Thrips pollination of Mesozoic gymnosperms

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Within modern gymnosperms, conifers and *Ginkgo* are exclusively wind pollinated whereas many gnetaleans and cycads are insect pollinated. For cycads, thrips are specialized pollinators. We report such a specialized pollination mode from Early Cretaceous amber of Spain, wherein four female thrips representing a genus and two species in the family Melanthripidae were covered by abundant *Cycadopites* pollen grains. These females bear unique ring setae interpreted as specialized structures for pollen grain collection, functionally equivalent to the hook-tipped sensilla and plumose setae on the bodies of bees. The most parsimonious explanation for this structure is parental food provisioning for larvae, indicating subsociality. This association provides direct evidence of specialized collection and transportation of pollen grains and likely gymnosperm pollination by 110–105 million years ago, possibly considerably earlier.

paleoecology | paleoethology | coevolution | plant–insect interactions

Mid-Mesozoic gymnosperms are a globally diverse assemblage of seed plants of which only four lineages persist today. Of these, about 600 species of conifers and the sole surviving ginkgophyte species, *Ginkgo biloba*, are obligately wind pollinated (1). By contrast, many of the about 100 gnetophyte species and somewhat over 300 species of cycads are insect pollinated (2, 3). Recent examination has documented the prominent, often obligate, insect mutualisms occurring among these two, latter gymnosperm clades (1–3) and the rarity of wind pollination (2, 4–6). For gnetophytes, a broad spectrum of small-sized, inconspicuous insects are pollinators, especially flies, but also moths, beetles, small wasps, thrips, and occasionally bees (2, 5, 6). Cycads are pollinated by equally specialized but, overall, more taxonomically circumscribed beetle lineages, especially weevils (3, 4), and a lineage of thrips (7–9). Occasionally, both insect groups pollinate the same cycad species (7, 8). Even so, Mesozoic evidence for insect pollination of gymnosperms has been sparse and indirect (1, 10–12), although the remaining seed-plant group, angiosperms, has received considerable support for pollination during the Late Cretaceous and Cenozoic (1, 13–16). Here, we report on four female thrips found in four pieces of Early Cretaceous (Albian) amber from Spain (*SI Text*), bearing abundant gymnospermous pollen associated with specialized body structures (Figs. 1 and 2). This unique gymnosperm–thrips association provides a distinctive pollination mode during the mid-Mesozoic that includes a specialized structure for collecting pollen, suggesting subsocial behavior and extending the breadth of nonangiospermous pollination mutualisms.

Thrips are minute, diverse insects that feed on pollen grains, plant tissues, fungi, and small arthropods (9, 17, 18), also known for their stereotyped punch-and-suck feeding style for extracting protoplasts from a variety of cell types and pollen grains (19). Historically, discussion of thrips as pollinators has been controversial, because these minute insects do not fit the general profile of an effective pollinator (9, 17, 18), although they now are documented as pollinators of basal angiosperms (15, 20) and eudicots such as dipterocarps (18). Individuals transport from several to a few hundred pollen grains to flowers (18) or cones (Table S1); for example, *Cycadothrips chadwicki* can deliver up to 5,700 pollen grains per ovule to *Macrozamia communis* cycad cones in an afternoon (8). Several species of *Cycadothrips* are efficient pollinators of endemic Australian *Macrozamia* cycads (7, 8, 21). Besides pollination of gnetaleans and cycads, thrips species are collected from male cones of conifers and are implicated in pollen feeding (22) but without effective pollination. No thrips or other insect ever has been reported as transferring pollen to modern, obligately wind-pollinated *Ginkgo biloba* (1).

Systematic Paleontology

The systematic paleontology is as follows: Insecta Linnaeus, 1758; Thysanoptera Haliday, 1836; Melanthripidae Bagnall, 1913; *Gymnopollisthrips* Peñalver, Nel & Nel gen. nov.; *Gymnopollisthrips minor* Peñalver, Nel & Nel gen. et sp. nov. (type species of genus, here designated); *Gymnopollisthrips maior* Peñalver, Nel & Nel sp. nov.

Etymology. The generic name is a combination of *Gymno*, referring to the gymnosperm origin of the vectored grains (Greek); *pollis* (Latin, meaning pollen); and *thrips* (Greek, meaning "woodworm"), which is a common suffix for thysanopteran genera and is of neutral gender. The specific epithets *minor* and *maior* (Latin) mean smaller and larger in size, respectively.

Diagnosis (Females). Specialized setae with small seriate rings that are regularly spaced along their length (ring setae) are distributed in a bilaterally symmetrical manner on certain body regions. Antennae are nine-segmented. Antennal segment II is asymmetrical with a small prolongation at the ventro-lateral apex. Antennal segments III and IV each have one rounded and large apical plate-like sensory area in lateral-external position. Antennal segments VI to IX are clearly distinct from each other. The head has ocellar setae I arising on a conical tubercle. The forewing is not falcate, but broad, slightly narrowed at the apex, with two complete, main longitudinal veins and five crossveins; the anterior fringe is short, and the posterior fringe is straight. The apex of the abdomen is elongated, not rounded. Abdominal

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Data deposition: The data and procedures reported in this paper corresponding to the scan parameters, reconstructed slices, 3D volume extraction, and resulting movie of the holotype specimen of *Gymnopollisthrips minor* are available online at the Paleontological Online Database of the European Synchrotron Radiation Facility, http://paleo.esrf.eu (amber inclusions and Spain sections).

