where overburden is thick and decreases vertical effective stress where overburden is thin. These pressure and stress profiles are created solely by differential loading and variations in rock properties (such as permeability and bulk compressibility) and do not require any other mechanism to lower the permeability and increase overpressure (*39*, *40*). The model provides a simple mechanism for overpressure generation and slope failure in basins around the world by providing an explanation for high overpressures that begin at shallow depth on the middle and lower slope. These results revitalize the hypothesis that overpressure contributes to slope geomorphology (*30–32*). The lateral flow predicted describes how compaction-driven flow can contribute to the distribution, diversity, and size of cold seeps and the communities that thrive on the solutes in the seep fluids.

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Timing the Radiations of Leaf Beetles: Hispines on Gingers from Latest Cretaceous to Recent

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Stereotyped feeding damage attributable solely to rolled-leaf hispine beetles is documented on latest Cretaceous and early Eocene ginger leaves from North Dakota and Wyoming. Hispine beetles (6000 extant species) therefore evolved at least 20 million years earlier than suggested by insect body fossils, and their specialized associations with gingers and ginger relatives are ancient and phylogenetically conservative. The latest Cretaceous presence of these relatively derived members of the hyperdiverse leaf-beetle clade (Chrysomelidae, more than 38,000 species) implies that many of the adaptive radiations that account for the present diversity of leaf beetles occurred during the Late Cretaceous, contemporaneously with the ongoing rapid evolution of their angiosperm hosts.

Insects and flowering plants (angiosperms) comprise most terrestrial biodiversity, and their trophic associations are dominant features of terrestrial ecosystems (*1*). Diagnostic insect damage on fossil angiosperms is a primary source of data for understanding the evolution of these associations and can also provide information complementary to insect body fossils on the times of appearance of insect lineages (*2*). Such insect damage is known almost exclusively from dicots (*3*, *4*), although monocots comprise ~22% of living angiosperm species (*5*) and are hosts to diverse groups of herbivorous insects (*6*, *7*). Among the best studied associations between insects and monocots is the specialized feeding of rolled-leaf hispine beetles (family Chrysomelidae, subfamily Hispinae, tribes Cephaloleiini and Arescini) in the semi-

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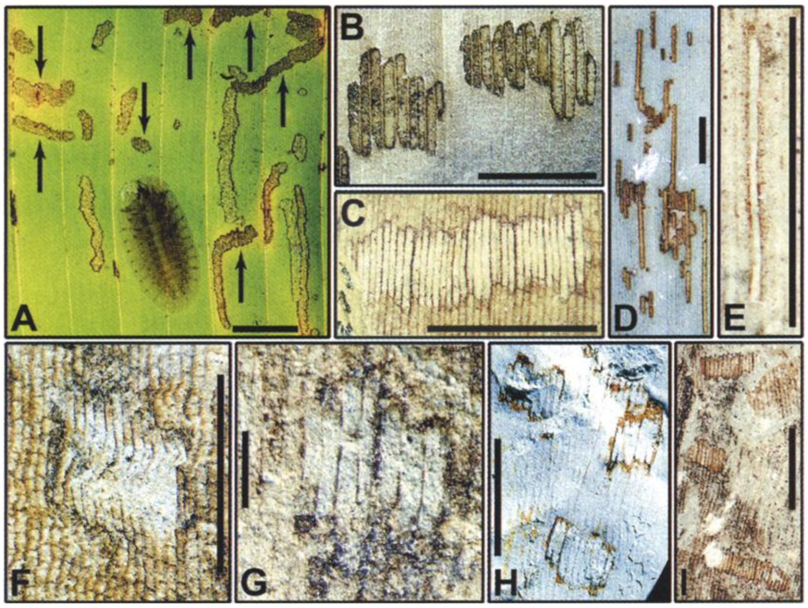

