Palaeoentomology 007 (6): 723–739
https://www.mapress.com/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.7.6.8
http://zoobank.org/urn:lsid:zoobank.org:pub:2891BF9C-B1FA-48AF-8777-B93CB185C9A9

Swarming behaviour and pollination by Cretaceous thrips (Insecta: Thysanoptera)

CONSTANZA PEÑA-KAIRATH[1, 2, *], ENRIQUE PEÑALVER[3], DAVID PERIS[4] & XAVIER DELCLÒS[1, 2]
[1]Departament de Dinàmica de la Terra i de l'Oceà, Facultad de Ciències de la Terra, Universitat de Barcelona (UB), c/Martí i Franquès s/n, 08028, Barcelona, Spain
[2]Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), 08028, Barcelona, Spain
[3]Instituto Geológico y Minero de España, CSIC, c/Cirilo Amorós 42, 46004, Valencia, Spain
[4]Institut Botànic de Barcelona, CSIC–CMCNB, Passeig del Migdia s/n, 08038, Barcelona, Spain
constanza.kairath@gmail.com; https://orcid.org/0000-0002-4877-7754
e.penalver@igme.es; https://orcid.org/0000-0001-8312-6087
david.peris@ibb.csic.es; https://orcid.org/0000-0003-4074-7400
xdelclos@ub.edu; https://orcid.org/0000-0002-2233-5480
**Corresponding author*

Abstract

Direct biotic interactions fossilize in low probability and are difficult to be recognized. This is because they normally occur over a brief time span and the conditions required for their fossilization are exceptional. Swarm behaviour in Thysanoptera (thrips) is a phenomenon that is not yet fully understood but is crucial for the survival and success of representatives of this order of insects. Moreover, the role of thrips as pollinators of gymnosperms had not gained significant attention until the Recent decline in insect populations, particularly pollinators, and the consequent impact on the flora that relies on them. Here we describe a thrips assemblage in Cenomanian Kachin amber (Myanmar, *ca*. 99 Ma), composed of both, females and males of the new species *Burmathrips engeli* **gen. et sp. nov.**, belonging to the family Stenurothripidae, that has been interpreted as a swarm. These specimens have *Cycadopites*-type pollen grains attached to their bodies, with additional associated grains, most likely detached, being abundant in the same amber flow, throughout the amber piece. Nowadays, hexapod aggregations are related to different activities like mating and courtship, but identifying this type of behaviour in the fossil record is difficult. This finding demonstrates the antiquity of mating-related swarming behaviour in thrips, which is consistent with that of their extant counterparts. It also provides direct evidence that gregariousness facilitated the prominent role of thrips as gymnosperm pollinators during the Cretaceous.

Keywords: amber, Cenomanian, gymnosperms, palaeobiology, Myanmar

Introduction

Thysanoptera is an order of small insects, commonly called thrips, with currently about 6,300 recognized species (McGavin & Davranoglou, 2022). It includes two suborders, Terebrantia and Tubulifera, comprising 35% and 65% of all thrips species respectively (Mound *et al*., 2022). All thrips, independently of their developmental stage, share a unique structural attribute: only the left mandible is fully developed, with the right mandible being resorbed during the embryonic stage (Heming, 1993). Even though these tiny insects are best known as agricultural and horticultural pests that can cause damage by feeding on plant tissues (Kirk, 1984), they have also diversified into grass, herb and floral herbivory, pollinivory, carnivory, and sporophagy (Terry, 2002), fulfilling different roles in ecosystems. Among the most significant behaviours and interactions are their ability to form aggregations and their role as effective pollinators of certain plants (Terry & Dyreson, 1996; Toon *et al*., 2020).

Aggregations in hexapods (true insects plus springtails, coneheads and two-pronged bristletails) are a common and diverse form of social behaviour, mostly in insects (Sullivan, 1981; Svensson & Petersson, 1992; Collett *et al*., 1998). These aggregations are associated with different activities such as mating, courtship, feeding, defence, and dispersion. If the aggregation is a body of organisms that move together, particularly in the context of dispersal or mating, it is often referred as swarming aggregations (Sullivan, 1981; Terry, 1997). Within the order Thysanoptera, it has been inferred that the main purpose of their aggregations is to locate breeding pairs (mate location) (Terry, 1997); therefore, in this work, we will refer to these aggregations in thrips as swarms. Some studies have analysed extant thrips swarms. In

Submitted: 26 Oct. 2024; accepted by D.-Y. Huang: 7 Nov. 2024; published: 20 Dec. 2024

Terebrantia, it is known that males form swarms in areas where females feed and lay eggs, with reports of fights between males for access to females (Terry & Gardner, 1990; Terry & Dyreson, 1996). Similarly, in Tubulifera, the suborder that includes all the eusocial species (Abbot & Chapman, 2017), males of the family Phlaeothripidae fight among themselves to defend areas where females form swarms for oviposition (Crespi, 1986, 1988).

The fossil record offers direct evidence of interactions between different organisms, allowing certain behaviours to be inferred (Arillo, 2007; Fraser *et al*., 2021). Amber, with its exceptional ability to preserve a wide variety of organisms in an almost intact state for millions of years, provides us with invaluable opportunities to study past terrestrial ecosystems and arthropod behaviours. Through the analysis of bioinclusions in this ancient resin, it has been possible to infer different interspecific and intraspecific relationships between animals, such as parental care (Sánchez-García *et al*., 2017), predation (Barden *et al*., 2020), or aggregation behaviour (Peris *et al*., 2020) and swarming related to mating and courtship (Sánchez-García *et al*., 2018).

Gymnosperms are generally considered to be wind-pollinated, although insect pollination has been demonstrated in both Gnetales and Cycadales (Bolinder *et al*., 2016; Toon *et al*., 2020) and Peña-Kairath *et al*. (2023) recently estimated that about 40% of gymnosperm species are pollinated in this fashion. The role of thrips as pollinators of gymnosperms has received increased attention during the past years, with particular emphasis on their close relationship with Cycadales (Mound & Terry, 2001; Terry, 2002; Terry *et al*., 2005; Toon *et al*., 2020). This interaction between thrips and gymnosperms has been described dating back even to the Early Cretaceous, with evidence of thrips carrying pollen grains on their bodies from the Albian amber of Spain (Peñalver *et al*., 2012), and from the Cenomanian amber of Myanmar (Guo *et al*., 2024; Peñalver *et al*., in press). The exceptional preservation of these records has provided unique insights into the origins of insect pollination, suggesting an early co-evolutionary relationship between thrips and gymnosperm plants.

Studying thrips and their role in pollination, along with an understanding of their swarming behaviour, offers a comprehensive perspective on their ecological and evolutionary interactions. Here we describe a new species of thrips belonging to the family Stenurothripidae (Terebrantia), and present new evidence of their pollination relationship with gymnosperms. Additionally, we describe the first direct evidence of intraspecific interaction in thrips in the fossil record, through the analysis of an assemblage composed of females and males in Cretaceous amber from Myanmar that is here interpreted as being a swarm.

Geological setting

The Kachin amber piece came from the Hukawng valley, Noije Hill, about 20 km southwest of Tanai, in the Hukawng Basin, in norther Myanmar (former Burma). This amber source is commonly referred in the literature as Burmese amber, but because ambers of different ages have been recently discovered in various deposits in Myanmar (Zheng *et al*., 2018) it is necessary to identify the exact deposit from which each amber piece was extracted. In this area, the amber is found in fine to very fine sandstones alternate with centimetric beds, which can rise 1 m thick, of silts and shales and micritic limestone clastic rocks, with thin limestone and muddy laminated carbonaceous beds containing the amber (Cruickshank & Ko, 2003). The clastic rocks that contain the amber were deposited in a nearshore marine environment, such as a bay or estuary, supported by the presence of brackish and marine invertebrates associated to the amber (Mao *et al*., 2018; Yu *et al*., 2019), and pholarid borings in the amber (Bolotov *et al*., 2021). The Kachin amber has been dated as early Cenomanian (98.79 ± 0.62 Ma) based on zircon studies by Shi *et al*. (2012), but see Cruickshank & Ko (2003) and Yu *et al*. (2019) for additional comments on the age of the deposits.

Material and methods

The fossil insects studied in this work are included in a single piece of Kachin amber from Myanmar, Cenomanian in age (*ca*. 99 Ma).

The piece was cut, polished, and embedded in epoxy resin ensuring his preservation and protection following the methodology of Corral *et al*. (1999). After the preparation the result is an amber fragment of 1.39 × 0.40 × 0.12 cm in size into a prism of epoxy resin 2.10 × 1.40 × 0.14 cm in size. The specimens were examined with reflected and transmitted light using an Olympus CX41 compound microscope. Photographs and drawings of the specimens were acquired using the same compound microscope with an attached sCMEX-20 digital camera and a camera lucida (Universitat de Barcelona, Barcelona, Spain). The photographs of pollen grains and the entire piece were taken using a digital camera attached to a compound microscope Olympus BX53 (IGME, CSIC, Valencia, Spain). The software HeliconFocus version 8.2.13 and Photoshop version 22.1.1 were used to prepare the photographs and composed figures.

Piece description

The amber bioinclusions correspond to a monospecific assemblage of thrips, comprising 10 females, five males and three specimens difficult to determine their sex.

The amber piece also contains one hemipteran. There are abundant pollen grains in the assemblage, also monospecific, based on their morphology. Some of the grains are attached to the body of some specimens and others are scattered around the swarm. All the specimens and pollen grains are eusyninclusions (Solórzano-Kraemer *et al.*, 2023), as they were embedded by the same resin flow (Fig. 1).

