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Chewed Leaves Reveal Ancient Relationship

God, the great British geneticist J. B. S. Haldane once remarked, must have “an inordinate fondness for beetles.” And certain beetles have an inordinate and, it turns out, historic fondness for ginger plants. Paleontologists have discovered how ancient this culinary preference really is by studying fossils of damaged leaves. The data help push back the time when a group of beetles called leaf beetles evolved their great diversity and demonstrate just how faithful some species can be to their favorite foods. The results are also convincing paleobotanists that they can sometimes glean more about their plant’s ancient past from a chewed-up leaf fossil than from a pristine one.

On page 291, paleobotanist Peter Wilf of the University of Michigan, Ann Arbor, Conrad Labandeira, a paleobiologist at the Smithsonian Institution’s National Museum of Natural History in Washington, D.C., and their colleagues describe a new beetle fossil based not on traces of the insect skeleton—in fact, the insect itself never even shows up in the fossil record—but on the distinctive gouges the beetles left when they munched on 11 ginger leaves many millions of years ago. The chew marks of the newly described *Cephaloleichnites strongi* prove that leaf beetles underwent rapid evolution and diversification more than 65 million years ago—far earlier than the oldest fossils of insect bodies suggest—possibly taking advantage of (and perhaps influencing) the rapid diversification among flowering plants occurring at the same time.

What’s more, *C. strongi* represents the earliest known rolled-leaf beetle species, hundreds of which today still are picky eaters, preferring just one of the ginger- and heliconia-like plants in the Zingiberales order. For decades, ecology students have learned about this impressive array of beetle-plant pairings, in which different rolled-leaf species adopt the same lifestyle but on their own distinct host plant. This new work adds “a historical dimension to this emblem of tropical biology,” says Brian D. Farrell, an insect evolutionist at Harvard University. Adds Phyllis Coley, a tropical ecologist at the University of Utah, Salt Lake City: “The beetles and the gingers are an extremely old and conservative pairing, which in turn suggests that each could have had profound selective effects on the other.”

As a young ecologist in the 1970s, Donald Strong—the fossil’s namesake—could not help but notice the vast variety of rolled-leaf beetles, whose larvae take up residence inside the young, curled leaves of gingers,

heliconias, and their relatives, plants that thrive in the understories of tropical forests of the Western Hemisphere. In particular, he was enchanted by what the beetles did to the leaf itself. Their damage becomes quite apparent as the leaf unfurls and serves as a lasting reminder of a beetle long gone. “It was an issue of artistry, how beautiful the damage was,” recalls Strong, now at the



Telltale jaws. From the characteristic chew marks left on fossilized leaves, researchers have identified an ancient beetle and its favorite food. Rolled-leaf beetles today still munch on ginger plants, as shown by the characteristic damage on this leaf from Panama.

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Over the next few decades, Strong documented the specialized associations among different beetles and particular plant species. Eventually, he learned to identify a beetle species from the leaf’s chew marks, which varied according to the size and shape of the particular beetle’s jaws.

Wilf came across Strong’s research in 1998, when he and Labandeira were studying a different sort of insect damage—tiny fossil pellets, mysterious specks of fossilized material found on 53-million-year-old fossil leaves he had collected from Wyoming. Until that time, Wilf hadn’t really noticed the chew marks. But when he and Labandeira took a second look at the leaves, “we realized the damage [seen by Strong in the modern leaves] matched beautifully with what we had,” Labandeira recalls. Moreover, the fossil leaves looked very much like some modern gingers. Even after millions of years, says Wilf, “[the beetles] are eating the same thing, and they are doing it the same way.”

Soon Labandeira found even older leaves bearing the telltale signs of the rolled-leaf beetle. While working with Kirk Johnson at the Denver Museum of Natural History, Labandeira noticed that some of Johnson’s fossils, whose identity he didn’t yet know, also had chew marks resembling *C. strongi*’s. And they, too, turned out to be fossil gingers. Because these fossils came from a North Dakota deposit dating back to the Late Cretaceous, “we now know this insect

is 20 million years older than if we just looked at body fossils,” Wilf points out.

These findings lend support to a theory proposed by Farrell in 1998. Farrell suggested that most plant-eating beetles likely evolved in parallel to flowering plants and therefore were quite diverse during the dinosaur’s heyday (*Science*, 24 July 1998, p. 555). But until now, there has been little supporting fossil evidence, as only one relevant beetle fossil exists from that time. Now researchers may be able to get around this lack of fossils by looking at insect damage instead, says Leo Hickey, a paleobotanist at Yale University: “The work shows the potential of an overlooked resource in [studying] the evolution of insects.” Inspired by this new work, Hickey expects that he and his botanical colleagues will be giving their plant fossils a second look for signs of insect activity. Coley agrees, noting that “it seems that the use of fossil damage patterns to infer ecological and evolutionary relationships is quite powerful.”

