A Carboniferous insect gall: Insight into early ecologic history of the Holometabola

(Pennsylvanian/Marattiales/*Psaronius*/herbivory/plant–insect interaction)

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ABSTRACT   Although the prevalence or even occurrence of insect herbivory during the Late Carboniferous (Pennsylvanian) has been questioned, we present the earliest-known ecologic evidence showing that by Late Pennsylvanian times (302 million years ago) a larva of the Holometabola was galling the internal tissue of *Psaronius* tree-fern fronds. Several diagnostic cellular and histological features of these petiole galls have been preserved in exquisite detail, including an excavated axial lumen filled with fecal pellets and comminuted frass, plant-produced response tissue surrounding the lumen, and specificity by the larval herbivore for a particular host species and tissue type. Whereas most suggestions overwhelmingly support the evolution of such intimate and reciprocal plant–insect interactions 175 million years later, we provide documentation that before the demise of Pennsylvanian age coal-swamp forests, a highly stereotyped life cycle was already established between an insect that was consuming internal plant tissue and a vascular plant host responding to that herbivory. This and related discoveries of insect herbivore consumption of *Psaronius* tissues indicate that modern-style herbivores were established in Late Pennsylvanian coal-swamp forests.

Holometabolous insects are the most diverse group of organisms and currently constitute 90% of all insect species. As a clade, the Holometabola is defined by the synapomorphy of a structurally and ecologically differentiated larva separated from the adult by a distinctive pupal stage (1), a condition known as complete metamorphosis. Primitive Holometabola are known from Early Permian body-fossils of ≈280 million years ago (Ma) that include the immediate stem groups of the Mecoptera, Neuroptera, and Coleoptera (see Table 1). While this early occurrence has been known for 70 years (2), little evidence has been available to address the life habits of the earliest known members of these clades. Virtually all autecological inferences regarding early Holometabola are uniformitarian projections into the Late Carboniferous of behaviors from plesiomorphic clades within modern insect orders (3, 4)

Our evidence for the earliest known insect gall and holometabolan insect consists of anatomically and three dimensionally preserved structures occurring in tree-fern petioles (5) of Late Carboniferous age (Pennsylvanian Subperiod). Insect gallers are geographically and ecologically diverse in the modern world and arose independently in numerous lineages within two hemipteroid and four holometabolous orders (6). Although galls have an under-appreciated fossil record (6, 7) and many examples are known from the Late Cretaceous and Cenozoic (7), three convincing occurrences have been recorded prior to the mid-Cretaceous ecological expansion of angiosperms (7). Whereas the fossil gall record extends this endophagous life habit into the Permian (7, 8), nothing is

known of the histological details of these galls, their structural comparisons to modern galls, or the identity of their culprits.

Geochronological Context and Techniques of Preparation

From 28 known occurrences of galled tree-fern petioles from the Upper Pennsylvanian Mattoon Formation of the Illinois Basin (unpublished data), 7 undistorted specimens have been intensively studied. These galls originate from the Calhoun and Berryville localities of the Calhoun coal-ball flora of east-central Illinois (10), and are ≈302 million years old (Ma), corresponding to the early Kasimovian Epoch of the Late Pennsylvanian, approximately equivalent to the Stephanian A of former European terminology (11). The Calhoun coal-ball flora is dominated by marattialean tree-ferns with subordinate arborescent components of medullosan seed-ferns, sigillarian lycopods, and calamitalean sphenopsids (10). The peat deposit was buried in a carbonate-rich environment marginal to an epicontinental sea, when Euramerica lay astride the Late Pennsylvanian equator (12). Although subsequent and rapid carbonate permineralization of plant tissues resulted in preservation of anatomically exceptional cellular detail, this preservational mode did not extend to the fauna. Nevertheless, widespread plant tissue damage and compositionally identifiable fecal pellets embedded in plant litter provide evidence for diverse arthropod-mediated interactions with vascular plants (5, 13, 14).

Preparation of plant tissues permineralized as coal balls involved initial sawing of coal balls into slabs, followed by grinding of the slab surface, acid etching in hydrochloric acid, and finally application of cellulose acetate peels to the etched surface (15). Permineralized coal balls were initially cut into 3- to 5-cm-thick slabs by a diamond-edged saw and then washed in detergent to remove excess cutting oil. The surface of each cleaned slab containing tree fern and other plant tissues of interest then was smoothed by 500 grit silicon carbide powder on a glass plate and then washed. After acid etching in 5% hydrochloric acid for 13 sec, the slab surface was again air-dried, followed by applying a cellulose acetate sheet onto the slab surface. This was done by flooding the surface with acetone, followed by immediate rolling of a sheet of cellulose acetate onto the surface prior to evaporation of the acetone. After several hours to one day the peel was removed. Glass microscopic slides (52 × 76 mm) were made by embedding a relevant region of the acetate peel, smooth-side-up, in Canada balsam.