The piece was acquired in 2010 by the AMBERIA group and entered the collection of the Palaeontology Laboratory of the Faculty of Earth Sciences, University of Barcelona. After this study, the piece is now housed in the Museum of Natural Sciences of Barcelona under the accession number MGB 95344.

Systematic palaeontology

Order Thysanoptera Haliday, 1836
Suborder Terebrantia Haliday, 1836
Family Stenurothripidae Bagnall, 1923

Genus *Burmathrips* Peña-Kairath, Peñalver & Delclòs gen. nov.; by present designation.
LSID: urn:lsid:zoobank.org:act:9CDABD59-B9EE-4972-BC41-3AB78588FF77

Type species. *Burmathrips engeli* Peña-Kairath, Peñalver & Delclòs **sp. nov.**

Etymology. The new generic name is a combination of Latin word *Burma* referring to the place origin of the amber deposit and *thrips* (Greek, meaning “woodworm”), which is a common suffix for thysanopteran genera and is of neutral gender.

Diagnosis (female). Antenna with nine antennomeres, striate sculpture on antennomeres II–IX, antennomere IX acuminate. Antennomeres III and IV inverted cone-shaped, stouter than the distal antennomeres; both antennomeres with a broadly based conical sensilla, strongly flattened laterally. Compound eyes are prolonged ventrally. Mesonotum with antero-lateral projections which resemble “shoulder pads”. Forewing narrow, having a crossvein between the two longitudinal veins at 2/5 of the wing length and lacking additional crossveins or these are very evanescent to be easily detected. Longitudinal veins slightly sclerotized, evanescent distally and with scarce setae. Hind wing with a slightly sclerotized longitudinal vein, present up to the distal fifth of the wing length, and lacking crossveins.

***Burmathrips engeli* Peña-Kairath, Peñalver & Delclòs sp. nov.**
(Figs 1–5)
LSID: urn:lsid:zoobank.org:act:E73521BC-FA89-4999-8451-39255E9E3951

Type material. Holotype female thrips (MGB 95344.1), allotype male thrips (MGB 95344.2), and 16 thrips as paratypes [nine females, four males and three specimens difficult to identify their sex (MGB 95344.3-18)]. Additional eusyninclusions are pollen grains attached to some thrips specimens and abundant isolated pollen grains around them, most likely detached, plus one hemipteran (nymphal Coccoidea; see Grimaldi & Vea, 2021).

Etymology. The species name honours the distinguished neo- and paleoentomologist and colleague Prof. Michael Engel.

Diagnosis. As for the genus.

Locality and horizon. Hukawng valley, Myanmar (Cenomanian, *ca*. 99 Ma).

Description. Holotype (female). Based on the holotype female (MGB 95344.1) with additional observations and characters from female paratypes between [brackets]. The specimen is complete (Fig. 2A, B), left and right hind legs are extended, left and right fore and mid legs are partly folded under the body. Antenna and body fully extended, right forewing spread and left forewing cannot be fully seen as it is overlapping with the body, the same as both hind wings (Fig. 2). Despite the abundance of female individuals in the swarm, this wing part is not visible in any of them due to overlapping or lateral views of them in the preparation.

The head is wider than long, dorsally with transverse striations at least posteriorly. Compound eyes prolonged ventrally (Fig. 2B), with many ommatidia (*ca*. 26 ommatidia visible in dorsal view); two short postocular setae visible behind each eye. The median ocellus is directed forwards and lateral ocelli close to compound eyes (Figs 2B, 3A).

Antenna (Fig. 2C) with nine antennomeres, antennomeres II–IX with transversal striation, II–VIII each one with at least one seta at the inner part and other one in the outer part; antennomeres I–IV stouter than distal antennomeres (Fig. 2C); antennomeres III–IV inverted cone-shaped and each with a conical sensilla broad at the base [strongly flattened laterally, thus slightly plate-shaped as observed in lateral views]. The antennomere IX large and slender, acuminate. Scapus protruding from the front of the head (Fig. 2C).

Mouth cone (Fig. 4A) large; with clypeus, labrum and labium visible, maxillary palps robust; labial palps short and two-segmented.

Pronotum wider than long, strongly adjoined to the head; [row with ten anteromarginal setae visible (12 estimated), and only five posteromarginal setae visible, two anteroangular setae visible (see Fig. 5A, B)], two long and stout posteroangular setae, one stouter and longer than the other, plus two additional short posteroangular setae (Figs. 3A, 5A, B). Mesonotum with anterior projections

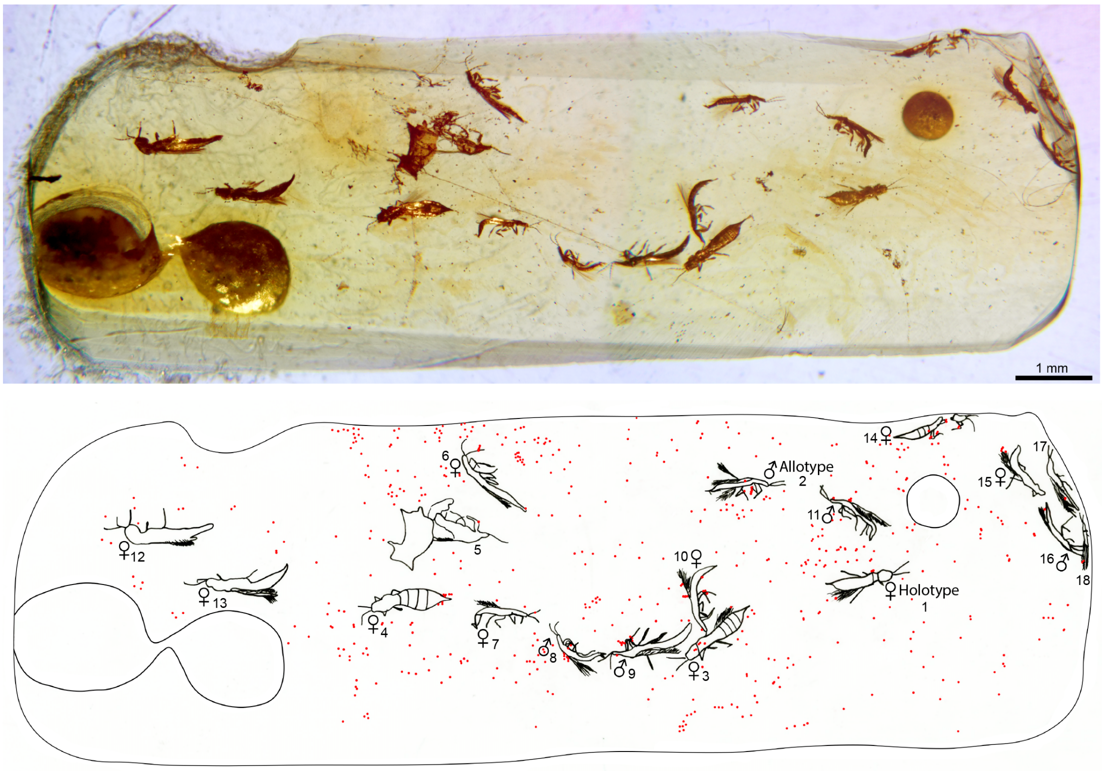

FIGURE 1. Burmese amber piece MGB 95344. Swarm composed of 18 type specimens of *Burmathrips engeli* **gen. et sp. nov.** (Stenurothripidae), with indication of the holotype female (♀) (MGB 95344.1) and allotype male (♂) (MGB 95344.2), as eusyninclusions, and females and males paratypes. The three specimens of unknown sex lack indication of their sex. The *Cycadopites*-type pollen grains are indicated by red dots. It is possible to observe borings made by pholarid bivalves. Photograph and camera lucida drawing at the same scale.

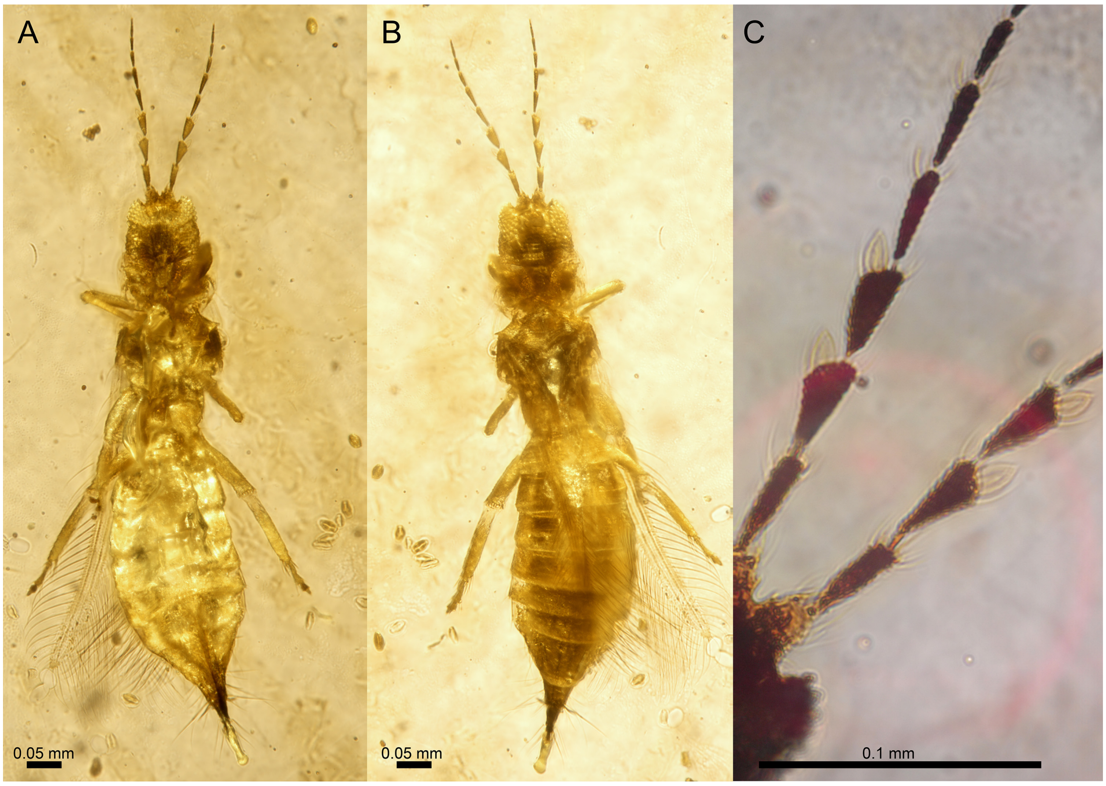

FIGURE 2. *Burmathrips engeli* **gen. et sp. nov.** (Stenurothripidae). Holotype female (MGB 95344.1) from Kachin amber, Upper Cretaceous (Cenomanian, *ca*. 99 Ma). **A**, Ventral habitus. **B**, Dorsal habitus. **C**, Antennae in dorsal view showing antennomeres III and IV with conical sensillae.

