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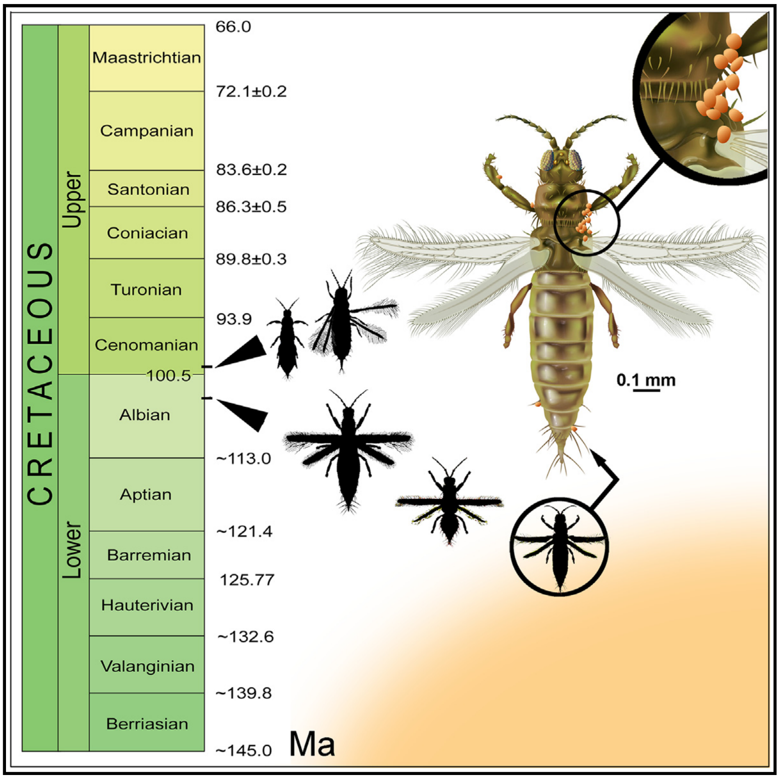
Diverse Mesozoic thrips carrying pollen during the gymnosperm-to-angiosperm plant-host ecological shift

Graphical abstract



Highlights

- New fossil thysanopteran insects identified as ancient pollinators of gymnosperms
- They belong to families which are pollinators of angiosperms in extant ecosystems
- Thysanopterans were diverse pollinators of gymnosperms during the Cretaceous
- These records are of the time of the gymnosperm-to-angiosperm plant-host shift

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In brief

Paleontology; Evolutionary processes; Evolutionary history

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Article

Diverse Mesozoic thrips carrying pollen during the gymnosperm-to-angiosperm plant-host ecological shift

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SUMMARY

Insects are important pollinators, and entomophilous pollination of gymnosperms occurred long before the Cretaceous radiation of angiosperms, but most extant pollination systems involve angiosperms. We studied four thrips of the extinct genus *Tethysthrips* present in Albian (Early Cretaceous) Spanish amber, one of which carried a patch of gymnosperm *Cycadopites* pollen grains, some of them attached around the mouthparts, providing direct fossil evidence of pollinivory and pollination. We describe the new species *Tethysthrips attenboroughi*, which belongs to the extant family Thripidae (suborder Terebrantia). In addition, we studied a *Cycadopites* pollen load in one specimen belonging to stem group Phlaeothripidae (suborder Tubulifera), from Cenomanian Burmese amber. This illustrates an ancient stage of gymnosperm plant host that most likely favored the later stage involving angiosperms. The absence of extant pollinators of gymnosperms in Thripidae and Phlaeothripidae, and in the terebrantian family Melanthripidae, which contain Cretaceous pollinators of gymnosperms, indicates impoverishment in their gymnosperm relationship.

INTRODUCTION

Plants and arthropods of the subphylum Hexapoda, which includes insects, represent two of the most diverse groups of organisms on Earth. They have been present together in terrestrial ecosystems at least since the Devonian. Remarkably, nearly 90% of angiosperm and approximately 40% of gymnosperm species rely on insect pollination for reproduction.[1] Insects play a key role in the survival of many plant species, facilitating fertilization and seed production.[2] It is noteworthy that even minute insects such as thrips (order Thysanoptera), many of which are pollen feeders, can make a substantial contribution to plant reproductive success.[3,4] The fossil record provides compelling evidence of insects serving as pollinators dating back to at least the Upper Jurassic period,[1] and possibly even considerably earlier if we consider indirect evidence.[5,6] Fossil deposits from the Permian have yielded evidence of insects that not only consumed pollen but also transported it.[7] Amber deposits offer direct and invaluable insights into ancient entomophily, preserving assemblages of insects and their pollen loads with remarkable detail. This exceptional preservation allows for the study of not only the preserved pollen loads but also the features of both the insects and the pollen grains. Some insect anatomical characteristics can be examined through functional morphology, while certain pollen grains exhibit characteristics indicative of entomophily, such as clumping due to their original stickiness.[8] Such well-preserved amber records date back to the Cretaceous period, specifically the Albian and Cenomanian stages. Essential to establish with confidence an intimate original relationship between the pollen grains and the insect body is a meticulous taphonomic analysis. To aid in the identification of fossil insect taxa associated with plant pollination, Peña-Kairath et al.[1] recently published a comprehensive review of this specific fossil record and outlined criteria for its analysis.

