Zootaxa 5162 (1): 001–036
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5162.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:94DAF833-90C6-4AC8-B92A-0313F173064B

New genera and species of Rohrthripidae (Thysanoptera: Tubulifera) from Burmese Cretaceous amber

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Abstract

The Rohrthripidae is a family of fossil tubuliferan thrips known exclusively from the Cretaceous. Despite typical tubuliferan features, these thrips show terebrantian character states, particularly on the wings and antennae, which have been interpreted as plesiomorphic. At present, the family includes only a single genus, with seven species. In the present study, 11 new species and four new genera of these ancestral thrips are described from Burmese Cenomanian amber: *Adstrictubothrips mirapterus* **gen. et sp. n.**, *Gemineurothrips microcephalus* **gen. et sp. n.**, *Gemineurothrips peculiaris* **gen. et sp. n.**, *Paralleloalathrips bivenatus* **gen. et sp. n.**, *Rohrthrips brachyvenis* **sp. n.**, *Rohrthrips multihamuli* **sp. n.**, *Rohrthrips pandemicus* **sp. n.**, *Rohrthrips rhamphorhynchus* **sp. n.**, *Rohrthrips setiger* **sp. n.**, *Sesquithrips markpankowskii* **gen. et sp. n.** and *Sesquithrips rostratus* **gen. et sp. n.** Furthermore, *Alavathrips moralesi*, a species from Spanish Cretaceous amber, is placed into the Rohrthripidae and its sex is reinterpreted as male. The present study, moreover, provides a tighter definition of the Rohrthripidae and a more detailed description of important character states. Finally, it is outlined why it makes taxonomic sense to distinguish Rohrthripidae from the modern Tubulifera, the Phlaeothripidae.

Key words: Burmite, Cenomanian, Thrips

Introduction

Rohrthripidae represents a family of fossil thrips within the thysanopteran suborder Tubulifera (Ulitzka 2018). At present, it comprises only a single genus, *Rohrthrips* Nel *et al.*, with seven species (ThripsWiki 2021a, Ulitzka 2019). These thrips are exclusively known from the Cretaceous with six species from Cenomanian Burmese amber and one, the generic type species *Rohrthrips libanicus* Nel *et al.*, from Early Cretaceous (Neocomian) Lebanese amber. The latter is considered the oldest known species in the Tubulifera.

The family Rohrthripidae has been established on the basis of plesiomorphic features (see Ulitzka 2019 and below) with respect to modern Tubulifera, all of which are assigned to only one further family, the Phlaeothripidae. The Phlaeothripidae is the largest family within the Thysanoptera, including 3769 extant and 20 fossil species; the latter dating back, however, no further than the Early Tertiary (ThripsWiki 2021b; Ulitzka 2018). All other thrips are associated with Terebrantia, the second thysanopteran suborder, which, according to the commonly accepted classification of Thysanoptera, comprises eight extant and four fossil families (Mound & Hastenpflug-Vesmanis 2021; ThripsWiki 2021b).

Regarding the relationship between the terebrantian families and Tubulifera, different hypotheses have been proposed (Mound *et al.* 1980) until Buckman *et al.* (2013) produced molecular evidence categorizing them as sister groups. In regard to morphological aspects, modern Tubulifera (i. e. Phlaeothripidae) are fundamentally distinct from members of Terebrantia (Bhatti 1988, 1998a, b, 2003; Ellington 1980; Moritz 2006; Mound 2009; Mound & Walker 1982; ThripsWiki 2021b). This also suggests that two main evolutionary lineages with considerable divergence have emerged within the Thysanoptera. In Rohrthripidae, however, some of the characteristic terebrantian features appear in association with a basic tubuliferan body structure (Nel *et al.* 2010; Ulitzka 2018). In this context, Ulitzka (2019) refers to six character states: (1) antennae nine-segmented; (2) abdominal sigmoid wing-retaining setae lacking; (3) fore wings with one or two well-developed longitudinal veins; (4) fringe cilia on wings arising from

Accepted by L. Mound: 4 Apr. 2022; published: 5 Jul. 2022

sockets; (5) wing coupling mechanism comprising both frenate and hamulate components (see also Bhatti 1993, p. 104); (6) wing membrane with rudiments of microtrichia (present only in *R. patrickmuelleri* Ulitzka).

Thus, particularly regarding their wing structure, Rohrthripidae has retained ancestral character states of "prototerebrantian" Thysanoptera, which are interpreted as plesiomorphic. These features also suggest that the wings of Terebrantia and Phlaeothripidae have evolved homologously, and they show that wing evolution in Phlaeothripidae is characterised overall by reduction. In Rohrthripidae these ancestral character states are visible as possible evolutionary intermediate stages towards recent Tubulifera (Ulitzka 2019). This mixture of character states involves problems in systematic and taxonomic interpretations, but it neither proves that Rohrthripidae is a stem group of Phlaeothripidae, nor that it is an obligatory sister group of the latter. Rather, Rohrthripidae might be one of many possible branches of an early diversification within Thysanoptera (Ulitzka 2019). Their ancestral nature, however, is also reflected in other findings. Former studies have shed light on the diet of Rohrthripidae and revealed that these thrips fed on fungal spores. In this way, they are highly consistent with the concept of Bhatti (1993) that characterizes the "Prototubulifera" as insects with cryptozoic habits seeking fungal hyphae and spores (Ulitzka 2019).

The first fossils of these remarkable Thysanoptera were interpreted as rare oddities (Nel *et al.* 2010; Ulitzka 2018). It soon became apparent, however, that these thrips had achieved considerable diversification during the Late Cretaceous; Ulitzka (2019) presented five new species from Burmese amber, all attributed to the genus *Rohrthrips*. Even though fossils of these early Tubulifera are not particularly common, the author's collection comprises at present more than 25 specimens. Some are fossilised in excellent condition and allow reliable assessment of their characteristics. These specimens are discussed in the following text. Some of them are attributable to already known species; some represent new species within the genus *Rohrthrips*; while others require the establishment of new genera within Rohrthripidae. The aim of the present paper, however, is not just to describe these fossils, but also to present a tighter definition of this group of ancestral Thysanoptera. Moreover, *Alavathrips moralesi* Peñalver *et al.* is placed in the Rohrthripidae. This species is based on a single small-sized specimen from Cretaceous (Upper Albian) amber from Spain, which shows exceptional preservation of the genitalia (Peñalver *et al.* 2022). However, it appears to have been misidentified as a female, inevitably leading to a complete misinterpretation of the inferred evolutionary achievements.

Age of Burmite

With the addition of the species described below, the Rohrthripidae now show quite remarkable diversity, but assessing biodiversity and speciation raises questions in the context of amber fossils. Burmite is about 99 million years old, and this oft-quoted age comes from radiometric dating of the volcanoclastic deposits of this amber (Cruickshank & Ko 2003; Shi *et al.* 2012). Regarding this age of amber and thus of its fossil inclusions, it is important to keep in mind that it represents a period and not just a point in the past (Sokol 2019). According to unpublished data by Bo Wang (in Sokol 2019), Burmite deposits span at least five million years – during which speciation may have happened. Hence, fossils with different character states may not necessarily represent two species that coexisted; one of these species could simply have lived later and even represent descendant of a more ancestral species. The latter fact implies that differentiation of species may blur, as transitional character states may occur which might be difficult to distinguish from intraspecific variations. On the other hand, cladogenesis of Thysanoptera is estimated with a rate of 0.0572 million years $^{-1}$ (Mayhew 2002); however, it might be even lower regarding exclusively fungivorous species (cf. Mayhew 2007). In view of this, the results of the present work are unlikely to be affected by speciation processes. The genera and species described below have been distinguished by features which are also commonly used for extant thrips. On present knowledge, the definite difference in these character states, a phenotypic expression of a different genotype, suggest the classification adopted here.

Material and methods

The Burmese amber inclusions discussed below are part of the author's Thysanoptera collection; all fossils in this collection are intended to be donated to the Bavarian State Collections for Paleontology and Geology, Munich, Germany. The male of *Rohrthrips jievenae* Ulitzka and the holotype female of *Sesquithrips markpankowskii* **gen. et**

sp. n. were donations from Mark Pankowski, Rockville, Maryland, USA; one of the syntypes of *Gemineurothrips microcephalus* **gen. et sp. n.**, the female of *Rohrthrips patrickmuelleri* Ulitzka, two paratypes of *Paralleloalathrips bivenatus* **gen. et sp. n.** and the paratype male of *S. markpankowskii* **gen. et sp. n.** have been purchased by the author on eBay from Terry Su, eBay username "burmite-miner" (https://www.ebay.com/usr/burmite-miner); all other inclusions have been generously donated by Patrick Müller, Käshofen, Germany. Detailed information on the fossils is included below. Numbers following a prefixed "MU-Fos-" refer to serial numbers in the author's collection. All holotypes of the following *Rohrthrips* species have been re-examined to create the included identification key: *R. breviceps* Ulitzka (MU-Fos-81/1), *R. burmiticus* Ulitzka (MU-Fos-53/1), *R. jiewenae* Ulitzka (MU-Fos-89/1), *R. maryae* Ulitzka (MU-Fos-88/1), *R. patrickmuelleri* Ulitzka (MU-Fos-80/1) and *R. schizovenatus* Ulitzka (MU-Fos-76/1). For comparisons with *R. libanicus* Nel *et al.*, detailed micrographs of the holotype were available.

The fossils — except for the holotype of *Rohrthrips multihamuli* **n. sp.**, which was too large (see below) — have been prepared according to Ulitzka (2015, 2021b). To increase visibility during microscopic examination, however, most samples have been ground much thinner than outlined in this earlier description. 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). Afterwards, 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 fossil of *R. multihamuli* **n. sp.** is too thick for the above treatment. Therefore, the amber was ground as close as possible towards the inclusion and then only varnished with Acrüdur R 40 single-component polyurethane resin (Adolff C.C. Rüegg GmbH & Co Hamburg, Germany) for safe conservation.

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 diffusor 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. Nik Sharpener Pro and Adobe Photoshop were used for final colour adjustment and sharpening.

Rohrthripidae Ulitzka, 2018

Adstrictubothrips gen. n.

Type species: *Adstrictubothrips mirapterus* **gen. et sp. n.**

Diagnosis. Abdominal segment X tubiform with a distinct constriction in the middle (Fig. 1). Antennae nine-segmented. Fore wings (Fig. 2) narrow, slightly bent forwards and broadened at base; first vein complete but bearing setae only in the basal two-thirds; second vein and cross-veins not developed; wing coupling hamulo-frenate. Fringe cilia distinctly thickened at base, but for the most part embedded into wing membrane, not on sockets; duplicated cilia present. Abdomen without sigmoidal wing retaining setae.

Adstrictubothrips shows modern tubuliferan character states in combination with plesiomorphic features like nine-segmented antennae and fore wings with a complete first vein. It therefore is allocated to Rohrthripidae. In contrast to most species of *Rohrthrips* the wing fringes in *Adstrictubothrips* are embedded for the main part into the wing membrane. A similar situation, however, has been also found in some species of *Rohrthrips*, eg *R. patrickmuelleri* or *R. schizovenatus* (Ulitzka 2019). Thus, this character state does not contradict the classification of the new genus within Rohrthripidae. *Adstrictubothrips* differs from *Rohrthrips* with regard to the narrow wings and the wing vein, which is furnished with setae only in the basal two-thirds of the wing length.

Etymology. The name of the new genus derives from the Latin words *adstrictus*, meaning "narrowed", and *tubus*, meaning "tube", as well as *thrips*, the usual term for a genus within Thysanoptera. The name refers to the constriction in the tube of the generic type specimen (Fig. 1).

Adstrictubothrips mirapterus gen. et sp. n.
(Figs 1–2, 35)

Female. Head slightly retracted under pronotum, thorax contracted, abdomen fully extended; head partially translucent, therefore maxillary stylets visible; left antenna with distal segments deformed; left wings overlapping body, right wings spread; both fore legs folded under body.

Colour (Fig. 1) brown to greyish brown, legs as well as antennal segments I, II and basal part of III concolourous with body; distal part of antennae dark brown as well as anterior part of head, pterothorax and tube. All major setae light brown, except s1–s3 at tergite IX and all anal setae, which are darker. Wing veins and fringes greyish brown (Fig. 2); fore wings shaded grey, hind wings lighter with a dark median streak.

Head (Figs 1, 35) retracted basally under pronotum; slightly wider than long, recessed behind eyes; basally sculptured with faint lines of transverse loose reticulation. Cheeks nearly straight, diverging slightly backwards and tapering sharply just before the base; laterally with some sparse and weak setae. Ocellar setae difficult to assess, one short pair visible close to hind ocelli; postocular setae far behind compound eyes, short but pointed. Eyes small, not prolonged ventrally. Hind ocelli close to compound eyes; far apart from each other; fore ocellus on a small hump far in front between antennal insertions. Antennae nine-segmented; segment I conically shaped; II inversely conical, apically with a small sensorium; III–VIII basally with a pedicle, then inverse conically shaped and tapering distally; IX style-shaped, at base nearly as wide as VIII distally. Sense cones difficult to assess; at least one inner and one outer present on III–V. Mouth cone short but pointed. Maxillary stylets (Fig. 35) wide apart but long (without maxillary bridge), their base visible close to hind margin of compound eyes. Pronotum wider than long; pronotal chaetotaxy as well as pterothoracic structure not assessable. Fore wings narrow (Fig. 2); somewhat widened in basal third; distally parallel and slightly bent forwards, tip bluntly rounded; anterior vein complete, with one small and two large setae in the basal two-thirds of the wing, apical setae lacking; second vein not developed; membrane without microtrichia. Fringe cilia straight; distinctly thickened at base; at fore wings embedded into the wing membrane, at hind wings, however, arising from tiny sockets. Duplicated cilia running parallel to normal wing fringes; present around wing apex, distally on posterior wing margin and one duplicated cilium on fore margin of wing. Clavus with paired setiform processes at tip. Hind wing without microtrichia and without any veins (Fig. 2). Fore legs (Fig. 1) with femora not enlarged; fore tibiae and tarsi not clearly assessable, however, fore tarsi with hamus. Mid and hind legs slender; tibiae each with a long dorsal seta and terminally each with a strong spine; mid and hind tarsi two-segmented; with a long recurved hamus. Abdominal tergites without wing-retaining setae; lateral setae weak, slightly curved and pointed. Pelta triangular, much wider than long, sculptured with lines of transverse loose reticulation. Abdominal segment IX dome-shaped; setae s1–s3 long and pointed; s2 slightly longer than tube. Abdominal segment X elongated tubular, but distinctly narrowed in the middle; with a terminal crown of anal setae, these shorter than tube.