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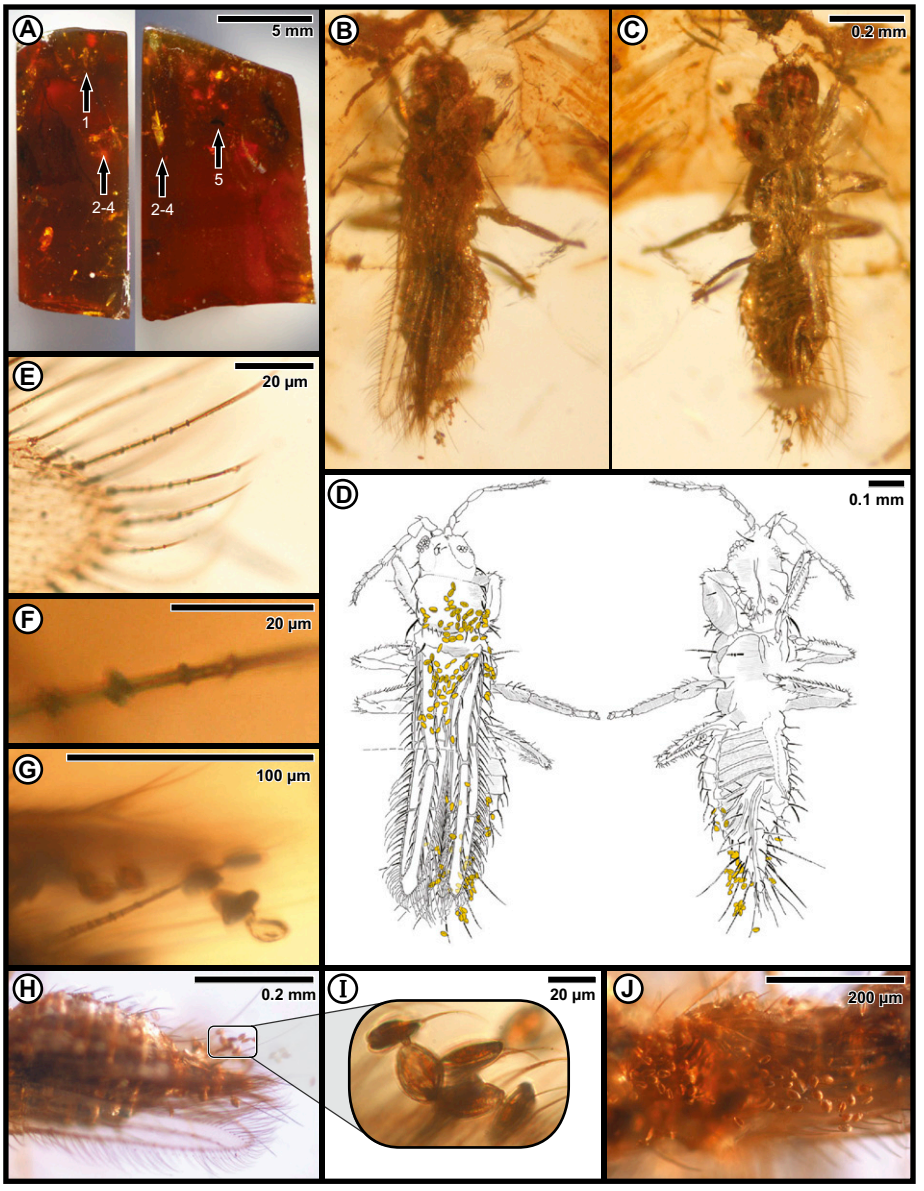

Fig. 1. Mesozoic pollinator association between a gymnosperm host plant and an insect pollinator from the Early Cretaceous of Spain. (*A*) Amber piece containing six specimens of the thrips genus *Gymnopollisthrips* (Thysanoptera: Melanthripidae), five of which are indicated by arrows (MCNA-9516). (*B*) Photographic image of *G. minor* with attached *Cycadopites*-type pollen grains (holotype MCNA-10731, intact female) in dorsal aspect. (*C*) Photographic image of *G. minor* and associated pollen in ventral aspect (same scale as *B*). (*D*) Camera lucida drawings of *G. minor*, based on *B* and *C* above. Wings in ventral view have been omitted for clarity; *Cycadopites* type pollen grains are indicated in orange. (*E*) Specialized ring setae of the distal forewing of *G. minor*. (*F*) Magnified ring seta from *E*, showing four rings. (*G*) Prominent ring seta of the distal abdomen of *G. minor*, showing the adherence of 12 clumped pollen grains of *Cycadopites*. (*H*) Detail of mostly clumped pollen grains from wing setae of *G. minor*. (*I*) Enlargement of grains in a clump of pollen attached to wing setae indicated in *H* at left. (*J*) Detail of *Cycadopites* type pollen grains on the dorsal surface of *G. minor* in *B* above.

segments IX and X have very long setae. Sclerotized ovipositor is upwardly curved.