Any Cretaceous fossil that exhibits evidence of insect pollination is relevant to understanding the details of the complex gymnosperm-to-angiosperm plant-host shift.[1,9–11] That shift, along with its timing, remains an area of limited comprehension.[12] The oldest records of insects carrying angiosperm pollen loads have been documented in Cenomanian Burmese amber.[10,11,13]

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However, even older records in amber containing direct evidence of gymnosperm pollination exist, predating the aforementioned findings by several million years. These records include two thrips species, a dipteran species, and a coleopteran species, all preserved in Albian Spanish amber.[8,9,14] A comprehensive understanding of the historical pollination processes involving gymnosperms and angiosperms plays a pivotal role in unraveling key factors contributing to the emergence of modern terrestrial ecosystems and the diversification of insects and plants.[15,16]

Thrips are minute and diverse insects, exhibiting a varied diet that encompasses pollen grains (of both gymnosperms and angiosperms, being pollinators of a variety of species of these two plant groups), plant tissues, fungi, and even small arthropods.[17,18] Remarkably, approximately 50% of thrips species exclusively feed on fungi, with a preference for hyphae, and, to a lesser extent, spores.[19] They have left a notable presence in Cretaceous amber deposits, primarily of taxa belonging to the suborder Terebrantia.

In this context, we present findings from three Cretaceous amber pieces originating from Spain, which harbor four terebrantian thysanopteran conspecific specimens belonging to the extinct genus *Tethysthrips.* One of these specimens carried a pollen load of the form genus *Cycadopites*, providing evidence of a previously unknown ancient insect pollinator, also being evidence of a case of ancient pollinivory, involving gymnosperm plants, potentially from the Cycadales, Ginkgoales, or Bennettitales groups. Additionally, we consider a previously published tubuliferan thysanopteran specimen carrying a pollen load of the same form genus from Burmese amber within this study. The new discoveries highly increase the diversity of Cretaceous pollinator thrips, and the fossil record of pollinivory allows us to represent a broader scenario of the early steeps of the entomophily.

RESULTS

Order Thysanoptera Haliday, 1836
Suborder Terebrantia Haliday, 1836
Family Thripidae Stevens, 1829
Genus *Tethysthrips* P. Nel, Peñalver, Azar, Hodebert & A. Nel, 2010

Type species

Tethysthrips hispanicus P. Nel, Peñalver, Azar, Hodebert & A. Nel, 2010

Note: the only specimen of *T. hispanicus* was “stored provisionally at the Museo Geominero (IGME), Madrid, Spain” with the collection number ES-07-11.[20] However, it has now been moved to the permanent institutional collection of the El Soplao Cave (Government of Cantabria, Spain) with the definitive collection number CES 451.

Tethysthrips attenboroughi Peñalver, Peña-Kairath, P. Nel & A. Nel nov. sp.

Figures 1, 2, and S1–S5

LSID: urn:lsid:zoobank.org:act:C8B1B7CA-7808-4EED-B560-D9166B9B4E9B

Diagnosis (female)

Antennal segment IX not subdivided; three pairs of post-ocular setae; pronotum with ten pairs of posteromarginal setae and lacking lateral setae; forewing with at least 20 setae on anterior longitudinal vein and at least 15 setae on posterior longitudinal vein.

Material

Holotype MCNA 12629a (female) (Figures 1 and 2) showing a pollen load, as eusyninclusion (sensu Solórzano-Kraemer et al.[21]) with paratype MCNA 12629b (female) (Figures 2 and S1A), distance only 1 mm between them, from Peñacerrada I. Additional material (not paratypes): MCNA 13046 (Figure S1B), sex indeterminate, from Peñacerrada II and MCNA 9503 (Figure S1C), sex indeterminate, from Peñacerrada I.

Type locality

Peñacerrada I amber outcrop (Moraza locality), Lower Cretaceous (upper Albian), Utrillas Group, Basque-Cantabrian Basin, Spain.[22–24] Based on additional material, this species has been also found in Peñacerrada II amber outcrop (Peñacerrada locality) of the same age.

Etymology

The specific epithet honors Sir David Frederick Attenborough, British naturalist and presenter of exceptional British Broadcasting Corporation nature documentaries, due to his pioneer career in the protection of the nature via the dissemination of the magnificence of the biosphere.

Description

For detailed anatomical description, see Data S1: Description of the new species, related to Figure 1.

Remarks

The only two previously known records of the genus *Tethysthrips*[20] are from Lebanese amber (Hammana/Mdeirij locality) (*T. libanicus*) and Spanish amber (El Soplao locality) (*T. hispanicus*), dating to the late Barremian and mid Albian, respectively. The new record from the late Albian amber of Peñacerrada I represents its youngest known occurrence. This gives the genus a known range of approximately 128–101 million years, as it is apparently absent from the rich Burmese amber paleoentomofauna. See Data S2: Thrips taxonomical remarks, related to Figure 1.

The pollen grains

There are 65 visible pollen grains on the dorsal side of the thrips specimen, both attached to and detached from the body. Twelve additional grains are visible on the ventral side, hidden by the body in dorsal view, and all of these last grains are in contact with the body, some contacting setae (Figure 3A). A few grains are entangled between the fringe cilia (Figure 3C), and other two are in contact to the abdomen. Some clumping can be observed in the assemblage (Figures 2B and 3B). The detached pollen grains are close around the thrips body, forming a small cloud-like arrangement. The furthest of these grains is present approximately 0.5 mm away from the distal end of the abdomen.