Measurements. Female (in microns): Body, length 794 (slightly contracted). Head, length 136; width 146. Eyes, length 50; width 31. Hind ocelli, diameter 9; distance between the hind ocelli 31. Postocular setae about 17 (difficult to measure). Distance between maxillary stylets (at base of head) 62. Pronotum, length 93; width 174. Pterothorax, largest width 174 (at level of mesothoracic spiracles). Abdomen, length 529; largest width 171 (segment VI); segment X (tube), length 99; basal width 28. Pelta, length 43; width 115. Setae on tergite IX, length s1 78; s2 109; s3 47. Antennae, length 255; length (largest width) of segment I 25 (25), II 31 (17), III 37 (22), IV 31 (19), V 31 (16), VI 33 (16), VII 26 (14), VIII 25 (12), IX 16 (6). Sense cones, length of inner (outer) on segment III 16 (15), IV 12 (15), V 12 (9); basal width of inner (outer) about 2 (3). Fore wings, length 498; width in the middle 31.

Material studied. Holotype female MU-Fos-134/1 (Figs 1–2, 35); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar. The holotype was donated by Patrick Müller and is deposited in the author's collection.

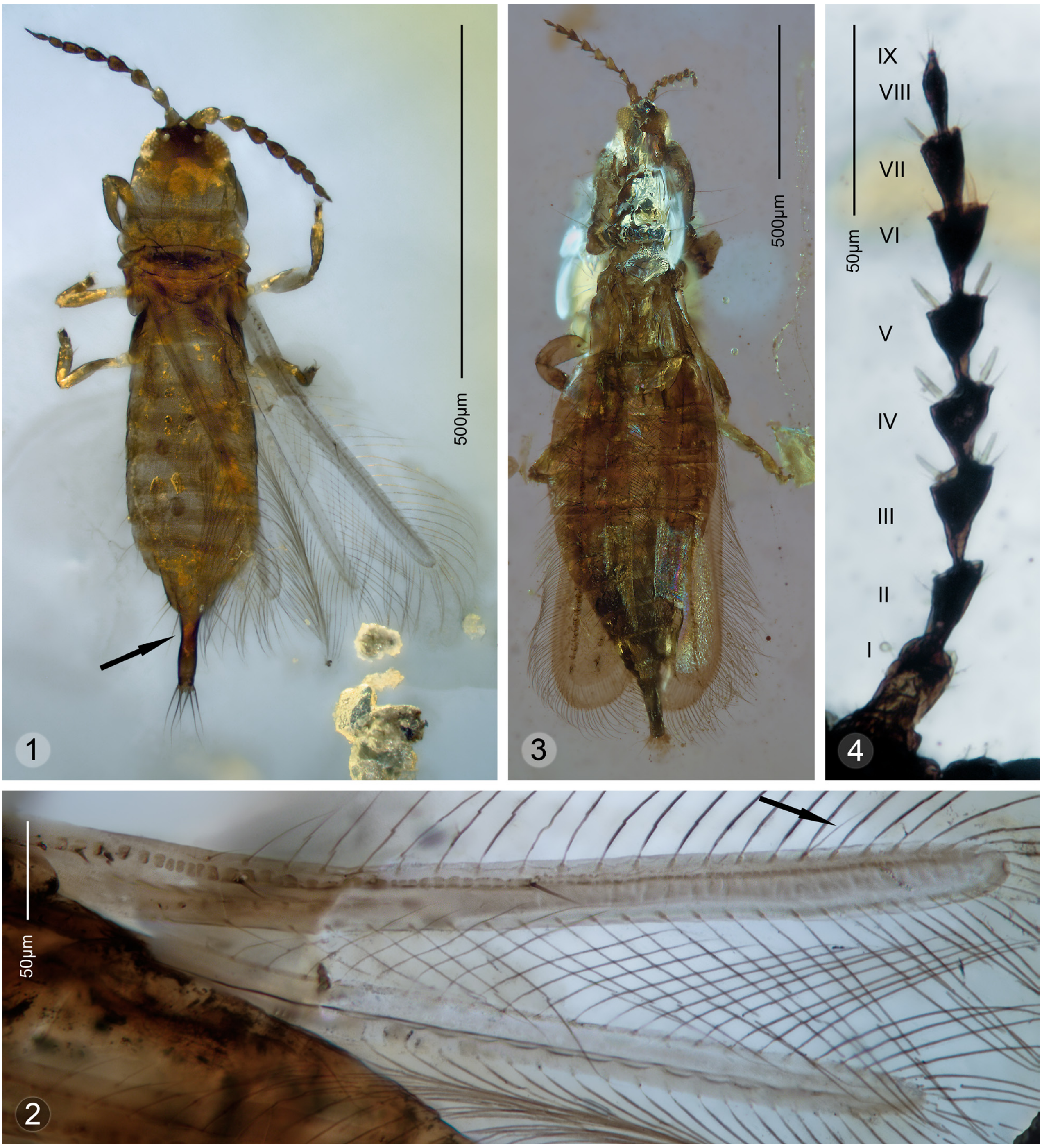
Syninclusions. Remnants of insect legs, plant detritus and stellate plant hair.

Etymology. The species epithet *mirapterus* comes from the Latin word *mirus*, meaning "strange", and the Greek word *πτερόν* (*pteron*), meaning "wing". It refers to the unusual wings of this species with a single vein bearing setae only in the basal two-thirds but not apically (Fig. 2).

Gemineurothrips gen. n.

Type species: *Gemineurothrips microcephalus* **gen. et sp. n.**

Diagnosis. Abdominal segment X tubiform, without a ventral median suture, but with a crown of apical anal setae. Antennae (Fig. 4) nine-segmented. Maxillary stylets lowly retracted into the head and wide apart (Fig. 36). Fore wings (Fig. 7) becoming progressively larger in distal half; with two parallel wing veins; both furnished with stout setae; cross-veins not developed. Fringe cilia at fore wings mainly retracted into the wing membrane, at hind wings partly arising from sockets; duplicated cilia present around wing apex (Fig. 29). Fore wing clavus with paired setiform



FIGURES 1–4. Rohrthripidae species. *Adstrictubothrips mirapterus* **gen. et sp. n.** 1–2: **(1)** holotype female dorsal view, indicated: constriction at the tube; **(2)** right wings, indicated: duplicated cilium on fore wing margin. *Gemineurothrips microcephalus* **gen. et sp. n.** syntype female (MU-Fos-145/1) 3–4: **(3)** dorsal view; **(4)** left antenna.

processes at tip and hind wing with basal recurved setae, wing coupling hamulo-frenate (Fig. 26). Abdomen without wing retaining setae. Fore tibiae with a strong distal spine. Anal setae much shorter than tube (Fig. 5).

Gemineurothrips shows character states of modern Tubulifera combined with plesiomorphic features like nine-segmented antennae and fore wings with two complete veins; it therefore is allocated to Rohrthripidae. Furthermore, wing coupling in *Gemineurothrips* is hamulo-frenate as it is in *Rohrthrips* (Fig. 25). Members of both genera have broadened wings; this feature distinguishes both from other Rohrthripidae. *Gemineurothrips* differs from *Rohrthrips* in having a complete second wing vein bearing stout setae (Fig. 7). Furthermore, the maxillary stylets are deeply retracted into the head capsule and close together in *Rohrthrips* (see Ulitzka 2018), whereas they are low in the head only and far apart in *Gemineurothrips* (Fig. 36). Finally, the pronotal chaetotaxy is different, with well-developed posteromarginal setae and a second pair of (much shorter) posteroangular setae in *Gemineurothrips*, whereas in *Rohrthrips* the posteromarginal setae are vestigial and only one pair of posteroangular setae is present.

Etymology. The name of the new genus derives from the Latin word *geminus*, meaning “twin”, the Greek word *νεῦρον* (*neuron*), meaning “vein”, and *thrips*, the usual term for a genus within Thysanoptera. It refers to the almost identical wing veins lying as “twins” in the fore wings of the generic type specimen (Fig. 7).

Gemineurothrips microcephalus gen. et sp. n.

(Figs 3–5, 26, 29)

Syntype female (MU-Fos-145/1; Figs 3–4). Body completely extended; right antenna bent downwards; wings closed over abdomen; right hind leg spread, others bent under body or head, respectively. Prothorax largely hidden, ventrally by a bubble and dorsally by a shiny reflective layer of air. *Syntype female* (MU-Fos-148/1; Figs 5, 26, 29). Body slightly inclined to the right, completely extended; right wings spread; hind wing, however, bent forwards; left wings partly torn, overlapping body; legs spread except for right fore and hind leg. Left side of pronotum covered by a shiny reflective layer; mesonotum torn away.

Colour (Fig. 5) of head, thorax and distal abdominal segments dark brown, rest of abdomen somewhat paler; antennae, legs and all major setae dark brown as well as wing veins and fringes; wing membrane uniformly light brown.

Head (Figs 3, 5) much longer than wide, with cheeks tapering straight towards base. One pair of long ocellar setae near the inner margin of antennal bases, projecting largely beyond the base of antennal segment III; a second pair close to the front margin of the eyes, much weaker and shorter. Postocular setae close to compound eyes; short and pointed. Compound eyes prominent; slightly prolonged ventrally. Ocelli small; on an ocellar hump; hind ocelli close to compound eyes; fore ocellus directed forwards. Antennae (Fig. 4) nine-segmented; segment I long and barrel-shaped; segment II asymmetrically bent outwards, without a pedicle; III–VII with a short pedicle at base, then slightly asymmetrical inverse cone shaped and flat at distal margin; VIII spindle-shaped; IX small, cone shaped, basally broadly joined to VIII. Sensorium at segment II not visible; number of sense cones of the following segments difficult to assess, at least one outer and one inner on III–V, one inner on VI and one outer on VII. Mouth cone short but pointed; maxillary palps not visible. Pronotum wider than long, trapezoidal; anteromarginal, mediolateral and posteromarginal setae not visible, anteroangular setae short; two pairs of posteroangular setae, inner pair short and stout, outer as well as epimeral setae and a pair of coxal setae long and hair-like. Mesonotum sculptured reticulate at front margin but striate in posterior half. Metanotum long; sculpture not assessable. Fore wings (Fig. 5) becoming progressively larger in distal half; with two parallel wing veins, both furnished with setae, but these stronger on second vein (Fig. 29); membrane distally smooth but fore wing clavus and base of hind wings with structures interpretable as microtrichia (Fig. 26). Fringe cilia straight; enlarged at base; for the most part deeply embedded into the wing membrane, on sockets only at the front margin of the hind wing. Duplicated cilia (Fig. 29) present around wing tips and apical margins of fore wing; on hind margin attached in an angle towards the body. Hind wings without veins. Wing coupling system hamulo-frenate with six hamuli (Fig. 26; MU-Fos-148/1 has four setiform processes at the fore wing clavus instead of two). Fore femora stout (Fig. 5); with a long hairlike ventral seta; fore tibiae with a long dorsal seta each and distally with a thorn-like process; fore tarsi with a strong tooth each and with hamus with bilateral pseudunguis (see Bhatti 1998a, p. 256) of which the outer claw is conspicuously long and slender. Mid and hind legs slender; tibiae with a long dorsal seta and terminally each with three strong spines; mid and hind tarsi two-segmented, with hamus. Abdominal tergites with three pairs of setae, s1 longer than s2 and s3; without wing-retaining setae; lateral setae pointed, recurved and long but delicate. Abdominal tergite I (pelta) not assessable; II without a dorsolateral suture; segment IX dome-shaped; setae s1–s3 long hair-like; s3 longest, protruding distally over tip of tube. Abdominal segment X elongated tubular, with a terminal crown of short anal setae.

Measurements. MU-Fos-145/1 (in microns): Body, length 2066. Head, length 233; largest width (across eyes) 163; width at base 95. Eyes, dorsal length 76, ventral length 82; width 57. Ocelli, diameter not measurable; distance 63. Inner ocellar setae 158, outer 32. Pronotum, length 258; width 315; anteroangular setae 50, outer (inner) posteroangular setae 189 (about 65, difficult to measure); epimeral setae 201; coxal setae 202. Pterothorax, largest width 302. Abdomen, length 1224; largest width 536 (segment III); segment X (tube), length 189; basal width 82. Setae on tergite IX, s1 245; s2 239; s3 290. Antennae, length 383; length (largest width) of segment I 56 (31), II 47 (22), III 53 (31), IV 47 (34), V 47 (34), VI 47 (31), VII 43 (22), VIII 34 (12), IX 9 (8). Sense cones, length of inner (outer) on segment III 19 (19), IV 22 (25), V 22 (22), VI 22 (–), VII – (19); basal width 4–6. Fore wings, length 1362; largest width 284.

Material studied. Two female syntypes; MU-Fos-145/1 (Figs 3–4) was donated to the author by Patrick Müller and MU-Fos-148/1 (Figs 5, 26, 29) was purchased by the author on eBay from Terry Su, eBay username "burmite-miner". Both specimens originate from amber mines in the Hukawng Valley, Kachin State, Myanmar and are deposited in the collection of the author.

Syninclusions. MU-Fos-145/1: threads of a spider's web, small particles of plant detritus as well as many brownish droplets and bubbles. MU-Fos-148/1: a small fly (Diptera), coprolites, plant detritus and a large brown fissured layer of unknown origin.

Etymology. The species epithet *microcephalus* comes from the Greek words *μικρός* (*mikrós*), meaning "small", and *κεφαλή* (*kephalon*), meaning "head". It refers to the remarkably small head of this species (Figs 3, 5).

Gemineurothrips peculiaris gen. et sp. n.

(Figs 6–7, 36)

Sex not determinable, as abdominal segments VII–X are lacking (Fig. 6). Body distended; left wings spread, right wings overlapping body, wing tip of left fore wing broken off; legs spread.