Results

The fossil galls are swollen parenchymatous abnormalities known only from the basal petioles (the form-genus *Stipitopteris*) that support and supply the broad, tripinnate fronds of the marattialean tree-fern *Psaronius chasei* Morgan (Fig. 1a)

Abbreviation: Ma, million years ago.
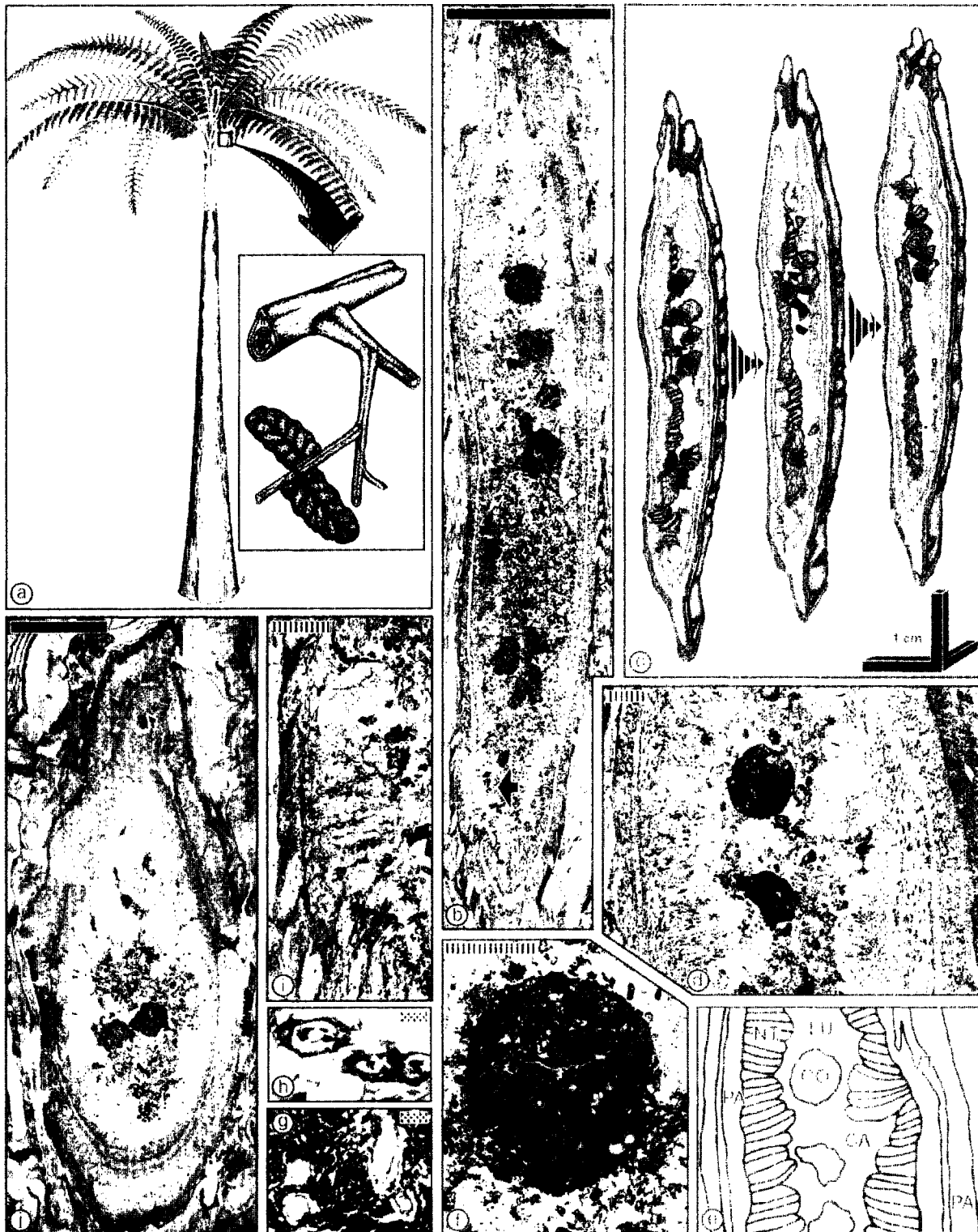[‡]To whom reprint requests should be addressed.