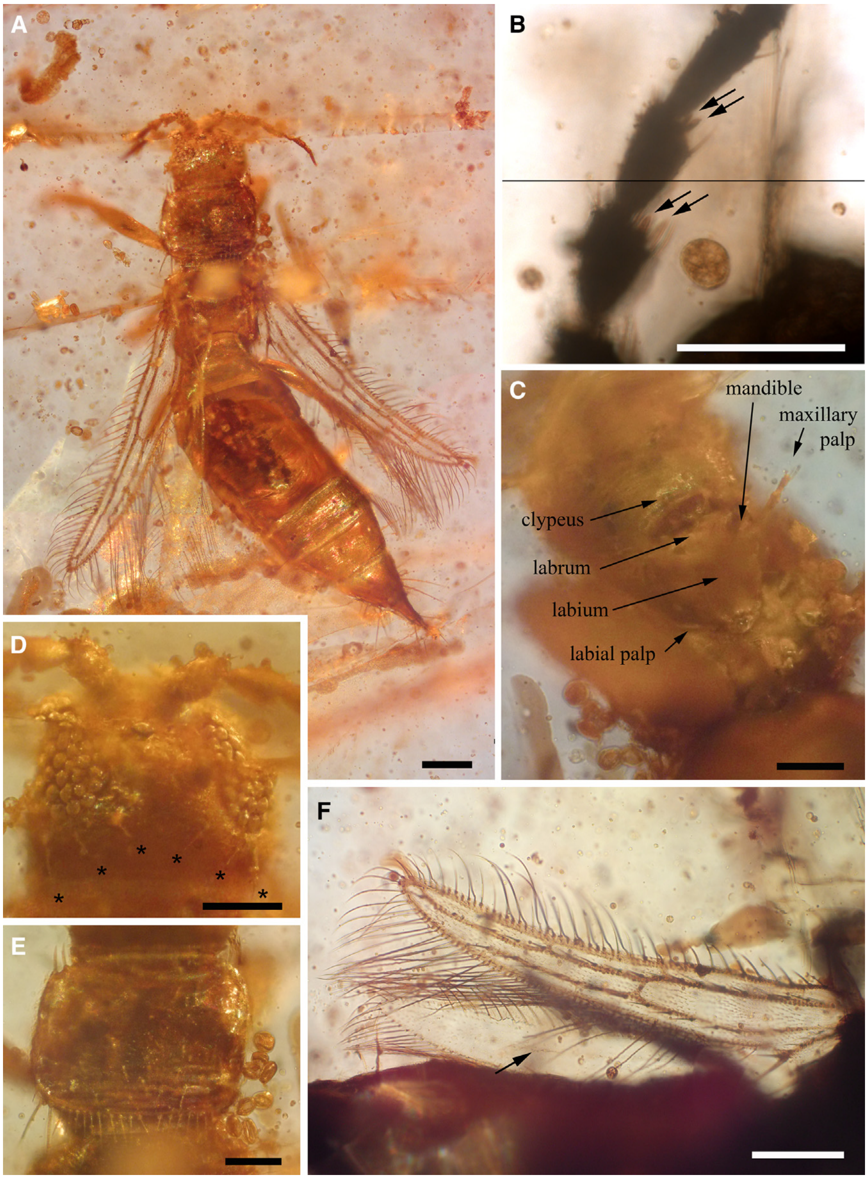

Figure 1. Anatomical features of holotype of *Tethysthrips attenboroughi* nov. sp. (Thripidae), Museo de Ciencias Naturales de Álava (MCNA) 12629a, female, in an amber fragment from upper Albian Peñacerrada I outcrop (Moraza, Burgos, Spain)

(A) Dorsal habitus.

(B) Antennal segments III and IV showing sensoria elongate and forked (pairs of arrows).

(C) Head in ventral view showing mouthparts and pollen grains attached; see camera lucida drawing in Figure 2D.

(D) Head in dorsal view showing three pairs of post-ocular setae (asterisks) and ommatidia.

(E) Chaetotaxy on pronotum and pollen grains attached to posteroangular setae (right).

(F) Right forewings and hind wings in ventral view (arrow indicates tenuous longitudinal vein of hind wing).

Scale bars 0.1 mm (A and F), 0.05 mm (B–E). All are image compositions (Photoshop CS2, version 9.0; www.adobe.com). See also Figures S3 and S4.

In addition to two grains attached to the distal abdomen and a few entangled within the fringe cilia, the majority of the pollen grains in contact with the body are densely concentrated on the pronotum, encompassing both the ventral and lateral surfaces, as well as the base of the head (Figures 1 and 2). The total number of pollen grains preserved in the assemblage is 77.

The pollen grains associated with *Tethysthrips* belong to the gymnosperm form genus *Cycadopites* Wodehouse emend. Fensome.[25] They are prolate to suboblate in shape and monosulcate, with a psilate exine surface (ca. 1 μm thick). They are small in size, averaging 24.0 μm long and 14.6 μm wide (n = 24), compared to species of pollen grains found in sedimentary rocks. In general, the grains have acute to rounded equatorial margins and elongate-oval sulci that extend their entire lengths (Figure 3).

Most of the pollen grains that are detached from the specimen's body have sulci that are wider at their ends and constricted toward the polar area, where their margins may overlap. In contrast, the grains that occur on the specimen have broad sulci at their midpoints (polar area). These differences are interpreted as result of two forms of grains from the same plant related to harmomegathy,[26] like in the pollen grains of the Jurassic species *Androstrobus balmei*.[27]

Additional evidence

We noted in the literature[28] a tubuliferan thrips of the stem group Phlaeothripidae with a load of pollen grains. We examined this remarkable specimen and found that it actually carried a pollen load as four clusters, three on the left antenna and one on left eye, of the gymnosperm form genus *Cycadopites* (total number of visible grains = 33) (Figures S6 and S7). The clumping of the grains in this case is very evident (Figure S7) but not noted in the original description of the thrips specimen. The ventral surface of the specimen is obscure, so it has not been possible to establish whether there is pollen on the mouth. The grains are small in size, averaging 22.6 μm long and 13.6 μm wide (n = 17).

