



*Zootaxa* 5489 (1): 001–203

<https://www.mapress.com/j/zt/>

Copyright © 2024 Magnolia Press

# Monograph

ISSN 1175-5326 (print edition)

**ZOOTAXA**

ISSN 1175-5334 (online edition)

<https://doi.org/10.11646/zootaxa.5489.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:9FB55FC2-4379-438A-9707-C20991DC7959>

# ZOOTAXA

5489

**Honoring Laurence Mound's 90<sup>th</sup> Birthday**

ADRIANO CAVALLERI (ED.)

*Universidade Federal do Rio Grande, Rio Grande, RS, Brazil.*

[✉ cavalleri\\_adriano@yahoo.com.br](mailto:cavalleri_adriano@yahoo.com.br); [🌐 https://orcid.org/0000-0003-4163-6745](https://orcid.org/0000-0003-4163-6745)

5489 (1): 099 – 106

**Late Cretaceous thrips (Thysanoptera) from Hti Lin amber**

MANFRED R. ULITZKA



Magnolia Press  
Auckland, New Zealand

*Published: 31 Jul. 2024*



## Late Cretaceous thrips (Thysanoptera) from Hti Lin amber

MANFRED R. ULITZKA

*Thrips-iD*, *Straßburger Straße 37A, 77652 Offenburg, Germany.*✉ [manfred.ulitzka@thysanoptera.de](mailto:manfred.ulitzka@thysanoptera.de); <https://orcid.org/0000-0002-2639-4867>

### Abstract

The present study provides a first investigation of fossil thrips from the Late Cretaceous. It deals with two specimens—*Avithrips yellae* **gen. et sp. n.** and *Campanithrips kyakhei* **gen. et sp. n.**—which are preserved as inclusions in Campanian Hti Lin (or Tilin) amber from Myanmar. Their taxonomic classification in the families Melanthripidae and Stenurothripidae, as well as an adhering pollen grain suggest that both thrips may have been associated with flowers.

**Key words:** Campanian, Melanthripidae, Stenurothripidae, Tilin amber

### Introduction

Amber from Myanmar mainly comes from the Hukawng valley (i.e. the Hukawng Basin), Kachin Province. This type of amber, known as ‘Burmite’ contains a unique paleontological diversity that has been described in numerous studies (e.g. Grimaldi *et al.* 2002; Ross *et al.* 2010; Guo *et al.* 2017; Ross 2019, 2020, 2021, 2022, 2023). Burmite is about 99 million years old (i.e. Cenomanian), and this oft-quoted age comes from radiometric dating of the volcanoclastic deposits of this amber (Cruikshank & Ko 2003; Shi *et al.* 2012). Other deposits of the same age are known from several regions in Myanmar, but unlike the Hukawng deposits, none of these sources have produced notable quantities of amber. Compared to typical Burmite, two types of amber from Myanmar, however, are notable due to their different ages: Hkamti amber from northern Myanmar, which is considered older (about 110 million years, i.e. Albian) and Hti Lin (or Tilin) amber, which is much younger, and is discussed in more detail hereafter (Zheng *et al.* 2018; Xing & Qiu 2020). The deposit of the latter, known as ‘Kyakhe’ (meaning ‘tiger bite’), was discovered in 2010–2011. It is part of the Cretaceous Kabaw formation and is located close to the township Hti Lin in the Magway Region of central Myanmar (21°41′44.6″N 94°5′47″E). Hti Lin amber is hosted in thin coal seams within shale layers and is usually found in pieces smaller than 10cm; it is mined at a depth of up to 15m to 20m (Tay *et al.* 2015). Zircons from a tuff sample collected just above one of the amber-bearing layers, yielded an age of  $72.1 \pm 0.3$  Ma, (i.e. very close to the Campanian-Maastrichtian boundary) suggesting an uppermost Campanian origin for the underlying amber-bearing layers. This age determination, furthermore, is supported by finds of ammonites of the genus *Sphenodiscus* preserved in nodules of brown sandstone underlying the amber layers; these ammonites are widely considered to be restricted to the Maastrichtian. According to these findings, Hti Lin amber is about 72.1 million years old and thus, at least 27 million years younger than Kachin amber, i.e. ‘Burmite’ (Zheng *et al.* 2018). Based on its chemical composition, Hti Lin amber originates from gymnosperms. Hence, it indicates that gymnosperms were still abundant in the equatorial forests of the latest Campanian, although Angiosperms diversified explosively during the mid-Cretaceous and became dominant in forests worldwide by the Maastrichtian (Zheng *et al.* 2018). At present, there is barely any knowledge from this period, as Campanian amber is not common with only a few occurrences worldwide (see Damgaard 2023). The amber of Hti Lin thus provides valuable insight into the vanishing—or at least considerably transforming—tropical forest of the latest Campanian and its biota. Zheng *et al.* (2018) analysed the inclusions of about 5kg of Hti Lin amber and found 52 arthropod and plant fossils. Among them, 34 insects were identified to order level, with a remarkable diversity of 12 families in Hymenoptera, Diptera, Hemiptera, Psocoptera, Coleoptera, Blattaria, Mantodea and Neuroptera. Thysanoptera have not been found so far.