G. minor Peñalver, Nel & Nel gen. et sp. nov

See Figs. 1 *B–D* and *H–J* and 2*I* and Movie S1.

Holotype. MCNA-10731 and paratype MCNA-9472, housed at the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain, are both complete females with pollen loads (*ca*. 140 and *ca*. 15 grains, respectively). The holotype was imaged by synchrotron holotomography to better study the pollen distribution (Movie S1).

Locality and Age. The specimens were collected from the Albian Peñacerrada I amber site, Escucha Formation, eastern area of the Basque–Cantabrian Basin, northern Spain (*SI Text*).

Diagnosis. As for the genus, additional characteristics include the following: plate-like sensory areas on antennal segments III and IV are longitudinally elongated and cover approximately half of the segment length. The pronotum is slightly rectangular, bearing two pairs of lateral setae. The forewing has *ca*. 18 setae on anterior longitudinal vein and *ca*. 16 setae on posterior longitudinal vein.

G. maior Peñalver, Nel & Nel sp. nov

See Fig. 2*A* and Figs. S1–S3.

Holotype. Specimen MCNA-9283, housed at the Museo de Ciencias Naturales de Álava, Vitoria–Gasteiz, Spain, is a complete female carrying *ca*. 137 pollen grains.

Locality and Age. Locality and age of *G. maior* are the same as those of *G. minor*.

Diagnosis. *G. maior* differs from *G. minor* by less setose antennae, strong setae on the dorsal side of the head, four pairs of lateral setae on a subcircular pronotum, a forewing with *ca*. 24 setae on anterior longitudinal vein and *ca*. 21 setae on posterior longitudinal vein, and plate-like sensory areas on antennal segments III and IV covering a third of the segment length. The area on segment III is longer than wide vs. wider than long on segment IV. In addition, *G. maior* is larger by one-third.