FIG. 1.   Host and structure of a Late Pennsylvanian gall from the Illinois Basin. (*a*) *Psaronius* tree fern (16), ≈7 m tall and host for the earliest known plant gall, with detail of a galled *Stipitopteris* petiole in *Inset* (after ref. 16). Specimen UIUC 31272-Bbot, slice 4, is represented in *b–i*. (*b*) Galled *Stipitopteris* specimen displayed in slightly oblique view, with plugged exit hole (arrow). (*c*) Reconstruction of specimen in *b*, calibrated by every fifth acetate peel of 75 successive peels; each slice in the figure represents 25 peels. (*d*) Detail of upper third region in *b* and *c*. (*e*) Anatomical interpretation of *d*: ca, catachord or undigested frass; co, coprolite; lu, gall lumen; nt, nutritive tissue; pa, unmodified parenchyma; vt, vascular tissue. (*f*) Detail of coprolite in *b–e*, showing gum-sac cells. (*g*) Detail of gum-sac cells in *f*. (*h*) Gum-sac cells in unmodified parenchyma. (*i*) Close-up of exit hole in *b*, plugged by nutritive tissue. (*j*) Specimen UIUC 8227-Bbot, slice 167. All specimens, including coal balls, acetate peels, and microscope slides are deposited in the Department of Plant Biology in the University of Illinois at Urbana-Champaign. [Solid scale bar = 1 cm; dashed scale bar = 1 mm; stippled bar = 0.1 mm (=100 μm).]

(16, 17). Galled *Stipitopteris* petioles range from 1.8 × 3.6 cm to 2.6 × 4.9 cm (Fig. 1 *b* and *j*) in maximal cross-sectional width

versus height, and extend to 24 cm long in one specimen. These galls possess a central lumen of excavated ground tissue

replaced by frass and are surrounded by nutritive tissue produced as a response by the host plant to endophagous herbivory (Fig. 1 b–e and j). Central lumen frass consists of wedge- or lens-shaped fragments of undigested ground tissue distributed among scattered but distinctive fecal pellets and empty regions that were postdepositionally replaced by calcite (Fig. 1 b, d, and j). These fecal pellets are cylindrical, about 1.5 times longer than wide, lack external surface features, and have jagged ends characterized by brittle fracture (Fig. 1 b–f and j). Each fecal pellet contains a distinctive, dark matrix of mostly collapsed cells interspersed among gum-sac cells (13) identical to those found in adjacent Stipitopteris ground tissue (Fig. 1 g and h). The lumens of most rhachises contain a few intact, cylindrical pellets, and many pellet fragments. A frequency distribution of those coprolite diameters with circular cross-sections, pooled from all measurable specimens (Fig. 2), demonstrates four distinct modes that probably represent four larval instars. Each mode is separated by an average factor of 1.33 (range = 1.47–1.23; $n = 102$). This value is consistent with intraspecific size increases in insect instars, codified as Przibram's Rule, and borne out in fecal pellet widths of modern beetle and moth species (18–20).

Encircling the lumen are adaxially oriented, bulbous tufts of nutritive tissue, each impinging on neighboring tufts to form a mostly continuous layer of variable thickness. Zones of contact between adjacent tufts exhibit a dark, opaque substance suggestive of trapped mucilage. Each tuft is a series of radial files of hyperplasic and occasionally hypertrophic cells whose longitudinal axes are aligned perpendicular to the abaxial, unmodified, bricklike parenchyma cells paralleling and immediately surrounding the vascular cylinder. There is evidence for an exit channel between the outer petiolar surface and the inner lumen in two specimens (Fig. 1i).