In our current knowledge the history of Thysanoptera *sensu stricto* dates back to the Triassic (Grimaldi *et al.* 2004). From this era, however, only two fossils have been described and another two from younger Jurassic deposits (see Ullitzka 2018, p. 550). During these periods, the Lophioneurida still were much more common and thus appear more frequently in fossil records. The latter insects represent an extinct group closely related to Thysanoptera (Ullitzka 2021). They are discussed as an immediate, ancestral thysanopteran clade, a stemgroup of modern thrips or an early paraphyletic lineage (Wang *et al.* 2009); the actual relationship between both, however, is a contentious issue (Grimaldi & Engel 2005). The decline of the Lophioneurida is evident since the Early Cretaceous, while the Thysanoptera finally became increasingly diverse (Zherikhin 2002). Today, this diversity is reflected in the fossils of various amber deposits, but only a few thrips have actually been studied in detail.

From Lower Cretaceous amber about a dozen species are known, most of which are even attributable to modern thysanopteran families (zur Strassen 1973; Nel *et al.* 2010, 2021; Peñalver & Nel 2010; Peñalver *et al.* 2012, 2022; see also Bhatti 2006). Numerous thrips are also known from the lower stages of the Upper Cretaceous, including twenty species—mainly Tubulifera—described from Cenomanian Burmite (Ullitzka 2018, 2019, 2022; Tong *et al.* 2019) and one species from the Turonian amber of New Jersey (Grimaldi *et al.* 2004). Particularly in Burmese Kachin amber, thrips are quite common, and it has to be noted that the author's collection contains at least 25 other new species (mainly Terebrantia) still awaiting their description. Moreover, one species (*Myanmarothrips pankowskiorum* Ullitzka) from this amber is known from countless chunks and it sometimes occurs with impressively high abundance; a phenomenon possibly caused by mass flights during swarming (Ullitzka 2018, 2023a).

No thrips species have yet been described from younger stages of the Upper Cretaceous (i.e. from Coniacium or later), and no fossil records of this insect order have been published either. The author's collection includes some specimens from Campanian amber, which was collected from a deposit at the Neuse River in North Carolina, USA (see Krynicki 2013; Szadziwski 2017; Ullitzka 2023b); but these have not yet been studied in detail. Thus, it is an open question how the Thysanoptera have evolved during the last periods of the Cretaceous, and how they adapted later to the new conditions resulting from the K-Pg extinction event. In general, the gap of about 24 million years between the early Campanian and the early Eocene poses great challenges to our understanding of the evolution of insect faunas (Zheng *et al.* 2018)—thrips faunas are no exception. With two new thrips species from Campanian Hti Lin amber, this work provides first clues to expand our knowledge regarding the Thysanoptera from the younger stages of the Upper Cretaceous.

## Material and Methods

The inclusions discussed below are part of the author's Thysanoptera collection. Both specimens were donations from Patrick Müller, Käßhofen, Germany. Detailed information on the fossils is included below. Numbers following a prefixed "MU-Fos-" refer to serial numbers in the author's collection.

Both fossils have been prepared according to Ullitzka (2015, 2023c). To increase visibility during microscopic examination, however, the samples have been ground much thinner than outlined in these earlier descriptions. Rough abrading was carried out using a water-fed flat lap; the fine works, however, were done by hand with wet grindstones (grit 3,000, 5,000 and 10,000). Afterward, the slices were polished with whiting (calcium carbonate powder) on a slightly moistened cotton cloth and finally embedded in XOR-Polyester-Resin (S-Kresin 2410, manufacturer: S u. K Hock GmbH, Regen, Germany) to prevent decomposition and oxidation of the amber.

The fossils were examined and measured using a Zeiss Stemi SV-11 Apo stereomicroscope and a Zeiss standard microscope with the following objectives: Zeiss Neofluar 6.3/0.20 160/-, Zeiss Plan 10/0.22 160/-, Zeiss Plan 16/0.35 Ph2 160/0.17, Nikon M Plan 20 0.4 ELWD 210/0 and Nikon M Plan 40 0.5 ELWD 210/0. Illumination involved merging transmission light with two or three white-light-LED incident illuminators. White paper was used as a diffuser for incident illumination to prevent reflections in the amber; different coloured paper sheets were inserted under the sample with transmission light to achieve better contrast between the inclusion and the yellowish amber. Images were taken with a digital camera (Canon EOS 70d) attached to the microscope, and these were produced using Helicon Focus software. Adobe Photoshop and Topaz Photo AI were used for final colour adjustment and sharpening.