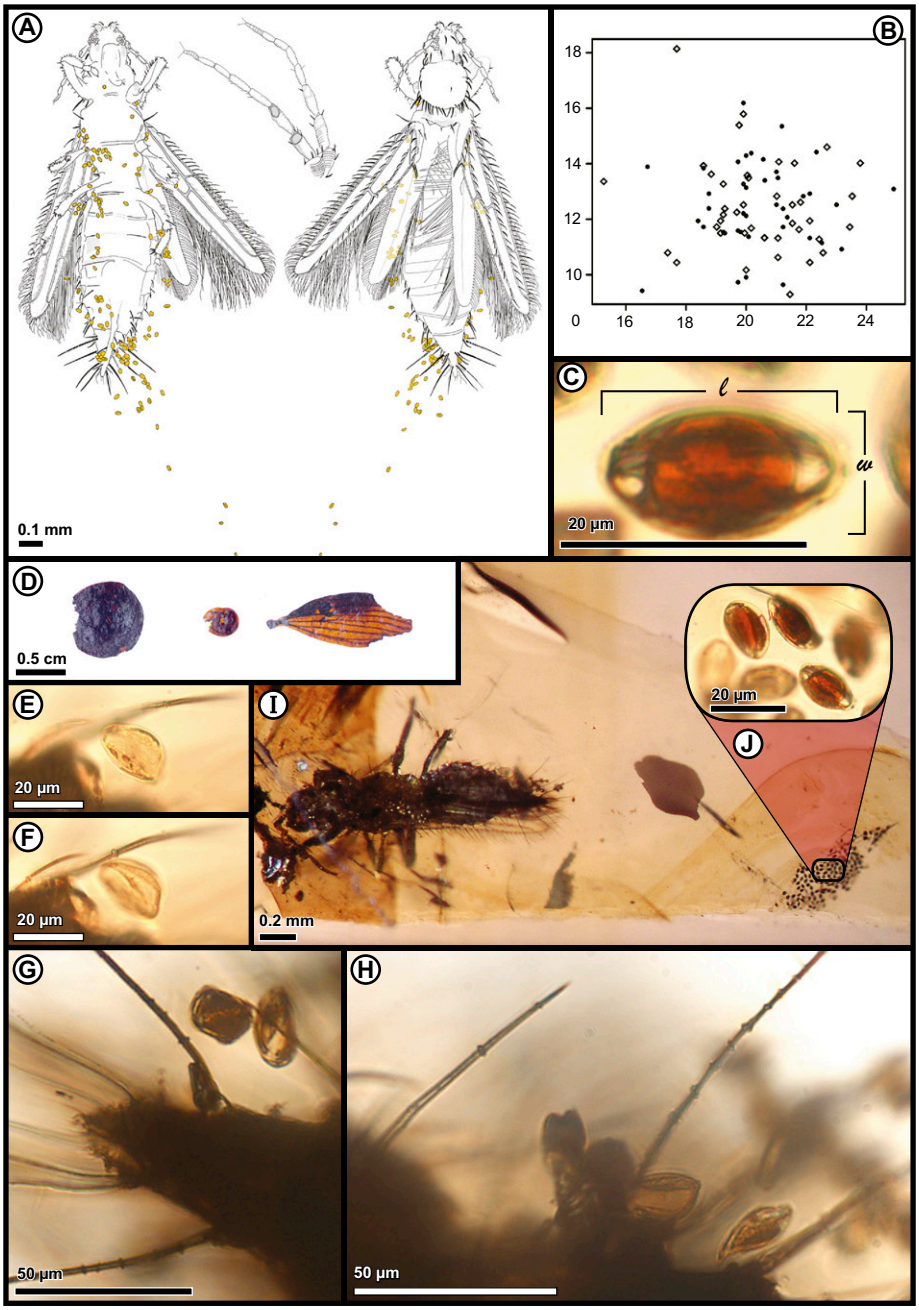

Fig. 2. Features of thrips and gymnosperm remains. (*A*) Camera lucida drawings of *Gymnopollisthrips maior* and detail of antennae showing the planated sensory structures on segments III to IV (segment III plus IV 130 µm in length); *Cycadopites*-type pollen grains are indicated in orange (holotype MCNA-9283, intact female). (*B*) Length (horizontal axis) and width (vertical axis) measurements in microns of pollen grains from *G. minor* (black circle) and *G. maior* (white square). Measurement scheme is provided in *C* below; data are available in Table S2. (*C*) Length (*l*) and width (*w*) measurements taken on pollen grains displayed in *B* above. (*D*) Two macerated ovulate organs of *cf Nehvizdyella* sp. and leaf of *Eretmophyllum* sp. from Spanish Albian deposits of amber. (*E*) Pollen grain attached to the base of a specialized ring seta of the abdominal margin of *G. minor*. (*F*) The same seta and pollen grain in *E* above but at a lower focal level, showing pollen grain margin attached to setal ring. (*G*) Pollen grain attached to the base of an abdominal ring seta. (*H*) Three abdominal ring setae, two with attached pollen grains at their bases. (*I*) Accumulation of *ca*. 150 *Cycadopites*-type pollen grains adjacent to a thrips, possibly attributable to falling pollen being concentrated in viscous resin. (*J*) Enlargement of several grains from cluster at *I*. *E*–*I* are from the holotype of *G. minor*.

Systematic Placement of the Genus

This genus (see *SI Text* for description of the subordinate species and detailed systematic placement) is attributable to the Aeolothripidae–Melanthripidae–Merothripidae group of families, supported by the wing venational synapomorphy: "capture of M by RP and the formation of a combined RP+M" (23). Attribution to the family Melanthripidae is supported by the presence of a projection in the anterior part of the vertex where ocellar setae I are situated, as in the genus *Ankothrips* (24), one of the four extant genera recognized within this family. *Ankothrips* also is characterized by the apex of antennal segment II ventro-laterally prolonged into a lobe, although this is weakly developed in some specimens. This character is present in the fossils as a pronounced asymmetry of segment II with a more developed ventro-lateral apex; however, it is shorter than in *Ankothrips*. Moreover, extant *Ankothrips* species frequently bear enlargement of plate-like sensoria on antennal segments III and IV, which is not as broad as in the fossils. Melanthripids appear phytophagous, feeding and breeding within flowers, and the pattern of host exploitation typically involves monophagy by most members (25). The twelve species of *Ankothrips* are from western United States, southwestern Africa, and Europe; monophagous host relationships seem to exist for some taxa, but one is common on *Yucca whipplei* (Agavaceae), another one on *Adenostema fasciculata* (Rosaceae) flowers, and the four European species are associated with the mature reproductive tissues of the conifers *Juniperus* and *Cupressus* (24).

Discussion

The female fossil specimens transported large quantities of pollen grains, similar to extant species of *Cycadothrips* but considerably more than loads borne by most angiosperm-pollinating

thrips (18) (Table S1). These data indicate that *Gymnopollisthrips* was an efficient transporter of pollen grains. The ability of thrips to carry pollen grains would depend on the stickiness of the grains (26) and the number and structure of their setae (18). *Gymnopollisthrips* has abundant, long, specialized setae containing seriate rings as a distinctive structural feature (*SI Text*). These setae are located only on external, protruding body parts and wing apices, which often exhibit attached single and clusters of pollen particularly at their bases (Fig. 2 *E–H*). We interpret ring setae as a unique structural modification of *Gymnopollisthrips* to increase the scope of thrips for attachment of pollen grains. That interpretation is based principally on their exclusive location on external, protruding parts of the body, with the higher surface area provided by the rings and the abundance and clumped nature of captured pollen grains. Indeed, thrips ring setae were a specialized structure for collecting pollen grains, unknown in modern insect species. Accordingly, pollen grains could be trapped passively or actively using stereotyped movements, although compelling evidence is not available. In addition, there are pollen grains concentrated on the dorsal or ventral regions of the body (Figs. 1 *B–D* and *H–J* and 2*A*). This distribution is consistent with initial attachment of pollen grains along the setae, followed by active relocation using the legs for better pollen transport that would prevent detachment during flight (*SI Text*). Remaining pollen on ring setae would represent less accessible grains and grain clumps.