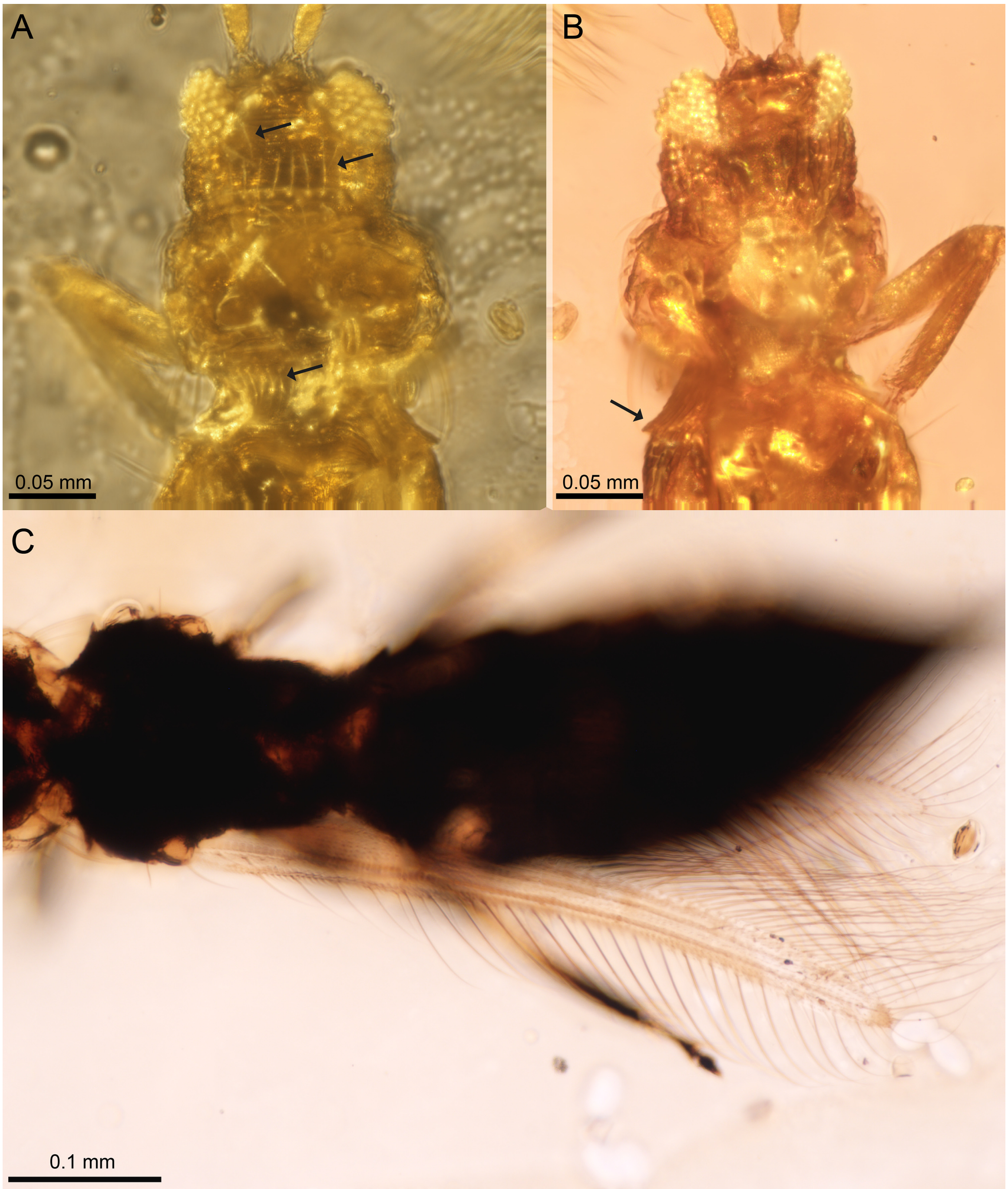

FIGURE 3. Holotype and paratype (females MGB 95344.1 and MGB 95344.3), in the piece MGB 95344, of *Burmathrips engeli* **gen. et sp. nov.** (Stenurothripidae). **A**, Head and pronotum of the paratype; arrows indicate posterocular in the head, anteromarginal and posteromarginal setae in the pronotum. **B**, Ventral view of the same paratype; arrow indicates "shoulder pads"-like structure. **C**, Holotype in dorsal view.

which resemble "shoulder pads" (Fig. 2A, B; [female paratype MGB 95344.4: Fig. 5A; female paratype MGB 95344.3: Figs 3B, 5B]); and with strong transverse striation. Metanotum without visible striation (Fig. 2A, B).

Forewing narrow, with two longitudinal veins poorly sclerotized and with ends evanescent, thus not visible a connection with the wing margin. Anterior vein ending near the wing apex with one small seta at the end arising from socket; number of setae variable (5 in the holotype, see Fig. 5C) [10 in one female paratype: Fig. 5D], mainly concentrated proximally. Posterior vein ending far from the wing apex, and with one small seta at the end arising from socket; number of setae variable (only one visible in the holotype, see Fig. 5C) [6–7 in one of the female paratypes: Fig. 5D], mainly concentrated distally.

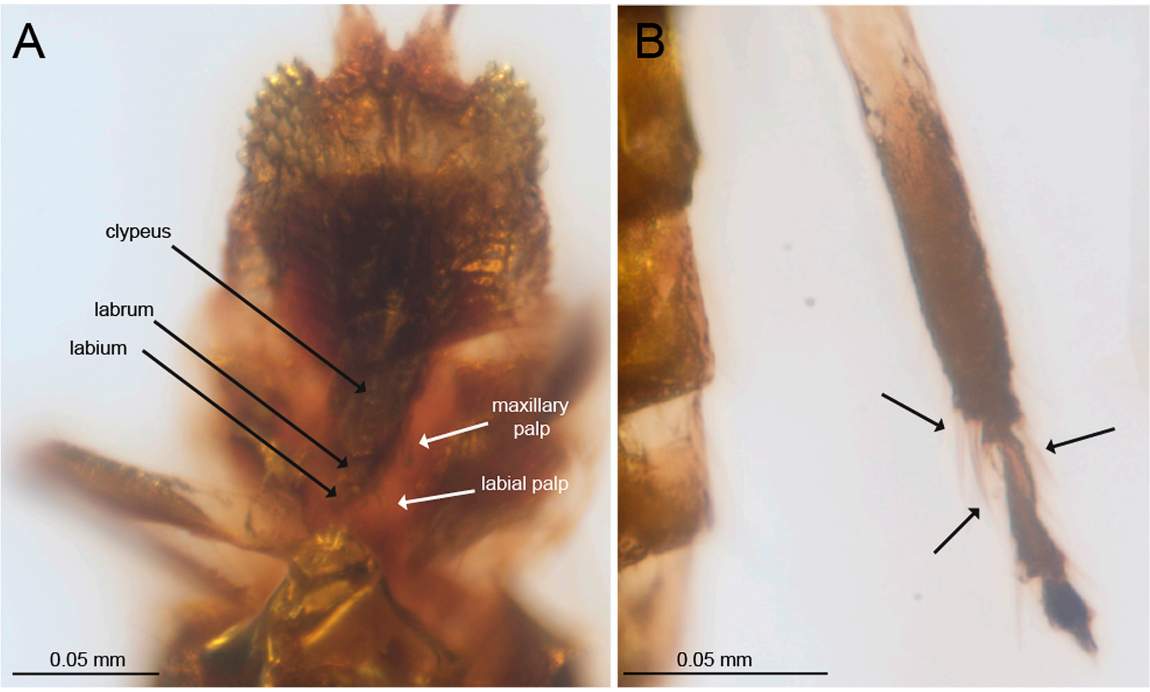

FIGURE 4. Holotype female MGB 95344.1 of *Burmathrips engeli* **gen. et sp. nov.** (Stenurothripidae). **A**, Head in ventral view showing the mouthparts. **B**, Right foreleg showing three stout spines in the tibia (arrows), with tarsus two-segmented, hamus, and bladder.

Crossvein between the two longitudinal veins, basally at two fifth of the wing length and inclined towards the base of the wing. Anteromarginal fringe cilia long and slender, six fringe cilia in the basal part of the wing smaller and distant from each other. Duplicated cilia between the long cilia up to the wing apex (Fig. 3C), strong wavy fringe cilia in the posterior wing margin. Clavus obscured due to overlapping.

Hind wing with the membrane fully covered with microtrichiae, with a slightly sclerotized longitudinal vein, present up to the distal fifth of the wing length, lacking crossveins (Fig. 3C); fringe cilia from posterior margin strongly wavy and longer than the straight ones of the anterior margin (Fig. 3C).