Discussion

The overall structure of Psaronius fronds was first figured and described by Stidd (17), who interpreted Stipitopteris specimens with anomalous tissues and contents as representing abnormal parenchymatic development. Lesnikowska (13) correctly identified the parenchymatic proliferation as evidence of herbivory. From comparisons with abiotically induced reaction tissue and all major types of extant galls, we conclude that the structure is demonstrably a gall. It possesses the three key features for assignment to an insect gall (6, 21, 22): (i) evidence for consumption of host plant tissue, such as a frass; (ii) host response of hypertrophic and/or hyperplasic tissue surrounding the evacuated area; and (iii) an exit hole from the lumen.
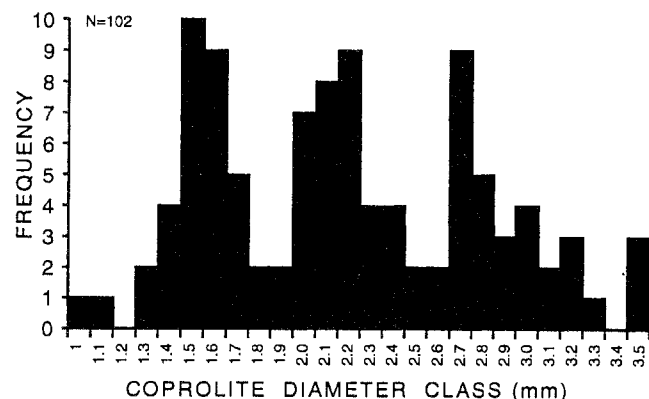

FIG. 2.   Frequency distribution of coprolite diameters with circular cross-sections, from the lumens of galled Stipitopteris rhachises. The sample is pooled from several specimens, and care was taken to select serial sections sufficiently separated in the same specimen to avoid measurement of the same coprolites. A total of 102 measurements were taken and assigned to the nearest tenth of millimeter.

Additionally, the structure exhibits tissue and organ specificity of a particular plant host. The first three criteria are anatomical features common to all arthropod gallers (mites and insects) but collectively disallow plant responses induced by viruses, bacteria, fungi or nematodes (21).

Identity of the Arthropod Galler. Several lines of evidence indicate that the galler was a holometabolous insect. First, relatively large, barrel-shaped, and solid fecal pellets with fractured ends, composed of undigested gum-sac cells and other adjacent tissue fragments, circumscribes the culprit as a holometabolous insect galler. Although some mites are gallers (6), they are not implicated since their fecal pellet sizes are smaller by approximately an order of magnitude (6, 23, 24). Apterygote, paleopterous, and orthopteroid insects are not gallers and, moreover, void fecal pellets that are irregularly shaped, spiral, spindle-shaped, or ellipsoidal (25). The only nonholometabolous insects that gall plants are hemipteroids that feed on vascular sap or cellular protoplasts. They are excluded since potentially galling, fluid-feeding lineages do not occur until the Early Permian (1, 26), and they excrete structureless fluid (27) or do not anally excrete (9) and lack a distinctive, well-developed zone of nutritive tissue surrounding the larval cavity (21). In contrast, large holometabolous larvae void excreta as a continuous, solid bolus and, because of rectal water uptake mechanisms, the fecal bolus exits in a relatively dry state that is subjected to considerable breakage (28, 29).

Additionally, the angular parenchyma fragments dispersed in the lumen, interpreted as macerated but undigested frass, indicates a mandibulate, endophytic insect. Modern borers and gallers do not ingest all the tissue they chew (30–32), resulting in the association of fecal pellets with wood fragments or wedges of adjacent parenchyma that are collectively termed frass. Last, we note the excavation of a considerable length of central ground tissue within an elongate fern rhachis, up to 24 cm in one specimen, replete with continuous nutritive tissue organized into lumen-invading tufts. Such endophagy reflects a life-habit characteristic of holometabolous larvae (21, 30, 33) that is extremely rare in other arthropod gallers (34). Although we cannot exclude the possibility that the galler was an extinct nonholometabolous insect, functional inference from extensive documentation of the life habits of modern gallers (4, 6, 21, 22, 30, 35, 36), and the absence of galling in extant myriapods and mandibulate nonholometabolous insects, restricts the culprit identity to a grublike holometabolous larva.

The most plesiomorphic clades of five major lineages (orders) of extant Holometabola are dominated by detritivorous or herbivorous larval life histories that are relevant to the presence of Late Pennsylvanian gallers (Table 1). None of these lineages are known from the Late Pennsylvanian (Fig. 3), although two taxa from the earlier Mazon Creek deposit in north-central Illinois have been interpreted as holometabolous by some (1, 37, 40). Only Neuroptera and Hymenoptera contain primitively herbivorous clades that are plausible candidates as the galler of Stipitopteris: Neuroptera, because of Early Permian stem-group representatives (1, 26, 41), and Hymenoptera, by virtue of the similarity in larval life habits with the Stipitopteris galler (Table 1) of blasticotomid and tenthredinid sawflies which are modern stem- and petiole-gallers in ferns (4, 42, 47, 48). While galled Stipitopteris resembles sawfly larval damage, the galler remains unassignable to any known extant lineage.

