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Permian *Circulipuncturites discinisporis* Labandeira, Wang, Zhang, Bek et Pfefferkorn gen. et spec. nov. (formerly *Discinispora*) from China, an ichnotaxon of a punch-and-sucking insect on Noeggerathialean spores

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ABSTRACT

The generic name *Discinispora* Wang, Zhang, Bek et Pfefferkorn was originally created for spores with an operculum-like structure that were found in a permineralized Noeggerathialean cone. Subsequently it was observed that up to three round and smooth openings can occur in different positions on the surface of a single spore. In light of the new observations, the previous interpretation as an operculum cannot be sustained. An interpretation implicating insect punch-and-sucking activity was suggested for these round structures. This new interpretation makes it necessary to withdraw the original diagnosis and the taxon. The insect-inflicted damage now is assigned to the ichnotaxon *Circulipuncturites discinisporis* Labandeira, Wang, Zhang, Bek et Pfefferkorn under the rules of the ICZN, rather than those of the ICBN that typified the insect-damaged host-plant spore.

1. Introduction

During an investigation of the morphology of the spores from the cone *Discinites sinensis* Wang, which is the sole petrified species of the Noeggerathiales and bears significant information on the systematic position of the order, a circular opening was recognized in a number of the microspores. Based on the consistent dimensions, morphology, and position of these circular apertures, it was interpreted as an original reproductive structure of the spore and this palynomorph was published as the new genus and species *Discinispora sinensis* Wang, Zhang, Bek et Pfefferkorn (Wang et al., 2004). However, during further study on the petrified noeggerathialean strobilus, it came to our attention that this structure might be the result of animal activity. It was not until recently that subsequent critical examination of in situ spores of *Discinites sinensis* Wang provided evidence that the opening could not be an operculum, that is, an integral part of the spore. Therefore, given this new interpretation, it is necessary to establish a new generic name for this insect-mediated damage according to the International Code of Zoological Nomenclature under Articles 2.1 and 10.5 (Ride et al., 1999). The name *Discinispora sinensis* Wang, Zhang, Bek et Pfefferkorn has to be abandoned as an empty name because spores of this cone that lack the circular damage described herein could be called *Deltoidospora* Miner, *Calamospora* Schopf, or *Punctatisporites* Ibrahim.

Our critical examination of the in situ spores of *Discinites sinensis* Wang is based on 1000 spores from two sporangia of the holotype (Wang, 2000, 2005). Methods have been described in detail by Wang (2000). For the current study, isolated sporangia were macerated with HF (36%) for about 24 h and washed with distilled water. Spores were etched with ethanol and coated with gold for observation in a LEO1530BP scanning electron microscope (SEM). The sporangia of *Discinites sinensis* Wang have been fragmental or broken to some degree due to weathering. There is not a certainly complete sporangium available for a critical investigation of the insect damage on sporangial walls.

2. Systematic paleontology

According to Article 10.3 of the International Code of Zoological Nomenclature (Ride et al., 1999), a name proposed for an ichnotaxon is a family group name, a genus-group name, or a species-group name,

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based on the way in which it is first established. We propose a genus-group name.

GENUS: *Circulipuncturites discinisporis* Labandeira, Wang, Zhang, Bek et Pfefferkorn.

Diagnosis: A circular orifice, 40–60 µm in diameter, representing severance of the spore wall and from one to three occurrences per spore that are variably positioned on the exposed surface.

Host plant: This distinctive damage occurs on the spores of *Discinites sinensis* Wang that belongs to the late Paleozoic Noeggerathiales.

Holotype: The spores of *Discinites sinensis* Wang figured by Wang et al. (2004, Plate I, Fig. 4), here refigured in Plate I, Fig. 1.

Type locality: Shitanjing, Shizuishan, Ningxia, China.

Stratigraphic horizon: The Lower Shihhotse Formation; Early Permian (Late Artinskian to Kungurian) in age.

Etymology: From the Latin (masculine): *circulus*, for "small circle," and *punctura*, for "hole."