## Sub-Order Terebrantia

### Melanthripidae Bagnall

#### *Avithrips* gen. n.

Type species. *Avithrips yellae* gen. et sp. n.

**Diagnosis.** Head with mouth cone exceptionally long, reaching back to the base of abdomen. Antennae nine-segmented with the distal segments fully distinct from each other; segments I–III distinctly stronger than distal segments; III distally with a structure interpreted as a transverse sensorium (sensoria not visible on IV). Setae on head and pronotum not assessable; one longer seta visible at the hind margin of pronotum. Fore wings with broadly rounded tips; front margin without wing fringes; longitudinal veins complete; with cross veins. Wing surface covered with microtrichia. Fore femora slender; fore tarsus without hamus. Abdominal segment VIII with ovipositor curved upwards.

Based on the above-mentioned character states of the fore wings and the shape of the ovipositor *Avithrips* gen. n. is attributed to Melanthripidae (see Bhatti 2006), even though some of the plesiomorphic features present in members of this thysanopteran family are not visible on the holotype due its lateral position in the amber matrix. Regarding the antennae, the basal segments of *Avithrips* gen. n. are stronger than usual in Melanthripidae. The shape of the structure on segment III, which is interpreted as a distal antennal sensorium, however, would support the here proposed classification.

With its long mouth cone *Avithrips* gen. n. resembles *Proboscisthrips mammuthoides* Ullrich from Baltic Eocene amber. However, the latter has the major setae on abdominal tergites IX and X much stronger. Moreover, the abdominal segment IX of *P. mammuthoides* is longer and covered with dense rows of microtrichia (Ullrich 2017). Most cephalic and pronotal setae of *Avithrips* gen. n. are not assessable and at least the head setae might be short. Regarding this feature, *Avithrips* gen. n. differs from most members of Melanthripidae, except for some species like *Cranothrips bellisi* Mound & Marullo (see Pereyra & Mound 2009). Compared to those, however, the antennae of *Avithrips* gen. n. are different.

**Etymology.** The name of the new genus comes from the Latin word *avis*, meaning ‘bird’ and *-thrips*, the usual term for a genus within Thysanoptera. It refers to the long and bird-beak-like mouth cone of the type species.

#### *Avithrips yellae* gen. et sp. n.

(Fig. 1)

**Female.** Preserved in lateral position in the amber matrix. Body fully distended; fore wings spread backwards, hind wings close to body and thus not assessable; hind legs spread, others bent under thorax. Head slightly turned to the right, with mouth cone directed backwards. Abdomen bent upwards; ovipositor protruding ventrally. Abdomen distally on the left side of the specimen covered with numerous tiny pyrite crystals.

**Colour.** Body, legs and antennae uniformly brownish, but in some parts difficult to assess due to shiny layers around the fossil; wing veins, fringes and setae dark; membrane of fore wing translucent with a light brownish shade.

**Head.** Vertex sculptured with transverse striae; without any long setae; compound eyes distinctly protruding at front margin, not prolonged ventrally; ocelli much larger than ommatidia; antennae attached ventrally. Mouth cone exceptionally long, reaching back to the base of abdomen; it could not be assessed whether the stylet-like structures in front of the mouth cone represent maxillae and the mandibula that have been squeezed out or slender maxillary palps. Antennae nine-segmented; segment I not assessable (covered laterally by compound eyes), II barrel shaped; III inversely conical at base and slightly tapering from the middle towards the distal edge; IV–V similarly shaped as III but much smaller (particularly IV), IV with a short pedicle; V–VI long and slender, VII vase-shaped; VIII about as long as VII, style-shaped. Sensoria not clearly assessable; III with a structure that may be interpreted as a transverse sensorium close to the distal edge. Pronotum long and slender; sculptured with transverse striae; with at least one pair of longer (presumably posteroangular) setae at hind margin. Fore wings, with at least two clearly visible