Colour (Fig. 6) uniformly brown, including antennae and legs; all major setae dark as well as wing veins (including costa) and fringes; wing membranes (Figs 6–7) with pronounced light brown wrinkles and dots of primary surface patterns (see Bhatti 1991, 1998c and Ulitzka 2019), hind wings with a paler streak along anterior margin.

Head (Figs 6, 36) wider than long; protruding at anterior margin over base of antennae. Cheeks slightly rounded and tapering towards base; with three pairs of weak setae. One pair of stout ocellar setae near the inner margin of antennal bases, their length protruding beyond base of antennal segment II; a second pair close to the front margin of the eyes, much weaker and shorter. Postocular setae close to compound eyes; short and pointed. Compound eyes small; prolonged ventrally. Hind ocelli close to compound eyes; fore ocellus directed forwards. Antennae nine-segmented; segment I barrel-shaped; segment II asymmetrically bent outwards, without a pedicle; III–VII with a short pedicle at base, then slightly asymmetrical inverse cone shaped and flat at distal margin; VIII spindle-shaped; IX tiny and style-shaped. Sensorium at segment II not visible; number of sense cones of the following segments difficult to assess, at least one outer and one inner on III–V, one inner on VI and one outer on VII. Mouth cone bluntly pointed, reaching back to fore margin of ferna. Maxillary stylets (Fig. 36) far apart and barely retracted into the head capsule. Maxillary palps two-segmented. Pronotum (Figs 6, 36) wider than long, trapezoidal; anteroangular, anteromarginal and mediolateral setae short, posteromarginal setae stout; two pairs of posteroangular setae, inner ones short and stout, outer as well as epimeral setae and a pair of coxal setae long and hair-like. Mesonotum weakly sculptured reticulate at front margin, smooth posteriorly of campaniform sensilla. Metanotum not assessable. Fore wings (Fig. 7) becoming progressively larger in distal half; with two parallel wing veins; both furnished with stout setae, these stronger on second vein; membrane without microtrichia. Fringe cilia (Fig. 7) straight; enlarged at base; for the most part deeply embedded into the wing membrane, on sockets only at the front margin of the hind wing. Duplicated cilia present around wing tips and apical margins of fore wing; on hind margin attached in an angle towards the body. Hind wing without microtrichia and without any veins. Wing coupling system hamulo-frenate; with a series of four hamuli at anterior margin close to base of hind wing. Fore femora stout (Fig. 6); with long hairlike ventral seta; fore tibiae distally with a thorn-like process; fore tarsi with a strong tooth and a hamus with bilateral pseudunguis (see Bhatti 1998a, p. 256). Mid and hind legs slender; tibiae with one long dorsal seta and terminally each with three strong spines; mid and hind tarsi two-segmented, with hamus. Abdominal tergites with three pairs of setae, s1 longer than s2 and s3; without wing-retaining setae; lateral setae pointed, recurved and long but delicate. Abdominal tergite I (pelta) not assessable; II without a dorsolateral suture.

Measurements. MU-Fos-142/1 (in microns): Length, head to abdominal segment VI 1683. Head, length 167; largest width (across eyes) 216. Eyes, dorsal length 98, ventral length 137; width 78. Hind ocelli, diameter 29; distance between the hind ocelli 127. Inner ocellar setae 127, outer 39. Pronotum, length 451; width 675; anteromarginal setae 29, anteroangular setae 20, mediolateral setae 29, outer (inner) posteroangular setae 294 (78), posteromarginal setae 147; epimeral setae about 210 (difficult to measure), coxal setae 233. Pterothorax, largest width 686. Abdomen, largest width 843 (segment IV); Antennae, length 399; length (largest width) of segment I 62 (56), II 50 (50), III 50 (47), IV 43 (47), V 47 (43), VI 48 (34), VII 48 (25), VIII 40 (9), IX 11 (3). Sense cones, length of inner (outer) on segment III 22 (19), IV 22 (25), V 22 (22), VI 28 (–), VII – (16); basal width 4–6. Fore wings, length 1195; largest width 274.

Material studied. Holotype MU-Fos-142/1 (Figs 6–7, 36); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar; donated by Patrick Müller and deposited in the author's collection.

Syninclusions. Small remnants of another arthropod, fungal hyphen, plant detritus and countless tiny brownish droplets.

Etymology. The species epithet *peculiaris* comes from the same Latin word meaning "peculiar". It refers to the unusual fore wings of this species (Fig. 7).

FIGURES 5–7. Rohrthripidae species. **(5)** *Gemineurothrips microcephalus* **gen. et sp. n.** syntype female (MU-Fos-148/1): dorsolateral view. *Gemineurothrips peculiaris* **gen. et sp. n.** holotype 6–7: **(6)** dorsal view; **(7)** left fore wing.

Differential diagnosis. The two species in this genus are already distinguished by their visual appearance. *G. peculiaris* is more robust, with a much broader head and thorax. The most striking difference, however, concerns their antennae. In *G. microcephalus* they are slender with the median segments much longer than wide and pedicellate, whereas in *G. peculiaris* they are short and stout.

Paralleloalathrips gen. n.

Type species: *Paralleloalathrips bivenatus* **gen. et sp. n.**

Diagnosis. Abdominal segment X tubiform, without a median suture, but with a crown of apical anal setae. Antennae (Fig. 8) nine-segmented. Fore wings (Fig. 10) narrow and straight; fore and hind margin completely parallel between clavus and tip; with two complete longitudinal veins, both furnished with setae; cross-veins not developed. Fringe cilia arising from sockets; duplicated cilia present around margin of wing apex and along distal part of posterior margin. Fore wing clavus with paired setiform processes at tip and hind wing with a basal recurved seta, wing coupling hamulo-frenate. Abdomen without sigmoidal wing retaining setae; abdominal tergite II with a pair of distinct dorsolateral sutures (Fig. 11).

Paralleloalathrips shows typical character states of modern Tubulifera in combination with plesiomorphic features like nine-segmented antennae and fore wings with two complete veins. It therefore is allocated to Rohrthripidae. Furthermore, wing coupling in *Paralleloalathrips* is hamulo-frenate as it is in *Rohrthrips* and *Gemineurothrips* **gen. n.** The new genus differs from both of the latter based on the narrow shape of the wings (Fig. 10), and from *Rohrthrips* additionally by the presence of a complete second wing vein bearing setae (cf. Ulitzka 2018, 2019). *Paralleloalathrips* and *Rohrthrips*, nevertheless, are possibly more closely related, as both have a pair of sutures dorsolaterally at the second abdominal tergite (Fig. 11). From *Adstrictubothrips* **gen. n.** the new genus differs by the presence of two complete wing veins and by the tube, which is not narrowed in the middle (Fig. 8).

Etymology. The name of the new genus derives from the Greek word *παράλληλος* (*parállēlos*), meaning "parallel", the Latin word *ala*, meaning "wing", and *thrips*, the usual term for a genus within Thysanoptera. It refers to the parallel wings of the generic type specimen (Fig. 10).

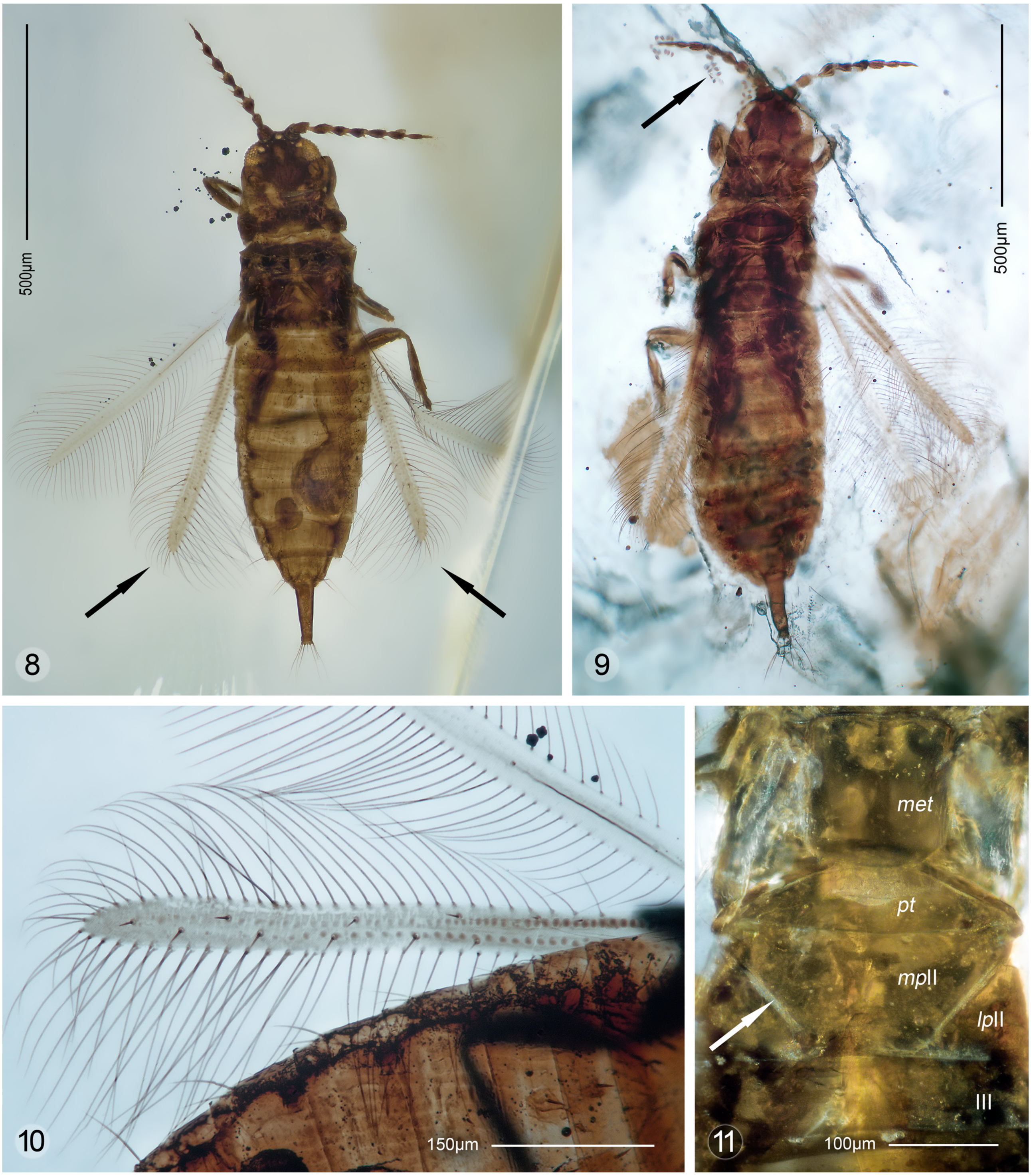
Paralleloalathrips bivenatus gen. et sp. n.

(Figs 8–11)

Female (Holotype). Body (Fig. 8) fully distended; pterothoracic tergites deformed and translucent, therefore their features difficult to assess; legs folded under body with exception of right hind leg; wings spread, hind wings lying in front of fore wings.

Colour (Figs 8–9) uniformly dark brown including antennae and legs; all major setae dark as well as wing veins and fringes; fore wings (Fig. 10) shaded greyish-brown, hind wings lighter with a dark median streak.

Head (Figs 8–9) wider than long, recessed behind the eyes, with cheeks slightly rounded in front, but almost straight and parallel towards base; cheeks with some sparse and weak setae; ocellar setae difficult to assess, one short pair clearly visible as well as the points of attachment of a second pair near the base of antennae. Eyes small, not prolonged ventrally. Hind ocelli close to compound eyes; far apart from each other; fore ocellus far in front between the antennal insertions. Antennae nine-segmented (Fig. 8); segment I barrel-shaped; II inversely conical, apically with a small circular sensorium; III–VII inverse conically shaped and tapering distally from level of sense cones; VIII spindle-shaped; IX style-shaped, at base much narrower than VIII distally. Outer sense cones stout, inner ones smaller; their number difficult to assess but at least one inner and one outer on III–VI and one outer on VII. Mouth cone short and rounded. Maxillary palps two-segmented; with three apical setae. Pronotum wider than long; pronotal chaetotaxy not assessable; most likely with two pairs of posteroangular setae, all of which are faint but long and pointed. Pterothorax dorsally as well as pelta not assessable. Fore wings (Fig. 10) straight and narrow, with fore and hind margin parallel between clavus and tip; tip softly pointed; anterior and posterior vein complete; both veins bearing 4–5 setae; membrane without microtrichia. Fringe cilia straight; arising from sockets. Duplicated cilia present around wing tips and apical margins of fore wing; with only a few cilia present at the fore margin; and about 14 cilia at hind margin attached in an angle towards the body. Clavus with paired setiform processes at tip. Hind wing without microtrichia and without any veins; base with one recurved seta. Fore legs (Fig. 8) with femora not enlarged; tibiae terminally with a strong spine-like seta; fore tarsi without teeth but with a small recurved hamus. Mid and hind legs slender; tibiae each with a long dorsal seta and terminally with at least one strong spine; mid and hind tarsi two-segmented. Abdominal tergites without wing-retaining setae; short mid-dorsal setae visible on tergites III–V; lateral setae weak, slightly curved and pointed. Abdominal segment IX dome-shaped; setae s1 curved upwards and stronger than s2 and s3; s3 longest, but somewhat shorter than tube. Abdominal segment X elongated tubular, with a terminal crown of anal setae, which are shorter than the tube (Fig. 8).



FIGURES 8–11. *Paralleloalathrips bivenatus* **gen. et sp. n. (8)** holotype female, dorsal view, fore wings indicated; **(9)** paratype female, indicated: fungal spores; **(10)** holotype female, left fore wing; **(11)** paratype male, basal abdominal tergites, indicated: dorsolateral grooves on tergum II (met: metanotum, pt: pelta, mpII: medial plate of tergum II, lpII: lateral plate of tergum II, III: tergum III).