Description: For a critical examination on the presence or absence of these orifices, two complete sporangia were isolated from the cone *Discinites sinensis* Wang, resulting in about 1000 spores after maceration. After checking our SEM observations, one to three circular openings per spore were found on more than 50 spores, of which six were selected and are shown in Plate I, Figs. 2–8. These orifices are usually circular (Plate I, Figs. 1–5, 6 for lower and left orifices, 7), although occasionally some are slightly irregular (Plate I, Fig. 6 for the upper-right orifice). The diameter typically ranges between 40 and 60 µm but the total range is between 10 and 80 µm. The apertures usually occur on the lateral and distal walls (Plate I, Figs. 1–6) but also on the proximal spore wall (Plate I, Figs. 7, 8). They always traverse all three layers of the spore wall (Wang et al., 2004). Occasionally spores have been incompletely penetrated, preserving a disk preserved in place prior to breakage (Plate I, Fig. 2) whereas other examples have the dislocated and fragmented disc occurring within the spore itself (Plate I, Fig. 4).

3. Remarks

The fact that these highly stereotyped, recurring, circular openings can occur at any orientation on the spore surface excludes the possibility that they are a functional part of the spore, such as an operculum. Thus, an alternative explanation has been sought. The highly regular, circular shape of the opening suggests a biological explanation, possibly by the action of an organism such as a fungus or an insect. Although fungal predation on spores is known (Sinclair et al., 1987), no known extant fungus produces the *Circulipuncturites discinisporis* type of damage.

Sporophagy is a common feeding habit among a variety of extant microarthropods, including springtails (Collembola), thrips (Thysanoptera), and major clades of holometabolous insects, particularly beetles (Coleoptera), sawflies (Hymenoptera) and moths (Lepidoptera). Much of the consumption of spores, including sporangial and synangial tissues, is accomplished by relatively large, mandibulate larval and adult external feeders, particularly beetles (Leschen and Lawrence, 1991). However, taxa with comparatively small adult and larval body sizes are known to consume spores within enclosed sporangia, including the curculionid weevils *Endalus celatus* and *Echinochnemus* sp. that bore small apertures for entry into sporocarps of *Marsilea* sp. (Board and Burke, 1971; Loyal and Kumar, 1977); the tenthredinid sawfly *Teichobia filicivora* that feeds in the sori of *Dryopteris borreri* and *Pteridium aquilinum* (Ottosson and Anderson, 1983); and the primitive oecophorid moth *Erineda aenea* on *Asplenium angustifolium*, which produces a hollowed indusium after feeding (Braun, 1918). Examples also are known from the fossil record, prominently the presence of pollen-laden coprolites within the pollen sacs of a pollen cone from the Middle Triassic of Antarctica (Klavins et al., 2005). In the present case, we have not seen any evidence that the sporangial wall was ruptured, but it is highly possible that certain apertures for entry into the sporangia are too small to recognize. No coprolites are detected. They might have been

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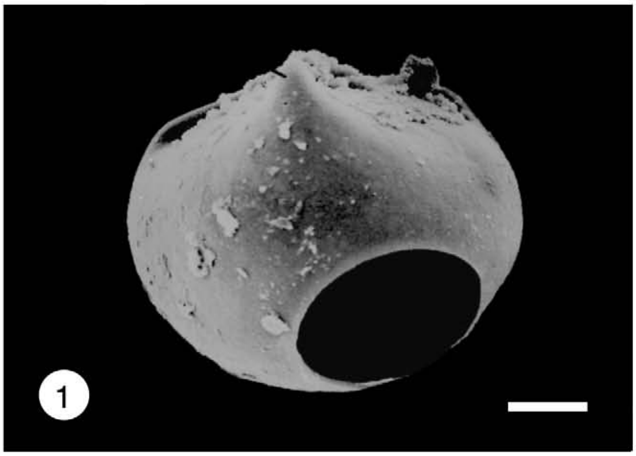
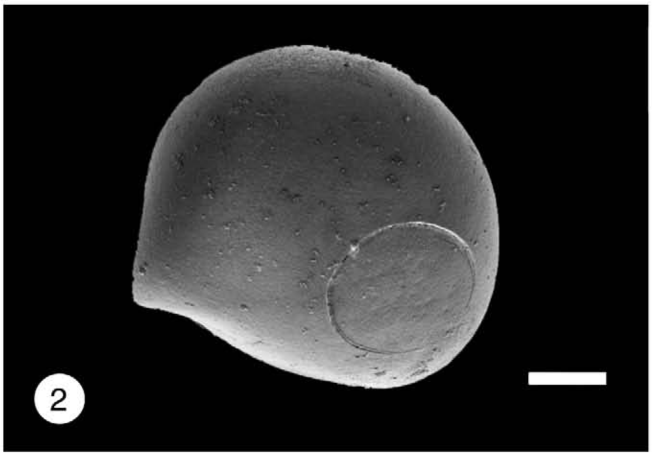
Plate I. Eight figures below show from one to three circular punctures of *Circulipuncturites discinisporis* Labandeira, Wang, Zhang, Bek and Pfefferkorn occurring on spores of *Discinites sinensis* Wang.