Late Pennsylvanian Life Habits of the Holometabola. Although holometaboly is postulated to have originated during the Pennsylvanian (49–52), three contrasting hypotheses have been proposed for the life habits of the ancestral holometabolous larva. One view, the campodeiform hypothesis, suggests that the ancestral holometabolan larva was cursorial, actively predaceous, possessed thoracic legs, and was similar to an aquatic megalopteran larvae with well-developed gills (51, 53–55). A second hypothesis posits a detritivorous, eruciform

Evolution: Labandeira and Phillips

Proc. Natl. Acad. Sci. USA 93 (1996)   8473

Table 1. Feeding habits and geochronological first occurrences of the most plesiomorphic clades of modern holometabolous insects whose larvae are primitively associated with plants

Order and common name	Most plesiomorphic extant clade or clades	Extant larval feeding type	Earliest occurrence (including stem-group)	Refs.
Mecoptera (scorpionflies)	Nannochoristidae	Exophagous; herbivorous or detritivorous	Early Permian	1, 26, 37
Diptera (flies)	Tipuloidea	Exophagous; detritivorous mostly on wood or litter	Late Permian	1, 26, 38
Lepidoptera (moths, butterflies)	Zeugloptera to Monotrysia	Mostly endophagous; as leaf miners, stem borers and gallers	Early Jurassic	1, 26, 39
Neuroptera (Planipennia) (lacewings, antlions)	lthonidae	Exophagous; apparently herbivorous on roots	Early Permian	1, 26, 40, 41
Hymenoptera (wasps, ants, bees)	Xyelidae	Exophagous or endophagous on leaves, or in cones, buds, or stems	Middle Triassic	1, 4, 26, 42

larva similar to a modern mecopteran or a primitive tenthredinoid caterpillar, possessing well-developed thoracic legs and abdominal prolegs, and feeding exophytically on detritus or possibly foliage (2, 40). This type of primitive larva was recently
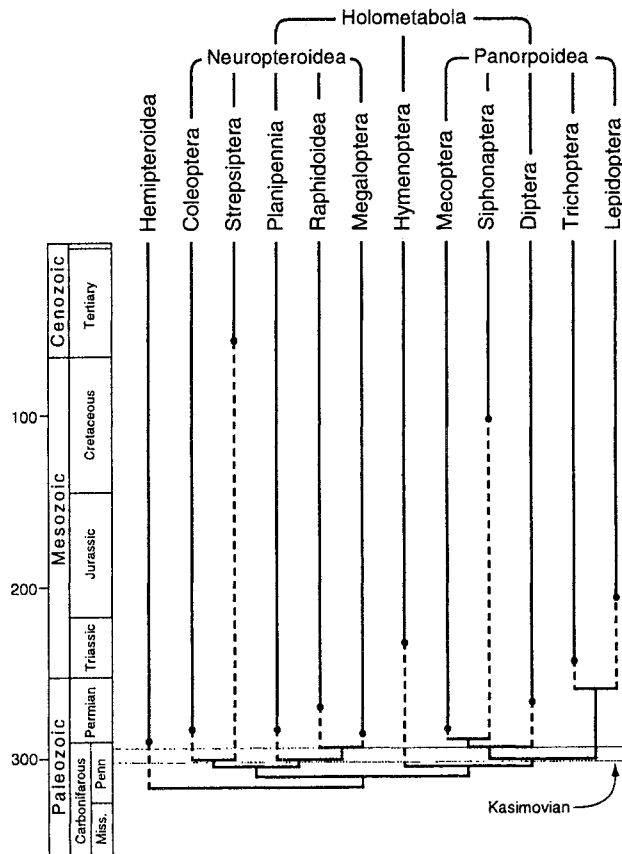

FIG. 3.   Temporal relationship of the Late Pennsylvanian *Stipitopteris* gall to the radiation of the Holometabola, based on the cladistic relationships of Hennig (1) and Kristensen (43, 44), calibrated by the earliest fossil occurrences (26, 45, 46) of constituent clades. Designations in panel at left indicate, from left to right, absolute age in millions of years, geologic era, and geologic period; the Carboniferous Period is subdivided into the Mississippian and Pennsylvanian subperiods (11). Cladogram symbols: dots represent first body fossil occurrences; solid lines record known presence from body fossils; and dotted lines record inferred presence based on sister-group relationships. The stippled bar designates the duration of the Kasimovian Epoch of the Late Pennsylvanian Subperiod (11); the Calhoun Coal is dated at 302 Ma (10) in the lower part of the interval.