Legs large and slender; hind leg with three stout distal spines on the tibia, stronger two of them in a pair, tarsus two-segmented in all the six legs with hamus present, vesicles cone-shaped (Fig. 4B).

Abdomen with 10 segments being segments VIII–X cone-shaped (Fig. 2). From segment V to VIII there is a small seta present on lateral posterior margin; abdomen slightly bent to the left at the apex; a pair of short stout setae on segment VIII and a pair of two large setae; ovipositor visible in segment VII; segments VIII, IX and X narrow in comparison to the others, segments IX and X with a pair of long setae, end of the abdomen with conical shape (Fig. 2A, B).

Description of main characters of the allotype (male) (MGB 95344.2, Fig. 6A)

Body and antennae fully extended at lateral side; antennae with nine antennomeres. Antennomeres III and IV inverted cone-shaped and each with a conical sensilla. Fore, mid, and hind legs blended, but fully visible; fore and hind wings partially extended and visible, the surface is fully covered with microtrichiae.

Forewing with two longitudinal veins with at least a crossvein between the longitudinal veins, posterior margin fringe cilia larger than the anterior margin ones and strongly wavy; hind wing with a longitudinal vein, fringe cilia on the posterior margin larger than the anterior margin ones and wavy.

Mesonotum with latero-anterior projections which resemble “shoulder pads”, larger than the ones present in the females. Abdomen slightly rotated, fully extended and visible laterally with X segments, VII segment with a ventral spine characteristic of males; segments IX and X with long setae.

Forelegs, mid legs and hind femora robust in comparison to females. Fore tibia with three stout setae, foretarsus two-segmented with hamus (Fig. 6B), bladder, and cone-shaped. At the apex of the abdomen the external genitalia are extruded and fully visible, but only the parameres can be identified (the genitalia could only be observed laterally, and the interpretation of other structures is more complex), which are very developed (Fig. 6C).

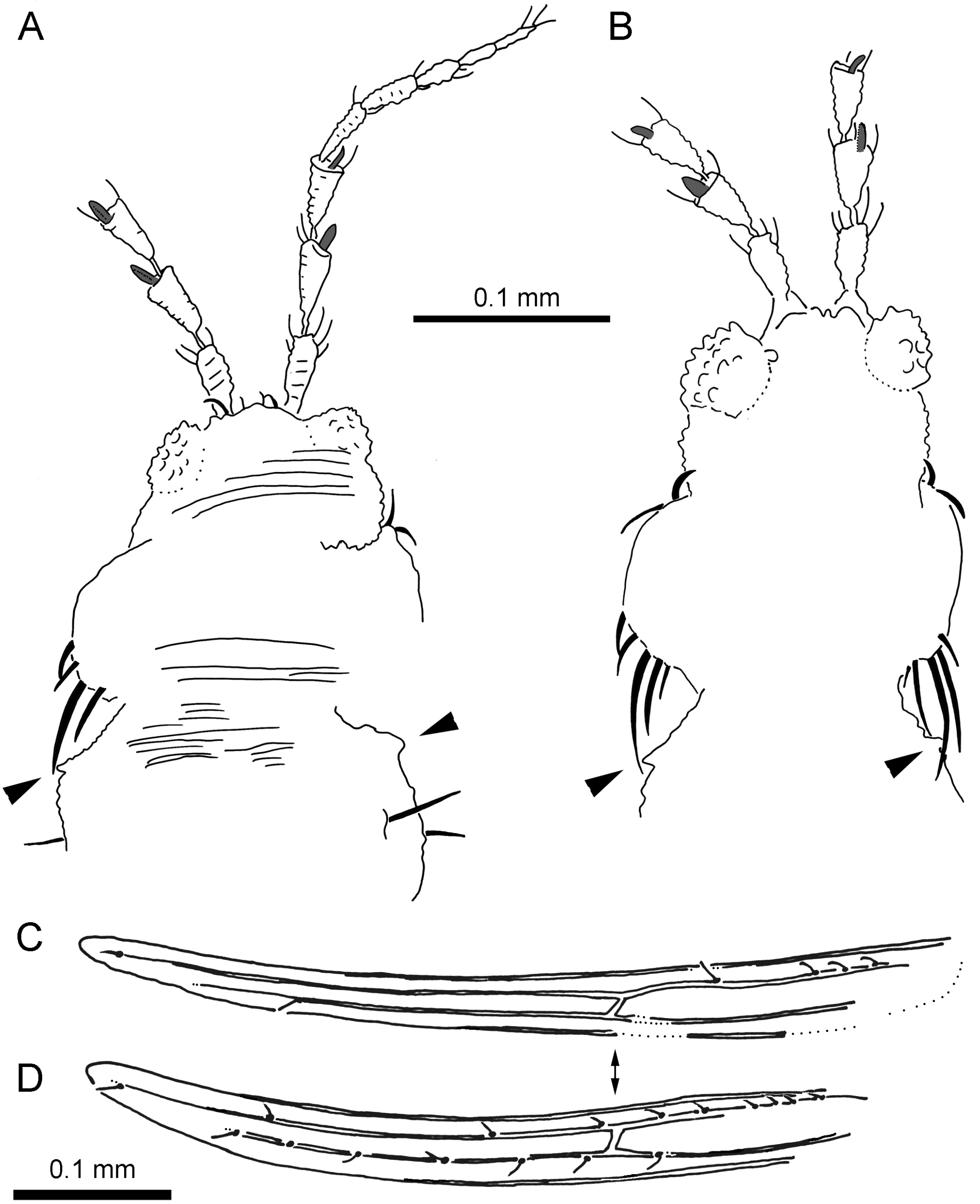

FIGURE 5. Holotype female and two paratype females of *Burmathrips engeli* **gen. et sp. nov.** (Stenurothripidae) in the amber piece (MGB 95344). **A**, **B**, Head and pronotum, arrowheads indicate antero-lateral mesonotal projections which resemble "shoulder pads", paratypes females MGB 95344.4 and MGB 95344.3, respectively. **C**, **D**, Forewings showing two longitudinal veins with sparse setae and only a conspicuous crossvein. Holotype MGB 95344.1 and paratype MGB 95344.4, respectively.

Measurements. All measurements for holotype female MGB 95344.1 and allotype male MGB 95344.2 in Table 1.

Description of pollen grains

There are at least 462 pollen grains as eusyninclusions in the amber piece, of which 46 are in contact with 14 thrips in the assemblage, both females and males, some of them forming clusters. The pollen grains attached to the specimens are prolate in shape; *ca.* 24.0 μm in length × 13.8 μm in width on average; range in length: 16.05–33.95 μm; range in width: 8.21–20.55 μm (all measurements in Table 2); monosulcate; sulcus elongate for the entire length of the grain; surface psilate in ornamentation. All pollen

FIGURE 6. Allotype male MGB 95344.2 of *Burmathrips engeli* **gen. et sp. nov.** (Stenurothripidae). **A**, Left side habitus of the complete specimen. **B**, Foreleg showing robust tibia with three spines (arrows), tarsus two-segmented, hamus and bladder. **C**, Extruded male genitalia with parameres very developed (arrows).