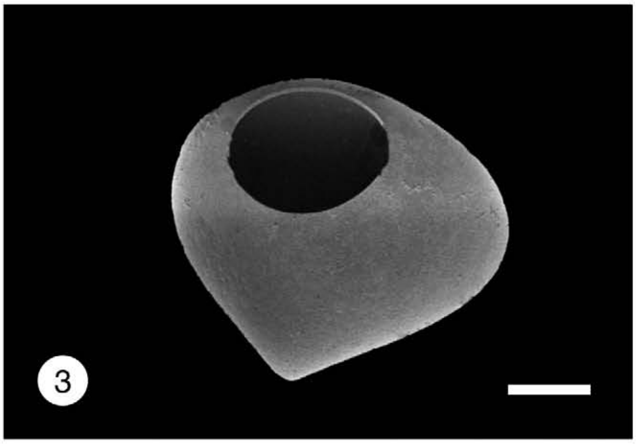
1. Holotype of *Circulipuncturites discinisporis*, figured in Wang et al. (2004; Plate I, Fig. 4) as *Discinispora sinensis* Wang, Zhang, Bek and Pfefferkorn. Scale bar = 20 µm.
2. An initially cut disk that did not separate from the spore wall. Scale bar = 20 µm.
3. An orifice on the distal wall, similar to the holotype. Scale bar = 30 µm.
4. An orifice with a diameter larger than half of the spore diameter. Scale bar = 30 µm.
5. Two orifices of different sizes on the lateral (left and smaller) and distal (right and larger) spore walls, respectively. Scale bar = 30 µm.
6. Three orifices of different sizes on the lateral distal wall, of which the upper-right one has a slightly irregular circular margin. Scale bar = 30 µm.
7. An orifice on the proximal spore wall. Scale = 30 µm.
8. Enlargement of the orifice in (7) at left, showing the aperture margin. Scale = 10 µm.

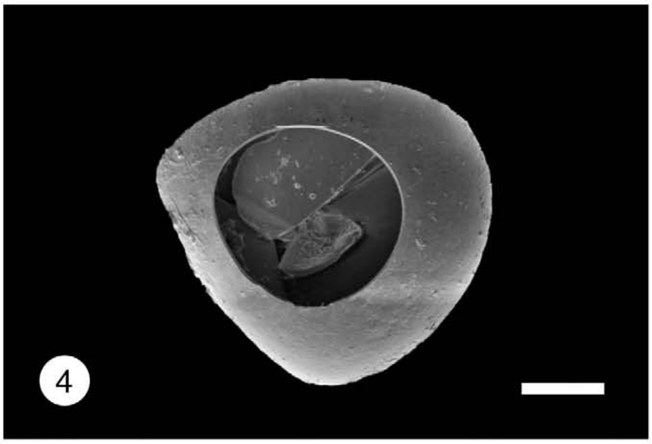
Plate II. At the left are modern (1) and Permian (2, 3) specimens of Thysanoptera; at the right are examples of thysanopteran damage to angiosperm pollen (4, 5), a leaf (6) and an ovule (7). (see on page 280)