Fig. 1. Recent and fossil (*Cephaloleichnites strongi*) hispine damage on Zingiberales (*29*). (A) is live; (B) and (D) are pressed specimens from the U.S. National Herbarium; (C), (E), (H), and (I) are from the early Eocene; and (F) and (G) are from the latest Cretaceous (*28*, *29*). (**A**) *Chelobasis perplexa* Baly larva feeding on a leaf of *Heliconia curtispatha* Petersen (collected in Chiriquí Province, Panama). The arrows indicate damage trails with irregular margins that are deployed perpendicular to leaf venation. (**B**) Hispine damage of the type noted by the arrows in (A) on *Heliconia vaginalis* Bentham [U.S. National Herbarium (US) 3134380, collected in Costa Rica]. (**C**) *C. strongi* (holotype) on *Zingiberopsis isonervosa* Hickey (USNM 498174). (**D**) Hispine damage on *Renealmia cernua* (Swartz) Macbride (Zingiberaceae), a close relative of *Zingiberopsis* (Fig. 3) (US 1153643, collected in Panama). Extended linear slot feeding is visible. (**E**) *C. strongi*, single slot of the type shown in (D) (USNM 498168). (**F** and **G**) *C. strongi* on *Z. attenuata* Hickey and Peterson [DMNH 19957, (F); DMNH 19959, (G)]. (**H** and **I**) *C. strongi* on *Z. isonervosa* [USNM 509718, (H); USNM 498169, (I)]. Scale bars in all panels equal 5 mm, except in (G), where the scale bar is 1 mm.

aquatic shaded habitat provided by the rolled juvenile leaves of gingers, heliconias, and their relatives (order Zingiberales) in understories of Neotropical forests (Fig. 1) (*8–13*). The feeding marks of larval rolled-leaf hispines are stereotyped (*9*) (Fig. 1) and remain intact on the mature unrolled leaves, increasing their potential for fossilization.

The family Chrysomelidae, or "leaf beetles," has ~38,000 described species (*14*) and a possible total diversity of >60,000 species (*15*). Most extant leaf beetles consume angiosperms, indicating a series of adaptive beetle radiations (*7*). The subfamily Hispinae (~6000 species) (*7*, *13*, *15–17*) is considered to be among the more derived and specialized groups within the Chrysomelidae (*6*, *7*). The Hispinae and its putative sister group (~5000 species) (Fig. 2) comprise a clade that includes most extant species of monocot-feeding beetles (*18*).

The body-fossil record of leaf beetles is virtually nonexistent during the Late Cretaceous (*7*, *19*), the time interval known for rapid evolution and diversification of angiosperms (*20*), and the record of most angiosperm-feeding Chrysomelidae is confined to the Cenozoic (*7*). The first appearance of Hispinae, in particular, is in the middle Eocene, and the rolled-leaf hispines have no fossil record (Fig. 2). This lack of temporal resolution limits understanding of the timing of chrysomelid radiations in relation to the evolution of angiosperm host plants, whose Cretaceous fossil records are far more complete than those of leaf beetles (*5*, *21*, *22*).

Here, we report diagnostic feeding patterns, of the type documented for larvae of living rolled-leaf hispines in Central America (*9*), on 11 specimens of latest Cretaceous and early Eocene *Zingiberopsis* (Fig. 1). This well-described leaf genus, a fossil member of the ginger family (Zingiberaceae), is known from Late Cretaceous through earliest Oligocene strata of North America and from the early Late Cretaceous of Germany (*23–26*). The nearest living relative of *Zingiberopsis* is considered to be the Asian genus *Alpinia* (*24*) (Fig. 3). Of the 11 insect-damaged specimens studied, 7 were *Z. isonervosa* from the early Eocene Wasatch Formation, Great Divide Basin, southwestern Wyoming (*26–28*). The remainder were three specimens of *Z. attenuata*, from the latest Cretaceous Hell Creek Formation, and a single specimen of *Z. isonervosa* from the early Eocene Camels Butte Member of the Golden Valley Formation; all four specimens are from the Williston Basin, southwestern North Dakota (*28*). The damage consists of individual (Fig. 1E) or sequential (Fig. 1, C and F through I) linear feeding strips that are bounded by reaction tissue and have asymmetrically rounded termini, as described in detail below (*29*). We propose the ichnotaxon *Cephaloleichnites strongi*, gen. et sp. nov., for the fossil insect damage (*29*).

The best fit of current phylogenetic data to the fossils suggests a basal member of a derived group, the Hispinae, feeding on a derived monocot host (Figs. 2 and 3). An adaptive trajectory within the phylogeny of Hispinae and their close relatives is depicted in Fig. 2, which starts on aquatic and semiaquatic dicots and then shifts to monocot host plants (stages 1 to 4 in Fig. 2) (*18*). *C. strongi* documents the extension of the semiaquatic life-style inland to the wet rolled-leaf habitat of Zingiberales (stage 5 in Fig. 2). Host shifts by higher hispine taxa occurred on terrestrial monocots and, for the "cassidoid" group, on dicots (stages 6 to 8 in Fig. 2).