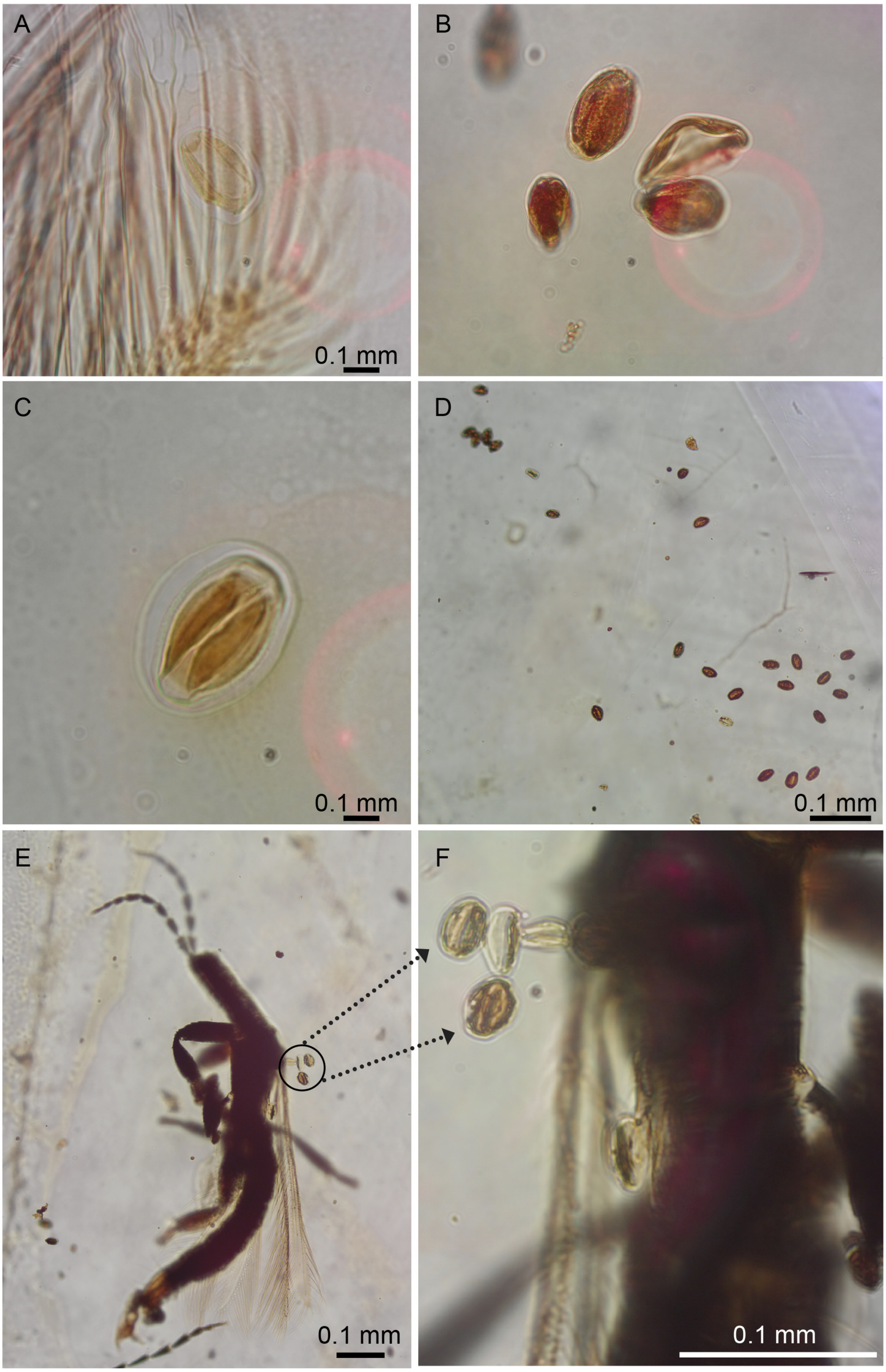

FIGURE 7. Pollen grains of the form-genus *Cycadopites* in the assemblage as eusyninclusions (sensu Solórzano-Kraemer *et al*., 2023). **A**, Single pollen grain in contact with the wavy fringe cilia of the forewing of one specimen. **B**, Some pollen grains are in contact among themselves forming clusters (one of them seems not psilate, but it is preservational). **C**, Single pollen grain with the sulcus fully visible. **D**, Isolated pollen grains in the assemblage, some of them forming clusters. **E**, **F**, Paratype male of *Burmathrips engeli* **gen. et sp. nov.** (Stenurothripidae), MGB 95344.8, with a cluster of pollen grains attached to the mesonotum.

TABLE 1. Measurements of the holotype female (MGB 95344.1) and allotype male (MGB 95344.2). All the measurements in microns.

Structure	Holotype female	Allotype male
Body length (antennae and male genitalia extruded not included)	775	337
Head length	88	93
Head width	104	-
Pronotum length	72	83
Pronotum width	116	-
Posteroangular setae lengths	50 and 32	-
Mesonotum length	107	118
Mesonotum width	153	-
Metanotum length	70	65
Metanotum width	104	-
Abdomen length	426	368
Abdomen largest width (segment IV holotype; segment III allotype)	46	38
Antenna length	274	248
Antenna segment I length	20	8
Antenna segment II length	35	33
Antenna segment III length	50	39
Antenna segment IV length	40	36
Antenna segment V length	33	35
Antenna segment VI length	31	31
Antenna segment VII length	21	21
Antenna segment VIII length	18	19
Antenna segment IX length	26	26
Forewing length	297	428
Forewing width	45	-
Hind wing length	-	356
Foreleg length	226	248
Midleg length	182	197
Hind leg length	264	285

grains show almost the same small size and the same shape, so it can be inferred that they originated from the same type of plant, or even from the same individual (Fig. 7). Based on the description of the pollen grains, these can be attributed to the form-genus *Cycadopites* Wodehouse emend. Fensome (Fensome, 1983) and could derive from a variety of Mesozoic groups of gymnosperms, such as—†Bennettitales, Ginkgoales and Cycadales (Balme, 1995; Zavialova & Van Konijnenburg-van Cittert, 2011).

Discussion

Burmathrips engeli **gen. et sp. nov.** possesses the distinctive characteristics of the family Stenurothripidae described by Schliephake (1990): the presence of conical sensillae on antennomeres III and IV, antenna with nine antennomeres freely connected, tarsomeres two-segmented with hamus, the forewing fully covered with microtrichiae and with two longitudinal veins nearly reaching the tip of the wing margin and wavy fringe cilia in the posterior margin. All these characteristics can be observed in both males and females of the type series in this fossil assemblage. However, they apparently lack some characters like the crossveins between longitudinal veins and the forewing margin, and lack of crossveins in the hind wings, even so they are most consistent with the family Stenurothripidae.

The new genus is distinguished from the rest of the genera in the family. It differs from *Stenurothrips* Bagnall, 1914 as the latter has elongated, cylindrical and tube-like tenth abdominal segment, which is not the case of *Burmathrips* **gen. nov.** *Scaphothrips* Strassen, 1973 has 10 antennomeres, while both *Rhetinothrips* Strassen, 1973 and *Progonothrips* Strassen, 1973 have 15 antennomeres.

TABLE 2. Measures of the pollen grains of the form-genus *Cycadopites* attached to the body of thrips in the fossil swarm.

	Length (μm)	**Width (μm)**	**Length (μm)**	**Width (μm)**
	26.3	16.9	22.3	10.9
	26.0	15.9	19.3	9.8
	23.9	20.6	20.3	11.3
	20.2	9.9	25.3	12.6
	22.4	9.9	23.2	15.9
	22.6	13.4	23.3	16.8
	21.8	13.4	28.6	14.9
	29.6	15.8	21.7	14.9
	22.8	13.6	21.4	16.3
	28.8	11.3	25.2	15.6
	22.8	10.9	17.6	9.7
	24.7	12.7	20.1	8.2
	24.5	16.3	19.1	15.9
	28.6	15.9	29.6	17.6
	27.7	14.4	33.9	9.6
	25.5	14.6	24.0	16.4
	19.3	12.6	21.6	14.7
	16.1	8.6	22.6	14.2
	27.1	12.9	24.3	15.2
	31.6	12.8	25.5	19.7
	25.5	15.7	21.6	11.3
	29.2	17.1	27.0	13.9
	23.3	13.2	17.2	9.5
Total Average	Length (μm): 24.0	Width (μm): 13.8		

In contrast, *Burmathrips* **gen. nov.** has nine antennomeres. Moreover, *Scaphothrips* has an unsegmented foretarsus, whereas the new genus has two-segmented foretarsus.

Burmathrips **gen. nov.** presents hamus in the foretarsus, which is absent in *Cenomanithrips* Tong, Shih & Ren, 2019, *Parallelothrips* Guo, Engel, Shih & Ren, 2024 and *Didimothrips* Guo, Engel, Shih & Ren, 2024. It also differs from *Neocomothrips* Strassen, 1973 that has three crossveins, while the new genus does not have crossveins.

Exitelothrips Strassen, 1973 and *Progonothrips* have broad forewings, while *Opadothrip*s has forewings that are broad at the apex. In contrast, *Burmathrips* **gen. nov.** has slender forewings that become narrower at the tip. The genus *Exitelothrips* has a longer antennomere II in comparison to the others. *Scudderothrips* Strassen, 1973 has a longer antennomere VII in comparison to the other known genera. These characteristics also are not present in *Burmathrips* **gen. nov.** Additionally, the new genus differs from *Cenomanithrips* in that the latter has forelegs without spines, whereas the new genus has three spines.

Burmathrips engeli **gen. et sp. nov.** exhibits sexual dimorphism, evident in the foreleg femur, which is more robust and wider in males compared to females. Also, the rapid distinction between males and females was easy in the studied assemblage thanks to the preservation of the male genitalia extruded. In extant Thysanoptera, sexual dimorphism has been observed in both Tubulifera (Crespi, 1986) and Terebrantia (Terry & Dyreson, 1996), but without indication in respect to the family Stenurothripidae up to our knowledge.

Swarm behaviour

In insects, two modes of swarming can be identified: 1) Dispersed swarming. In this type males search for and pair with females while in flight and in sufficient density. This typically occurs in sites where females are emerging, feeding, ovipositing, or dispersing; and 2) Crowded swarming. In this mode, males are strongly clumped within a small portion of the volume where females are available and they tend to fly at a station for a prolonged period (Sullivan, 1981; Svensson & Petersson, 1992). Research has shown that swarming behaviour may involve various types of pheromones to attract the opposite sex (Milne *et al*., 2002; Kirk & Hamilton, 2004; Niassy *et al*., 2019), and is likely that swarming in insects improves their mating success (Neems *et al*., 1992).

Swarm behaviour has been observed in families of both thysanopteran suborders, where aggregations are common and presumably associated with mate location (Terry, 1997). However, studies are limited due to the small size and elusiveness of thrips as well as the difficulty of distinguishing species and sex under field conditions (Terry & Gardner, 1990). Males of *Frankliniella occidentalis* Pergande, 1895 (Terebrantia: Thripidae) swarm in landmark-based swarm sites and/or possibly areas where females feed and have oviposition resources (Terry & Gardner, 1990). Male fighting related to mating has also been described in that species (Terry & Dyreson, 1996). Males of *Hoplothrips pedicularius* Haliday, 1836 and *H. karnyi* Hood, 1914 (Tubulifera: Phlaeothripidae) have been also observed fighting within swarms using front legs in the female's oviposition areas in order to increase mating success (Crespi, 1986, 1988).

The presence together of 18 monospecific specimens, males and females, in the same resin flow as eusyninclusions, and in a small amber piece, is direct evidence of the partial entrapment in resin of a thrips swarm. By analysing and describing the Cretaceous thrips swarm in the Kachin amber piece, it can be inferred that the primary objective was mating at a site with resource availability. This inference is supported by the abundant presence of both females and males together, the presence of abundant pollen grains (an important food resource), and the fact that they were all embedded in the same resin flow, indicating they were trapped simultaneously (eusyninclusions). Sexual dimorphism can be weakly identified based on the difference in femur size of all legs, being in males slightly more robust than in females, concluding that fights between males is only a possibility.