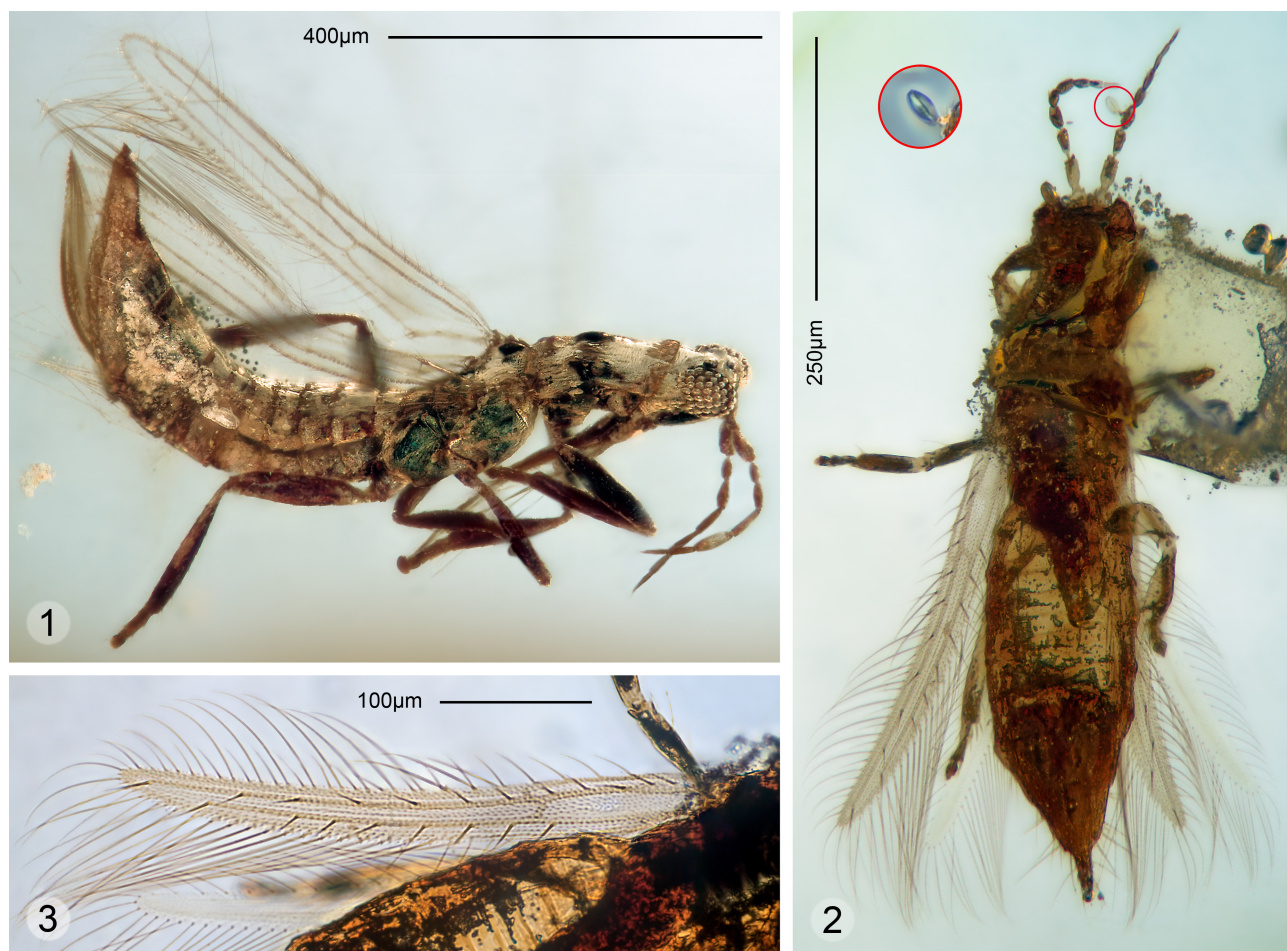
cross-veins and two faint structures also interpretable as cross-veins; first vein with number of setae not assessable; second vein with 9 setae; costa with about 25 setae; wing fringes present only on the posterior margin; fringe hairs straight. All legs long and slender; tarsi two-segmented; fore tarsus without a hamus. Abdominal segment VIII with a distinctly strong, broad and upwards curved ovipositor.

**Measurements.** Female (in microns): Body, length 835. Head, length 80. Eyes, length 65. Hind ocelli, diameter 15; fore ocellus, diameter 10. Mouth cone, length 295. Pronotum, length 140; posteroangular (?) setae about 30 (difficult to measure). Abdomen, length 480. Ovipositor, length 260. Antennae, length about 250; length (largest width) of segment I and II not measurable, III 35 (15), IV 25 (10), V 30 (10), VI 35 (10), VII 35 (10), VIII 30 (10), IX 30 (5). Fore wings, length 525; largest width 65.

**Material studied.** Holotype female MU-Fos-128/1; inclusion in Hti Lin amber, Magway Region, Myanmar. The holotype was donated by Patrick Müller and is located in the author's collection.

**Syninclusions.** Some small droplets, air bubbles and brownish stains of unknown origin; numerous pyrite crystals along the left side of the distal abdominal segments of the thrips inclusion.

**Etymology.** *A. yellae* **gen. et sp. n.** is dedicated to Yella Bernet, in gratitude for all the precious moments and her loving and constant companionship.



**FIGURES 1–3.** New Terebrantia from Hti Lin amber. (1) *Avitrips yellae* **gen. et sp. n.** holotype female (MU-Fos-128/1), lateral view. (2–3) *Campanithrips kyakhei* **gen. et sp. n.** holotype female (MU-Fos-129/1); (2) dorsal view, encircled red: pollen grain attached to the antenna of the thrips; (3) left fore wing.

