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# Stem Borings and Petiole Galls from Pennsylvanian Tree Ferns of Illinois, USA: Implications for the Origin of the Borer and Galler Functional-Feeding-Groups and Holometabolous Insects

by

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with 16 plates, 10 text-figures and 1 table

## Zusammenfassung

In den Tiefländern des höchsten Ober-Carbons lebte eine gleichförmige euramerische Florengemeinschaft. Feuchte Standorte wurden von pfahlartigen Bärlappbäumen beherrscht. Daneben kamen Baum- und Samenfarne zusammen mit Sphenopsiden und seltenen Cordaiten vor. In diesen taxonomisch und physiognomisch unterschiedlichen Pflanzengemeinschaften bauten Abfallfresser die pflanzliche Biomasse ab. Als im höheren Ober-Carbon die *Psaronius*-Baumfarne die Bärlappgewächse als vorherrschende Florenelemente ablösten, gab es eine deutliche Zunahme in Mannigfaltigkeit und Intensität von Pflanzenfressertypen. Diese Verschiebung zugunsten der Herbivoren wird durch die signifikante Zunahme von Arthropoden Coproliten in der Torfstreu belegt, deren Entstehung am ehesten durch die Tätigkeit von Pflanzenfressern zu erklären ist. Gleichbedeutend ist auch der frühe Nachweis von form- und wirtsspezifischen Beschädigungen, die durch herbivore Insekten verursacht wurden. Wir beschreiben hier zwei dieser Phänomene als neu errichtete Ichnogenera, nämlich *Pteridiscaphinchnos*, ein von einem Abfallfresser erzeugtes Tunnel- und Miniergangartiges Netzwerk in *Psaronius*-Stämmen aus dem mittleren und oberen Abschnitt des Ober-Carbons, und *Pteriditorichnos*, eine längliche Galle im Wedelstiel des obercarbonischen *Psaronius chasei*, die von einer herbivoren endophytischen Larve eines holometabolen Insektes erzeugt wurde.

Der in *Psaronius*-Stämmen bohrende *Pteridiscaphinchnos* erscheint im höheren Mittel-Pennsylvanium in *Psaronius* sp. („layered cells morphotype") und im oberen Pennsylvanium in *P. magnificus* und *P. chasei*. Diese so bezeichnende Stammbohrung wurd durch Ausräumen des Grundparenchyms charakterisiert, das durch Kot aus ellipsoidischen Coproliten von 1,0 × 3,0 mm und mazerierte Fragmente von verdautem Parenchym ersetzt wird. Sämtliche bekannt gewordenen Exemplare treten zwischen längsgerichteten bis gebogenen Gefäßsträngen im Inneren des Gefäzylinders auf. Das Fehlen von Wundgewebe bezeugt einen post-mortem-Verzehr eines verhältnismäßig weichen und nährstoffreichen Parenchyms. Die Anlage des Netzwerks aus Miniergängen ging auf der anderen Seite dem Zerfall des Stammes voraus, da nämlich das verholzte Gewebe, wie Sklerenchym, Gefäße und Teile des Wurzelmantels noch in ihrer Struktur erhalten blieb und von Fressern gemieden wurde. Wenn man von der Geometrie der Bohrgänge, der Struktur der Coproliten und dem Verhalten von heute in den Stämmen von Baumfarnen lebender Insekten ausgeht, dürften die Erzeuger von *Pteridiscaphichnos* am ehesten eine Schabe oder ein schabenartiges Kerbtier gewesen sein.

Die aus dem höheren Ober-Carbon stammende Galle *Pteriditorichnos* ist allein von der Wirtspflanze *Psaronius chasei* bekannt, wo sie an der Wedelstielen auftritt. Die Galle umfaßt einen Hohlraum, der durch die Beseitigung von Grundparenchym in der Stielachse entstand. Teilweise wurde er von Reihen aus hypertrophierten Zellen ersetzt, die als strahlenförmige, aneinanderstoßende Büschel eine differenzierte Calluszone bildeten. Das von diesem Callus umgebende Lumen enthält Kot, der aus Coproliten und mazerierten Parenchympartikeln besteht. Faßförmige Coproliten von 1,5 × 2,5 mm Größe haben eine glatte Oberfläche auf der Längsseite; die Enden aber sind unregelmäßig. Sie enthalten deutlich erkennbare Zellen, wie sie in dem umgebenden Callus und in dem nicht modifizierten Parenchym vorkommen. Allem Anschein nach bohrte ein endophytisches Insekt durch das Mark des Stielparenchyms, was die Bildung von Callus hervorrief, der dann von dem Insekt verzehrt wurde. Ausgehend von der dreidimensionalen Form der Galle, der besonderen Natur der Coroliten und der reichen Dokumentation von heutigen gallenbildenden Arthropoden deuten wir den fossilen Erzeuger als Larve eines holometabolen Insektes.

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Obwohl diese älteste Galle solchen tenthredinoiden Hymenopteren (Pflanzenwespen, Gallwespen) ähnlich ist, kann man sie dennoch keiner lebenden Holometabolenlinie zuordnen.

Zwar wurden Körperfossilien von wahrscheinlichen Holometabola aus obercarbonischen Schichten erwähnt, doch können erstmals an Hand des Spurenfossils *Pteriditorichnos* die Lebensgewohnheiten eines erdgeschichtlich frühen holometabolen Insektes genauer dokumentiert werden. Wegen ihrer außergewöhnlich guten anatomischen Erhaltung und ihres verhältnismäßig hohen geologischen Alters (höheres Ober-Carbon) ist diese von einer Insektenlarve erzeugte Pflanzengalle wichtig, um die Lebensgewohnheiten der Larven der öltesten Holometabla zu ergründen: 1. Der holometabole Gallenerzeuger lebte in einem klimatisch gleichmäßigen, tropisch-humiden Sumpfwald mit Torfstreu. 2. Endophytische Gallenbildung in Wedelstielen war wohl die älteste bekannt gewordene Lebensweise der Holometabola-Larven. Ferner dürften solche in Stämmen ihre Gallen erzeugende Formen oder ähnliche endophytische Gruppen zumindestens eine der ursprünglichen Lebensweisen der Holometabola darstellen. 3. Die Behauptung von Lameere, die später noch von Malyshev erweitert wurde, wird gerechtfertigt: Das Eindringen in das Gewebe primitive Gefäßpflanzen (besonders von Pteridophyten) war wesentlich mit dem holometabolen Entwicklungsstadium der Insekten verbunden.

Die hier vorgelegten Daten zeigen nicht nur das Auftreten eines Stammbohrers und eines herbivoren Gallenerzeugers im Paläozoikum, sondern sie dokumentieren auch die innige Wechselbeziehung zwischen Wirtspflanze und pflanzenfressendem Eindringling bis in der höhere Ober-Carbon zurück.

Schlüsselwörter: Carbon – Insekten – Blattopteriformia – Holometabola – Pflanzenfresser – Pteridophyten.

## Summary

Latest Middle Pennsylvanian, lowland, equatorial communities of Euramerica occurred in equable, wetland habitats with peat substrates dominated by pole-like lycopod trees amid subdominant tree ferns and seed ferns, along with sphenopsids and rare cordaites. In these taxonomically diverse and physiognomically varied communities detritivores overwhelmingly channeled plant biomass from primary production to reduced organic matter. However, by the Late Pennsylvanian, when *Psaronius* tree ferns replaced lycopods as dominant floral elements, there was a dramatic increase in the spectrum and intensity of herbivore functional-feeding-groups. This shift toward the importance of herbivores is supported by a significant increase of arthropod coprolites in peat litter whose origin is most parsimoniously explained by herbivory. Equally important are the earliest documented occurrences of highly stereotyped and host specific plant damage caused by herbivorous insects. We describe two of these distinctive interactions as the newly established ichnogenera *Pteridiscaphichnos*, a detritivore-created, tunnel-and-gallery network in Middle- and Late Pennsylvanian *Psaronius* stems; and *Pteriditorichnos*, an elongate petiole gall from the frond of the Late Pennsylvanian *Psaronius chasei*, caused by an herbivorous and endophytic larval holometabolan.

The *Psaronius* stem-boring, *Pteridiscaphichnos*, occurs in the late Middle Pennsylvanian form "layered cells morphotype" and the Late Pennsylvanian species *Psaronius magnificus* and *P. chasei*. This distinctive stem boring is characterized by evacuated ground parenchyma replaced by frass of ellipsoidal coprolites 1.0 mm × 3.0 mm in average size and macerated fragments of processed but unconsumed parenchyma. All known specimens occur among linear to arcuate vascular strands interior to the outer sclerenchyma cylinder. The lack of reaction tissue indicates postmortem consumption of relatively soft, nutrient-rich parenchyma, although construction of the tunnel-and-gallery network preceded significant decomposition of the trunk since lignified tissues, such as sclerenchyma, vascular tissue and part of the root mantle, were still structurally sound and were avoided by the detritivores. Based on the geometry of the boring, coprolite structure, and the life-habits of modern ecologic analogs inhabiting tree fern trunks, the culprit of *Pteridiscaphichnos* is attributed to a roach or roach-like insect.

The Late Pennsylvanian gall, *Pteriditorichnos*, is known only on *Psaronius chasei* hosts, and occurs in basal frond petioles. The structure of this gall consists of a lumen formed by removal of ground parenchyma through the petiolar axis, and its partial replacement by files of hypertrophied cells organized into radiating, impinging tufts that define a differentiated zone of callus. The lumen, encapsulated by callus, contains regions with frass consisting of coprolites and macerated parenchyma fragments. Barrel-shaped coprolites average 1.5 mm × 2.5 mm in size, have smooth longitudinal surfaces but ragged ends, and contain recognizable cell types found in the surrounding callus and unmodified parenchyma. All lines of evidence indicate that an endophytic insect tunneled through medullary petiolar parenchyma, which induced plant response by production of callus, and was followed by insect consumption of the callus. Based on the three-dimensional structure of this gall, the particulate nature of the coprolites, and an extensive literature documenting known gall-making arthropods, we identify the culprit as a holometabolous larva. Although this earliest known gall resembles those made by extant tenthredinoid Hymenoptera, it is unassignable to any modern lineage of Holometabola.

Although possible body fossils of the Holometabola have been mentioned in Pennsylvanian strata, *Pteriditorichnos* provides the first high-resolution, trace-fossil documentation of the life-habits of any Paleozoic larval holometabolan. Because of its exceptional anatomical preservation and Late Pennsylvanian age, this larval-induced gall is important in assessing existing hypotheses regarding the ancestral life-habits of the earliest larval Holometabola. Evidence indicates: 1. That the larval holometabolan galler occurred in a climatically equable, tropical, and humid swamp forest with a peat substrate. 2. That endophytic petiole galling is the earliest known life-habit for the Holometabola, and that stem galling or a related endophytic guild was an ancestral/behavior for this clade. 3. The prediction of Lameere, later elaborated by Malyshev, is vindicated: the endophytic penetration of tissues in primitive vascular plants (especially pteridophytes) was integrally associated with the holometabolous condition. These data indicate not only the occurrence of a stem borer and a herbivore galler during the Paleozoic, but also document the presence of an intimate interaction between a herbivore and its responding plant host as early as the Late Pennsylvanian.

Key words: Carboniferous – insects – Blattopteriformia – Holometabola – herbivores – pteridophytes.

## Contents

## 1. Introduction

The two most diverse clades occurring today – vascular plants and insects – provide impressive ecological structure to modern terrestrial ecosystems. Yet little is known of the origins and the historical record of interactions between these two groups, despite extensive recent interest directed toward understanding myriad associations between flowering plants and holometabolous insects. It is in this context of understanding the vast ecological repertoire of insects on plants that the locus of our investigation is placed in Pennsylvanian-age (= Late Carboniferous) swamp forests of equatorial Euramerica. In these deposits there is now evidence for highly stereotyped interactions between archaic insects and coal-swamp tree ferns.

## 1.1. Theoretical and Historical Context

Recent approaches toward understanding the historical association between vascular plants and insects have overwhelmingly emphasized cladistic inference based on the congruence of plant host and insect herbivore phylogenies. Intellectually robust insights have been derived from these approaches, particularly when well-corroborated cases of parallel diversification are demonstrated, such as two noteworthy analyses for chrysomelid beetles and their lamiaceous (FARRELL & MITTER, 1990) and asclepiadaceous (FARRELL, 1991) plant hosts. However, all such studies of tandem cladogenesis (MITTER & FARRELL, 1991; FARRELL & MITTER, 1993) and biogeographic examinations of the antiquity of plant host/insect herbivore associations – for example, OPLER (1973) for lepidopteran leaf miner/oak interactions, and MORAN (1989) for the aphid/barberry/sumac system – indicate origins during the mid-Tertiary. A few studies (LINSLEY, 1963; ZWÖLFER, 1978; WOOD, 1982; PELLMYR, 1992) suggest more distant Cretaceous associations. From this body of research it is clear that discerning interactions of older, preangiospermous, Mesozoic and Late Paleozoic hosts and their herbivores will rely less on cladistic inference of parallel phylogeny, and more on direct evidence of the fossil record (THOMAS, 1985; LABANDEIRA & BEALL, 1990; CHALONER et al., 1991; SCOTT et al., 1992). Increasingly, this will occur, if for no other reason, than many older Mesozoic and Paleozoic clades are now extinct. This state of affairs was perceptively rendered by SWAIN in 1978, who said (p. 4):

> "Nor, in my opinion, is it sensible to concentrate, as most authors have done, only on angiosperms and modern insects, for they are much too closely interlinked to explain all evolutionary processes."

Although examination of fossil evidence from plant/insect interactions in older Mesozoic and Paleozoic deposits is a direct approach, in most cases identification of the responsible insect interactor is tenuous or impossible. This is attributable to well-preserved, insect-damaged plant tissues commonly occurring in depositional environments and under taphonomic conditions unfavorable for insect preservation. Ironically, while insects are rarely preserved in flagrante delicto on damaged plants, the perception that the fossil record of interactions is poor (MITTER & FARRELL, 1991; FARRELL & MITTER, 1993) is perhaps unduly pessimistic. Examples are available that the preservation of insect damage on plants can be exceptionally good (CRANE & JARZEMBOWSKI, 1980; KOZLOV, 1988; this report). While direct inspection of the fossil record incurs some liabilities, in selected cases it can provide conclusions apparently not amenable to cladistically-based inferences. Fossils are an available and valuable resource for testing explicit hypotheses regarding the interactions between vascular plants and insects.

Cladistic tests of plant/insect interactions have overwhelmingly involved herbivores on angiosperms. Analogously, there has been only modest efforts in applying direct fossil evidence to associations between preangiospermous plants and insects. For these and other reasons, many statements have been made regarding the presence or absence of Paleozoic insect herbivores. The overwhelmingly received hypothesis is that there was minimal herbivory, if at all, during the Paleozoic in general and the Carboniferous in particular (HUGHES & SMART, 1967; SMART & HUGHES, 1973; COX, 1974; HAMILTON, 1978; ROLFE, 1980; STRONG et al., 1984; SOUTHWOOD, 1985; BEERBOWER et al., 1987; SHEAR, 1991; SHEAR & KUKALOVÁ-PECK, 1991; INGROUILLE, 1993). Apparent validation of this view originates from two sources. First is the claim of scant empirical evidence for insect external-foliage-feeding (COX, 1974; STRONG et al., 1984; SHEAR & KUKALOVÁ-PECK, 1991) and other functional-feeding-groups (SHEAR, 1991) particularly in Carboniferous floras (but see AMEROM, 1966; AMEROM & BOERSMA, 1971; SWAIN, 1978; LABANDEIRA & BEALL, 1990). Second, there is theoretical support from studies documenting the formidable physiological and biochemical barriers that insects have to overcome as they jump the "herbivory hurdle" (SOUTHWOOD, 1973; STRONG et al., 1984), and consequently it has been inferred that there was a long evolutionary prelude to the eventual colonization of plants by insect herbivores sometime after the Carboniferous (SOUTHWOOD, 1985; also see PLUMSTEAD [1963] and SRIVASTAVA [1987] for counterexamples). Implicit in this hypothesis is the absence during the Paleozoic of highly host- and tissue-specific functional-feeding-groups, such as stem gallers, leaf miners and cambium borers – a view that has been explicitly supported as commentary by specialists in leaf mining (HERING, 1951; JOLIVET, 1986) and galling (MAMAEV, 1975; ROSKAM, 1992), among others (STRONG et al., 1984; SCHLÜTER, 1987).

Consistent with this view has been very little evidence challenging the omnipresence of detritivore-based ecosystems in Pennsylvanian wetlands. For the earlier Pennsylvanian, considerable data supports the observation that primary productivity was being overwhelmingly routed through detritivores rather than herbivores (Rolfe, 1985; Phillips & Cross, 1991; DiMichele & Hook, 1992; Labandeira & Phillips, 1992; Labandeira et al., 1997). However, this model is becoming less likely for the late Moscovian to Gzelian (Text-Fig. 1). Recent anecdotal documentation of functional-feeding-groups during the later Pennsylvanian indicates the presence of leaf-chewing (Scott & Taylor, 1983; Labandeira & Beall, 1990; Scott et al., 1992), piercing-and-sucking (Labandeira & Phillips, 1996a), spore and sporangial consumption (Meyen, 1984; Scott et al., 1985; Rothwell & Scott, 1988), galling (this report; Labandeira & Phillips, 1996b), and possible leaf-mining (Müller, 1982; Boucot, 1990; Labandeira & Beall, 1990), although currently the impact of these feeding strategies on plant tissues remains unquantified. What is remarkable about this spectrum of interactions is that they are early representatives of modern functional-feeding-groups, even though both host and herbivore interactors are taxa of premodern, Paleozoic clades. Nevertheless, in a brief review of research to date, Shear (1991) stated that: "Fossil evidence for Carboniferous insects feeding by chewing on living vegetative parts is weak" (p. 287). In this paper we provide new data and interpretations that address Shear's (1991) assessment.

In 1899 the Belgian entomologist Lameere stated that "…l'holométabolisme est dû à la pénétration de l'Insecte à l'intérieur de tissus végétaux." (p. 632), perhaps the earliest statement regarding the endophytic ancestral life-habits of the Holometabola. Long after Lameere's initial postulation (1899) and subsequent reiterations (1908, 1917), Hennig (1981) mused that "it is remarkable that no fossils that definitely belong to the Paraneoptera or Holometabola are known from the Carboniferous" (p. 167, transl. A. C. Pont), even though previous phylogenetic studies informally placed the holometabolan evolutionary radiation during the Carboniferous (for example, Handlirsch, 1906-1908; Tillyard, 1926; Crampton, 1931; Martynov, 1938; Chen, 1946; Heslop-Harrison, 1958; Carpenter, 1971, 1977; Hinton, 1977). It is revealing that Malyshev (1968) subsequently revived Lameere's ideas and placed them in the context of the evolution of life-habit stages from a primitive mecopteran to a symphytan hymenopteran, only to be admonished by Mamaev (1975) for positing Carboniferous endophytic larvae. Eventually, as fossil holometabolous lineages were discovered closer to the Permo-Carboniferous boundary, the notion of Carboniferous Holometabola (and an implicit evolutionary radiation) became more acceptable. Currently there is possible body-fossil evidence for Carboniferous Holometabola, principally an undescribed, apparently external-detritus-feeding, eruciform larva from the late Myachkovskian (Kukalová-Peck, 1991), and a reinterpretation of the venation of the Pennsylvanian fossils *Metropator* and *Fatjanoptera* as holometabolans (Martynova, 1961; Hennig, 1981; Willmann, 1989; Aspöck, 1998; but see Carpenter, 1965).

### 1.2. Previous Work

Investigations of teratological plant tissues from Euramerican Carboniferous lycopods, ferns and seed-ferns were made mostly early during the past century (Williamson, 1880; Weiss, 1904; Stopes, 1907; Holden, 1910, 1930; Wilkinson, 1930), although it is unlikely that most of this permineralized damage was mediated by arthropods. Recently there has been interest regarding the role of detritivores in degradation of coal-swamp plant tissues, with evidence supplied from coprolites (Scott, 1977; Baxendale, 1979) and borings in wood and parenchyma (Cichan & Taylor, 1982; Rothwell & Scott, 1983). Attempts have been made to identify the detritivores responsible for the comminution of these tissues (Rolfe, 1980; Scott & Taylor, 1983; Taylor & Scott; 1983) and to ascertain the trophic pathways resulting in the eventual reduction of primary productivity to coal deposits (Scott, 1980; Beerbower, 1985). Additionally there has been a greater focus on documentation of herbivory, such as borings of ovular tissue in *Samaropsis* seeds (Sharov, 1973), reinterpretation of spore-containing masses as coprolites (Meyen, 1984; Rothwell & Scott, 1988), documentation of bite marks with reaction tissue in seed-fern pinnules (Müller, 1982; Labandeira & Beall, 1990), evidence for stylet insertion traces into vascular tissue (Taylor & Scott, 1983; Lesnikowska, 1989; Labandeira & Phillips, 1996a), and suggestive leaf mining in seed-fern pinnules (Potonié, 1921; Müller, 1982; Boucot, 1990; Labandeira & Beall, 1990). Although some of this documentation has been contested (Shear, 1991; Shear & Kukalová-Peck, 1991; see Edwards & Selden [1991] for geologically older records), these discoveries broaden understanding of above-ground, especially canopy, insect consumption of live plant tissues.

Both plant-insect interactions described in this report have an important, but limited history of documentation. The first, a coprolite-packed, galleried boring in *Psaronius magnificus* stems, was first figured from a Late Pennsylvanian locality in southeastern Ohio (ROTHWELL & SCOTT, 1983; SCOTT & TAYLOR, 1983; SCOTT et al., 1992). Later, the same interaction type was figured for the "layered cells morphotype" of *Psaronius* (LESNIKOWSKA, 1989) by LABANDEIRA & BEALL (1990) for a Herrin Coal specimen from the late Middle Pennsylvanian of southern Illinois. The second interaction type, a petiole gall from the petiole (*Stipitopteris*) of *Psaronius chasei*, was initially documented by STIDD (1971), who interpreted it as abnormal parenchymatic growth. These and other specimens from the Late Pennsylvanian Calhoun Coal were later discussed and figured by LESNIKOWSKA (1989, 1990), who correctly recognized that they were prima facie evidence for insect herbivory.

## 2. Materials and Methods

Studies of Pennsylvanian-age coal-swamp floras of the Illinois Basin have a long and distinguished history. Although this report focuses on a relatively neglected aspect of these studies – plant-insect interactions – our methodology principally has been borrowed and occasionally modified from previously used techniques of specimen preparation and illustration. One exception, discussed below, is use of a computer-based system for low-magnification photodocumentation of specimens.

### 2.1. Stratigraphy and Geochronology

The fossil material examined in this report consists of original and insect-altered plant tissues that were carbonate-permineralized and structurally preserved as peat in coal balls in two Euramerican, Middle Pennsylvanian-age, coal-swamp deposits in Illinois (Text-Fig. 1). The Herrin Coal occurs in the middle of the Carbondale Formation (Kewanee Group), and was deposited during the late Myachkovskian Stage of the late Moscovian Series (HARLAND et al., 1990). Within the midcontinent of North America this deposit is part of the Desmoinesian Series, and is equivalent to late Westphalian D Stage of European terminology (Text-Fig. 1; PHILLIPS & PEPPERS, 1984). This stratigraphic placement corresponds to an absolute age of 307 Ma (HESS & LIPPOLT, 1986). The Herrin Coal extends over much of the Illinois Basin and represents one of the most extensive coal units of Pennsylvanian age.

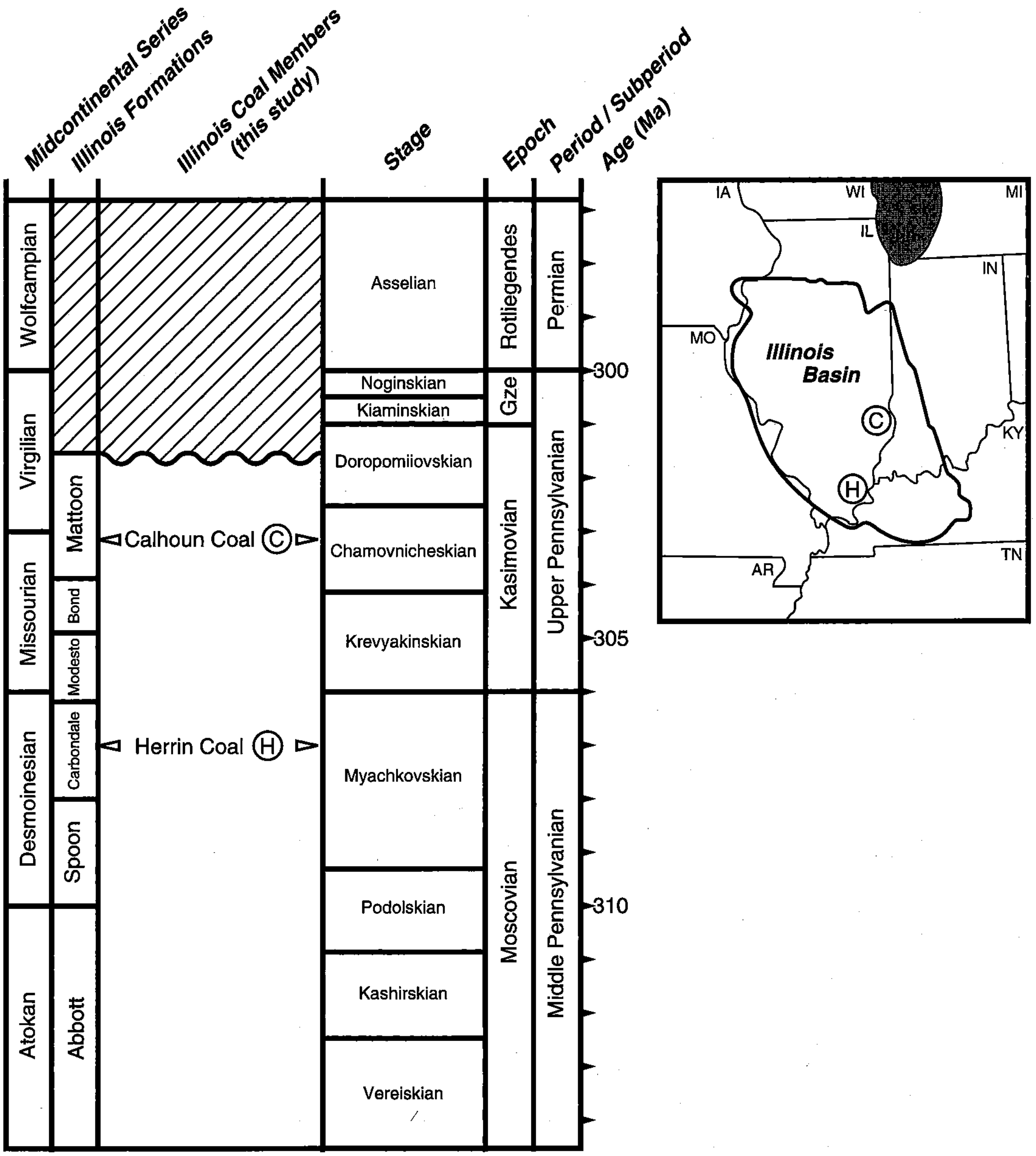
By contrast the Upper Pennsylvanian Calhoun Coal is a geographically restricted deposit of Late Pennsylvanian age. The Calhoun Coal occurs in the lower part of the Mattoon Formation (McLeansboro Group), and was deposited during the Dorogomilovskian Stage of the Kasimovian Series (HARLAND et al., 1990). In midcontinental North America this deposit occurs within the Missourian Series, equivalent to the Stephanian A Stage of European terminology (Text-Fig. 1; PHILLIPS & PEPPERS, 1984). This assignment is equivalent to an absolute age of 302 Ma (HESS & LIPPOLT, 1986).

### 2.2. Specimen Processing and Illustration Techniques

Coal balls were sawed from 3 to 5 cm thick slices, after which the cut surfaces were smoothed, and then etched for making acetate peels (PHILLIPS et al., 1976). All illustrated specimens originate from cellulose acetate peels and microscope slides of acetate peels, housed at the Paleobotany Laboratory of the University of Illinois at Urbana-Champaign (UIUC), Department of Plant Biology. Each peel has been assigned a UIUC identification number that designates accession number, cut surface, and number within a peel series.

#### 2.2.1. Photodocumentation

Photodocumentation was done by two different processes. Peels mounted on microscope slides were photodocumented by magnifications greater than 2X, using standard black-and-white, high contrast photography. The photographic apparatus was an Olympus SZH stereomicroscope attached to an automatic photographic system with Polaroid 4 × 5 film. Negative and print development was done by standard darkroom techniques. Images magnified by less than 2X were done by scanning an uncleared acetate peel at 300 dots per inch by a Hewlett-Packard ScatJet II flatbed scanner and a Macintosh computer. The images were imported into Adobe Photoshop™ software. Once within Photoshop™, the images were modified analogously to standard



Text-Fig. 1. Stratigraphic, geochronologic, and geographic context of the Herrin and Calhoun Coals. Correlations between Midcontinental chronostratigraphic and lithostratigraphic units, and European-based epochs and stages may be approximate in some cases. Abbreviation: Gze, Gzelian.

photographic techniques to achieve suitable contrast, resolution, and brightness. The processed scanned images were printed on linotronic film at 2700 dots per inch and at 150 lines per inch and then stripped onto photographic plates of line art illustrations.

### 2.2.2. Three-Dimensional Reconstructions

Three-dimensional reconstructions were rendered manually by camera lucida tracings of selected acetate peels at 6X magnification. For most same-surface reconstructions, the tracing of every fifth peel of a peel series was used. Of these, the first five camera lucida tracings, representing a composite of peels 1, 6, 11, 16, 21 and a coal-ball thickness corresponding to 25 peels, was assembled into a unit such that each successive peel was diagonally offset to the upper-right to provide a sense of depth. Three-dimensionality was achieved by connecting the same features within these five peel tracings, followed by fleshing with stipple shadowing to render the topography, orientation, and surface texture of structures such as coprolites, callus and unmodified parenchyma. Internal, undigested frass surrounding the coprolites were excluded from the reconstruction to allow for clarity in the recognition of each coprolite and various plant tissues. This process was repeated for reconstruction of a second unit representing the next five acetate peel tracings of the same specimen, namely peels 26, 31, 36, 41, 46, and so on. This method was used to reconstruct various specimens into a total of three (Figs. 9-12, 60-62, 70-72), five (Figs. 47-51) or six (Figs. 39-44) successive units.

There were two modifications of this general technique. First, specimens revealing the details of coprolite distribution in *Psaronius* trunk tissues (Figs. 13-16, 21-24) were prepared with the same technique as above, except every tenth peel was used, and the resulting reconstruction was rendered as a block figure and not as separated serial units. Second, continuous coal-ball specimens of *Psaronius* trunks and frond petioles were represented by successive cut faces of slices from the same coal ball. (Figs. 1-12, 28-38), providing a considerably coarser-grained perspective of insect-damaged plant organs.

### 2.2.3. Procedure for Measuring Coprolite Size

From three specimens displaying stem detritivory, large populations of coprolites were measured. The coprolites in these specimens were distributed in a random, three-dimensional orientation within the plant tissues. Consequently measurements of coprolite width and length for each sample population of coprolites asymptotically converged upon true coprolite size. The upper limit of the scatter plot distribution for each sampled population was taken as the maximum coprolite size. For those coprolites that were longitudinally to longitudinal-obliquely positioned, widths and lengths were measured as maximum diameters of minor and major axes, respectively. Such coprolites were ellipsoidal or parabolic in cross section, albeit sometimes truncated. For those coprolites that were transversely sectioned and displaying a circular or slightly ellipsoidal form, only widths (diameters) were taken. This protocol was also applied to measurement of plant anatomical structures, such as petiole diameters.

## 2.3. Definitions of Terminology

There have been disparate views on the structural circumscription of galls (STUBBS, 1987; SPOONER, 1990; REDFERN, 1992; MANI, 1992), depending on the number and specificity of the attributes included in the definition (WILLIAMS, 1994). We will use GAGNÉ's (1989: 90) more inclusive definition of a gall, as “ ... any predictable and consistent plant deformation that occurs in response to feeding or other stimulus by foreign organisms.“

We are using the term, larva, in its American and British, rather than Continental European, entomological and etymological usage, namely, to refer to any prepupal stage of a member of the Holometabola (see CHINA et al., 1958). Accordingly, the term, nymph, refers to the preadult stages of an insect that is not a member of the Holometabola (SNODGRASS, 1954; DAVIES, 1958).

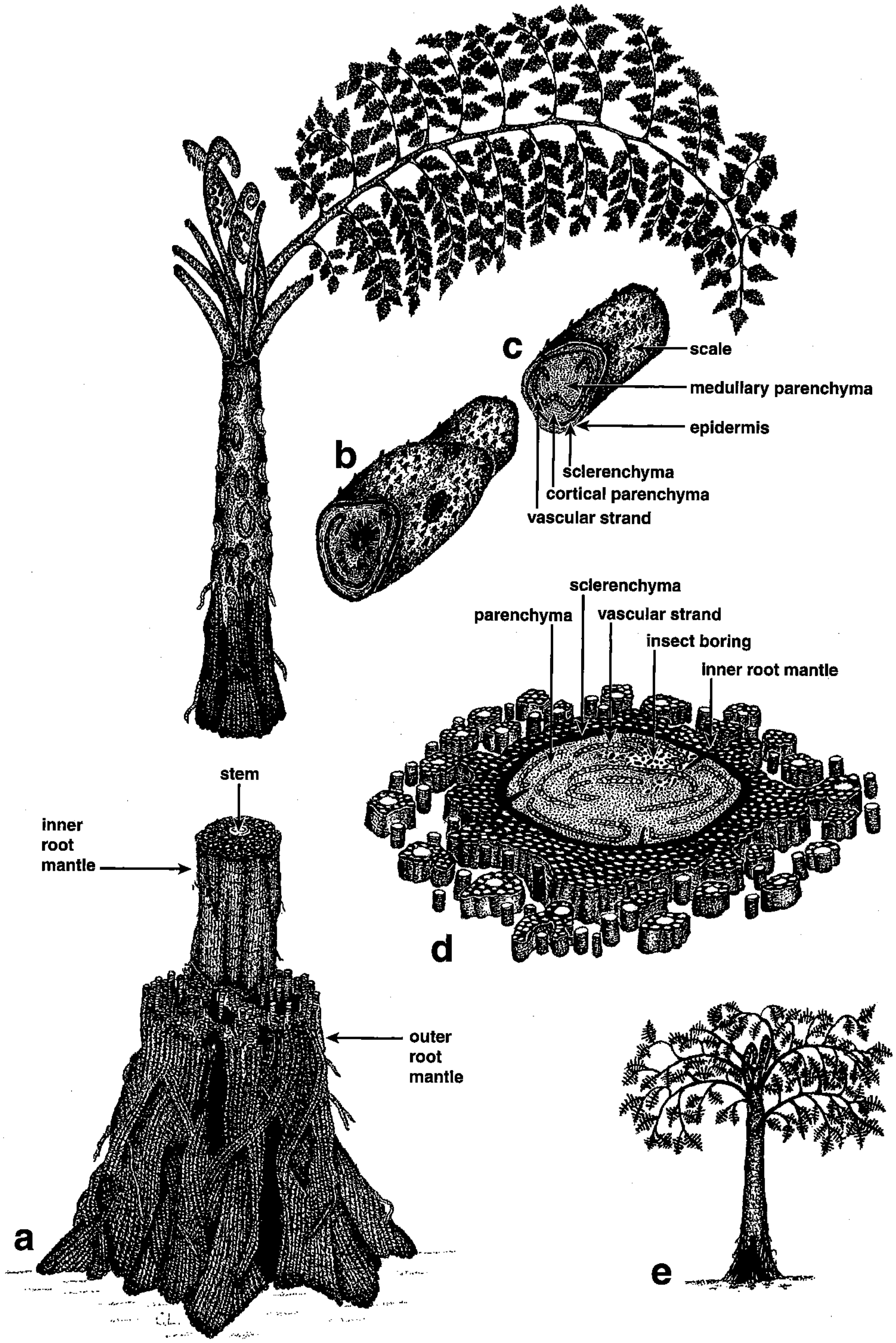
The term coprolite will define any type of insect excrement that has been preserved as a fossil, regardless of its size (WOOD, 1980; but see EL-BAZ [1968] for a size distinction). In this report, the preservational style is three-dimensional permineralization that reveals the tissue structure of coprolitic contents. By contrast, a fecal pellet, is recent insect excrement that has not been fossilized. The term frass is used to designate all products generated in the course of feeding, including fecal pellets, chewed but undigested plant tissue fragments, and potentially body parts. Undigested plant fragments are termed catachord (HEADRICK & GOEDEN, 1993). For lack of appropriate and analogous terms, the terms frass and catachord will also to refer to fossil material.

# 3. The Structure and Ecology of *Psaronius*

One of the most prominent and extensively studied members of Pennsylvanian swamp forests is *Psaronius*, a marattialean tree fern that was a subdominant component in some lycopod-dominated, late Middle Pennsylvanian coal swamp forests (Text-Fig. 2). *Psaronius* subsequently became dominant in these peat-forming wetlands after the extinction event that extirpated almost all Euramerican lycopod species at the end of the

Text-Fig. 2. Reconstruction of Late Pennsylvanian coal-swamp vegetation of the Calhoun Flora, from the Illinois Basin (c. 302 Ma). The large tree at center is *Psaronius chasei* MORGAN; to its side is *Medullosa* sp.; sigillarian lycopods and calamites occur in the background. Drawing by Mary Parrish.

Myachkovskian (PHILLIPS et al., 1974, 1985). In more elevated, deltaic and fluvial habitats with mineral soils, the ecological expansion of *Psaronius* commenced during the earlier Myachkovskian Stage, approximately 1.5 million years earlier than the corresponding ecological replacement in the lowland coal-swamp forests with peat soils (PFEFFERKORN & THOMSON, 1982). Because of the salient role that *Psaronius* provided in the structuring of later Pennsylvanian wetland communities, and particularly because of its paradigm role as a host for diverse interactions between a vascular plant and its consumers (two of which are recorded herein), this section provides a brief sketch of the biology of *Psaronius*.



Text-Fig. 3. Reconstruction of *Psaronius chasei* Morgan from a Late Pennsylvanian coal-swamp forest of the Illinois Basin. a: Sectioned view of trunk and portion of crown, including one complete frond. b: Basal region of petiole, showing a galled region. c: Basal region of petiole, showing an ungalled region. d: Cross-section of trunk (stem and root mantle), about one-third of the way from the base to the crown region, with stem-boring indicated. e: Younger sporophyte. The principal sources are Morgan (1959), Stidd & Phillips (1968), Stidd (1971), Ehret & Phillips (1977), and Stewart & Rothwell (1993).

### 3.1. Anatomical Description of *Psaronius*

*Psaronius* was a Paleozoic representative of the Marattiales, an ancient lineage of eusporangiate, homosporous ferns currently represented by six or seven genera of large, unbranched forms mostly with tuberous, erect stems and generally pinnately compound fronds as long as 4 m (Mabberly, 1993; Stewart & Rothwell, 1993). Modern marattialeans occur often near streamsides, in humid, lowland to midmontane, pantropical forests (Parris, 1976; Page, 1979). Most species of the Pennsylvanian to Permian *Psaronius* were columnar trees; some early forms were undoubtedly less than a meter tall (DiMichele & Phillips, 1977). Late Pennsylvanian species were up to 16 m tall (Stidd, 1974) and bore a basally-flaring trunk up to 1m in diameter supporting a crown of lacy, multipinnate fronds up to 6 m long that abscised basally (Text-Fig. 3a; Stidd, 1971; Rothwell, 1991). The basal trunk consisted of a relatively small, centrally located stem and a surrounding massive root mantle. The stem was circular to elliptical in cross-section and a few mm to cm in diameter basally, expanding upward to 13 cm in diameter apically (Morgan, 1959; Mickle, 1984b; Lesnikowska, 1989; see West [1917] for an example of a modern marattialean). The stem was usually surrounded by a well-developed, lignified sclerenchyma cylinder, which in turn was enveloped by outer cortical tissues and epidermis with scales (Morgan, 1959; Mickle, 1984b; Text-Fig. 3d). The polycyclic dictyostele of the *Psaronius* stem contained from two to ten or more vascular cycles (Moon, 1939; Stidd & Phillips, 1968; Rothwell & Blickle, 1982; Mickle, 1984b), each cycle of which consisted of amphiphloic, endarch-maturing meristeles bearing scalariform tracheids, parenchyma, and phloem (Morgan, 1959; Mickle, 1984b; Lesnikowska, 1989). The meristeles were separated from other adaxially-concentric meristeles of the same cycle by regularly arranged gaps of parenchyma, but were connected by strands of vascular tissue (West, 1917; Morgan, 1959; Stidd, 1974; Mickle, 1984b). Departing petiolar traces provided a characteristic dissected appearance to the dictyostele. Some histological variation occurred within the ground parenchyma among morphotypes, including the presence or absence of lysigenous lacunae, resin ducts, and tannin cells clustered around meristeles (Mickle, 1984b; Lesnikowska, 1989).

The *Psaronius* stem was largely supported by a root mantle consisting of a dense inner root zone that surrounded the stem subapically and increased in thickness and diameter basally (Text-Fig. 2; Morgan, 1959; Ehret & Phillips, 1977). Roots of the inner mantle zone adhered to each other by a matrix of interstitial parenchyma, in contrast to those of an outer root zone which were larger and mostly separate from each other (Morgan, 1959; Ehret & Phillips 1977; Mickle, 1984a). The outer root zone contributed most of the basal trunk diameter and produced lateral roots that penetrated the surrounding soil substrate and anchored the tree (Ehret & Phillips, 1977; Lesnikowska, 1989).

The canopy of *Psaronius* was constantly expanding in size during ontogeny (Mickle, 1984b). Frond emergence was characterized by croziers that were circinately unfurled to produce tripinnate or quadripinnate mature fronds usually 2 to 3m long. Individual fronds however exhibited transitions from a quadripinnate condition proximally to a monopinnate condition terminally (Stidd, 1971). Each frond axis, known as *Stipitopteris* (Grand'Eury, 1877), consisted of a basal petiole that became dorsally flattened as a rhachis distally (Text-Fig. 3b,c), pinnae of which bore *Pecopteris*-type foliage (Brongniart, 1828). Radiate synangiate fructifications on *Pecopteris* pinnules are known as *Scolecopteris* (Zenker, 1837) and contained spores that have been assigned to several form-genera (Courvoisier & Phillips, 1975; Lesnikowska, 1989). Combinations of these form-genera and some of their subsidiary form-species that refer to trunks, petiole/rhachis elements, fertile foliage, synangia, and spores have been assigned to particular, whole-plant, *Psaronius* species (Stidd, 1971; Mickle, 1984b; Lesnikowska, 1989; Pryor, 1993). Originally the form-genus, *Psaronius*, referred to certain Paleozoic marattialean trunks (Cotta, 1832), although it is now widely understood to refer to a whole-plant assemblage.