Measurements. Female MU-Fos-125/1 (in microns): Body, length 1225. Head, length 151; width 207. Eyes, length 56; width 40. Hind ocelli, diameter 16; distance between the hind ocelli 68. Ocellar setae not measurable. Pronotum, length 152; width 233; posteroangular setae about 75. Pterothorax, largest width 267. Abdomen, length 804; largest width 310 (segment III); segment X (tube), length 143; basal width 47. Setae s3 on tergite IX 140. Antennae, length 327; length (largest width) of segment I 31 (37), II 31 (22), III 48 (31), IV 37 (22), V 43 (25), VI 40 (22), VII 40 (19), VIII 37 (11), IX 20 (3). Sense cones, length of inner (outer) on segment III 16 (20), IV 14 (20), V 12 (16), VI – (12), basal width of inner (outer) about 2 (4). Fore wings, length 696; width in the middle 40.

Male (Paratype). Body fully distended; head slightly compressed; antennae inclined to the right; wings spread, but right hind wing bent forwards; legs spread except for right fore leg; thorax and basal segments of abdomen ventrally hidden by a large bubble of air.

Similar to female in colour and body structure; somewhat larger. Fore femora slightly enlarged. Pronotum with two pairs of long posteroangular setae. Pelta broad; abdominal tergite II with a pair of distinct dorsolateral sutures slanting posteriorly inwards (Fig. 11). Abdominal sternite IX with hypandrium and androsternite (see Bhatti 1998b); X ventrally at base with a triangular recess (see Priesner 1968).

Measurements. Male MU-Fos-149/1 (in microns): Body, length 1401. Head, length 176; width 220. Pronotum, length 163; width 258; inner and outer posteroangular setae about 80. Abdomen, length 850; largest width 346 (segments III and IV); segment X (tube), length 151; basal width 51. Antennae, length 365. Fore wings, length 835; width in the middle 50.

Material studied. The holotype female MU-Fos-125/1 (Figs 8, 10) and the paratype female MU-Fos-133/1 have been donated to the author by Patrick Müller; the paratype female MU-Fos-124/1 (Fig. 9) as well as the paratype male MU-Fos-149/1 (Fig. 11) were purchased by the author on eBay from Terry Su, eBay username "burmite-miner". All specimens are inclusions in Burmese amber and originate from mines in the Hukawng Valley, Kachin State, Myanmar. The holotype and all paratypes are deposited in the collection of the author.

Syninclusions. MU-Fos-124/1: about 30 fungal spores around the left antenna of the thrips (Fig. 9), one mite, plant detritus as well as some stellate plant hairs, tiny droplets and many cracks limiting the visibility of the thrips; MU-Fos-125/1: a beetle (Coleoptera, Staphylinidae, Scydmaeninae), remnants of two insect legs, a mite, plant detritus and some pyrite crystals close to the thrips; MU-Fos-133/1: one midge, many tiny droplets; MU-Fos-149/1: bubbles of air and some tiny brownish droplets.

Etymology. The species epithet *bivenatus* comes from the Latin prefix *bi*, meaning "two", and the Latin word *venatus*, meaning "with veins". It refers to the two complete wing veins of this species (Fig. 10).

Rohrthrips Nel, Peñalver, Azar, Hodebert & Nel, 2010

Type species: *R. libanicus* Nel, Peñalver, Azar, Hodebert & Nel, 2010

Diagnosis. Abdominal segment X tubiform, without a median suture, but with a crown of long apical anal setae. Antennae nine-segmented. Maxillary stylets deeply retracted into the head capsule and close together (Fig. 37; Ulitzka 2018, 2019). Fore wings becoming progressively larger in distal half (Figs 12–13, 18); with a first vein bearing setae and, in some species, additionally with a second much shorter vein without setae (Fig. 18); cross-veins not developed; wing tips broadly rounded. Fringe cilia in most species arising from sockets. Duplicated cilia present around wing apex; running parallel to normal wing fringes. Fore wing clavus with paired setiform processes at tip and hind wing with basal recurved setae, wing coupling hamulo-frenate (Fig. 27). Abdomen without sigmoidal wing retaining setae; abdominal tergite II with a pair of distinct dorsolateral sutures (Fig. 30). The latter feature is rarely found in Tubulifera and has not been documented so far in *Rohrthrips* (see discussion below); it is also present in *Paralleloalathrips bivenatus* **gen. et sp. n.**

Rohrthrips brachyvenis sp. n.

(Fig. 12)

Female (Syntype MU-Fos-138/1). Body fully distended; right wings spread, left wings twisted and overlapping abdomen; all legs bent, left hind leg folded under abdomen; dorsal parts of head (vertex) and some pronotal major setae torn off. Syntype MU-Fos-139/1; sex not determinable because distal abdominal segments are obscured. Body distended; wings spread; right wings distally hidden by a crack; all legs except left hind leg bent; fore legs folded under the head.

Colour (Fig. 12) uniformly brown including antennae and legs; all major setae dark as well as wing veins and fringes; wings largely translucent, but fore wings with an elongate brownish spot along distal part of vein towards anterior wing margin.

Head wider than long; slightly prolonged in front of the small compound eyes. Cheeks protruding behind eyes; rounded and tapering towards base; with about 3 pairs of faint lateral setae. One pair of ocellar setae visible close to base of antennae; pointed, about as long as antennal segment I. Postocular setae far behind compound eyes; pointed, long and stout. Compound eyes small; not prolonged ventrally. Ocelli not visible. Antennae nine-segmented; segment I barrel-shaped; segment II asymmetrically bent outwards, basally with a short pedicle; III–VII with a longer pedicle at base, then symmetrical inverse cone shaped and tapering distally from level of sense cones, VIII spindle-shaped, IX style-shaped. Segment II with a small distal sensorium; number of sense cones of the following segments difficult to assess, at least two outers and two inners on III and one outer and one inner on IV–VI. Mouth cone short and rounded. Maxillary palps three-segmented. Pronotum wider than long, trapezoidal; anteroangular, mediolateral and posteroangular setae long and pointed, anteromarginal and posteromarginal setae minute; epimeral setae longer than other pronotal major setae. Mesonotum sculptured coarsely reticulate; mesonotal setae not visible. Fore wings (Fig. 12) becoming progressively larger in distal half; anterior vein reaching costa in front of apex (at about four fifths of the wing length), bearing some faint setae (their number and length different in each syntype); second vein not developed; membrane without microtrichia. Fringe cilia straight; slightly enlarged at base but embedded into the wing membrane, not on sockets. Duplicated cilia present around apical margin of wing; running parallel to normal wing fringes. Hind wing without microtrichia and without any veins. Wing coupling system hamulo-frenate; with a series of 3–4 hamuli at anterior margin close to base of hind wing. Fore legs with femora stout; fore tarsi with a strong tooth and a strong hamus. Mid and hind legs slender. All femora with one long ventral and all tibiae with one long dorsal seta; mid and hind tibiae terminally each with three spines; mid and hind tarsi two-segmented, with hamus. Abdominal tergites without wing-retaining setae; lateral setae pointed, recurved, long but delicate; setae s3 on IV–VII conspicuously longer than other lateral setae. Abdominal tergite I (pelta) not assessable; II with a dorsolateral suture slanting laterally inwards; segment IX conical, with setae s2 very long, protruding over tip of tube; gynosternal plates with aciculae recognizable. Abdominal segment X (tube) moderately long and slightly extended at base; with terminal crown of long anal setae about as long as tube.

Measurements. Female MU-Fos-138/1 (in microns): Body, length 2038. Head, length 189; largest width 227. Eyes, length 70; width 32. Ocellar setae 41. Pronotum, length 246; width 441. Pterothorax, largest width 410. Epimeral setae 164. Abdomen, length 1254; largest width 461 (segment IV); segment X (tube), length 221; basal width 69. Setae on tergite IX, s1 189; s2 328; s3 107. Antennae, length 525; length (largest width) of segment I 51 (31), II 61 (34), III 87 (40), IV 71 (34), V 69 (28), VI 60 (22), VII 62 (19), VIII 42 (12), IX 22 (6). Sense cones, length of inner (outer) on segment III 22&19 (22&19), IV 22 (25), V 16 (16), VI 9 (9); basal width of sense cones on III and IV about 5. Fore wings, length 1137; largest width 294; vein length 892.

Measurements added from syntype MU-Fos-139/1: Body, length 2000. Pronotal anteromarginal setae 88, mediolateral setae 82, posteroangular setae 63; epimeral setae 189.

Material studied. Syntype female MU-Fos-138/1 (Fig. 12); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar. Purchased by the author on eBay from Terry Su, eBay username "burmite-miner"; deposited in the author's collection. Syntype MU-Fos-139/1; inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar; donated by Patrick Müller; deposited in the author's collection.

Syninclusions. MU-Fos-138/1: plant detritus, stellate plant hairs. MU-Fos-139/1: remnants of a fly (Diptera) and small brownish droplets of unknown origin.

Etymology. The species epithet *brachyvenis* comes from the Greek word *βραχύς* (*brachys*), meaning "short", and the Latin word *vena*, meaning "vein". It refers to the short wing vein of this species (Fig. 12).

Rohrthrips breviceps Ulitzka, 2019
(Fig. 13)

Male (MU-Fos-144/1). Body slightly contracted; wings spread, except right hind wing, which overlaps the abdomen; both fore legs and left mid and hind legs bent under head and body, respectively.

Very similar to the holotype in colour and body structure, but somewhat longer and with broader abdomen (see Ulitzka 2019, p. 29). Wings (broken off in the holotype male); with fore wings becoming progressively larger in distal half (Fig. 13). Wing vein shortened, extending only to base of distal wing rounding; not converging with costa; furnished with some setae; second vein not developed. Wing membrane without microtrichia. Fringe cilia straight; some arising from sockets, particularly at the distal margin of the fore wing. Duplicated cilia present around apical margin of wing; running parallel to normal wing fringes. Hind wing without any veins. Wing coupling system hamulo-frenate; number of hamuli not assessable.

Measurements. Male MU-Fos-144/1 (in microns): Body, length about 1377 (slightly contracted). Head, length 137; largest width 206. Eyes, length 63; width 44. Ocellar setae 44; postocular setae 56. Pronotum, length 159; width 391; anteroangular setae 30, mediolateral setae about 65 (not clearly visible), posteroangular setae about 96, epimeral setae 125. Pterothorax, largest width 353. Abdomen, length 813; largest width 431 (segment V); segment X (tube), length 196; basal width 83. Setae on tergite IX, s1 147, s2 broken off, s3 270. Antennae, length 440. Fore wings, length 921; largest width 206; length of vein 735.

Material studied. Male MU-Fos-144/1 (Fig. 13); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar; donated to the author by Patrick Müller; deposited in the author's collection.

Syninclusions. A beetle (Coleoptera: Limnichidae), remnants of another insect, a branched plant trichome, some bubbles of air and brownish streaks of unknown origin.

Rohrthrips jiewenae Ulitzka, 2019
(Fig. 14)

Male. Body fully distended; head laterally compressed; several pronotal setae broken off; right wings slightly spread, left fore wing broken off in the middle, left hind wing twisted and overlapping abdomen; legs folded under body or head, respectively, except for left mid and hind leg; pterothorax concealed by a bubble of air; tube at tip broken off.

Similar to female in colour, size and body structure but more slender, with longer antennae and less setae on the first wing vein. Sense cones short as in female (see Ulitzka 2019, p. 30).

Measurements. Male MU-Fos-93/1 (in microns): Body, length about 1607 (tip of tube broken off). Head, length 170; largest width 164 (laterally compressed). Eyes, length 63. Ocellar setae 42; postocular setae about 57. Pronotum, length 220; width 296; posteroangular setae about 50 (difficult to measure); epimeral setae 70. Pterothorax, largest width 284. Abdomen, length >915 (tip of tube missing); largest width 314 (segment IV); segment X (tube), length not measurable; basal width 52. Setae on tergite IX, s3 221 (others broken off at tips). Antennae, length 380. Fore wings, length 1185; largest width 190.

Material studied. Male MU-Fos-93/1 (Fig. 14); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar; donated to the author by Mark Pankowski; deposited in the author's collection.

Syninclusions. Stellate plant hairs, plant detritus.

Rohrthrips multihamuli sp. n.
(Figs 15, 27, 38)

Female. Abdomen slightly contracted; head bent upwards, its left side at base slightly dented; body partially covered by a reflective layer that gives an excellent impression of the sculptured structure; tube and parts of the wings difficult to assess due to cracks and bubbles; fore wings spread, hind wings overlapping body, left fore leg folded under body.

Colour uniformly dark brown including antennae and legs; all major setae dark as well as wing veins and fringes; wings very weakly shaded greyish brown, largely translucent.