## Stenurothripidae Bagnall

### *Campanithrips* **gen. n.**

Type species. *Campanithrips kyakhei* **gen. et sp. n.**

**Diagnosis.** Head with eyes protruding over the base of antennae. Antennae nine-segmented with the distal segments fully distinct from each other; segment III distally with broad sense cone (sensoria not visible on IV). Setae on head and pronotum not assessable (at least some longer posteromarginal or posteroangular setae present). Mouth cone short and rounded. Fore wings with softly pointed tips; hind and front margin with straight wing fringes; costal setae long, about as long as wing width in the middle; both longitudinal veins complete but with a slightly larger gap between the penultimate and the distal seta; with two (visible) cross veins. Fore wing surface with microtrichia. Fore femora slender; fore tarsi with hamus.

Based on the above-mentioned character states of the fore wings and the broad sense cones *Campanithrips gen. n.* is attributed to Stenurothripidae (see Bhatti 2006). At present, this family comprises ten fossil and three extant genera (Mound & Hastenpflug-Vesmanis 2021). *Campanithrips gen. n.* differs from all fossil genera by the straight fringes on the hind margin of the fore wings (Schliephake 1990, p. 180; Peñalver & Nel 2010; Tong *et al.* 2019; Guo *et al.* 2024) and is thus more similar to extant forms. Compared with extant *Holarthrothrips* Bagnall and *Oligothrips* Moulton the new genus has less setae on the wing veins, but these are much longer and stronger than in *Heratythrips* Mound & Marullo.

**Etymology.** The name *Campanithrips gen. n.* refers to the Campanian origin of amber and is combined with *-thrips*, the usual term for a genus within Thysanoptera.

### ***Campanithrips kyakhei gen. et sp. n.***

(Figs 2–3)

*Female.* Preserved in dorso-ventral position. Body fully distended; wings slightly spread apart from body, laterally overlapping abdomen on the right side. Hind legs and left mid leg spread, others bent under body or head, respectively. Posterior right side of head and thorax largely hidden by opaque streaks and bubbles. Left antenna bent inwards; most antennal segments permeated by air inclusions. Median parts of abdomen translucent.

**Colour.** Body, legs and antennae uniformly yellowish brown; major body setae pale, fringes and wing setae dark; wings shaded, veins slightly darker than wing membrane.

Head (Fig. 2) about as long as wide, with compound eyes largely protruding anteriorly. Sculpture, ocelli and head setae not assessable. Mouth cone short and rounded. Antennae 9-segmented; segment I slightly conical; II basally with a short but rather strong pedicle, then reverse conically widened and almost parallel in the middle, apically with a narrow, recessed ring; III with a pedicle at base, then inverted conical, distally asymmetrical due to the attachment of a large exterior sense cone. IV–VI (including VII on the left) decreasing in diameter, rounded, each much longer than wide. Sense cone on IV not assessable, only its area of attachment visible; V–VII with long setae; VIII inverse conical; XI style-shaped. Pronotum wider than long; pronotal chaetotaxy as well as pterothoracic structure not assessable. Fore wings (Fig. 3) narrow but somewhat widened in basal third, distally from the middle slightly bent forwards, tip softly pointed; with two cross veins (RP1 not visible or not developed; see Nel *et al.* 2012); first vein with a complete row of 12, second vein with 8 setae, both veins offset by a gap between the last and the penultimate, giving the impression of one missing seta; costa with a row of 18 long setae; wing fringes straight; wing membrane with microtrichia; clavus not assessable. Hind wing (Fig. 3) setae straight; membrane without microtrichia. Fore legs with femora not enlarged; femora and tibiae with curved setae on outer edge; fore tarsi not clearly assessable, however, with hamus. Mid legs slender; femora with 3, tibiae with 4 long ventral setae; tarsi two-segmented. Hind legs slender; tibiae with a row of 3 setae and a pair of distal spines; tarsi two-segmented. Abdomen not assessable in terms of sculpture and chaetotaxy; segments VIII and IX cone-shaped, X distinctly prolonged; distal abdominal setae long and pointed; ovipositor strong.

**Measurements.** Female (in microns): Body, length 665. Head, length 80; largest width 100. Eyes, length 55; width about 35. Pronotum, length and setae not measurable; width 110. Pterothorax not measurable. Abdomen, length 405; largest width 145 (segment V); segment X length 40. Setae on tergite IX, s1 45, s2 30, s3 55. Antennae, length 180; length (largest width) of segment I 15 (15), II 35 (15), III 25 (10), IV 25 (10), V 20 (10), VI 20 (10), VII 15 (10), VIII 15 (5), IX 15 (5). Sense cones (segment III), length 5; basal width 5. Fore wings, length 455; width in the middle 35; costal setae about 30.

**Material studied.** Holotype female MU-Fos-129/1; inclusion in Hti Lin amber, Magway Region, Myanmar. The holotype was donated by Patrick Müller and is stored in the author's collection.