Entire fronds supported by *Stipitopteris* eventually abscised, leaving an outer ovoidal scar of sclerenchyma and a characteristic, inner U- or V-shaped scar representing the vascular tissue trace. The U- or V-shaped vascular strand configuration of the petiole distally acquired hooklike, enrolled ends, and eventually became W-shaped in cross-section, as it supplied the terminal part of the rhachis (Stidd, 1971, 1974). The *Stipitopteris* petiole and rhachis consisted almost entirely of parenchymatic ground tissue that embedded the vascular tissue (Text-Fig. 3c). The cellular orientation of this ground parenchyma paralleled the petiolar axis, had a bricklike appearance consisting of regularly arranged sheets of squarose to mostly rectangular cells, and was often interrupted by distinctive gum-sac cells, layered cells, tannin cells, or lacunae, depending on the *Stipitopteris* morphotype (Stidd, 1971; Lesnikowska, 1989). In some forms, polygonal, gum-sac cells with opaque, resinous interiors occurred sporadically throughout the parenchyma; in others layered cells containing dark contents that concentrically parallel the cell wall were deployed as a broad zone of sclerenchyma projecting adaxially from the vascular strand; whereas in others polygonal, pigmented, tannin cells were dispersed in the parenchyma (Lesnikowska, 1989, 1990). Lacunae of one morphotype occurred as cylindrical cavities in the parenchyma between the vascular strand and the sclerenchyma sheath (Lesnikowska, 1989).

## 3.2. *Psaronius* Autecology

As a subdominant or dominant plant in Pennsylvanian wetland ecosystems, *Psaronius* is important for understanding the autecology between a Paleozoic vascular plant and other associated plants. *Psaronius* is also the most intensively studied example of a Paleozoic plant host harboring a local insect community of detritivorous and herbivorous arthropods. The collective documentation of these diverse, autecological interactions between *Psaronius* and other organisms considerably exceeds current knowledge of any other Paleozoic plant.

### 3.2.1. Interactions With Other Plants

*Psaronius* was an important tree in Pennsylvanian coal-swamp and adjacent wetland ecosystems, and it apparently had important interactions with adjacent plants. Indirect inferences can be made from assessing changes in peat biovolume allocated to particular plant taxa in vertical transects of a single coal seam (e.g., Phillips et al., 1985; DiMichele et al., 1991; Pryor, 1993). Such studies indicate that in several abiotically unstable habitats *Psaronius* was a dominant genus.

An alternative approach for understanding the interactions of *Psaronius* with other plants is an examination of specific physical associations between *Psaronius* and other plants that may have used the scraggly root mantle as an anchor or for mechanical support. Because of anastomosing cavities created by the entangled fibrous roots of the outer root mantle, *Psaronius* was an ideal substrate for the penetration, attachment, and eventual anchoring of lianas, scrambling shrubs and possibly epiphytes (Mickle, 1984b). Physical evidence for an attached plant within the *Psaronius* outer root mantle comes from the fern *Tubicaulis berthieri* (Sahni, 1935) as well as *Ankyropteris scandens* (Stenzel, 1889) which were positioned "fairly high" on *Psaronius* trunks (Mickle, 1984b). Additional associates embedded in root mantle have been documented for taxa as diverse as the seed-fern liana *Medullosa endocentrica* (Pryor, 1993), the sphenopsid *Sphenophyllum* (Mickle, 1984b), the scrambling, seed fern *Callistophyton poroxyloides* (Pryor, 1993), and a possibly epiphytic fern, *Botryopteris forensis*, that bore large, globose fructifications (Rothwell, 1991). Notably, most of these associates possessed long, root-entrapped stems approximately 4.0 to 6.0 mm in diameter and were incapable of being structurally supported without *Psaronius* trunks for mechanical support and root mantle envelopment.

Evidence has been presented by Mickle (1984a) for decay of *Psaronius* stems basally while the stem apex continued to grow and expand its canopy foliage. Apparently sufficient nutrients and water was mobilized by the exterior root mantle to supply the middle and upper region of a stem. The decomposition of the basal stem probably provided ideal microhabitat space for the establishment and maintenance of commensal plants. Notably, this phenomenon also occurs in modern filicalean tree ferns such as *Cibotium, Sadleria*, and *Cyathea*, which have crowns "... that become epiphytes on their own dead stems" with water supplied by "... living and adventitious roots that grow down through the trunk into the soil" (Carlquist, 1975: p. 35, 36).

### 3.2.2. Interactions With Arthropods

Ongoing documentation of altered and damaged *Psaronius* tissues and coprolites that contain diverse *Psaronius*-attributed constituents provide evidence for the occurrence of five insect and mite functional-feeding-groups interacting with *Psaronius* during the Late Pennsylvanian (Labandeira & Beall, 1990; Labandeira, 1990b, 1998a, 1998b; Labandeira & Phillips, 1992, 1996a, 1996b). These functional-feeding-groups include generalized detritivory by oribatid mites and insects on decaying tissues (Scott & Taylor, 1983; Rothwell & Scott, 1983; Labandeira & Beall 1990; Phillips & Cross, 1991; Labandeira et al., 1997; see Section 5.0

herein) and four types of insect herbivore interactions. The herbivore functional-feeding-groups are (1) external-foliage-feeding, indicated by occasional coprolites found in peat litter with high concentrations of pecopteroid trichomes, (2) spore and sporangia consumption (SCOTT et al., 1985), indicated by the presence of *Psaronius*-attributed spores and sporangial walls, (3) petiole and rhachis galling in medullary parenchyma as discussed in Section 6.0 herein (also see LESNIKOWSKA, 1990), and (4) piercing-and-sucking as evidenced by stylet sheath tracks through petiolar cortical parenchyma (Figs. 42-44; LESNIKOWSKA, 1989; LABANDEIRA & PHILLIPS, 1996a). Currently no evidence exists for surface-fluid-feeding, although at least two extant marattialean genera bear petiolar nectaries (BONNIER, 1879; FIGDOR, 1891; FAHN, 1979). Leaf miners have not been documented on *Psaronius* foliage, although they have been suggested as culprits on contemporaneous seed-fern foliage (MÜLLER, 1982; LABANDEIRA & BEALL, 1990). Thus, an ecologically diverse assemblage of insects and mites were interacting in behaviorally stereotyped and tissue-specific ways with *Psaronius* during the Late Pennsylvanian. Although variations of the mandibulate and piercing-and-sucking mouthpart types constrained the spectrum of feeding modes by excluding the diverse surface-fluid-feeding strategies of modern insects (LABANDEIRA, 1990a), it is notable that frond pinnules, medullary petiolar parenchyma, vascular bundle sap, spores, and sporangia were all targets by herbivores (LABANDEIRA, 1998b). Additionally, postmortem stem parenchyma and various lignified tissues of the entire plant were consumed by detritivores.

*Psaronius* is a paradigm plant for Pennsylvanian plant/insect interactions. Despite examination of significant volumes of biomass in several Midcontinent and Appalachian coal-ball deposits, other plants of comparable stature, including sphenopsids and cordaites apparently lacked the broad spectrum of feeding damage found in *Psaronius*. Reasons for this relatively depauperate representation on other plants may include the presence of herbivore-deterring chemical defenses; the absence of extensive, nutritionally rewarding tissues which are replaced by wood in cordaites (COSTANZA, 1984) and to a lesser degree in lycopods (DIMICHELE, 1979); and rapid and weedy growth strategies (MICKLE, 1984a,b) that would hinder herbivore colonization. In spite of the relatively high level of herbivore attack of *Psaronius*, it was subdominant to dominant in Euramerican wetlands during the later Pennsylvanian.

### 3.3. *Psaronius* Synecology

Tropical to subtropical Euramerican coal swamps during the Pennsylvanian were basically structured by five, major taxa – lycopods, sphenopsids, seed ferns, tree ferns, and cordaites – each of which represented a physiognomic solution to existence in unstable, wetland habitats. Lycopods were dominant during the Middle Pennsylvanian whereas tree ferns became ecologically ascendant after the major extinctions at the end of the Middle Pennsylvanian (PHILLIPS et al., 1974, 1985; DIMICHELE et al., 1991). In these freshwater ecosystems, characterized by low pH and nutrient availability, anoxic soil conditions, and occasional to constant flooding, there was sufficient topographic and edaphic heterogeneity for the assembly of several community types. These species assemblages were primarily determined by the presence of standing water and soil moisture gradients that ranged from streamside, often inundated habitats to more emergent, better drained sites (DIMICHELE et al., 1991). Nevertheless, dominant plants from all communities were constructed of cheaply-designed structural tissues that provided for an arborescent growth-habit in unstable, nutrient-poor habitats (PHILLIPS & CROSS, 1991). For example, trunk rigidity was achieved variously among the major taxonomic groups not only by axially located wood, but to a great extent by other reinforcing cortical tissues such as sclerenchyma, bark, and massive root mantles. Of these constructional strategies, the dominant, pole-like lycopod trees were constructed mostly of bark (PHILLIPS et al., 1985). By contrast, *Psaronius* and medullosan seed ferns were subdominants in these forests (CROSS & PHILLIPS, 1990). For *Psaronius*, construction of a sclerenchyma-enclosed stem that lacked secondary tissues was an unique solution for achieving arborescence.

Under the regionally more drier and seasonal conditions of Late Pennsylvanian coal-swamps, *Psaronius* constituted approximately 75 percent of preserved peat by biovolume (PHILLIPS & PEPPERS, 1984; PHILLIPS et al., 1985). This dominance also extended to extrapaludal habitats (MICKLE, 1984b; PHILLIPS & CROSS, 1991; PRYOR, 1993) in sites with exposed but undoubtedly wet soils. Physiognomically, Late Pennsylvanian forests were dominated more by trees bearing nonsecondary supportive tissues than Middle Pennsylvanian coal-swamp forests, which were generally dominated by taxa structurally supported by bark and/or wood – namely lycopods or cordaites (CROSS & PHILLIPS, 1990). The coal-swamp forest represented by the Calhoun Flora was relatively nondiverse and geographically confined, compared to earlier, Middle Pennsylvanian forests such as the Herrin Flora. Although Euramerican, *Psaronius*-dominated, coal-swamp ecosystems largely disappeared during the end of the Pennsylvanian, *Psaronius* survived into the Permian in other equatorial paleocontinents, such as North China (Yao et al., 1994). However, by Early Permian time, *Psaronius* tree ferns coexisted with callipterid ferns, walchian conifers, taenopterid cycadophytes and gigantopterid pteridiphylls (Cross & Phillips, 1990).

## 4. Systematic Paleontology

According to recent changes in the third edition of the Code of Zoological Nomenclature (Ride et al., 1985) ichnotaxa are recognized as valid, as long as the described material are fossil and not the recent work of animals (see Rindsberg, 1990). Legitimate ichnotaxa include "… burrows, borings, galls, nests, worm tubes, cocoons, [and] tracks, …" (Ride et al., 1985: Art. 1a, 1b[7]; Glossary, p. 267, 276). Although type species are not necessary to fix ichnogenera, we are designating type species for each of our two new ichnogenera.

Several reasons support our choice to designate these unique feeding traces as Linnean binomials. The antiquity of each of these trace fossils virtually precludes the possibility that they will be rediscovered as a stem-boring or gall created by a modern insect taxon. Moreover, since there exists a tradition of naming Upper Paleozoic, insect-mediated plant damage as Linnean binomials (Vialov, 1975), including external-foliage-feeding (Amerom, 1966; Amerom & Boersma 1971), leaf mines (Müller, 1982), pollen-containing coprolites (Meyen, 1984; Rothwell & Scott 1988), and possible galls (Amerom, 1973), our designations formalize a more complete picture of the extent of Upper Paleozoic insect-plant interactions. Lastly, our formalized designations provide a useful, commonly understood name to which subsequent treatments of Paleozoic plant-insect interactions can refer to unambiguously (Chaloner et al., 1991).

### 4.1. Ichnogenus *Pteridiscaphichnos* Labandeira & Phillips, novum

Generic Diagnosis: Coprolite-packed borings in the stems of Paleozoic marattialean tree ferns consisting of anastamosing tunnels and galleries, resembling the habitation burrows of extant wood roaches and termites. Borings are characterized by the evacuation of parenchymatous tissues only and the avoidance of all other tissues.

*Pteridiscaphichnos psaronii* n. ichnosp.

Plate 1, Figs. 1–8; Plate 2, Figs. 9–12; Plate 3, Figs. 13–18; Plate 4, Figs. 21–27; Plate 16, Fig. 88

Derivation of name: Greek, *πτεριος* (a kind of fern) + *σκαπηος* (a hollowed-out structure) + *ιχνος* (track or trail) and *Psaronius*, the host plant of this trace fossil.

Holotype: UIUC slide 22,415 (Fig. 88), corresponding to UIUC coal-ball peel no. 38048-Cbot (see Figs. 2, 7, 13–16), is housed at the Paleobotanical Facility, Department of Plant Biology of the University of Illinois at Urbana-Champaign.

Type locality: Peabody Eagle Surface Mine, Shawneetown, Gallatin County, Illinois; Shawneetown 7½' Quad., Section 9, T10S, R9E.

Horizon: For UIUC-22622, 22686, 38048 (including holotype) and 38842: Kewanee Group, Desmoinesean Series, Carbondale Formation, Herrin (No. 6) Coal. For UIUC 10765: McLeansboro Group, Missourian Series, Mattoon Formation, Calhoun Coal. For OU-2111, 2117, and 2121-2123: Monongahela Group, Virgilian Series, Monongahela Formation, Redstone or Pittsburgh Coal.

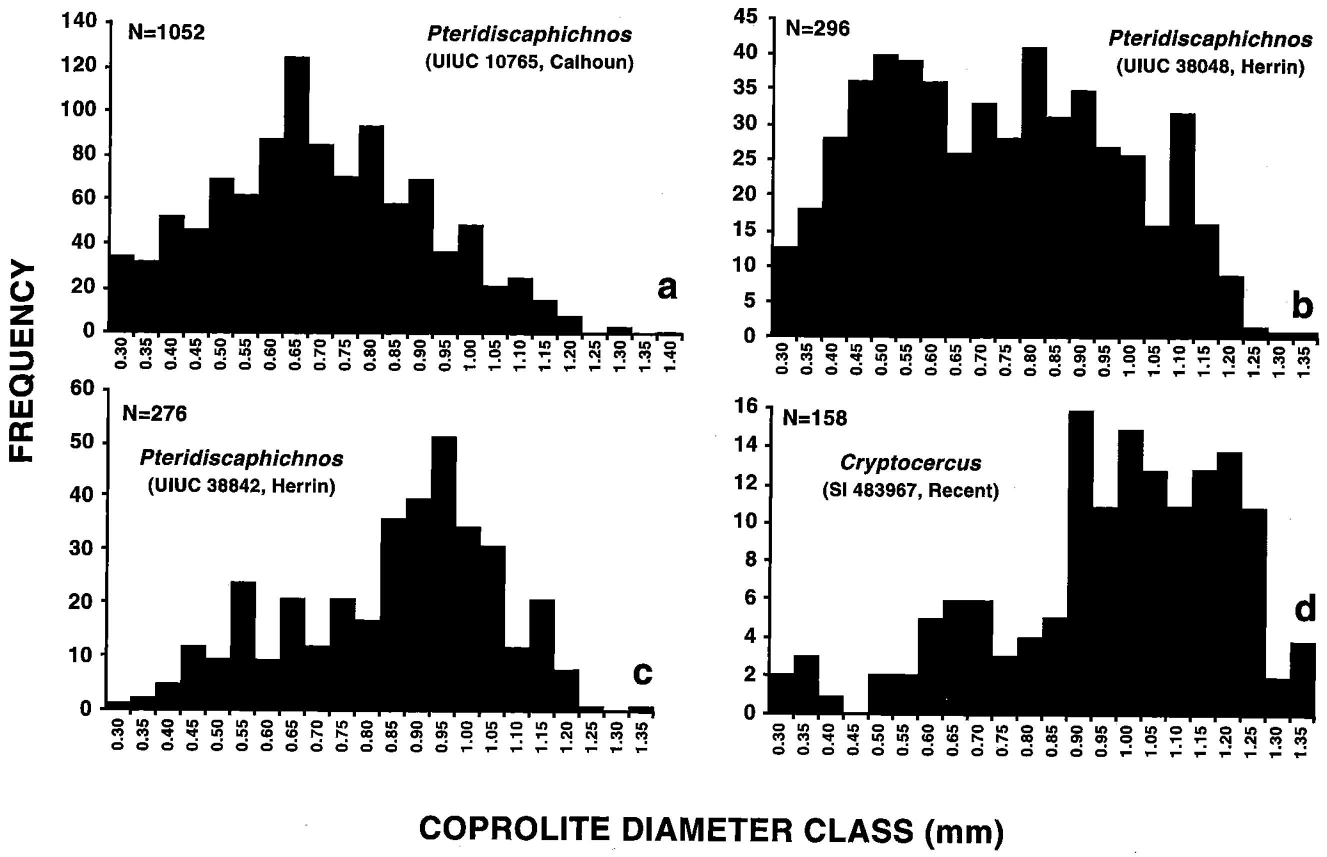
Age: Carboniferous Period, Pennsylvanian Subperiod; all specimens range from Middle to Upper Pennsylvanian, corresponding to the Myachkovskian and Chamovnicheskian Stages of Harland et al. (1990). This is equivalent to an geochronological age of approximately 307 to 300 Ma (Hess & Lippolt, 1986).

Occurrence: Five known specimens occur from the Illinois Basin on the "layered cells morphotype" (Lesnikowska, 1989) of the host plant *Psaronius chasei* Morgan 1959. One specimen (Rothwell & Scott, 1983), not studied for this report, is known from eastern Ohio on *Psaronius magnificus* (Herzer) Rothwell & Blickle 1982.

Referrable material:

1983: Scott & Taylor (Fig. 8B).
1983: Taylor & Scott (Fig. 5, top left).
1983: Rothwell & Scott (Plate I, figs. 1 to 9).
1990: Labandeira & Beall (Fig. 5D).
1992: Scott et al. (Figs. 13, 15).
2001: Labandeira (Fig. 1.3.9.4h).

This report. UIUC-22622 and 22686: Sahara Coal Co. Inc. Mine No. 6, near Carrier Mills, about 8 km SW of Harrisburg, Saline County, Illinois; Harrisburg 7½' Quad., SW 1/2, Section 19, T9S, R6E. UIUC-38048 and 38842: Peabody Eagle Surface Mine, Shawneetown,



Text-Fig. 4. Frequency distribution histograms of coprolite diameters for Late Pennsylvanian *Pteridiscaphichnos* and modern *Cryptocercus*. a: *Pteridiscaphichnos* (UIUC-10765) from the Late Pennsylvanian Calhoun Coal; b: *Pteridiscaphichnos* (UIUC-38048) from the Middle Pennsylvanian Herrin Coal; c: *Pteridiscaphichnos* (UIUC-38842) from the Middle Pennsylvanian Herrin Coal; d: modern *Cryptocercus* (NMNH slides 483967-9 and 483967-10) from North Carolina.

Gallatin County, Illinois; Shawneetown 7½' Quad., Section 9, T10S, R9E. UIUC-10765: Berryville, Lawrence County, Illinois; Sumner 15' Quad., SW 1/4, NE 1/4, NW 1/4 Section 7, T2N, R13W.

Specimen designations: UIUC = University of Illinois at Urbana-Champaign Department of Plant Biology (Paleobotany Collections), Urbana, Illinois; OU = Ohio University Department of Botany, Athens, Ohio.

Description: Borings consisting of galleries linked by tunnels in marattialean tree-fern stems, characterized by local and extensive excavation of ground parenchyma. Reaction tissue absent. Galleries and tunnels containing distinctive, ellipsoidal-elongate coprolites, macerated but apparently undigested, angular parenchyma fragments, and space subsequently replaced by calcite. Geometry of boring typified by galleries ranging up to 7 mm × 20 mm × 30 mm in dimensions, connected by tunnels apparently 2.5 mm in maximum width. Consumed tissue consisting only of ground parenchyma; adjacent inner root mantle, sclerenchyma and its internal extensions, and internal meristeles not consumed or otherwise altered. Parenchyma rich in gum sac cells avoided, but occasionally consumed.

Coprolites ellipsoidal-elongate in longitudinal section (maximum dimensions: 1.2 mm diameter × 4.0 mm long), circular to infrequently somewhat subhexagonal in cross-section (maximum diameter modes are 0.65 mm, 0.9 mm and 1.1 mm for UIUC specimens 10765, 38842 and 38048, respectively). Contents consisting entirely of packed cell walls of degraded parenchyma; some coprolites with periodic meniscate concentrations of packed cellular material, indicating multiple food boluses per original fecal pellet. Three-dimensional orientation of coprolites random in galleries; in tunnels coprolites arranged randomly or often end-to-end, in a file. Several instar stages are indicated by frequency histograms of coprolite diameters greater than 0.3 mm (Text-Fig. 4a-c).

Differential Diagnosis: See Section 5.4. for extensive treatment.

## 4.2. Ichnogenus *Pteriditorichnos* LABANDEIRA & PHILLIPS, novum

Generic Diagnosis: Galls containing frass and reaction tissue (callus) occurring in petioles of marattialean tree ferns. Characeristic axial lumen packed with distinctive cylindrical coprolites interspersed among angular fragments of macerated petiolar parenchyma; reaction tissue zone mostly surrounding the lumen and characterized by radiating tufts of distinctively modified cells within a larval chamber with maximum dimensions of 1.5 cm diameter by ca. 9 cm. long. Galls superficially resembling those of some extant symphytan Hymenoptera.

### *Pteriditorichnos stipitopterii* n. ichnosp.

Plate 5, Figs. 28–32; Plate 6, Figs. 33–38; Plate 7, Figs. 39–41; Plate 8, Figs. 42–44; Plate 9, Figs. 45–51; Plate 10, Figs. 52–59; Plate 11, Figs. 60–62; Plate 12, Figs. 63–69; Plate 13, Figs. 70–72; Plate 14, Figs. 73–80; Plate 15, Figs. 81–87; Plate 16, Figs. 93–95.

Derivation of Name: Greek, *πτεριος* (a kind of fern) + *τορος* (a borer) + *ιχυος* (track or trail), and *Stipitopteris*, the form-genus of the host organ that encapsulates this trace fossil.

Holotype: UIUC-slide 22,634 (Fig. 93), corresponding to peel no. 8227-Bbot (see Figs. 39–44), is housed at the Paleobotanical Facility, Department of Plant Biology of the University of Illinois at Urbana-Champaign.

Type locality: Berryville, Lawrence County, Illinois; Sumner 15' Quad., SW 1/4, NE 1/4, NW 1/4, Section 7, T2N, R13 W.

Horizon: McLeansboro Group, Desmoinsean Series, Mattoon Formation, Calhoun Coal.

Age: Carboniferous Period, Upper Pennsylvanian Subperiod, corresponding to the Kasimovan Stage. This is equivalent to a geochronological age of approximately 302 Ma (LIPPOLT & HESS, 1986).

Occurrence: Twenty-eight known specimens occur on the host plant *Psaronius chasei* MORGAN 1959.

Referrable material:

1971: STIDD, Plate 26 (Figs. 86, 89, 90; Plate 27, figs. 92–94, 97, 99; Plate 28, figs. 100–104; ?Plate 31, figs. 138, 139).
1989: LESNIKOWSKA (Figs, 46–49).
1990: LESNIKOWSKA (Fig. 2, a to e).
1996b: LABANDEIRA & PHILLIPS (Fig. 1).
1998b: LABANDEIRA (Fig. 1a).
1999: LABANDEIRA (Fig. 12b).
2001: LABANDEIRA (Fig. 1.3.9.4e).

This report: UIUC 2865, 7165, 7167, 7253 and 8227; USNM 483609 (4 specimens), 483610, 483611 (2 specimens), 483612, 43613 and 483614: Berryville, Lawrence County, Illinois; Sumner 15' Quad., SW 1/4, NE 1/4, NW 1/4, Section 7, T2N, R13 W. UIUC 30814, 30823 (2 specimens), 30839, 31010, 31205, 31272 (3 specimens), 31939, 35206, 35248: Calhoun, Richland County, Illinois; Sumner 15' Quad., NE 1/2 Section 32, T3N, R14W.

Specimen designations: UIUC = University of Illinois at Urbana-Champaign Department of Plant Biology (Paleobotany Collections), Urbana, Illinois; USNM = National Museum of Natural History Department of Paleobiology, Washington, D.C.

Description: Galls ranging from 1.0 to 2.5 cm in diameter, occurring along medial longitudinal axes of tree-fern petioles, proximal to their trunk attachment. Reaction tissue (callus) present. Galls characterized by an axial lumen up to 1.5 cm in maximum diameter, created from excavated ground parenchyma, and surrounded by a distinctive reaction tissue organized into centrally-directed tufts of reaction tissue consisting of parallel files of hypertrophied and frequently hyperplasic cells. Reaction tissue also distinguished by thin cell walls, cell axes directed radially toward petiolar axis, a glassy texture, and wisps of opaque material (trapped mucilage) occurring between adjacent tufts. Reaction tissue zone generally surrounds the central lumen up to a thickness of 0.5 cm, although occasionally it is absent. Rare exit holes and bite marks in reaction tissue present (Figs. 66, 95).

Axial lumen bears frass of distinctive coprolites and macerated parenchyma, and space subsequently replaced by calcite. Coprolites barrel-shaped, often fragmented, consisting of digested, unmodified parenchyma (including distinctive gum sac cells with recognizable opaque centers) and digested reaction parenchyma. Shape cylindrical, about 1.7 times longer than diameter, distinguished by circular cross-sections and smooth longitudinal surfaces but ragged transverse surfaces at ends. Diameters range from 1.0 to 3.5 mm, but deployed in three (instar-related) size classes with diameter modes at 1.5, 2.2 and 2.7 mm. Abundant parenchyma frass interspersed among coprolites and space in lumen, consisting of wedge- and spindle-shaped fragments of extracted unmodified and reaction parenchyma.

Differential Diagnosis: See Section 6.5. for extensive treatment.

## 5. *Pteridiscaphichnos*, an Early Stem-Boring

In this section we establish the defining characteristics of a stem boring, provide an overview of the ecology of modern stem-borers in ferns, and then describe the distinguishing features of *Pteridiscaphichnos*. We then focus on possible culprits that may have been responsible for *Pteridiscaphichnos*, provide evidence that a cockroach-like insect created this distinctive boring, and conclude by documenting the current knowledge about the fossil record of stem-boring and the ecological implications of *Pteridiscaphichnos*.

### 5.1. Modern Borers and the Definition of a Stem Boring

Endophytic insects that bore into relatively hardened plant tissues possess particular body morphologies for living within highly structured, three-dimensional tissues (CYMOREK, 1968). They also bear trophic specializations for processing lignified or other indurated tissues as food sources (MEESS, 1924; CYMOREK, 1968). These adaptations are a consequence of subsisting on a food source that is of very poor quality (SOUTHWOOD, 1973; WOOD, 1978; MARTIN, 1983, 1991). Lignified tissues frequently must be nutritionally enhanced by the establishment of plant-fungal interactions for exploitation by xylophagous stem borers (NORRIS, 1978; MADDEN & COUTTS, 1978). In these associations between the insect and the tunnel-dwelling fungus, there often is a symbiosis, in which the insect disperses spores in return for a higher quality fungal food than nutritionally poor, unaltered wood (CROWSON, 1984; GILBERTSON, 1984).

As an endophytic functional-feeding-group, the autecological breadth of borers ranges from boring through fresh coniferous or dicotyledonous wood, often to the detriment of the plant host (HICKIN, 1975; MAMAEV, 1977; CROWSON, 1981), to boring through the comparatively softer pith parenchyma of grasses, aquatic reeds and ferns (GRAY, 1970, 1972), and tunnelling in subterranean roots (GREHAN, 1989). In all instances borers are differentiated from gallers that may occur in the same tissues by the lack of plant reaction tissue (DREGER-JAUFFRET & SHORTHOUSE, 1992). Borers frequently are located in an axial plant organ, such as a root, stem or reproductive strobilus, and are thus ecologically differentiated from miners, which occupy tissues such as leaves, floral appendages and two-dimensional epidermal surfaces on stems and other organs. Miners, like borers, do not induce reaction tissue (HERING, 1951). Accordingly a borer is defined as an endophage occurring in tissues of axial plant organs that does not induce response tissue from its plant host.

The lack of response tissue in borers is attributable to several causes: (i) either the tissue being bored is dead within a living plant, such as punky wood, or (ii) the tissue is alive but does not respond to the endophage, or (iii) the plant and thus its constituent tissues are recently dead, a condition that may not differ significantly from a live host for many borers. These tissues are generally nutrient poor. Although many endophytic arthropods consume more nutritionally rewarding meristematic tissues, including various stem cambia (SPENCER, 1990), their usual designation as "cambium miners" is more appropriately rendered as cambium borers (HERING, 1951; REDFERN & ASKEW, 1992). Thus, the distinction between a borer and a miner sometimes is tenuously delimited, and instances of autecologic shifts from one functional-feeding-group to the other are known in species with hypermetamorphic larvae. In such species, one instar may occupy and feed on a different organ than a previous instar within the same host plant.

### 5.2. The Ecology of Borers and Modern Ferns

Many modern ecosystems contain ferns, including lianoid, epiphytic and arborescent species, as prominent components. On tropical and subtropical islands and on continents at higher, climatically equitable elevations in the tropics, ferns frequently are subdominant and dominant elements in undergrowth and in tree canopies (PAGE, 1979). Although most attention on fern herbivory has centered on bracken (see Section 6), there is considerable documentation for the importance of detritivores in the decomposition of organs, especially stems, petioles and rhachises, from diverse fern taxa (SWEZEY, 1922, 1954; ZIMMERMAN, 1948; SCHEDL, 1968; MAY, 1973; KUSCHEL, 1982; PAULAY, 1985). One of the historically most studied subtropical ecosystems with a high proportion of fern species is Hawai'i, in which ferns, especially cyatheaceous tree ferns, form dominant elements (SWEZEY, 1954) in a closed canopy, montane, wet forest known as *Metrosideros/Cibotium* Tree Fern Forest (WAGNER et al., 1990). Additionally, herbaceous and shrub-statured native Hawaiian ferns form an important component of the ground cover (WAGNER et al., 1990).

In Hawai'i, a diverse detritivore community of insects is responsible for the transformation of live fern tissue into organic litter. Host-specific borers of *Cibotium* tree ferns, including at least 25 species of aglycerid and curculionid weevils (SWEZEY, 1922, 1954; HOWARTH & MULL, 1992), invade petioles and trunks and consume parenchymatous tissue in various stages of decay. Other associates include nitidulid beetles (SHARP, 1881; SWEZEY, 1954), yponomeutid and pyralid larvae (MEYRICK, 1935; SCOBLE 1992), and, as external feeders, minimally six species of the sap-sucking, cixiid bug *Oliarus* (SWEZEY, 1906, 1922). Although adult and larval weevils and larval lepidopterans bore extensively as they consume fern parenchyma soon after plant death, little is known of their autecologies, such as their feeding pattern within rhachises and trunks. Since Hawai'i lacks native termites, cockroaches and webspinners (HOWARTH & MULL, 1992), it is highly likely that these orthopteroid detritivores, frequently associated with pteridophyte decomposition in other regions, are replaced by holometabolous insects in Hawai'i.

In the subtropical Caribbean region, there has been modest documentation of insect associates on dead fern axes, much of it collated and summarized by ROTH & WILLIS (1960). At least seven genera of cockroaches are associated with decaying frond bases or trunks of ferns (Anonymous, 1893; HEBARD, 1917, 1920; SEÍN, 1923; REHN & HEBARD, 1927; PRINCIS & KEVAN, 1955), including species that apparently construct tunnels in parenchyma of tree-fern stems. Interestingly, freshly fallen monocot trees that lack wood and achieve structural support by fiber bundles and sclerenchyma, such as banana, various palms and bamboo, are frequented by the same cockroach species typically found in tree ferns. Other arthropod taxa, such as mites and millipedes, have been documented in decaying fern tissues in tropical and subtropical ecosystems (GERSON, 1979).

In temperate regions the insect-mediated decomposition of fern rhizomes has been most extensively studied in England (ELTON, 1966; FRANKLAND, 1966, 1976) and, to a lesser extent, the United States (Beer 1955; Roth & WILLIS, 1960). Again, many of these studies have focused exclusively on bracken. In England, bracken forms the dominant component in the physiognomically distinctive Bracken/Bramble Glade Community (ELTON, 1966). Bracken pinnules, rhachises and stems accumulate as litter that slowly changes into peaty humus (TANSLEY, 1939) – a situation which inhibits the establishment of other plants. In this community bracken litter harbors glomerid millipedes that consume bracken tissue that have been degraded by fungi (VAN DER DRIFT, 1950). Other fauna associated with bracken petioles and stems include oribatid mites, diverse collembolans, and other millipedes (FRANKLIN, 1966, 1976; KÜHNELT, 1976). The bracken detritivore fauna is considerably more diverse than the adjacent fauna on decomposing dicotyledonous litter (ELTON, 1966).

The insect that provides a close ecological analog to *Pteridiscaphichnos* is *Cryptocercus*, a cockroach which penetrates slightly decomposing to punky logs of dicotyledonous and coniferous woods at low to high elevations of the Appalachian Range (CLEVELAND et al., 1934; SEELINGER & SEELINGER, 1983; NALEPA, 1984, pers. comm.) and the Pacific Northwest (CLEVELAND et al., 1934). *Cryptocercus* nymphs and adults produce a complex, anastomosing gallery system oriented parallel to the wood grain that is occasionally interconnected by transverse tunnels (NALEPA, 1984). Although the phylogenetically related termites (GRASSÉ & NOIROT, 1959; THORNE & CARPENTER, 1992) consume both live and dead tissue of both woody and herbaceous plants (WOOD, 1978), termites are not known to bore into live or dead fern petioles, although this is possible because of their broad dietary spectrum and several species are known as feeders in decomposing plant litter (SNYDER, 1915; WOOD, 1978). By contrast, numerous ant species throughout the tropics are mutualists in the rhizomes of polypodiaceous ferns (YAPP, 1902; GÓMEZ, 1974; BEATTY, 1985; HÖLLDOBLER & WILSON, 1990).

### 5.3. Stem Boring Structure and Host of *Pteridiscaphichnos*

Two distinctive features are associated with *Pteridiscaphichnos*. First is the unique structure of the boring and its contents. Second is the occurrence of the gallery and tunnel network only in the stems of Middle to Late Pennsylvanian *Psaronius* trunks from the Illinois and North Appalachian Basins. The unique structural features and host specificity of *Pteridiscaphichnos* collectively define it as a distinctive stem boring on a singular host taxon in time and space.

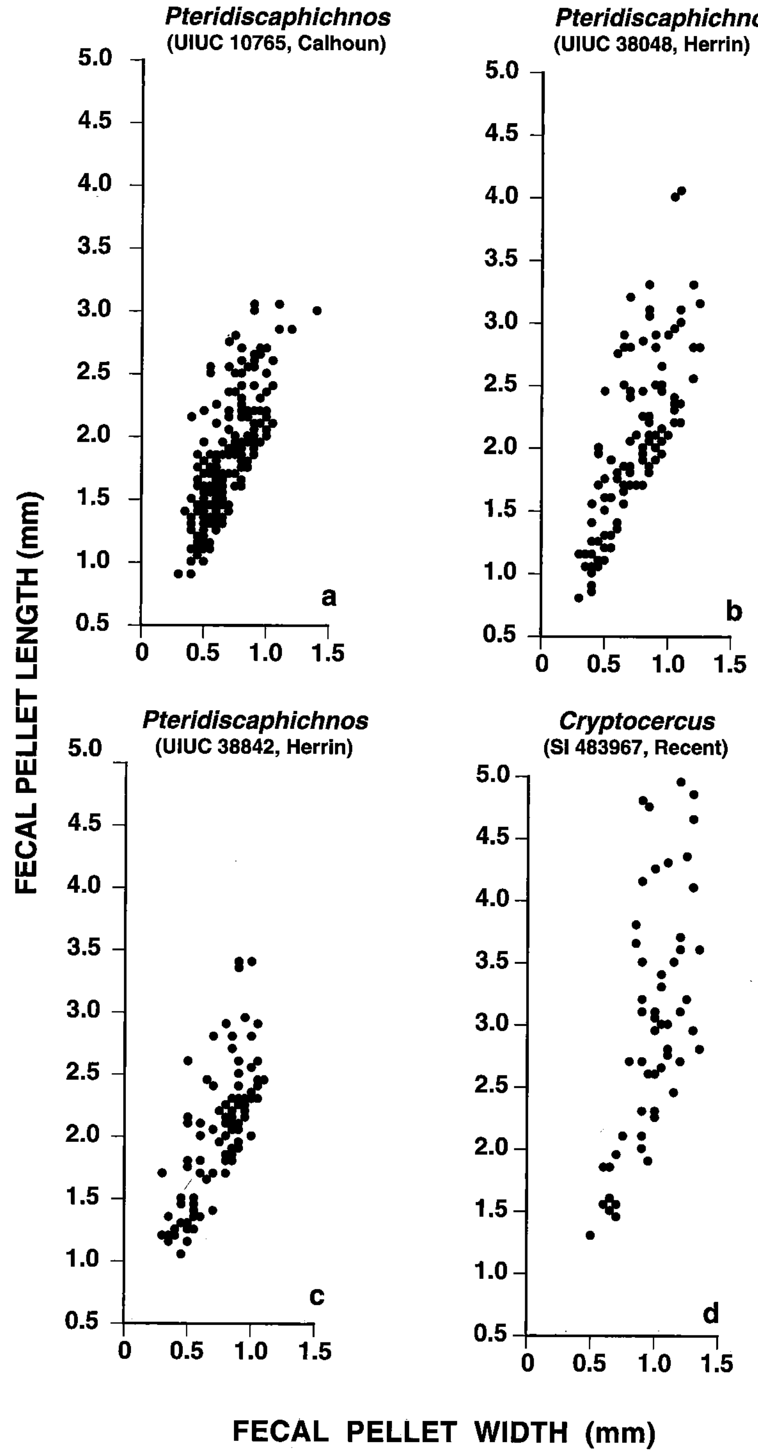
### 5.3.1. Structure of the Boring

Of the structural criteria that define *Pteridiscaphichnos* as a stem boring, there are two categories of evidence. First is a system of galleries and tunnels excavated from parenchyma that are bounded by relatively resistant tissues (Figs. 1–17, 21–26), and second is the resulting coprolites of highly constant shape and internal structure occurring as clusters in galleries (Figs. 18, 25–27) and often serially in tunnels (Fig. 19). These two structural criteria occur repeatedly for each of our five studied specimens of *Pteridiscaphichnos*. It also occurs for a specimen from the North Appalachian Basin (ROTHWELL & SCOTT, 1983), also referrable to *Pteridiscaphichnos*.

*5.3.1.1. Gallery Geometry.* The arthropod-mediated borings occur in the upper regions of *Psaronius* stems that ranged from approximately 6 cm (UIUC-38842) to 13 cm (UIUC-10765) in diameter. The borings are located within the stem parenchyma of *Psaronius* and consist of relatively expansive galleries linked to each other by narrower tunnels (Figs. 1–8, 21). Both galleries and tunnels are physically bounded by abundant vascular tissue arranged in laminate meristeles that parallel the stem axis, and by an external sclerenchyma sheath and its occasional internal extensions, which separates the stem proper from an adventitiously-produced root mantle (Figs. 1–17, 21–26). Gallery size and shape is variable and consist of dense accumulations of mostly randomly-oriented coprolites formed by the consumption of stem parenchyma in enclosed regions (Figs. 13–18, 21–26). These enclosed regions of relatively soft and nutritious parenchyma are bounded by resistant lignified or otherwise indurated tissues; entrance into and from these galleries were afforded by gaps in the sclerenchyma or xylary tissue where there was a continuity of stem parenchyma (e.g., Figs. 13–16). Like the variable dimensions of the galleries, tunnel diameters range from a minimum width of 2.0 mm for Middle Pennsylvanian, Herrin specimens UIUC-38048 and 38842 (Figs. 1–8, 13–16, 21) to 6.0 mm and 9.0 mm for Herrin specimens UIUC-22622 and UIUC-22686, respectively. However, in the Late Pennsylvanian, Calhoun specimen UIUC-10765 (Figs. 9–12, 21–26) and apparently the Redstone specimens OU-2111, 2117, and 2121 to 2123 (ROTHWELL & SCOTT, 1983), stem parenchyma was extensively consumed, obliterating original tunnels. The tunnels are several times the width of their largest constituent coprolites; presumably an average width of 4 to 6 mm approximates the greatest cross-sectional dimension of the arthropod borer. It is apparent that the geometry of *Pteridiscaphichnos* is controlled by the location of three major stem tissues: parenchyma which is consumed, creating the space for galleries and tunnels, and the much more solid sclerenchyma and xylary tissue which is avoided and forms the encircling walls.

Since the geometry of the gallery-and-tunnel network is largely determined by the xylary and sclerenchymatous anatomy of the *Psaronius* stem, it has a certain predictable quality. Galleries largely occur in parenchymatous regions subtended by C- or U-shaped sclerenchyma sheaths in departing frond traces (Figs. 2, 3, 6, 7, 13–17, 21–24; see also STIDD, 1971); although they are not as highly stereotyped as the axially-located *Stipitopteris* galls (see Section 6). Typical dimensions for any one traceable, complete gallery is approximtely 2.0 cm by 2.5 cm (Figs. 2–6, 13–16). Unlike the location of the expansive galleries, much of the tunneling is randomly determined and probably represents opportunistic pathways of consumable parenchyma delimited occasionally by surrounding resistant tissues. Tunnels generally avoid the mucilage-rich concentrations of gum sac cells external to the outer phloem of meristeles, described as "layered cells" by LESNIKOWSKA (1989). No evidence of callus and of exit or entry channels have been found, despite extensive searching. Additionally there is no indication of fungal symbioses involved in cellulolytic breakdown; apparently only nonlignified, parenchymatic tissue was consumed.

*5.3.1.2. Frass.* In addition to gallery-and-tunnel geometry, coprolites and interspersed fragments of comminuted but undigested plant tissue characterize *Pteridiscaphichnos* (Figs. 18, 25–27). The cylindrically elongate coprolites have rounded to bluntly tapering ends and occur in both galleries and tunnels of *Pteridiscaphichnos*. Their orientation within the galleries is generally random, but they occasionally occur in parallel or subparallel fashion, as serially arranged elements (Figs. 13–16, 21–24). Their shape is generally circular in cross-section, although a minor fraction appears subhexagonal to even hexagonal (Fig. 27). The coprolites possess smooth, uninterrupted surfaces and do not bear the longitudinal sulci of many holometabolous larvae (WEISS & BOYD, 1950, 1952). Internally, unlike the irregular shapes of apterygote fecal pellets, most coprolites are homogenous, consist of randomly packed, mostly identifiable cell-wall material of stem parenchyma. There is no evidence for the incorporation of xylary tissue, sclerenchyma fibers or the distinctive gum sac cells (LESNIKOWSKA, 1989) in these coprolites. A significant fraction of coprolites have a periodic, densely packed,



Text-Fig. 5. Bivariate scatter plot of coprolite width and lengths for Pennsylvanian *Pteridiscaphichnos* and modern *Cryptocercus*. a: *Pteridiscaphichnos* (UIUC-10765) from the Late Pennsylvanian Calhoun Coal; b: *Pteridiscaphichnos* (UIUC-38048) from the Middle Pennsylvanian Herrin Coal; c: *Pteridiscaphichnos* (UIUC-38842) from the Middle Pennsylvanian Herrin Coal; d: modern *Cryptocercus* (UMNH slides 483967-9 and 483967-10) from North Carolina.

meniscate structure that is indicative of the sequential incorporation of separate food boluses into a single fecal pellet during formation (Fig. 20; FROST, 1928). Other coprolites are serially and sequentially arranged within a tunnel, separated by small spaces, indicating either continual extrusion of separate fecal pellets in rapid succession by the same individual or extrusion at longer intervals of time by a relatively immobile individual (Fig. 19). Both phenomena – coprolites with internal packing, and the serial arrangement of coprolites within a tunnel – indicate periods of continuous feeding by the borer. All *Psaronius*-enclosed coprolites are intact and did not undergo prepreservational brittle fracture, dessication or oxidation, unlike many coprolites in the surrounding litter.

