costa Rica), along the banks of the Rio Bayano, Rio Chepo in the Bayano region of Panama, and in the Limon area of Costa Rica (Limon Province), but these populations are much less dense than in the two Panama Canal populations referred to above. The Limon population of *H. mariae* is the only other in which *Chelobasis* adults regularly reside in and eat the rolled leaves, but there are no *Chelobasis* larvae on this host in the Limon area. The larvae, and most adults of *Chelobasis perplexa* and *Nymphaescus separatus* are found on the other, more abundant *Heliconia* species in the area. *H. mariae* is intermixed with these other *Heliconia* species, of which *H. imbricata* is the most abundant. At La Selva and Rio Frio in Costa Rica, and in the Panamanian Bayano, *Chelobasis* virtually ignores the relatively rare *H. mariae*. The La Selva situation is particularly interesting in this regard as the *H. mariae* population is intermixed with a large and very dense population of *Heliconia imbricata*. Leaves of individuals of these two host species touch, yet fewer than one in 20 leaves of *H. mariae* bear rolled-leaf hispine damage, and those that are eaten are damaged only lightly, not extensively as are the *H. imbricata* leaves. *Chelobasis perplexa* attacks *Heliconia imbricata*, but

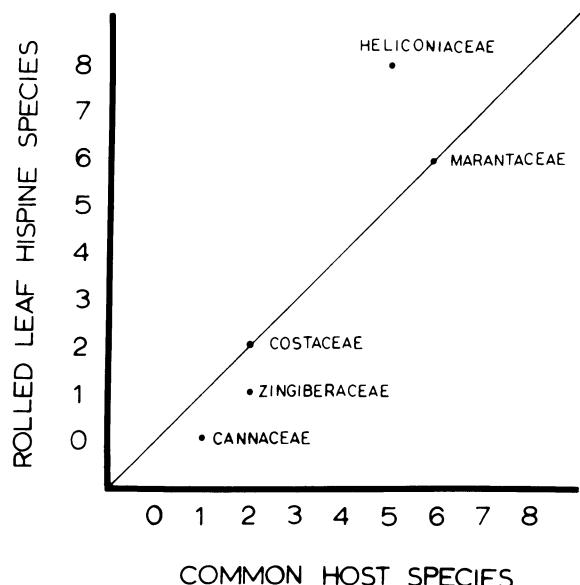


FIGURE 6. The number of rolled-leaf hispine species as a function of the number of common species in their host family, at Finca La Selva. These beetle species are usually restricted to a single Zingiberales family.

there are no rolled-leaf hispine larvae on the *H. mariae* plants. Adults of *C. perplexa* that are experimentally placed in rolled leaves of *H. mariae* soon leave and eat very little of the rolled leaf. Adults of this hispine species transplanted between *H. imbricata* rolled leaves as a control eat extensively from the leaf and remain for several days, as they would had they not been transplanted. This pattern is not peculiar. All locally rare Zingiberales are ignored by all but the most host-general rolled-leaf hispines.

There is an additional pattern of species-richness which occurs among the rolled-leaf hispines of the various Zingiberales families. On a local level, host families represented by a greater number of species are attacked by more species of these beetles. This situation is illustrated in fig. 6 from Finca La Selva in Costa Rica. Host species diversity of the families is given as the number of locally abundant, large species. For *Heliconia*, the common species at this site are *H. latispatha*, *H. imbricata*, *H. pogonantha*, *H. crenulata*, and *H. diffcilis* (Stiles 1975). The rare *Heliconias* at La Selva (*H. Wagneriana*, *H. mariae*, "H-17", and "H-16") have no unique hispine species, only the polyphagous *Cephaloleia vicina*, *C. puncticollis*, and *C. nigripicta*. These rare *Heliconias* are not necessary for the maintenance of the polyphagous hispine populations because the majority of the beetle individuals are on the common *Heliconia* species. If the rare *Heliconias* were removed from La Selva it is likely that the num-

ber of hispine species would not change. Only the larger Marantaceae species have associated hispines, and the common species at La Selva are *Calathea lutea*, *C. similis*, *C. inocephala*, *C. insignis*, *C. warscewicza*, *C. marantafolia*, and *Ischnosiphon c.f. cerotus* (Kennedy 1974). The common *Costus laevis* and *C. malorteanus* (Maas 1972) are both large. There are two common but unidentified species of Zingiberaceae at La Selva, one with basal inflorescences and one with the inflorescences at shoot tips. There is also one species of Cannaceae, *Canna lutea*. In fig. 6, the hypothetical relationship in which the number of hispine species is equal to the number of common, large hosts species in these families is indicated with a line (slope = 1). Because many of the beetle species attack more than one host species within a family, the points should not fall directly upon this line of slope = 1. In this regard, notice that the *Heliconiaceae* is above the line, the next two families, the Marantaceae and the Costaceae, are virtually on the line, and the last two are below. This implies that the host families with the greatest absolute number of hispine species also have the greatest number relative to the number of suitable and available host species. I interpret this pattern of hispine diversity among the host families to be the result of several factors. First, the average size of individuals in the Marantaceae is smaller than those in the Heliconiaceae, and the Costaceae and Zingi-

beraceae are smaller than the Marantaceae. I suspect that the size of the leaf is the important characteristic in this pattern; coexisting hispine species in these leaves always use the leaf in different ways (Strong, in press) and a larger leaf allows more subdivision. Second, I suspect that the hispine species-pool for these families in Middle America has the same rank-order as does the species richness on the families in fig. 6. My collections show this trend, and although they are not complete, it is reasonable to accept them as an indication of the relative richness of these insects. In summary, I would suspect that the families in the Zingiberales with fewer associated hispine species within sites also have fewer beetle species for the entire Middle American region, and that host species in these families are smaller, and less abundant within sites.

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On behalf of the officers, staff, and membership of the Association for Tropical Biology, I would like to acknowledge with gratitude the ATB members listed below who have, as of 1 June 1977, contributed sums in excess of their dues to the Publication Fund. These contributions serve to subsidize the reduced-dues rates in various parts of the world, a procedure which allows members in those areas to participate fully in the ATB. A portion of these funds are also used to distribute BIOTROPICA to a few libraries in tropical areas where economic restraints preclude access to the journal through regular subscription.

W. DONALD DUCKWORTH, *Executive Director, Washington, D.C.—1 June 1977*

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