**Syninclusions.** Parts of an insect leg, some small brownish droplets, air bubbles, brownish stains of unknown origin, numerous tiny crystal-like particles and a pollen grain (Fig. 3) attached to the right antenna of the thrips inclusion (similar in shape to pollen of extant *Cycas* or respectively Cycadaceae; length 22, width 9 microns (see APSA Members 2007; Vovides *et al.* 2021).

**Etymology.** The species epithet *kyakhei* was chosen in honour of the amber deposit ‘Kyakhe’ (meaning ‘tiger bite’) from which this fossil originates.

## Conclusion

Both families, to which the new genera are assigned, have existed at least since the Mid Cretaceous and are still present in the current faunas (Peñalver *et al.* 2012; Tong *et al.* 2019; Nel *et al.* 2021). Their extant members are phytophagous, feeding and breeding within flowers (Mound & Tree 2020 a, b), and this might lead to the assumption that the fossil species described here may have also been flower-living. The latter presumption seems to be supported by the *Cycas*-like pollen grain adhering to the antenna of *C. kyakhei* **gen. et sp. n.**, and it is known that some extant thrips are associated with Cycads and even contribute to their pollination (Mound & Terry 2001; see also Peñalver *et al.* 2012). In contrast, no food and thus habitat preference can be deduced from the long mouth cone of *A. yellae* **gen. et sp. n.** Similarly shaped mouth cones are known from flower-living species (e.g. *Rhinothripiella ctenifera* zur Strassen) as well as from leaf feeders (e.g. *Neohydathrips catenatus* (Hood)) and also from species associated with fungi (e.g. *Poecilothrips albopictus* Uzel). Up to date, no correlations between this character state and foraging or ingestion have been studied.

The two specimens studied here provide a first insight into the Thysanoptera of the Late Cretaceous and allow some conclusions to be drawn. Further investigation, however, will be necessary to understand the Thysanoptera faunas of this important era of transition.

## Acknowledgements

I would like to thank Patrick Müller, Kāshofen, Germany for his generous donations of the specimens described in this paper. Furthermore, I express my sincere thanks to Laurence A. Mound, CSIRO, Canberra, Australia for numerous discussions inspiring this work. I also would like to thank Bert Vierbergen, Netherlands Institute for Vectors, Invasive plants and Plant health, Wageningen, Netherlands for the idea of naming the genus with the remarkably long mouth cone *Avithrips*. Moreover, I am grateful to Derek Binns, Hastings, UK for the linguistic revision of this paper.

## References

- APSA Members (2007) *The Australasian Pollen and Spore Atlas. Version 1.0*. Australian National University, Canberra. Available from: <https://apsa.anu.edu.au/samples/sample.php?id=301-4-4> (accessed 29 December 2023)
- Bhatti, J.S. (2006) The classification of Terebrantia (Insecta) into families. *Oriental Insects*, 40, 339–375. <https://doi.org/10.1080/00305316.2006.10417487>
- Cruickshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, 21, 441–455. [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)
- Damgaard, A.L. (2023) Amber – a window to the past: More than 150 different types of amber in the world. Available from: <https://amber-fossils.com/types-and-mines> (accessed 27 February 2023)
- Grimaldi, D.A., Shmakov, A. & Fraser, N. (2004) Mesozoic thrips and early evolution of the order Thysanoptera (Insecta) *Journal of Paleontology*, 78, 941–952. [https://doi.org/10.1666/0022-3360\(2004\)078%3C0941:MTAEEO%3E2.0.CO;2](https://doi.org/10.1666/0022-3360(2004)078%3C0941:MTAEEO%3E2.0.CO;2)
- Grimaldi, D.A. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, Cambridge, New York, Melbourne, 755 pp.
- Grimaldi, D.A., Engel, M.S. & Nascimbene, P.C. (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, 3361, 1–71. <https://hdl.handle.net/2246/2914>