Pollen grains associated with the thrips are monosulcate, psilate in ornamentation, prolate to suboblate in shape, and minute in size (average 20.4 μm long and 12.6 μm wide). Each grain shows acute to rounded polar margins and generally an elongate-oval external sulcus for the entire length of the grain. Often the sulcus is wider at its ends and constricted toward the equatorial area where its margins may overlap. The sulcus margin is simple but sometimes folded. The exine is on average 1.3 μm thick. The pollen grains belong to the gymnosperm form-genus *Cycadopites* and, in general, has a slightly smaller size than Jurassic and Cretaceous specimens of the genus, such as *C. follicularis*, *C. durhamensis*, and principally *C. fragilis* (*SI Text*).

Evidence strongly supports a ginkgoalean or possibly cycad as the source of the *Cycadopites* pollen on *Gymnopollisthrips*. These two affiliations are based mostly on: (*i*) macrofloral abundance and the taphonomic context of *Eretmophyllum* (Fig. 2*D*) in relevant, Albian Spanish amber outcrops, indicating a ginkgoalean assignment; and (*ii*) some pollen structural features that suggest a cycadalean affinity (Fig. 2*C* and *SI Text*). Ginkgoaleans and cycads are dioecious, having separate male and female organs, often on different individuals.

Apart from the abundance of pollen grains of the same morphotype on thrips bodies and the presence of specialized setae (*SI Text*), these grains show features consistent with insect pollination. Stickiness, minute size, and clumping suggest an insect pollination system based on correlates with extant insect-pollinated seed plants (15, 26–28). These pollen features have been associated with insect pollination in ancient angiosperms (16, 29). Intergrain stickiness evidently caused the observed clumping, suggesting that a pollenkitt-like substance was present on the pollen surface, analogous to some extant cycads, which are pollinated by both insects and aerial transfer (28). Extant gymnosperms lack adhesive surface compounds or other clumping-induced structures (26), indicating that modern gymnosperms may be poor analogs for the variety of reproductive modes during the Cretaceous (11). Nevertheless, several basal lineages of Early Cretaceous angiosperms apparently were pollinated by insects vectoring clumped pollen (15, 16, 29).

We infer that a *Gymnopollisthrips*–gymnosperm active pollination mutualism was present at Peñacerrada I, also based on analogous, similar pollen grains occurring in several extant *Cycadothrips–Macrozamia* mutualisms from Australia, and on the small size and the lack of *Cycadopites* in the amber-bearing sediment consistent with gymnospermous entomophilous pollen (7, 8). Additionally, pollen grains identical in structure and size (Fig. 2 *B* and *C* and Tables S2 and S3) were transported by both species of *Gymnopollisthrips*, suggesting that these taxa were accessing the same gymnosperm species or minimally the same host genus, implicating possible monophagy. The uniquely specialized ring setae of female *Gymnopollisthrips* would have afforded better fitness for the initial collection and secondary transport of pollen, evidently functionally equivalent to the hook-tipped sensilla and plumose setae on bee bodies (30) used by females to capture and vector distant pollen grains for larval food provision.

The value of ring setae would have operated under multiple selective regimes. The inferred active transportation of pollen grains could be explained as parental food provisioning for larvae, which perhaps promoted subsocial colony formation (31). The identified insect pollinator belongs to a distinct genus of the family Melanthripidae, an extant clade of the order Thysanoptera. Modern thrips show varied behaviors that can include parental care ranging from solitary to gregarious, colonial, subsocial, and eusocial habits, the last of which can exhibit morphologically and behaviorally specialized individuals into castes (31–33). Scarce but direct evidence of parental care/eusociality in insects has been reported only in Cenozoic ambers, principally ants, but never in Cretaceous amber, possibly attributable to preservational limitations. In contrast, these behaviors have been widely inferred from structural proxy characters.

The hypothesized presence of subsocial behavior, reinforced by parental care, has not been found in extant Melanthripidae. By comparison, some modern thrips species are subsocial (31, 32) whereas others, especially some Phlaeothripidae, are eusocial with all life-stages congregating, such as in gall chambers (33). Although the microhabitat of *Gymnopollisthrips* larvae remain uncertain, sites amid host-plant interstices seem most reasonable. Ginkgoalean pollen organs generally lack protection for larvae, albeit their ovulate organs and associated vegetative structures would provide concealed enclosures for larval development. A pollination system in which there was transport of pollen by a female thrips that ended in larval feeding on an ovulate cone is more consistent with a ginkgoalean rather than a cycad host, in which the larvae would have fed directly on the male cones. In addition, ovulate reproductive organs assigned to the form-genus *Nehvizdyella* (Fig. 2*D*), affiliated with *Eretmophyllum* foliage, are common in several Early Cretaceous Spanish amber deposits (*SI Text*). This proposed system differs from recent *Cycadothrips* and *Macrozamia* mutualisms, including taxa inferred to have diversified during the later Miocene (34). The differences include absence of a specialized structure in *Cycadothrips* to attach pollen grains and the pattern of adults and larvae inhabiting principally pollen cones that eventually emit a strong, repugnant odor inducing individuals to leave the male plant and visit the ovulate cone. This timed "push" of pollen cones overlaps with the "pull" of ovulate cones causing short-distance flights that result in pollination (21).