Coprolite size is highly variable, representing a tenfold size increment between the smallest and largest size classes. Populations of coprolites with only circular to subhexagonal cross-sectional areas from UIUC specimens 38048, 38842 and 10765, as well as the modern woodroach *Cryptocercus*, are plotted on a bivariate plot (Text-Fig. 5). Size scaling within these size classes is positively allometric. When populations from each of the three *Pteridiscaphichnos* specimens and modern *Cryptocercus* are plotted univariately (Text-Fig. 4), there is some evidence for slightly size-overlapping instar stages, a phenomenon which has been documented for fecal pellets of various insects (GOSSWALD, 1935; NOLTE, 1939; SARDESEI, 1969). Maximum dimensions of the coprolites from the presumed adult instar is 1.0 × 3.1 mm for all three coal-ball samples (Text-Fig. 5), with rare coprolites approaching 4.0 mm long without any change in width. Together with coprolite shape, these dimensions are consistent with fecal pellet sizes from many modern nonholometabolous clades, particularly orthopteroids (Text-Figs. 4, 5; CLEVELAND et al., 1934; WEISS & BOYD, 1950; SCOTT, 1964; VASU, 1965; BHATIA & CHANDRA, 1967).

It is noteworthy that uncharacteristic, apparently macerated, parenchymatic material occurs among coprolites within *Pteridiscaphichnos*. The presence of undigested plant tissue fragments is known for a wide spectrum of modern insect borings (HICKIN, 1975; MAMAEV, 1977; PEARCE 1987). The infilling of gallery space with comminuted plant fragments is consistent with our interpretation of *Pteridiscaphichnos* as an insect boring.

### 5.3.2. Host Specificity

The known occurrence of *Pteridiscaphichnos* is confined to the "layered cells" morphotype of *Psaronius* from the Middle Pennsylvanian Herrin Coal of the Illinois Basin (LESNIKOWSKA, 1989), to the Upper Pennsylvanian *P. chasei* MORGAN 1959 from the Calhoun Coal of the Illinois Basin, and *P. magnificus* (HERZER) ROTHWELL & BLICKLE 1982 from the Redstone Coal of the North Appalachian Basin (Text-Fig. 6). Despite extensive scanning of plant organs in these and other Pennsylvanian coal-ball deposits, this interaction has not been found in any other plant species, including seed ferns, calamites, lycopods and cordaites. The taxonomic specificity of *Pteridiscaphichnos* on *Psaronius* is also paralleled by its predilection for stem parenchyma and the avoidance of more resistant, less nutritious tissues in the same host organ. The location of damage of all five *Psaronius* individuals is toward the upper, canopy end of the trunk, since both Middle Pennsylvanian specimens contain relatively thick stems and a consistently thin inner root mantle (1.5 cm for UIUC-22622, 2.0 cm for UIUC-22686, 1.0 cm for UIUC-38048, and 0.6 cm for UIUC-38842) and damage on the larger Upper Pennsylvanian specimen only bore a root mantle thickness of 2.5 cm. Although other documented examples of *Psaronius* individuals with much thicker inner root mantles exist for other specimens of these species (MORGAN, 1959), they invariably contain hollowed stems resulting from rotting of the stem while the plant was alive (MICKLE, 1984a). CARLQUIST (1975) has documented the same phenomenon in modern filicalean ferns. Thus, confinement of *Pteridiscaphichnos* to the upper stem axis, near the canopy may be a consequence of in vivo rotting of the lower trunk region – a feature noted in extant marattialean ferns (SHOVE, 1900). It is noteworthy that this interaction type occurs in both the "layered cells" morphotype of *Psaronius* from the Middle Pennsylvanian and *P. chasei* and *P. magnificus* of the Late Pennsylvanian; it is not known from other *Psaronius* species. This may suggest a connection within one or more anagenetically evolving lineages (Text-Fig. 6).

The specificity of *Pteridiscaphichnos* for *Psaronius* hosts is based on (i) a taxon-specific preference, (ii) a preference for a particular tissue type to the exclusion of other tissues in the same organ, and (iii) apparent selection for stems exceeding a minimum diameter that are closer to the canopy than they are to the ground. While such pronounced, host plant specificities are unusual for detritivores in modern ecosystems (DETHIER, 1954; ROTH & WILLIS, 1960; FUTUYMA, 1976; WOOD, 1978), it is possible that this interaction represents an early glimpse into a novel detritivore life-habit by a large arthropod entering a new functional-feeding-group via stem-boring. Since modern ecologic analogs use intestinal bacteria and protozoans for breakdown of plant tissues

Modern diplopods are a dominant macrodetritivore component in most terrestrial ecosystems (KÜHNELT, 1976; WALLWORK, 1976; CRAWFORD, 1992), and are instrumental in decomposing leaf and stem litter in grassland (BAILEY & MENDONÇA, 1990) and forest (ROMELL, 1935; LYFORD, 1943; MARCUZZI, 1970) soils. This ability has been documented for log decomposition, where diplopods are frequently found in cavities of rotted wood (BLACKMAN, 1922; BANERJEE, 1967). Significantly, decomposition of bracken by diplopods in temperate forests is well documented (ELTON, 1966; FRANKLIN, 1966), including the tendency to inhabit decaying petioles (ELTON, 1966; FRANKLIN, 1976) and stems (KÜHNELT, 1976) for either food, shelter, or both. Whereas ellipsoidal to cylindrical diplopodan fecal pellets, particularly glomerids, polydesmids and julids (ZACHARIAE, 1965; MARCUZZI, 1970; SLEEMAN & BREWER, 1972; PAULUSSE & JEANSON, 1977; RUSEK, 1985) are similar in geometry to those described for *Pteridiscaphichnos*, other shapes are known, such as the truncated cones of *Glomeris* (ZACHARIAE, 1965; NICHOLSON et al., 1966). Based on the ecological evidence from Pennsylvanian and Recent ecosystems, the only credible myriapod fabricator of *Pteridiscaphichnos* is a very small, adult, julid diplopod with a maximum body width of approximately 4 to 6 mm, given the estimated diameter of the *Pteridiscaphichnos* tunnel system that link the galleries. Tunnel widths of modern *Cylindroiulus* vary between 1.0 and 1.5 mm in soils dominated by *Aesculus* leaf litter (PAULUSSE & JEANSON, 1977).

### 5.4.2. Parainsecta

Parainsects encompass proturans, collembolans and possibly diplurans (KUKALOVÁ-PECK, 1987, 1991), all of which are microarthropods occurring in litter-rich, subcortical and fungal microhabitats (ANDRÉ, 1983). Proturans bear piercing mouthparts, are liquid feeders, and are poorly known ecologically, although some species are known to pierce mycelia for food (KÜHNELT, 1976; MOORE, 1988). Some are known to subsist on ferns (HEUNGENS, 1967). Collembolans are considerably better known, consuming plant litter altered by various epiphyllous and endophyllous fungi, as well as the fungi itself, in the form of mycelia and spores (POOLE, 1959; CHRISTIANSEN, 1964; ELTON, 1966). Colembolan fecal pellets are generally rich in macerated fungi and mineral particles (KILBERTUS & VANNIER, 1979), and are opaque and spheroidal, with an irregularly lobed surface and range in size from 30µm in smaller species to somewhat over 100 µm in larger species (ZACHARIAE, 1963; RUSEK, 1975, 1985). When compared to mite fecal pellets, those of collembolans are noticeably larger and bear a pronounced lobate surface (RUSEK, 1975, 1985); additionally they are considerably smaller than almost all detritivorous or herbivorous insect pellets. Japygid diplurans are primarily a predatory group, although other diplurans are herbivorous or detritivorous (CONDÉ & PAGÉS, 1991), and some campodeids subsist on live plant roots (CARPENTER, 1988).

Proturans lack a fossil record (CARPENTER, 1992), and a single pre-Tertiary occurrence of a dipluran, apparently a predatory species, was described from the Middle Pennsylvanian of Illinois (KUKALOVÁ-PECK, 1987). Collembolans are known from the Early Devonian (WHALLEY & JARZEMBOWSKI, 1981; JARZEMBOWSKI, 1991) and Early Permian (RIEK, 1976), although they have never been recovered from Pennsylvanian age deposits. Undoubtedly they were important components as microdetritivores in Pennsylvanian coal swamp ecosystems, and may have been responsible for smaller coprolites in coal-ball litter horizons from several Euramerican deposits. Nevertheless, their fecal pellet size and geometry (ZACHARIAE, 1963; PAWLUK, 1985; RUSEK, 1985) is significantly different from the coprolites of *Pteridiscaphichnos*.

### 5.4.3. Blattodea

Blattodeans (cockroaches) are an ancient insect lineage that are important consumers of plant litter and other detritus in tropical to warm-temperate ecosystems with appreciable seasonal or permanent accumulations of decaying plant tissues. On rare occasions blattodeans are herbivores and can consume fern foliage (JONES, 1987). As detritivores with frequently extremely eclectic diets, blattodeans can occur on almost any substrate of decaying tissue (ROTH & WILLIS, 1960), and are often encountered in logs of punky wood (REHN & HEBARD, 1910; SEÍN, 1923; CLEVELAND et al., 1934; PRINCIS & KEVAN, 1955; GRANDCOLAS, 1993), decaying litter (REHN & HEBARD, 1927), carrion (FROGGATT, 1906; BEI-BENKO, 1950) and even cave guano (ROTH & WILLIS, 1960). They are attracted to decaying cortical and medullary tissues of trunks and petioles, especially decaying monocots and tree ferns, where they feed on softer parenchyma while avoiding more indurated vascular and structural tissues

(Anonymous, 1893; HEBARD, 1917, 1920; LEPESME, 1947; WOLCOTT, 1950; FRANKLAND, 1976; JONES, 1987). In the tropics and subtropics, blattodeans are locally responsible for a significant share of the conversion of dead, nonlignified, plant tissues into fecal pellets. These pellets in modern adult blattodeans are relatively constant in shape, although there is a great range in size among nymphal instar and adult stages . Most species produce ellipsoidal pellets about two or three times as long than wide (Figs. 19, 20, 89, 90). Typical adult blattodean pellets possess dimensions of 1.0 mm × 2.5 mm or somewhat less to 1.4 mm × 4.0 mm, and are ellipsoidal to cylindrical, with rounded (Fig. 90) to tapered (Fig. 89) ends and frequently diminutive, longitudinal striae (SWEETMAN, 1965; COCHRAN, 1973; SCOTT, 1977). Smaller blattodean species include the blatellids *Shawella couloniana* (SAUSSURE) whose adult fecal pellet dimensions are around 0.45 mm × 0.75 mm; and *Blatella germanica* (L.), with ellipsoidal and slightly hexagonal uric acid pellets that range from 0.5 mm × 0.75 to 1.25 mm × 2.25 mm in size (HARTNACK, 1943; SCOTT, 1964; COCHRAN, 1973). The primitive cryptocercid, *Cryptocercus punctulatus* SCUDDER, possesses relatively long fecal pellets with tapering ends, round to subhexagonal cross-sections (Figs. 19, 20, 89), and dimensions of 1.5 mm × 5.5 to 7.0 mm (CLEVELAND et al., 1934; NALEPA, pers. comm.). The blaberid *Blaberus* was recorded as producing pellets averaging 1.0 mm × 3.0 mm (SCOTT, 1977; Fig. 90). However, since virtually all blattodeans are generalist detritivores – albeit some have plant tissue preferences – no distinguishing features consistently differentiate fecal pellets of various species.

Pennsylvanian age blattodeans were small to large, dorsiventrally flattened insects whose nymphs bore laterally projecting, immovable wings. Although modern blattodeans are almost always oöthecate and lack an external ovipositor (NALEPA & BELL, 1997), Paleozoic blattodeans possessed long, stylate, and externally conspicuous ovipositors (MARTYNOV, 1938; SHAROV, 1966; VISHNIAKOVA, 1968) for inserting eggs into soil (LAURENTEAUX, 1951) and possibly other substrates. The valves of Paleozoic ovipositors have been homologized to the internal valves of modern oöthecate lineages (NEL, 1929; but see VISHNIAKOVA [1968] who was aware of NEL's work), thus demonstrating phylogenetic continuity between Paleozoic and modern blattodeans. It is possible that plant tissues were used for Pennsylvanian blattodean oviposition (BRONGNIART, 1889; ZALESSKY, 1939, 1953), similar to some modern orthopterans (CHOPARD, 1938). This possibility results from fossil ovipositors with apparently ridged (but not sawtooth) valves that are typically associated with egg insertion into plant tissues. Like modern forms, Pennsylvanian-age blattodeans are assumed to have inhabited the litter zone (SCOTT & TAYLOR, 1983; ROLFE, 1985) and fed on co-occurring plants (GOLDENBERG, 1877). In 1879 Scudder reiterated GOLDENBERG's view on the subject:

> "Such a food-plant for the palaeozoic cockroach he (GOLDENBERG, 1877) would discover in the tree-like *Noeggeranthia*, or the *Cordaites* of the period; just as the ally of the former, the sago palm, furnishes food to the cockroaches of to-day." (p. 37, insertion ours)

Within modern Blattodea, the most plesiomorphic lineage is the wingless Cryptocercidae (CLEVELAND et al., 1934; GRASSÉ & NOIROT, 1959; MCKITTRICK, 1964; HENNIG, 1981; NALEPA, 1984; BOUDREAUX, 1987; THORNE & CARPENTER, 1992; KAMBHAMPATI, 1995; but see GRANDCOLAS & DELEPORTE, 1992; GRANDCOLAS, 1994). The Cryptocercidae probably consists of five species (NALEPA, pers. comm.), *Cryptocercus relictus* BEI-BENKO (1950) from eastern Manchuria in China and western Primorsk Province of Russia, *C. primarius* BEI-BENKO from Sichuan Province of China, a northern and a southern species of *C. punctulatus* SCUDDER from the Appalachian region of northeastern Alabama to north-central Virginia, and an undescribed species of *Cryptocercus* from the Pacific Northwest (CLEVELAND et al., 1934; BEI-BENKO, 1950; THORNE, 1990; KAMBHAMPATI et al., 1996). *Cryptocercus punctulatus* has been intensively studied since it is notable for its termite-like structural features, its harboring of gut endosymbionts that digest wood, and for building a termite-like gallery system in logs of various stages of decay (SNYDER, 1915; CLEVELAND et al., 1934; HAMILTON, 1978; SEELINGER & SEELINGER, 1983; NALEPA, 1984). Although the Cryptocercidae lack a fossil record, these structural, behavioral, and gut-biotal features are paralleled in primitive Isoptera (termites) and have been used as evidence that *Cryptocercus* is a very plesiomorphic clade within the Blattodea (MCKITTRICK, 1964; NALEPA, 1984; THORNE & CARPENTER, 1992; GRANDCOLAS & DELEPORTE, 1992; BANDI et al., 1995) and that its ancestors were primitively associated with wood during the Paleozoic (MAMAEV, 1971; GRASSÉ & NOIROT, 1959; THORNE, 1990). Extant cryptocercids construct a gallery system of irregularly-shaped chambers 20 to 30 mm wide and 50 to 70 mm long (CLEVELAND et al., 1934) connected by approximately 14 mm diameter tunnels that are wide enough to allow passage of a single adult (SEELINGER & SEELINGER, 1983). Although chamber shape is not constant, it is frequently delimited by log shape and wood grain; tunnels by contrast are generally oriented transverse to the chamber axes and cut across the wood grain (SEELINGER & SEELINGER, 1983; NALEPA, 1984). Occasionally structural boundaries of compacted but fragile frass plugs separate gallery systems (Nalepa, 1984), with each system occupied by a single family unit consisting of a mated adult pair and 15 to 35 nymphs (CLEVELAND et al., 1934; SEELINGER & SEELINGER, 1983; NALEPA, 1984). Early instar nymphs have been observed feeding proctodeally (NALEPA, 1984) and engaging in coprophagy (CLEVELAND et al., 1934) – behaviors that result in the larval innoculation of gut endosymbionts necessary for cellulose digestion. Once wood consumption commences, nymphs produce wood debris and fecal pellets that resemble accumulations of wood slivers intermixed among ellipsoidal to cylindrical, occasionally subhexagonal fecal pellets with tapering ends (Figs. 91, 92). Although the exact number of molts is not known, nymphs probably undergo 10 to 12 molts prior to adulthood (NALEPA, pers. comm.) in a process that is completed in five to six years.

Xylophagy and wood gallery construction has been documented for other blattodean clades, particularly the derived panesthine blaberids (FROGGATT, 1906; GURNEY, 1937; CHOPARD, 1952; GRASSÉ & NOIROT, 1959; MATSUMOTO, 1988) and blatellids (GRANDCOLAS, 1993, 1995). However, when gallery system geometry, frass characteristics (including fecal pellet shape), and microhabitat are considered, the greatest similarity exists between extant *C. punctulatus* from the central Appalachian Mountains and *Pteridiscaphichnos* of the Middle to Late Pennsylvanian from the Illinois Basin. Although the plant taxa that are invaded are taxonomically incongruous and separated by 300 million years – modern pinaceous and fagaceous hardwoods versus the unlignified parenchyma of marattiaceous tree ferns – the life habits of both culprits are apparently congruent. In fact, the chamber dimensions and coprolite lengths of *Pteridiscaphichnos* differ from *Cryptocercus* only by somewhat smaller values for the former. These data and comparisons suggest that an ancestral blattodean ecologically similar to *Cryptocercus* was probably the responsible fabricator of *Pteridiscaphichnos*.

### 5.4.4. Isoptera

Isopterans, or termites, are a clade responsible for considerable degradation of plant structural tissues, especially wood, and recycling it back to the soil in tropical and temperate regions (WILSON, 1992a,b). This ecologic success is probably attributable to the exploitation of a major food resource that historically was used minimally by other animals (GREENSLADE, 1985), with the exception of oribatid mites. Although best known for wood consumption, isopterans commonly consume several forms of plant tissues, including live wood, undecomposed but recently dead wood, decomposing wood, litter, humus, fungi, and ungulate feces (GRASSÉ & NOIROT, 1959; LEE & WOOD, 1971; EDWARDS, 1974; WOOD, 1976, 1978; GREENSLADE, 1985; ABE, 1987; NOIROT, 1992). Of these dietary feeding strategies, ingestion of damp wood is most primitive (GRASSÉ & NOIROT, 1959; WOOD, 1978; GREENSLADE, 1985), as is nest construction within the same food source item (WOOD, 1978). More derived feeding strategies include litter consumption, ungulate coprophagy, and humivory; similarly, derived nest-building behaviors are soil-based nests and construction of gallery systems in the upper branches of standing trees (WOOD, 1978; NOIROT, 1992).

Associated with dietary strategy and nest construction behavior is fecal pellet consistency. In plesiomorphic groups such as the Hodotermitidae and Kalotermitidae, feces are solid, pelletal, hexagonal to subhexagonal in cross-section (BANKS & SNYDER, 1920; WEIDNER, 1956; SWEETMAN, 1965; SLEEMAN & BREWER, 1972; ROHR et al., 1986) and may contain plant fragments (WOOD, 1978). The most derived condition is semiliquid feces, such as that found in the Termitidae, which use their feces in gallery construction and overall nest infrastructure (ABE, 1987). Lastly, plesiomorphic isopterans such as Kalotermitidae and Hodotermitidae construct gallery systems of chambers and interconnecting tunnels in wood that are parallel with the grain and are partitioned into separate units by concentrated piles of frass mixed with earth (SNYDER, 1915; BANKS & SNYDER, 1920; PEARCE, 1987). This is similar to gallery systems constructed by *Cryptocercus*. These primitive gallery systems generally occur in heartwood, in which there is preferential consumption of larger-celled, thicker-walled and softer spring wood. This results in smaller-celled, thinner-walled and harder summer wood remaining as characteristic "ribbons" interspersed among frass accumulations containing fecal pellets of finely digested wood (SNYDER, 1915; PEARCE, 1987).

Several factors – including traditional notions of the antiquity of the Isoptera, the known fossil record of isopterans, and the occurrence of *Pteridiscaphichnos* – collectively present a dilemma regarding the presence of Paleozoic Isoptera and the possibility of ascribing *Pteridiscaphichnos* to an ancient isopteran. Because traditional evidence has linked the Blattodea and Isoptera phylogenetically (McKittrick, 1964; Hennig, 1981; Boudreaux, 1987; Kristensen, 1989), it has been inferred that the Isoptera must extend back to the Pennsylvanian (Grassé & Noirot, 1959; Koch, 1967; Hennig, 1981; Thorne, 1990). Thorne & Carpenter (1992) and Kambhampati (1995) found Isoptera more distantly related, with an Isoptera + (Mantodea + Blattodea) topology, which also suggests antiquity to the Pennsylvanian. Alternative proposals include a Permian or Triassic origin based on a worldwide Pangean distribution (Boudreaux, 1987; Abe, 1987; Krishna, 1990), or a late Mesozoic origin immediately before the fragmentation of Gondwanaland (Emerson, 1955). Nevertheless, the overwhelming bulk of isopteran fossils originate from Eocene or younger deposits (Krishna, 1990) and only several pre-Cenozoic termite body-fossils have been described, all from compression fossils of the earlier Cretaceous and assigned to the plesiomorphic Hodotermitidae, albeit one may be a mastotermitid (Emerson, 1967; Krishna, 1990). At least three Cretaceous amber deposits contain known and mostly figured, but undescribed, isopteran fossils (Schlee & Dietrich, 1970; Zherikin & Sukasheva, 1973; Schlüter, 1978). In addition, two Cretaceous woods are known with well-preserved, hexagonal coprolites: a *Diospyros* log from the Late Cretaceous of Texas (Rohr et al., 1986), and an undetermined gymnosperm from the mid-Cretaceous of British Columbia (Labandeira, pers. observ.). Given the sudden and relatively dense appearance of isopteran body- and trace-fossils during the earliest Cretaceous, and their continuation to the Recent, the occurrence of an approximately 170 million year gap between the divergence of Isoptera and Blattodea and the first appearance of isopteran fossils appears anomalous (see Hennig, 1981). This is particularly so, given the relatively high preservation potential of isopteran wings and their galleries and coprolites in fossil woods. Although this anomaly has been explained as isopteran occupation of a specialized habitat (Boudreaux, 1987) or by preservational biases (Shear & Kukalová-Peck, 1990), an alternative explanation is that the Paleozoic-derived isopteran lineage did not evolve structural, behavioral and ecological traits typifying a modern isopteran facies until the Late Mesozoic (Thorne, 1990; Wilson, 1992b). Accordingly, this premodern isopteran lineage possibly has been misdiagnosed in the pre-Cretaceous fossil record.

Ironically, several similarities exist between modern isopteran behaviors and the construction of *Pteridiscaphichnos*. These include the avoidance of more lignified cortical tissues, similarity in tunnel and chamber geometry, subhexagonal shape of some *Pteridiscaphichnos* coprolites, and microhabitat type. However, given the unlikely occurrence of Paleozoic isopterans that were behaviorally, ecologically or taxonomically similar to modern isopterans, it is provisionally reasonable to infer that *Pteridiscaphichnos* was made by a stem-group isopteran. If so, such a taxon may have been morphologically similar to and ecologically indistinguishable from a *Cryptocercus*-like blattodean.

### 5.4.5. Orthopteroidea

Among orthopteroid insects, there are six generalized, detritivorous to herbivorous clades that are candidates for the construction of *Pteridiscaphichnos*. These are Embioptera (webspinners), Grylloblattodea (rock crawlers), Zoraptera (angel insects), Dermaptera (earwigs), Phasmida (stick insects) and Orthoptera (grasshoppers and crickets). The Embioptera are tropical to warm-temperate, gregarious forms with elongated, minimally pigmented bodies that construct silk-lined galleries and tunnels in cryptic habitats such as soil openings, under litter, and within bark cavities. Embiopteran gallery systems are constructed such that an approximately 2 mm wide cylindrical body is accommodated by tunnels that connect more expansive chambers. Although embiopterans have a generally accepted Tertiary fossil record (Carpenter, 1992), the Late Permian Sheimiidae has been assigned to this group (Hennig, 1981; Rohdendorf, 1991; Kukalová-Peck, 1991), which may indicate Paleozoic roots for this order. Grylloblattodeans, by contrast, occur in cool-temperate to polar environments, mostly inhabiting cryptic, subalpine microhabitats, including talus and infrequently rotting logs (Rentz, 1991a). Most apparently are detritivorous, and others consume plant material (Pritchard & Scholefield, 1978), but they are not known to be endophagous or otherwise construct gallery systems. Grylloblattodeans of modern aspect lack a fossil record, although three Paleozoic families have been assigned to the order, including the Liomopteridae (Rohdendorf & Rasnitsyn, 1980), which is coeval with *Pteridiscaphichnos*. Zorapterans are unpigmented, colonial detritivores that have a fossil history extending to the Oligocene (Poinar, 1988). Although they apparently occur in sawdust and construct tunnel and gallery systems in fallen logs (Riegel, 1963; Shetlar, 1978; O'Neill et al., 1987; Kukalová-Peck & Peck, 1993), very little is known of the life-habits of these cryptic insects. Their universally small size (Rentz, 1991c) precludes their production of the relatively large fecal coprolites of *Pteridiscaphichnos.* The Dermaptera are tropical to warm-temperate, and are associated with plant debris, although some taxa are predatory and others are ectoparasitic (Rentz & Kevan, 1991). Most are omnivorous detritivores and consume considerable dead plant food; a few are herbivorous or saprophagous. Dermapterans are not endophagous, nor do they create gallery systems in the soil or in plant tissues. Their earliest fossil occurrence is the Early Jurassic Sinemurian Stage (Whalley, 1985). Phasmids are strict ectophages of tropical areas; virtually all are obligate herbivores (Fig. 93), although some occur on litter (Key, 1991). They are not known to burrow, tunnel or frequent cryptic microhabitats, predominately because of their large size. Their fecal pellets are generally large and spheroidal (Fig. 92) to ellipsoidal. The geochronologically earliest phasmids are known from the Middle Triassic Ladinian Stage. Consequently, for several reasons – the lack of endophagy or construction of gallery systems, inappropriateness of habitat preferences, and absence of a Paleozoic fossil record – the Embioptera, Grylloblattodea, Zoraptera, Dermaptera and Phasmida are unlikely candidates for creating *Pteridiscaphichnos.*

The Orthoptera are a reasonable culprit for the construction of *Pteridiscaphichnos.* Orthopterans are dominantly phytophagous (Brues, 1972; Strong et al., 1984), although a few species are insectivorous or detritivorous. Strict endophagy is unknown in orthopterans, and they generally avoid confined, cryptic locations, since orthopterans subsist mostly on accessible foliar material. Nevertheless, orthopterans have pronounced cylindrical-stylate or laterally compressed, ridged to sawtooth ovipositors that are used for egg insertion into soil or plant substrates, respectively (Rentz, 1991b). Several examples of orthopteran insertion of eggs into plants have been documented (Jensen, 1909; Fulton, 1915; Ramme, 1927), although nymphs developing from eggs deposited into stem parenchyma have exit tunnels that always open to the outside (Fulton, 1915; Chopard, 1938). Endophagous consumption of live or dead stem parenchyma is inconsistent with known ensiferan structure since nymphs bear markedly cumbersome appendages in confined spaces, such as saltatorial hindlegs, long filiform antennae, and laterally projecting wing buds. However, several fossorial and epigeic orthopterans are known to invade live plant tissues to a limited extent, including gryllotalpids (Tindale, 1928; Jones, 1987; Rentz, 1995) and raphidiophorids (Buller, 1867).

Virtually all orthopteran fecal pellets are elongate, subcylindrical to elliptical shape, have a coarsely textured and irregularly sculptured surface, and possess ends ranging from truncate to blunt to acuminate with emergent, threadlike stringers (Fig. 92; Brown, 1937; Weiss & Boyd, 1950; Gangwere, 1962). Considerable intraspecific variation exists for these features, depending on diet (Gangwere & Morales-Agacino, 1964; Bhatia & Chandra, 1967; Paranjape, 1985) and feeding interval (Frost, 1928; Gangwere & Morales-Agacino, 1964). Fecal pellet consistency can range from dry to moist, depending on composition and aerial exposure (Brown, 1937; Whitman, 1990). Whereas modern orthopteran fecal pellet shape ranges from the more equant pellets of crickets (1.5 mm × 2.5 mm; Sweetman, 1965) to elongate cylinders of some acridid grasshoppers (1.0 mm × 3.5 mm; Brown, 1937), the coprolites of *Pteridiscaphichnos* are within the size and shape range of an average-sized modern orthopteran. Although modern orthopteran fecal pellets do possess general size and shape characteristics, they lack identifiable, taxon-specific features within the modern fauna (Gangwere, 1962; Gangwere & Morales-Agacino, 1964), even though dichotomous keys have been developed to identify limited numbers of species with economic importance (Vasu, 1965; Sweetman 1965).

The earliest known orthopteran family, the Oedischiidae, has been described from the Middle Pennsylvanian (Zeuner, 1939; Sharov, 1971a). These Orthoptera subsequently experienced an initial burst of diversification of five families during the Early Permian and three additional families during the Late Permian, followed by a more dramatic radiation that commenced during the Early Mesozoic (Labandeira & Sepkoski, 1993; Labandeira, 1994). Oedischiids, contemporaneous with *Pteridiscaphichnos*, were several centimerers long and bore prominent ovipositors and saltatorial hind legs but lacked stridulatory organs and tegmenous forewings. Although Sharov (1971a) indicates that oedischiids were predaceous, Shear & Kukalová-Peck (1990) suggest that they were detritivorous. If they were ecologically similar to modern orthopterans, oedischiid nymphs could have inhabited microhabitats such as recently fallen tree fern trunks and produced fecal pellets consistent with those of *Pteridiscaphichnos.*

### 5.4.6. "Protorthoptera"

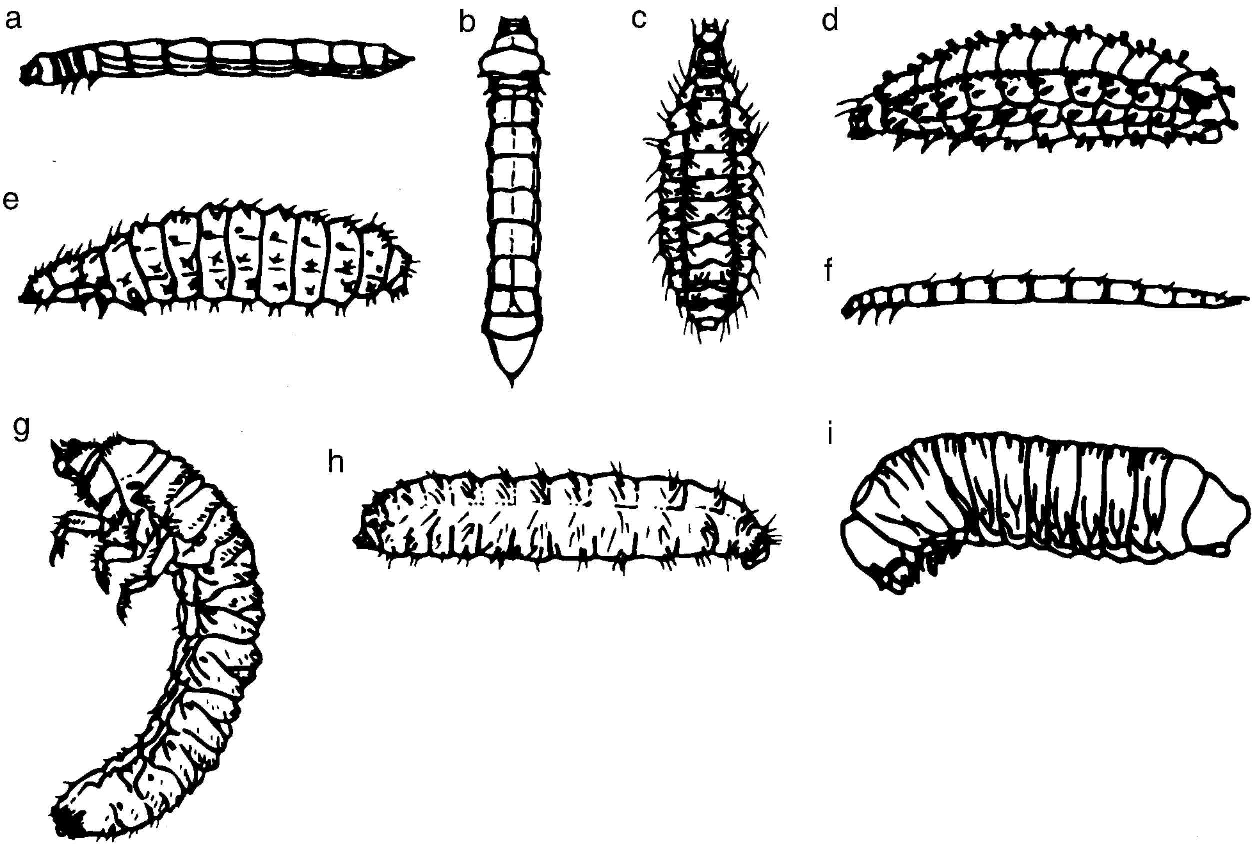
The Protorthoptera, as traditionally constituted, is a polyphyletic assemblage of lineages with a generalized, orthopteroid facies (CARPENTER, 1992; KUKALOVÁ-PECK & BRAUCKMANN, 1992). Several researchers are disassembling the Protorthoptera and allocating segregate lineages to plecopteroids, blattoids, orthopteroids, hemipteroids, and, with difficulty, holometabolans (ROHDENDORF & RASNITSYN, 1980; KUKALOVÁ-PECK, 1991; KUKALOVÁ-PECK & BRAUCKMANN, 1992). As a result, protorthopterans currently comprise about 45 families of almost exclusively Paleozoic clades that were diverse during the Middle Pennsylvanian to Early Permian (LABANDEIRA, 1994). While the relative paucity of Late Pennsylvanian protorthopteran families may be artifactual, their general abundance and diversity in later Pennsylvanian and earlier Permian biotas suggest that, with the possible exception of blattoids, they were the dominant mandibulate occupant of the detritivore/herbivore feeding niche and may have been responsible for foliage feeding damage on *Neuropteris* and other seed ferns (SCOTT & TAYLOR, 1983; LABANDEIRA & BEALL, 1990). They probably were the producers of numerous ellipsoidal coprolites in Middle and Late Pennsylvanian coal-ball litter horizons. According to BURNHAM (1986) and KUKALOVÁ-PECK & BRAUCKMANN (1992), the plant-feeding Geraridae are the best documented of protorthopterans and possessed a short, ridged, exserted ovipositor that functioned in cutting plant stems (KUKALOVÁ-PECK, 1987, 1991). However, like modern orthopteroids, it is parsimonious to consider newly hatched nymphs as ectophages rather than endophages on pith parenchyma. In summary, although significantly anecdotal evidence associates protorthopterans with feeding on plants, like the Oedischiidae of the Orthoptera, numerous difficulties are encountered in postulating relatively large, appendiculate insects in confined, endophytic microhabitats.

### 5.4.7. Holometabola

*Pteridiscaphichnos* antedates by 15 million years the earliest, well-documented, conventionally assigned body fossil of an holometabolan. However, there are three body fossils that are possible exceptions to this diachroneity: First is a possible eruciform, polypod larva with apparent mecopteroid and hymenopteran features, known from late Middle Pennsylvanian strata (KUKALOVÁ-PECK, 1991; see also WILLMANN, 1998). Second is the reassignment of the Early Pennsylvanian *Metropator* to the Mecoptera, and third is the reassignment of the Late Pennsylvanian *Fatjanoptera* to the Raphidioptera (MARTYNOVA, 1961; ROHDENDORF & RASNITSYN, 1980; HENNIG, 1981; WILLMANN, 1989; but see CARPENTER, 1992). If any of these possibilities are confirmed as holometabolous, presence of Myachkovskian-age Holometabola would have implications for the potential culprit of *Pteridiscaphichnos*.

Attribution of *Pteridiscaphichnos* to an holometabolous larva is based on inferred life-habit and behavior of a fossil endophage occupant. It is significant that lineages of primitive holometabolans possibly may have been contemporaneous with *Pteridiscaphichnos*. Although verification of authentic Pennsylvanian holometabolan body-fossils remains elusive, many have presented evidence and arguments that primitive holometabolans occupied Paleozoic plant tissues, becoming borers, gallers, or other endophages (LAMEERE, 1899, 1917; MALYSHEV, 1968; MAMAEV, 1971; HAMILTON, 1978; KIREJTSHUK, 1989). In fact, most plesiomorphic lineages in free-living, nonparasitic, holometabolan clades are either litter inhabitants or are associated with endophagy, including stem gallers, wood borers, and leaf miners. (See Text-Fig. 7 for representative modern examples.) Several of these clades, including Mecopteroidea, Coleoptera and Neuroptera, have their earliest known occurrences during the Early Permian (CROWSON, 1981; KUKALOVÁ-PECK & WILLMANN, 1990; CARPENTER, 1992) and are conceivable candidates for *Pteridiscaphichnos* damage.

*5.4.7.1. Miomoptera.* The mandibulate Miomoptera, among the smallest of Pennsylvanian and Permian insects, have been assigned variously to the plecopteroids (MARTYNOV, 1937; BOUDREAUX, 1987), hemipteroids (CARPENTER, 1992) or holometabolans (ROHDENDORF & RASNITSYN, 1980; KUKALOVÁ-PECK, 1991). ROHDENDORF & RASNITSYN (1980) have proposed that miomopteran larvae were endophytic in the strobili of gymnosperms – a microhabitat that shares some limited similarities to *Pteridiscaphichnos*. However, if SHAROV's (1957) assignment of the nymph *Permonympha* to the Miomoptera is correct (ROHDENDORF & RASNITSYN, 1980, but also see CARPENTER, 1992), it is highly unlikely that such a highly appendiculate insect inhabited fern trunks in close quarters. In this regard, HINTON (1948) discusses the basic conflict between endophagy and possession of developed, external wings or other appendages.



Text-Fig. 7. Larvae of plesiomorphic clades of extant holometabolous lineages that are primitively associated with herbivory. The figures are redrawn from the originals and not to scale; b and c are dorsal views, all others are left lateral views. a, Coleoptera (Cupedidae): *Cupes concolor* WESTWOOD, from SNYDER (1913); b, *Coleoptera* (Cupedidae): *Cupes clathratus* SOLSKY, from FUKUDA (1938); c, Lepidoptera (Micropterygidae): *Neomicropteryx nipponensis* ISSIKI, from YASUDA (1962); d, Lepidoptera (Micropterygidae): *Micropteryx calthella* (L.), from LORENZ (1961); e, Coleoptera (Rhysodidae): *Omoglymmus americanus* (LAPORTE), from LAWRENCE (1991); f, Mecoptera (Nannochoristidae): *Nannochorista* sp., from BYERS (1991); g, Neuroptera (Ithonidae): *Ithone fusca* NEWMAN, from TILLYARD (1922b); h, Diptera (Tipulidae): *Ctenophora dorsalis* WALKER, from FOOTE (1991); i, Hymenoptera (Xyelidae): *Xyelecia nearctica* ROSS, from SMITH (1967).

*5.4.7.2. Mecoptera.* The earliest assured mecopteran, or scorpionfly, is of Late Permian age (WILLMANN, 1989), although protomeropids and related lineages that possess mecopteroid synapomorphies (WILLMANN, 1989) are known from the earliest Permian of the Czech Republic (KUKALOVÁ-PECK & WILLMANN, 1990). The life habits of modern mecopteran larvae are poorly known; nannochoristids are wireworm-shaped, aquatic, and insectivorous (Text-Fig. 7f; PILGRIM, 1972; BYERS, 1991) whereas other mecopteran larvae are eruciform, terrestrial and generally detritivorous either on plants or animals (CURRIE, 1932; APPLEGARTH, 1939; SETTY, 1939; EVANS 1942; BYERS, 1963; GASSNER, 1963). With the possible exception of KUKALOVÁ-PECK's (1991) mecopteroid-hymenopteran larva, an apparent external-foliage-feeder, nothing is known of Paleozoic mecopteran larvae. Modern mecopteran larvae generally occur in litter or soil, and avoid endophytic microhabitats. Additionally, we know of no known documentation of mecopteran larval fecal pellets, although the expectation of all holometabolan larvae is the presence of barrel-shaped fecal pellets with ends of irregular, fractured surfaces, and not the ellipsoidal coprolites of *Pteridiscaphichnos*. We conclude that a mecopteran was not responsible for *Pteridiscaphichnos*.

*5.4.7.3. Coleoptera.* The earliest known coleopterans (beetles) originate from middle Lower Permian deposits of the Czech Republic and Russia (PONOMARENKO, 1969; SHEAR & KUKALOVÁ-PECK, 1990). They resemble modern cupedids (CROWSON, 1981), which conventionally have been assigned to the most plesiomorphic lineage of extant Coleoptera (HAMILTON, 1978; CROWSON, 1981). Modern cupedid larvae (Text-Fig. 7a,b) bore into wood (Blackman, 1922; Fukuda, 1938,1941) and probably engage in fungal symbioses. Nevertheless, recent phylogenetic analysis by Kukalová-Peck & Lawrence (1993) have identified the adephagan Rhysodidae as the most plesiomorphic coleopteran lineage (see also Beutel, 1993), and rhysodids also have wood-boring larvae (Text-Fig. 7e; Bell, 1985). Known rhysodid fossils, however, extend only to the Tertiary (Poinar, 1992). While coleopterans lack a known Pennsylvanian fossil record, given the primitive facies of Lower Permian "protocoleopterans", and the primitivity of larval wood boring in modern coleopteran taxa (Ponomarenko, 1969; Crowson, 1981; Kirejtshuk, 1991), it is conceivable that a lightly sclerotized ancestor created *Pteridiscaphichnos* during Pennsylvanian times and escaped detection as body-fossils. However, primitive coleopteran larvae are noncommunal and create linear to serpentine tunnels occupied by a single individual that backfills its tunnel with wood fragments (Snyder, 1913; Fukuda, 1938, 1941; Neboiss, 1968; Bell, 1985) – a feature that is very different from the *Psaronius* tunnel-and-gallery system. Other, advanced, coleopteran larvae such as Curculionidae bore into the petioles of tree ferns and monocots with fleshy piths (Swezey, 1922; Herms, 1926; Lepesme, 1947), but belong to clades that evolved during the early Mesozoic. Consequently, as in the Mecoptera, the geometry of the boring and fecal pellet structure is inconsistent with coleopteran culprit.