Pollination

Gymnosperm plants are currently pollinated by diverse groups of insects (Tang, 1987; see Toon *et al*., 2020). Extant species of beetles and thrips are identified as the main pollinators of Cycadales (Mound & Terry 2001; Terry, 2001; Toon *et al*., 2020; Terry *et al*., 2021). These pollinators live in obligate mutualism with their cycad host species where they feed, mate, lay eggs, and complete their larval development on the cones (see Mound & Terry, 2001). Notably, most cycad pollinators use only the pollen cone as brood site, where adults feed and larvae develop on sporophyll tissue or pollen (Terry, 2023). This is important, as pollinivory is often considered an evolutionary precursor to biotic pollination (Labandeira, 1998, 2000).

The pollination process in Cycadales is known as the "push-pull" mechanism, where insects are initially attracted to the cones by low concentration of volatile organic compounds (VOCs) and then repelled by higher concentrations of these same compounds (Terry *et al*., 2007; Salzman *et al*., 2020; Terry, 2023; Salzman *et al*., 2024). Both pollen cones and ovulated cones undergo daily cycles of increased respiration and thermogenesis, which leads to elevate VOCs emissions (Terry *et al*., 2016; Salzman *et al*., 2020). This "push-pull" pollination mechanism appears to be ancestral in the Cycadales lineage (Salzman *et al*., 2020, 2024; Peris *et al*., 2024). The genus *Cycadothrips* Mound, 1991 utilizes the cycad pollen cones of specific host plants for mating and larval development, feeding exclusively on pollen from their host. This behaviour is an example of obligate pollination mutualism, sometimes referred to as a brood-site pollination system (see Terry *et al*., 2021).

There is direct evidence of entomophilous pollination in some gymnosperm plant groups in the fossil record, *i.e*. Cycadales, Ginkgoales and/or the fossil Bennettitales, where the analyses of the pollen grains attached to the insects are key to understand this type of mutualistic relationship (*e.g*., Peñalver *et al*., 2012, 2015; Peris *et al*., 2017, 2020; Lin *et al*., 2019; Tihelka *et al*., 2021; Peña-Kairath *et al*., 2023). In addition, it has been inferred that the insect pollination of gymnosperms existed since the Carboniferous, more than 300 million years ago (Peris *et al*., 2024).

Nowadays there is no evidence that the unique representative of Ginkgoales in extant ecosystems, *i.e. Ginkgo biloba* L. (1771), is pollinated by insects. However, there are observations of Diptera and Hymenoptera visiting the reproductive organs of this species (Saunders, 2018). In addition, the analysis of their ovular secretions revealed has sugar concentrations similar to other ambophilous species (Nepi *et al*., 2017).

The †Bennettitales are known for their flower-like strobili (Labandeira *et al*., 2007), for some of their ovulate organs with elongate micropyles, most likely a feature for pollination by long-proboscid insects (Labandeira, 2010), and for cones that produced relatively small, boat-shaped and monosulcate pollen grains (Osborn & Taylor, 1995). Bennettitalean strobili of the †Cycadeoideaceae family taxa were closed, so not open to the dissemination of pollen by wind, thus required other mechanisms to transfer the pollen grains (Crepet, 1974 in Labandeira *et al*., 2007). These characteristics have led to consider this group to have been entomophilous plants (Labandeira *et al*., 2007). In fact, different findings support this consideration, such is the case of pollen grains, possibly attributed to †Bennettitales, attached to the dipteran species *Buccinatormyia magnifica* from the Albian Spanish amber (Peñalver *et al*., 2015), the beetle species *Cretaretes minimus* from Cenomanian Kachin amber (Peris *et al*., 2020), and, from the same amber (Lin *et al*., 2019), the mecopteran species *Parapolycentropus paraburmiticus*.

TABLE 3. Fossil species of Thysanoptera described to date, all of them preserved in amber, and recognized as pollinators of gymnosperms during the Cretaceous following the criteria stablished by Peña-Kairath *et al*. (2023).

Thrips species	Pollen grains associated to thrips	Age	Country	References
Gymnopollisthrips maior	Ginkgoales/Cycadales	late Albian (early Cretaceous)	Spain	Peñalver *et al*. (2012)
Gymnopollisthrips minor	Ginkgoales/Cycadales	late Albian (early Cretaceous)	Spain	Peñalver *et al*. (2012)
New species of *Tethysthrips*	Cycadales/Ginkgoales/Bennettitales	early Albian (early Cretaceous)	Spain	Peñalver *et al*. (in press)
Parallelothrips separatus	Cycadales/Ginkgoales/Bennettitales	early Cenomanian (late Cretaceous)	Myanmar	Guo *et al*. (2024)
Paralleloalathrips bivenatus	Cycadales/Ginkgoales/Bennettitales	early Cenomanian (late Cretaceous)	Myanmar	Peñalver *et al*. (in press)
Burmathrips engeli **gen. et sp. nov.**	Cycadales/Ginkgoales/Bennettitales	early Cenomanian (late Cretaceous)	Myanmar	This work

The fossil record of the pollination relationship between thrips and gymnosperms has expanded significantly, particularly with the increased focus on amber assemblages (Table 3). In this new contribution, the presence of *Cycadopites*-type pollen grains in great quantity in the whole amber piece, as well as attached to the body of several female and male specimens, suggests that these insects were in contact with the male reproductive organ of a plant short before the entrapment in the resin of some individuals of a swarm.

Conclusion

The analysed amber piece from Kachin amber provides direct evidence of swarm behaviour in Thysanoptera dating back at least *ca*. 99 million years. The presence of abundant pollen grains in the described amber assemblage allows to infer that since ancient times at least some species of these insects have visited the male reproductive organ of the host-plant during swarming, as pollen ingestion promotes higher fitness in females and is a key nutritional factor for the growth, development, and reproduction of thrips in general (Trichilo & Leigh, 1988). This mutualistic relationship is based on the plants providing the insects with food, oviposition and mating sites, and at the same time, the plant is pollinated by the thrips.

Following the criteria outlined by Peña-Kairath *et al*. (2023), *Burmathrips engeli* **gen. et sp. nov.** can be classified as pollinator, since it meets the requirements of having pollen attached to the body and specialized structures, based on their asymmetrical mouthparts used for sucking out the contents of pollen grains (Kirk, 1984). With the addition of Stenurothripidae as pollinating insect family in the fossil record, together with the recent findings of *Parallelothrips separatus* also in Stenurothripidae (Guo *et al*., 2024) and the new species of *Tethysthrips* in Thripidae and the revision of *Paralleloalathrips bivenatus* in Phlaeothripidae (Peñalver *et al*., in press), the total number of pollinating insect families in the fossil insect record is increased up to 18 (Peña-Kairath *et al*., 2023). This number is expected to continue growing also with new discoveries currently under study.

Acknowledgments

This work is a contribution to the project "CREI": PID2022-137316NB, funded by MICIU/AEI/10.13039/501100011033 and by ERDF/EU. C.P.-K, D.P. and X.D. thanks the project 2021SGR-349, from the Secretary of Universities and Research (Government of Catalonia), for financial support. C.P.-K is funded by the National Agency for Research and Development (ANID) Scholarship Program, Doctorado en el Extranjero, BECAS CHILE 2020-Folio 72210321. D.P thanks the project PID2023-151735NA-I00, funded by MCI/AEI/10.13039/501100011033/FEDER and the project RYC2022-037026-I, from the MCIN/AEI/10.13039/501100011033 and FSE+, for financial support.

References

Abbot, P. & Chapman, T. (2017) Sociality in aphids and thrips. *In*: Rubenstein, D.R. & Abbot, P. (Eds), *Comparative social evolution*. Cambridge University Press, pp. 154–187. https://doi.org/10.1017/9781107338319.007

Arillo, A. (2007) Paleoethology: fossilized behaviours in amber. *Geologica Acta*, 5 (2), 159–166. https://doi.org/10.1344/105.000000301

Bagnall, R.S. (1914) On *Stenurothrips succineus* gen. et sp. nov., an interesting Tertiary thysanopteron. *Geological Magazine*, 6 (1), 483–485. https://doi.org/10.1017/S0016756800153294

Bagnall, R.S. (1927) LXXIV.—Contributions towards a knowledge of the European Thysanoptera.—III. *Annals and Magazine of Natural History*, Series 9, 20 (120), 561–585. https://doi.org/10.1080/00222932708655491

Balme, B.E. (1995) Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology*, 87 (2-4), 81–323. https://doi.org/10.1016/0034-6667(95)93235-X

Barden, P., Perrichot, V. & Wang, B. (2020) Specialized predation drives aberrant morphological integration and diversity in the earliest ants. *Current Biology*, 30 (19), 3818–3824. https://doi.org/10.1016/j.cub.2020.06.106

Bolinder, K., Humphreys, A.M., Ehrlén, J., Alexandersson, R., Ickert-Bond, S.M. & Rydin, C. (2016) From near extinction to diversification by means of a shift in pollination mechanism in the gymnosperm relict *Ephedra* (Ephedraceae, Gnetales). *Botanical Journal of the Linnean Society*, 180 (4), 461–477. https://doi.org/10.1111/boj.12380

Bolotov, N., Aksenova, O.V., Vikhrev, I.V., Konopleva, E.S., Chapurina, Y.E. & Kondakov, A.V. (2021) A new fossil piddock (Bivalvia: Pholadidae) may indicate estuarine to freshwater environments near Cretaceous amber-producing forests in Myanmar. *Scientific Reports*, 11, 6646. https://doi.org/10.1038/s41598-021-86241-y

Brown, B.V. & Pike, E.M. (1990) Three new fossil phorid flies (Diptera: Phoridae) from Canadian Late Cretaceous Amber. *Canadian Journal of Earth Sciences*, 27, 845–848. https://doi.org/10.1139/e90-087

Collett, M., Despland, E., Simpson, S.J. & Krakauer, D.C. (1998) Spatial scales of desert locust gregarization. *Proceedings of the National Academy of Sciences of the United States of America*, 95 (22), 13052–13055. https://doi.org/10.1073/pnas.95.22.13052

Corral, J.C., López Del Valle, R. & Alonso, J. (1999) El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, norte de España). Su colecta y preparación. *Estudios del Museo de Ciencias Naturales de Álava*, 14 (2), 7–21.