DISCUSSION

The significance of the pollen loads

Our understanding of the biology of thrips families, especially the tubuliferan family Phlaeothripidae, remains limited.[19] This deficiency also extends to pollination activity, highlighting the lack of comprehensive knowledge about extant pollinator thrips

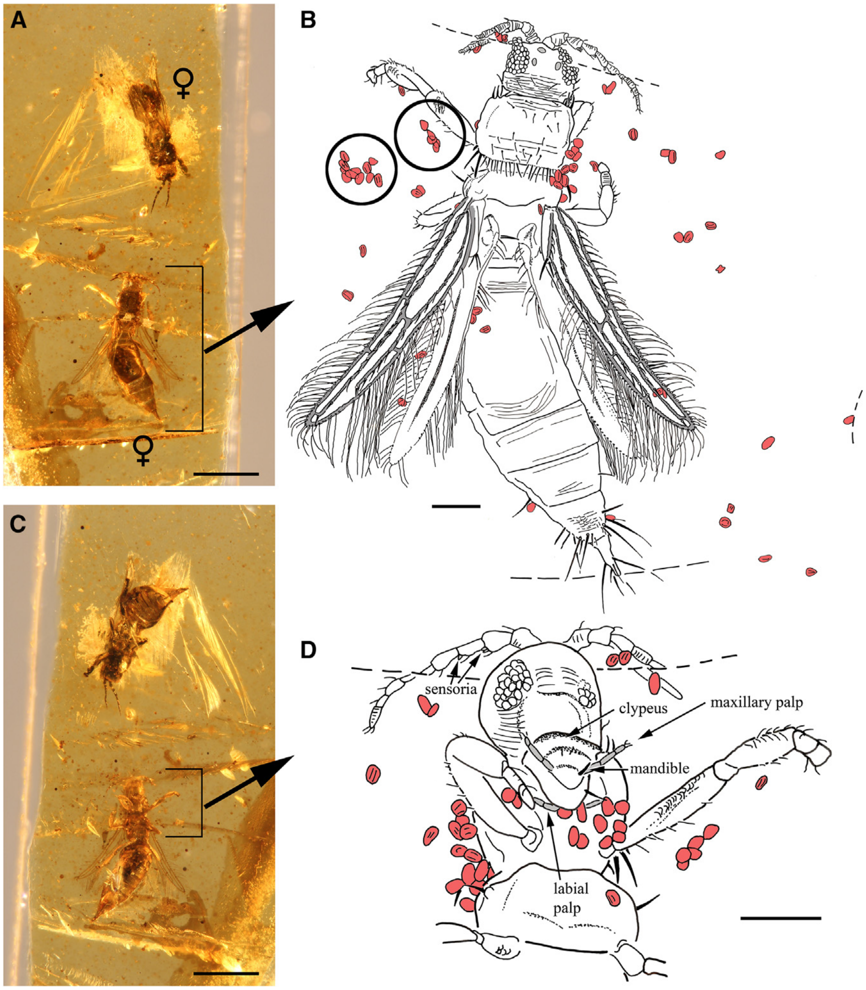

Figure 2. Holotype, MCNA 12629a, female, and paratype, MCNA 12629a, female, of *Tethysthrips attenboroughi* nov. sp. (Thripidae) in same amber fragment from upper Albian Peñacerrada I outcrop (Moraza, Burgos, Spain)

(A) Holotype and paratype in dorsal views.

(B) Drawing of holotype habitus with *Cycadopites* pollen grains (red colored) observed in dorsal view, some of them forming groups by contact (two main groups encircled) indicating clumping due to stickiness (forewing venations and margins gray colored).

(C) Holotype and paratype in ventral views.

(D) Drawing of holotype head and anterior part of thorax with *Cycadopites* pollen grains (red colored) observed in ventral view, several of them in contact or very close to mouthparts (antennal sensoria and palps gray colored).

Scale bars 0.5 mm (A and C), 0.1 mm (B and D). (A) and (C) are image compositions (Photoshop CS2, version 9.0; www.adobe.com).

species. Several factors have contributed to this knowledge gap, including the historical neglect of thrips in pollination studies.[19,29] Furthermore, there is ambiguity regarding which thrips families harbor definitive pollinator species.[30,31] Uncertainty persists in some cases regarding whether any thrips family comprises extant pollinator species for both angiosperms and gymnosperms. For example, while it is well documented that the family Thripidae includes extant pollinators of angiosperms,[3] certain occurrences of thripids in gymnosperm reproductive organs are challenging to interpret, including those described by Mound & Palmer,[32] which they considered as likely pollinivores. Based on the presently available data, we could consider that extant Aeolothripidae have species that pollinate gymnosperms (cycads), whereas Thripidae, Melanthripidae, and Phlaeothripidae pollinate angiosperms (see Table S3 in Wardhaugh[31] for Melanthripidae). The cases of Aeolothripidae and Thripidae are well documented, but caution is advised when considering the other two families, as future research may reveal interesting potential cases, including those involving gymnosperms.