The present-day occurrence of rolled-leaf hispines on six of the eight families of Zingiberales (*13*) raises the question of the order of colonization within Zingiberales. Plant chemistry is thought to be a primary constraint and selective force on the host shifts of Chrysomelidae and other herbivorous beetles (*30*). The Zingiberaceae as a group possess well-developed phytochemistry, and several compounds with potentially defensive uses have been extracted from *Alpinia* leaves in particular, including tannins, phenols, alkaloids, and diverse terpenes (*31*). In contrast, leaves of *Heliconia*, a relatively basal member of the Zingiberales (Fig. 3) that is host to a high diversity of rolled-leaf hispines (*8*), are notably lacking in defensive compounds, and experimental data show negligible effects of *Heliconia* chemistry on the larval development of rolled-leaf hispines (*11*). Correspondingly, we have also observed, in herbarium collections, a relatively low frequency and intensity of hispine damage on Zingiberaceae in comparison to *Heliconia*. The preceding evidence suggests an initial colonization of basal, chemically "simple" Zingiberales, which led to the diverse associations with living *Heliconia*, followed by adaptive radiations of specialized hispines on the Zingiberaceae by the Maastrichtian or earlier.

C. strongi predates the body-fossil record of Hispinae by ~20 million years, documenting the Cretaceous origins of the group (Fig. 2). As the fossil records of many living lineages of monocots begin in the Campanian and Maastrichtian (*5*), our data demonstrate the presence and trophic activity of derived, specialized, monocot-feeding beetles near the time of the first appearances of present-day host groups. In addition, the recent discovery of a fossil sagrine beetle (*19*) indicates the presence of the sister group to the hispines by