The *Gymnopollisthrips*–gymnosperm mutualism occurred toward the end of the third phase of the plant–insect associational fossil record (1), established in the wake of the end Permian extinction and replaced by the mid-Cretaceous angiosperm ecological expansion (13). Our discovery shows that within this interval, some thrips lineages may have been among the "primeval pollinators" (9). This antiquity of thrips as pollinators (9) has been based on recent cycad-pollinating *Cycadothrips* as a member of a basal or otherwise early-appearing thysanopteran clade (35). This issue merits further investigation for several reasons. Firstly, the phylogeny of major thrips clades related to *Cycadothrips* remains unresolved. Secondly, it may be premature to extend phylogenetic inference (36, 37) from the biology of recent *Cycadothrips* (7, 8) to taxa of Mesozoic thrips (38–40). Current evidence indicates that *Cycadothrips* may have acquired plant associational attributes with *Macrozamia* host species relatively

recently (34). Thirdly, the three extant species of *Cycadothrips* live only on species of the Australian genus *Macrozamia*. A relationship between *Macrozamia* and the *Lepidozamia–Encephalartos* sister clade would suggest a 200–135 Ma (largely Jurassic) age for the "*Macrozamia*" lineage (41). The oldest documented fossils of this cycad genus are from the Paleogene of Australia (42), suggesting a latter diversification and possibly a rather recent age for *Cycadothrips* as well (34). Lastly, the abundance and diversity of other cycad hosts, some representing ancient Mesozoic lineages, lack pollinating thrips, consistent with a recent, Australian origin for the *Cycadothrips–Macrozamia* association. These considerations indicate that major biological differences exist between the gymnosperm–*Gymnopollisthrips* and the cycad–*Cycadothrips* mutualisms, and ecologically uniformitarian extensions from the recent to the Mesozoic are premature.

Nevertheless, the Thysanoptera is a likely ancient group of gymnosperm pollen feeders, indicated by the possible consumption of Late Permian noeggerathialean spores by representatives of the stem-group Thripida (43) and subsequent pollinator associations that evolved with two or three, major, seed-plant clades. These associations are as follows: (*i*) between angiosperms and principally thripids (plus possibly Melanthripidae on gymnosperms and angiosperms) that presumably commenced during the Early Cretaceous angiosperm radiation (15, 20); (*ii*) between modern cycads and *Cycadothrips* (7, 8) that may have mid-Cretaceous antecedents (38–40); and (*iii*) between Early Cretaceous ginkgoaleans or cycads and the fossil melanthripids reported herein (Fig. 3). Circumstantial evidence for mid-Cretaceous angiosperm–thrips associations includes early angiosperm floral structure consistent with thrips pollination (15, 18, 20), and the presence of the earliest known Thripidae and Phlaeothripidae (40), many members of which currently are angiosperm pollinators (17, 18) (Table S3). For earliest angiosperms, small insects such as thrips could have been pollinators of small, inconspicuous flowers dominated by the rewards of pollen and perhaps thermogenesis, volatile scents, but avoiding nectarial secretions, oils, and resins (5, 13, 20). Although it is uncertain whether additional seed plant–thrips associations other than the gymnosperm–melanthripid association were established during the Mesozoic, it is evident that several, modern thysanopteran genera associated with angiosperms were present by the Early Eocene (38). The ancient associations between gymnosperms and their insect pollinators were extinguished either through loss of their plant hosts or exist today on cycads, possibly as depauperate relicts. Our study also indicates that modern gymnosperms may be poor analogs for understanding the diversity of pollination modes in their Mesozoic relatives.

Methods

The specimen preparation, photography, and synchrotron imaging procedure followed the following steps. Amber initially was screened for inclusions, then embedded in a stable epoxide resin under vacuum, and finally ground and polished with a water-fed flat lap. Embedding stabilizes the amber, preventing oxidation and permitting an accurate viewing of the bioinclusion. Subsequently, photomicrography was performed with a digital camera attached to a stereomicroscope (Olympus BX51). Later specimens were drawn using a drawing tube Olympus U-DA attached to the stereomicroscope. One holotype specimen was imaged at the BM05 beamline of the European Synchrotron Radiation Facility at Grenoble, using propagation phase-contrast X-ray synchrotron microtomography. Procedure details are provided in *SI Text*.