- Guo, D., 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>
- Guo, M., Xing, L., Wang, B., Zhang, W., Wang, S., Shi, A. & Bai, M. (2017) A catalogue of Burmite inclusions. *Zoological Systematics*, 42 (3), 249–379.  
<https://doi.org/10.1186/zs.201715>
- Krynicky, V.E. (2013) Primitive ants (Hymenoptera: Sphecomyrminae) in the Campanian (Late Cretaceous) of North Carolina (USA). *Life: The Excitement of Biology*, 1, 156–165.  
[https://doi.org/10.9784/LEB1\(3\)Krynicky.03](https://doi.org/10.9784/LEB1(3)Krynicky.03)
- Mound, L.A. & Marullo, R. (1999) Two new basal-clade Thysanoptera from California with Old World affinities. *Journal of the New York entomological Society*, 106, 81–94.
- Mound, L.A. & Hastenpflug-Vesmanis, A. (2021) All genera of the world: Order Thysanoptera (Animalia: Arthropoda: Insecta). *Megataxa*, 6 (1), 2–69.  
<https://doi.org/10.11646/megataxa.6.1.2>
- Mound, L.A. & Terry, I. (2001) Thrips pollination of the Central Australian Cycad, *Macrozamia macdonnellii* (Cycadales). *International Journal of Plant Sciences*, 162, 147–154.  
<https://doi.org/10.1086/317899>
- Mound, L.A. & Tree, D.J. (2020a) *Thysanoptera Australiensis – Thrips of Australia*. Lucidcentral.org, Identic Pty Ltd., Queensland. Available from: [https://keys.lucidcentral.org/keys/v3/thrips\\_australia/keys/Thysanoptera\\_Families/key/thysanoptera\\_families/Media/Html/entities/Stenurothripidae.htm](https://keys.lucidcentral.org/keys/v3/thrips_australia/keys/Thysanoptera_Families/key/thysanoptera_families/Media/Html/entities/Stenurothripidae.htm) (accessed 29 December 2023)
- Mound, L.A. & Tree, D.J. (2020b) *Thysanoptera Australiensis – Thrips of Australia*. Lucidcentral.org, Identic Pty Ltd., Queensland. Available from: [https://keys.lucidcentral.org/keys/v3/thrips\\_australia/keys/Thysanoptera\\_Families/key/thysanoptera\\_families/Media/Html/entities/Melanthripidae.htm](https://keys.lucidcentral.org/keys/v3/thrips_australia/keys/Thysanoptera_Families/key/thysanoptera_families/Media/Html/entities/Melanthripidae.htm) (accessed 29 December 2023)
- Nel, P., Azar, D., Prokop, J., Roques, P., Hodebert, G. & Nel, A. (2012) From Carboniferous to Recent: wing venation enlightens evolution of thysanopteran lineage. *Journal of Systematic Palaeontology*, 10 (2), 385–399.  
<https://doi.org/10.1080/14772019.2011.598578>
- Nel, P., Peñalver, E., Azar, D., Hodebert, G. & Nel, A. (2010) Modern thrips families Thripidae and Phlaeothripidae in Early Cretaceous amber (Insecta: Thysanoptera). *Annales de la Société entomologique de France, New Series*, 46 (1–2), 154–163.  
<https://doi.org/10.1080/00379271.2010.10697651>
- Nel, P., Schubnel, T., Perrichot, V. & Nel, A. (2021) *Ankothrips*, the most ancient extant thrips genus (Thysanoptera, Melanthripidae). *Papers in Palaeontology*, 15, 825–837.  
<https://doi.org/10.1002/spp2.1320>
- 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 of the United States of America*, 109 (22), 8623–8628.  
<https://doi.org/10.1073/pnas.1120499109>
- Peñalver, E., Nel, A. & Nel, P. (2022) An apterous Tubulifera (Insecta, Thysanoptera, Phlaeothripidae) preserved in Spanish Cretaceous amber. *Historical Biology*, 34 (8), 1381–1387.  
<https://doi.org/10.1080/08912963.2021.2023139>
- Peñalver, E. & Nel, P. (2010) *Hispanothrips* from Early Cretaceous Spanish amber, a new genus of the resurrected family Stenurothripidae (Insecta: Thysanoptera). *Annales de la Société Entomologique de France*, 46, 1–10.  
<https://doi.org/10.1080/00379271.2010.10697649>
- Pereyra, V. & Mound, L.A. (2009) Phylogenetic relationships within the genus *Cranothrips* (Thysanoptera, Melanthripidae) with consideration of host associations and disjunct distributions within the family. *Systematic Entomology*, 34, 151–161.  
<https://doi.org/10.1111/j.1365-3113.2008.00445.x>
- Ross, A.J., Mellish, C., York, P. & Crighton, B. (2010) *Burmese amber*. In: Penny, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 208–235.
- Ross, A.J. (2019) Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology*, 2 (1), 22–84.  
<https://doi.org/10.11646/palaeoentomology.2.1.5>
- Ross, A.J. (2020) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019. *Palaeoentomology*, 3 (1), 103–118.  
<https://doi.org/10.11646/palaeoentomology.3.1.14>
- Ross, A.J. (2021) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2020. *Palaeoentomology*, 4 (1), 57–76.  
<https://doi.org/10.11646/palaeoentomology.4.1.11>
- Ross, A.J. (2022) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2021. *Palaeoentomology*, 5 (1), 27–45.  
<https://doi.org/10.11646/palaeoentomology.5.1.4>
- Ross, A.J. (2023) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2022. *Palaeoentomology*, 6 (1), 22–40.