illustrated by Kukalová-Peck (40, 45) from the Middle Pennsylvanian of Illinois. Finally, an older hypothesis suggests that the ancestral larval holometabolan was an eruciform grub with poorly developed thoracic legs and abdominal prolegs, occurring endophytically within plant tissues, and most likely a stem-borer or galler similar to a modern tenthredinoid or cephoid sawfly (35, 56, 57). Our data supports the presence of such an endophytic, grublike larva during the Late Pennsylvanian. The presence of these ecologically specialized larvae, in conjunction with recent developmental evidence indicating that campodeiform larvae are primitive within Holometabola (58, 59), supports a view that holometabolous larvae were already morphologically and ecologically differentiated by Late Pennsylvanian times. It is noteworthy that evidence now suggests that the larvae of early lineages of Holometabola interacted with plants, endophytically as grubs and possibly exophytically as caterpillars.

In particular, the galled *Stipitopteris* fronds support Lameere's hypothesis (3) for endophytic holometabolous larvae in Pennsylvanian swamp forests, elaborated by Malyshev (4) who suggested that such larvae were mecopteroid, sawflylike ancestors. Our data are inconsistent with various assessments that posit the origin of the galling life habit contemporaneously with the angiosperm radiation (35, 36, 60–62). The presence of a *Psaronius* galler provides direct evidence for the presence of intimate autecological coupling between an endophagous larval insect and a histologically responding vascular plant 175 million years earlier, during the Late Pennsylvanian.

The Extent of Herbivory During the Latest Pennsylvanian. Our documentation of gallers on *Psaronius* frond rhachises is paralleled by the presence of several other herbivore functional feeding groups on the same host plant (5). Evidence now exists for piercing-and-sucking of vascular tissue of the same frond rhachises (5, 13, 63), as well as external foliage feeding on pinnules, rhachis epidermal scales, and sporangia, apparently by mandibulate insects (ref. 5; unpublished data). Collectively these data indicate that diverse insect dietary guilds were established on *Psaronius* tree ferns during the beginning of the Late Pennsylvanian, and virtually all above-ground live tissues were targeted for consumption by herbivores. Additionally, insect and mite detritivores were consuming, respectively, the stem parenchyma and root mantle tissue of *Psaronius* trunks (5, 14, 64).

This emerging picture of the partitioning of diverse tissues by herbivores on *Psaronius* tree ferns during the Late Pennsylvanian, contradicts widespread notions that emphasize a lack of evidence for Pennsylvanian and even Early Permian herbivory (40, 60, 61, 65–67), with the possible exception of consumption of megaspores, seeds, or fructifications (4, 40, 62, 66). By contrast, these and coordinate data indicate that,

excepting the absence of leaf miners, the herbivores of *Psaronius* formed a modern-style community of diverse insect consumers targeting specific tissues of the same host plant (68). Although the exact taxonomic identities of coeval insect species cannot be associated with the distinctive types of plant damage documented in this and related studies, the ecological *roles* of these taxonomically unknown insect herbivores can be established independently, thus revealing an otherwise inaccessible fossil record of early plant–insect interactions. As primary data for the interactions of insects with plants, well-preserved herbivore-mediated damage of plant tissue and analysis of coprolite contents not only provides illuminating glimpses into ancient autecological associations, but is the only direct way of establishing how early insect herbivores dietarily subdivided their food resources.