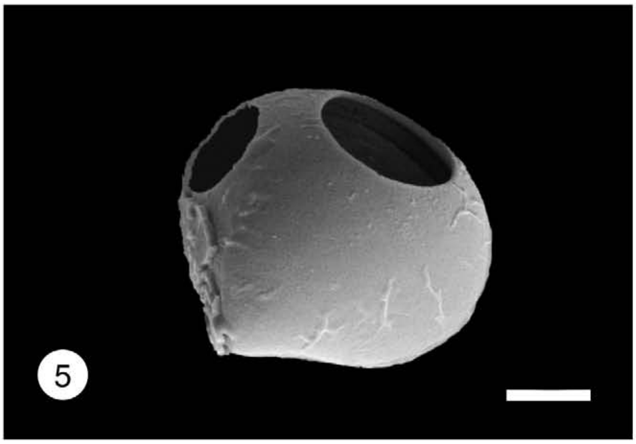
1. The punch-and-suck feeding technique in *Thrips vulgatissimus* Haliday (Thripidae) above and *Aeolothrips intermedius* Bagnall (Aeolothripidae) below, showing the head profile and position of the mouthcone and associated mouthparts during puncture of a pollen grain. From Kirk (1997), reproduced with permission by the Commonwealth Agricultural Board International, London, U.K. Scale bars = 100 mm.
2. An early Middle Permian (Roadian) lophioneurid, *Lophiocypha incompleta* Vishniakova, from Soyana, Ural Region, Russia. The arrow points to mouthcone and styletal mouthparts. From Vishniakova (1981), reproduced with permission by the Russian Academy of Sciences. Scale bar = 1 mm.
3. A dorsal view of the head, mouthparts and antennae of a different specimen of *Lophiocypha incompleta* Vishniakova but from the same locality than shown in (2) above. From Vishniakova (1981), reproduced with permission by the Russian Academy of Sciences. Scale bar = 100 µm.
4. A SEM micrograph of a pollen grain of *Malva sylvestris* L. (Malvaceae), exhibiting a central collapsed area following a feeding puncture. From Kirk (1997), used with permission by the Commonwealth Agricultural Board International, London, U.K. Scale bar = 20 µm.
5. A drawing of the specimen in (4) above, showing the envelope of the circular collapsed area. From Kirk (1996), used with permission from the Company of Biologists, Ltd., U.K. Scale bar = 20 mm.
6. A SEM micrograph showing a circular damaged area and a central figure-8 puncture by *Limothrips cerealium* Haliday (Thripidae) on a *Triticum aestivium* L. (Poaceae) leaf. From Kirk (1997), used with permission by Commonwealth Agricultural Board International, London, U.K. Scale bar = 5 µm.
7. SEM micrograph of a feeding puncture of *Frankliniella bispinosa* (Morgan) (Thripidae) on a *Citrus sinensis* Pers. (Rutaceae) ovary, showing a circular damaged area with (left arrow) and without (right arrow) a saliva plug. From Childers and Achor (1991), reproduced with permission by the Entomological Society of America. Scale bar = 10 µm.