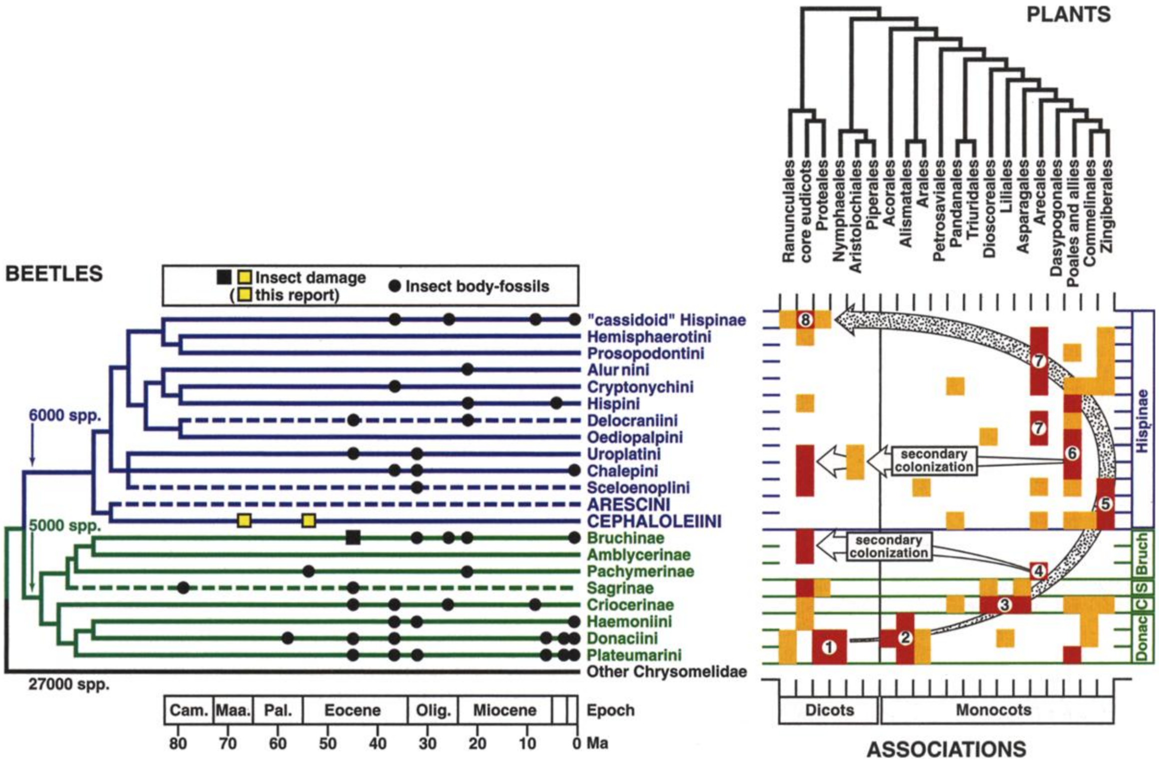

Fig. 2. Hypothesized evolutionary colonization of angiosperms by hispine beetles and their immediate ancestors, with the corresponding fossil record of beetles and their feeding damage (*19*, *36*). At the left is a phylogeny of hispine tribes (blue) (*13*) and subfamilies and tribes of its putative sister group (green) (*37*), with an empty branch representing all other Chrysomelidae; dashed lines indicate groups without published phylogenies, inserted on the basis of morphological evidence (*38*). Approximate numbers of described species (spp.) are indicated for these three branches, using (*14*) for the total of 38,000 and (*7*) for the blue and green clades. The two tribes of rolled-leaf hispines are in capital letters. Relevant body fossils of insects are almost entirely confined to Cenozoic Lagerstätten. At the top right is a cladogram of all major monocot lineages and several representative clades of basal dicots, which is a compromise topology among recently hypothesized evolutionary relationships based on both molecular and morphological characters (*39*–*41*). The lower right indicates dominant (red squares) and subdominant (orange squares) plant hosts for chrysomelid clades at the left (*6*, *42*–*44*); numbered red clusters represent inferred major colonization stages. The matrix reflects larval herbivory, almost all of which is deployed as external feeding or leaf mining. The overall trajectory of primitive aquatic dicot to advanced monocot to core eudicot host colonization is indicated by the stippled arrow; secondary colonizations of core eudicots (*43*), as supported by beetle phylogenies, are designated by smaller arrows (*6*, *45*). The colonization of core eudicots by "cassidoid" hispines is primary (*43*, *44*). The actual history of colonization is undoubtedly more complex than depicted, and the time scale refers only to fossil occurrences, not to branching events. The blank sections of the time scale are "Pliocene" and "Pleistocene," from left to right. Cam. = Campanian; Maa. = Maastrichtian; Pal. = Paleocene; Olig. = Oligocene; Donac = Donaciinae; C = Criocerinae; S = Sagrinae; Bruch = bruchoid complex.

the Campanian (Fig. 2). Taken together, the Cretaceous hispine and sagrine occurrences indicate a high likelihood that many other clades of leaf beetles evolved well before the terminal Cretaceous.

Angiosperm diversity exceeded that of other groups of land plants by the early Late Cretaceous (*20*). The rapid evolution of angiosperms continued throughout the Late Cretaceous (*22*), and 44% of extant angiosperm orders have Cretaceous fossil records, including most living lineages (*21*). Thus, Cretaceous radiations of leaf beetles occurred during an extended interval of evolutionary innovation for angiosperms, suggesting the possibilities of plant-beetle coevolution or of adaptive beetle radiations that closely followed the diversification of angiosperms. Supporting the latter hypothesis is Farrell's contrast of the diversities of sister groups of gymnosperm- and angiosperm-feeding beetles (*7*), leading to his estimate that radiations of beetles on angiosperms were responsible for the evolution of ~100,000 living beetle species.

Rolled-leaf Hispinae and Zingiberales have maintained a stereotyped, highly specialized plant-animal interaction in the New World for >66 million years, surviving the mass extinctions of plants at the end of the Cretaceous (*32*) and profound climate changes throughout the Cenozoic (*33*). This longevity supports findings of high phylogenetic conservatism for host associations in living Chrysomelidae (*34*) and in the exploitation of ecological niches over evolutionary time (*35*). Finally, the exclusively subtropical and tropical distribution of the extant interaction provides further evidence for warm climates in the Western Interior of North America during the Late Cretaceous and early Eocene (*23*, *26*, *32*).

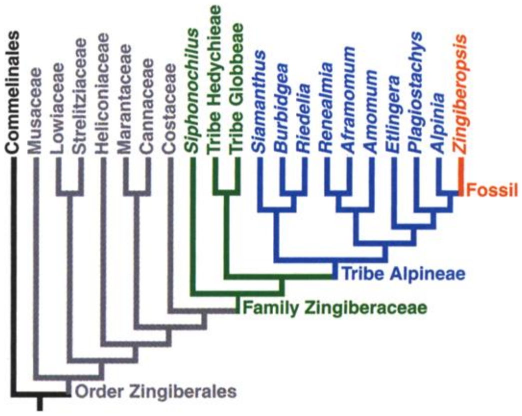

Fig. 3. The phylogenetic relationships of the families of the order Zingiberales and the major clades of the family Zingiberaceae, with a hypothesized placement for the fossil ginger *Zingiberopsis*. Commelinales is used as the outgroup. The cladogram of living taxa is derived from parsimony analyses of morphological and molecular (*rbcL*, *atpB*, *matK*, 18S RNA, and internal transcribed spacer regions) characters (*39*, *46*). *Zingiberopsis* is inserted as a sister to its living relative with the greatest morphological similarity, *Alpinia* (*23*, *24*).