*5.4.7.4. Neuroptera.* Neuropterans (sensu stricto) have been recovered from middle Lower Permian deposits of the Czech Republic (Kukalová-Peck, 1991) and remain relatively nondiverse until the end of the Triassic, after which a modest diversification ensued (Labandeira & Sepkoski, 1993; Labandeira, 1994). As in other holometabolan groups, the earliest fossil neuropterans are allied to lineages that are assessed as plesiomorphic in the modern insect fauna. The Ithonidae is generally considered as the most plesiomorphic extant neuropteran lineage (Withycombe, 1922; Popov, 1973; Kukalová-Peck, 1991) and correspondingly its larvae exhibit the only nonpredaceous behavior in the order (Text-Fig. 7g), subsisting on plant tissues, probably roots and litter (Gallard, 1932; Smithers, 1979). Ithonid-like, adult neuropterans are known from various localities of the Permian (Tillyard, 1922a; Carpenter, 1992), although nothing is known of Permian neuropteran larvae. Like the Mecoptera and Coleoptera, evidence for Pennsylvanian Neuroptera is wanting, and because of a mismatch between typical holometabolan and *Pteridiscaphichnos* coprolites, it is highly unlikely that a neuropteroid insect produced *Pteridiscaphichnos.*

### 5.4.8. Taxonomic Assignment of the Probable Culprit

Three principal criteria are used for assignment of the *Psaronius* tunnel-and-gallery maker to a particular taxon. They are (i) the location, geometry and contents of the gallery system, (ii) the inferred life-habit of the culprit, based on microhabitat paleoecology, and (iii) the general environmental and temporal provenance of the gallery. Collective application of these criteria indicate that the most reasonable and parsimonious assignment of the culprit is to the Blattodea, although if Isoptera existed during the Paleozoic, they also would be a candidate. Other potentially relevant groups include myriapods, some noncarnivorous orthopteroids, and holometabolans. The only possible myriapod group of concern are millipedes, which are almost exclusively detritivores. Millipedes are not known stem-borers, and only rarely feed on fresh plant tissue. Orthopteroid groups other than Blattodea and Isoptera comprise taxa that either lack Paleozoic and often Mesozoic fossil records, or do not construct gallery systems in plant tissues. While one family of Orthoptera was present during the Middle Pennsylvanian, it is an unlikely candidate because of difficulties involved with projecting appendages in confined spaces. By contrast, a larval holometabolan culprit would be inconsistent because of the coprolite structure of *Pteridiscaphichnos.*

Based on an evaluation of all the evidence, the maker of the *Psaronius* gallery-and-tunnel system is parsimoniously assigned to the Blattodea, especially a *Cryptocercus*-like cockroach (Cleveland et al., 1934; Seelinger & Seelinger, 1983; Nalepa, 1984). However, because of poor understanding of blattodean life-habits, other more derived, xylophagous and gallery-constructing subclades, such as panesthiine blaberids (Grassé & Noirot, 1959; Matsumoto, 1988), zetoborine blaberids (Grandcolas, 1995), and possibly blatellids (Chopard, 1952; Grandcolas, 1993) should also be considered as ecological models. Notably, cryptocercid blattodeans have traditionally been considered termite-like since they are xylophagous, use a diverse gut fauna to digest cellulose, construct tunnel-and-gallery systems, and exhibit some features of primitive sociality (McKittrick, 1964; Seelinger & Seelinger, 1983; Nalepa, 1984).

## 5.5. Implications of Stem-Boring Detritivores in Coal-Swamp Ecosystems

*Pteridiscaphichnos* is illustrative of the initial ecological expansion of detritivory from simpler, wood- and parenchyma-boring mites during the Early and Middle Pennsylvanian to considerably larger, cockroach-sized insects able to process large regions of tree trunks during the latest Middle and Late Pennsylvanian. Excluding any direct evidence for millipede, collembolan or other insect degraders of Pennsylvanian plant tissues, this stem-boring detritivore represented a second syndrome of the comminution of trunk tissues. The combination of mites and the *Pteridiscaphichnos* culprit undoubtedly provided a more efficient system of reducing mostly tree-derived organic matter to the end-product of plant detritus and coal.

### 5.5.1. Trees As an Ancient Habitat for Insects

There are three categories of evidence that provide constraints for regarding trees as an ancient habitat for insects. These types of evidence, one direct and two indirect, are (i) knowledge of the life-habits and stem-tunneling and wood boring geometry of modern arboricolous and xylophagous insects, particularly for primitive insects whose hosts are primitive plant taxa, (ii) direct evidence of insect body structures during the Pennsylvanian and Permian that are associated with living under bark or in trunk tissues, and (iii) direct information derived from coprolite laden wood borings and other tissue damage in Pennsylvanian trees. From these three, albeit data-limited, approaches, reasoned inferences can be made regarding the role that trees provided for the initial colonization by insects of microhabitats occurring under bark, and endophytically in stem tissues.

Modern postmortem degradation of lignified supportive tissues is accomplished by mites, myriapods, and tree-dwelling insects. Insect degraders include several orthopteroid clades, and, prominently, holometabolan clades that bore principally into wood, periderm and cambium (see Section 5.4). Notably, both groups are dominated by plesiomorphic lineages (MAMAEV, 1971; RASNITSYN, 1971a,b; HAMILTON, 1978; CROWSON, 1981). For primitive, detritivorous insect clades, wood is frequently a primitive life-habit; for example, in the Blattodea, the plesiomorphic cryptocercids construct galleries in decomposing logs (SEELINGER & SEELINGER, 1983; NALEPA, 1984), as do the more apomorphic panesthiine blaberids (O'NEILL et al., 1987; MATSUMOTO, 1988; SCRIVENER et al., 1989). Among the Isoptera, the most plesiomorphic extant families are wood-inhabiting and xylophagous, whereas the most apomorphic lineages build nests in soil and consume humus (ABE, 1987; NOIROT, 1992). Termite-like zorapterans, apparently a primitive lineage related to Blattodea (KUKALOVÁ-PECK & PECK, 1993), live in rotting logs (GURNEY, 1938; RIEGEL, 1963), although presently there is no convincing evidence of gallery or tunnel construction. Of these three orders, modern blattodeans occur during the Pennsylvanian, and are known to bore and construct galleries in modern pteridophytes (HEBARD, 1917; FRANKLAND, 1976; JONES, 1987). Blattodeans are important detritivores of stems and petioles of tree ferns, palms, and other pithy, nonwoody arborescent monocots (Anonymous, 1893; HEBARD, 1917; SWEZEY, 1922, 1954; SEÍN, 1923; LEPESME, 1947; FRANKLAND, 1976; LASEBIKAN, 1977). Current data however does not indicate any insect detritivore selectivity for these host plants.

For the Holometabola, the modern association between phylogenetic primitivity and endophytic life-habits in several lineages provides empirical support for the claim that endophagy was a primitive condition in ancestral Holometabola – an association that was extended to the Pennsylvanian and Permian by some (LAMEERE, 1908; MALYSHEV, 1968; RASNITSYN, 1971a; ROHDENDORF & RASNITSYN, 1980). Basal groups of several modern orders are phytophagous and frequently occur inside plant tissues as wood-borers, stem-gallers, leaf miners, or as detritivores associated with decaying wood or litter (Text-Fig. 7). Examples include the Cupedidae and Rhysodidae for Coleoptera; Xyelidae and Tenthredinoidea for Hymenoptera; Tipulidae, Pachyneuridae and Axmyiidae for the Diptera, and many nonditrysian Lepidoptera. Some of these groups are associated with nonangiospermous trees, such as xyelid sawflies and agathiphagid moths on conifers and blasticotomid and selandriinid sawflies on ferns.

Several structural characteristics of Pennsylvanian and lower Permian insects indicated generalized to intimate associations with plants, including dorsoventral flattening, presence of effective piercing-and-sucking mouthparts, and ovipositors modified into laterally-compressed valves with sawtooth ridges. A few lineages of Pennsylvanian protorthopterans, and, conspicuously, Lower Permian protocoleopterans such as Tschekardocoleidae, display pronounced dorsoventral flattening (Ponomarenko, 1969; Crowson, 1981) similar to that illustrated by Peyerimhoff (1909) for modern cupedid beetles occurring under bark. Second, a diversity of piercing-and-sucking palaeodictyopteroid beaks are known from the late Paleozoic, ranging from mouthparts that are small and delicate, with needle-like stylets, to large and robust ensembles with thick, proximally expanded stylets (Sharov, 1971b,1973; Müller, 1978; Kukalová-Peck, 1987). While it is unclear which of these variations were used by taxa piercing plants for sap, there is independent evidence from stylet tracks in *Psaronius* petioles and herbaceus fern stems (Scott & Taylor, 1983; Lesnikowska, 1989; Labandeira & Phillips, 1996a). Additionally there has been the suggestion that others were probably feeding on spores from gymnospermous cones (Rohdendorf & Rasnitsyn, 1980). Lastly, the occurrence of laterally-flattened, valvate ovipositors with serrated ridges among various palaeodictyopteroids (also possessing piercing-and-sucking beaks) indicates that some oviposition targeted plant tissues, some of which were lignified, judging from the robustness of some ovipositor apparati (Carpenter, 1971; Kukalová-Peck, 1991).

Current knowledge of borings associated directly with Pennsylvanian plants consist overwhelmingly of small (60 to 80 µm) tunnels constructed by oribatid mites (Kubiena, 1955; Baxendale, 1979; Scott & Taylor, 1983; Labandeira et al., 1997). These tunnels occur principally in moderately decayed cordaite, lycopod, and calamite wood, and to a lesser extent in parenchymatic tissue within lycopod leaf-cushions, medullosan petioles and tree-fern roots. Other associations of Pennsylvanian trees with endophagous insects are the much larger tunnel-and-gallery *Pteridiscaphichnos* system probably caused by cockroach-like insects in three species of *Psaronius* trunks, and the holometabolan-induced *Pteriditorichnos* galls in *P. chasei* petioles (see Section 6.0). These types of endophytic interactions are complemented by other organs that simultaneously were experiencing attack, including pinnules, sporangia and roots (Labandeira & Beall, 1990; Chaloner et al., 1991).

These three classes of evidence suggest that a dynamic and varied assemblage of insects were interacting with trees as early as the late Middle Pennsylvanian, and became important during the Late Pennsylvanian. During the late Middle Pennsylvanian, available evidence indicates mite borings in diverse lignified tissues, cockroach-like borings in *Psaronius* stem parenchyma, consumption of spores from tree-fern sporangia and gymnospermous cones, external-foliage-feeding on tree-fern and seed-fern pinnules, and possible seed predators on *Samaropsis* seed-fern seeds. During the Late Pennsylvanian, evidence supports the addition of piercing-and-sucking on *Psaronius* frond petioles, the galling of frond petioles by a vermiform larva, and continuation at elevated levels of Middle Pennsylvanian herbivory. These data indicate that virtually all major tissue types of trees, which constitute 95 percent of the biomass in Pennsylvanian coals (Phillips et al., 1985), were being exploited as food resources during Late Pennsylvanian times. This widening of the food resource envelope is reflected in a shift from the omnipresent detritivore trophic loop of earlier coal-swamp ecosystems (Rolfe, 1980, 1985) immediately prior to the Middle/Late Pennsylvanian extinctions. During the Late Pennsylvanian the dominant, coal-swamp vegetation of the recovery phase harbored an expanded suite of herbivores. This inaugurated the first, major herbivore trophic link probably since the earliest forests originated during the Middle Devonian.

### 5.5.2. Nutrient Recycling During the Pennsylvanian

The two types of plant/insect interactions of this report are paleoenvironmentally contextualized by five empirical observations of Middle to Late Pennsylvanian swamp floras in Euramerica. First, there is a pronounced reduction in seam thickness and geographic extent of coal units above this boundary (Phillips & Peppers, 1984). The biovolume of Late Pennsylvanian coals, both individually and collectively, is considerably less than that of Middle Pennsylvanian coals. Second, there is a demonstrable shift toward drier climate during the Late Pennsylvanian, based on independent geological data (Phillips et al., 1985), and there is some indication that seasonality was augmented. Third, a pronounced floral turnover characterizes the Middle to Late Pennsylvanian boundary – one that resulted in a dramatic shift from lycopod-dominated to tree fern-dominated coal swamps (Phillips et al., 1974; Pfefferkorn & Thomson, 1982). Fourth, accompanying this floristic change was a significant drop in floral taxonomic diversity (Phillips et al., 1985). The relatively high plant diversity occurring in the late Middle Pennsylvanian Herrin coal flora was never regained during Late Pennsylvanian floras, such as those represented by the Calhoun Coal. Last, there is an increase in herbivore functional-feeding-groups and herbivory feeding intensity in Late Pennsylvanian floras (Labandeira & Phillips, 1992; Labandeira, 1998b). It

1984; Ananthakrishnan & Raman, 1989; West & Shorthouse, 1989). This histological alteration is accomplished first by normal growth inhibition and later by new-growth inhibition in hyperplasic tissue near the larva, and finally by hypertrophy more distally (Plumb, 1953; Mani, 1964; Meyer, 1987). For many galls these processes result in a distinctive proliferation of tissue under the control of the juvenile insect occupant. The more primitive type of cellular modification is callus proliferation, which is induced by an internal wound that is caused, for example, by insect consumption of parenchymatic tissue. Insect-induced callus is a type of reaction tissue that consists of hyperplasic and sometimes hypertrophied tufts of mostly equant cells that is proximal to the feeding larva and sometimes is radially oriented toward a central cavity which is occupied by a nymph or larva (Ananthakrishnan & Raman, 1989; Mound, 1994). However the most advanced type of cellular differentiation is the formation of nutritive tissue, which comprises a distinctive zone of activated cells that is defined by organellar criteria and is organized generally into layers rich in proteins, lipids, and carbohydrates (Meyer, 1969; Rohfritsch, 1992), often consumed as food by an encapsulated nymph or larva (Trotter, 1934; Fourcroy & Braun, 1967; Rohfritsch, 1974, 1977; Rohfritsch & Shorthouse, 1982; Raman & Ananthakrishnan, 1983; Shorthouse, 1986; Bronner, 1992). Nutritive tissue is produced by those hemipteroid and holometabolous insects forming complex galls, although in cecidomyiids and aphids it functions as a transport layer for moving solutes to the larva (Kirst & Rapp, 1974; Rohfritsch, 1992). In most instances, the cropping of gall nutritive tissue by endophagous mandibulate or piercing-and-sucking immatures stimulates further production of more nutritive tissue by the plant (Loux & Meyer, 1967; Rohfritsch, 1971, 1975a,b; Ananthakrishnan & Raman, 1989).

Essentially the insect/plant gall relationship represents a temporary symbiosis. The galling insect uses its ovipositor or mouthparts to wound a particular hostplant organ during an appropriate developmenal stage (Shively, 1948; Hori & Miles, 1977; Rey, 1992). The gall results from the defense response of the host plant. This host plant response is controlled by the insect, and possibly other mutualistic associates such as fungi (Haridass, 1987), and consists of tissue proliferation and frequent physical enlargement in the immediate area of the affected plant organ. Tissue differentiation includes the formation of nutritive tissue and the commensurate modification of other tissues that are physiologically essential for the maintenance of nutritive tissue. During the period when the larva is surrounded by nutritive tissue, the gall enlarges and matures (Bronner, 1977; Hori & Miles, 1977; Rohfritsch & Shorthouse, 1982; Cornell, 1983). With the exception of cecidomyiids and aphids, the subsequently produced, additional nutritive tissue is consumed by endophage occupants until their juvenile development is completed (Rohfritsch, 1992).

Fern galls, characterized by minimal to pronounced organ enlargement and production of callus and nutritive tissue, are worldwide and produced by all major clades of angiosperm-galling insects (Houard, 1920; Docteurs van Leeuwen, 1938; Wieczorek, 1973; Spencer, 1990; Gerson, 1996). Fern pinnules are especially susceptable to attack by mites (Nalepa, 1909, 1924; Docteurs van Leeuwen-Reijnvaan & Docteurs van Leeuwen, 1926; Houard, 1933) and dipterans (Gerson, 1979; Brown & McGavin, 1982; Aderkas & Peterson, 1987; Kolomoets et al., 1989; Spencer, 1990). By contrast, the gallers of fern stems, petioles, and rhachial midribs include taxa as diverse as the pyralid *Undulambia* (Lepidoptera) on the North American leatherleaf fern *Polystichium* (Kuitert & Dekle, 1962; Short et al., 1971; Munroe, 1972), the gelechiid *Paltodora* (Lepidoptera) on European bracken (Meess, 1924), the drosophilid *Drosophila* (Diptera) on Australian bracken (Shuter, 1990), the anthomyiid *Chirosia* (Diptera) on British bracken (Cameron, 1930, Collin, 1955; Brown & McGavin, 1982), an unidentified cecidomyiid (Diptera) on Venezuelan *Alsophila* (Karsch 1880), and the cryptic tenthredinid *Heptamelus* and the blasticotomid *Blasticotoma* (Hymenoptera) on Eurasian bracken (Meijere, 1911; Ermolenko, 1964; Shaw & Bailey, 1991). Curculionoids (weevils) are particularly notable worldwide as endophytic inhabitants of fern petioles and frond midribs; at least ten genera are borers and gallers of live ferns ranging from polypodiaceous lianas to massive tree ferns (Anderson, 1941; Swezey, 1922, 1954; Schedl, 1961, 1968; Gray, 1970, 1972; Board & Burke, 1971; Julien et al., 1987). Roots are attacked and bored less frequently; the best documented case are hepialiids (Viette, 1948; Grehan, 1989), with some species producing borings up to 30 cm long (Barrett, 1895), and evacuating all live medullary parenchyma, leaving only an outer cylinder of structural tissue.

The robust stems of ferns, especially the Polypodiaceae, are often domiciles for ant endophytes. As a result of hollowing the interiors of tuberous fern stems, ants create teratological enlargement of the stem, usually without production of callus or nutritive tissue (Yapp, 1902; Senn, 1910; Hageman, 1969; Gómez, 1974,1977;

Jermy & Walker, 1975; Hölldobler & Wilson, 1990). These cavities generally have relatively smooth inner surfaces (Senn, 1910), although Ridley (1910) has described the presence of callus in stems of Singaporean *Polypodium*, a phenomenon also described for ant cavities by Bailey (1922) in a verbenaceous lianas from central Africa and by Wheeler (1942) in polygonaceous trees from Panama. The attraction of ants to ferns is induced by carbohydrate-rich secretions from extrafloral nectaries (Darwin, 1877; Figdor, 1891; Douglas, 1983; Cooper-Driver, 1990), in return for which the ants provide formidable herbivore protection (Hölldobler & Wilson, 1990). Although these diverse fern/ant interactions are universally considered a mutualism, whether the general phenomenon of galling is commensalism or parasitism is an issue that still engenders debate (Price et al., 1986, 1987; Mani, 1992).

### 6.3. Gall Structure and Host of *Pteriditorichnos*

Three classes of evidence demonstrate that *Pteriditorichnos* is a stem gall. They are, in decreasing order of importance, (i) qualitative features of the interior structure of *Pteriditorichnos* and host plant anatomy, (ii) constancy in shape and size consistent with a gall origin, and (iii) specificity in host plant tissue type, organ location, and taxonomic affinity.

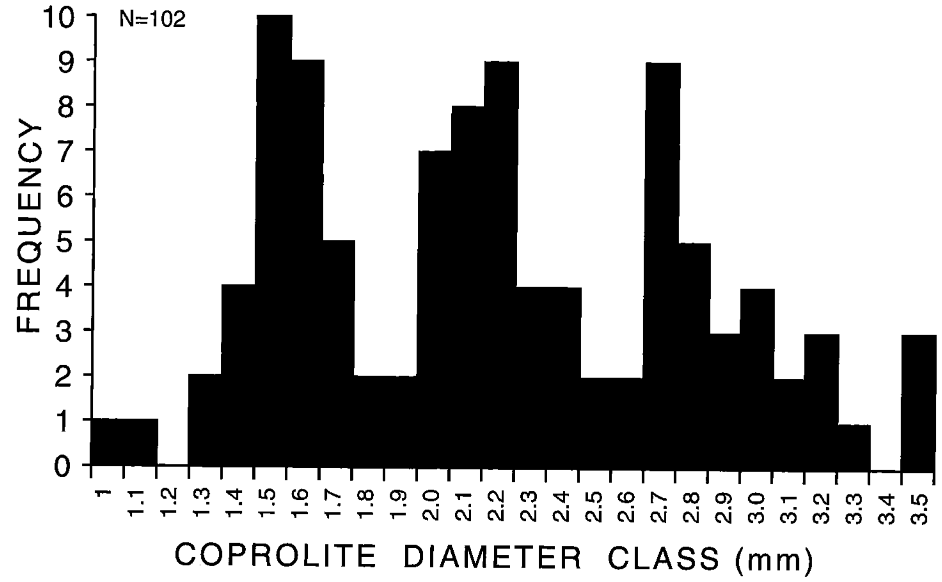
#### 6.3.1. Structure of the Gall

Several structural features of *Pteriditorichnos* are highly stereotyped and are known to occur in all specimens. These features include (i) presence of an elongate, tube-shaped lumen that is approximately centered on the vascular axis of *Stipitopteris*; (ii) presence of a frass infilling in the lumen, consisting of apparently undigested parenchyma fragments and distinctive, barrel-shaped coprolites, (iii) characteristic, parenchymatous, gum-sac cells occurring in both the lumen coprolites and in unaltered medullary and cortical parenchyma; and (iv) a characteristic zone of new cell layers surrounding the lumen and derived from medullary parenchyma that is interrupted by (v) apparent exit holes in two specimens.

*6.3.1.1. Lumen.* The cylindrically elongated central lumen occurs in all specimens, ranging in width from 0.5 to 1.5 cm and reaching a documentable maximum length of about 18 cm in specimen UIUC-8227 (Figs. 33–38). The termination of the *Pteriditorichnos* lumen is evident in a few longitudinal sections, although specimen UIUC-30823 (Figs. 60–65), illustrates best longitudinal diminution of the lumen diameter. Because of the marked constancy in diameter within and among specimens, this central, paraxial lumen is interpreted as the larval chamber, whose minimum diameter was controlled in life by the width of the larval insect occupant and maximum diameter was determined by additional space needed for lateral larval movement and cropping of interior parenchymatic and newly formed tissue. Additionally, the larval chamber is packed with considerable material that is interpreted as derived from a mandibulate larval insect.

Advanced, modern insect galls are characterized by the presence of one or multiple chambers housing endophages that subsist on surrounding nutritive tissue. These chambers may consist of a single, axially elongate lumen in the example of many stem, root or cone galls, or they may consist of one to often as many as hundreds of chambers in spheroidal galls attached to plant organs such as leaves and stems. For larval insects with functional mandibles, such as tenthredinoid Hymenoptera, Coleoptera, and Lepidoptera, the gall inhabitants modify their chambers by cropping the encompassing callus or nutritive tissue and processing the food into unconsumed macerated debris and distinctive fecal pellets resulting from digestion of parenchyma through a gut. This produces an internal ovoidal to elongate cavity with relatively smooth walls and regions of frass accumulations. Larval insects that fluid-feed and possess extraintestinal digestion, such as hemipterans and dipterans, lack frass accumulations. Of all modern galls, *Pteriditorichnos* most closely resembles the stem galls of sawflies, or tenthredinoid hymenopterans, and to a lesser extent, certain beetles. Although a modern analog is the elongate gall produced by the sawfly *Heptameleus ochroleuceus* (Stephens) on bracken fern fronds, *Pteriditorichnos* was produced by a much larger and massive larva that apparently tunneled more extensively than modern *Heptamelus*.

*6.3.1.2. Frass.* Packed within the lumen is frass that was deposited by the larval occupant. The frass consists of two components: comminuted but undigested, angular parenchyma fragments compositionally identical to the surrounding lumen tissue; and relatively dense and packed, cylindrical coprolites. The undigested accumulations



Text-Fig. 8. Frequency-distribution histogram of diameters of coprolites in specimens of Late Pennsylvanian *Pteriditorichnos* galls occurring in the Calhoun Coal. Data represents a pooling of all samples.

of parenchymal fragments are ubiquitously and randomly dispersed throughout the lumen, and are interrupted by irregularly shaped vacuities (Figs. 58, 59; 66–69; 80). By contrast, the one to several coprolites in many lumen cross-sections are arranged into clusters whose axes are subparallel with the lumen axis (Figs. 47–51; 60, 63, 69; 70, 73). Frequency-distribution histograms of coprolite diameters exhibit three discrete and pronounced modes (Text-Fig. 8), indicating instar development. These coprolites are cylindrical in shape, are approximately 1.7 times as long as they are wide, and range in diameter from less than 1.0 to 3.5 mm in diameter (Text-Fig. 8). Although they are circular and rounded in transverse-section (Figs. 45, 55, 59; 70, 73, 79, 80), they are transversely truncated by irregular surfaces (Figs. 60–66, 69), indicating brittle fracture of an extruded, relatively dry bolus stream. This fracturing has also resulted in angular coprolite fragments. Those that retain circular cross-sections lack any indication of a pinched-off or rounded terminus. They also exhibit a recurring and diagnostic internal texture of occasional, angular, randomly organized fragments of cellularly identifiable parenchyma tissue embedded in a matrix of dark, amorphous material (Figs. 45, 68, 79), and surrounded by a more refractory coprolite rim (Headrick, 1993, in litt.) This possibly crystalline rim may represent evidence of a peritrophic membrane. Some coprolites contain distinctive gum sac cells of the adjacent cortical and medullary parenchyma (Figs. 68, 76, 79). These relatively indigestible gum sac cells are characterized by a center of opaque resin surrounded by a rigid cell wall, indicating that some coprolites were derived by consumption of the surrounding unaltered parenchyma (Fig. 77). Since gum sac cells occur in only some coprolites and the callus typically lacks gum sac cells, we infer that they represent the products of the initial consumption of axial parenchyma, prior to the production of callus.

Modern insects exhibit a variety of fecal pellet organization, sizes and shapes. Fecal pellets range from rod-shaped structures that are rounded at both ends in Collembola (Kilbertus & Vannier, 1979), to disorganized and angular forms in Archaeognatha (Headrick, 1993, in litt.), to those with ovoidal shapes with irregular surfaces, lenticular and even spiral-shaped structures in various orthopteroids and some larval beetles (Gangwere, 1962; Gangwere & Morales-Agacino, 1964; Jeanson, 1975; Starzyk, 1977; Paranjape, 1985), to elongate cylindrical solids produced by many holometabolan larvae (Hodson & Brooks, 1956; Weiss & Boyd, 1950, 1952; Sweetman, 1965; Pant et al., 1981). Fecal pellets of many holometabolan larvae are barrel-shaped and bear fragemented ends (Figs. 95, 96), unlike the ovoidal or otherwise pinched-off fecal pellets of nonholometabolous insects and holometabolous adults. Fecal pellets of many holometabolan larvae are modified by rectal pads into deep, longitudinal sulci interrupted by regularly arranged lobes (Morris, 1942;

Hodson & Brooks, 1956; Weiss & Boyd, 1950, 1952; Solomon, 1977; Starzyk, 1977) that are asterisk-shaped in cross-section (Figs. 99, 100), or into elongate, ribbon- or rod-shaped pellets (Eckstein, 1939; Solomon, 1977; Starzyk, 1977) or irregular, stringy structures with projecting fibrous or woody elements (Cymorek, 1968; Solomon, 1977).

Although lack of an extensive data base of fecal pellet structure in modern insects disallows direct comparison of coprolites in *Pteriditorichnos* to a specific modern insect clade, several features indicate that it closely resembles a generalized holometabolan larva (Headrick, 1993, in litt.). First, the presence of barrel-shaped coprolites with fractured ends that are about 1.7 times as long as their diameter widths (Figs. 44, 49, 66) indicates that defecation occurred as a continuous bolus in a semirigid state by a larval holometabolan. Many holometabolan larvae possess rectal water uptake mechanisms that leave the feces relatively dry (Frost, 1928; Cymorek, 1968), and thus they are susceptible to further fragmentation as the fecal column is extruded anally and subjected to breakage forces (Hay, 1968). This extrusion mechanism is found only in larval holometabolan insects and is qualitatively different from defecation in other insects in which food boluses are packaged into discrete units and voided as ovoidal or lenticular packages, or more rarely spiral shapes. The lack in *Pteriditorichnos* coprolites of pronounced longitudinal sulci that normally would impart a characteristic asterisk-shaped cross section (Weiss & Boyd, 1950, 1952) is noteworthy, and thus excludes those larvae with longitudinal rectal muscles, such as some Lepidoptera (Gösswald, 1935; Hodson & Brooks, 1956), some symphytan Hymenoptera (Morris, 1942), and certain clades from other holometabolan orders. (Compare *Pteriditorichnos* of Figs. 45, 59, 58, 66 and 79 to folivorous Lepidoptera of Figs. 99 and 100, noting that fecal pellets of xylovorous Lepidoptera in Fig. 98 are circular in cross-section). Second, the clustered, near-parallel packing of the coprolites within the lumen (Figs. 39–44; 60–66, 69) indicates a preferred direction of progression of the endophage within the lumen. The presence of clear evidence for coprolite size classes (Text-Fig. 8) suggests that the responsible endophage comprised four instar stages, and is similar to fecal pellet size in modern holometabolan larvae that are discrete and size-classed (Escherich, 1931; Gösswald, 1935; Nolte, 1939; Sardesai, 1969). Additionally, size-increase ratios between modes of *Pteriditorichnos* coprolite populations (Text-Fig. 8) average a factor of 1.33 (range = 1.23 to 1.47; N = 122), comparable to fecal pellet size-increase ratios for modern holometabolan larvae (Nagasawa, 1957; Sardesai, 1969). Third, the presence of angular and macerated tissue fragments among the coprolites (Figs. 46, 58, 67, 78, 82) indicates a mandibulate endophytic borer or galler. Modern mandibulate borers and gallers do not ingest all tissue they chew (Holmes, 1954; Hay, 1968; Smith, 1970), the unconsumed fraction is termed "sapwood chips" (Starzyk, 1977) for wood borers, or "catachord" (Headrick & Goeden, 1993) for bud gallers. The juxtaposition in *Pteriditorichnos* of dense and refractory coprolites among unconsolidated plant tissue fragments is very similar to frass structure in modern stem gallers. Finally, the presence of a refractory, crystalline-appearing halo around each coprolite may indicate a peritrophic membrane, and thus assignment to either a myriapod or hexapod.

*6.3.1.3. Callus.* A neoformed callus of variable thickness, ranging up to 3.2 mm, generally surrounds the central lumen. (Compare Figs. 39–44 to Figs. 47–51 for thickness end-members.) The elongate shape of the proliferated cells and their transverse orientation with respect to normal, unaltered parenchyma provides a diagnostic criterion for its recognition. This distinctive zone consists of a wound callus of medullary, parenchymatic cells deployed into hemispherical tufts; each tuft is an agglomeration of several to about 25 vertical, uniseriate files of elongate cells (Figs. 57, 66, 80, 85, 86) that may occasionally be cross-cut by a resin canal (Fig. 67). For each file of cells, the cell axes are radially directed toward the central gall axis. This zone, which consists of multiple stratiform layers that completely encircles the lumen in most specimens, but is only partially expressed in UIUC-specimens 31010 (Figs. 47–49, 52-54) and 30823 (Figs. 60–65) and specimen no. 1 of 31272 (Figs. 70–75).

Bulbous tufts frequently appear crowded within the callus zone, and exhibit more vigorous proliferation once they are free within the lumen and unencumbered by lateral constraints. Arcuate and linear zones of contact between individual tufts contain dark material (Figs 39–44; 79; 82, 83; Lesnikowska, 1990) that probably represent trapped mucilage as actively expanding and radiating tufts impinged on each other. Some of these tufts bear cuspate truncations of their lumen-exposed ends (Fig. 66), indicating consumption by an endophage occupant with mandibulate mouthparts. In three specimens, linear passages are oriented approximately perpendicular to the lumen axis and crosscut all medullary and cortical tissues (Figs. 30; 73, 78; 81–84, 87). These passages have a diameter approximately from 0.4 to 0.8 times that of their respective lumen diameter, and they are interpreted as exit holes.

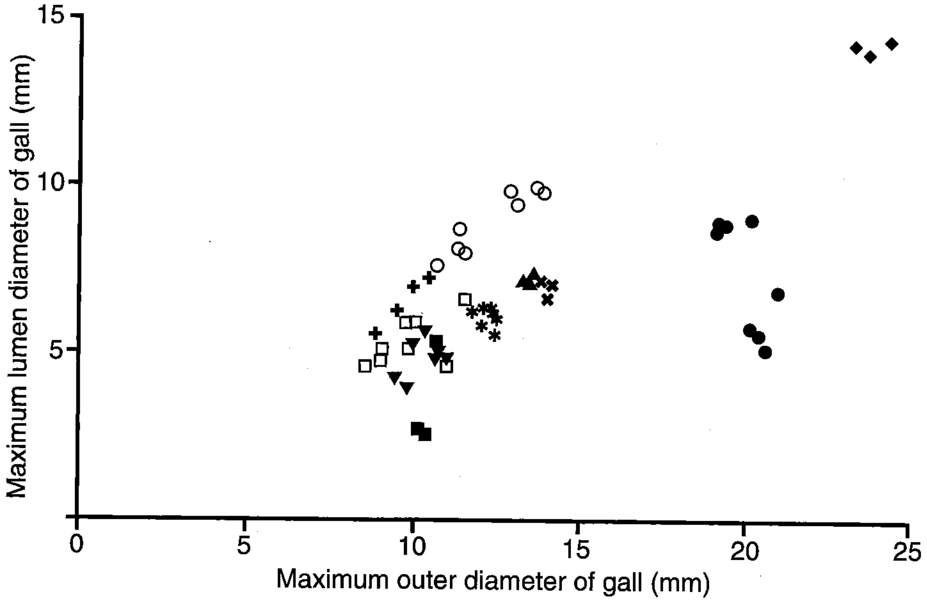
Importantly, the histology of callus in *Pteriditorichnos* exhibits differences to abiotically generated wound tissue as well as similarities to nutritive tissue of typical advanced galls. *Pteriditorichnos* callus is significantly different from mechanically-induced wound reaction parenchyma described by Holden (1912, 1916) for modern filicalean ferns. The key features of endophage-induced callus that distinguishes it from abiotically-inflicted wound tissue include uniseriate, parallel files of cells, cell files organized into tufts, and the layering of proliferated tissue into identifiable strata that are several cells deep. Variations of these features depend on wound localization, type of wounding behavior, and the age of the attacked organ. By contrast, although *Pteriditorichnos* is characterized by presence of callus generated internally by an insect, it exhibits similarities to typical nutritive tissue of advanced galls. Gross cellular and histological similarities include cell wall thickening, elongation of hyperplasic cells as uniseriate files comprising tufts oriented perpendicular to the medullary parenchyma stratum and toward the larval chamber, and the deployment of the callus as a distinctive and frequently continuous layer surrounding the larval cavity. These features of *Pteriditorichnos* callus are shown in Fig. 95, where they are compared to typical callus occurring in cortical parenchyma, consisting of equant, unthickened cells that are characterized by variable growth trajectories and result from a reaction to stylet piercing by a paleodictyopterid insect (Labandeira & Phillips, 1996a). Notably, in the same specimen (UIUC-8227-Bbot), *Pteridotorichnos* callus occurs as a stratum of differentiated cells similar to nutritive tissue. Since nutritive tissue in modern galls is defined by specific features of organellar modification and the elevation of carbohydrate, lipid and soluble protein levels in cellular protoplasts, the secondary parenchyma of *Pteriditorichnos* cannot be definitively assigned to nutritive tissue. It highly resembles the "nutritive zone" of thysanopteran galls that lack typical nutritive tissue, described by Ananthakrishnan & Raman (1989).

The presence of cellular proliferation around the larval chamber in *Pteriditorichnos* confirms that it is a stem gall, and not a stem mine or a stem boring. Modern stem mines occur in parenchymatous tissues, but they do not induce cellular proferation, whereas stem borings mostly are found in more indurated tissues, especially wood, and are associated with structural tissues that are normally dead and are incapable of responding to endophage stimuli. However, one unique Neotropical association, documented by Wheeler (1921), involves endophytic *Pseudomyrmex* ants and the leguminous ant-plant tree *Tachigalia*. Although these ants consume normal, live tissue referred to as "nutritive parenchyma" in the petioles of *Tachigalia* (Wheeler, 1921: 92, pls. 3, 4), this tissue does not exhibit hyperplasia, hypertrophy and other organizational features of galls. The characteristic pattern of hyperplasic and hypertrophied cellular growth organized into vertical cell files, the aggregation of these cell files into tufts, and the layered orientation of these tufts adjacent to the endophage chamber, occurs in most tenthredinid, coleopteran, lepidopteran, and cyclorrhaphous dipteran galls. Consequently the pattern of callus formation per se lacks features for identifying the galler.

### 6.3.2. Size and Shape

The results of bivariate relationships that express ratios of several gall-associated variables indicate that *Pteriditorichnos* is within the modern range of insect galls (Text-Fig. 9). The variables measured are maximum gall diameter, lumen diameter, callus or nutritive zone thickness, and maximum coprolite diameter. In all instances the same mensuration method was used for both *Pteriditorichnos* and modern galls.

*Pteriditorichnos* has a somewhat smaller maximum lumen diameter compared to modern galls of similar maximum outer diameters (Text-Fig. 9). Nevertheless its transverse dimensions are well within the range of modern galls (Text-Fig. 9; Headrick, 1993, in litt.). Although *Pteriditorichnos* extended to 18 cm in length, modern galls, mostly from hemipteroid taxa, do approach this dimension (Cosens, 1912; Newstead & Cummings, 1913; Karny, 1922; Anthony, 1974); in some cases galls measure from 3 to 4 cm in diameter and extend 10 cm or more in length. Notably, *Pteriditorichnos* lacks pronounced external swelling, although several modern stem galls, mostly characterized by larval consumption of medullary stem parenchyma, also lack significant gall enlargement (Trotter, 1934; Lengerken, 1941; Holmes, 1954; Claridge, 1961; Grover, 1988; Zerova et al., 1991; Skuhrava & Skuhravy, 1992). These data, coupled with overall geometry of *Pteriditorichnos*, indicate that a gall origin is the soundest explanation.



Text-Fig. 9. Bivariate scatter plot of maximum outer diameter versus maximum lumen diameter of *Pteriditorichnos* and two recent galls. Solid symbols represent fossil *Pteriditorichnos* galls: ● = UIUC-8227-Bbot, ■ = UIUC-31272a-Bbot, ▲ = UIUC-31272b-Bbot, ◆ = UIUC-8227-Fbot, ▼ = UIUC-31272b-Ctop, ✱ = UIUC-31272c-Ctop, × = UIUC-30823-Dbot, ✚ = UIUC-31010-Dbot. Outlined symbols indicate modern galls: ❑ = USNM-483976, *Pachypsylla venusta* Osten Sacken (Hemiptera: Psyllidae) on desert hackberry, *Celtis pallida* Torr.; and ○ = USNM-483975, *Epiblema strenuana* (Walker) (Lepidoptera: Tortricidae) on common sunflower, *Helianthus annuus* (L.). Both modern galls were collected from Foard Co., Texas.

### 6.3.3. Host Specificity

Extensive effort during the past thirty years has been undertaken to qualitatively and quantitatively characterize the botanical composition of permineralized coal-ball deposits from Euramerica throughout the Pennsylvanian Subperiod (Phillips et al., 1985; DiMichele et al., 1985, 1991). These endeavors have resulted in an extensive inventory of all known coal-ball associated plants, including the incidental discovery and description of many new species. Although paleobotanically-trained researchers may have overlooked or miscategorized plant/animal interactions, we feel that structures as prominent and conspicuous as *Pteriditorichnos* at least would have been photodocumented in the literature, as Stidd did for *Pteriditorichnos* in 1971. Given this history, as well as the extensive and directed survey that the authors have made for locating plant/animal interactions in several, major coal ball deposits, we feel confident that all known *Pteriditorichnos* specimens are confined to Late Pennsylvanian *Stipitopteris* petioles of Euramerican *Psaronius* tree ferns. Twenty-eight known specimens of *Pteriditorichnos* have been recorded out of a pool of at least 450 *Stipitopteris*, suggesting an incidence rate of six percent or less. This fact alone belies a singular pattern of host specificity, indicating that the endophage responsible for *Pteriditorichnos* probably was monophagous.

In addition to host specificity based on taxonomic affiliation, there is strong evidence for organ- and tissue-specificity as well. All known specimens of *Pteriditorichnos* indicate that the endophage galler occurred only in the medullary (axial) parenchyma of basal *Stipitopteris* petioles. With the exception of exit holes, all examples of *Pteriditorichnos* indicate that the vascular cylinder was avoided, and that feeding was limited to medullary parenchyma along the petiolar axis. A thin zone of medullary parenchyma immediately adaxial of the vascular cylinder was also avoided. Apparently only the petiolar base was affected (Text-Figs. 2, 3b). Petiolar diameters smaller than about 1 cm are unaffected in all specimens we have observed. The obvious exception of exit holes indicates that other tissues were consumed during the process of gall abandonment. This is a behavior exhibited by modern monophagous endophages since they must leave their gall to complete their life cycle.

A high percentage of modern galling endophages are monospecific, galling only the same plant species or a group of closely related species (Mani, 1964; Abrahamson & Weis, 1987; Fernandes, 1987; Dreger-Jauffret nymphs, would disallow endophagous gall formation as a viable life-habit. Additionally, presumed palaeodictyopteroid excretion of digested fluid food as nonparticulate, possibly formless, fecal pellets is inconsistent with coprolites in *Pteriditorichnos*.

We have observed cell proliferation and callus formation associated with mouthpart stylet tracks by paleodictyopterans in cortical parenchymatous and vascular tissue of *Stipitopteris* (LABANDEIRA & PHILLIPS, 1996a; Plate 16, fig. 95). Although these structures lack key features associated with galls, and feeding is ectophagous, their presence provides a second example of cellular reaction to insect feeding in *Stipitopteris* (LABANDEIRA & PHILLIPS, 1996a). Also, it should be noted that some Early Permian diaphanopterodeans possessed sawtooth ovipositors (CARPENTER, 1971; KUKALOVÁ-PECK, 1991;) that undoubtedly were used to insert eggs into live plant tissue (SHEAR & KUKALOVÁ-PECK, 1990). This type of palaeodictyopteroid ovipositor is not preserved in known Late Pennsylvanian deposits, but may have been present. If so, then the life-habits of palaeodictyopteroid nymphs may have been more ecologically diverse than previously realized.

### 6.5.3. Orthopteroidea

The only known group of Orthoptera contemporary with *Pteriditorichnos* was the Oedischiidae, a group of average-to large sized saltatorial forms with nonserrated, external ovipositors and generalized mandibulate mouthparts (BOUDREAUX, 1987) that have variously been interpreted as specialized for detritivory, herbivory or insectivory (SHAROV, 1971a; SHEAR & KUKALOVÁ-PECK, 1990). Oedischiid nymphs are unknown.

Diverse modern orthopterans lack true endophagy. However, several examples of orthopteran leaf rollers are known (MCATEE, 1908; KARNY, 1923; CHOPARD, 1938), resulting in foliar curling and near complete enclosure of a grasshopper, but apparently without intratissue boring or galling. Additionally, instances are known of live plant consumption characterized by significant excavation of indurated stem tissue. For example, the Australian mole crickets *Cylindracheta* and *Gryllotalpa* have been recorded from "...stems in plants" (TINDALE, 1928: 25), and in sugar cane stems (HUSSEY et al., 1969), respectively. Of the New Zealand Raphidiophoridae, the genus *Deinacrida* apparently bores into wood with large, powerful mandibles (BULLER, 1867), and although capable of macerating wood, there is no evidence for an endophytic life-habit. Similarly, Frost stated that the cricket *Cylindrodes campbelli* "...bores into wood" (FROST, 1936: 104). WELLS (1921) observed that the orthopteran *Meconema varium* FABRICIUS induced rosette galls on oak stems, but provided no documentation. Lastly, some species of orthopterans can induce tissue reaction up to 4 cm deep in plant stems by abdominal extension during oviposition of eggs into exposed breaks of woody or herbaceous stems (RAMME, 1927; CHOPARD, 1938). Other grasshoppers oviposit into live plant tissues, including stems and leaf midribs (CHOPARD, 1938), but upon hatching there is no evidence that the nymphs are endophytic. Evidently intratissue location of eggs serves as prehatching protection and such microhabitats are not targeted for a nymphal food source.