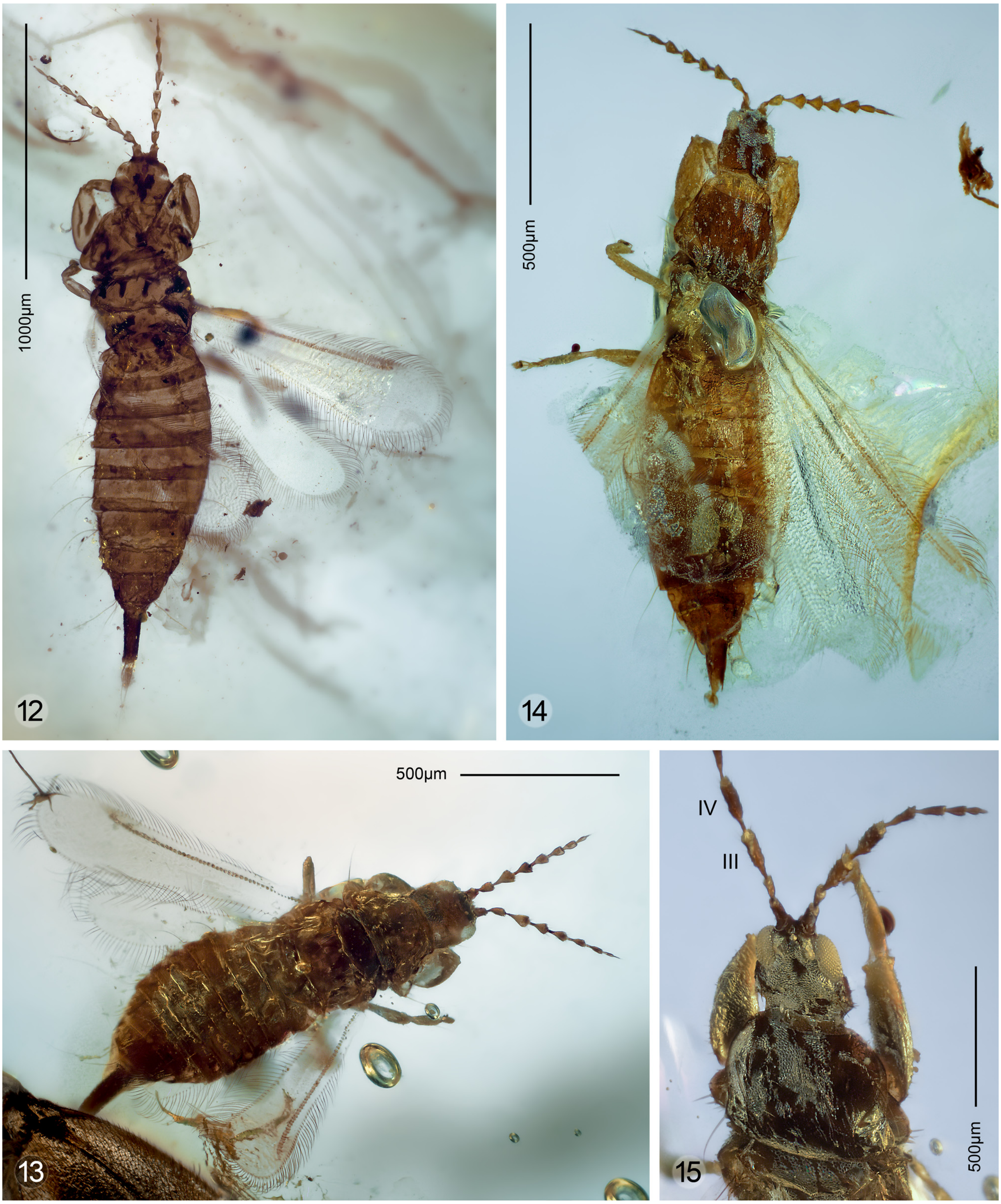
Head (Fig. 15) as long as wide; recessed behind the eyes; sculptured with fine reticulations. Cheeks nearly straight, diverging backwards and tapering sharply after a lateral ridge towards base; furnished with tubercles bearing short stout setae. Ocellar setae not assessable, two points of attachment visible near base of each antenna. Postocular setae far behind compound eyes; pointed, long and stout. Eyes large, laterally occupying about half of the head length; not prolonged ventrally. Ocelli arranged on a distinct ocellar hump, with fore ocellus protruding towards front and hind ocelli close to compound eyes. Antennae nine-segmented (Figs 15, 38); segment I long, broadened at base, inverse funnel-shaped; II inversely conical, with a campaniform sensillum close to apex; III and IV basally with a long pedicle, distally cylindrical; V basally with a long pedicle, then inversely conical and ventrally with a pointed projection bearing a seta at apex; VI–VIII basally with a short pedicle, then inverse conical and slightly tapering towards apex, each with a short projection ventrally (somewhat similar to some species of extant *Anactinothrips* Bagnall (see Retana-Salazar 2009); IX conical, broadly attached to VIII. All antennal segments bearing many setae, particularly III and IV. Sense cones tiny, difficult to see and to distinguish from setae; their number not determinable. Mouth cone short and rounded. Maxillary stylets not assessable. Pronotum trapezoidal, wider than long; sculptured finely reticulate; with notopleural suture complete. Pronotal anteromarginal and posteromarginal setae vestigial; anteroangular setae recurved and pointed; mediolateral, posteroangular and epimeral setae distinctly long, hairlike and finely pointed. Mesonotum and metanotum sculptured reticulate; metanotum with a pair of long median setae far behind front margin of plate. Fore wings becoming progressively larger in distal half; anterior vein reaching costa at about three quarters of the wings' length, distally expanded to a brown elongated mark, furnished with a row of 12 setae and distally with three terminal setae close to costa; second vein not developed; membrane anteriorly at base clearly with some sparse microtrichia (Fig. 27), distal part of the wing membrane smooth. Fringe cilia straight; slightly enlarged at base but embedded into the wing membrane, not on sockets. Duplicated cilia present around apical margin of wing; running parallel to normal wing fringes; on sockets or at least not deeply retracted into wing membrane. Hind wings at base clearly with some sparse microtrichia (Fig. 27), distal part of the wing membrane smooth and without any veins. Wing coupling system hamulo-frenate; hamulate component consisting of a row of six (right) and seven (left) hamuli at anterior margin close to base of hind wing (Fig. 27). Fore legs (Fig. 15) with femora enlarged; tibiae dorsally with a long hair-like seta; fore tarsi with a strong tooth and with hamus. Mid legs slender; tibiae each with a long dorsal seta and terminally with two strong spines; mid and hind tarsi two-segmented. Abdominal tergites without wing-retaining setae, but with fine long and recurved dorsal and lateral setae; sculpture of tergites reticulate (assessable only in some parts). Abdomen with tergite I (pelta) broad, shape of fore margin not assessable (covered by hind margin of metanotum); tergite II with a dorsolateral suture slanting laterally inwards; VIII with sternal gynosternites clearly visible. Segment IX conical, tergal setae s1 (broken off, preserved near tube) stouter than s2 and s3; s2 longest, but much shorter than tube. Abdominal segment X tubular, long and slender, with a terminal crown of anal setae, which are shorter than the tube.

Measurements. Female (in microns): Body, length 2800. Head, length 274; largest width 274. Eyes, length 132; width 63. Hind ocelli, diameter 25; distance between the hind ocelli 50. Postocular setae about 60 (difficult to measure). Pronotum, length 340; width 447; anteroangular setae 50, mediolateral setae 208, posteroangular setae 206 and epimeral setae 164. Pterothorax, largest width 539. Abdomen, length 1760; largest width 566 (segment III); segment X (tube), length 460; basal width 78. Setae on tergite IX, s1 186; s2 380; s3 196. Antennae, length 744; length (largest width) of segment I 68 (31), II 62 (28), III 133 (43), IV 133 (37), V 114* (28), VI 93* (22), VII 65* (20), VIII 57* (12), IX 28 (6) [all measurements taken on right antenna; segments indicated with * have been measured from segment base to tip of the distal projections]. Fore wings, length 1352; largest width 343.

Material studied. Holotype female MU-Fos-137/1 (Figs 15, 27, 38); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar. The holotype was donated by Patrick Müller and is deposited in the author's collection.

Syninclusions. A mite (attached?) dorsally to the abdomen of the thrips; remnants of an insect, a plant trichome, many air bubbles around the thrips inclusion.

Etymology. The species epithet *multihamuli* refers to the wing coupling system comprising a remarkable number of hamuli (Fig. 27).



FIGURES 12–15. *Rohrthrips* spp. **(12)** *Rohrthrips brachyvenis* **sp. n.** holotype female, dorsal view; **(13)** *Rohrthrips breviceps* male, dorsal view (Note: the median shading makes the tube appear narrow, but the lighter edges are part of the tube, which actually is broad at base); **(14)** *Rohrthrips jiewenae* male, dorsal view; **(15)** *Rohrthrips multihamuli* **sp. n.** holotype female, head and pronotum, antennal segments III–IV indicated with roman numerals.

***Rohrthrips pandemicus* sp. n.**

(Fig. 16)

Female aptera. Body extended, slightly dorsoventrally compressed; left antenna distally of segment II broken off; all legs spread, tibia and tarsus of left mid leg lacking; some segments of right antenna dorsoventrally compressed; sense cones of right antenna as well as numerous setae of thorax and abdomen torn off but for the most part conserved near the body.

Colour (Fig. 16) including antennae, head and legs uniformly light brown.

Head wider than long; sculpture hardly assessable, but rather smooth; produced in front of anterior margin of small eyes, with cheeks slightly rounded behind eyes; cheeks lacking setae. One pair of ocellar setae visible close to base of antennae; pointed, somewhat longer than antennal segment I. Postocular setae far behind compound eyes; pointed, long and stout. Compound eyes reduced to a few facets only. Ocelli not developed. Antennae nine-segmented; segment I barrel-shaped; segment II asymmetrically bent outwards, basally with a short, stout pedicle; III–VI symmetrical and short, inverse conically shaped and tapering distally from level of sense cones, III with very slender pedicle; VII and VIII inverse cone-shaped, distally flat, IX style-shaped. Sensorium on segment II not visible; sense cones of the following segments torn off and preserved close to the segments; one inner and one outer on III–V, one outer on VI and one inner on VII. Mouth cone short and rounded. Palps not assessable. Pronotum broad, wider than long, trapezoidal; posteroangular as well as epimeral setae long and pointed, anteromarginal, mediolateral and posteromarginal setae not visible. Wings not developed. Fore legs with femora stout; fore tarsi with a strong tooth and a hamus. Mid and hind legs slender. All femora with one long ventral and all tibiae with one long dorsal seta; mid and hind tibiae distally each with three spines; mid and hind tarsi two-segmented, with hamus. Abdominal tergites smooth; with lateral setae long, pointed; setae s3 on IV–VII longer than other lateral setae. Abdominal tergite I (pelta) broadly trapezoidal; segment IX conical, with setae s3 about as long as tube. Abdominal segment X (tube) conically extended towards base; its sculpture not assessable; with a terminal crown of anal setae shorter than tube.

Measurements. *Female aptera* (in microns): Body, length 1686. Head, length 183; width 202. Eyes, length 32; width 32. Ocellar setae 63; postocular setae 76. Prothorax, length 264; width 453; posteroangular setae about 80 (difficult to measure); epimeral setae 94. Abdomen, length 1078; largest width 519 (segments V); segment X (tube), length 235; basal width 100. Setae s3 on tergite IX about 280. Antennae, length 400; length of segment I 53, II 50, III 71, IV 53, V 40, VI 40, VII 40, VIII 34, IX 16 (width not given due to dorsoventral compression). Sense cones, length of inner (outer) on segment III – (19), IV 16 (16), V 14 (16), VI – (19); basal width about 5.

Material studied. Female *aptera* MU-Fos-146/1 (Fig. 16); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar; donated to the author by Patrick Müller; deposited in the author's collection.

Syninclusions. Two mites, remnants of other arthropods, different plant trichomes, many tiny brownish droplets; some air bubbles and brown streaks of unknown origin.

Etymology. The species epithet *pandemicus* comes from the Greek words *πᾶν* (*pan*) meaning "all" and *δῆμος* (*demos*) meaning the "common people" in sense of the 'crowd'. The word "pandemic" is used for an infectious disease that has spread across a large region affecting a substantial number of individuals. The new species is dedicated to all mankind suffering at present under the Covid-19 pandemic.

Note. Despite being described here as a new species this specimen may represent the micropterous form of *R. maryae* or possibly *R. breviceps*. If further finds clarify the position the name will disappear in revision, just as hopefully Covid-19 will disappear in a not-too-distant future.

***Rohrthrips patrickmuelleri* Ulitzka, 2019**

Female. Body slightly contracted; pronotum dorsoventrally compressed; wings overlapping abdomen; legs folded under body or head, respectively, except for right fore leg and left mid leg.

Very similar to the holotype female in colour, size and body structure (see Ulitzka 2019, p. 32); wings somewhat shorter. This female enhances the characterisation of the species by its coarse reticulate pronotal sculpture; in the holotype this feature is preserved only at the posterior margin of the pronotal plate.

Measurements. Female MU-Fos-115/1 (in microns): Body, length 1470. Head, length 190; largest width 202. Eyes, length 82. Ocellar setae 32. Pronotum (dorsoventrally compressed), length 214; width 396; posteroangular setae about 107; epimeral setae 107. Pterothorax, largest width 378. Abdomen, length 921 (slightly contracted); largest width 473 (segment III); segment X (tube), length 151; basal width 63. Setae on tergite not measurable. Antennae, length 390. Fore wings, length 963; largest width 201.

Material studied. Female MU-Fos-115/1; inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar; purchased by the author on eBay from Terry Su, eBay username "burmite-miner", and deposited in the author's collection.

Syninclusions. Four mites, large aggregations of fungal hyphae and some spores, stellate plant hairs, plant detritus and many air bubbles.

Rohrthrips rhamphorhynchus **sp. n.**

(Figs 17, 37)

Sex not determinable, distal abdominal segments ventrally obscured. Body distended except for mesonotum, which is somewhat retracted under pronotum; left wings spread but broken off at about one-third of wing length; right fore wing spread, right hind wing overlapping body; legs spread except for right fore and hind leg, which are folded under head and body, respectively. Tube broken off at tip.

Colour (Fig. 17) uniformly dark brown, including antennae and legs; all major setae dark as well as wing veins and fringes; wings shaded brownish, slightly paler at base.