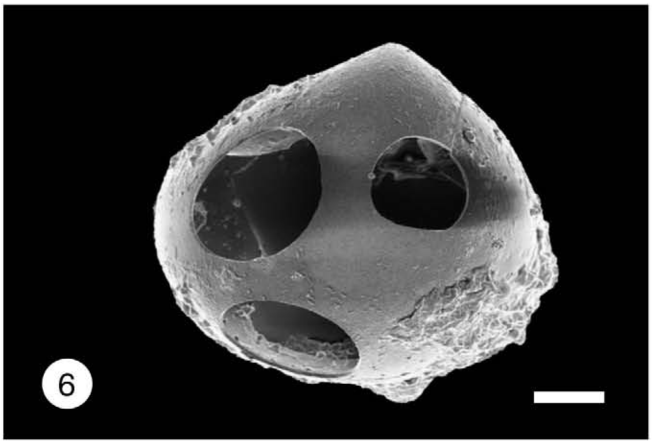


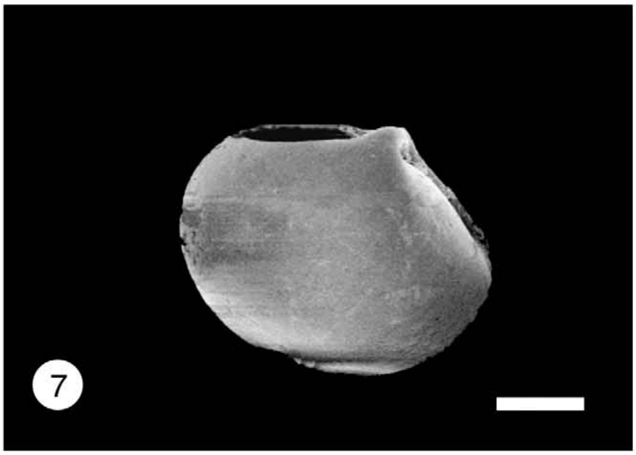












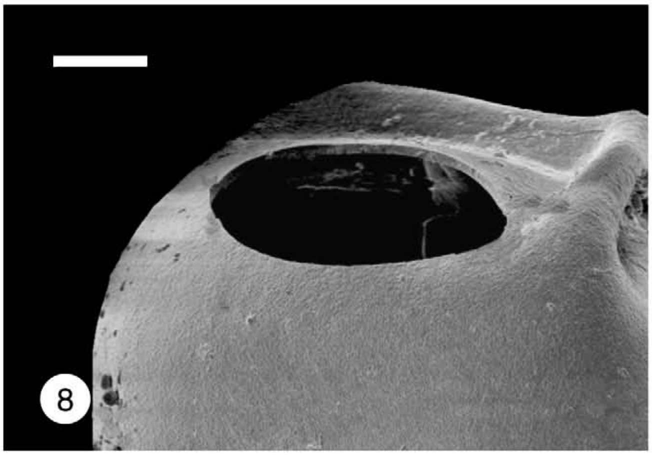


Plate I

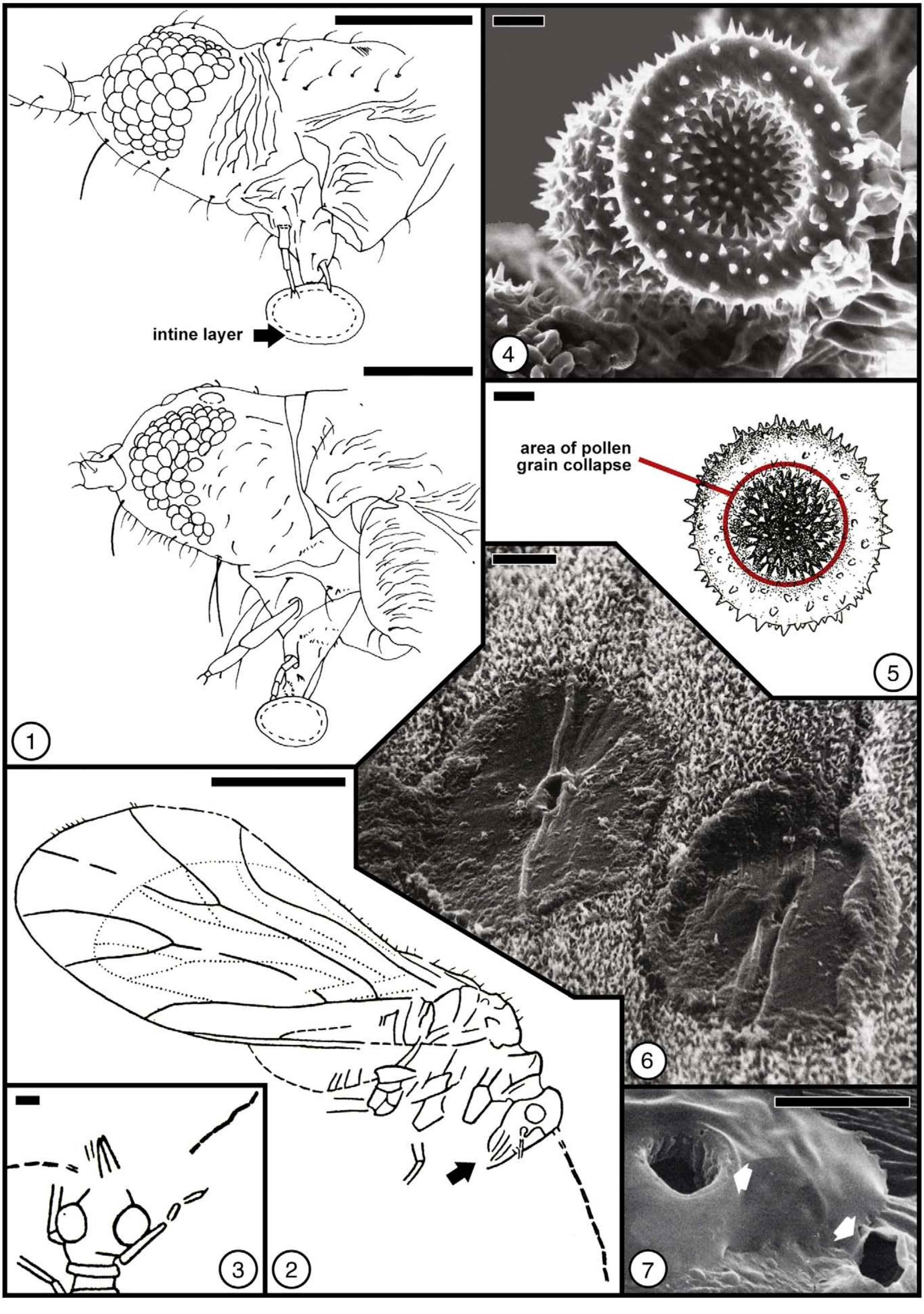


Plate II (*caption on page 278*).

lost during maceration. The spores are considered to be nearly but not fully mature, since they are in situ and completely mature spores would have been dispersed (Wang, 2005).

After a review of the modern literature on phytophagous insects, we noted similarities between the circular openings of *Circulipuncturites discinisporis* on Permian spores of *Discinites sinensis* Wang and similar damage inflicted on a variety of modern angiosperm pollen by thrips (Grinfel'd, 1960; Kirk, 1984, 1985, 1987, 1997; Plate II, Fig. 1). Thrips are a moderately speciose group of hemipteroid, piercing-and-sucking insects constituting the order Thysanoptera, and are comprised of approximately 4500 described species that are rarely longer than 3 mm in body length (Lewis, 1973, Ananthakrishnan, 1984). Thysanoptera are associated predominantly with plants, and are common associates of flowering plants (Kirk, 1997, Childers, 1997) and cycads (Terry, 2001). Their economic importance is considerable because of their damage to surface tissues, frequently as circular damaged areas in epidermis (Plate II, Fig. 6), mesophyll, parenchyma, and ovular surfaces (Plate II, Fig. 7) in plants of natural and managed ecosystems (Kirk, 1997; Childers, 1997; Kindt, 2004).