### 6.5.4. Blattodea and Isoptera

The modern blattoid assemblage consists of the closely-related cockroaches (Blattodea), termites (Isoptera) and mantids (Mantodea) (NALEPA, 1991; THORNE & CARPENTER, 1992) as well as possibly the more distantly associated angel insects (Zoraptera) and earwigs (Dermpatera) (KUKALOVÁ-PECK, 1991). With the exception of the blattodeans and zorapterans, the three other orders have earliest occurrences during the Mesozoic. Blattodeans are a very conspicuous element of the Pennsylvanian biota, and in many fossil deposits coeval with *Pteriditorichnos* are the most abundant insect component. Modern blattodeans deposit their eggs either in leathery oöthecae if they are oviparous or in a membrane if they are ovovivaparous, rather than the Paleozoic-Mesozoic mode of egg extrusion into a substrate by a long ovipositor. Anatomical studies have indicated that blattoid ovipositors, while long, did not have ridged or sawtooth margins (ZALESSKY, 1939; BEKKER-MIGDISOVA, in ROHDENDORF, 1991; VISHNIAKOVA 1973), and were probably used for oviposition in substrates other than plant tissues. Additionally, the flat body structure of cursorial blattoid nymphs and adults indicates a likely role as a litter detritivore. Notably, the modern wood roach *Cryptocercus* bores into dead woods and establishes a gallery system, as do modern termites and apparently zorapterans (LEE & WOOD, 1971; GREENSLADE, 1985; RENTZ, 1991c; see Section 5). Although these xylophagous taxa are endophages, and termites are known to consume live food (BANKS & SNYDER, 1920), none are known to be gallers, despite considerable autecological research by economic entomologists.

### 6.5.5. "Protorthoptera" and Plecopteroids

The undoubtedly polyphyletic order "Protorthoptera" consists of a diverse assemblage of approximately 45 families of Lower Pennsylvanian to rare Early Triassic terrestrial mandibulate insects (LABANDEIRA, 1994). Although many taxa of traditional protorthopterans recently have been transferred to other neopterous assemblages (RASNITSYN & ROHDENDORF, 1980; SHEAR & KUKALOVÁ-PECK, 1990; KUKALOVÁ-PECK & BRAUCKMANN 1992), the unassigned remainder exhibits a generalized, uncharacteristic neopterous facies, including mandibulate mouthparts, generalized wing venation, and a ridged ovipositor (SHAROV 1971a; KUKALOVÁ-PECK & BRAUCKMANN, 1992). Although little is known of protorthopteran autecology, it is most reasonable to infer that the nymphs were structurally similar to the adults, possessing long antennae, wing pads, and lateral abdominal appendages. By contrast, the related plecopteroids are characterized by aquatic nymphs, but, like protorthopterans, adults are free-living and ectophagous.

### 6.5.6. Hemipteroidea

The hemipteroid assemblage is a taxonomically diverse complex of five orders dominated by various specializations for fluid feeding. These specializations range from typically mandibulate mouthpart elements modified into styliform structures in hemipteroid ancestors (KUKALOVÁ-PECK, 1991; KUKALOVÁ-PECK & BRAUCKMANN, 1992), to the highly integrated, ensheathed mouthparts of hemipterans (sensu lato). According to KUKALOVÁ-PECK & BRAUCKMANN (1992), the geochronologic range of hemipteroids extends to the Early Pennsylvanian by recognition of wing, mouthpart and head features of taxa that formerly were included in the "Protorthoptera". Little is known of the subadult life-habits of these primitive hemipteroids, other than that for Myachkovskian-age herdinid nymphs which possessed well-developed, posterolaterally projecting wings, abdominal exites and caudal cerci – a habitus incompatible with an endophage existence.

Psocopterans, phthirapterans, thysanopterans and hemipterans (sensu lato) are derived hemipteroids and the last two orders contain modern taxa that are prominent gallers on vascular plants. Psocopterans are principally detritivorous and occur in litter and under bark, whereas phthirapterans are vertebrate ectoparasites. The earliest occurrences of both thysanopterans and hemipterans are Permian, although an origin during the Late Pennsylvanian is reasonable. Nevertheless, hemipteroid fluid feeding results in fecal material characterized by amorphous masses that lack particulate structure (STOREY & NICHOLS, 1937; BROADBENT, 1951; HORSFIELD, 1978). Thus, the hemipteroid type of excreta is qualitatively different from *Pteriditorichnos* coprolites (DIXON, 1985; DOLLING, 1991) that contain abundant fragments of macerated parenchyma tissue. Equally important is the qualitatively distinctive nature of virtually all hemipteran galls, which lack the tissue differentiation and thus well-developed cecidogenic tissue that occurs in holometabolan galls (KÜSTER, 1911; DREGER-JAUFFRET & SHORTHOUSE, 1992). Additionally, only one known thysanopteran has been implicated in a recent stem gall (KARNY 1922; MOUND & CRESPI, 1992); all other thysanopterans are principally leaf gallers and to a lesser extent bud gallers (ANANTHAKRISHNAN, 1978; ANANTHAKRISHNAN & RAMAN, 1989). In hemipterans, virtually all galling taxa produce leaf and bud galls, although several galls are known from petioles, such as psyllid galls on *Celtis* and pemphigid aphids on *Populus*. Based on these collective considerations, it is highly unlikely that *Pteriditorichnos* was caused by an hemipteroid.

### 6.5.7. Holometabola

The most structurally, taxonomically and ecologically diverse clade of insects of all time is the Holometabola, comprising in excess of 88 percent of all extant insects (HINTON, 1963). The spectacular dominance of holometabolans in terrestrial ecosystems is attributable to an unique apomorphy – namely, the presence of complete metamorphosis wherein a generally vermiform larva is morphologically and ecologically separated from its nominal winged adult stage by a pupal resting stage. The holometabolan radiation during the Permian (Text-Fig. 10) was contemporaneous with older paleopterous and orthopteroid lineages that survived a taxonomic pruning at the end of the Late Pennsylvanian. The taxonomically distinctive Permian insect fauna is distinguished from a Pennsylvanian insect fauna, rich in palaeodictyopteroids, dragonflies, roaches and "protorthopterans" that is almost entirely known from Euramerican, clastic-dominated equatorial swamp forests. Several authors have indicated that holometabolans should occur in Upper Pennsylvanian deposits (LAMEERE, 1899, 1908, 1917; CRAMPTON, 1931; CHEN, 1946; SHAROV, 1966; MALYSHEV, 1968; HENNIG, 1981; LAWRENCE & NEWTON, 1982; WILLMANN, 1989), and some have expressed surprise that no undoubtedly holometabolan forms have been discovered from Pennsylvanian strata (HENNIG, 1981; CARPENTER, 1992). There now are three lines of body-fossil evidence that suggest that holometabolans were present during the Middle to Late Pennsylvanian, namely reassignment of *Metropator* and *Fatjanoptera* to the Holometabola (MARTYNOVA, 1961; RASNITSYN & ROHDENDORF, 1980; SHEAR & KUKALOVÁ-PECK, 1990; but also see CARPENTER, 1992) and an undescribed, apparently eruciform larva (KUKALOVÁ-PECK, 1991). Additionally there is an instance of holometabolan-implicated, herbivore endophagy – namely possible leaf-mines from diverse medullosan pinnules from the Myachkovskian of Illinois (LABANDEIRA & BEALL 1990) and Germany (MÜLLER 1982). The implications of these discoveries will be discussed in Section 7.

Excluding the above possible exceptions and perhaps the enigmatic Miomoptera, all holometabolan orders have post- Pennsylvanian earliest known occurrences. The Early Permian radiation of holometabolans apparently involved taxa whose descendants currently constitute two of the three major branches of the Holometabola. These include the mecopterans of the Panorpoidea, and neuropterans, raphidioideans and ancestral coleopterans of the Neuropteroidea; good evidence for the Hymenoptera does not occur until the Middle Triassic (Text-Fig. 10). The life-habits of these Early Permian groups are poorly known, although the adults were probably free-living and ectophagous, based on fossil occurrences and extensive documentation of the ecology of modern forms. Only a single Permian larva, a probable coleopteran, has been described (SHAROV, 1953; ACHTELIG, 1981; but see LAWRENCE & NEWTON, 1982). In this section we consider only those holometabolan orders that possess in their most plesiomorphic subclades larval life-habits that are ecologically similar to a putative stem-endophyte living during the Upper Pennsylvanian.

*6.5.7.1. Miomoptera.* Although the Lower Pennsylvanian to Lower Jurassic Miomoptera are considered primitive hemipteroids by CARPENTER (1992), several authors have assigned the group to the Holometabola because of their combination of panorpoid and hymenopteran venational features (SHEAR & KUKALOVÁ-PECK 1990; RASNITSYN, 1994, in litt.). Five families of Late Pennsylvanian miomopterans are known from Euramerica, including the controversial *Metropator*, which has been assigned to the Mecoptera by some (TILLYARD, 1926, but also see WILLMANN, 1989). The Miomoptera were relatively nondiverse and probably inconspicuous element in Late Pennsylvanian biotas.

Adult miomopterans are small to very small forms with short abdomens, hypognathous heads and mandibulate mouthparts (ROHDENDORF & RASNITSYN, 1980; SHEAR & KUKALOVÁ-PECK, 1990). They may have been spore feeders on gymnospermous cones (RASNITSYN, 1980) or more likely generalist detritivores or herbivores. Although there is the suggestion that miomopteran immatures (presumably larvae) developed inside gymnospermous reproductive structures (ROHDENDORF & RASNITSYN, 1980), the only known miomopteran immature is *Permonympha* (SHAROV, 1957), which possessed a body facies inconsistent with an endophytic existence. Regardless of their status as holometabolans or not, it is very unlikely that they were the culprit for production of *Pteriditorichnos.*

*6.5.7.2. Mecoptera.* The Mecoptera are one of the most plesiomorphic clades of the Holometabola, an assessment that is supported by their possession of many plesiomorphies within the Holometabola and the relatively high diversity of mecopterans and their immediate ancestors during the Early Permian (KUKALOVÁ-PECK & WILLMANN, 1990). The most plesiomorphic extant family, the Nannochoristidae (KRISTENSEN, 1989; BYERS, 1991), have larvae that are wireworm-shaped (Text-Fig. 7f), apparently insectivorous, and occur in terrestrial or aquatic habitats (PILGRIM, 1972; BYERS, 1991). Larvae of other mecopteran families are eruciform and display feeding habits of scavenging, herbivory on mosses and leafy liverworts (BYERS, 1987), or rare insectivory (CURRIE, 1932; SETTY, 1939; BYERS, 1963); no known extant larval mecopteran is endophytic. Notably, diverse, widely-accepted mecopteran-like forms appear in the Early Permian, and an undescribed Myachkovskian-age eruciform larva with mecopteroid affinities has been figured by KUKALOVÁ-PECK (1991; also see WILLMANN, 1998). Also, there has been frequent mention of the mecopteroid features of the Miomoptera in general and the Kinderscoutian (earliest Pennsylvanian) *Metropator* in particular (TILLYARD, 1926; CARPENTER, 1965; SHAROV, 1966; HENNIG, 1981; WILLMANN, 1989; KUKALOVÁ-PECK 1991). The difficulty in taxonomic assignment of these taxa may indicate that there was a complex of Late Pennsylvanian and Early Permian mecopteroid lineages that lacked apomorphies now considered to define the Mecoptera or any other extant mecopteroid clade. These generalized holometabolan lineages were the referents that LAMEERE (1899, 1908, 1917), MALYSHEV (1968), and ROHDENDORF & RASNITSYN (1980) alluded to in their discussions of the origin of endophagy during the Pennsylvanian.

*6.5.7.3. Diptera.* Like other major holometabolan lineages, the Diptera consist of a structurally and taxonomically diverse assemblage that has invaded virtually every terrestrial and aquatic habitat. Within the Diptera, it is generally accepted that the craneflies, comprising the superfamily Tipuloidea, are the most plesiomorphic extant clade (HENNIG 1973, WOOD & BORKENT, 1989; KRIVOSHEINA, 1991; COURTNEY, 1991; but see ROHDENDORF, 1974). This conclusion is bolstered by the tipuloid fossil record, which extends to the Late Triassic (OLSEN et al., 1978; KOVALEV, 1984; KRZEMINSKI, 1992). Although these Triassic occurrences have conventionally been considered the earliest definitive Diptera, other studies have indicated that the early Late Permian taxa Permotanyderidae and Permotipulidae are most appropriately assigned to the stem-group of the Diptera (OLDROYD, 1964; WOOTTON & ENNOS, 1989; WILLMANN, 1989; but see KRZEMINSKI, 1992). However, these Permian taxa have two pairs of well-developed wings and are probably not tipuloids.

Modern tipuloids comprise two families, the Trichoceridae and the exceedingly diverse Tipulidae, the larvae of which collectively occur in ecologically disparate microhabitats, ranging from fully aquatic to obligately terrestrial (OLDROYD, 1964; KRIVOSHEINA, 1969), and including specialized life-habits such as leaf-mining (SWEZEY, 1915). Most tipuloid larvae are detritivores, occurring in water, or in wet situations generally in litter, soil or decaying plant tissues (KRIVOSHEINA, 1969; FOOTE, 1991). Many are xylophagous or mycophagous wood-decomposers that burrow or bore into woods of all stages of decay (KRIVOSHEINA, 1969, 1991). Although tipuloid larvae, or maggots, are generally diminutive compared to the larger eruciform larvae of coleopterans, hymenopterans and lepidopterans, a few wood-associated forms are atypically robust (Text-Fig. 7h). No generalizations regarding the ancestral life-habit of tipuloid larvae can be made because of the broad ecological spectrum they currently inhabit. It should be noted that the larvae of other basal and plesiomorphic dipteran lineages such as Axmyiidae and Pachyneuridae, also occur in decomposing wood. Thus, it can be concluded that detritivory, including wood decomposition, was the most likely larval life-habit of Triassic dipterans and their immediate Permian ancestors. Because of the relatively late appearance of the earliest known fossil Diptera and their near absence in live plant tissues (but see SWEZEY 1915), we exclude dipterans as the maker of *Pteriditorichnos*.

*6.5.7.4. Lepidoptera.* The Lepidoptera constitute the most herbivorous clade of holometabolans: over 99 percent of all lepidopteran species feed on plants in some form (STRONG et al., 1984). Lepidopteran associations with plants are intimate and complex, involve both larvae and adults that range from plesiomorphic groups such as micropterygids to derived groups such as butterflies. Interestingly, Early Jurassic micropterygoid moths are the earliest known, indisputable lepidopterans (WHALLEY, 1986), and they also are the most plesiomorphic of extant lepidopterans (KRISTENSEN, 1984; but see SHIELDS [1993]). The Lepidoptera share a sister-group relationship with the Trichoptera (HENNIG, 1981; KRISTENSEN, 1991), whose earliest occurrence is 35 million years earlier, during the Middle Triassic. Complicating this sister-group relationship is the poorly resolved systematic status of the mostly Permian "Paratrichoptera", which can be interpreted either as a sister group to the Lepidoptera + Trichoptera, or more likely, an assortment of unrelated, generalized panorpoid families that are unassignable to any modern panorpoid lineage (HENNIG, 1981). Permian paratrichopterans apparently resemble generalized panorpoids and, by inference, probably had terrestrial larvae (WHALLEY, 1978). WHALLEY (1978) envisions a relatively early and subsequent differentiation of these paratrichopteran larvae into varied plant microhabitats, including stem-boring, whereas the corresponding adults did not acquire recognizable lepidopteran or trichopteran features until the mid Mesozoic.

Considerable attention has been focused on the dietary habits of modern micropterygid larvae. Larval micropterygids (Text-Fig. 7c,d) are feeders on liverworts, mosses, leaf detritus, herbaceous dicots, and probably on fungi (TILLYARD, 1923; LORENZ, 1961; YASUDA, 1962; CARTER & DUGDALE, 1982; TUSKES & SMITH, 1984; DAVIS, 1987). There is no evidence for endophagy; nor is there significant host selectivity by particular species. Although the lineage encompassing micropterygids is traceable to the Early Jurassic, and includes several Cretaceous and Tertiary occurrences, it is unclear whether the nonselective, ectophagous diet and occupation of epiedaphic habitats is traceable to the Paleozoic. By contrast, although trichopteran adults are terrestrial, their larvae are obligately aquatic and feed on detritus, and, less commonly, on live plants. With regard to *Pteriditorichnos*, the only insight that the most plesiomorphic extant lepidopteran can provide is that possibly the life-habits of the ancestral Trichoptera + Lepidoptera larva was terrestrial and a generalized herbivore or detritivore. Additionally, based on fossil evidence, it was during the later Mesozoic and Cenozoic during which at least 17 lepidopteran lineages, including the Tortricidae (Figs. 96 and 97), began to gall vascular plants, producing nutritive tissue that histologically resembles some features of *Pteriditorichnos* callus. Collectively this evidence indicates that a larva of a lepidopteran or its immediate ancestor probably was not involved in producing the *Pteriditorichnos* gall.

*6.5.7.5. Neuroptera.* The Neuroptera – herein used in the narrow sense, equivalent to Planipennia – share with the coleopteroid and mecopteroid lineages a relatively early origin during the Early Permian. Three families representing a modest neuropteran diversity are known from the Sakmarian Stage, although no known larvae have been recovered. Recent neuropteran larvae are overwhelmingly terrestrial and carnivorous, although the two notable exceptions are the aquatic Sisyridae, feeding on sponges and byrozoans, and the root-feeding, Ithonidae (Text-Fig. 7g). The Ithonidae are widely considered as the most plesiomorphic, extant neuropteran family (WITHYCOMBE, 1924; MEINANDER, 1972). Consideration of the life-habits of ithonids is essential for establishing the ancestral larval life-habit in the Neuroptera. If the Ithonidae are truly rhizophagous or detritivorous (GALLARD, 1932; SMITHERS, 1979; FAULKNER, 1990; but see TILLYARD [1922b] and RIEK [1974]), then it is possible that the obligate carnivory in the remaining sixteen or so families (minus the Sisyridae) may be secondary. However, it also is more likely that carnivory is primitive within the Neuroptera, since the sister-group of the Neuroptera, the Megaloptera, has obligate larval carnivory, as does the Raphidioidea, which is the probable sister-group to the Neuroptera + Megaloptera (BOUDREAUX, 1987). Under this phylogenetic topology, the Ithonidae is viewed as dietarily derived, while retaining several structural plesiomorphies (OSWALD, pers. comm.). However, ithonid herbivory on roots (FAULKNER, 1990) is phylogenetically too far removed from the life-habits the *Pteriditorichnos* culprit for a meaningful comparison.

*6.5.7.6. Coleoptera.* Beetle-like insects are first encountered in the fossil record from Early Permian (Sakmarian) strata and are conventionally represented by five families. Debate exists whether these families of beetle-like insects are plesiomorphic members of the traditionally-accepted, most plesiomorphic coleopteran subclade, the Archostemata (PONOMARENKO, 1971; CROWSON, 1981; CARPENTER, 1992); or whether they represent an ancestral, paraphyletic lineage (KUKALOVÁ, 1969; KUKALOVÁ-PECK, 1991); or even if they are an assemblage of forms representing the stem-group of the Coleoptera (HENNIG, 1981; KUKALOVÁ-PECK & LAWRENCE, 1993). Nevertheless, Early Permian, beetle-like fossils possess a body facies very similar to modern Cupedidae (PEYERIMHOFF, 1909; PONOMARENKO, 1969; VULCANO & PEREIRA, 1975; CROWSON, 1976), arguably the most primitive extant coleopteran lineage. Little is known of Permian beetle-like larvae (SHAROV, 1953; PONOMARENKO, 1969; LAWRENCE & NEWTON, 1982), and determination of larval life-habits is dependent on the autecologies of extant descendant lineages.

It is noteworthy that the Adephaga also has been proposed as the most plesiomorphic coleopteran suborder (VULCANO & PEREIRA, 1975; KUKALOVÁ-PECK & LAWRENCE, 1993). The Adephaga contains an endophytic, wood-associated family, the Rhysodidae, which probably is its most plesiomorphic subclade (CROWSON, 1981; BEUTEL & ROHGHLEY, 1988; but also see BELL & BELL [1962] and BEUTEL [1993] for a differing interpretation). Although the Rhysodidae only have a Tertiary fossil record, they apparently possess primitive characters relative to the more derived caraboid and hydradephagan clades. Recently, the Late Permian holometabolan larva, *Permosialis* (SHAROV, 1953), although once considered a megalopteran (HENNIG, 1981), has been reassigned to the aquatic adephagan family Gyrinidae (ACHTELIG, 1981; BEUTEL, 1993). This specimen may represent one of the oldest holometabolan larvae, with the possible exception of KUKALOVÁ-PECK's (1991) undescribed Middle Pennsylvanian form. *Permosialis* has all the features of an holometabolan larvae, including an inverted, Y-shaped cranial suture, a vermiform shape, and abdominal, gill-like appendages. It was probably insectivorous.

Early Permian beetle fossils of the Tschekardocoleidae are dorsoventrally flattened as adults and presumably inhabited subcortical habitats or rotting logs (PONOMARENKO, 1969, 1971; CROWSON, 1981). Curiously, within both the modern Archostemata and the Adephaga, the most plesiomorphic subclades – the Cupedidae and Rhysodidae respectively – consist of members whose adults are dorsoventrally flattened and inhabit bark and dead wood habitats, and whose larvae (Text-Fig. 7a,b,e) are wood borers or otherwise inhabit dead, frequently punky, wood (VANIN & COSTA, 1978; LAWRENCE, 1989) This suggests that a xylophagous, endophytic larval life-habit may be ancestral, and wood-associated fungivory the ancestral diet (Crowson, 1981; Kiretjshuk, 1991). None of these wood-associated clades contain gallers, though boring in tough wood is present in some species (Blackman, 1922; Hickin, 1975; Hamilton, 1978). Coleopteran lineages that currently have galling species probably did not originate until the Late Triassic or Jurassic (Crowson, 1981; Lawrence & Newton, 1982; Lawrence, 1989). All known gall-forming Coleoptera are members of the post-Paleozoic suborder Polyphaga and largely induce stem or petiole galls without formation of typical nutritive tissue with cells rich in proteins and sugar (Shorthouse & Lalonde, 1984). This presumably is because mandibulate larvae rapidly damage host tissue prior to its differentiation. Instead of nutritive tissue, callus-like secondary parenchyma is produced. Consequently, while coleopteran larval xylophagy and occurrence within wood is consistent with endophytic life-habits in other holometabolan lineages (Mamaev, 1977; Hamilton, 1978), it is possibile that the *Pteriditorichnos* galler may have been an early coleopteran lineage.

*6.5.7.7. Hymenoptera.* The earliest occurrence of undisputed Hymenoptera is from Middle Triassic strata, and consists of xyelid sawflies (Rasnitsyn, 1980) that are members the most plesiomorphic extant hymenopteran group, the symphytans. Extant xyelid larvae (Text-Fig. 7i) are external-foliage-feeders on conifers and amentiferous angiosperms, or are wood borers and gallers in conifers (Evans, 1987). Like many xyelid larvae, endophagous life-habits also occur in other related clades of the Symphyta, including extant Tenthredinidae, Blasticotomidae, Siricidae, Xiphydriidae, Anaxyelidae and Cephidae. Although the endophages of most of these groups are wood borers in angiosperms (Blackmann, 1922), many occur in conifers (Smith, 1967; Rasnitsyn, 1977b; Gauld & Bolton, 1988) and even ferns (Ludwig, 1891; Togashi, 1989; Shaw & Bailey, 1991). Notably, several extant symphytan lineages have evolved stem- or petiole boring and galling in ferns (Forsius, 1926; Simmonds, 1967), including *Blasticotoma filiceti* Klug (Blasticotomidae) and *Heptameleus ochroleuceus* (Tenthredinidae: Selandriinae), among others, which bore into the petioles and stems of extant Polypodiaceae. A tenthredinoid stem borer or galler is known from Baltic amber (Rasnitsyn, 1977b) and blasticotomids have a fossil record extending to the Oligocene (Zhelochovlzev & Rasnitsyn, 1972). The plesiomorphic status and early appearance of symphytans in the hymenopteran fossil record (Malyshev, 1968), and their current association with fern lineages that originate during the Early Mesozoic (Taylor & Taylor, 1993; Stewart & Rothwell; 1993) indicate that this association is ancient. The association of *Blasticotoma* and the asplenaceous lady-fern, *Athyrium filix-femina*, has been described by Malyshev (1968):

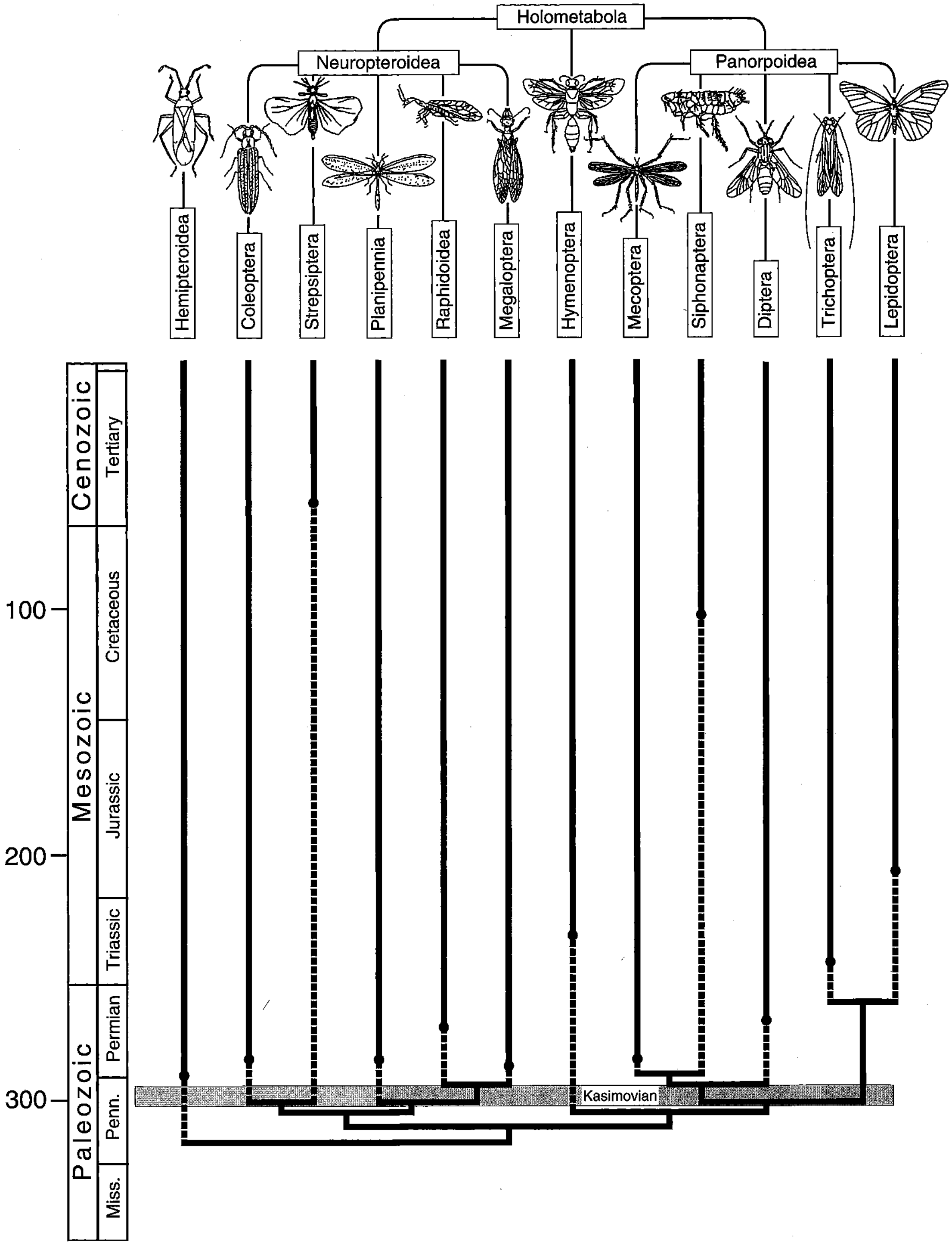
> "The larva of this rare sawfly develops in the hollow of the leaf petiole of the fern *Athyrium filix-femina*, and secretes small blobs of foam which surround the petiole. The primitive morphological characteristics of this sawfly thus correspond to its archaeic endophytic relationship to the fern." (Malyshev, 1968, p. 19; transl. from Russian by B. Uvarov]

Unfortunately, other than *Pteriditorichnos*, no other insect stem gall on a fern has been described from the fossil record.

Considerable intensive documentation of the development, anatomy, histology and cytology of symphytan galls in a plethora of modern seed plants (Cameron, 1885; Smith, 1968, 1970; Narenden, 1984; Price, 1992) has provided a comprehensive baseline for comparison to *Pteriditorichnos*. *Pteriditorichnos* is consistent with those symphytan galls that are relatively noninflated and are elongate galls within stems. Several symphytan clades have members that produce elongate, axial, stem-borings with internal gall tissue, such as some tenthridinids on woody dicot twigs (Smith, 1968, 1970), blasticotomids on nonarborescent fern petioles (Ermolenko, 1964; Shaw & Bailey, 1991), and cephids on grass stalks (Soloman & Randall, 1978; Roskam, 1992). Most other symphytan stem galls are more ovoidal, site-specific, and have sedentary occupants unaltered by consumption of adjacent axial parenchyma. Of all modern insect galls, *Pteriditorichnos* is most structurally similar to elongate axial stem galls made by symphytan Hymenoptera. However, the rather large size of *Pteriditorichnos* galls, with a maximum size: 1.5 cm diameter by 18 cm. long, and the absence of symphytans prior to the Middle Triassic clouds assignment of *Pteriditorichnos* to primitive, endophytic Hymenoptera.

### 6.5.8. Taxonomic Assignment of the Probable Culprit

Two lines of evidence are available for describing the endophage responsible for producing *Pteriditorichnos*. First is the basic structure of the gall itself, including shape, size, contents and anatomy. Second is our knowledge



Text-Fig. 10. Temporal relationship of the Late Pennsylvanian (Kasimovian) *Pteridiscaphichnos* to the radiation of the Holometabola, based on cladistic relationships (Hennig, 1981; Kristensen, 1989, 1991) and earliest fossil appearances (Labandeira, 1994) of Holometabola subgroups. Cladogram symbols: dots denote first fossil occurrences; solid lines record known presence from fossils; dotted lines record inferred presence based on sister-group relationships; stippled bar provides the duration of the Kasimovian Epoch of the Late Pennsylvanian. Abbreviations: Miss = Mississippian (Lower Carboniferous), Penn = Pennsylvanian (Late Carboniferous).

of the Late Pennsylvanian fossil insect record, both from the fossils themselves, as well as from comparative anatomical and ecological features of modern plesiomorphic taxa from holometabolan lineages (Text-Fig. 7) that are recorded from or are presumed to have originated during the late Pennsylvanian and Permian. We have excluded ecologically uninformative holometabolan lineages such as the animal-parasitic Strepsiptera and Siphonaptera, and the aquatic Trichoptera – groups which secondarily acquired life-habits absent from more basal Holometabola (Text-Fig. 10).

Evidence from the *Pteriditorichnos* gall and from the taxonomic spectrum of extant galling insects indicates that the culprit was a vermiform holometabolan larvae. This is generally consistent with the fossil insect record, although the occurrence of completely-metamorphosing insect lineages contemporaneous with *Pteriditorichnos* is a conclusion that still receives only tentative support from relevant body-fossils. Also, given the fossil gall structure and the habitus of extant plesiomorphic groups of major holometabolan clades, we conclude that the *Pteriditorichnos* culprit was an eruciform, holometabolan larva similar to extant tenthredinoid stem-gallers. Nevertheless, we emphasize that, in lieu of any body fossil evidence, the *Pteriditorichnos* larva is unassignable to any modern holometabolan clade.

### 6.6. Historical Approaches Toward Understanding Insect Galling on Ferns

A highly integrated association during the Late Pennsylvanian between an endophytic herbivore and a marattialean tree fern in a floristically ancient coal swamp has implications for the evolution of fern/arthropod interactions. *Pteriditorichnos*, in addition to several other *Psaronius*/arthropod interactions occurring during the Late Pennsylvanian (SCOTT et al, 1985; LABANDEIRA & PHILLIPS, 1992, 1996a; LABANDEIRA et al., 1997; LABANDEIRA, 1998b) constitutes our best window in deciphering Paleozoic associations between a fern and its arthropods. Our only other comparable case example is Recent fern/arthropod associations, which host the same functional-feeding-groups of arthropods as those of other vascular plants. Although a direct comparison of Recent fern/arthropod interactions to the Late Pennsylvanian is tempting, it is essential to recognize that during the intervening 300 million years, there has been major taxonomic realignments for both fern and arthropod clades, and that the synecological framework of ecosystems has been so modified that wetland communities from the two periods are biotically incomparable (LABANDEIRA & BEALL, 1990; BEHRENSMEYER, et al, 1992). However, certain autecological and functionally-based comparisons can be ascertained between Late Pennsylvanian and modern fern/arthropod associations.

#### 6.6.1. Arthropod Herbivory on Marattialean Ferns

The Marattiales, whose fossils extend from the Mississippian, form subdominant or dominant elements in many Pennsylvanian and Early Permian floras (PHILLIPS et al., 1974; PFEFFERKORN & THOMSON, 1982; THOMAS, 1985). Paleozoic marattialean ferns were unbranched tree ferns up to 16 meters tall, mantled with a dense, thick buttress of adventitious roots (MORGAN, 1959; STIDD & PHILLIPS, 1968; see Section 3), and contributed to canopy formation during the Middle to Late Pennsylvanian (CROSS & PHILLIPS, 1990). Their modern descendants are more diminutive, mostly with short, tuberous, stems that lack a dense root mantle, and are confined to riparian habitats at lower elevations in equable, tropical forests (PARRIS, 1976; PAGE, 1979). The lineage comprising modern marattialean ferns probably originated during the Permian (HARRIS, 1931; but see STIDD [1971] and GAO & THOMAS [1993]), and consists of several genera comprising approximatley 200 species that are placed in the single family, Marattiaceae. Little is known of modern marattialean interactions with arthropods. By contrast, exhaustive effort has been devoted to the insect associates of one genus of filicalean fern – *Pteridium aquilinum* (KUHN), or bracken, which is near cosmopolitan in distribution and is a serious agricultural weed in regions of livestock grazing (MEIKLE, 1937; BRAID, 1959). Extensive worldwide documentation exists of the insect herbivores on bracken (LAWTON, 1976; LAWTON & MACGARVIN, 1985; WINTERBOURN, 1987; COMPTON et al., 1989; SHUTER, 1990; SHUTER & WESTOBY, 1992), a feature attributable to its economic importance and unique candidacy as a widely-distributed, nonangiospermous model system for investigating the geographical patterns of insect functional-feeding-groups.

Literature-based references to herbivory on extant marattialeans consist of casual textual or pictorial documentation of galls, leaf mines and stem borings, frequently in the context of a larger botanical study. An intensive search of the available literature has produced only five documented examples of endophagous mite and insect interactions with the Marattiaceae. These are a petiolar gall of undetermined origin on a Brazilian *Archangiopteris* sp. (Christ & Giesenhagen, 1899), an unspecified, but probable eriophyid, pinnule gall on an Indonesian *Angiopteris evecta* (Forster) Hoffmann (Docteurs von Leeuwen & Docteurs von Leeuwen-Reijnvan, 1926), the curculionid stem borer, *Miocalles sternalis*, occurring on *Angiopteris rapensis* from Rapa Island (Paulay, 1985), and species of the agromyzid leaf-mining genera *Phytoliriomyza* sp. on *Marattia douglassi* from Hawaii (Swezey, 1954; Spencer, 1990) and *Tropicomyia* sp. on *Angiopteris evecta* from Kerala, southern India (Spencer, 1990). Additionally, a cursory search of marattiaceous specimens in the herbarium of the University of Illinois at Urbana-Champaign has revealed considerable pinnule damage, including galls, but especially external-foliage-feeding in the form of cuspate margin feeding and probable curculionid window feeding on *Angiopteris lygodifolia* Rosenstock from Taiwan and *Marattia laxa* Kunze from Vera Cruz, Mexico. Skeletonization was also noted on *Marattia attenuata* Labillardière from New Caledonia.

Although these data superficially indicate that extant Marattiaceae are minimally consumed by herbivores, we suggest that this is more apparent than real, and reflects a lack of interest and study rather than a genuine biologic pattern (Auerbach & Hendrix, 1980). Furthermore, the development of an extensive network of lysigenous mucilage canals and tannin ducts in modern and ancient marattialean ferns (Brebner, 1902; West, 1915; Lesnikowska, 1989) is consonant with antiherbivore defense. It is possible that these physiological mechanisms of herbivore avoidance are associated with biochemical evidence indicating that the Marattiaceae are poorly defended biochemically (Imai et al., 1969; Hikino et al., 1973). This contrasts to the elevated biochemical defense and perceived under-representation of insects particularly on bracken (Kaplanis et al., 1967; Hendrix, 1975, 1977) and ferns in general (Brues, 1920, 1972; Soo Hoo & Frankel, 1964; Elton, 1966; Southwood, 1973; Swain & Cooper-Driver, 1973; Balick et al., 1978; Hendrix, 1980; Ottosson & Anderson, 1983). Nevertheless, recent evidence indicates that, even with a considerable battery of secondary defense, ferns are as intensely utilized as angiosperms by herbivores (Swezey, 1922; Lawton, 1976, 1978; Rowell, 1978; Balick et al., 1978; Gerson, 1979; Auerbach & Hendrix, 1980; Rowell et al., 1983; Jones, 1983; Hendrix & Marquis, 1983). Despite the detailed studies of herbivory on bracken (for example, Lawton, 1976; Kirk 1977; Winterbourn, 1987; Compton et al., 1989; Shuter, 1990; Shuter & Westoby 1992), there is a special need to address the detection and documentation of insect herbivores on modern marattiaceous ferns.

This paucity of documentation for arthropod interactors on modern marattialean ferns can be contrasted with what is currently known about Late Pennsylvanian marattialean tree ferns. To date, there is evidence for the following on *Psaronius*: oribatid mite borers (Cichan & Taylor, 1982; Labandeira et al., 1997); large trunk borer (Rothwell & Scott, 1983; this paper); petiole galler (Labandeira & Phillips, 1996b; this paper); external-foliage-feeders, principally in the form of *Pecopteris* folivores and *Scolecopteris* sporangiavores (Labandeira, 1998b); and a piercer-and-sucker (Labandeira & Phillips, 1996a). No reliable evidence exists as yet for a leaf miner. Clearly, *Psaronius* is a model system for a diversity of functional-feeding-groups during the Late Pennsylvanian and our knowledge of its diverse arthropods possibly exceeds that of any single modern marattialean species. This is attributable to the excellently preserved permineralized state of Late Pennsylvanian, *Psaronius*-bearing coal balls, as well as the inattention by modern ecologists to document arthropod interactors on modern, arborescent ferns.

### 6.6.2. The Origin of the Galler Functional-Feeding-Group

In this section we provide an evolutionary and ecological context for the origin of galling. We examine the Mesozoic and Paleozoic fossil-gall record, discuss hypotheses and nutritional pathways for the origin of insect galling, and lastly, cite and contrast two case studies – dipteran cecidomyiids and hymenopteran symphytans – as possible analogs for the origin of *Pteriditorichnos*. Curiously, although there is a considerable literature devoted to establishing and testing various hypotheses for the origin of plant galls, to date no fossil data has been included in the mainstream of discussions on gall origins. Much of the earlier literature on fossil plant teratologies – for example, Williamson, 1880; Weiss, 1904; Stopes, 1907; Holden, 1910 – has been interpreted as consequences from physical trauma; Berry (1923) provides a provisional but useful summary.

Virtually all discussions of the fossil record of insect galls point to the origin of galling as a functional-feeding-group during the Cretaceous (Cockerell, 1890; Brues, 1972; Möhn, 1960; Paclt, 1972; Mamaev, 1975; Strong et al., 1984; Ananthakrishnan, 1984; Gagné, 1984, 1989; Roskam, 1985; Ananthakrishnan & Raman, 1989) or even the Tertiary (Zwölfer, 1978; Roskam, 1992), during an interval that is associated with the initial diversification or subsequent expansion of angiosperms. Although some suggest that recent fern gallers are indicative of a considerably more ancient association (Karny, 1926; Docteurs van Leeuwen, 1938; Cooper-Driver, 1978; Tahvanainen & Niemelä, 1987), others have provided limited but important fossil evidence for pre-Cretaceous galls (Larew, 1986, 1992; Boucot, 1990; Scott et al., 1994). Malyshev (1968), on paleontological, comparative behavioral, and phylogenetic grounds, claimed a Pennsylvanian age for the origin of primitive symphytan galls on pteridophytes. Except for these notable exceptions, the near-exclusive focus on the association of galling taxa with angiosperms and the extrapolation of this pattern to a Cretaceous origin of galling needs to be reassessed. In fact, Malyshev's (1968) hypothesis, postulating a Pennsylvanian age of origin for galling for at least one clade, may be closer to the truth for other galling clades as well.