Crepet, W.L. (1974) Investigations of North American cycadeoids: the reproductive biology of *Cycadeoidea*. *Palaeontographica, Abt. B, Palaöphytologie*, 148, 144–169.

Crespi, B.J. (1986) Territoriality and fighting in a colonial thrips, *Hoplothrips pedicularius*, and sexual dimorphism in Thysanoptera. *Ecological Entomology*, 11 (2), 119–130. https://doi.org/10.1111/j.1365-2311.1986.tb00286.x

Crespi, B.J. (1988) Risks and benefits of lethal male fighting in the colonial, polygynous thrips *Hoplothrips karnyi* (Insecta: Thysanoptera). *Behavioral Ecology and Sociobiology*, 22, 293–301. https://doi.org/10.1007/BF00299845

Cruickshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, 21 (5), 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5

Fensome, R.A. (1983) *Miospores from the Jurassic–Cretaceous Boundary Beds, Aklavik Range, Northwest Territories, Canada: Incorporating taxonomic reviews of several groups of Mid- to Late Mesozoic miospores*. Doctoral thesis, University of Saskatchewan, Saskatoon, Canada.

Fraser, D., Soul, L.C., Tóth, A.B., Balk, M.A., Eronen, J.T., Pineda-Munoz, S., Shupinski, A.B., Villaseñor, A., Barr, W.A., Behrensmeyer, A.K., Du, A., Faith, J.T., Gotelli, N.J., Graves, G.R., Jukar, A.M., Looy, C.V., Miller, J.H., Potts, R. & Lyons, S.K. (2021) Investigating biotic interactions in deep time. *Trends in Ecology & Evolution*, 36 (1), 61–75. https://doi.org/10.1016/j.tree.2020.09.001

Grimaldi, D.A. & Vea, I.M. (2021) Insects with 100 million-year-old dinosaur feathers are not ectoparasites. *Nature Communications*, 12, 1469. https://doi.org/10.1038/s41467-021-21751-x

Guo, D.W., Engel, M.S., Shih, C. & Ren, D. (2024) New stenurothripid thrips from mid-Cretaceous Kachin amber (Thysanoptera, Stenurothripidae). *ZooKeys*, 1192, 197–212. https://doi.org/10.3897/zookeys.1192.117754

Haliday, A.H. (1836) An epitome of the British genera in the order Thysanoptera with indications of a few of the species. *Entomological Magazine*, 3, 439–451.

Heming, B.S. (1993) Structure, function, ontogeny and evolution of feeding in thrips (Thysanoptera). *In*: Schaefer, C.W. & Leschen, R.B. (Eds), *Functional Morphology of insect feeding*. Thomas Say Publications in Entomology, pp. 3–41. https://doi.org/10.4182/WEEJ5334.1993.3

Hood, J.D. (1914) Studies in tubuliferous Thysanoptera. *Proceedings of the Biological Society of Washington*, 27, 151–172.

Kirk, W.D.J. (1984) Pollen-feeding in thrips (Insecta: Thysanoptera). *Journal of Zoology*, 204 (1), 107–117. https://doi.org/10.1111/j.1469-7998.1984.tb02364.x

Kirk, W.D.J. & Hamilton, J.G. (2004) Evidence for a male-produced sex pheromone in the western flower thrips *Frankliniella occidentalis*. *Journal of Chemical Ecology*, 30, 167–174. https://doi.org/10.1023/B:JOEC.0000013189.89576.8f

Labandeira, C.C. (1998) How old is the flower and the fly? *Science*, 280, 57–59. https://doi.org/10.1126/science.280.5360.57

Labandeira, C.C. (2000) The paleobiology of pollination and its precursors. *Paleontological Society Papers*, 6, 233–270. https://doi.org/10.1017/S1089332600000784

Labandeira, C.C. (2010) The pollination of Mid Mesozoic seed plants and the early history of long-proboscid insects. *Annals of the Missouri Botanical Garden*, 97 (4), 469–513. https://doi.org/10.3417/2010037

Labandeira, C.C., Kvaček, J. & Mostovski, M.B. (2007) Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms. *Taxon*, 56 (3), 663–695. https://doi.org/10.2307/25065852

Lin, X.D., Labandeira, C.C., Shih, C., Hotton, C.L. & Ren, D. (2019) Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber. *Nature Communications*, 10 (1), 1–14. https://doi.org/10.1038/s41467-019-09236-4

Linné, C. von (1771) *Mantissa plantarum altera generum editionis VI et specierum editionis II*. Laurentius Salvius, Holmiae [= Stockholm], pp. [1–7], pp. 144–588.

Mao, Y.Y., Liang, K., Su, Y.T., Li, J.G., Rao, X., Zhang, H., Xia, F.Y., Fu, Y.Z., Cai, C.Y. & Huang, D.Y. (2018) Various amberground marine animals on Burmese amber with discussions on its age. *Palaeoentomology*, 1 (1), 91–103. https://doi.org/10.11646/palaeoentomology.1.1.11

McGavin, G.C. & Davranoglou, L.-R. (2022) *Essential Entomology*. Oxford University Press, 314 pp.

Milne, M., Walter, G.H. & Milne, J.R. (2002) Mating aggregations and mating success in the flower thrips, *Frankliniella schultzei* (Thysanoptera: Thripidae), and a possible role for pheromones. *Journal of Insect Behavior*, 15, 351–368. https://doi.org/10.1023/A:1016265109231

Moulton, D. (1933) *Oligothrips oreios* a new genus and species of thrips belonging to the family Opadothripidae Bagnall. *Pan-Pacific Entomologist*, 9, 139–140.

Mound, L. (1991) The first thrips species (Insecta, Thysanoptera) from cycad male cones, and its family level significance. *Journal of Natural History*, 25 (3), 647–652. https://doi.org/10.1080/00222939100770411

Mound, L.A. & Marullo, R. (1998) Two new basal-clade Thysanoptera from California with old world affinities. *Journal of the New York Entomological Society*, 106 (2/3), 81–94.

Mound, L.A. & Terry, L.I. (2001) Thrips pollination of the central Australian cycad, *Macrozamia macdonnellii* (Cycadales). *International Journal of Plant Sciences*, 162 (1), 147–154. https://doi.org/10.1086/317899

Mound, L.A., Wang, Z.H., Lima, É.F. & Marullo, R. (2022) Problems with the concept of "pest" among the diversity of pestiferous thrips. *Insects*, 13 (1), 1–17. https://doi.org/ 10.3390/insects13010061

Neems, R.M., Lazarus, J. & McLachlan, A.J. (1992) Swarming behavior in male chironomid midges: a cost-benefit analysis. *Behavioral Ecology*, 3 (4), 285–290. https://doi.org/10.1093/beheco/3.4.285

Nepi, M., Little, S., Guarnieri, M., Nocentini, D., Prior, N., Gill, J., Tomlinson, B.P., Ickert-Bond, M., Pirone, C., Pacini, E. & von Aderkas, P. (2017) Phylogenetic and functional signals in gymnosperm ovular secretions. *Annals of Botany*, 120 (6), 923–936. https://doi.org/10.1093/aob/mcx103

Niassy, S., Tamiru, A., Hamilton, J.G., Kirk, W.D., Mumm, R., Sims, C., De Kogel, W.J., Ekesi, S., Maniania, N.K., Bandi, K., Mitchell, F. & Subramanian, S. (2019) Characterization of male-produced aggregation pheromone of the bean flower thrips *Megalurothrips sjostedti* (Thysanoptera: Thripidae). *Journal of Chemical Ecology*, 45, 348–355. https://doi.org/10.1007/s10886-019-01054-8

Osborn, J.M. & Taylor, T.N. (1995) Pollen morphology and ultrastructure of the Bennettitales: in situ pollen of Cycadeoidea. *American Journal of Botany*, 82 (8), 1074–1081. https://doi.org/10.1002/j.1537-2197.1995.tb11573.x

Peña-Kairath, C., Delclòs, X., Álvarez-Parra, S., Peñalver, E., Engel, M.S., Ollerton, J. & Peris, D. (2023) Insect pollination in deep time. *Trends in Ecology & Evolution*, 38 (8), 749–759. https://doi.org/10.1016/j.tree.2023.03.008

Peñalver, E. & Nel, P. (2010) *Hispanothrips* from Early Cretaceous Spanish amber, new genus of the resurrected family Stenurothripidae (Insecta: Thysanoptera). *Annales de la Société Entomologique de France*, 46 (1-2), 138–147. https://doi.org/10.1080/00379271.2010.10697649

Peñalver, E., Arillo, A., Pérez-de la Fuente, R., Riccio, M.L., Delclòs, X., Barrón, E. & Grimaldi, D.A. (2015) Long-proboscid flies as pollinators of Cretaceous gymnosperms. *Current Biology*, 25, 1917–1923. https://doi.org/10.1016/j.cub.2015.05.062

Peñalver, E., Labandeira, C.C., Barrón, E., Delclòs, X., Nel, P., Nel, A., Tafforeau, P. & Soriano, C. (2012) Thrips pollination of Mesozoic gymnosperms. *Proceedings of the National Academy of Sciences*, 109 (22), 8623–8628. https://doi.org/10.1073/pnas.1120499109

Peñalver, E., Peña-Kairath, C., Barrón, E., Nel, P., Nel, A., Delclòs, X., Peris, D., Solórzano-Kraemer, M.M. & Rodrigo, A. (in press) Diverse Mesozoic thrips carrying pollen during the gymnosperm to angiosperm plant-host ecological shift. *iScience*.