The distinctive ensemble of downwardly directed, asymmetric, fluid feeding mouthparts in the Thysanoptera consists of a central, tapering mouthcone that houses a single, stout mandibular stylet and two, more gracile maxillary stylets that are used to channel imbibed fluids into the esophagus (Risler, 1957; Mickoleit, 1963; Heming, 1993). Feeding on plants typically targets the protoplasts of individual cells in surface tissues, but also pollen. For pollen, thysanopterans use the punch-and-suck mechanism (Kirk, 1984), activated by powerful cibarial musculature within the head capsule, and characterized by an initial probe along the outer wall by the mandibular stylet (Heming, 1993). The pollen grain is secured by the mouthcone, maxillary and labial palps (Plate II, Fig. 1) and is buttressed by robust prothoracic legs from the right and left sides (Grinfel'd, 1960; Kirk, 1984). After penetration and subsequent insertion of channeled maxillary stylets, the protoplast is imbibed (Chisholm and Lewis, 1984), often as the pollen grain is held in midair attached to the mouthcone opening. Thrips also invade the confined interstices of fructifications, gaining purchase and feeding on individual pollen grains anchored to a solid substrate surface by prothoracic legs, palps, and an adpressing mouthcone (Kirk, 1996). After styletal withdrawal, a circular region of surface damage is accentuated, accompanied by pollen wall collapse within a circular area (Childers and Achor, 1991; Plate II, Figs. 4, 5). Frequently there is evidence of initial stylet penetration, in the form of a figure-8 hole representing the dual puncture events initially by the mandibular stylet and thereafter by the paired maxillary stylets (Chisholm and Lewis, 1984; Kirk, 1997). This distinctive type of microscale piercing-and-sucking damage occurs at the cellular level and has been difficult to document unambiguously in the plant fossil record.