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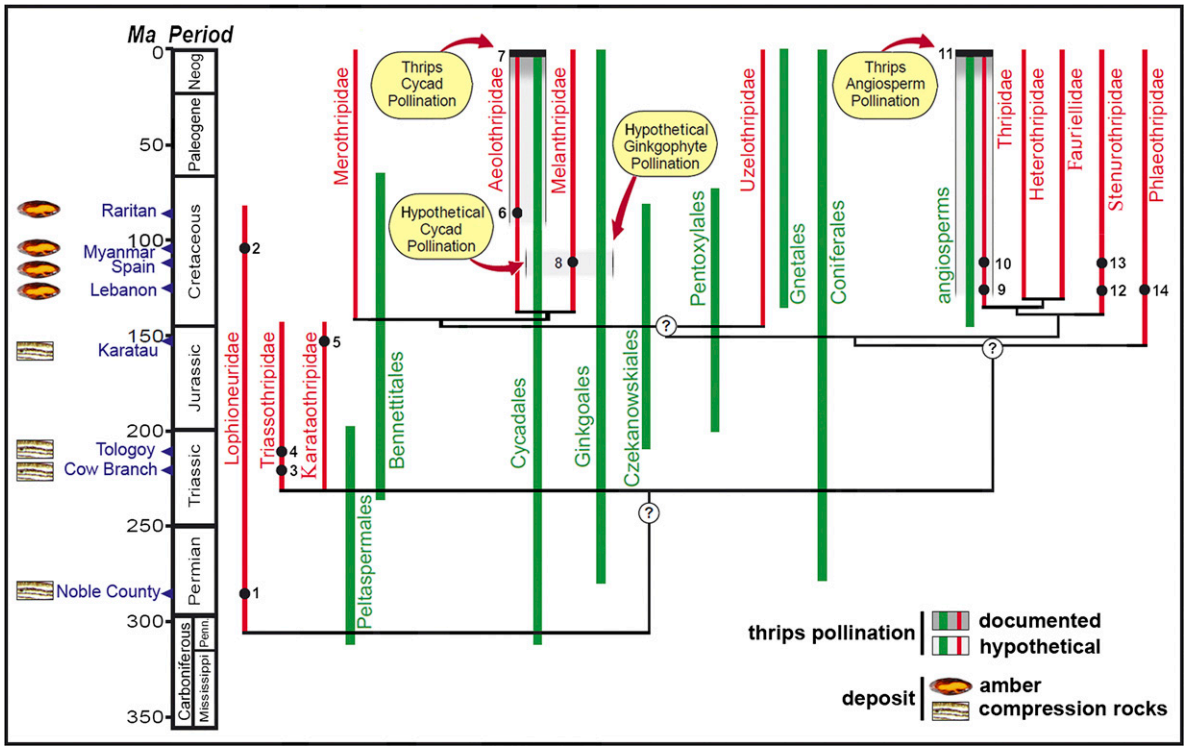

Fig. 3. Hypothesis of thysanopteran–seed plant pollinator relationships, indicating the colonization of cycads, angiosperms, and probable ginkgoaleans. The numbered fossil and modern occurrences of thrips taxa are as follows: 1, *Cyphoneurodes patriciae*; 2, *Burmacypha longicornis*; 3, *Triassothrips virginicus*; 4, *Kazachothrips triassicus*; 5, *Karataothrips jurassicus*; 6, *Cretothrips antiquus*; 7, extant *Cycadothrips chadwicki*; 8, *Gymnopollisthrips minor*, *G. maior*; 9, *Tethysthrips libanicus*; 10, *Tethysthrips hispanicus*; 11, several extant genera; 12, several occurrences in Lebanese amber; 13, *Hispanothrips utrillensis*; and 14, *Rohrthrips libanicus*. References and additional data supporting the numbered thrips fossil and modern occurrences, thysanopteran phylogeny, and the geological age of plant groups are provided in *SI Text*.