Convincing evidence (Boucot, 1990; Larew, 1992) exists for insect galls during the Pennsylvanian to the Middle Jurassic (Table 1). These galls occur on various organs from diverse vascular plant clades, including *Stipitopteris* petioles from a Late Pennsylvanian *Psaronius* tree fern (this study), *Odontopteris* pinnules from an Early Permian medullosan seed fern (Potonié, 1893; Larew, 1992; Scott et al., 1994), an *Aethophyllum* stem from an Early Triassic conifer (Grauvogel-Stamm & Kelber, 1996); and *Wielandiella* pinnules from a Middle Jurassic bennettialean (Harris, 1942; Alvin et al., 1967). Possible Middle Pennsylvanian, sphenopsid stem galls on shoots bearing *Paracalamostachys* fructifications (Thomas, 1969) may also be an example. These latter structures are bulbous expansions at the termini of stems that have been proposed as galls by Weiss (1876) and

Table 1. Fossil Record of Late Carboniferous to Mid-Cretaceous Arthropod Plant Galls.

| Period<br>Epoch<br>Stage[1] | Class<br>Order<br>whole plant | galled<br>plant organ | arthropod<br>galler | deposit and<br>location | reference |
|---|---|---|---|---|---|
| Cretaceous<br>Upper<br>Cenomanian | Magnoliopsida<br>[unknown] | leaf | Insecta | Steinkohlen Fm.,<br>Czech Republic | Fritsch, 1882;<br>Fritsch, 1901;<br>Vakhrameev, 1991 |
| Cretaceous<br>Upper<br>Cenomanian | Magnoliopsida<br>Fagales<br>*"Quercus"* | leaf,<br>*"Quercus"* | Insecta<br>?Hymenoptera | Dakota Fm.,<br>Kansas, USA | Lesquereaux, 1892;<br>Berry, 1923 |
| Cretaceous<br>Lower<br>Albian | Magnoliopsida<br>Hamamelidales<br>*"Sassafras"* | leaf,<br>*"Sassafras"* | Insecta<br>?Hymenoptera | Patapsco Fm.,<br>Maryland, USA | Hickey &<br>Doyle, 1977;<br>Larew, 1992 |
| Jurassic<br>Middle<br>Bajocian | Cycadopsida<br>Bennettitales<br>*Wielandiella* | leaf<br>*Anomozamites* | Insecta<br>Holometabola | Yorkshire Flora,<br>England | Harris, 1942;<br>Alvin et al., 1967;<br>Vakhrameev, 1991 |
| Triassic<br>Late<br>Carnian | Gymnospermopsida<br>[unknown]<br>*Dechellyia* | leaf<br>*Dechellyia* ? | Insecta<br>Acarina | Chinle Fm.,<br>Arizona, USA | Ash, 1997 |
| Triassic<br>Middle<br>Ladinian | Gymnospermopsida<br>Coniferales<br>*Aethophyllum* | stem<br>*Aethophyllum* | Insecta<br>Holometabola | Voltzia Sandstone<br>France | Grauvogel-Stamm &<br>Kelber, 1996 |
| Permian<br>Lower<br>Sakmarian | Gymnospermopsida<br>Medullosales<br>*Medullosa* | leaf<br>*Odontopteris* | Arthropoda<br>indeterminate | Thuringer Beds,<br>Germany | Potonié, 1893;<br>Larew, 1992;<br>Scott et al., 1994 |
| Carboniferous<br>Pennsylvanian<br>Chamovnichskian | Filicopsida<br>Marattiales<br>*Psaronius* | petiole<br>*Stipitopteris* | Insecta<br>Holometabola | Mattoon Fm.,<br>Illinois, USA | Stidd, 1971;<br>Lesnikowska, 1990;<br>Labandeira & Phillips,<br>1996b; [this paper] |

[1] From Harland et al., (1990)

Amerom (1973), and they are curiously similar to gall-induced, terminal expansions occurring in extant *Equisetum* (Humbert, 1945). However, their status as galls requires further verification.

There undoubtedly are relatively recently-evolved insect clades that have interacted in tandem with angiosperms since the Cretaceous. Examples include several lepidopteran clades, probably the Cecidomyiidae (also see Fernandes & Price [1991] and Fernandes [1992] for biogeographical approaches) and possibly the Phylloxeridae (Schlüter, 1987). Others, however, such as aphidoid Homoptera, symphytan Hymenoptera and curculinoid Coleoptera, probably have a substantial pre-Cretaceous history. Anecdotal evidence, such as the above gall occurrences, and a recent nepticuloid (Lepidoptera) leaf mine on a lanceolate leaflet from an Upper Jurassic/Lower Cretaceous seed fern (Rozefelds, 1988) supports this. Additionally, a recent geochronological examination of insect taxonomic and mouthpart morphological diversity demonstrates that the rise of both taxonomic and morphological diversity considerably preceded the appearance of angiosperms (Labandeira, 1990a), and actually levelled during the spectacular radiation of angiosperms (Labandeira & Beall, 1990; Labandeira & Sepkoski, 1993). Collectively these data indicate that several clades of insect gallers on vascular plants existed prior to the rise of flowering plants during the Early Cretaceous.

Six hypotheses have been proposed to explain the origin of insect galls on vascular plants (Price et al., 1986, 1987; Grover, 1988). These hypotheses can be characterized as to whether the identity of the benefactor is the plant, the galler, both, or none. Since *Pteriditorichnos* is the earliest known gall, and bears evidence for a dynamic insect/host feedback system, it provides a basis for accepting or rejecting any of the six hypotheses of gall origins.

Bequaert's (1924) nonadaptation hypothesis states that galls have no adaptive value in plants. However, the *Pteriditorichnos* galler does appear to have resulted in extensive hollowing out of axial parenchyma in the basal regions of some *Psaronius* frond elements. This reasonably would contribute to structural failure of the frond. Also, inferred mobilization of metabolic machinery for the production of callus would divert limited resources from other vegetative or reproductive functions. The plant protection hypothesis (Küster, 1911; Mani, 1964; Rohfritsch & Shorthouse, 1982; Kraus et al., 1993), which maintains that plant defense is achieved by encapsulating an endophage to minimize plant damage, is similarly inconsistent with *Pteriditorichnos* structure. The *Pteriditorichnos* galler however was never encapsulated by a secondary indurated tissue, such as sclerenchyma, induced by the galling occupant; nor was it completely sedentary during its occupancy within the petiole. The oldest hypothesis of gall origin is the mutual benefit hypothesis (Cockerell 1890; Nolte, 1954; Leatherdale, 1955), which holds that galls act as protection to both the host plant and plant galler. With the exception of agaonid wasp galls on *Ficus*, studies on modern taxa have not demonstrated any benefit of galls to the plant (e.g., Abrahamson & McCrea, 1986). Similarly, it is not evident how the *Pteriditorichnos* galler would benefit its *Psaronius* host.

A currently favored hypothesis, the nutrition hypothesis, states that the high nutritional content of galls, when compared to adjacent ungalled tissue, confers a direct advantage to the galler, to the detriment of the host (Paclt, 1972; Sedlag, 1988; Hartley & Lawton, 1992). Fig. 95 documents two examples of callus present on the same *Psaronius* specimen – one representing typical callus induced by stylet penetration of cortical parenchyma by a paleodictyopteran and resulting in the proliferation of variously-oriented, hyperplasic, equant cells (see Labandeira & Phillips [1996a] for details); and a second example of a gall consisting of files of hypertrophic, elongated cells originating from medullary parenchyma, organized into characteristic tufts, and oriented perpendicular to adjacent, unaltered, bricklike parenchyma. This second type of callus in *Psaronius* petioles and rhachises is histologically similar to nutritive tissue in many modern galls (Figs. 96 and 97); both include files of elongate cells organized into tufts and formation into a zone many cell layers thick (Fourcroy & Braun, 1967; Rohfritsch, 1974, 1975a, 1977; Rey, 1979, 1992; Raman & Ananthakrishnan, 1983). However, in modern galls nutritive tissue is defined by organellar criteria and by elevated levels of carbohydrates, lipids and soluble proteins (Cameron, 1885; Rohfritsch, 1977; Shorthouse, 1986; Bronner, 1992) – features which are impossible to discern in *Pteriditorichnos*. Thus, although *Pteriditorichnos* lacks the verification necessary to conclude that it produced nutritive tissue, the presence of a nutritive-like callus characterized by a distinctive hyperplasia and hypertrophy that is histologically differentiable from other types of insect-induced callus, indicates that it is consistent with the nutrition hypothesis. Nevertheless, few data demonstrate whether modern (and certainly ancient) gallers necessarily derive any advantage from the high quality of nutritive tissue (Price et al., 1987).

The adaptive significance of galls in the following two hypotheses postulate protection of the galler at the expense of the plant. The microenvironmental hypothesis (Cameron, 1885; Felt, 1965) states that endophagy shelters the gall occupant from inclement external conditions, especially temperature and humidity (ABRAHAMSON & MCCREA, 1986; CORNELL, 1989) or even fire (KOTEJA, 1986). Supportive evidence in modern ecosystems includes the preferential abundance of galls in more extreme environments when their diversity is assessed along geographical gradients (CORNELL, 1989; FERNANDES & PRICE, 1991). In Late Pennsylvanian wetland ecosystems, there is strong evidence for relatively dry, aseasonal environments with possible periodic flooding by marine incursions and possible fire (PHILLIPS & PEPPERS, 1984; PHILLIPS et al., 1985; DIMICHELE et al., 1985). *Pteriditorichnos* is consistent with the microenvironmental hypothesis. The enemy hypothesis (WEIS et al., 1985; HAWKINS, 1988; PRICE & PSCHORN-WALCHER, 1988) asserts that galls are protective enclosures to avoid the ravages of external parasitoids. Recent studies are equivocal, with evidence for (PRICE & PSCHORN-WALCHER, 1988) and against (HAWKINS, 1988; HARTLEY & LAWTON, 1992) the creation of enemy-avoiding space. Nevertheless, there is no evidence for a parasitoid guild during the Late Pennsylvanian, and the major taxonomic component of modern parasitoids of gallers – diverse clades within less advanced Hymenoptera Apocrita – have their earliest occurrences during the Middle Jurassic (RASNITSYN, 1980; GAULD & BOLTON, 1988). In summary, the occurrence of a Late Pennsylvanian stem-gall on *Psaronius* is tentatively consistent with the nutritional and microenvironmental hypotheses, and is not supportive of the nonadaptational, plant protection, mutual benefit or enemy hypotheses.

There are two hypothesized pathways by which gallers evolved as a functional-feeding-group (PRICE et al., 1987; GROVER, 1988; ROSKAM, 1992; GASSMANN & SHORTHOUSE, 1992). They are (i) via sedentary external feeders, which explains the origin of hemimetabolous gallers (Thysanoptera, aphidid and psyllid Homoptera, mirid Heteroptera) and the holometabolan Cecidomyiidae, Anthomyiidae and symphytan Hymenoptera, and (ii) via leaf miners and stem borers. The sedentary-external-feeder to gall route is logically connected to the microenvironmental and nutritional hypotheses, and supports the increased advantage offered by microhabitat enclosure. To a lesser degree, enhanced food resources would accrue to an external feeder that became an endophage.

The leaf miner/stem borer to galler route is postulated for the origin of galls in several holometabolan groups, including the dipteran Anthomyiidae, Tephritidae and Agromyzidae and various lepidopteran clades. This route does not invoke the microenvironmental hypothesis since leaf miners and stem borers are already microenvironmentally protected. However, the sudden production of callus or nutritive tissue by a leaf-miner could result in gall formation that may measurably augment diet quality and quantity for the endophage. Similarly, apparent "simple" or "primitive" stem galls in anthomyiid (GASSMANN & SHORTHOUSE, 1982) and tephritid (LALONDE & SHORTHOUSE, 1984) dipterans and in curculionid coleopterans (SHORTHOUSE & LALONDE, 1984) start out as pith borings that only subsequently become transformed into galls, as callus or other proliferated tissue which becomes grazed by the larval occupant. *Pteriditorichnos* structure, and preliminary evidence for the absence of leaf miners on *Psaronius* suggests that the route taken by the *Pteriditorichnos* culprit to achieve endophagy was through external feeding. The possible occurrence of leaf mines on contemporaneous seed ferns has been suggested (MÜLLER, 1982; LABANDEIRA & BEALL, 1990).

Two specific examples are herein cited to document the transition from external feeding to endophage galling. These are the origin of galling in the Cecidomyiidae (MAMAEV, 1975; GROVER, 1988), an event that probably occurred during the Early Cretaceous; and the origin of the gallicolous Symphyta (MALYSHEV, 1968; ROHDENDORF & RASNITSYN, 1980; ROSKAM, 1992), an event that presumably transpired sometime during the late Paleozoic. Although these two clades of stem gallers possess different autecologies – cecidomyiids are sedentary, mouthhook-bearing fluid feeders that are encapsulated by a larval cavity and symphytans are mandibulate chewers that tunnel through stems – their suggested entry into the galler functional-feeding-group from an external feeder shares some autecological similarities.

The best documented study of a transition from external feeding to gall endophagy is the Cecidomyiidae or gall midges. Free-living, fungivorous Mycetophilidae, or fungus gnats, are the sister-group to the Cecidomyiidae (HENNIG, 1973; GAGNÉ, 1989; but see WOOD & BORKENT [1989] and COURTNEY [1991] for more unresolved cladistic relationships). Within the Cecidomyiidae, free-living fungivory, larval biting mouthparts, and larval intestinal digestion is plesiomorphic (MAMAEV, 1964, 1975; GAGNÉ, 1989). More apomorphic lineages are detritivorous and phytophagous, including the vast majority which are gall formers. These gall formers comprise the most apomorphic clades; their larvae possess piercing-and-sucking mouthparts in the form of mouthhooks and extraintestinal digestion. Based on the ecological distribution of gallicolous cecidomyiid taxa and their phylogenetic relationships, MAMAEV (1975) postulated that the transition from external phytophagy to gall endophagy involved two routes. One was damage to tree trunks that incurred establishment of saprophytic fungi and concomitant necroses of adjacent plant tissues; and the other is invasion of flowers (or similar structures), which was an simpler route for gall establishment on hosts. The passage from external feeding to gall-formation was presumably linked with the early appearance of angiosperms during the Early Cretaceous (MAMAEV, 1964). Extant cecidomyiid taxa that gall ferns and conifers are apparently secondary invaders.

Compared to the angiosperm-focused perspective for MAMAEV's (1975) cecidomyiids, MALYSHEV (1968) opts for a different tack, and emphasizes the geologically ancient conifer- and fern host associations of primitive sawfly clades, suggesting that symphytan stem-galling originated among the pteridophyte- and gymnosperm-dominated swamp forests of the Late Pennsylvanian. MALYSHEV has postulated that the Mecopteroidea, the sister-clade of the Hymenoptera, ancestrally possessed eruciform, exophytic, detritivorous larvae, one clade of which was transformed into eruciform, endophytic, and parenchyma-devouring larvae that are currently represented by the Cephidae. Cephids are a modern clade of dominantly stem-boring symphytans. Since extant mecopteran larvae nominally subsist on litter detritus (BYERS, 1987, 1991), but readily become sporivorous when placed on a spore rich substrate, MALYSHEV (1968) concluded that the transition from mecopteran saprophagy to primitive hymenopteran phytophagy involved a sporivorous transitional phase. Moreover, modern mecopteran and xyelid larvae and adults obligately or facultatively consume gymnosperm and angiosperm pollen (SHIPEROVICH, 1925; BENSON, 1945; GAULD & BOLTON, 1988). Accordingly, these sporivorous, cryptic larvae of litter and bark gradually shifted to consumption of photosynthetic plant tissue – a trend paralleled with the evolution of the ovipositor saw in primitive Holometabola, such as Hymenoptera, for insertion of eggs into plant tissue (SMITH, 1968, 1970; RASNITSYN, 1971a; KUKALOVÁ-PECK, 1991). Unlike many modern neonate symphytans that emerge from tissue-embedded eggs and become external-foliage-feeders, cephids remain endophagous and consume pith parenchyma, generally without becoming gallers. Cephids are stem-borers in mostly woody Rosaceae and Poaceae, and presumably are the analog for the transition from an external-foliage-feeder to a stem-galler. Moreover, the existence of at least two modern species of cephid stem gallers (ROSKAM, 1992) indicates that, for at least two angiosperm hosts, a transition occurred from simple pith consumption to the added generation and consumption of secondary parenchymatic tissue. Notably, larvae of several related families, such as the tenthredinids *Heptameleus* and *Strombocerus* (SHAW & BAILEY, 1991) and the blasticotomids *Blasticotoma* and *Runaria* (MEIJERE, 1911; ERMOLENKO, 1964; TOKASHI, 1989) are initial borers in fern petioles that subsequently elicit galling responses.

Part of this difference in approach between MAMAEV's explanation for the origin of cecidomyiid gallers and Malyshev's symphytan taxa is contingent on the different geological durations of these two clades. Cecidomyiid body fossils have an earliest documented occurrence during the Hauterivian Stage of the Early Cretaceous (SCHLEE & DIETRICH, 1970) whereas the earliest symphytans are known from the Ladinian Stage of the Middle Triassic (RASNITSYN, 1975). Nevertheless, within a diverse clade of galling taxa, there is a tendency to see less diverse subclades on gymnosperm hosts as groups that recently acquired these hosts (MAMAEV, 1975) rather than as survivors of an older, ancestral gymnosperm host complex that has produced a subsequent radiation on flowering plants (MALYSHEV, 1968). In the case of both cecidomyiids and symphytans, rigorous, host-independent cladistic testing of these alternative views needs to be done.

### 6.6.3. Extension of LAMEERE 's and MALYSHEV's Hypotheses

Both LAMEERE (1899, 1908, 1917) and MALYSHEV (1968) provided similar hypotheses regarding the larval habitat of the ancestral Holometabola, and the ancestral Hymenoptera, respectively (see also RASNITSYN, 1971a). Both hypotheses were predictive statements based on analyses of comparative morphology and behavior of extant taxa, as well as their distribution in the fossil record. When *Pteriditorichnos* is used as a test of these hypotheses, it is notable that there is a striking resemblance of *Pteriditorichnos* to the larval habitat postulated by LAMEERE for the ancestral Holometabola, and particularly for the larval habitat suggested by MALYSHEV (1968) for the ancestral symphytan that was transitional between a detritus-consuming mecopteroid and an endophagous cephid-like symphytan. MALYSHEV (1968) placed the acquisition of endophagy during the transition from a primitive mecopteroid to a primitive symphytan, indicating that stem-boring by nongalling cephids represented the most ecologically primitive life-habit in extant Hymenoptera. Although *Pteriditorichnos* suggests a link to a tenthredinid-like pleurocecidium resulting from tunneling (see HOUARD [1903] for examples), it is more advanced than the simple, cephid-like stem boring suggested by MALYSHEV. *Pteriditorichnos* was a true galler.

Both hypotheses were temporally and ecologically located in Pennsylvanian age swamp forests. Whereas LAMEERE (1899, 1908) was not specific as to the identity of the plant host, MALYSHEV (1968) suggested that fern stems were the likely host of his hypothetical larva. Interestingly, both these predictions spatiotemporally contextualize the *Pteriditorichnos* galler and its plant host. The availability of holometabolous galling taxa still remains consistent with both LAMEERE and MALYSHEV's predictions, since some Pennsylvanian body-fossils are suspect holometabolans (ROHDENDORF & RASNITSYN 1980) and an Early Permian stem-group to the Mecoptera recently has been documented (KUKALOVÁ-PECK & WILLMANN, 1990). Apparently holometabolous insects were available for endophytic colonization of plant tissues immediately before the diversification of several Holometabola lineages during the Lower Permian.

## 7. General Discussion

Our study presents three salient results that have important implications for the development of detritivory and herbivory in Pennsylvanian coal-swamp forests and for the origin of the most taxonomically diverse lineage of all time. First, we document a tunnel-and-gallery system resulting from the selective consumption by a blattoid insect of stem parenchyma from at least three species of *Psaronius* tree ferns during the Middle and Late Pennsylvanian. Second, we describe the host-specific, endophytic consumption of live axial parenchyma in *Psaronius chasei* petioles during the Late Pennsylvanian. Third, we provide evidence that establishes a larval holometabolan as the galler of these *P. chasei* petioles. For each of these results, there has been a relevant, indeed prolific, literature that has presented detailed phylogenetic and life-habit studies that have contextualized some of our findings. Ironically, in most of these discussions, historical scenarios have been established with minimal reference to a frequently relevant body-fossil record, and without mention of the trace-fossil record of plant-insect interactions.

For a modern perspective on arthropods responsible for degradation of wood, oribatid mites and termites are the most widely-cited culprits. Whereas abundant evidence supports the degradation of Pennsylvanian wood by (probably) oribatid mites (BAXENDALE, 1979; LABANDEIRA & BEALL, 1990; CHALONER et al., 1991; SCOTT et al., 1992; LABANDEIRA et al., 1997), there has been no body- or trace-fossil evidence for the occurrence of termites until the Early Cretaceous (ROHR et al., 1986; LACASA-RUIZ & MARTÍNEZ-DELCLÒS, 1986; KRISHNA, 1990). Although some modern termites are known to subsist on nonwoody parenchyma (WOOD, 1976, 1978), such tissue is also degraded by other insects, prominently blattodeans, where they occur in tree ferns, palms, and other tropical, arborescent monocots (SEÍN, 1923; SWEZEY, 1922, 1954; ROTH & WILLIS, 1960; LASEBIKAN, 1977). By contrast, a few lineages of modern blattodeans – such as the subsocial and plesiomorphic Cryptocercidae (CLEVELAND et al., 1934; SEELINGER & SEELINGER, 1983; NALEPA, 1984), but also apomorphic panesthine blaberids (MATSUMOTO, 1987, 1988; SCRIVENER et al., 1989), zetoborine blaberids (GRANDCOLAS, 1995), and possibly blatellids (CHOPARD, 1952; GRANDCOLAS, 1993) – are xylophagous and construct tunnel-and-gallery networks similar to primitive termites. Moreover, if our assignment of *Pteridiscaphichnos* to a blattodean culprit is correct, then the role of blattodeans as the only major Pennsylvanian insect group responsible for the degradation of nonwoody and possibly woody tree trunks (GRASSÉ & NOIROT, 1959; MAMAEV, 1971) may partly explain the ubiquitous presence of blattodeans in virtually all well-sampled Pennsylvanian insect deposits (CARPENTER, 1980; JARZEMBOWSKI, 1987). Overwhelmingly occurring as isolated tegmina and membranous hindwings, blattoids were probably not only conventional litter detritivores, but also consumers of postmortem stem tissues (SCUDDER, 1879). In a recent study of a late Middle Pennsylvanian clastic swamp from England, TODD (1991) found that blattodeans constituted 77 percent of all insects, but they were associated with lycopod and not fern vegetation.

By the Early Permian, blattoids became a relatively minor faunal component (WOOTTON, 1990; LABANDEIRA & SEPKOSKI, 1993). Well-described insect faunas are represented by new lineages of palaeodictyopteroids, "protorthopterans", and emerging hemipteroid and holometabolous taxa. Coincidentally, this decrease in blattodean abundance corresponds to a drastic reduction in the volume and geographic extent of extensive coal-swamp deposits (PHILLIPS et al., 1974, 1985). We suggest that insect detritivores were not more effectively recycling nonphotosynthetic biomass during the Permian, but rather abiotic factors were not conducive toward the formation of vast, euxinic, tropical, peat-accumulating coal swamps. Notably, during the Early Permian, groups belonging to modern orders, such as Psocoptera and especially archostematan Coleoptera, were probably intimately associated with dead wood (PONOMARENKO, 1971; HAMILTON, 1978; CROWSON, 1981; NEW, 1987), and supplanted blattodeans as major wood decomposers. Also, based on the recent validation of two Late Permian fossils as true Diptera (WOOTTON & ENNOS, 1989), it is highly likely that plesiomorphic dipteran lineages such as Tipulidae, Axmyiidae, and Pachyneuridae (COURTNEY, 1991) that are associated with wood degradation (PÉREZ, 1910; KRIVOSHEINA, 1969, 1991), were also added to this guild during the Late Permian and Triassic. The possibility also exists that fungi achieved a greater role in wood degradation during the Mesozoic, especially in wet forests where currently they are of greater importance than most insects (JONES et al., 1995).

The delay in the appearance of fossil termites is a vexing issue. Although the culprit responsible for *Pteridiscaphichnos* consumed nonlignified tissues with little cellulose, and phylogenetic and physiologic evidence indicates that Permian wood-associated Coleoptera and Diptera may have been more mycophagous than xylophagous (though see GRIFFITHS & CHESIRE, 1987); endosymbiont-mediated, holometabolous xylophagy may not have appeared until the Triassic. During the Late Triassic to Early Cretaceous, siricid sawflies (RASNITSYN, 1980) and beetle taxa such as buprestids (WEIDLICH, 1986; ALEKSEEV, 1993), bostrichids, cerambycids (DMITRIEV & ZHERIKIN, 1988), and curculionoids (WHALLEY, 1985; JARZEMBOWSKI, 1990) originated, modern representatives of which possess endosymbiont-laden, alimentary pouches (KOCH, 1967; MISRA & SEN-SARMA, 1985; KUKOR & MARTIN, 1983, 1986; MARTIN, 1983, 1991). The earlier part of this interval is corroborated by the first documented fossil beetle-like tunnels occurring in Middle- and Late Triassic woods of Arizona (WALKER, 1938) and Germany (LINCK, 1949). Thus, wood-boring within live trees may have been a guild that was not occupied during the Paleozoic, although decaying wood was consumed by mites (BAXENDALE, 1979; GOTH & WILDE, 1992; LABANDEIRA et al., 1997) and blattoid insects during the Pennsylvanian and Permian.

The biology of the *Pteriditorichnos* galler resembles most closely extant tenthredinoid sawflies, particularly the poorly-documented, rare, and plesiomorphic *Blasticotoma* of the Blasticotomidae (GAULD & BOLTON, 1988; SHAW & BAILEY, 1991). To a lesser extent it resembles modern coleopteran and lepidopteran gallers. In both the Pennsylvanian and Recent cases, fern petioles are attacked initially by eggs that are oviposited into or on petiolar tissue, and after penetration of the petiole the developing larva consumes medullary parenchyma as it tunnels through the petiolar axis. As the larva creates a lumen from its boring, tufts of callus bearing histological similarities to nutritive tissue radiate and form the surface of the lumen, partially infilling the cavity; simultaneously (at least in *Blasticotoma*) mucilaginous froth oozes from a basal exit hole (BENSON, 1952; ERMOLENKO, 1964; SHAW & BAILEY, 1991). Pupation occurs within the petiole, at least for *Blasticotoma*, after the larva has constructed an exit hole (GAULD & BOLTON, 1988). For both extant *Blasticotoma* and the culprit of *Pteriditorichnos*, the interaction between the host and galler is taxon-specific, highly stereotyped, and reciprocal; physiological outcomes are characterized by a predictable and an exact sequence of initial galler induction followed by a host response that, in turn, causes a galler response. The existence of this intimate system of a plant host/insect galler interaction in Pennsylvanian-age coal-swamps is unanticipated, based on our review of the extensive modern gall literature. The discovery of *Pteriditorichnos* forces a serious re-evaluation of many assumptions regarding the geochronologic recentness of plant/gall interactions (MAMAEV, 1975; ZWÖLFER, 1978; ANANTHAKRISHNAN, 1984; JOLIVET, 1986; SCHLÜTER, 1987; ROSKAM, 1992), and particularly the widespread claim that the initial origin of insect galling represents a phenomenon limited to the angiosperm radiation.

*Pteriditorichnos* is a gall that is most parsimoniously attributed to a holometabolan larva. Consequently, data from this trace-fossil are a unique, rare, and informative paleontological window into the life-habits and associated behavior of one of the earliest documented holometabolous insects. It predates the traditional appearance of the Holometabola in earliest Permian strata by 10 million years, although KUKALOVÁ-PECK (1991) has figured a slightly older, possible eruciform larva, but it remains undescribed. Early Permian body fossils are attributable to modern holometabolan orders such as Mecoptera, Megaloptera and probably Coleoptera, but *Pteriditorichnos* is not assigned to an order since body parts have not been recovered. Nevertheless, the exceptional preservational context of *Pteriditorichnos* – preservation that cannot be obtained from conventional body fossils – allows for inferences regarding the autecology and behavior of one of the earliest holometabolan insects. Parenthetically, for virtually all fossil insect deposits, these two aspects – morphological and sometimes anatomical data found as body fossils versus behavioral and ecological data retrieved from trace fossils – are almost always mutually exclusive. Very rarely are the two types of fossil information preserved simultaneously and satisfactorily in the same deposit.

A voluminous and exasperating literature of original research and commentary has been published on the origin of insect metamorphosis, beginning at the turn of this century (for example, LAMEERE, 1899, 1908; PÉREZ, 1910; BERLESE, 1913; POYARKOFF, 1914) and continuing into mid-century in articles by CRAMPTON (1931), CHEN (1946), HINTON (1948, 1953, 1963), AUBERT (1950), SNODGRASS, (1954) and HESLOP-HARRISON (1958). *Pteriditorichnos* cannot address the complex developmental processes involved in the original transformation of preadult internal wing buds into adult external wings. However, *Pteriditorichnos* can offer constraints on various published speculations regarding the likely paleoclimate and habitat of at least some primitive Holometabola, as well as the life-habits and a limited description of the earliest known holometabolous larva for which there is ecological data.

A widespread observation is that the origin of insect holometaboly occurred during the Pennsylvanian (TILLYARD, 1918; CRAMPTON, 1931; CHEN, 1946; NOVAK, 1955; HESLOP-HARRISON, 1958; HENNIG, 1981; LAWRENCE & NEWTON, 1982; KUKALOVÁ-PECK, 1991). Most of these explanations propose a causal link between holometaboly and an initial increase in seasonality that later became pronounced during the Early Permian. On this view, holometaboly represented an "adaptation" to food resources that became differentially deployed in habitat space during the seasonal course of a year (TILLYARD, 1926; HANDLIRSCH, 1925; CRAMPTON, 1931; HINTON, 1977; STADNITSKY, 1991). Accordingly, the aseasonal, warm, humid coal-swamp forests centered on the Middle Pennsylvanian equator of Euramerica were an inappropriate environment for the spatiotemporal division of food resources, and thus for the origin of the Holometabola. Although the *Pteriditorichnos* gall occurred during the Late Pennsylvanian, if it originated during the late Middle Pennsylvanian, before the onset of the Second Drier Interval (PHILLIPS et al., 1985; Text-Fig. 1) the seasonality hypothesis would be an unlikely explanation (SHEAR & KUKALOVÁ-PECK, 1990; see also SEHNAL et al., 1996). This view is supported if the interpretation of certain Pennsylvanian adult body-fossils are indeed members of the Holometabola (TILLYARD, 1926, WILLMANN, 1989; KUKALOVÁ-PECK 1991). However, if holometaboly originated during the Late Pennsylvanian within tree-fern dominated forests during the Second Drier Interval, then significant seasonality and xeric conditions would have been associated with the early occurrence of holometaboly. Notably, *Pteriditorichnos* was produced by an endophytic larva, a condition that many maintain would have been an ideal life-habit for avoidance of climatic fluctuation and dessication. We suspect that the balance of evidence indicates that holometaboly originated during the late Middle Pennsylvanian at the latest, for purposes other than a response to increasing seasonality.

Three different hypotheses regarding the life-habits and external morphology of the ancestral holometabolous larva have been proposed. One view, currently disfavored, suggests that the ancestral holometabolan larva was a cursorial, campodeoid-polypod form similar to an aquatic megalopteran larva with well developed gills (BERLESE, 1913; BRADLEY, 1942; CHEN, 1946; GHILAROV, 1957; TOMS, 1984a, 1984b). A second hypothesis states that the primitive holometabolan larva was exophytic, detritivorous, and eruciform, similar to a modern primitive mecopteran or an exophytic tenthredinoid hymenopteran (TILLYARD, 1926; SHEAR & KUKALOVÁ-PECK, 1990). This view gains support if KUKALOVÁ-PECK's (1991) undescribed insect is indeed an exophytic caterpillar. Lastly, an older hypothesis suggests that the ancestral larval holometabolan was endophytic, eruciform, and an oligopod, most likely a stem borer, and possessed reduced appendages similar to the grub of an endophytic tenthredinoid hymenopteran (LAMEERE, 1899, 1908; MARTYNOV, 1925; SHAROV, 1966; MALYSHEV, 1968). Evidence from *Pteriditorichnos* suggests the last hypothesis. By contrast, although the polypod theory is still a viable alternative, it lacks trace- or body-fossil evidence from the Pennsylvanian, and it would be difficult to differentiate a megalopteran-like larva from a small myriapod, even under the good preservational conditions found in many Pennsylvanian compression deposits. Although KUKALOVÁ-PECK's presumed caterpillar is a serious contender, we conclude that the evidence indicates that the ancestral holometabolous larva was more likely an eruciform oligopod inhabiting and interacting with the medullary tissues of vascular plants, most likely pteridophytes.

## 8. Conclusions

We conclude the following five points from our examination of two unique types of insect-mediated damage on Euramerican tree-fern hosts. These conclusions include descriptions of two new ichnogenera to accommodate distinctive plant damage types on tree-fern hosts. Equally important is the significance of these plant-insect interactions for the evolution of the galler functional-feeding-group and the Holometabola. *Psaronius* tree ferns are our best window into a Paleozoic vascular plant harboring diverse mite and especially insect interactions, and consequently has important implications for reassessing orthodox tenets regarding the paleobiology of plant/insect interactions.

1. Three distinctive Middle- and Late Pennsylvanian morphotypes of the tree fern *Psaronius* were bored by a detritivorous roach or roach-like insect, producing a characteristic pattern of tunnels and galleries in stem parenchyma. This distinctive trace-fossil boring is described by the ichnogenus, *Pteridiscaphichnos*. Evidence indicates that, although the attack was postmortem, the responsible borer was tissue-specific, consuming unlignified stem parenchyma and avoiding indurated sclerenchyma, vascular tissue, and root mantle.

2. The frond petioles of the Late Pennsylvanian tree fern *Psaronius chasei* were galled by an endophytic, eruciform, holometabolous larva. These distinctive galls, assigned to the ichnogenus *Pteriditorichnos*, consist of an axially extensive, petiolar lumen of evacuated medullary parenchyma, surrounded by adaxially-radiating, proliferating tufts of hypertrophied files of cells arranged into a layer of callus. This, and the occurrence in the lumen of coprolites containing digested adjacent parenchyma, clearly indicate that the initial consumption of petiolar parenchyma was by an endophytic herbivore capable of limited tunneling. The stereotyped response of the plant to this insect attack was the production of cell proliferation by a process analogous to many modern, galled plants.

3. From evidence based on the internal structure of Late Pennsylvanian tree-fern petiole galls and the inferred life-habit of the galler based on the gross structure and size of the gall, we conclude that the culprit was a holometabolous larva. This culprit, however, is unassignable to any modern lineage, although the gall structure is suggestive of a tenthredinoid hymenopteran. There are several implications from this conclusion. First, the earliest known occurrence of holometaboly is during the Late and probably late Middle Pennsylvanian, amid aseasonal and wet coal-swamp forests, rather than seasonally xeric, dry, more upland, extrabasinal floras of the conifer- and cycadophyte-dominated Early Permian. Second, our earliest behavioral and autecologic evidence for the Holometabola provides strong evidence that endophytic stem galling was an ancestral life-habit. Third, the existence of a holometabolous larva galling Late Pennsylvanian tree-fern petioles provides strong support for intimate and response-driven host-plant/herbivore interactions occurring among the earliest, diverse insect faunas known.

4. Based on findings from this study, in conjunction with previously described interactions and our ongoing research, it is now evident that *Psaronius* was a host plant that was significantly attacked by at least five insect functional-feeding-groups, comparable to its modern marattialean descendants. Current evidence has been observed for detritivore boring in stem parenchyma, petiole galling, piercing-and-sucking into petiolar vascular tissue, folivory on pecopterid pinnules, and sporangia- and spore consumption of scolecopterid fructifications. The only major functional-feeding-groups not yet observed on *Psaronius* that occurs in its modern descendants is leaf mining and perhaps external-fluid-feeding. Collectively these results demonstrate that specific tissue types and organs of *Psaronius* were being partitioned by herbivore insects in discrete and manifold ways in Pennsylvanian coal-swamp forests. Thus, most of the modern functional-feeding-groups now typically associated with post-Paleozoic insects and angiospermous plants, were in existence during the Pennsylvanian.

5. The results of this study challenges two recent views regarding the historical record of plant/insect interactions. The first is that little evidence exists for herbivory during the Paleozoic. The second is that highly specific herbivore syndromes on vascular plants, such as galls, were phenomena that originated only in coordination with the angiosperm radiation. Accordingly, the occurrence of intimate nonangiosperm/insect interactions invariably were the result only of subsequent and secondary invasions. Our ongoing and close scrutiny of Pennsylvanian plants indicate that these views are unfounded.

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## Explanation of Plates

For details of preparation of these plates, including photodocumentation, three-dimensional reconstructions, and abbreviations, see Section 2 of this paper. Scale bar conventions are: solid bars represent one centimeter, striped bars represent one millimeter, and stippled bars represent 0.1 millimeter (= 100 µ).

The following abbreviations, used in Plates 1 to 16, refer to anatomical structures of the *Psaronius* trunk and frond petiole, and other features resulting from interactions with insects. Reference to anatomical terms can be found in Stidd (1971), Lesnikowska (1989, 1990) and Stewart & Rothwell (1993). Examples of the interaction features in modern plants may be found in Mani (1964), Larew (1982), Meyer & Maresquelle (1983), Meyer (1987), Shorthouse & Rohfritsch (1992) and Headrick & Goeden (1993).

| Anatomical Structures | |
|---|---|
| cp | cortical parenchyma |
| gs | gum sac cell |
| me | meristele |
| mp | medullary parenchyma |
| pa | parenchyma |
| ph | phloem |
| rc | resin canal |
| rm | root canal |
| sc | sclerenchyma |
| sr | stigmarian root |
| vs | vascular strand |

| Interaction Features | |
|---|---|
| ca | callus |
| co | coprolite |
| cr | cropped callus |
| ct | catachord |
| eh | exit hole |
| fr | frass |
| lu | lumen of gall |
| nt | nutritive tissue |
| st | stylet track |
| tm | trapped mucilage |
| tu | tuft of callus tissue |

## Plate 1

Figs. 1–8. *Pteridiscaphichnos psaronii* gen. et sp. nov., in the three-dimensionally reconstructed stem of the "layered cells" morphotype of *Psaronius*. In the three-dimensional drawings (Figs. 2–7), the peripheral root mantle is depicted as open ovoidal figures interspersed among a matrix, sclerenchyma as white bands, meristeles as black bands, and parenchyma as stipple. Zones of fecal-pelleted *Pteridiscaphichnos* are indicated by clusters of black ellipsoids. Specimen UIUC-38048 from the Herrin Coal, near Carrier Mills, Illinois. Each illustrated peel corresponds to the upper surface of a coal-ball slab.

1. Coal-ball slabs of specimen UIUC-38048 assembled in sequence to show the orientation of the *Psaronius* trunk.
2. Bottom of preserved *Psaronius* trunk. Section B-bot. (Peel 1.)
3. Continuation of *Psaronius* trunk into the adjacent slab, with reconstruction of a region bearing *Pteridiscaphichnos*. Section C-bot. (Peel 11.)
4. Next, adjacent slab, with one area of *Pteridiscaphichnos* nestled along the outer sclerenchyma sheath in lower-left region. Section D-bot. (Peel 1.)
5. Slab connecting D-bot and A-side.
6. Section A-side. (Peel 1.)
7. Slab above A-side, showing surface-etched *Pteridiscaphichnos*.
8. Three-dimensional reconstruction of detail from boring in section C-bot; enlarged in Plate 3, fig. 13.

## Plate 2

Figs. 9–12. *Pteridiscaphichnos psaronii* gen. et sp. nov. in the three-dimensionally reconstructed, somewhat flattened trunk of *Psaronius chasei* MORGAN. Specimen UIUC-10765 from the Calhoun Coal, Berryville, Illinois. Each illustrated peel corresponds to the upper surface of a coal-ball slab.

9. Section B-top, peel 4. The pith parenchyma is replaced by frass containing densely packed coprolites; only vascular traces, sclerenchyma bands, and root mantle are present.
10. Section C-top, peel 67. Note the contrast between the root mantle thickness and the diameter of the stem.

11 Section C-bot, peel 65. Peel reversed for projection as a "D-top" image.

12. Three-dimensional reconstruction of detail from boring in Section C-bot; enlarged in Plate 4, fig. 21.

## Plate 3

Figs. 13–16. *Pteridiscaphichnos psaronii* gen. et sp. nov. from stem of the "layered cells" morphotype of *Psaronius*. From specimen 38048-C; Herrin Coal, near Carrier Mills, Illinois.

13. Three dimensional reconstruction of trunk region in specimen UIUC-38048, section C-bot, This reconstruction shows preferential consumption of pith parenchyma and avoidance of root mantle, sclerenchyma, and meristeles.
14. Control peel no. 60 for Fig. 13 above.
15. Control peel no. 30 for Fig. 13
16. Control peel no. 1, forming the face (section C-bot) of Fig. 13 above.

Figs. 17–18. *Pteridiscaphichnos psaronii* gen. et sp. nov. from stem of the "layered cells" morphotype of *Psaronius*. From specimen UIUC-38842-D; Herrin Coal, Carbondale Formation, Shawneetown, Illinois.

17. Section D-bot, peel 134; slide UIUC-22,658. Detail of root stem with evidence of *Pteridiscaphichnos* damage. The only tissues remaining are root mantle, sclerenchyma sheath, and some sheath-adhering parenchyma.
18. Section D-bot, peel 134; slide UIUC-22,658. Close-up of fecal pellet cluster lodged among the abaxial sclerenchyma sheath (above) and adaxial meristeles (center and below).

Figs. 19–20. Fecal pellets of modern *Cryptocercus punctulatus* (Blattodea: Cryptocercidae) on *Pinus* (pine), from western North Carolina.

19. Longitudinal, oblique and transverse sections of representative fecal pellets. (USNM slide 483967-9.)
20. Transverse section of fecal pellet; note subhexagonal shape. (USNM slide 483967-7.).

## Plate 4

Figs. 21-27. *Pteridiscaphichnos psaronii* gen. et sp. nov. from the stem of *Psaronius chasei* MORGAN. All documentation from specimen UIUC-10765; Calhoun Coal, Berryville, Illinois.

21. Three dimensional reconstruction of trunk region for specimen UIUC-10765, peel of the original B-bot surface. This reconstruction exhibits preferential consumption of pith parenchyma and avoidance of root mantle, sclerenchyma, and meristeles.
22. Control peel no. 60 for Fig. 21 above.
23. Control peel no. 30.
24. Control peel no. 1, forming the face (section/B-bot) of Fig. 21 above.
25. Section C-bot, peel 56; slide UIUC-22,669. *Pteridiscaphichnos* boring showing unconsumed root mantle and sclerenchyma, with stem parenchyma replaced by coprolites, and postmortem roots growing between outer sclerenchyma sheath and removed stem parenchyma.
26. Section B-bot, peel 73; slide UIUC-22,665. Same as 25, but exhibiting three layers of unconsumed sclerenchyma.
27. Section B-bot, peel 73; slide UIUC-22,665. Close-up of randomly oriented coprolites.

## Plate 5

Figs. 28–32. *Pteriditorichnos stipitopterii* gen. et sp. nov. from the three-dimensionally reconstructed, cross-sectioned petiole of *Psaronius chasei* MORGAN, using the top peel from the upper surface of each successive coal-ball slab. Dark black line on peel sections at right represents the anatomical boundary of the petiole. Specimen no. 2 of UIUC-30823; Calhoun Coal, Calhoun, Illinois.

28. Section B-top. (Peel 1.)
29. Lumen containing three conspicuous coprolites. Section C-top. (Peel 1.)
30. Discontinuous zone of callus, organized into discrete tufts that are separated by frass. Section D-top. (Peel 1.)
31. Section E-top. (Peel 1.)
32. Section F-top. (Peel 2.)

## Plate 6

Figs. 33–38. *Pteriditorichnos stipitopterii* gen. et sp. nov. from the three-dimensionally reconstructed, cross-sectioned petiole of *Psaronius chasei* MORGAN, using the top peel from the upper surface of each successive coal-ball slab. Specimen UIUC-8227; Calhoun Coal, Berryville, Illinois.

33. Section A. (Peel 4) + Btop. (Peel 1.) Peels were combined for composite image.
34. Section C-top. (Peel 3.)
35. Section D-top. (Peel 1.) Portion of lumen and outer tissues replaced by calcite.
36. Section E-top. (Peel 5.)
37. Section F-top. (Peel 1.)
38. Section G. (Peel 2.)

## Plate 7

Figs. 39–41. *Pteriditorichnos stipitopterii* gen. et sp. nov. from the three-dimensionally reconstructed, cross-sectioned petiole of *Psaronius chasei* MORGAN. Specimen UIUC-8227-B; Calhoun Coal, Berryville, Illinois.