Out of the six specimens belonging to the genus *Tethysthrips* that have been documented to date in diverse Cretaceous ambers, only one herein studied displays a pollen load, comprising a total of 77 grains of the form genus *Cycadopites*. These pollen grains may have derived from plant species within the Cycadales or Ginkgoales, among other gymnosperms as Bennettitales.[8,9] It is highly likely that all of the detached pollen grains in that individual were originally part of a single pollen patch. Remarkably, some of the attached grains are situated at a distance of 38 microns from the mandibles (Figures 1C and 2D). This observation suggests that these grains came into contact with the insect body during pollinivory[17] (Figure 4). Grimaldi et al.[11] previously described a similar record from Cenomanian Burmese amber, involving a stinging wasp and angiospermous pollen grains. Furthermore, Labandeira[33] has explained that pollen consumption was often the evolutionary precursor to pollination (see Figure 4).

The clumping of pollen grains within the assemblage (Figures 2B and 3B) remains apparent even after the immersion in resin and short displacement from the thrips body. This phenomenon strongly indicates the presence of a sticky substance on the pollen surfaces, resembling a pollenkitt-like substance. Pollenkitt is a sticky material that facilitates the adhesion of pollen grains to each other and to the bodies of pollinators. The clumping of pollen grains results in more effective pollination,[34] and the stickiness significantly enhances the thrips' capacity to transport pollen.[35] Clumping of pollen grains has been documented in Upper Cretaceous pollen grains associated with the basal angiosperm lineage of water lilies, such as *Praenymphaeapollenites cenomaniensis*, associated with pollinator nitiduloid beetles.[10] It appears that clumping has also been recorded in eudicot *Tricolporoidites*, which constitutes the pollen load of a stinging wasp (as seen in the mandible in Figure 2B of Grimaldi et al.[11]). Notably, both of these records were discovered in

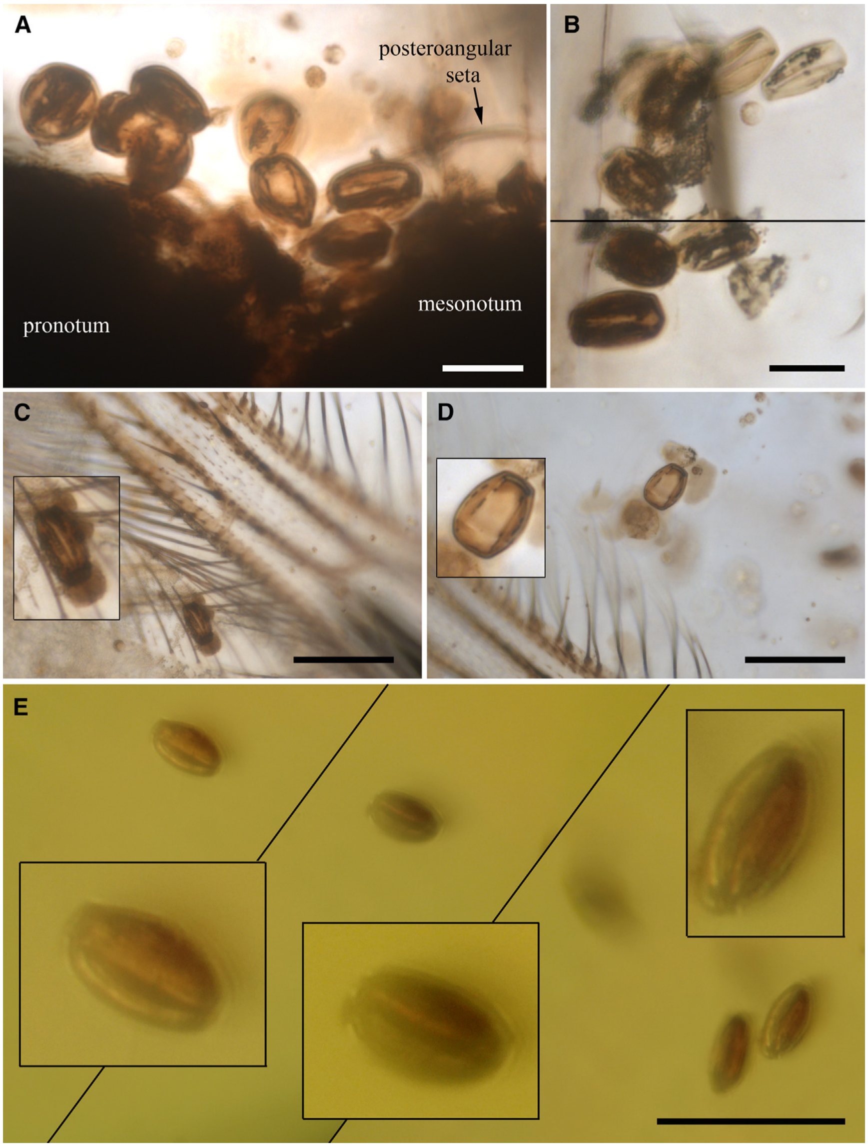

Figure 3. Load of *Cycadopites* pollen grains on or close to the *Tethysthrips attenboroughi* nov. sp. body, holotype (female), piece MCNA 12629, found in upper Albian Peñacerrada I amber (Moraza, Burgos, Spain)

(A) Cluster attached to thorax surface and to one of its posteroangular setae showing broad sulci at their equatorial areas.

(B) Detached cluster close body showing sulci wider at its ends and evidencing clumping due to stickiness.

(C) Prolate grain entangled between fringe cilia of wings with narrow, elongate sulcus.

(D) Detached, isolated pollen grain close to forewing with oval sulcus broad at equatorial area.

(E) Portion of a stele of detached pollen grains well-showing their 3-dimension morphology (insets with three selected grains enlarged).