Pergande, T. (1895) Observations on certain Thripidae. *Insect Life*, 7, 390–395.

Peris, D., Pérez-de la Fuente, R., Peñalver, E., Delclòs, X., Barrón, E. & Labandeira, C.C. (2017) False blister beetles and the expansion of gymnosperm-insect pollination modes before angiosperm dominance. *Current Biology*, 27, 897–904. https://doi.org/10.1016/j.cub.2017.02.009

Peris, D., Labandeira, C.C., Barrón, E., Delclòs, X., Rust, J. & Wang, B. (2020) Generalist pollen-feeding beetles during the Mid-Cretaceous. *iScience*, 23, 100913. https://doi.org/10.1016/j.isci.2020.100913

Peris, D., Postigo-Mijarra, J.M., Peñalver, E., Pellicer, J., Labandeira, C.C., Peña-Kairath, C., Pérez-Lorenzo, I., Sauquet, H., Delclòs, X. & Barrón, E. (2024) The role of thermogenesis in the origin of insect pollination. *Nature Plants*, 10, 1297–1303. https://doi.org/10.1038/s41477-024-01775-z

Priesner, H. (1924) Bernstein-Thysanopteren. *Entomologische Mitteilungen*, 13 (4-5), 130–151.

Salzman, S., Crook, D., Crall, J.D., Hopkins, R. & Pierce, N.E. (2020) An ancient push-pull pollination mechanism in cycads. *Science Advances*, 6 (24), eaay6169. https://doi.org/10.1126/sciadv.aay6169

Salzman, S., Whitaker, M., Sierra, A., Bustos Díaz, D.E., Cibrián-Jaramillo, A., Liu, Y., Barona Gómez, F., Zhang, S.Z., Sahu, S. & Villarreal, J.C. (2024) New insights on cycad biology and evolution. *Authorea Preprints*. https://doi.org/10.22541/au.170750032.26264089/v1

Sánchez-García, A., Delclòs, X., Engel, M.S., Bird, G.J., Perrichot, V. & Peñalver, E. (2017) Marsupial brood care in Cretaceous tanaidaceans. *Scientific Reports*, 7, 4390. https://doi.org/10.1038/s41598-017-04050-8

Sánchez-García, A., Peñalver, E., Delclòs, X. & Engel, M.S. (2018) Mating and aggregative behaviors among basal hexapods in the Early Cretaceous. *PLoS One*, 13 (2), e0191669. https://doi.org/10.1371/journal.pone.0191669

Saunders, M.E. (2018) Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. *Insect conservation and diversity*, 11 (1), 13–31. https://doi.org/10.1111/icad.12243

Schliephake, G. (1990) Beiträge zur Kenntnis fossiler Fransenflügler (Thysanoptera) aus dem Bernstein des Tertiär. 1. Beitrag: Stenurothripidae. *Zoologie*, 2 (4), 163–184. https://doi.org/10.1007/BF02985981

Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L. & Li, X.H. (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research*, 37, 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Solórzano-Kraemer, M.M., Peñalver, E., Herbert, M.C., Delclòs, X., Brown, B.V., Aung, N.N. & Peretti, A.M. (2023) Necrophagy by insects in *Oculudentavis* and other lizard body fossils preserved in Cretaceous amber. *Scientific Reports*, 13, 2907. https://doi.org/10.1038/s41598-023-29612-x

Strassen, R. zur (1973) Fossile Fransenflügler aus mesozoischem Bernstein des Libanon (Insecta: Thysanoptera). *Stuttgarter Beiträge zur Naturkunde*, (A), 256, 1–51.

Sullivan, R.T. (1981) Insect swarming and mating. *The Florida Entomologist*, 64 (1), 44–65. https://doi.org/10.2307/3494600

Svensson, B.G. & Petersson, E. (1992) Why insects swarm: testing the models for lek mating systems on swarming *Empis borealis* females. *Behavioral Ecology and Sociobiology*, 31, 253–261. https://doi.org/10.1007/BF00171680

Tang, W. (1987) Insect pollination in the cycad *Zamia pumila* (Zamiaceae). *American Journal of Botany*, 74 (1), 90–99. https://doi.org/10.1002/j.1537-2197.1987.tb08582.x

Terry, L.I. (1997) Host selection, communication and reproductive behaviour. *In*: Lewis, T. (Ed.), *Thrips as crop pest*. CAB International, Wallingford, UK, pp. 65–118.

Terry, L.I. (2001) Thrips and weevils as dual, specialist pollinators of the Australian cycad *Macrozamia communis* (Zamiaceae). *International Journal of Plant Sciences*, 162 (6), 1293–1305. https://doi.org/10.1086/321929

Terry, L.I. (2002) Thrips: the primeval pollinators. *In*: Marullo, R. & Mound, L.A. (Eds), *Thrips and tospoviruses: Proceedings of the 7th International Symposium on Thysanoptera.* Australian National Insect Collection, Canberra, pp. 157–162.

Terry, L.I. (2023) Pollination: Multimodal signaling in a co-dependent thermogenic gymnosperm system. *Current Biology*, 33 (9), R353–R356. https://doi.org/10.1016/j.cub.2023.03.051

Terry, L.I. & Dyreson, E. (1996) Behavior of *Frankliniella occidentalis* (Thysanoptera: Thripidae) within aggregations, and morphometric correlates of fighting. *Annals of the Entomological Society of America*, 89 (4), 589–602. https://doi.org/10.1093/aesa/89.4.589

Terry, L.I. & Gardner, D. (1990) Male mating swarms in *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). *Journal of Insect Behavior*, 3 (1), 133–141. https://doi.org/10.1007/BF01049200

Terry, L.I., Moore, C.J., Roemer, R.B., Brookes, D.R. & Walter, G.H. (2021) Unique chemistry associated with diversification in a tightly coupled cycad-thrips obligate pollination mutualism. *Phytochemistry*, 186, 112715. https://doi.org/10.1016/j.phytochem.2021.112715

Terry, L.I., Roemer, R.B., Booth, D.T., Moore, C.J. & Walter, G.H. (2016) Thermogenic respiratory processes drive the exponential increase of volatile organic compound emissions in *Macrozamia* cycad cones. *Plant, Cell & Environment*, 39 (7), 1588–1600. https://doi.org/10.1111/pce.12730

Terry, L.I., Walter, G.H., Donaldson, J.S., Snow, E., Forster, P.I. & Machin, P.J. (2005) Pollination of Australian *Macrozamia* cycads (Zamiaceae): effectiveness and behavior of specialist vectors in a dependent mutualism. *American Journal of Botany*, 92 (6), 931–940. https://doi.org/10.3732/ajb.92.6.931

Terry L.I., Walter G.H., Hull C. & Moore C. (2008) Responses of pollinating thrips and weevils to specific *Macrozamia* cycad cone volatiles. *In*: Vovides, A.P., Stevenson, D.W.M. & Osborne, R. (Eds), *The 7th International Conference on Cycad Biology*. Memoirs of The New York Botanical Garden, 97. The New York Botanical Garden Press, New York, pp. 346–371.

Terry, L.I., Walter, G.H., Moore, C., Roemer, R. & Hull, C. (2007) Odor-mediated push-pull pollination in cycads. *Science*, 318 (5847), 70. https://doi.org/10.1126/science.1145147

Tihelka, E., Li, L., Fu, Y., Su, Y., Huang, D. & Cai, C. (2021) Angiosperm pollinivory in a Cretaceous beetle. *Nature Plants*, 7 (4), 445–451. https://doi.org/10.1038/s41477-021-00893-2

Tong, T., Shih, C. & Ren, D. (2019) A new genus and species of Stenurothripidae (Insecta: Thysanoptera: Terebrantia) from mid-Cretaceous Myanmar amber. *Cretaceous Research*, 100, 184–191. https://doi.org/10.1016/j.cretres.2019.03.005

Toon, A., Terry, L.I., Tang, W., Walter, G.H. & Cook, L.G. (2020) Insect pollination of cycads. *Austral Ecology*, 45 (8), 1033–1058. https://doi.org/10.1111/aec.12925

Trichilo, P.J. & Leigh, T.F. (1988) Influence of resource quality on the reproductive fitness of flower thrips (Thysanoptera: Thripidae). *Annals of the Entomological Society of America*, 81 (1), 64–70. https://doi.org/10.1093/aesa/81.1.64

Yu, T.T., Thomson, T., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F.Y., Zhang, H.C., Wang, B. & Dilcher, D. (2019) An ammonite trapped in Burmese amber. *Proceedings of the*

National Academy of Sciences, 116 (23), 11345–11350. https://doi.org/10.1073/pnas.1821292116

Zavialova, N. & Van Konijnenburg-van Cittert, J.H.A. (2011) Exine ultrastructure of in situ peltasperm pollen from the Rhaetian of Germany and its implications. *Review of Palaeobotany and Palynology*, 168, 7–20. https://doi.org/10.1016/j.revpalbo.2011.09.007

Zheng, D.R., Chang, S.-C., Perrichot, V., Dutta, S., Rudra, A., Mu, L., Thomson, U., Li, S.C., Zhang, Q., Zhang, Q.Q., Wong, J., Wang, J., Wang, H., Fang, Y., Zhang, H.C. & Wang, B. (2018) A Late Cretaceous amber biota from central Myanmar. *Nature Communications*, 9, 3170. https://doi.org/10.1038/s41467-018-05650-2