39. Lumen containing a packed cluster of subparallel coprolites. (Peels 1-20.)
40. Example with zone of callus that is continuous and considerably thicker than in other specimens, for example UIUC-31010 D-bot in Plate 9. (Peels 25–45.)
41. Peels 50–70.

## Plate 8

Figs. 42–44. Continuation of *Pteriditorichnos stipitopterii* gen. et sp. nov. from the three-dimensionally reconstructed, cross-sectioned petiole of *Psaronius chasei* MORGAN. Specimen UIUC-8227-B; Calhoun Coal, Berryville, Illinois.

42. Combined peels 75, 80, 85, 90 and 95.
43. Combined peels, 100, 105, 110, 115 and 120. A well-developed stylet track that terminates in vascular tissue occurs at the right margin. See also Fig. 95.
44. Combined peels 125, 130, 135, 140 and 145.

## Plate 9

Figs. 45–46. *Pteriditorichnos stipitopterii* gen. et sp. nov. from the petiole of *Psaronius chasei* MORGAN. Specimen UIUC-31010; Calhoun Coal, Calhoun, Illinois.

45. Section D-bot, peel 85. Close-up of ovoidal coprolite.
46. Section D-top, peel 5; UIUC slide 22,249. Close-up of sclerenchyma, parenchyma, vascular strand and callus surrounding gall lumen.

Figs. 47–51. *Pteriditorichnos stipitopterii* gen. et sp. nov. from the three-dimensionally reconstructed, obliquely sectioned petiole of *Psaronius chasei* MORGAN. Specimen UIUC-31010-D; Calhoun Coal, Berryville, Illinois. For associated scans of the top peel of each series, see Plate 10, figs. 52–56.

47. Combined peels 1, 5, 10, 15 and 20. A petiole with a very thin zone of medullary parenchyma and a corresponding large lumen.
48. Combined peels 25, 30, 35, 40 and 45.
49. Combined peels 50, 55, 60, 65 and 70. Several coprolites exhibit furrows on their external surfaces.
50. Combined peels 75, 80, 85, 90 and 95.
51. Combined peels 100, 105, 110, 115 and 120. Subparallel clustering of coprolites is evident at the upper region of the lumen.

## Plate 10

Figs. 52–56. *Pteriditorichnos stipitopterii* gen. et sp. nov. Associated peels for three-dimensional reconstruction in Plate 9, figs. 47 to 51 of from the petiole of *Psaronius chasei* MORGAN. Specimen UIUC-31010 D-top; Calhoun Coal, Calhoun, Illinois. (Peels 1, 25, 50, 75, 100)

Figs. 57–59. Detail of gall structures in Specimen 31010 D-top.

57. Close-up of centrally-located, prismatic callus surrounded by opposite-oriented, brick-like, parenchyma. (Peel 40.)
58. Cluster of ellipsoidal, entire coprolites at top and fragmentary, angular coprolites at bottom. Note thick sclerenchyma sheath and adjacent, inconspicuous vascular strand. (Peel 20.)
59. Cluster of ellipsoidal, entire coprolites at left, and smaller, coprolitic fragments at right. (Peel 85.)

## Plate 11

Figs. 60–62. *Pteriditorichnos stipitopterii* gen. et sp. nov. from the three-dimensionally reconstructed, obliquely sectioned petiole of *Psaronius chasei* MORGAN. Specimen no. 2 of UIUC-30823-D; Calhoun Coal, Calhoun, Illinois. For associated scans of peels, see Plate 12, figs. 63-65.

60. Subparallel clustering of fecal pellets displayed at central region of the lumen. (Peels 1-20.)
61. Peels 25-45.
62. The callus almost encircles the entire lumen. (Peels 50-70.)

## Plate 12

Figs. 63–65. Associated peels for three-dimensional reconstruction in Plate 11, figs. 60 to 62, of *Pteriditorichnos stipitopterii* gen. et sp. nov. from the petiole of *Psaronius chasei* MORGAN. Peels are from the original D-bot surface of specimen no. 2 of UIUC-30823; Calhoun Coal, Calhoun, Illinois.

63. Peel 1.
64. Peel 25
65. Peel 50.

Figs. 66–69. Detail of gall structures associated with Section D-bot.

66. Cluster of fragmented and intact coprolites. Note region of callus that has been cropped by an apparent bite. (Peel 25.)
67. Resin canal in callus. (Peel 2.)
68. Detail of coprolite with digested gum-sac cells. (Peel 2.)
69. Cluster of fragmented and intact coprolites. (Peel 5.)

## Plate 13

Figs. 70–72. *Pteriditorichnos stipitopterii* gen. et sp. nov. from the three-dimensionally reconstructed, obliquely sectioned petiole of *Psaronius chasei* MORGAN. Specimen no. 1 from UIUC-31272-B; Calhoun Coal, Calhoun, Illinois. For associated scans of peels, see Plate 14, figs. 73-75.

70. Absence of callus in several regions. The exit hole occurring in Fig. 78 is present at this level. (Peels 1-20).
71. Well-developed exit hole at lower-left. (Peels 25-45).
72. Exit hole in Fig. 71 is not present at this level. (Peels 50-70)

## Plate 14

Figs. 73–75. Associated peels for Plate 13, figs. 70 to 72, of *Pteriditorichnos stipitopterii* gen. et sp. nov. from the petiole of *Psaronius chasei* MORGAN. Peels are from the original B-bot surface of specimen no. 1 from UIUC-31272; Calhoun Coal, Calhoun, Illinois.

73. Peel 1. Arrow indicates exit hole enlarged in Fig. 78.
74. Peel 25.
75. Peel 50.

Figs. 76–80. Histological and cellular detail of *Pteriditorichnos stipitopterii* gen. et sp. nov. from the petiole of *Psaronius chasei* MORGAN. Specimen no. 1 from UIUC-31272 B-bot.

76. Gum-sac cells in coprolite. (Section B-top, peel 4; UIUC slide 22,734.)
77. Structurally identical gum-sac cells in unaltered parenchyma. (Section B-top, peel 4; UIUC slide 22,734.)
78. Enlargement of exit hole in Fig. 73. Note plug of tissue. (Section B-top, peel 4; UIUC slide 22,734).
79. Coprolite, showing gum-sac cells and adjacent tufts of callus. (Section B-top, peel 4; UIUC slide 22,734).
80. Cross-section of gall showing, from abaxial to adaxial, cortical parenchyma, vascular strand, medullary parenchyma, callus, and lumen with coprolites and catachord. (Section B-bot, peel 84; UIUC slide 22,655).

## Plate 15

Figs. 81–88. Histological and cellular detail of exit holes and callus from *Pteriditorichnos stipitopterii* gen. et sp. nov. in the petiole of *Psaronius chasei* MORGAN. Specimen no. 2 from UIUC-31272; Calhoun Coal, Calhoun, Illinois.

81. Entire petiole with lumen of frass and exit hole at center-left (arrow). (Section C-top, peel 121; UIUC slide 22,661.)
82. Enlargement central lumen region in Fig. 81, showing exit hole. (Section C-top, peel 120, UIUC slide 22,662.)
83. Additional enlargement of Fig. 82, showing exit hole with plug of callus. Note central linear region of trapped mucilage bounded by tufts of callus above and below. (Section C-top, peel 120; UIUC slide 22,662.)
84. Close-up of exit hole, with callus plug. (Section B-top, peel 4; UIUC slide 22,734.)
85. Partly infilled lumen with digitate extensions of callus. (Section B-bot, peel 98; UIUC slide 22,667.)
86. Close-up of callus with digitate extensions in Fig. 85. (Section B-bot, peel 98; UIUC slide 22,667.)
87. Close-up of same exit hole in Fig. 84. Plug of callus well-developed. (Section B-bot, peel 98; UIUC slide 22,667.)

## Plate 16

Fig. 88. Holotype of *Pteridiscaphichnos psaronii* LABANDEIRA and PHILLIPS, ichnogenus et ichnospecies novum. Mounted peel UIUC-38048-Cbot on UIUC slide 22,415.

Figs. 89–92. Recent fecal pellets of adult orthopteroid insects.

89. Several representative fecal pellets of *Cryptocercus punctulatus* SCUDDER, on *Pinus* (pine) from western North Carolina, in various orientations. (Slide USNM-483967-9.)

90. Various sections of fecal pellets of *Blaberus giganteus* (Blattodea), on artificial diet. (Slide USNM 483971-7.)

91. Various sections of fecal pellets of *Heterojapyx dilatata* (Phasmida), on *Hedera* (ivy). (Slide USNM 483970-5.)

92. Various sections of fecal pellets of *Romalea guttata* (Orthoptera), on *Phaseolus* (bean) and *Lactuca* (lettuce). (Slide USNM 483972-1.)

Fig. 93. Holotype of *Pteriditorichnos stipitopterii* LABANDEIRA and PHILLIPS, ichnogenus et ichnospecies novum. (Peel UIUC-8227-Bbot on UIUC slide 22,634.)

Fig. 94. Typical, ungalled petiole of *Psaronius chasei* MORGAN, somewhat compressed laterally. (Peel UIUC 31272-Bbot on UIUC slide 22,736.)

Fig. 95. Cross-section of a *Psaronius chasei* MORGAN petiole, showing callus resulting from a paleodictyopterid insect piercing cortical parenchyma at right (LABANDEIRA & PHILLIPS, 1996b), and callus resulting from the *Pteriditorichnos* galler of medullary parenchyma at left. Note the histological difference between these two callus formations. Same specimen as Fig. 93. (Peel UIUC 8227-Bbot on UIUC slide 22,676.)

Figs. 96–97. Recent gall of Lepidoptera.

96. Partial transverse section of stem gall of *Epiblema strenuana* (WALKER) (Lepidoptera: Tortricidae) on *Helianthus annuus* (L.) (common sunflower, Asteraceae). Foard Co., Texas. (Slide USNM 483975-3).

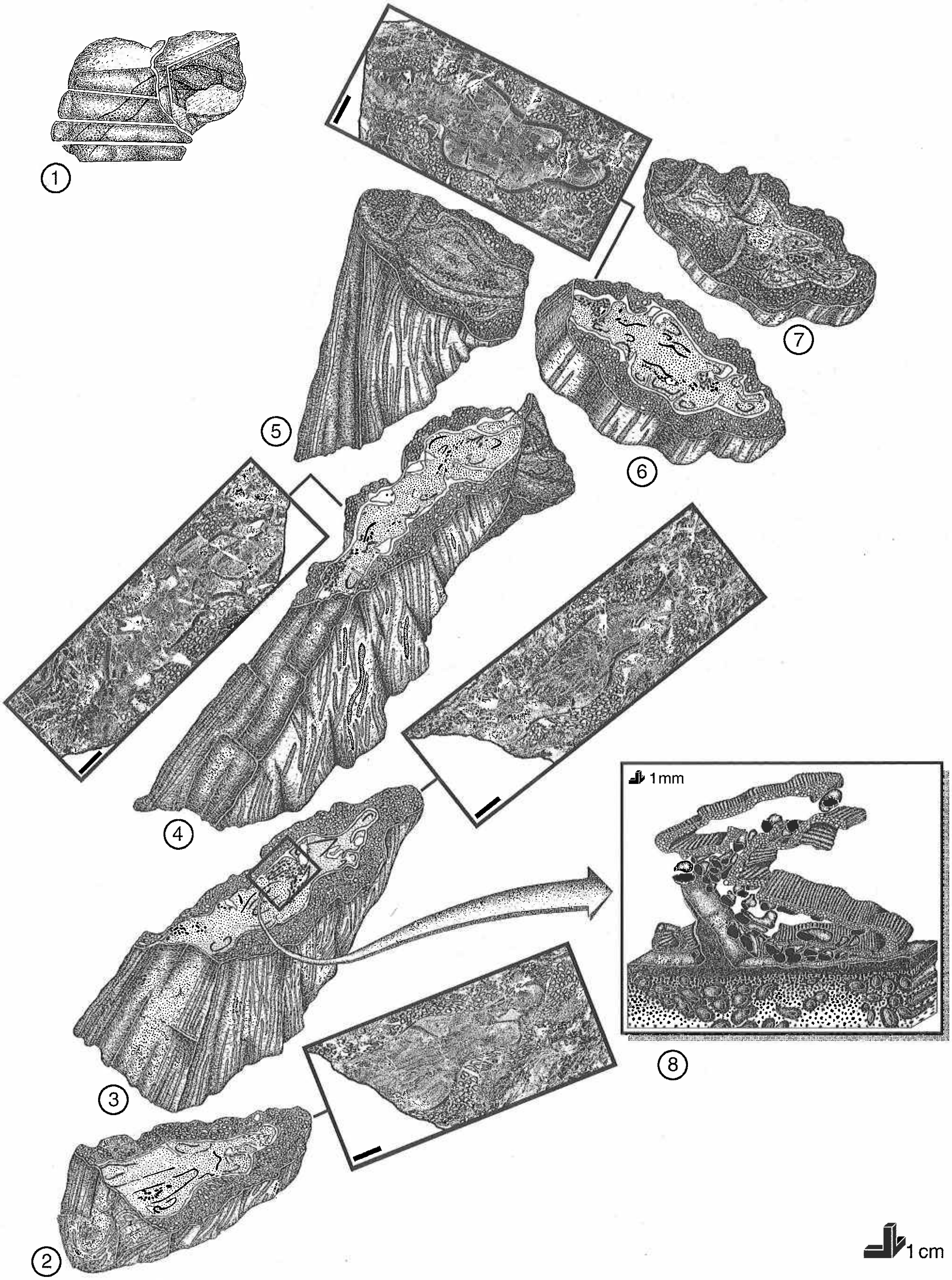
97. Enlargement of outlined region at left of Fig. 97, showing the presence of nutritive tissue.

Figs. 98–100. Recent fecal pellets of lepidopteran insect larvae.

98. Various sections of fecal pellets of *Solecampa liburna* GRAY (Lepidoptera: Noctuidae) on *Quercus* (oak). Note pellets with circular transverse sections at upper right and center. (Slide USNM 483973-5.)

99. Transverse section of fecal pellet of *Bombyx mori* (L.) (Leipdoptera: Bombycidae) on *Morus alba* (mulberry). (Slide USNM 483968-5.)

100. Transverse section of fecal pellet of *Hyalophora cecropia* (L.) (Lepidoptera: Saturniidae) on *Kalmia latifolia* (mountain laurel). (Slide USNM 483974-5.)



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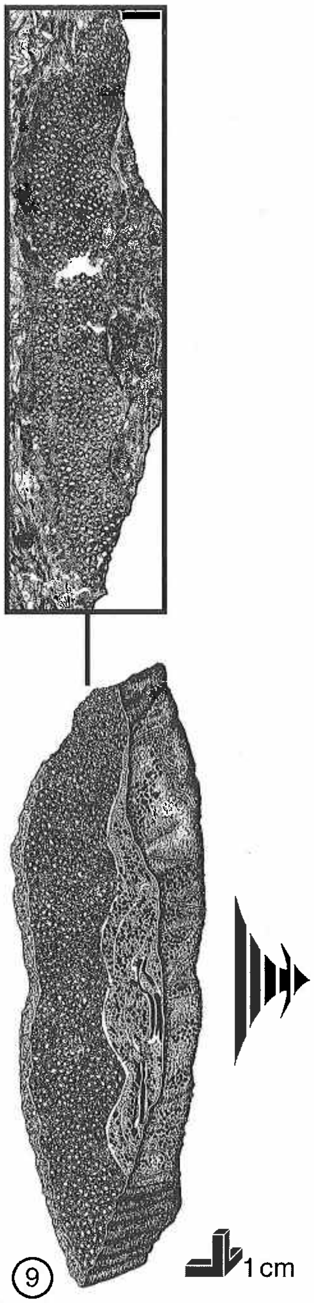

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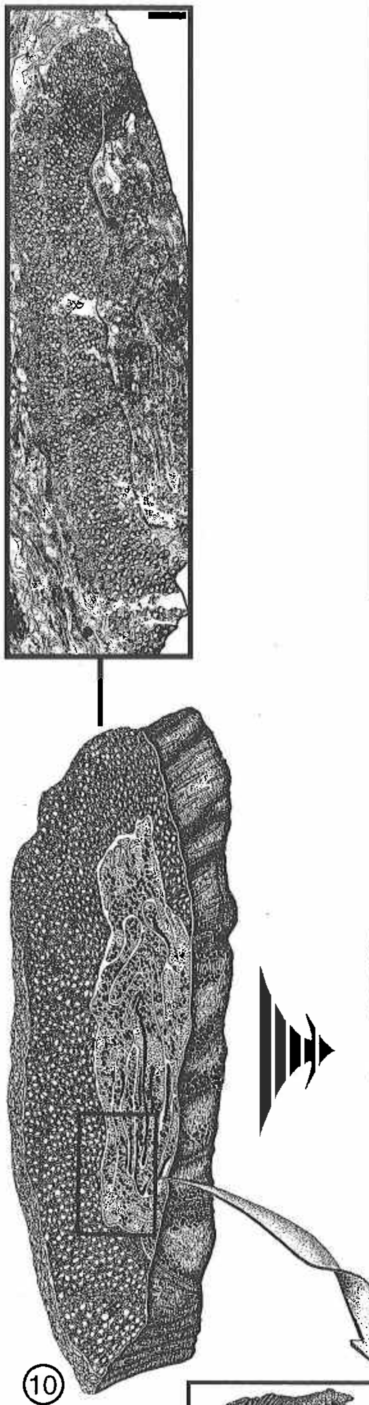

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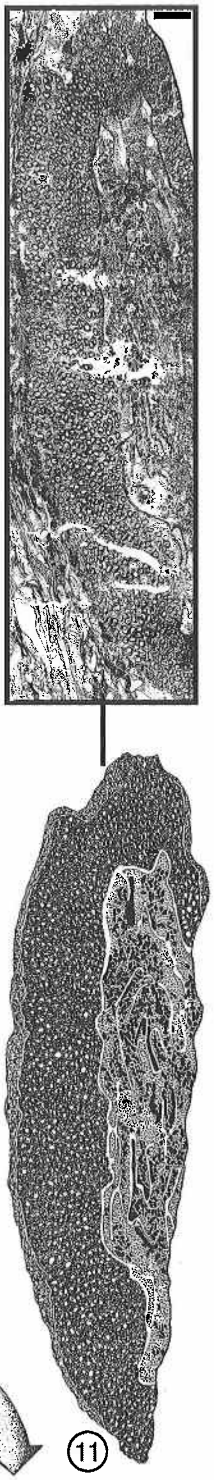

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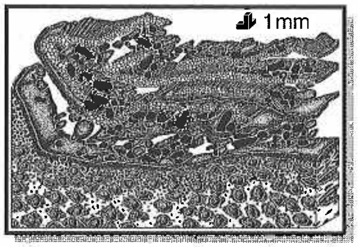

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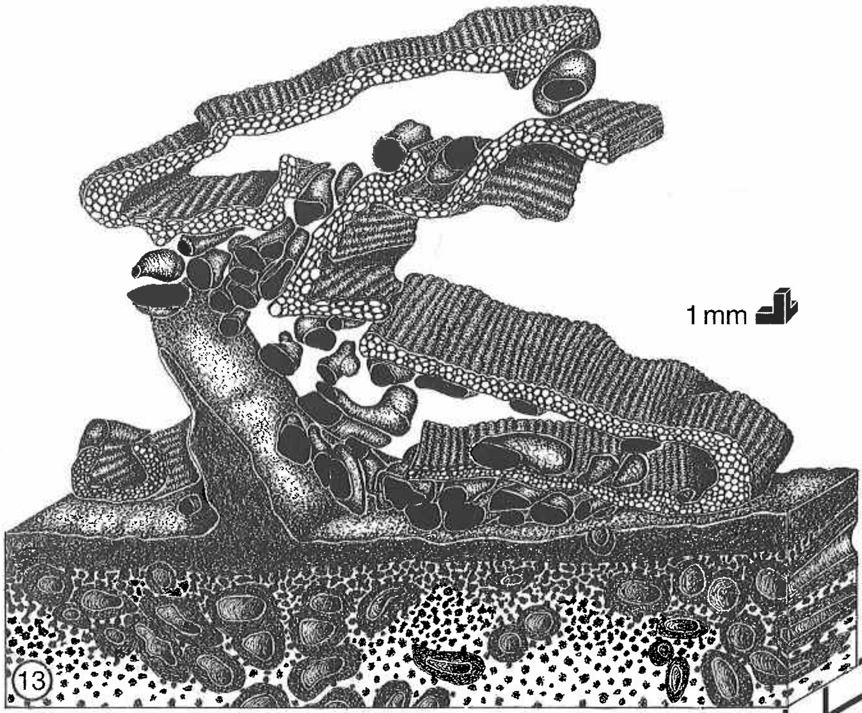

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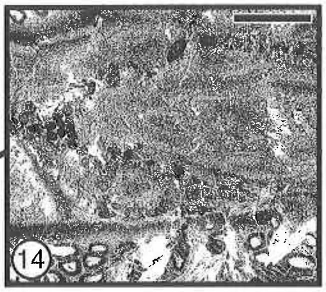

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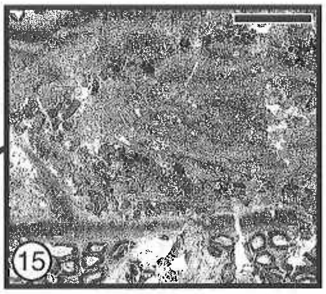

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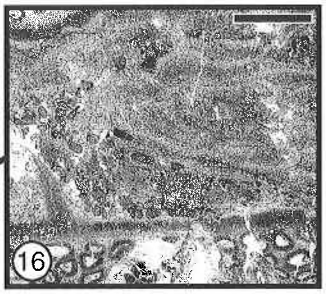

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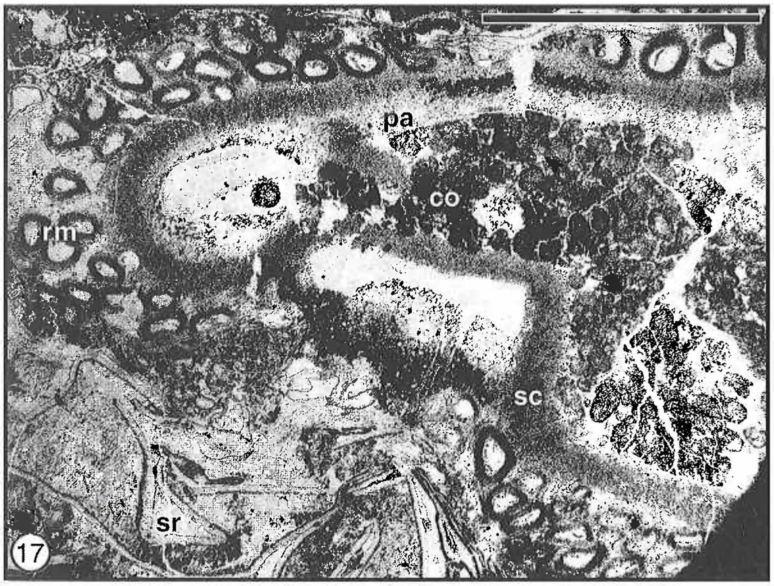

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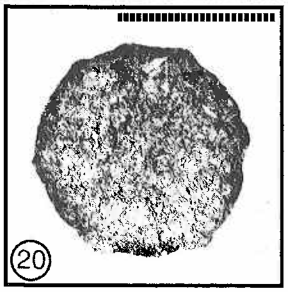

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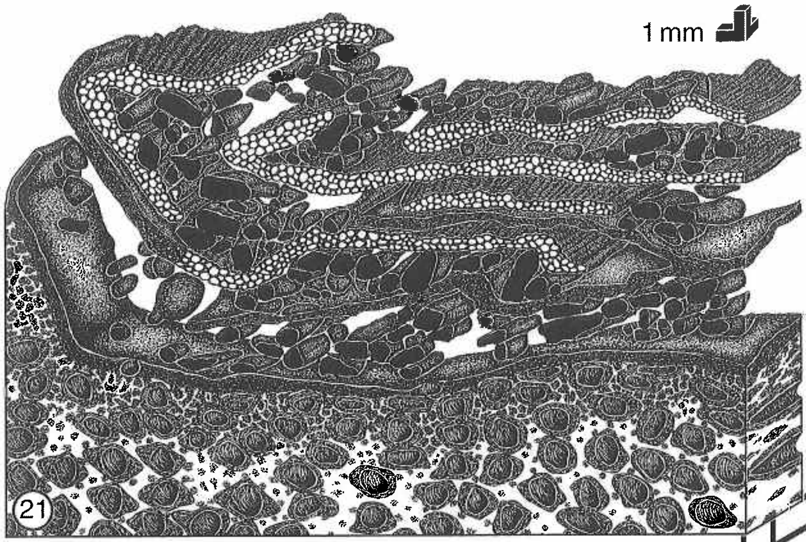
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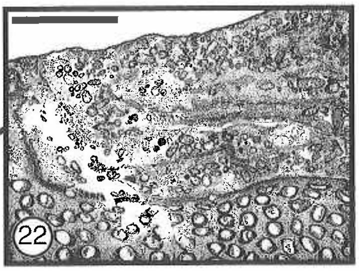
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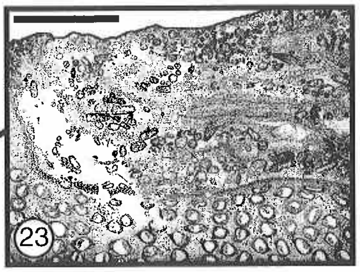
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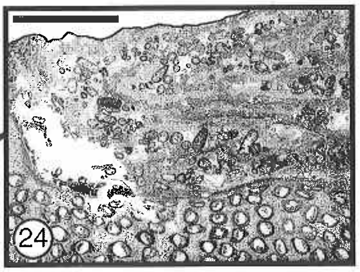
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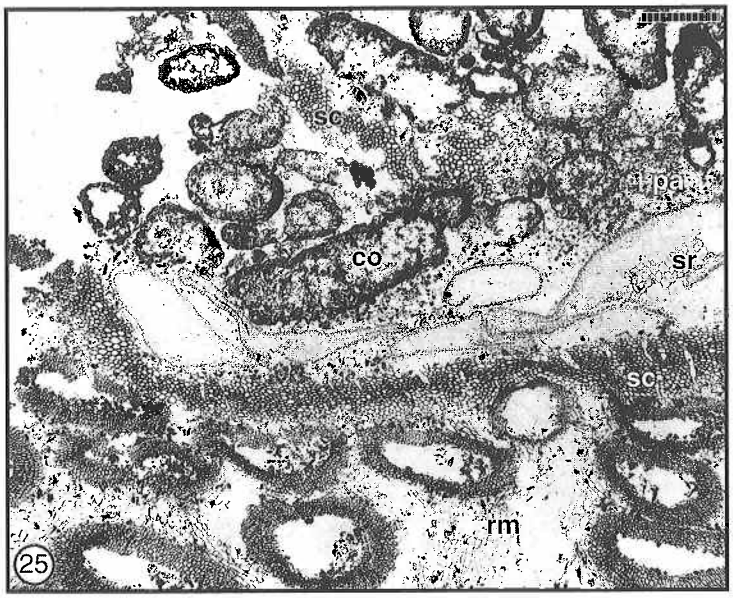
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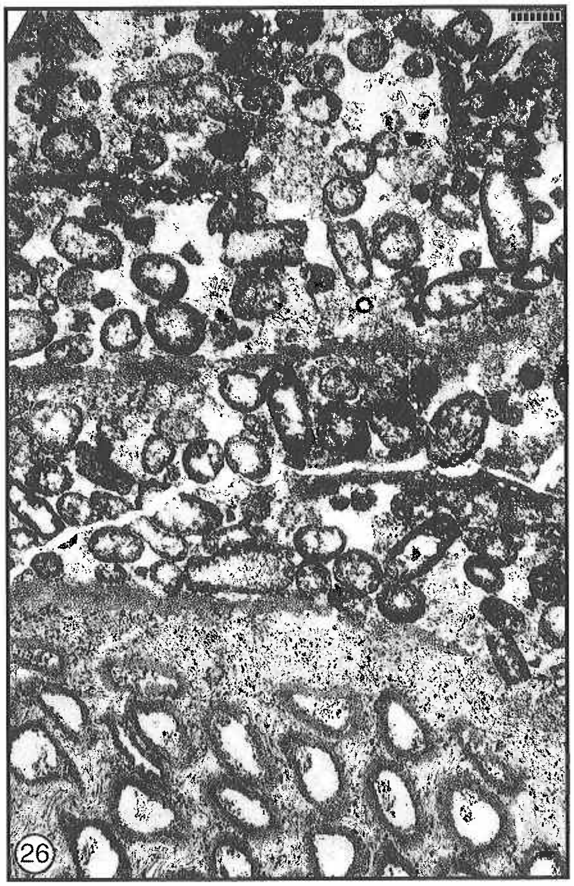
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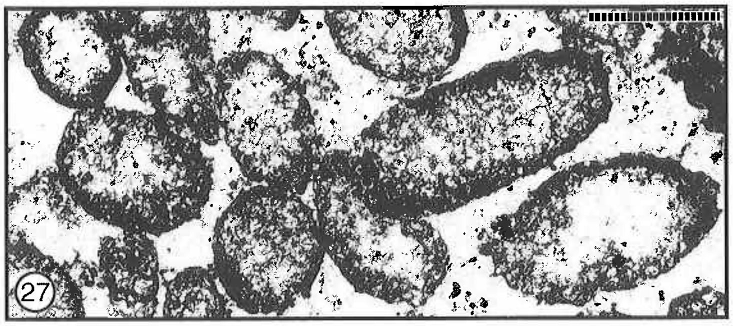
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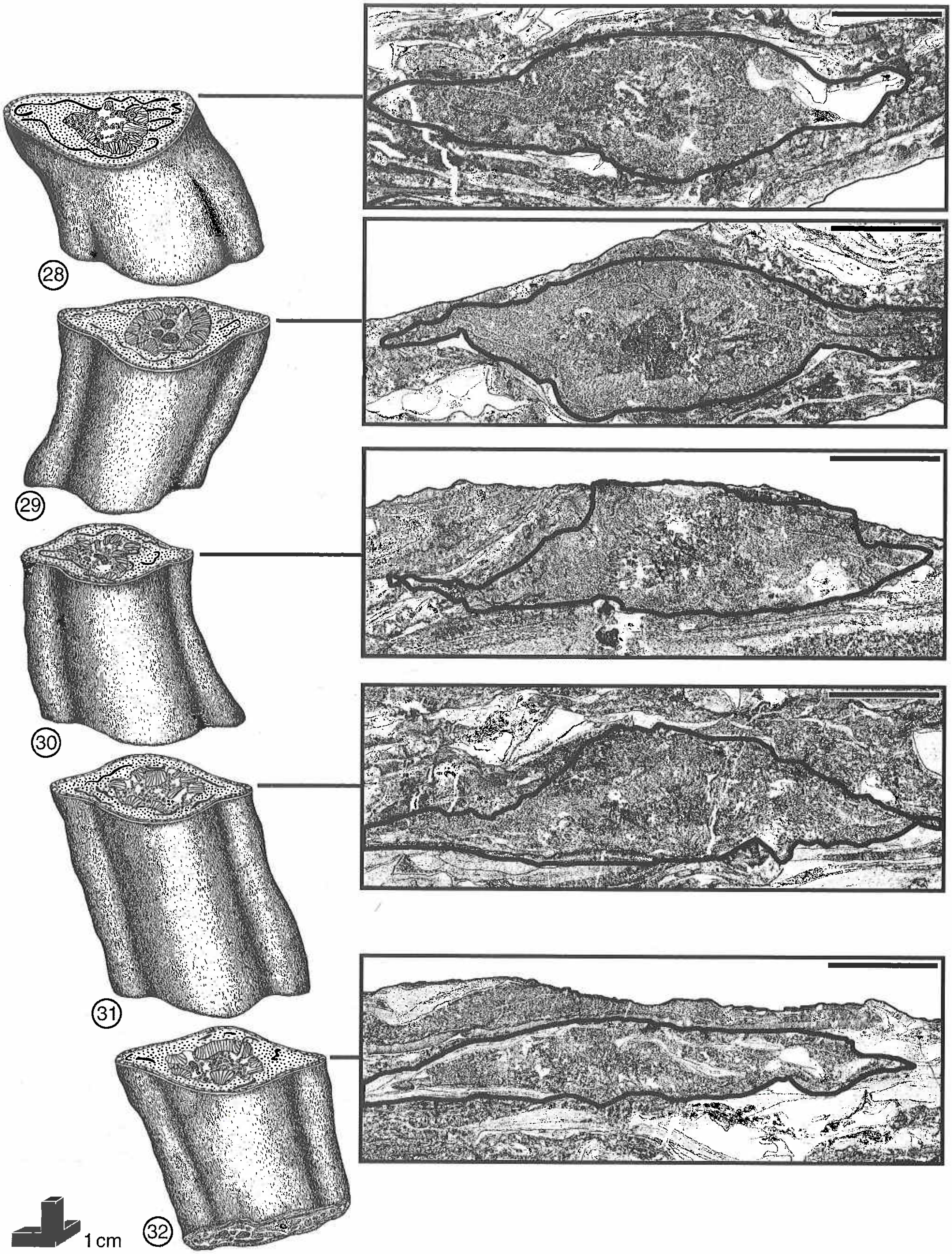

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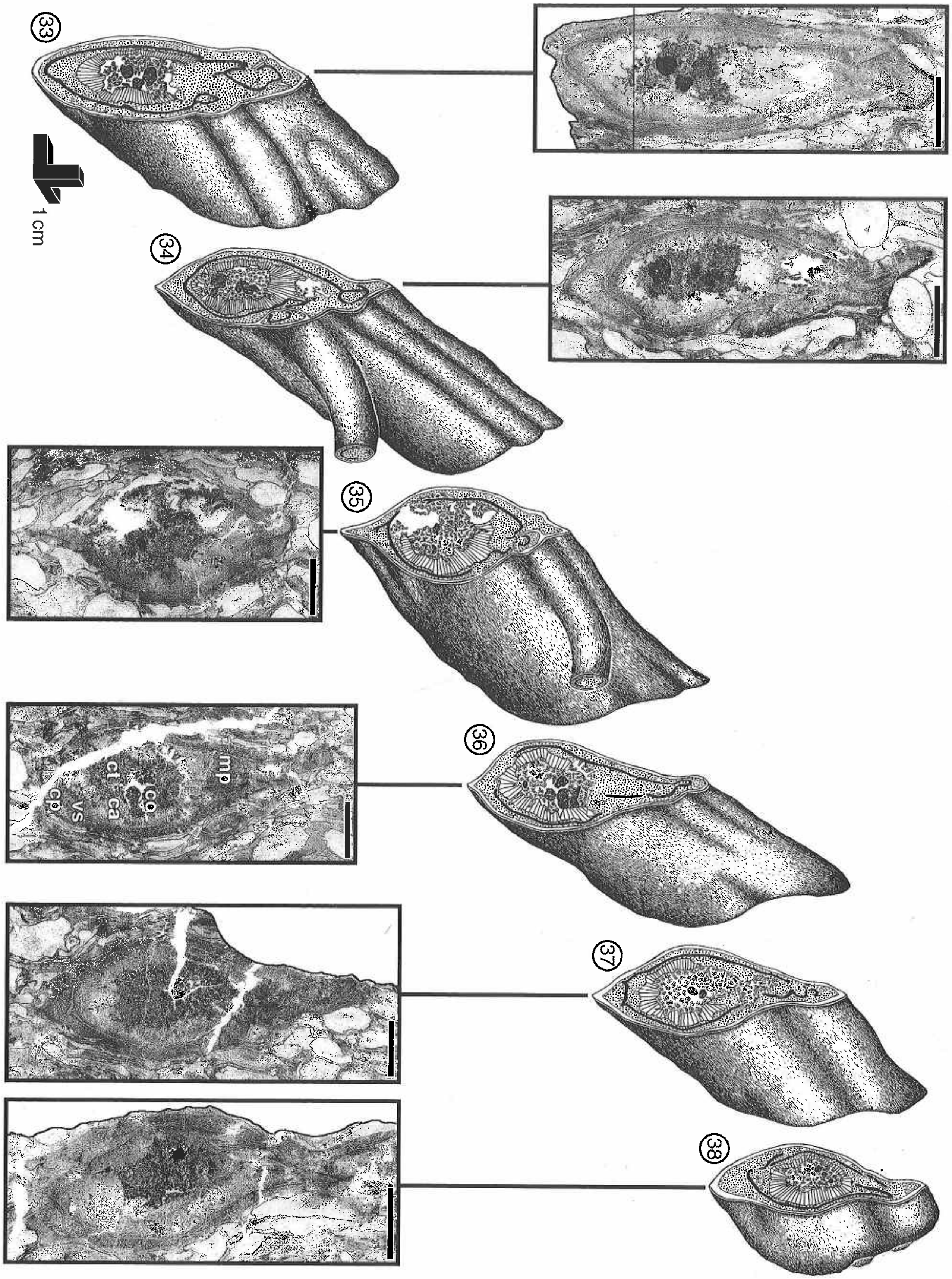

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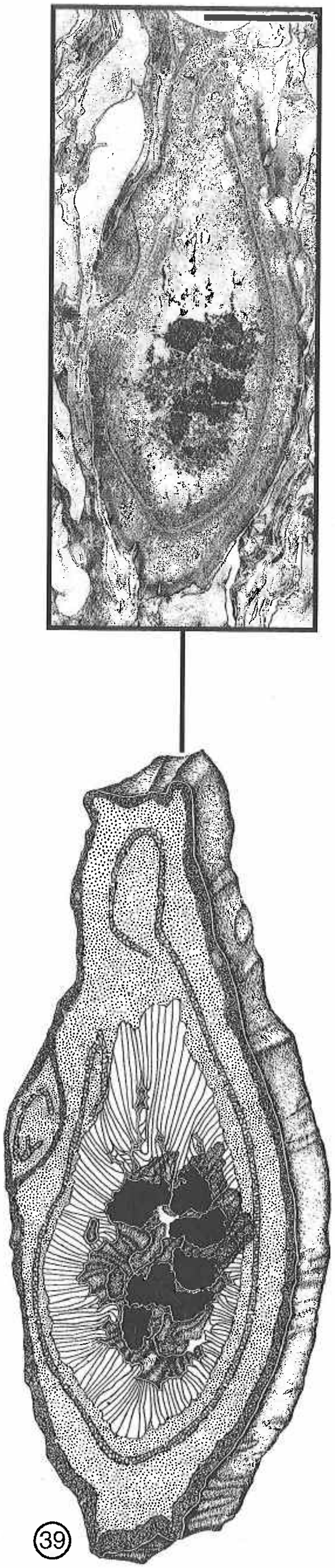

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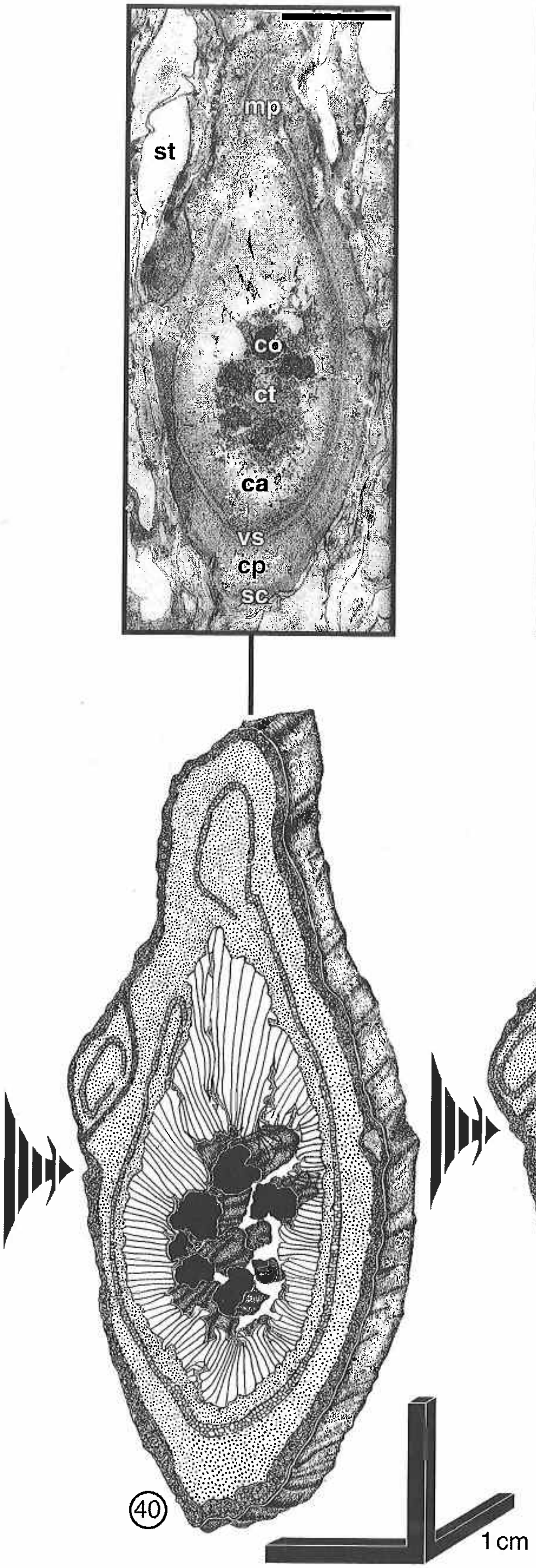

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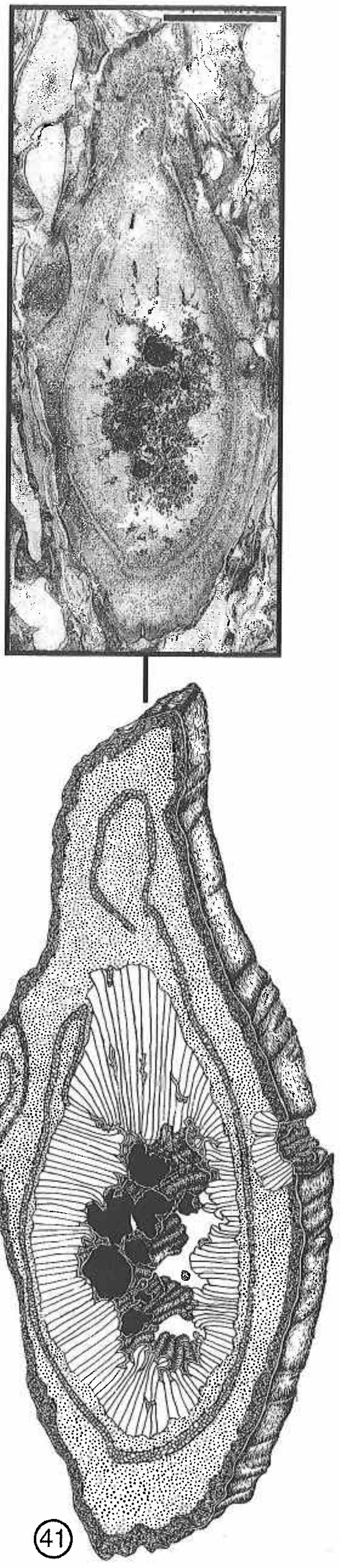