Scale bars 20 μm (A and B), 50 μm (C–E). (B) and (E) are image compositions with thin black lines separating micrographs of the same view but taken at different focal planes (Photoshop CS2, version 9.0; www.adobe.com).

Cenomanian Burmese amber. The newly discovered instances of pollen clumping in pollen loads associated with both gymnosperms and angiosperms during the Albian and Cenomanian periods, respectively, carry evolutionary implications for entomophilous pollination.[34] Interestingly, pollenkitt has only been reported on angiosperm pollen grains in extant biota.[8,35] However, it is noteworthy that clumping has been described in a few gymnosperms, particularly in Cycadales.[36,37]

The stickiness, minute size (but a few extant entomophilous pollen grains are big), and clumping of the pollen grains strongly suggest a pollination relationship involving this extinct genus *Tethysthrips*. This case bears a striking resemblance to the inferred pollination cases involving the extinct genera *Gymnopollisthrips* and *Parallelothrips* (Figure 4). *Gymnopollisthrips* belongs to the family Melanthripidae[8] and was discovered in the same Albian amber locality as the *Tethysthrips* specimens from the family Thripidae. The genus *Parallelothrips* has been recently described as new in the extant family Stenurothripidae based on specimens preserved in Cenomanian Burmese amber.[38] Unlike *Gymnopollisthrips*, which exhibits anatomical specializations for transporting pollen grains to a colony—evidencing pollinivory in both adults and immatures—*Tethysthrips* and *Parallelothrips* lack any anatomical specializations related to pollen loads (Figure 4).

Ulitzka[28] described several new taxa in the fossil tubuliferan family Rohrthripidae, including the species *Paralleloalathrips bivenatus* based on four complete specimens from Burmese amber. However, the monophyly of Rohrthripidae is questionable, as there is no apomorphy to support the group as a clade. Therefore, we consider these Cretaceous amber tubuliferans as stem group Phlaeothripidae. According to Ulitzka, the paratype specimen MU-Fos-124/1 of *P. bivenatus* exhibits a spot of ca. 30 fungal spores,[28] mainly around the left antenna. However, after our observation under the optic microscope of this specimen, we reinterpret these palynomorphs as pollen grains of the gymnosperm form genus *Cycadopites* (Figures 4, S6, and S7).

Both the newly discovered fossil record within the Thripidae family and *Paralleloalathrips bivenatus* from the stem group Phlaeothripidae satisfy the criteria outlined by Peña-Kairath et al.[1] to be considered two additional insect groups at the family level with ancient pollinators: (1) "pollen attached to the body"; (2) "pollinator extant lineage," considering that extant Thripidae and Phlaeothripidae contain pollinators of

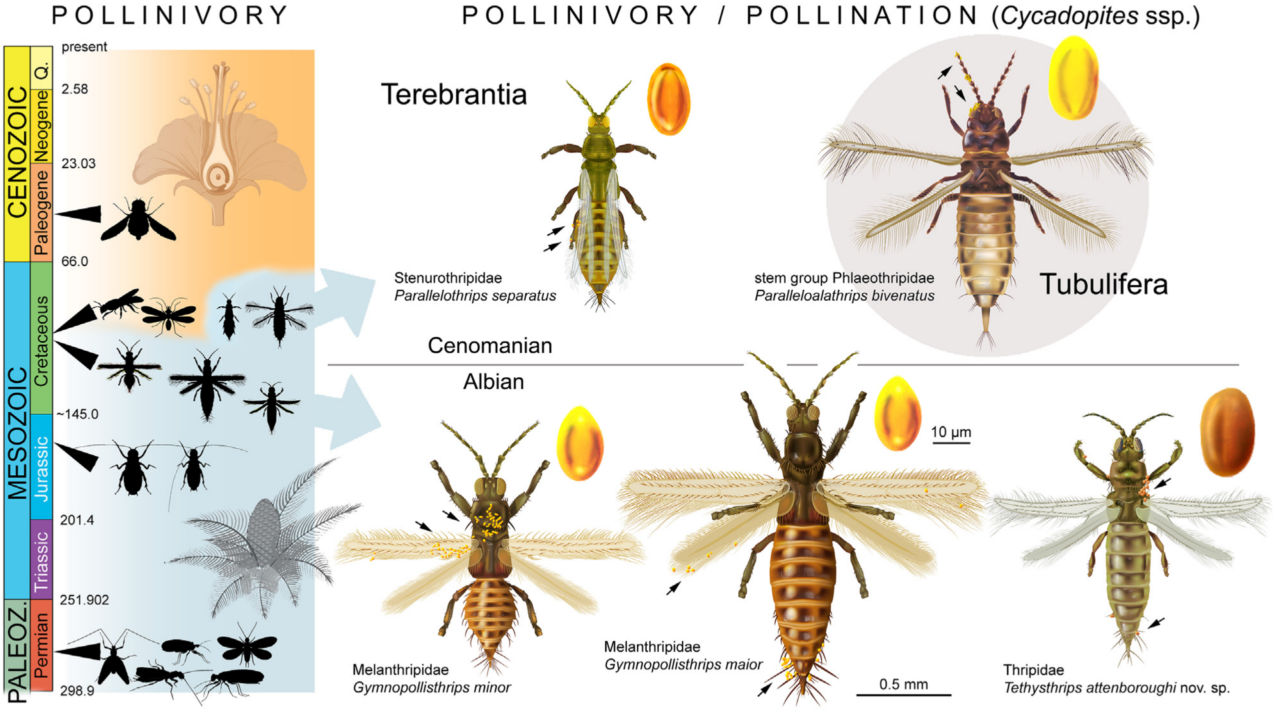

Figure 4. Insect pollinivory evidence in the fossil record segregated between gymnosperm (blue area) and angiosperm (orange area) pollen and detail of five Cretaceous thysanopteran species having gymnosperm pollen loads constituted by the form genus *Cycadopites*