The occurrence of multiple holes of *Circulipuncturites discinisporis* for particular *Discinites sinensis* spores may indicate a hard-wired feeding behavior. Repetitive feeding routines are generally common among insects (Chapman, 1982), and have been specifically documented from three-dimensional sections in piercing-and-sucking taxa such as the aphid *Aphis fabae* (Hemiptera), which produce radiating multiple probes from the same localized stylet insertion point for targeting individual cell protoplasts (Tjallingii and Hogen Esch, 1993). This is a stereotyped feeding pattern that has been found in Early Devonian land plants as well, attributed to an unknown microarthropod (Labandeira, 2002, Fig. 2.8d). A parallel example occurs for modern thrips, which produce linear tracks of stylate puncture marks on leaf surfaces, indicating a repetitive puncturing of epidermal tissue along particular ambulatory trajectories, such as *Selenothrips rubrocinctus* on the cashew *Anacardium occidentale* (Fennah, 1963). This repeated pattern of linear punctures extends to the Late Permian of South Africa, expressed by Damage Type 138 (Labandeira et al., 2007, p. 10), which occurs along the intersection of midrib and blade for particular glossopterid foliage. An alternative explanation for the occurrence of these multiple probes on Permian spores is related to ingestion limitations based on spore protoplast volumes that would exceed a single feeding event. Such a hypothesis remains untested because the body size and digestive tract volume of the hypothetical feeding insect remains unknown.

Punch and sucking has originated independently multiple times among small microarthropods. In addition to Thysanoptera, punch-and-suckers presently include members of forcipine biting midges (Diptera: Ceratopogonidae) that similarly have robust piercing mouthparts (Downes, 1955; Labandeira, 2005). As well, piercing-and-sucking may occur among members of primitively entognathan insects such as the Protura and some springtails (Schaller and Wolter, 1963; François, 1969), and in certain small beetles such as the Leiodidae, Eucinetidae and Cerylonidae (Besuchet, 1972; Vit, 1981; Pakaluk, 1987). These assemblages of taxa have developed gracile, multistylate, piercing-and-sucking mouthparts for consumption of fungal hyphae, algal filaments and plant cells, and are known to ingest intact spores and pollen grains (Labandeira, 1997), but have not been suspected of consuming pollen protoplasts through punch-and-sucking. Primitively entognathous insects are both known from the terrestrial Paleozoic (Riek, 1976; Greenslade, 1986), and Protura and probably piercing-and-sucking springtails were present during the Permian; however, it is not clear that the mouthparts of any members of these groups were capable of punch-and-sucking. In addition, the presence of a circular hole, with beveled edges on the surface of the lycopod megaspore *Setisisporites* sp. (Scott et al., 1992), has been recorded during the Middle Pennsylvanian, preceding the earliest occurrence of the basal thysanopteran clade, Lophioneuridae, by ~30 My, suggesting damage inflicted by another insect group, probably a piercing-and-sucking paleodictyopteroid with truncate stylate mouthparts. By contrast, from what is known of beetle phylogeny and their Permian fossil record, the occurrence of *Circulipuncturites discinisporis* damage antedates considerably the inferred earliest occurrences of beetle culprits that could have produced similar spore damage.

The most likely culprit is the Lophioneuridae, an immediate, ancestral clade of the Thysanoptera, or possibly a closely related stem-group or early paraphyletic lineage (Zherikhin, 2000; Grimaldi et al., 2004; Grimaldi and Engel, 2005; Labandeira, 2006). The Lophioneuridae bore a mouthcone housing relatively symmetrical mandibular and maxillary stylets and bearing typical maxillary and labial palps (Vishniakova, 1981); judging from mouthpart structure, punch-and-suck feeding was likely. The earliest lophioneurid occurrence is *Cyphoneurodes patriciae* Beckemeyer from the Early Permian (Artinskian) Wellington Formation of Elmo, Kansas (Beckemeyer, 2004), after which they are variably represented elements in later Permian and Triassic deposits (Plate II, Figs. 2, 3; Becker-Migdisova et al., 1991; Grimaldi et al., 2004), becoming rare thereafter, and achieving relict status into the mid Cretaceous. The last known, surviving taxon is *Burmacypha longicornis* Zherikhin from the Early Cretaceous (late Albian) from Burmese amber in northern Myanmar (Zherikhin, 2000).

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