1. Hennig, W. (1981) *Insect Phylogeny* (Wiley, New York).
2. Tillyard, R. J. (1926) *Am. J. Sci.* **11,** 133–164.
3. Lameere, M. (1908) *Ann. Soc. Entomol. Belgique* **52,** 127–147.
4. Malyshev, S. I. (1968) *Genesis of the Hymenoptera and the Phases of their Evolution* (Methuen, London).
5. Labandeira, C. C. (1991) *Geol. Soc. Am. Abstr. Prog.* **23,** A405.
6. Ananthakrishnan, T. N., ed. (1984) *Biology of Gall Insects* (Oxford/IBH, New Delhi).
7. Larew, H. G. (1992) in *Biology of Insect-Induced Galls*, eds. Shorthouse, J. D. & Rohfritsch, O. (Oxford Univ. Press, New York), pp. 50–59.
8. Potonié, R. (1893) *Abh. König. Preuss. Geol. Landes* **9,** 1–299.
9. Livingstone, D. (1978) *J. Ind. Acad. Wood Sci.* **9,** 39–45.
10. Phillips, T. L., Peppers, R. A. & DiMichele, W. A. (1985) *Int. J. Coal Geol.* **5,** 43–109.
11. Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G. & Smith, D. G. (1990) *A Geologic Time Scale 1989* (Cambridge Univ. Press, Cambridge), pp. 42–46.
12. Rowley, D. B., Raymond, A., Parrish, J. T., Lottes, A. L., Scotese, C. L. & Ziegler, A. M. (1985) *Int. J. Coal Geol.* **5,** 17–42.
13. Lesnikowska, A. D. (1990) *Palaios* **5,** 76–80.
14. Labandeira, C. C. & Beall, B. S. (1990) in *Arthropod Paleobiology*, ed. Mikulic, D. G. (Univ. of Tennessee Press, Knoxville), pp. 214–256.
15. Phillips, T. L., Avcin, M. J. & Berggren, D. (1976) *Ill. State Geol. Surv. Educ. Ser.* **11,** 1–40.
16. Morgan, J. (1959) *Ill. Biol. Monogr.* **27,** 1–108.
17. Stidd, B. M. (1971) *Palaeontographica* **134B,** 87–123.
18. Eckstein, K. (1939) *Forstarchiv* **15,** 268–271.
19. Nagasawa, S. (1957) *Botyu-Kagaku Kyoto Univ. Inst. Ins. Control* **22,** 176–182.
20. Sardesai, J. B. (1969) *Ann. Entomol. Soc. Am.* **62,** 662.
21. Meyer, J. & Maresquelle, H. J. (1983) *Anatomie des Galles* (Gebrüder Borntraeger, Berlin).
22. Fernandes, G. W. (1987) *Rev. Bras. Entomol.* **31,** 379–398.
23. Westphal, E. (1977) *Marcellia* **39,** 193–375.
24. Kühnelt, W. (1976) in *Soil Biology with Special Reference to the Animal Kingdom*, eds. Kühnelt, W., Walker, N., Butcher, J. W. & Laughlin, C. (Faber, London), pp. 126–216.
25. Gangwere, S. K. (1962) *Eos* **38,** 247–262.
26. Labandeira, C. C. (1996) *Contrib. Biol. Geol. Milwaukee Publ. Mus.* **88,** 1–71.
27. Storey, H. H. & Nichols, R. F. W. (1937) *Proc. R. Entomol. Soc. London* **12A,** 149–150.
28. Cymorek, S. (1968) *Rec. 18th Annu. Conv. Br. Wood Preserv. Assoc.* **18,** 161–170.
29. Hay, C. J. (1968) *Ann. Entomol. Soc. Am.* **61,** 255–258.
30. Holmes, N. D. (1954) *Can. Entomol.* **86,** 159–167.
31. Starzyk, J. R. (1977) *Z. Angew. Entomol.* **83,** 269–281.
32. Headrick, D. H. & Goeden, R. D. (1989) *Proc. Entomol. Soc. Wash.* **91,** 594–603.
33. Smith, E. L. (1970) *Ann. Entomol. Soc. Am.* **63,** 36–51.
34. Newstead, R. & Cummings, B. F. (1913) *Ann. Mag. Nat. Hist.* **11,** 306–308.
35. Roskam, J. C. (1992) in *Biology of Insect-Induced Galls*, eds. Shorthouse, J. D. & Rohfritsch, O. (Oxford Univ. Press, New York), pp. 34–49.
36. Mamaev, B. M. (1975) *Evolution of Gall Forming Insects—Gall Midges* (The British Library, Boston Spa).
37. Willmann, R. (1989) *Abh. Senckenb. Naturforsch. Ges.* **544,** 1–153.
38. Courtney, G. W. (1991) *Syst. Entomol.* **16,** 137–172.