The 15 insect groups represented as silhouettes showing fossil evidence of pollinivory (and perhaps pollination as well) are from the bottom and left to right (silhouettes not at the same scale): Permian, *Sojanidelia florea* (Paoliidae), *Tschekardaenigma pollinivorum* (Grylloblattodea family indet.), *Parapsocidium uralicum* (Psocidiidae), *Idelopsocus diradiatus* (Hypoperlidae), and *Sellardsiopsis conspicua* (Palaeomanteidae); Jurassic, *Aboilus amplus* and *Aboilus* sp. aff. *dilutus* (Prophalangopsidae); Cretaceous, the three Albian terebrantian thrips species represented in detail on the right, *Prosphex anthophilos* (Aculeata indet.), *Psocorrhyncha burmitica* (Archipsyllidae), and the two Cenomanian thrips species represented in detail on the right, one terebrantian and one tubuliferan (encircled); and Paleogene, *Hirmoneura messelense* (Nemestrinidae). The five thysanopterans represented on the right are four species in three genera of three Terebrantia families from upper Albian Peñacerrada I amber (Spain) and Cenomanian Burmese amber (Myanmar) and the only known species of a Tubulifera with direct evidence of pollination, from Burmese amber. Coloration of the five thrips species and pollen grains are conjectural. Arrows indicate some patches of pollen grains adhered to the bodies based on the amber records available. The five species reconstructions are of females, despite the stenurothripid specimen with a load being a male. The thrips are at the same scale, and the enlarged pollen grains (these last represented with their average sizes) as well.

angiosperms (but not of gymnosperms); and (3) presence of "specialized structures," based on their peculiar sucking mouthparts. Regarding point 3, Grinfel'd[39] hypothesized that the asymmetrical mouthparts of Thysanoptera evolved as an adaptation to sucking pollen (and fungi), a small and resistant food source that can be efficiently pierced by their single mandible (see detailed discussion in Nel et al.[40]). The case of the species *Parallelothrips separatus* differs, because it belongs to the extant family Stenurothripidae without known pollinator species and thus only satisfies the criteria 1 and 3, but these criteria are sufficient to consider it an ancient pollinator.[1] Additional Burmese amber assemblages of new stenurothripid taxa with *Cycadopites* loads are under study by the authors of the present work. With the inclusion of these three newly identified groups, the total number of insect groups at the family level containing evidence of pollinator species in the fossil record reaches 18, implying a notable increase of 20% (see Figure 4A in Peña-Kairath et al.[1]). Moreover, thrips can be confidently regarded as ancient pollinators,[30,41] with their pollinivory and pollination histories dating back at least 105 million years, and possibly even earlier.

The gymnosperm-to-angiosperm plant-host ecological shift

Up to now, no fossil thrips carrying angiosperm pollen grains have been discovered. The current fossil record involving this insect group and gymnosperm pollen grains is limited to the Albian-Cenomanian. Burmese amber, dating to the Cenomanian (99 Ma), is rich in thrips, including tubuliferans like the specimen carrying pollen grains studied here. It also features notable records of other insect groups carrying angiosperm or gymnosperm loads, some of which represent the earliest records involving angiosperm pollen. It is important to highlight that, by the Cenomanian, angiosperms had become abundantly established lineages with more species than other plants.[15,42] An analysis of the abundant and highly diverse angiosperm flora preserved in Burmese amber, in contrast to records from slightly older ambers, could illuminate the onset of the Angiosperm Terrestrial Revolution. That term was established by Benton et al.,[15] and they estimated that this series of profound changes in the terrestrial ecosystems began around 100 Ma and lasted for approximately 50 million years (Late Cretaceous to early Paleogene).[15] Such an analysis could also shed light on the ecological impact on another key group of terrestrial organisms: the arthropods, which are abundantly and diversely preserved in the same amber. Comparing the arthropod fauna in Burmese amber with that of slightly older ambers could be key to understanding the dramatic changes that occurred in these two groups and their coevolutionary trends prior to the end of the Cretaceous. This could also contribute to explain the remarkable temporal mismatch between the origin and initial diversification of angiosperms and the similar processes of their key insect pollinators, a topic discussed by Asar et al.[43]

The fact that the extant families Melanthripidae, Thripidae, and Phlaeothripidae can be considered the only families which contain extant representatives that pollinate angiosperm plants, but none of gymnosperms, reinforces the idea that the order Thysanoptera experimented important biological changes during the Angiosperm Terrestrial Revolution. The present research of some Cretaceous thrips species provides insight into a preceding phase of gymnosperm plant host, which most likely favored the later additional phase of angiosperm plant host.[9,10] Different gymnosperm plants use volatile organic compounds as a signaling device that attracts thrips looking for food, mating sites, and heat as a reward.[44] CO_2 or humidity levels could have also played a role as attractants,[45] although these have been less studied. Odors and heat may have been key components for the early evolution of reproductive systems in seed plants by attracting pollinating insects,[46] probably since the Carboniferous.[47] During the Angiosperm Terrestrial Revolution, there was a high diversification of taxa, ecological behaviors, new signals and rewards, and colonization of new ecospaces in insects,[15,16,18,48] but also impoverishment of some ecological behaviors as is the entomophily involving gymnosperms.