Head (Fig. 37) about as long as wide; projecting over antennal bases; protruding in front of eyes and incised anteriorly and posteriorly to eyes; sculpture difficult to assess, but coarse reticulations are clearly visible laterally. Cheeks slightly convex; each with two weak lateral setae. One pair of stout ocellar setae attached on a distinct tubercle near the outer margin of antennal bases, longer than antennal segment I; a second pair close to the front margin of the eyes, much weaker and shorter. Postocular setae far behind compound eyes; pointed, long and stout. Eyes small but protruding at front margin; laterally occupying about one quarter of the head length; slightly prolonged ventrally. Hind ocelli close to compound eyes, fore ocellus not visible. Antennae nine-segmented; segment I long, broadened at base, cone-shaped; II inversely conical, sensorium not assessable; III–VIII with a pedicle at base, then inverse cone shaped and distally flat, IX conical and broadly attached to VIII. Sensorium on segment II not visible; number of sense cones of the following segments difficult to assess, at least one outer and one inner on III–VI and one inner on VII. Mouth cone long, slender and pointed, protruding over base of prosternum (Figs 17, 37). Maxillary stylets retracted to hind margin of compound eyes, running close together and parallel towards the mouth cone; left mandibula long and curved, right mandibula vestigial. Maxillary palps not visible. Pronotum (Fig. 37) trapezoidal, wider than long; pronotal posteroangular and epimeral setae long and finely pointed; other pronotal setae not visible. Mesonotum not assessable; metanotum with a pair of strong setae far behind front margin of plate. Fore wings (Fig. 17) becoming progressively larger in distal half; with two veins. First wing vein shortened, extending only to base of distal wing rounding; furnished with five dispersed small setae (only one seta in distal wing half about as long as distance between wing vein and fore margin of wing); second vein developed in basal third only, without any setae. All wings basally with some microtrichia, especially hind wings; distal parts of wing membrane smooth. Fringe cilia straight; arising from sockets. Duplicated cilia present around apical margin of wing; running parallel to normal wing fringes. Hind wing without any veins. Wing coupling system hamulo-frenate; hamulate component consisting of two hamuli at anterior margin close to base of hind wing (the setiform process on the right wing has three setae instead of only two). Fore legs with femora enlarged (Fig. 17); tibiae dorsally with a long hair-like seta; fore tarsi with a strong tooth and with hamus. Mid legs slender. All femora with one long ventral and all tibiae with one long dorsal seta; mid and hind tibiae terminally each with three spines; mid and hind tarsi two-segmented, with hamus. Abdominal tergites without wing-retaining setae, but with fine long and recurved dorsal and lateral setae; sculpture not assessable. Abdomen, tergite I not assessable; tergite II with a dorsolateral suture slanting laterally inwards. Segment IX conical, tergal setae s1 stout but tips broken off, much stronger than s2 (also with tips broken off) and s3, which are long, hair-like and finely pointed. Abdominal segment X tubular, tip broken off.

Measurements. MU-Fos-140/1 (in microns): Body, length >1410 (tip of tube broken off). Head, length 140; largest width 142. Eyes, length 50; width 31. Hind ocelli, diameter 12; distance between the hind ocelli 30. Ocellar setae s1 65; s2 19. Postocular setae 81. Pronotum, length 183; width 179; posteroangular setae about 70–80 (difficult to measure) and epimeral setae 108. Pterothorax, largest width 290. Abdomen, partial length (segments I–IX)

668; largest width 347 (segment III); segment X (tube; tip broken off), length < 112; basal width 25. Setae on tergite IX, s1 and s2 with tips broken off; s3 294. Antennae, length 429; length (largest width) of segment I 74 (31), II 50 (28), III 62 (31), IV 50 (31), V 50 (31), VI 50 (25), VII 43 (24), VIII 28 (14), IX 22 (12). Sense cones, length of inner (outer) on segment III 19 (22), IV 16 (19), V 12 (12), VI 12 (12), VII 12 (–); basal width of inner (outer) about 4 (5) (measured on segment III). Fore wings, length 1078; largest width 196.

Material studied. Holotype female MU-Fos-140/1 (Fig. 17); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar. The holotype was donated by Patrick Müller and is deposited in the author's collection.

Syninclusions. Remnants of another insect, plant trichomes, one of which is attached to the thrips' antenna.

Etymology. The species epithet *rhamphorhynchus* comes from the Greek words *ῥάμφος* (*rhamphos*), meaning "beak" and *ῥύγχος* (*rhynchos*), meaning "snout". It refers to the long and pointed mouth cone of this species (Figs 17, 37).

Rohrthrips setiger sp. n.

(Fig. 18)

Female. Body extended, distal abdominal segments, however, directed to the right; pronotum dented on the left side; right fore wing slightly spread, right hind wing turned under body, left wings overlapping body; right hind leg folded under abdomen, other legs bent but well visible; anterior and mediolateral setae of pronotum as well as major head setae not visible (whether broken off or vestigial).

Colour uniformly dark brown, including antennae and legs; all major setae dark as well as wing veins and fringes; wings shaded brownish.

Head longer than wide; slightly prolonged in front of and incised behind compound eyes; sculpture not clearly assessable, some parts give the impression of a coarse reticulation. Cheeks straight, barely tapering towards head base; with a few short lateral setae (their number not assessable). One pair of ocellar setae visible close to base of antennae; pointed, about as long as antennal segment I. Postocular setae not visible. Eyes slightly protruding at front margin; laterally occupying somewhat more than one third of the head length; not prolonged ventrally. Hind ocelli large and close to compound eyes, fore ocellus much smaller and directed forwards. Antennae nine-segmented; segment I barrel-shaped; segment II asymmetrically bent outwards, basally with a stout pedicle; III–VII with a much more slender pedicle at base, then inverse cone shaped and tapering distally from level of sense cones; VIII spindle-shaped; IX style-shaped. Sensorium on segment II not visible; sense cones of the following segments deformed, their number difficult to assess, at least one outer and one inner on III–V, one inner on VI and one inner on VII. Mouth cone pointed, long but not reaching base of prosternum. Maxillary palps not assessable. Pronotum wider than long, trapezoidal; anteroangular and mediolateral setae very short (or broken off), posteroangular setae long and pointed, anteromarginal and posteromarginal setae minute; epimeral setae long and hair-like, longer than other pronotal major setae. Mesonotum sculptured finely reticulate; mesonotal setae not visible. Fore wings becoming progressively larger in distal half; with two veins (Fig. 18). First wing vein reaching costa near wing apex; furnished with 13 dispersed setae (six of these setae in distal wing half are about as long as distance between the wing vein and fore margin of wing, or even longer); second vein developed in basal third only, without any setae. Fringe cilia straight, for the most part slightly enlarged at base but embedded into the wing membrane, only some fringes – particularly on hind wings – clearly on sockets. Duplicated cilia present around apical margin of wing; running parallel to normal wing fringes. Hind wing without any veins. Wing membrane of fore and hind wings without microtrichia. Wing coupling system hamulo-frenate (number of hamuli not assessable). Fore legs with femora enlarged, but not as stout as in other species; fore tarsi with a strong tooth and a strong hamus. Mid and hind legs slender. All tibiae with one long dorsal seta; mid and hind tibiae terminally each with three spines; mid and hind tarsi two-segmented, with hamus. Abdominal tergites without wing-retaining setae; lateral setae pointed, recurved, long but delicate; setae s3 on IV–VII conspicuously longer than other lateral setae. Basal abdominal segments not assessable (hidden by wings); IX conical, with setae s2 long but shorter than tube. Abdominal segment X (tube) long and evenly widened towards base; with terminal crown of short anal setae (shorter than half the length of the tube).

Measurements. Female (in microns): Body, length 1960. Head, length 255; largest width 206. Eyes, length 87; width 49. Hind ocelli, diameter 19; distance between the hind ocelli 76; fore ocellus, diameter 13. Ocellar setae 38.

Pronotum, length 246; width not measurable (dented on right side); posteroangular setae about 20 (difficult to measure) and epimeral setae 164. Pterothorax, largest width 328. Abdomen, length 1040; largest width 510 (segment III); segment X (tube) length 270; basal width 76. Setae on tergite IX, s1 107; s2 252; s3 202. Antennae, length 533; length (largest width) of segment I 71 (28), II 68 (28), III 81 (34), IV 68 (31), V 68 (28), VI 56 (19), VII 53 (19), VIII 46 (16), IX 22 (9). Sense cones not measurable. Fore wings, length 1088; largest width 255.

Material studied. Holotype female MU-Fos-147/1 (Fig. 18); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar; purchased by the author on eBay from Terry Su, eBay username "burmite-miner"; deposited in the author's collection.

Syninclusions. Numerous hairs of another arthropod; small particles of plant detritus, small dark droplet and many crystals of pyrite around the thrips inclusion.

Etymology. The species epithet *setiger* comes from the Latin words *seta*, meaning "bristel", and *gerere*, meaning in the character of the suffix *-ger* "furnished with". It refers to the wing vein of this species that is furnished with numerous longer setae (Fig. 18).

Differential diagnosis. *Rohrthrips* now comprises 12 species that can be distinguished primarily by their wing veins and the length-to-width ratio of their tubes. In contrast to all other species *R. libanicus*, *rhamphorhynchus* **sp. n.** and *setiger* **sp. n.** have an additional but shorter second vein on the fore wings (see Figs 17–18 and Ulitzka 2018, p. 556 Fig. 13). *R. libanicus* from Lebanese amber can be distinguished from the latter two species from Burmese amber by its shorter tube. Within the species from Burmite, *R. rhamphorhynchus* **sp. n.** has a long and slender mouth cone protruding over the base of the prosternum (Fig. 37), whereas the mouth cone in *R. setiger* **sp. n.** is much shorter. These species, moreover, can be distinguished by the number of setae on their first wing vein: In *R. setiger* **sp. n.** the vein has much more stout setae (13); in *R. rhamphorhynchus* **sp. n.** it is less setose (four short and one longer setae). The species with only one wing vein may be classified into two groups with regard to the shape and length-to-width ratio of their tubes. The first group contains species with a short and bulky tube (length-to-width ratio 2.3–2.5): *R. breviceps*, *R. maryae* and *R. patrickmuelleri*; in contrast, the second group contains species with a long and slender tube (length-to-width ratio 3.2–5.9): *R. brachyvenis* **sp. n.**, *R. burmiticus*, *R. jiewenae*, *R. multihamuli* **sp. n.** and *R. schizovenatus* (see also Ulitzka 2019). In the first group, *R. breviceps* (Fig. 13) may be distinguished by its conspicuously short head, the shortened wing vein (0.8 of wing length) and the smaller body size (1.3mm). Some character states of this species, however, are similar to those of *R. maryae* and *R. patrickmuelleri*, such as the length of the epimeral setae in *R. patrickmuelleri*, and in *R. maryae* the head, which is also somewhat wider than long. However, both of the latter species are larger yet their antennae are much shorter. *R. maryae* and *R. patrickmuelleri* may be distinguished by their wings. In both species the wing vein meets the costa close to the wing apex. In *R. patrickmuelleri*, however, the vein is colourless subbasally and coloured pale greyish-brown distally and it is conspicuously straight except for the short bending close to its tip. In contrast, the vein is dark brown in the distal two thirds and curved forwards from the middle of its length in *R. maryae*. Furthermore, the wings of the latter species are broader apically and it is much larger than *R. patrickmuelleri,* with the abdomen conspicuously broad.

In the second group *R. multihamuli* **sp. n.** differs significantly from all other species; on the one hand by its large size (2.8 mm) and on the other hand by the shape of antennal segments III and IV, which are not inversely conical but cylindrically elongated (Figs 15, 38). *R. burmiticus* and *R. jiewenae* differ from *R. brachyvenis* **sp. n.** and *R. schizovenatus* with regard to their long wing vein reaching the costa at base of the wing tip rounding. These species are quite similar regarding their body shape and structures; however, they are clearly distinguished by the conspicuously short sense cones in *R. jiewenae*. In *R. brachyvenis* **sp. n.** and *R. schizovenatus* the wing vein is shortened. In *R. schizovenatus* it hardly reaches the last quarter of the fore wing and it is apically split into two branches, each ending with a terminal seta. Furthermore, *R. schizovenatus* has a very long and slender tube (length-to-width ratio about 5.1) and antennal segment III is strikingly long (>100µm). In *R. brachyvenis* **sp. n.** antennal segment III and the tube (length-to-width ratio about 3.2) are shorter. Furthermore, the wing vein in this species is not split and slightly longer, reaching the last fifth of the wing (Fig. 12). *R. brachyvenis* **sp. n.**, moreover, is the only species of *Rohrthrips* that clearly shows four sense cones on antennal segment III. However, this feature should be considered with great care. In other species, further sense cones may also be present but may lie completely above or below the segment and thus remain hidden. *R. pandemicus* **sp. n.**, finally, is the only micropterous species within that genus (Fig. 16). It has no ocelli, and its compound eyes are reduced to a few ommatidia only. Most likely, however, it is not a distinct species but the micropterous form of *R. maryae* or possibly *R. breviceps*.

FIGURES 16–18. *Rohrthrips* spp. **(16)** *Rohrthrips pandemicus* **sp. n.** holotype female aptera, dorsal view; **(17)** *Rohrthrips rhamphorhynchus* **sp. n.** holotype, dorsal view, indicated: second vein at base of fore wing; mouth cone outlined white; **(18)** *Rohrthrips setiger* **sp. n.** holotype female, right fore wing, indicated: second wing vein at base.

Sesquithrips gen. n.

Type species: *Sesquithrips rostratus* **gen. et sp. n.**

Diagnosis. Abdominal segment X tubiform. Antennae nine-segmented, with segments VIII and IX broadly joined. Fore wings broadened in basal half, distally with parallel margins and with broadly rounded tip; first vein complete, bearing setae; second vein present but ending approximately in the middle of the wing with a distinct terminal seta (Fig. 22). Fore wings with fringe cilia embedded into wing membrane; duplicated cilia present; wing coupling not assessable. Hind wings distally with posterior margin of wing membrane serrate into small teeth, each carrying a fringe cilium at tip attached on a tiny socket (Fig. 23). Abdomen without sigmoidal wing retaining setae.

Sesquithrips shows modern tubuliferan character states in combination with plesiomorphic features like nine-segmented antennae and fore wings with longitudinal veins. It therefore is allocated to Rohrthripidae. Similar as mentioned for *Adstrictubothrips* **gen. n.**, the fringes in *Sesquithrips* **gen. n.** are embedded for the most part into the wing membrane (Fig. 22). Only at the serrate posterior margin of the hind wings are they clearly attached on tiny sockets (Fig. 23). *Sesquithrips* **gen. n.** differs from *Rohrthrips* and *Gemineurothrips* **gen. n.** with regard to the narrow shape of the wings. Furthermore, the dorsolateral sutures found in members of *Rohrthrips* and *Paralleloalathrips* **gen. n.** at abdominal segment II (see below) are not developed in this new genus. Moreover, *Sesquithrips* **gen. n.** is easily distinguished from the latter genus and from *Adstrictubothrips* **gen. n.** by the second wing vein, which ends in the middle of the fore wing with a stout terminal seta (Fig. 22).

Etymology. The name of the new genus derives from the Latin prefix *sesqui*, meaning "one and a half", and *thrips*, the usual term for a genus within Thysanoptera. It refers to the wing venation with a complete first vein and a second vein extending only half the length of the fore wing (Fig. 22).