39. Scoble, M. J. (1992) *The Lepidoptera: Form, Function and Diversity* (Oxford Univ. Press, Oxford), pp. 171, 192–195.
40. Shear, W. A. & Kukalová-Peck, J. (1990) *Can. J. Zool.* **68,** 1807–1834.
41. Gepp, J. (1984) *Proc. First Int. Symp. Neuropterol.*, 183–239.
42. Gauld, I. D. & Bolton, B., eds. (1988) *The Hymenoptera* (Oxford Univ. Press, Oxford), pp. 87–97.
43. Kristensen, N. M. (1989) in *The Hierarchy of Life*, eds. Fernholm, B., Bremer, K. & Jörnwall, H. (Elsevier, Amsterdam), pp. 295–306.
44. Kristensen, N. M. (1991) in *The Insects of Australia: A Textbook for Student's and Research Workers*, eds. Naumann, I. D., Carne, P. B., Lawrence, J. F., Nielsen, E. S., Spradbery, J. P., Taylor, R. W., Whitten, M. J. & Littlejohn, M. J. (Cornell Univ. Press, Ithaca, NY), Vol. 1., pp. 125–140.
45. Kukalová-Peck, J. (1991) in *The Insects of Australia: A Textbook for Student's and Research Workers*, eds. Naumann, I. D., Carne, P. B., Lawrence, J. F., Nielsen, E. S., Spradbery, J. P., Taylor, R. W., Whitten, M. J. & Littlejohn, M. J. (Cornell Univ. Press, Ithaca, NY), Vol. 1., pp. 141–179.
46. Carpenter, F. M. (1992) in *Treatise on Invertebrate Paleontology*, eds. Kaesler, R. L., Brosius, E., Keim, J. & Priesner, J. (Geol. Soc. of Am., Boulder, CO/Univ. of Kansas Press, Lawrence), Part 4, Vols. 3/4, pp. xxi, 1–655.
47. Togashi, I. (1989) *Proc. Entomol. Soc. Wash.* **91,** 406–413.
48. Shaw, M. R. & Bailey, M. (1991) *Entomologist* **110,** 103–109.
49. Tillyard, R. J. (1918) *Proc. Linn. Soc. N.S.W.* **43,** 265–319, 626–657.
50. Crampton, G. C. (1931) *Entomologist* **64,** 154–158, 171–174.
51. Chen, S. H. (1946) *Trans. R. Entomol. Soc. London* **97,** 381–404.
52. Lawrence, J. E. & Newton, A. F., Jr. (1982) *Annu. Rev. Ecol. Syst.* **13,** 261–290.
53. Berlese, A. (1913) *Redia* **9,** 121–137.
54. Ghilarov, M. S. (1957) *Zool. Zh.* **36,** 1683–1697 (in Russian).
55. Toms, R. B. (1984) *J. Entomol. Soc. South Afr.* **47,** 169–276.
56. Martynov, A. V. (1925) *Z. Morphol. Ökol. Tiere* **4,** 465–501.
57. Sharov, A. G. (1966) *Basic Arthropodan Stock with Special Reference to Insects* (Pergamon, London).
58. Panganiban, G., Nagy, L. & Carroll, S. B. (1994) *Curr. Biol.* **4,** 671–675.
59. Svacha, P. (1994) *Dev. Biol.* **154,** 101–117.
60. Karny, H. H. (1926) in *The Zoocecidia of the Netherlands East Indies*, eds. van Leeuwen-Reijnvaan, J. & van Leeuwen, W. M. (Drukkerij de Unie, Jakarta), pp. 37–47.
61. Zwölfer, H. (1978) *Sonderb. Naturwis. Ver. Hamburg* **2,** 7–50.
62. Strong, D. R., Lawton, J. H. & Southwood, T. R. E. (1984) *Insects on Plants: Community Patterns and Mechanisms* (Harvard Univ. Press, Cambridge, MA), pp. 31–45.
63. Labandeira, C. C. & Phillips, T. L. (1996) *Ann. Entomol. Soc. Am.* **89,** 157–183.
64. Labandeira, C. C., Phillips, T. L. & Norton, R. A. (1996) *Palaios* **11,** in press.
65. Cox, B. (1974) *Nature (London)* **249,** 615–616.
66. DiMichele, W. A. & Hook, R. W. (1992) in *Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals*, eds. Behrensmeyer, A. K., Damuth, J. D., DiMichele, W. A., Potts, R., Sues, H.-D. & Wing, S. L. (Univ. of Chicago Press, Chicago), pp. 206–325.
67. Hughes, N. F. (1994) *The Enigma of Angiosperm Origins* (Cambridge Univ. Press, Cambridge), pp. 45–46.
68. Labandeira, C. C. (1996) *Paleontol. Soc. Spec. Publ.* **8,** 227 (abstr.).