Limitations of the study

Considering the limitations of the fossil record, this study was conducted exclusively on two individuals with pollen loads, each from a different suborder of the Thysanoptera order. More of these rare specimens, if discovered, would better support the conclusions of this paper. Additionally, to classify an insect species as a pollinator in the extant biota, controlled experiments are needed to observe whether the plants visited by these insects increase their fruit and seed productivity compared to control groups.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to the lead contact, Enrique Peñalver, (e.penalver@igme.es).

Materials availability

Amber specimens and repository. Four studied specimens of thrips are present in three amber fragments. The piece MCNA 12629, from Peñacerrada I, in a fragment of amber 5 × 3 × 1 mm in size into a prism of epoxy resin 22 × 14 × 1 mm in size, contains two female thrips MCNA 12629a-b, one of them with pollen load (MCNA 12629a). Two isolated thrips of indeterminate sex are present in pieces MCNA 13046, from Peñacerrada II, in a fragment of amber 6 × 6 × 1 mm into a prism 22 × 15 × 1 mm, and MCNA 9503, from Peñacerrada I, in a fragment of amber 9 × 4 × 1 mm into a prism 22 × 15 × 1 mm. The four specimens belong to the same genus and are conspecific. No eusyninclusions were detected in these pieces, apart from the insects and pollen grains together in the piece MCNA 12629. The specimens are deposited at the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain, abbreviated as MCNA herein.

The Burmese type specimen of the species *Paralleloalathrips bivenatus*, MU-Fos-124/1, currently is in a German private collection, but it will be housed in a German public museum in the nearest future as indicated in Ulitzka.[28] The specimen was gently sent to one of us (M.M.S.-K.) by Dr. Manfred Ulitzka for review.

Data and code availability

- Data on the new taxon has been deposited at ZooBank at https://zoobank.org and are publicly available since the date of publication with the LSID: urn:lsid:zoobank.org:act:C8B1B7CA-7808-4EED-B560-D9166B9B4E9B.
- The paper does not report original code.
- Any additional information required to reanalyze the data reported in this article is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

E.P. designed the project, prepared the figures, wrote the original draft, and supervised the manuscript; E.P., C.P.-K., P.N., and A.N. identified the Spanish fossil insects; E.B. identified the pollen grains; E.P., C.P.-K., E.B., P.N., A.N., X.D., D.P., M.M.S.-K., and A.R. analyzed the data, contributed to the discussion, and edited the manuscript; E.P., X.D., and D.P. acquired the funding.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- METHOD DETAILS
  - ○ Laboratory methodology
  - ○ Imaging

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Taxonomical data on the new taxon named *Tethysthrips attenboroughi*	Zoobank (LSID)	urn:lsid:zoobank.org:act:C8B1B7CA-7808-4EED-B560-D9166B9B4E9B
Biological samples (fossils)		
Tethysthrips attenboroughi nov. sp. (Thripidae), complete fossil body of a female with pollen load (holotype)	Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain	MCNA 12629a
Tethysthrips attenboroughi nov. sp. (Thripidae), complete fossil body of a female (paratype)	Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain	MCNA 12629b
Tethysthrips attenboroughi (Thripidae), complete fossil body of sex indeterminate (no type specimen)	Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain	MCNA 13046
Tethysthrips attenboroughi (Thripidae), complete fossil body of sex indeterminate (no type specimen)	Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain	MCNA 9503
Paralleloalathrips bivenatus (stem group Phlaeothripidae), complete fossil body of a female with pollen load (paratype)	Dr. Manfred Ulitzka private collection, Germany	MU-Fos-124/1

METHOD DETAILS

Laboratory methodology

The three Spanish amber fragments were prepared and included in Epoxy resin (EPO-TEK 301) for visibility and curation.[49] This resulted in polished regular prisms of epoxy resin.

Two compound microscopes Olympus BX51 and BX53 were used to examine the pollen grains and the insects.

The four thrips specimens in Spanish amber are intact and dorsal and ventral views are available to observation. In one of the specimens, MCNA 12629a, virtually all the key features are well visible. That specimen only has the proximal half of the abdomen collapsed dorsally and the anterior part of the head and antennae sectioned by an internal amber crack and slightly displaced.

The pollen grains are described following the works by Punt et al.[50] and Hesse et al.[51]

Imaging

Photographs of the general specimenś habitus were taken with a digital camera Canon EOS 650D using the software "Macrofotografía", version 1.1.0.5 (IGME-CSIC, Madrid, Spain). The software created composite photographs by integrating sequential images obtained at different focal planes. Micrographs of the morphological structures and the pollen grains were taken using a digital camera attached to a compound microscope Olympus BX53 and the drawings of the holotype using an attached camera lucida tube to the same compound microscope (IGME-CSIC, Valencia, Spain). Micrographs of the Burmese type specimen of the species *P. bivenatus* were also taken using the same compound microscope, but they are not clear due to poor original preparation of the specimen. Photography was enhanced using Photoshop CS2 version 9.0 (www.adobe.com) to increase contrast to assist in viewing and the composite figures were prepared also using the same software.

Figure 4 uses the geological time chart from GSA Geologic TimeScale, version 6.0, updated October 2022 (https://www.geosociety.org/GSA/GSA/timescale/home.aspx). Reconstructions of the five thrips is art by José Antonio Peñas, with the scientific assistance of the first author (E.P.). Illustrate composition and silhouettes and plant drawings by the authors using Photoshop CS2, version 9.0 (www.adobe.com), Adobe Illustrator 2021 and the online software https://www.biorender.com.