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1. Labandeira CC (2010) The pollination of Mid Mesozoic seed plants and the early history of long-proboscid insects. *Ann Mo Bot Gard* 97:469–513.
2. Wetsching W, Depisch B (1999) Pollination biology of *Welwitschia mirabilis* Hook. *Phyton* 39:167–183.
3. Schneider D, Wink M, Sporer F, Lounibos P (2002) Cycads: Their evolution, toxins, herbivores and insect pollinators. *Naturwissenschaften* 89:281–294.
4. Procheş Ş, Johnson SD (2009) Beetle pollination of the fruit-scented cones of the South African cycad *Stangeria eriopus*. *Am J Bot* 96:1722–1730.
5. Kato M, Inoue T (1994) Origin of insect pollination. *Nature* 368:195.
6. Meeuse ADJ, De Meijer AH, Mohr OWP, Wellinga SM (1990) Entomophily in the dioecious gymnosperm *Ephedra aphylla* Forsk. (=*E. alte* C.A. Mey.), with some notes on *Ephedra campylopoda* C.A. Mey. III: Further anthecological studies and relative importance of entomophily. *Isr J Bot* 39:113–123.
7. Mound LA, Terry I (2001) Thrips pollination of the Central Australian cycad, *Macrozamia macdonnellii* (Cycadales). *Int J Plant Sci* 162:147–154.
8. Terry I (2001) Thrips and weevils as dual, specialist pollinators of the Australian cycad *Macrozamia communis* (Zamiaceae). *Int J Plant Sci* 162:1293–1305.
9. Terry I (2002) *Thrips and Tospoviruses: Proceedings of the Seventh International Symposium on Thysanoptera*, eds Marullo R, Mound LA (Australian National Insect Collection, Canberra), pp 157–162.
10. Klavins SD, Kellogg DW, Krings M, Taylor EL, Taylor TN (2005) Coprolites in a Middle Triassic cycad pollen cone: Evidence for insect pollination in early cycads? *Evol Ecol Res* 7:479–488.
11. Labandeira CC, Kvaček J, Mostovski MB (2007) Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms. *Taxon* 56:663–695.
12. Ren D, et al. (2009) A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. *Science* 326:840–847.
13. Grimaldi D (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Ann Mo Bot Gard* 86:373–406.
14. Ramírez SR, Gravendeel B, Singer RB, Marshall CR, Pierce NE (2007) Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. *Nature* 448:1042–1045.
15. Friis ES, Crane PR, Pedersen KR (2011) *Early Flowers and Angiosperm Evolution* (Cambridge Univ Press, Cambridge, UK).
16. Hu S, Dilcher DL, Taylor DW (2012) *Evolution of Plant–Pollinator Relationships*, ed Patiny S (Cambridge Univ Press, Cambridge, UK), pp 165–236.
17. Kirk WDJ (1997) *Thrips As Crop Pests*, ed Lewis T (Commonwealth Agricultural Board International, Wallingford), pp 119–174.
18. Lewis T (1973) *Thrips, Their Biology, Ecology and Economic Importance* (Academic Press, New York).
19. Kirk WDJ (1984) Pollen-feeding in thrips (Insecta: Thysanoptera). *J Zool* 204:107–117.
20. Thien LB, Azuma S, Kawano S (2000) New perspectives on the pollination biology of basal angiosperms. *Int J Plant Sci* 161:225–235.
21. Terry I, Walter GH, Moore Ch, Roemer R, Hull C (2007) Odor-mediated push-pull pollination in cycads. *Science* 318:70.
22. Mound LA, Palmer JM (1990) Two new Thripidae (Thysanoptera) from the male flowers of *Araucaria* and *Casuarina* in Australia and Hawaii. *Entomol Mon Mag* 126: 1–7.
23. Nel P, et al. (2012) From carboniferous to recent: Wing venation enlightens evolution of thysanopteran lineage. *J Syst Palaeontol*, in press.
24. Bailey SF (1940) A review of the genus *Ankothrips* D.L. Crawford. *Pan-Pac Entomol* 16: 97–106.
25. Pereyra V, Mound LA (2009) Phylogenetic relationships within the genus *Cranothrips* (Thysanoptera, Melanthripidae) with consideration of host associations and disjunct distributions within the family. *Syst Entomol* 34:151–161.
26. Pacini E, Hesse M (2005) Pollenkitt—its composition, forms and function. *Flora* 200: 399–415.
27. Pacini E, Franchi GG, Ripaccioli M (1999) Ripe pollen structure and histochemistry of some gymnosperms. *Plant Syst Evol* 217:81–99.
28. Hall JA, Walter GH (2011) Does pollen aerodynamics correlate with pollination vector? Pollen settling velocity as a test for wind versus insect pollination among cycads (Gymnospermae: Cycadaceae: Zamiaceae). *Biol J Linn Soc Lond* 104:75–92.
29. Hu S, Dilcher DL, Jarzen DM, Taylor DW (2008) Early steps of angiosperm–pollinator coevolution. *Proc Natl Acad Sci USA* 195:240–245.
30. Thorp RW (2000) The collection of pollen by bees. *Plant Syst Evol* 222:211–223.
31. Moritz G (2002) *Thrips and Tospoviruses: Proceedings of the Seventh International Symposium on Thysanoptera*, eds Marullo R, Mound LA (Australian National Insect Collection, Canberra, Australia), pp 259–267.
32. Kiester AR, Strates E (1984) Social behaviour in a thrips from Panama. *J Nat Hist* 18: 303–314.
33. Morris DC, Mound LA, Schwarz MP, Crespi BJ (1999) Morphological phylogenetics of Australian gall-inducing thrips and their allies: The evolution of host-plant affiliations, domicile use and social behaviour. *Syst Entomol* 24:289–299.
34. Nagalingum NS, et al. (2011) Recent synchronous radiation of a living fossil. *Science* 334:796–769.
35. Mound LA, Morris DC (2007) The insect order Thysanoptera: Classification *versus* systematics. *Zootaxa* 1668:395–411.
36. Bryant HN, Russell AP (1992) The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philos Trans R Soc London Ser B* 337:405–418.
37. Nel A (1997) The probabilistic inference of unknown data in phylogenetic analysis. *Mém Mus Natl Hist Nat* 173:305–327.
38. Grimaldi DA, Shmakov A, Fraser N (2004) Mesozoic thrips and early evolution of the order Thysanoptera (Insecta). *J Paleontol* 78:941–952.
39. Shmakov AS (2008) The Jurassic thrips *Liassothrips crassipes* (Martynov, 1927) and its position in the system of the order Thysanoptera (Insecta). *Paleontol J* 42:47–52.
40. Nel P, Peñalver E, Azar D, Hodebert G, Nel A (2010) Modern thrips families Thripidae and Phlaeothripidae in Early Cretaceous amber (Insecta: Thysanoptera). *Ann Soc Entomol Fr* 46:154–163.
41. Chaw SM, Walters TW, Chang CC, Hu SH, Chen SH (2005) A phylogeny of cycads (Cycadales) inferred from chloroplast *matK* gene, *trnK* intron, and nuclear rDNA ITS region. *Mol Phylogenet Evol* 37:214–234.
42. Carpenter RJ (1991) *Macrozamia* from the early Tertiary of Tasmania and a study of the cuticles of extant species. *Aust Syst Bot* 4:433–444.
43. Wang J, Labandeira CC, Zhang G, Bek J, Pfefferkorn HW (2009) 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. *Rev Palaeobot Palynol* 156:277–282.