<https://doi.org/10.11646/palaeontomology.6.1.6>

- Schliephake, G. (1990) Beiträge zur Kenntnis fossiler Fransenflügler (Thysanoptera, Insecta) aus dem Bernstein des Tertiär. 1. Beitrag: Stenurothripidae. *Zoology (Journal of Pure and Applied Zoology)*, 2, 163–184.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. (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>
- zur Strassen, R. (1973) Fossile Fransenflügler aus mesozoischem Bernstein des Libanon (Insecta: Thysanoptera). *Stuttgarter Beiträge zur Naturkunde*, 256, 1–51.
- Szadziewski, R., Krynicki, V.E. & Krzemiński, W. (2017) The latest record of the extinct subfamily Eoptychopterinae (Diptera: Ptychopteridae) from Upper Cretaceous amber of North Carolina. *Cretaceous Research*, 82, 1–5.  
<https://doi.org/10.1016/j.cretres.2017.10.011>
- Tay, T.S., Kleismantas, A., Nyunt, T.T., Minrui, Z., Krishnaswamy, M. & Ying, L.H. (2015) Burmese amber from Hti Lin. *Journal of Gemmology*, 34 (7), 606–615.  
<https://doi.org/10.15506/JoG.2015.34.7.606>
- 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>
- Ulitzka, M.R. (2015) Two new species of Aeolothripidae from Baltic Tertiary amber (Insecta: Thysanoptera). *Palaeodiversity*, 8, 89–94.
- Ulitzka, M.R. (2017) Revision of the fossil Melanthripidae from Baltic Tertiary (Eocene) amber including a new genus (Insecta: Thysanoptera). *Entomologische Zeitschrift*, 127, 205–212.
- Ulitzka, M.R. (2018) A first survey of Cretaceous thrips from Burmese amber including the establishment of a new family of Tubulifera (Insecta: Thysanoptera). *Zootaxa*, 4486 (4), 548–558.  
<https://doi.org/10.11646/zootaxa.4486.4.8>
- Ulitzka, M.R. (2019) Five new species of *Rohrthrips* (Thysanoptera: Rohrthripidae) from Burmese amber, and the evolution of Tubulifera wings. *Zootaxa*, 4585 (1), 27–40.  
<https://doi.org/10.11646/zootaxa.4585.1.2>
- Ulitzka, M.R. (2021) All genera of the world: Order †Lophioneurida—fossil out-groups of Thripida (Animalia: Arthropoda: Insecta). *Megataxa*, 6 (1), 70–72.  
<https://doi.org/10.11646/megataxa.6.1.3>
- Ulitzka, M.R. (2022) New genera and species of Rohrthripidae (Thysanoptera: Tubulifera) from Burmese Cretaceous amber. *Zootaxa*, 5162 (1), 1–36.  
<https://doi.org/10.11646/zootaxa.5162.1.1>
- Ulitzka, M.R. (2023a) Thrips-*iD*: †*Myanmarothrips pankowskiorum*. Available from: <https://www.thrips-id.com/en/myanmarothrips-pankowskiorum/> (accessed 9 March 2023)
- Ulitzka, M.R. (2023b) Thrips-*iD*: Fossils. Available from: <http://www.thrips-id.com/en/photo-video/fossils/> (accessed 11 March 2023)
- Ulitzka, M.R. (2023c) Thrips-*iD*: Fossile Thripse. Available from: <http://www.thrips-id.com/de/sammlung/fossile-thripse/> (accessed 11 March 2023)
- Vovides, A.P., Guevara, R., Coiro, M., Galicia, S. & Iglesias, C. (2021) Pollen morphology of the Megamexican cycads reveals the potential of morphometrics to identify cycad genera. *Botanical Sciences*, 99 (1), 182–197.  
<https://doi.org/10.17129/botsci.2696>
- Wang, J., Labandeira, C.C., Zhang, G., Bek, J. & Pfefferkorn, H.W. (2009) Permian *Circulipuncturites discinispuris* Labandeira, Wang, Zhang, Bek et Pfefferkorn gen. et spec. nov. (formerly *Discinispora*) from China, an ichnotaxon of a punch-and-sucking insect on Noeggerathialean spores. *Review of Palaeobotany and Palynology*, 156, 277–282.  
<https://doi.org/10.1016/j.revpalbo.2009.03.006>
- Xing, L. & Qiu, L. (2020) Zircon U-Pb age constraints on the mid-cretaceous Hkamti amber biota in northern Myanmar. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 558, 109960.  
<https://doi.org/10.1016/j.palaeo.2020.109960>
- Zheng, D., Chang, S.-C., Perrichot, V., Dutta, S., Rudra, A., Mu, L., Kelly, R.S., Li, S., Zhang, Q., Zhang, Q., Wong, J., Wang, J., Wang, H., Fang, Y., Zhang, H. & Wang, B. (2018) A Late Cretaceous amber biota from central Myanmar. *Nature Communications*, 9, 1–6.  
<https://doi.org/10.1038/s41467-018-05650-2>
- Zherikhin, V.V. (2002) *Order Thripida Fallen, 1914 (=Thysanoptera Haliday, 1836). The Thrips*. In: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston and London, pp. 133–143.