Sesquithrips markpankowskii gen. et sp. n.

(Figs 19–20)

Female (Holotype). Head slightly bent downwards, abdomen contracted (Fig. 19); right wings spread but hind wing hidden by fore wing; left wings partially overlapping body, hind wing covered by fore wing except for tip; left fore leg and right hind leg folded under body.

Colour (Fig. 19) uniformly dark brown, including antennae and legs; all major setae dark as well as wing veins and fringes; fore wings shaded brown, paler from the middle towards base and at the extreme tip; hind wings largely covered by fore wings, at least pale brownish at tip.

Head (Fig. 19) broad, much wider than long; dorsally sculptured with transverse reticulations. Cheeks converging slightly rounded towards base; laterally with spine-like setae arising from small tubercles. Ocellar setae not visible; postocular setae far behind compound eyes, tiny, pointed. Eyes small, longer than wide, not prolonged ventrally. Ocelli large; hind ocelli close to compound eyes and far apart from each other; fore ocellus between antennal insertions, directed forwards. Antennal bases far apart. Antennae nine-segmented; segment I conically shaped; II large, inversely conical, apically with a small circular sensorium; III–VIII basally with a pedicle, then inverse conically shaped and sharply tapering distally; IX style-shaped, broadly attached to VIII. Sense cones difficult to assess; at least one inner and one outer present on III–VI and one outer on VII. Mouth cone short and rounded (Fig. 19). Maxillary palps two-segmented. Pronotum trapezoidal, wider than long; chaetotaxy not assessable. Mesonotum sculptured with fine transverse lines; metanotum reticulate. Fore wings narrow, somewhat broadened in basal half and bluntly rounded at tip; anterior vein complete, bearing seven setae in distal half; second vein ending with a distinct terminal seta in the middle of the wing; wing membrane without microtrichia. Clavus with paired setiform processes at tip. Fringe cilia straight; embedded into wing membrane, except at posterior distal margin of hind wings, where the wing margin is serrate with small teeth, each carrying a fringe cilium at tip attached on a tiny socket. Fore wings with duplicated cilia around wing tip and along distal part of posterior wing margin; running parallel to normal wing fringes. Fore legs with femora not enlarged, apically with external margin sharply curved into a tooth-like protuberance; fore tibiae not clearly assessable; tarsi without tooth but with a recurved hamus. Mid and hind legs slender; tibiae each with a long dorsal seta; mid and hind tarsi two-segmented. Abdominal tergites without wing-retaining setae; lateral setae stout, slightly curved and pointed. Tergite I (pelta) D-shaped, much wider then long, sculptured with lines of transverse loose reticulation. Abdominal segment IX dome-shaped; setae s1 stout and pointed, sharply recurved at tip; s2 and s3 finely pointed, shorter than tube. Abdominal segment X tubular, with margins parallel; with a pair of campaniform sensilla close to apex and with a terminal crown of anal setae, these much shorter than tube; ventral median pair of anal setae stout with cannula-like tips.

Measurements. Female (in microns): Body, length 990 (abdomen contracted). Head, length 105; width 167; distance between antennal bases 22. Eyes, length 47; width 37. Hind ocelli, diameter 16; distance between the hind ocelli 31. Pronotum, length 109; largest width 189. Pterothorax, largest width 226 (at level of mesothoracic spiracles). Abdomen, length 536; largest width 245 (segment II); segment X (tube), length 124; width 31. Pelta, length 56; width about 190 (difficult to measure). Setae at tergite IX, length s1 34; s2 56; s3 74. Antennae, length 249; length (largest width) of segment I 31 (27), II 34 (25), III 37 (22), IV 34 (22), V 34 (22), VI 28 (17), VII 22 (12), VIII 19 (9), IX 10 (5). Sense cones, length of inner (outer) on segment III 6 (9), IV 9 (16), V 6 (12), VI 6 (9), VII – (9); basal width of inner (outer) about 2 (3) (measured on segment III). Fore wings, length 517; width at terminal seta of cross vein 53.

Male (Paratype). Body (Fig. 20) fully distended; wings bent upwards so that they appear shorter in projection than they are in reality, right wings and left hind wing spread, left fore wing overlapping body; all legs folded under head and body, respectively, except for right mid leg; median part of abdomen ventrally hidden by a large air bubble.

Very similar to female but smaller and much more slender. Pronotum with short posteromarginal setae. Fore tarsi without tooth. Abdominal sternite IX with hypandrium and androsternite clearly visible (see Bhatti 1998b). Fore femora not enlarged; fore tibiae not clearly assessable; tarsi without tooth but with a recurved hamus. Fore wings shorter as in female; with less duplicated cilia; first vein of fore wing with less setae; posterior distal margin of hind wings serrate with small teeth, but not as pronounced as in female.

FIGURES 19–20. *Sesquithrips markpankowskii* **gen. et sp. n. (19)** holotype female, dorsal view, mouth cone outlined white; **(20)** paratype male, dorsal view, mouth cone outlined white. (Note: The wings of the male are bent upwards and, therefore, longer than visible on the photo).

Measurements. Male (in microns): Body, length 853. Head, length 84; width 118; distance between antennal bases 21. Eyes, length 31; width 25. Pronotum, length 72; largest width 130; posteromarginal setae 16. Abdomen, length 559; largest width 152 (segment II); segment X (tube), length 81; width 25. Setae at tergite IX, length s1 34; s2 47; s3 62. Antennae, length 255. Fore wings, length 350; width at terminal seta of cross vein 37.

Material studied. Holotype female MU-Fos-134/1 (Fig. 19); inclusion in Burmese amber; purchased by Mark Pankowski on eBay and donated to the author. Paratype male MU-Fos-141/1 (Fig. 20); inclusion in Burmese amber; purchased by the author on eBay from Terry Su, eBay username "burmite-miner". Both fossils originate from Hukawng Valley, Kachin State, Myanmar and are deposited in the author's collection.

Syninclusions. MU-Fos-134/1: Plant detritus, small droplets and brownish stains of unknown origin. MU-Fos-141/1: A springtail (Collembola), parts of a mite, two coprolites, stellate plant hairs (some in a large aggregation), plant detritus, some tiny air bubbles.

Etymology. The new species is dedicated in gratitude to Mark Pankowski for his continuous and invaluable support in my work on fossil Thysanoptera.

Sesquithrips rostratus gen. et sp. n.

(Figs 21–23)

Female. Body (Fig. 21) fully distended, head and thorax partially concealed by a vertical crack, basal abdominal segments deformed; left wings spread, right wings for the most part overlapping body; right hind leg and tarsus of left fore leg folded under body.

Colour (Fig. 21) uniformly light brown to brown, including antennae and legs; wing veins and fringes dark as well as anal setae; major body setae, however, almost translucent and therefore difficult to see; fore wings shaded brownish, paler from the middle towards base; hind wings brownish, slightly paler than fore wings.

Head broad, wider than long; dorsally sculptured with transverse reticulations. Cheeks broadened behind eyes, converging slightly rounded towards base; laterally with spine-like setae arising from small tubercles. Ocellar setae difficult to assess; one short pair visible close to fore ocellus, one pair just before hind ocelli; postocular setae far behind compound eyes, pointed. Eyes small, about as wide as long, not prolonged ventrally. Ocelli large; hind ocelli close to compound eyes and far apart from each other; fore ocellus between antennal insertions, directed forwards. Antennal bases close together. Antennae nine-segmented; segment I conically shaped; II inversely conical, apically with a small sensorium; III–VII basally with a pedicle, then inverse conically shaped and tapering distally, somewhat oval in appearance but rather short; VIII with a pedicel, distally broadly joined to IX, giving the impression of one single segment. Sense cones not preserved, only some large attachment points visible. Mouth cone long and pointed, protruding to middle of mesosternum (Fig. 21). Maxillary palps two-segmented. Pronotum wider than long. Major pronotal setae pointed; epimeral and posteroangular setae longer than others; anteromarginal setae vestigial. Mesonotum and metanotum reticulate. Fore wings narrow, somewhat broadened in basal half and bluntly rounded at tip; anterior vein complete, bearing six stout setae in distal two-thirds; second vein ending with a distinct stout terminal seta in the middle of the wing (Fig. 22); wing membrane without microtrichia. Clavus with paired setiform processes at tip, their length not assessable. Fringe cilia straight; embedded into wing membrane, except at posterior distal margin of hind wings, where the wing margin is serrate into small teeth, each carrying a fringe cilium at tip attached on a tiny socket (Fig. 23). Fore wing with nine duplicated cilia from tip along distal part of posterior margin, running parallel to normal wing fringes, and one single duplicated cilium on fore margin. Fore legs with femora not enlarged, apically with external margin sharply curved into a tooth-like protuberance; fore tibiae not clearly assessable; tarsi without tooth but with a recurved hamus. Mid and hind legs slender; tibiae each with a long dorsal seta; mid and hind tarsi two-segmented. Abdominal tergites without wing-retaining setae; lateral setae almost straight and pointed. Tergite I not assessable; IV–VII sculptured loose reticulate at anterior margin but with transverse lines posterior to setae s1. Abdominal segment IX conical, sculptured with 5–6 transversal lines; setae s1 blunt, s2 and s3 finely pointed; s1–s3 shorter than tube. Abdominal segment X tubular, with margins parallel; with a terminal crown of anal setae, these much shorter than tube.

Measurements. Female (in microns): Body, length 970. Head, length 109; width 130. Eyes, length 40; width 40. Hind ocelli, diameter 13; distance between the hind ocelli 25. Pronotum, length 133; largest width 177. Pronotal setae (length), anteromarginals 9, anteroangulars 16, mediolaterals 22, posteroangulars 31, posteromarginals 28;

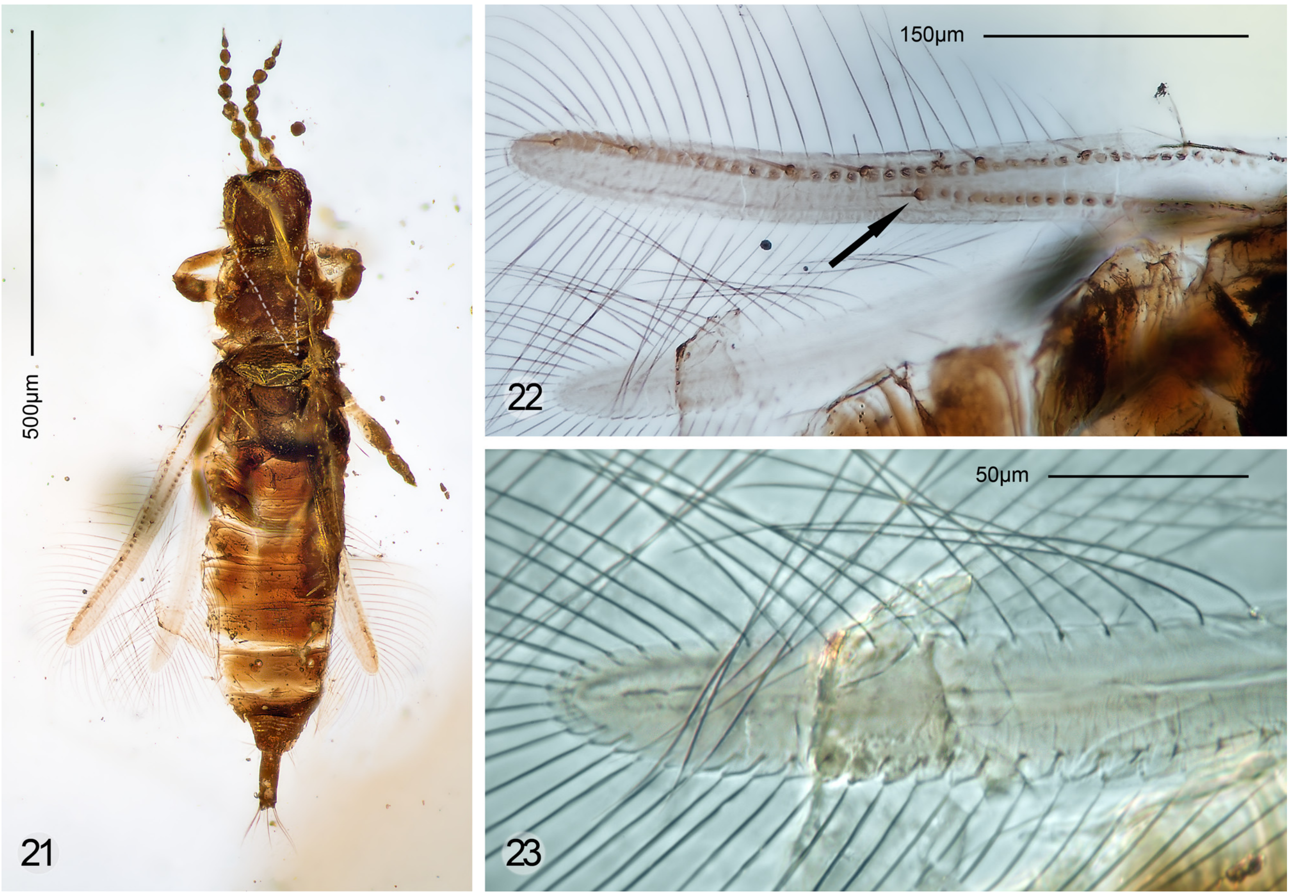
epimeral setae 34. Pterothorax, largest width 192 (at level of mesothoracic spiracles). Abdomen, length about 570 (not measurable due to deformed basal segments); width 202 (at segment V, anterior segments broader due to deformation); segment X (tube), length 90; width 28. Setae on tergite IX, length s1 47; s2 56; s3 62. Antennae, length 229; length (largest width) of segment I 25 (25), II 34 (19), III 34 (22), IV 33 (33), V 28 (22), VI 25 (19), VII 25 (16), VIII 19 (9), IX 12 (5). Fore wings, length 485; width at terminal seta of cross vein 40.

Material studied. Holotype female MU-Fos-136/1 (Figs 21–23); inclusion in Burmese amber from Hukawng Valley, Kachin State, Myanmar. The holotype was donated by Patrick Müller and is deposited in the author's collection.