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29. **Genus:** *Cephaloleichnites*, gen. nov., subfamily Hispinae. **Genotypical species:** *Cephaloleichnites strongi*, sp. nov. **Generic diagnosis:** The genus pertains to fossil traces of insect feeding consisting of linear strips, each confined entirely within the space between adjacent parallel veins such that leaf-tissue strata between parallel veins are removed and only the upper epidermis typically remains (Fig. 1). Strips are bordered by dark reaction tissue of the host plant. Terminations of strips are usually asymmetrically rounded. The average strip length is 2.1 mm ($\sigma = 0.83$ mm, minimum = 0.81 mm, maximum = 6.3 mm, $n = 279$). Eocene strip lengths are shorter (mean of 1.9 mm for the Wasatch Formation, $n = 209$; mean of 2.0 mm for the Golden Valley Formation, $n = 42$) than those from the Cretaceous (mean of 3.5 mm, $n = 28$). Strips are occasionally single (Fig. 1E), nearly always consecutive, and characterized by series of strips occupying adjacent pairs of parallel veins so as to form a continuous and en échelon damage field. Single strips and consecutive strips can co-occur on a single specimen (USNM 498168), as they do on modern examples (Fig. 1D). The series of end points of consecutive strips is very roughly linear, resulting in an overall squarish or otherwise quadrilateral feeding feature that has a ragged irregular margin. The angle of the feature's margin to the parallel veins of the host plant is typically perpendicular but can be angled up to 30° from perpendicular. The maximum number of consecutive strips found is 34, on the holotype. **Species diagnosis:** Diagnosis is the same as that for the genus, because of monotypy. **Repository:** All type and referred material is housed in the paleobotanical type collections of the USNM (National Museum of Natural History, Smithsonian Institution) and the DMNH. **Holotype:** USNM 498174 (Fig. 1C). **Type locality:** USNM loc. 41352. **Referred material:** DMNH 19957, 19959, and 19960 (DMNH loc. 2092); USNM 498168 (USNM loc. 41362), 498169 through 498173 (USNM loc. 41352), and 509718 (USNM loc. 14048). **Etymology:** *Cephaloleia* Chevrolat is the only extant genus of rolled-leaf Hispinae known to feed on Zingiberaceae today (*9*), although both rolled-leaf tribes, the Cephaloleiini and the Arescini, generate similar leaf damage on other Zingiberales [*ichnos*: trail, track (Greek); *strongi*: named for D. R. Strong Jr., for his seminal papers on the modern analog association]. **Discussion:** The fossil and modern damage are equivalent, and only the rolled-leaf hispines are known to produce the relevant damage patterns on living Zingiberales. *Cephaloleichnites* indicates a probable tribal affinity but not a formal tribal classification. *C. strongi* in all probability spatiotemporally represents more than one larval beetle species. Feeding is accomplished by "scraping the ventrally-directed, scoop-shaped, toothed mouthparts reciprocally across the plant surface" (*9*, p. 158). Adult hispines leave similar damage on the same hosts as larvae, but the margin of the damage field typically is more smooth (*9*). The fossil damage was first noted in table 1 of (*27*, p. 2154) as "strip-feeding between secondary veins (*Zingiberopsis*)." This ichnotaxonomic description is provided for by W. D. L. Ride and others [W. D. L. Ride *et al.*, Eds., *International Code of Zoological Nomenclature* (International Trust for Zoological Nomenclature, London, ed. 4, 1999), article 1.2.1].
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37. The phylogeny is based on (*7*) for subfamilial relationships and on (*17*) and work by I. S. Askevold [*Can. J. Zool.* **68**, 2135 (1990)] for hispine and donaciine tribal groupings, respectively. Resolution of subfamilial relationships is based on morphological and molecular data, donaciine relationships are based on morphological data only, and hispine relationships are based on molecular data only.
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