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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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13. Eq. 3 is derived in material coordinates and tracks the solid grains during burial.
14. For sediments that are unloading or reloading, the bulk compressibility is assumed to be $0.44 \times 10^{-3} \text{ MPa}^{-1}$.
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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 fea-

tures 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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aquatic shaded habitat provided by the rolled juvenile leaves of ginger, heliconias, and their relatives (order Zingiberales) in understories of Neotropical forests (Fig. 1) (8–13). The feeding marks of larval rolled-leaf hispinas 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 hispinas 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 hispinas 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

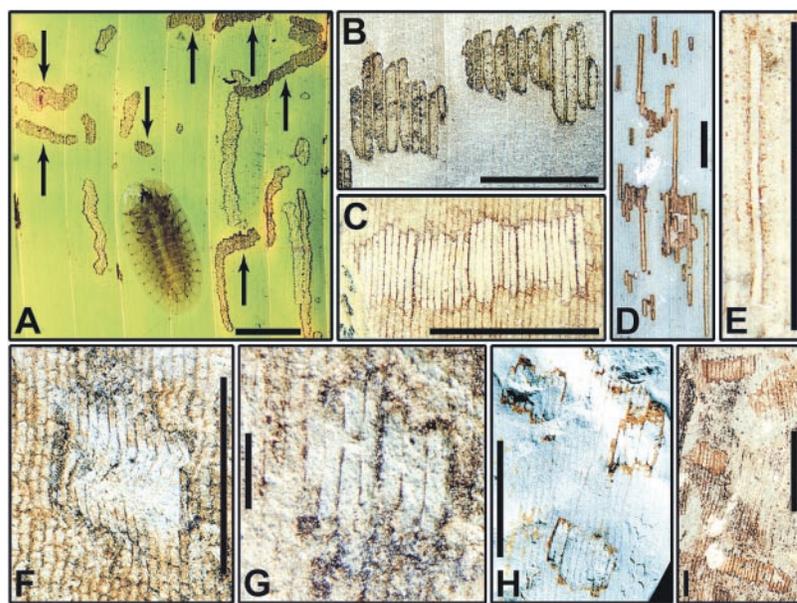


Fig. 1. Recent and fossil (*Cephaloleichnites strongi*) hispine damage on Zingiberales (29). (A) is live; (B) and (D) are pressed specimens from the U.S. National Herbarium; (C), (E), (H), and (I) are from the early Eocene; and (F) and (G) are from the latest Cretaceous (28, 29). (A) *Chelobasis perplexa* 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* Benthham [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.

sp. nov., for the fossil insect damage (29).

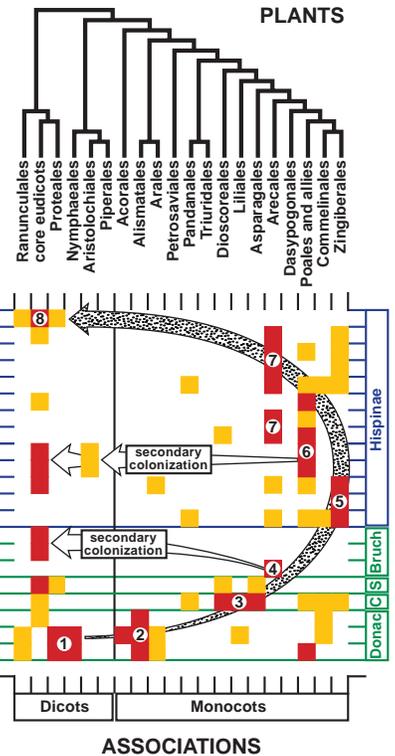
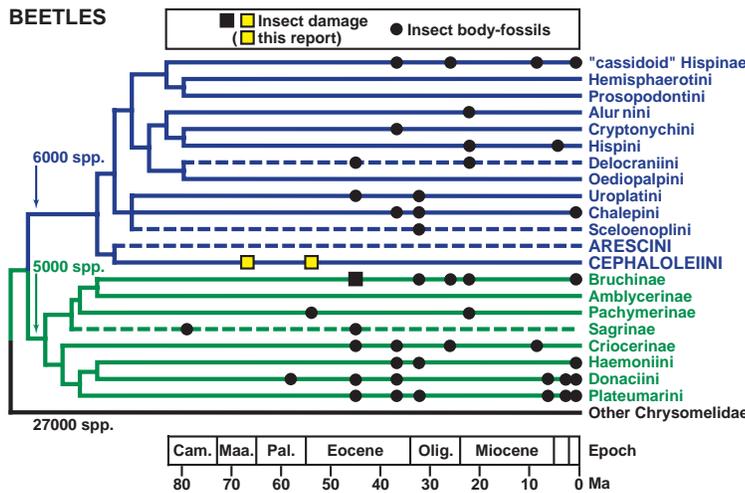
The best fit of current phylogenetic data to the fossils suggests a basal member of a derived group, the Hispinae, feeding on a derived monocot host (Figs. 2 and 3). An adaptive trajectory within the phylogeny of Hispinae and their close relatives is depicted in Fig. 2, which starts on aquatic and semiaquatic 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 hispinas 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 hispinas (8), are notably lacking in defensive compounds, and experimental data show negligible effects of *Heliconia* chemistry on the larval development of rolled-leaf hispinas (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 hispinas 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 hispinas 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 (39–47). 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

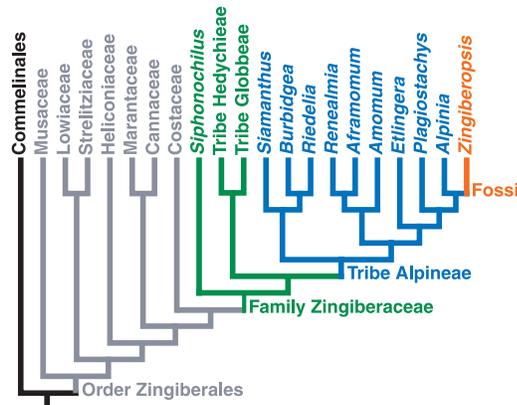


monocot to core eudicot host colonization is indicated by the stippled arrow; secondary colonizations of core eudicots (43), as supported by beetle phylogenies, are designated by smaller arrows (6, 45). The colonization of core eudicots by "cassidoid" hispines is primary (43, 44). The actual history 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 = Sagrainae; Bruch = bruchoid complex.

the Campanian (Fig. 2). Taken together, the Cretaceous hispine and sagraine 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 co-evolution 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 rRNA, 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 hispinines 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 hispinines 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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