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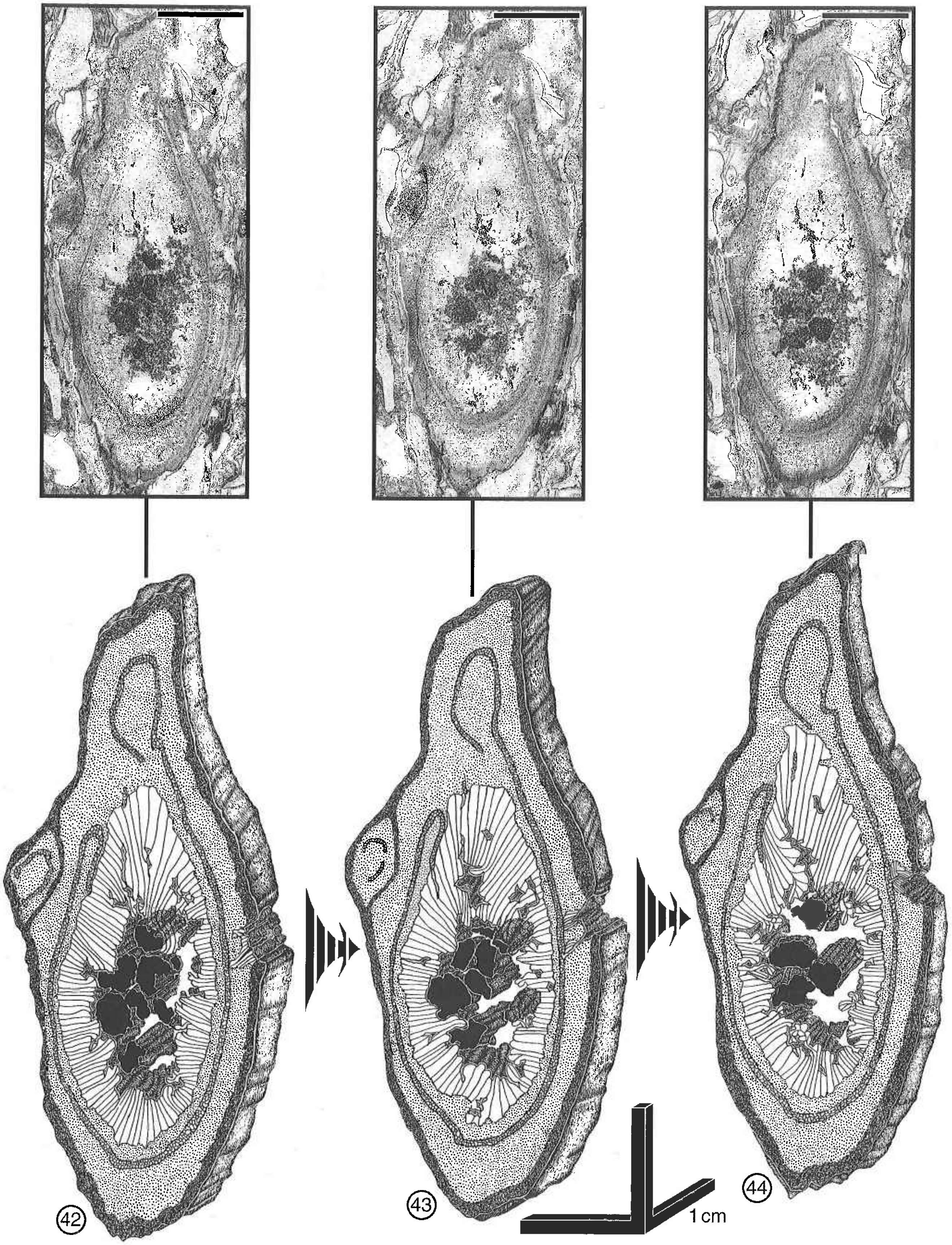

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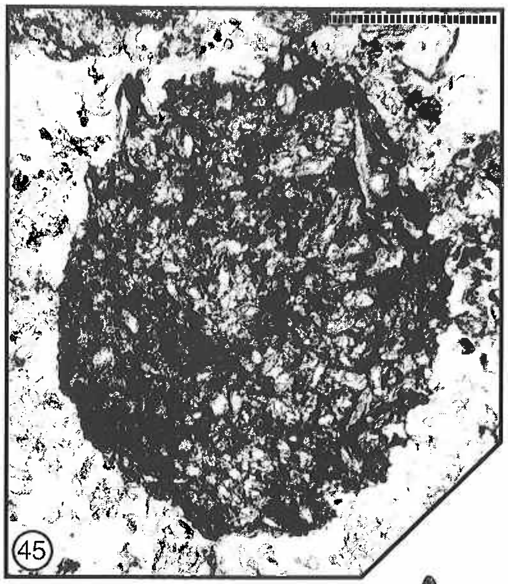

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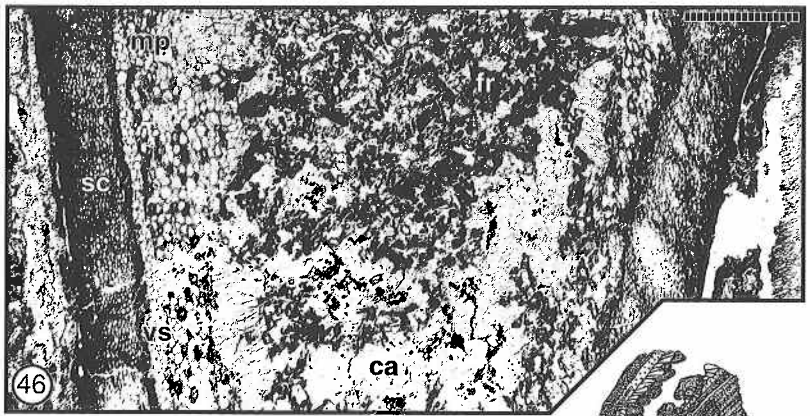

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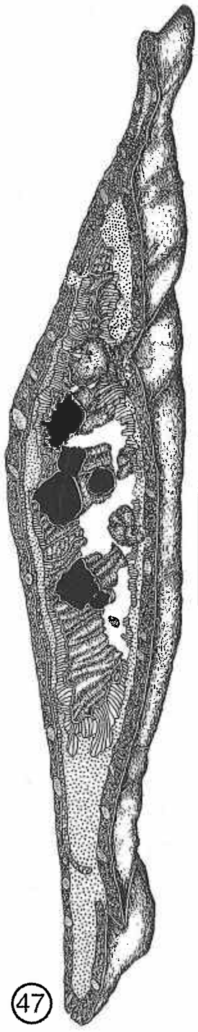

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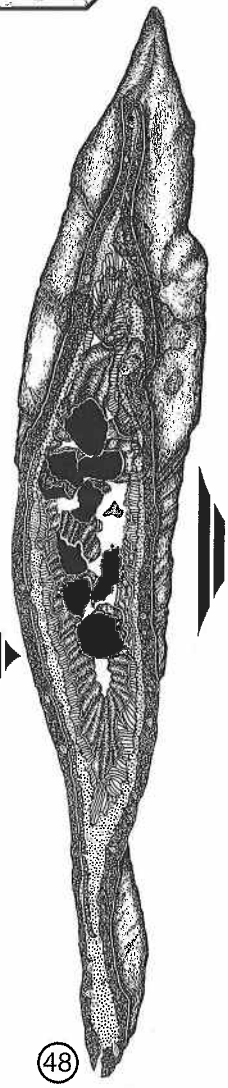

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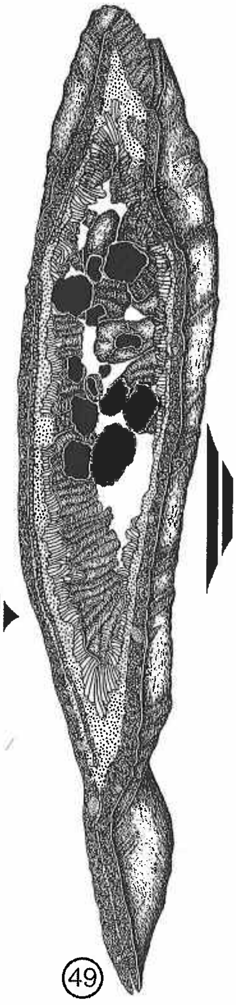

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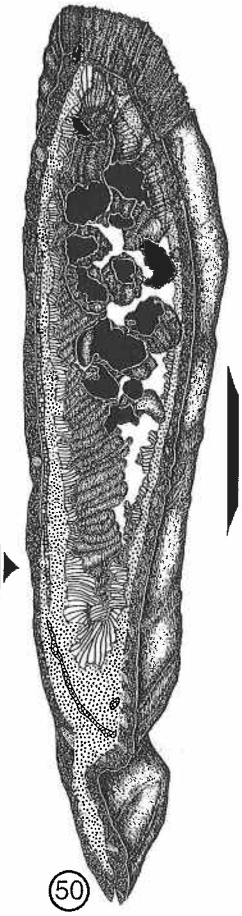

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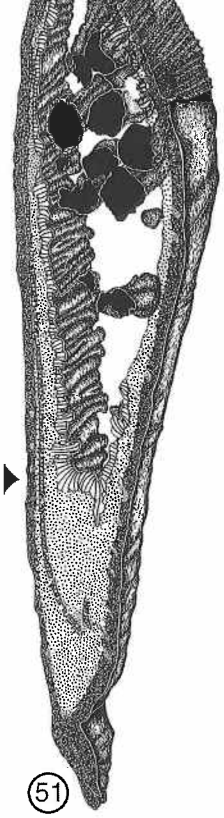

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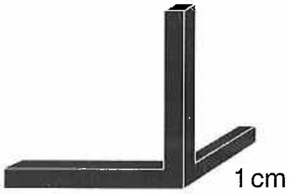

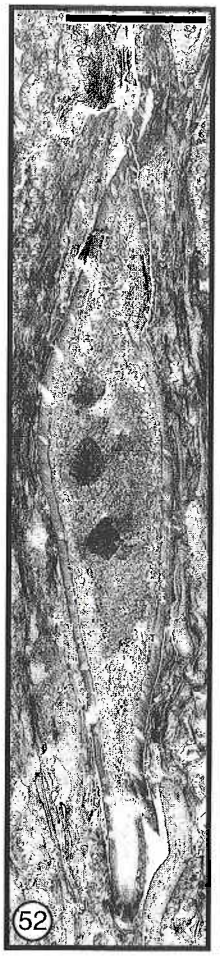
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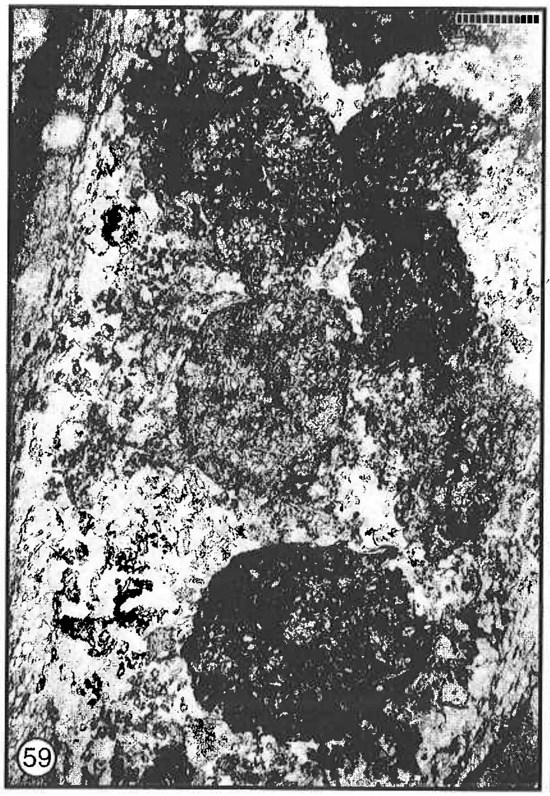
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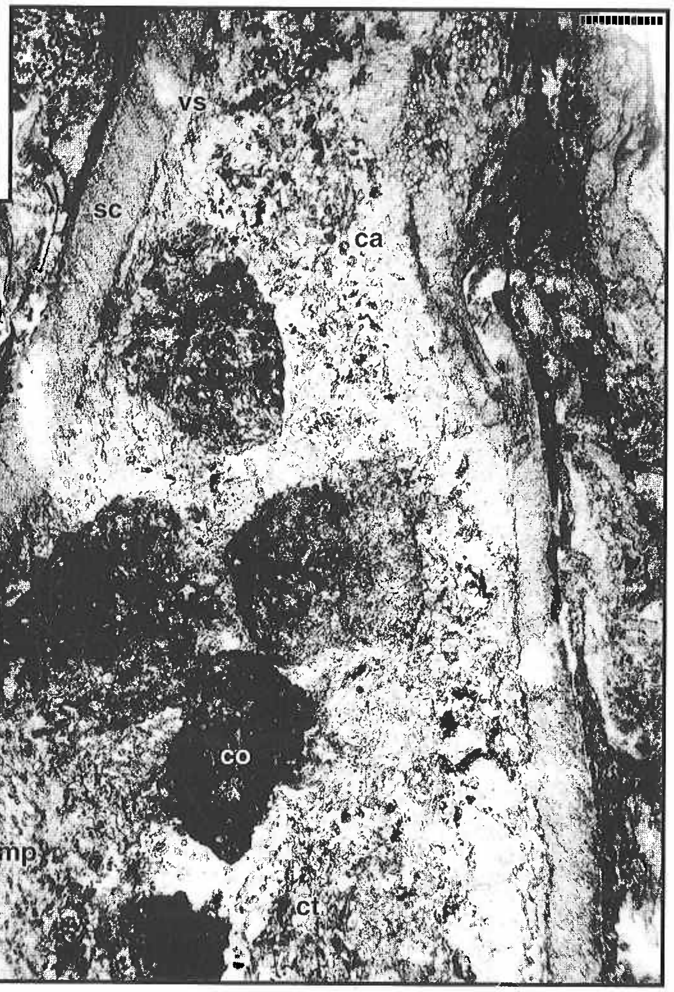
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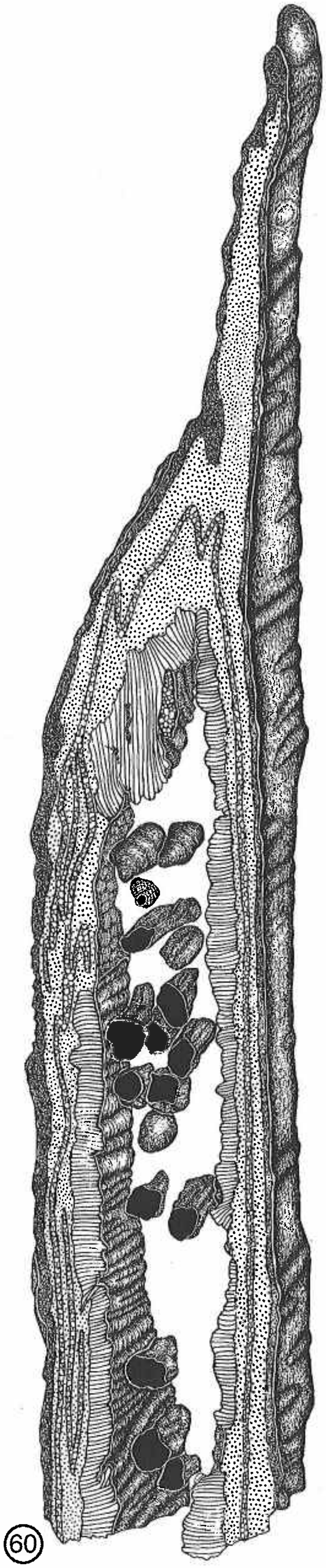

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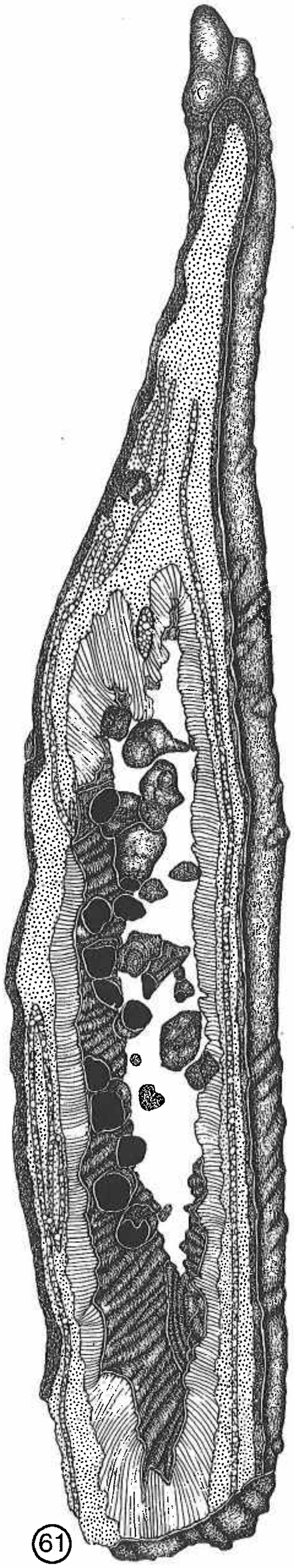

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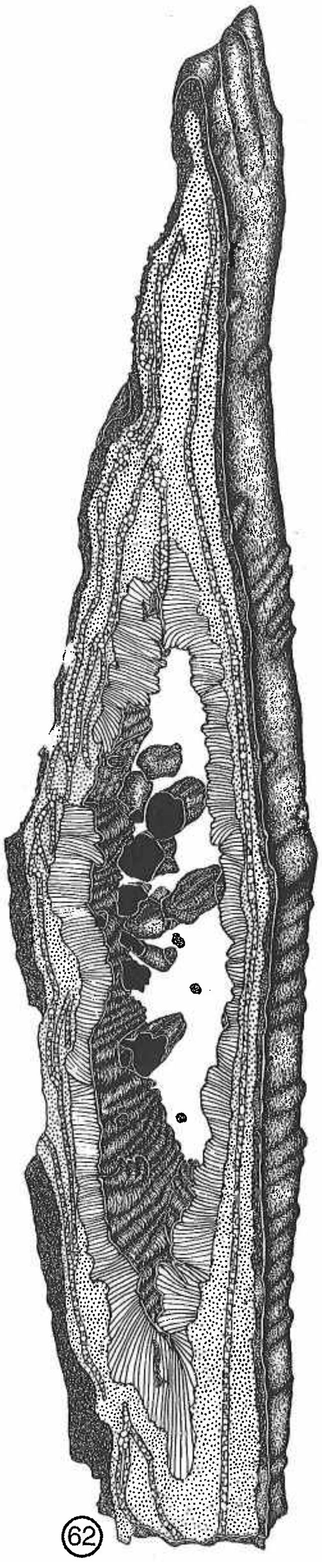

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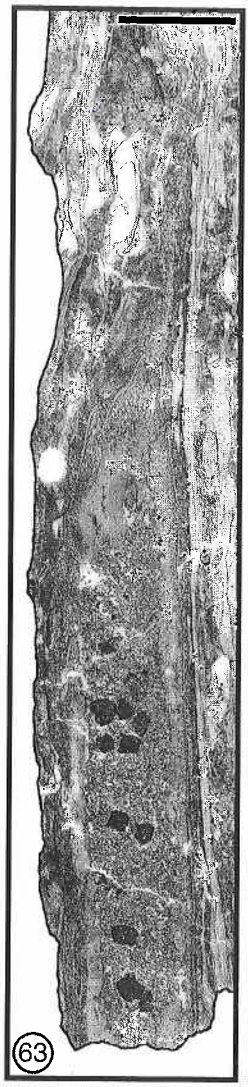

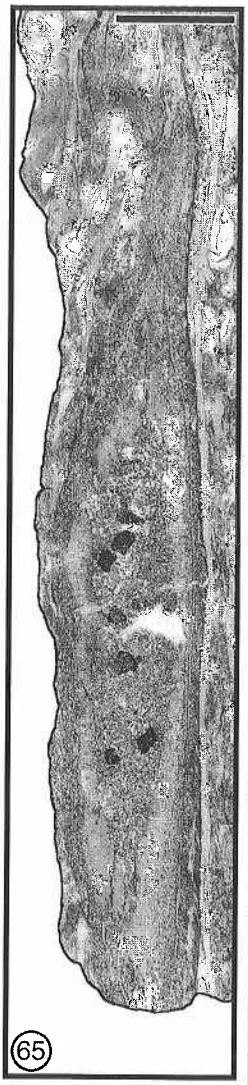

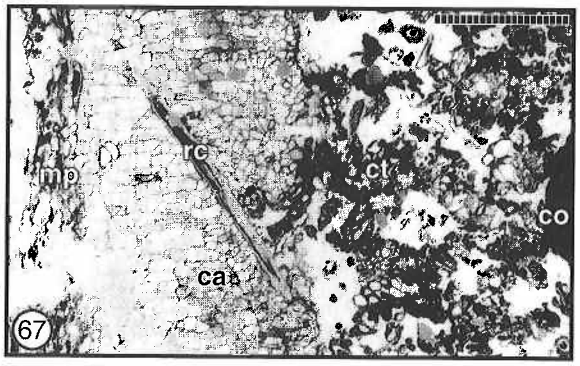

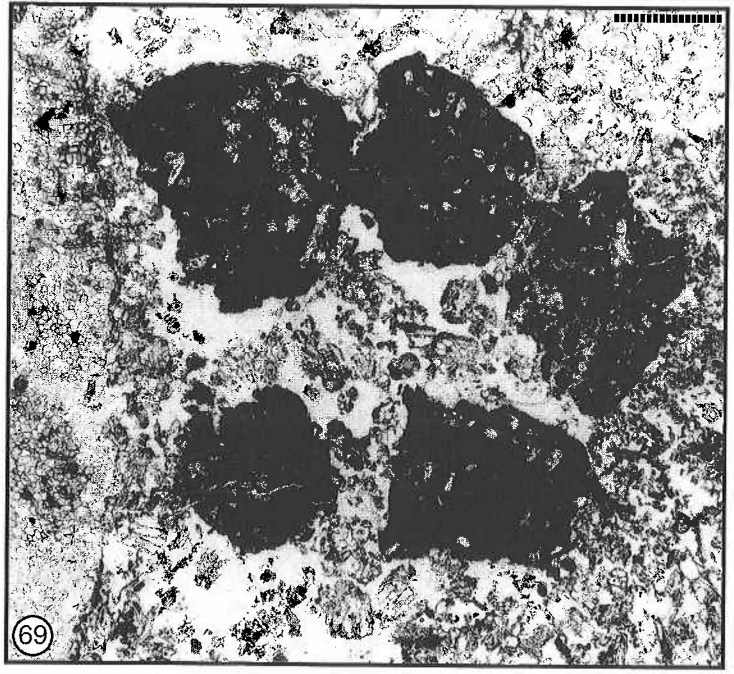

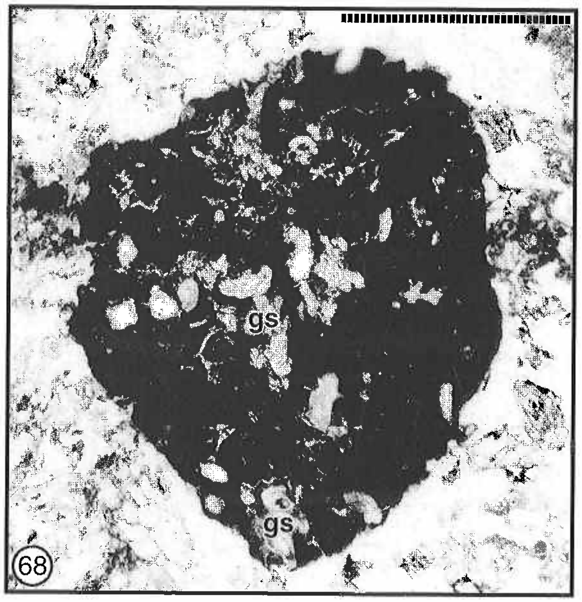

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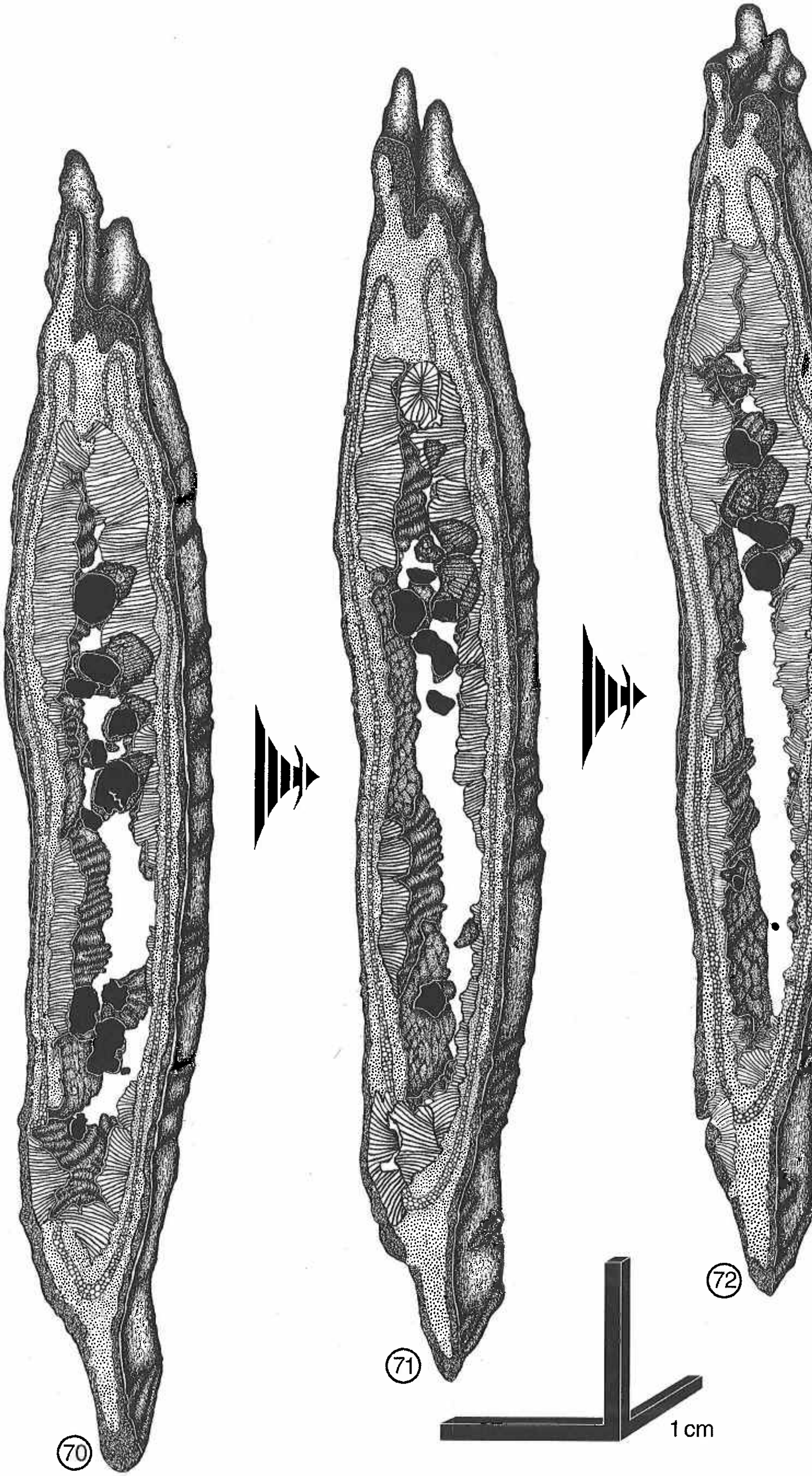

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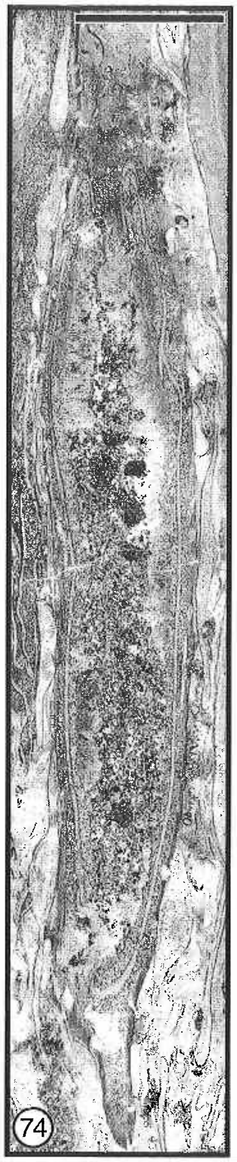
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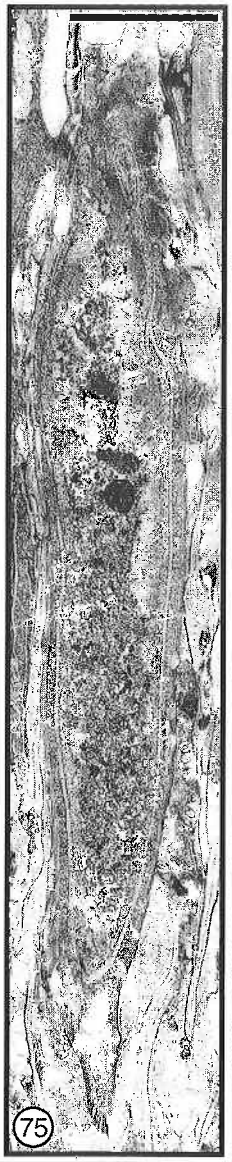
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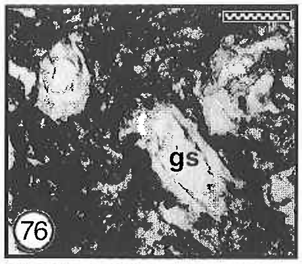
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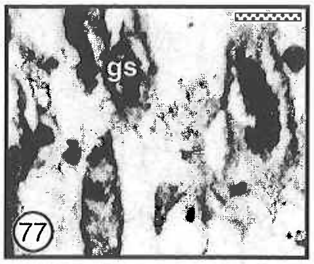
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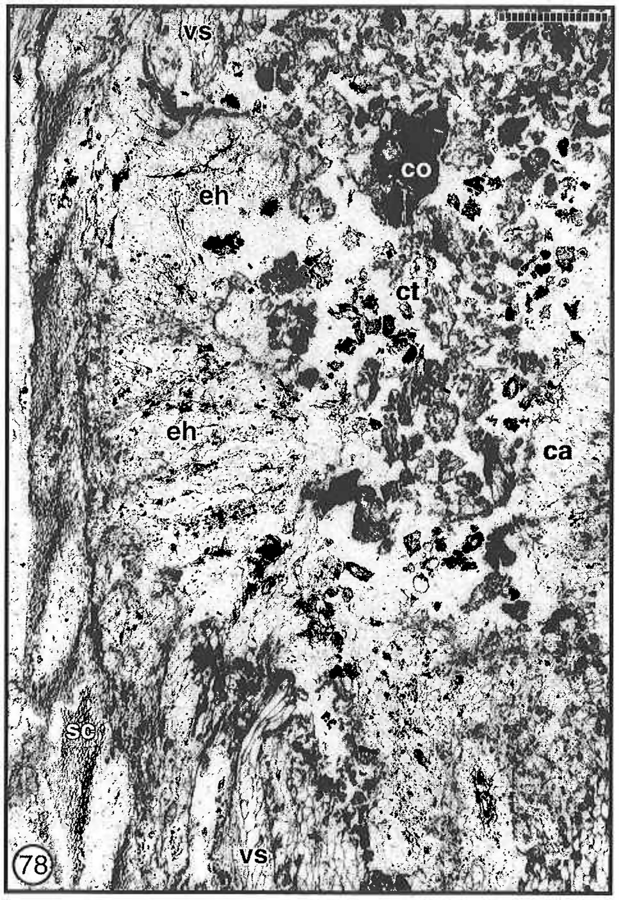
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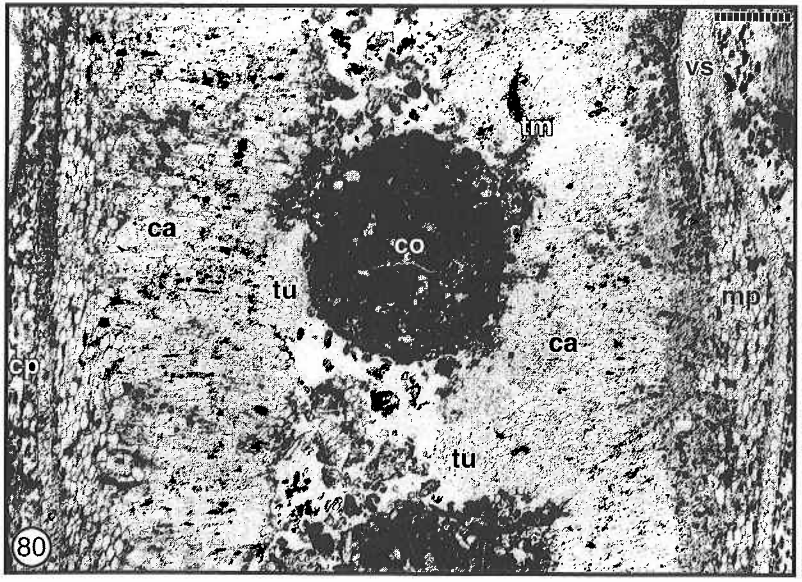
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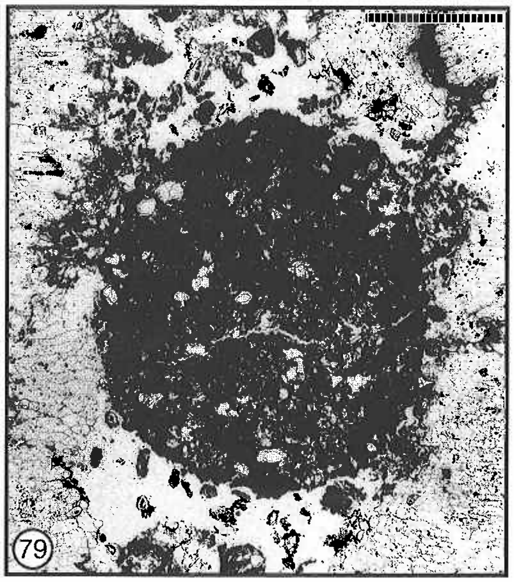
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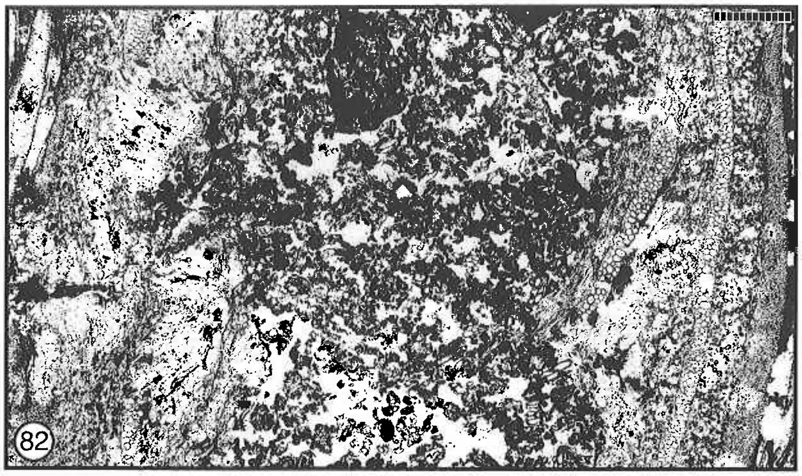

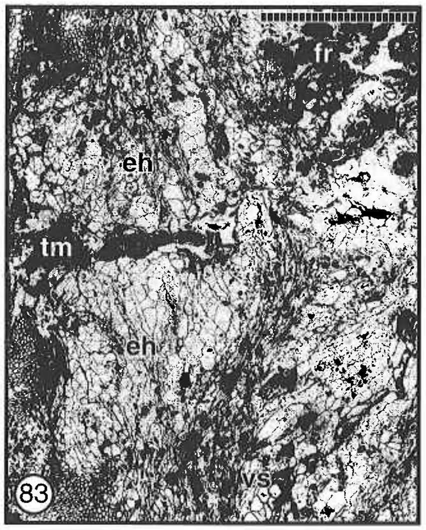

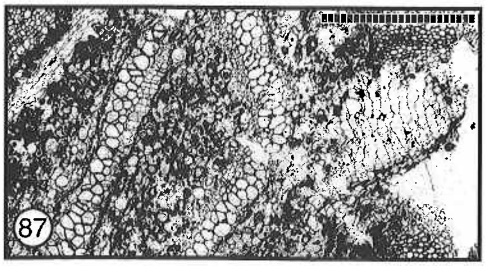

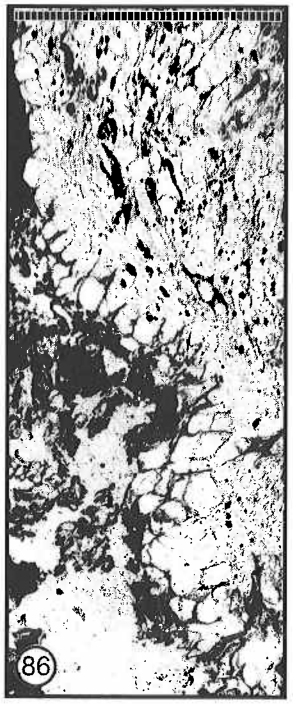

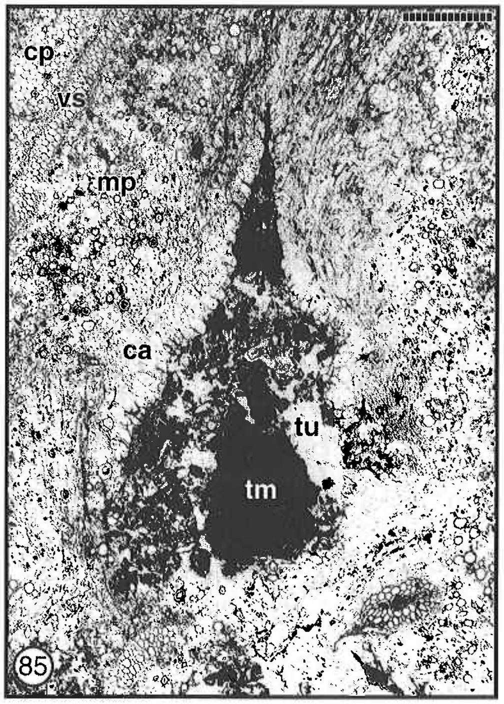

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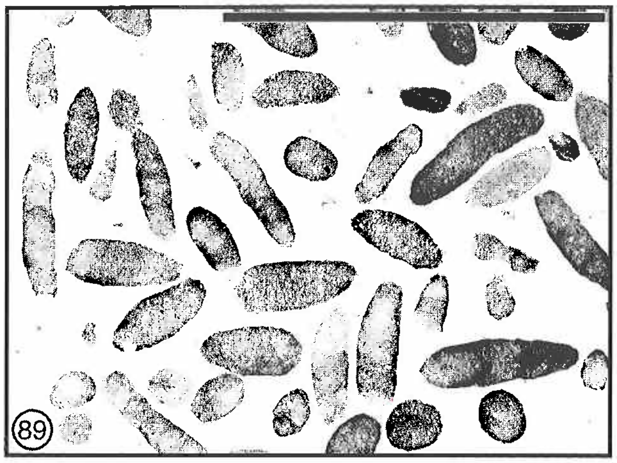
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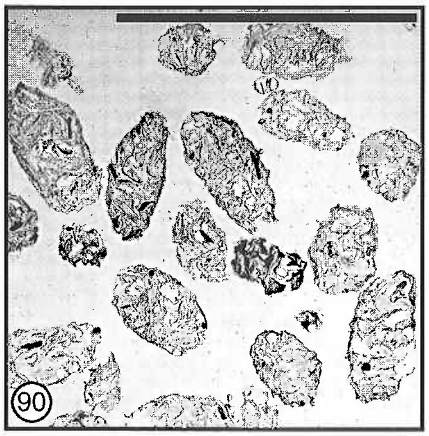
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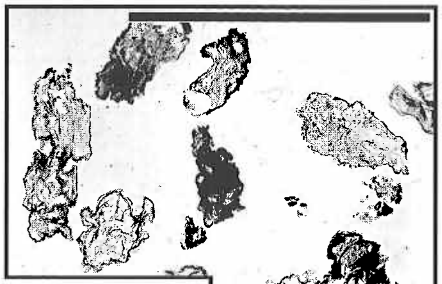
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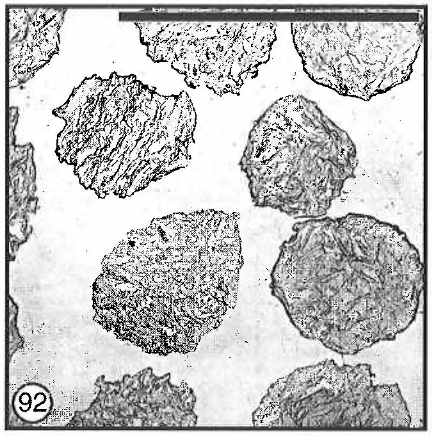
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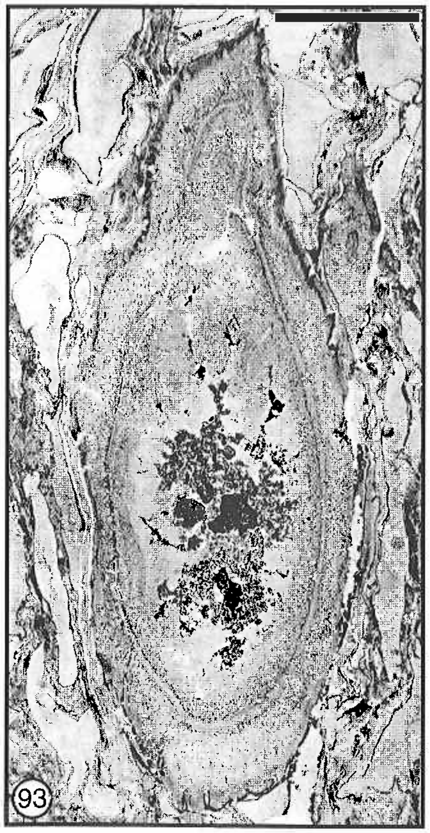
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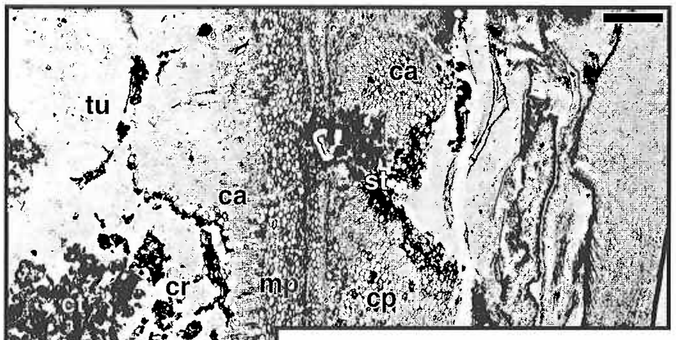

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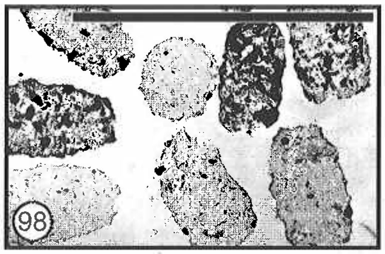
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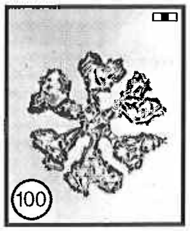
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