Syninclusions. Remnants of different insects, stellate plant hairs and particles of plant detritus as well as some small droplets, air bubbles and brownish stains of unknown origin.

Etymology. The species epithet *rostratus* comes from the Latin word *rostrum*, meaning "beak". It refers to the long and pointed mouth cone of this species (Fig. 21).

Differential diagnosis. The two species are already distinguished by their visual appearance. *S. markpankowskii* **gen. et sp. n.** is more robust, with a much broader head and shorter pronotum. The most striking difference between the two species, however, is the shape of their mouth cone, which is long and pointed in *S. rostratus* **gen. et sp. n.** but short and rounded in *S. markpankowskii* **gen. et sp. n.** (see Figs 19–21). Furthermore, antennal segments VIII and IX are broadly joined in *S. rostratus* **gen. et sp. n.** whereas they are more clearly separated in *S. markpankowskii* **gen. et sp. n.**



FIGURES 21–23. *Sesquithrips rostratus* **gen. et sp. n.** holotype female. **(21)** dorsal view, mouth cone outlined white; **(22)** left wings, indicated: distinct seta at distal end of second wing vein; **(23)** serrate hind margin of left hind wing.

Key to genera and species of Rohrthripidae

R. pandemicus excluded.

1. Fore wings narrow, distally never wider than at base (cf. Figs 2, 10, 22) 2

-. Fore wings becoming progressively larger in distal half, broadly rounded at tip (cf. Figs 7, 12, 18) 5

2. Fore wings parallel and straight, with two complete veins, both with setae; fore wing fringe cilia arising from sockets (Fig. 10) . . . . *Paralleloalathrips bivenatus*

-. Fore wings slightly bent forwards, broadened towards base; either with only one vein or additionally with a second vein ending approximately in the middle of the wing; fore wing fringe cilia embedded into the wing membrane (Figs 2, 22) 3

3. Fore wings with first vein only, which does not bear any distal setae; tube constricted (Figs 1, 2) . . . . *Adstrictubothrips mirapterus*

-. Fore wings with a shorter second vein, which ends with a prominent seta approximately in the middle of the wing (Fig. 22); distal setae on first vein present; hind wings with posterior distal margin of wing membrane serrate (Fig. 23) (*Sesquithrips*) 4

4. Mouth cone short and rounded (Figs 19, 20); antennal segment IX clearly separated from VIII; robust species . . . . *S. markpankowskii*

-. Mouth cone long and pointed (Fig. 21); antennal segment IX broadly joined to VIII; gracile species . . . . *S. rostratus*

5. Fore wings with two complete veins, both furnished with setae (Fig. 7); pronotum (Fig. 36) with two pairs of posteroangular setae (inner pair much shorter) and well-developed posteromarginal setae; fore coxae each with a long hair-like seta (*Gemineurothrips*) 6

-. Fore wings with one long wing vein only (Figs 12, 13); second vein, if developed, reduced to basal half of wing, without any setae (Figs 17, 18); pronotum with one pair of posteroangular setae, posteromarginal setae vestigial (Fig. 37); fore coxae without long setae (*Rohrthrips*) 7

6. Antennal segment I about twice longer than wide; median antennal segments at least 1.4 times longer than wide (Fig. 4), with a slender pedicel; inner ocellar setae protruding beyond base of antennal segment III; head narrow . . . . *G. microcephalus*

-. Antennal segment I scarcely longer than wide; median antennal segments about as long as wide (Fig. 6), without a distinct pedicel; inner ocellar setae protruding beyond base of antennal segment II; head broad . . . . *G. peculiaris*

7. Fore wings with a distinct second vein near base (Figs 17,18) 8

-. Fore wings without a second vein (Figs. 12, 13) but sometimes with an elongated shading near base (Fig. 14) or with some scattered stains 10

8. From Lebanese amber; tube no more than 2.8 times longer than basal width . . . . *R. libanicus*

-. From Burmese amber; tube slenderer, more than 3.3 times longer than wide (Fig. 18) 9

9. Mouth cone long, slender and pointed, protruding over base of prosternum (Fig. 17); first wing vein with about 4 very small setae and with one distal seta as long as the distance between the vein and the anterior margin of the wing; small species (body length about 1.5mm) . . . . *R. rhamphorhynchus*

-. Mouth cone shorter, not reaching base of prosternum; first wing vein with about 13 dispersed stout setae, several as long as the distance between the vein and the anterior margin of the wing (Fig. 18); large species (body length about 1.9mm) . *R. setiger*

10. Tube short and bulky, about 2.3–2.5 times longer than wide (cf. Fig. 16) 11

-. Tube long and slender, about 3.2–5.9 times longer than wide (Fig. 12) 13

11. Head very short, about 1.4–1.5 times wider than long; antennal length about 0.3 the body length; wing vein hardly extended to base of rounding of wing tip; about 0.8 times as long as fore wing; small species (body length about 1.3 mm) (Fig. 13) . . . . *R. breviceps*

-. Head longer; first vein extended to base of rounding of wing tip; larger species (body length over 2.1 mm) 12

12. Head about as long as wide; wing vein pale along entire length; smaller species (body length about 1.6 mm) . . . . *R. patrickmuelleri*

-. Head about 1.25 times wider than long; wing vein distally dark; large species (body length about 2.1 mm) . . . . *R. maryae*

13. First vein long, reaching costa at base of rounding of wing tip (Fig. 14); length of antennal segment III about 50–70 microns; smaller species (body length about 1.5–1.6mm) 14

-. First vein short, distally not reaching last fifth of fore wing (Fig. 12); antennal segment III long (87–133 microns); large species (body length over 2.0mm) 15

14. Sense cones on antennal segments short (not longer than 10 microns) . . . . *R. jiewenae*

-. Sense cones on antennal segments longer (longer than 15 microns) . . . . *R. burmiticus*

15. Antennal segment III and IV distally cylindrical-elongated (Figs 15, 38); sense cones tiny, hardly distinguishable from setae; ocelli on a distinct ocellar hump; hamulate part of wing coupling system with six or seven hamuli (Fig. 27); very large species (body length about 2.8 mm) . . . . *R. multihamuli*

-. Antennal segment III and IV distally inverse conical (cf. Fig. 4); sense cones stout, easy to distinguish from setae; ocellar hump lacking; wing coupling with less hamuli; large species (body length about 2.0 mm) 16

16. Wing vein short, hardly reaching last quarter of fore wing, apically split, with two terminal setae; tube very long and slender (about 5.1 times as long as wide at base) antennal segment III conspicuously long (about 100 microns) . . . . *R. schizovenatus*

-. Wing vein longer, reaching almost last fifth of fore wing; not diverged into two branches; tube shorter (about 3.2 times as long as wide at base); antennal segment III shorter (less than 87 microns) . . . . *R. brachyvenis*

Discussion

Note: *Alavathrips moralesi* Peñalver *et al.*, a species recently published as a member of Phlaeothripidae, is included in the following discussion. The data used for this purpose are from Peñalver *et al.* (2022).

While the finds mentioned in Ulitzka (2018, 2019) involved species clearly belonging to the genus *Rohrthrips*, some of the specimens of the present work have required the establishment of new genera. The most important generic differences include the shape of the wings and the wing venation, the position of the maxillary stylets and the presence or absence of sutures on abdominal tergite II. These character states, however, hardly allow conclusions to be drawn about the relationship between the genera. Members of *Rohrthrips* and *Gemineurothrips* **gen. n.**, for example, are rather similar with regard to their body and wing shape (compare Figs 7, 18), but they differ distinctly concerning chaetotaxy of the head and pronotum, and particularly in the position of their maxillary stylets (Figs 36, 37). The latter are deeply retracted into the head capsule and close together in *Rohrthrips*, whereas they are low in the head and far apart in *Gemineurothrips* **gen. n.** On the other hand, *Rohrthrips* and *Paralleloalathrips* **gen. n.** also share distinct character states like paired grooves on abdominal tergite II. This uncommon structure might indicate a possible closer relationship between these genera. In other features, such as the shape of the wings, the wing veins and the pronotal chaetotaxy, however, they differ considerably from each other (compare Figs 10, 18). Therefore, any cladistic interpretation would inevitably lead to contradictions, since it is currently impossible to judge which character states should be considered with greater weight. Moreover, we should not be misled into a systematic characterisation by the reduced number of wing veins: two in *Gemineurothrips* **gen. n.** (Fig. 7) and *Paralleloalathrips* **gen. n.** (Fig. 10), one and a second short one in *Sesquithrips* **gen. n.** (Fig. 22) and in some *Rohrthrips* (Fig. 18), one in *Adstrictubothrips* **gen. n.** (Fig. 2) and most members of *Rohrthrips* (Figs 12–13), and finally none in all *Phlaeothripidae* (Fig. 28). This listing does not imply a testable conclusion indicating that taxa with more reduced wing veins are necessarily more closely related to Phlaeothripidae.

Evolution is seen mainly as a model based on branches, as such a system is easy to comprehend. This simplification results in trees of life that have become central in life sciences and try to summarise the history of organisms in cladistic diagrams. More comprehensive depictions, such as the "coral of life" (see Podani 2019), reflect evolutionary realities much more precisely, but have received little attention so far due to their complex nature. Moreover, no molecular information can be included plotting fossil taxa, and thus their allocation to phylogenetic trees shows at most who is sister to whom; the resulting cladograms, therefore, are by no means a reconstruction of phylogeny (Podani 2019). Furthermore, inheritance seems much more complicated as depicted in cladograms. What we define as "forks" in cladistics are expressions of traits becoming character states (Via & Lande 1985). In the case of a reduced trait, however, its genetic information is not lost at this point, but the propensity to express this trait may be severely diminished — sometimes it reappears when it fits certain conditions, or later coincidentally in atavisms to remind us that the information lies quiescent within the genome (Hall 1995). Such happenings resulting in anastomoses between different taxa or within a group of taxa cannot be depicted in cladograms because their basic characteristic namely is ramification (Podani 2019). This may also apply to the reduction of wing veins within Rohrthripidae, which are not likely to have degenerated simply from one generation to the next, nor continuously from one species to another. Rather, the reduction of wing veins within Tubulifera seems to be subject to phenotypic plasticity. This kind of plasticity enables a single genotype to produce various phenotypes in response to different environmental conditions. Further genetic change, as a result, may not be required or slowed down to adapt to new conditions (Pfennig 2021). Cladistic classification based on the wing veins within Tubulifera, therefore, would not be provable, or rather, would simply be wrong.

According to Ulitzka (2018), the early evolution of Tubulifera might have produced much diversity, with most species wiped out again later, as in all groups of organisms. Recent Phlaeothripids, therefore, represent just a few long branches that once came out of this "bush" of diversity long ago. More broadly, this paraphyly involves a natural transitional stage in the evolution of taxa, one that occurs regularly along with holophyly (Hörandl & Stuessy 2010). When a new holophyletic group arises, it usually coexists for some time with its paraphyletic stem groups. Therefore, paraphyly and holophyly represent relational and temporal evolutionary stages. Paraphyletic groups exist at all levels of diversification, and they have traditionally been recognized because of their descent-based similarity. Peñalver *et al.* (2022) suggested Rohrthripidae as a synonym of Phlaeothripidae. It seems, however, too simplistic and not helpful for practicable taxonomy and classification to insist on cladistic systems based on autapomorphies. Thus, for practical purposes the proposed synonymy of Rohrthripidae with the Phlaeothripidae is not supported.

The present findings available allow some general conclusions to be drawn about certain character states of the Rohrthripidae.

Antennae. The antennae of all species found so far are nine-segmented. Sense cones, similar to those of Phlaeothripidae, are present on antennal segments III–VI or III–VII (Fig. 4). In extant species, both number and shape of these sense cones represent reliable species-specific characteristics and are commonly used for identification (Mound & Marullo 1996; Schliephake & Klimt 1979). Even assuming that the number of sense cones in Rohrthripidae is species-specific, at most their shape and size are reliable features in fossils. Their number, in contrast, is often hard to assess, particularly if these thin-walled trichomes are poorly preserved. To separate *R. jiewenae* and *R. burmiticus*, however, their size is an important and helpful feature. The pedicle (antennal segment II) in Thysanoptera bears dorsally a typical external structure of a sensillum campaniforme (Moritz 1997). This structure, already difficult to recognize in slide-mounted extant thrips, is rarely preserved in fossils. In Rohrthripidae it is located in the distal half of the pedicle, as in most members of Phlaeothripidae (Fig. 38; see Mound & Marullo 1996). The fact that it is not visible in a specimen as tiny as the holotype of *A. moralesi* seems hardly surprising (see Peñalver *et al.* 2022, p. 5). In this specimen, furthermore, the authors give a different number of segments on the left (9) and right (8) antenna. The apparently lower number on the right, however, is explained by the deformation of the last segments obviously leading to a hidden suture. This hypothesis is supported by the position of the large distal sense cone, which is never located on the last segment (see Peñalver *et al.* 2022, p. 2, Fig. 4c and p. 5 Fig. 3b). The antennae of *A. moralesi* are interpreted here as nine-segmented and, therefore, this species is included into Rohrthripidae.

Maxillary stylets. A further important feature in classifying extant Tubulifera is the position and length of the maxillary stylets (Mound & Marullo 1996). In fossils these organs are rarely preserved and thus only have been examined in a few specimens. In summary, however, they are slender in Rohrthripidae, resembling those of Phlaeothripinae rather than Idolothripinae, although they feed like the latter on fungal spores (Stannard 1957; Mound & Palmer 1983; Ulitzka 2019). At present knowledge, in *Rohrthrips* the maxillary stylets are close together and retracted to the level of the hind margin of the compound eyes (Fig. 37; Ulitzka 2018, p. 556 Fig. 12); in *Adstrictubothrips* **gen. n.** they are also deeply retracted but farther apart (Fig. 35), whereas in *Gemineurothrips* **gen. n.** they are low in the head and far apart from each other (Fig. 36). A maxillary bridge as seen in many Phlaeothripids has not been recognized so far.

Pronotal chaetotaxy. A character consistently used in thrips classification is the pronotal chaetotaxy (Priesner 1964). With regard to fossils, however, it often proves to be of little help. Sometimes it remains unclear whether setae are vestigial or simply broken off at their base. Even in clear amber, setae may be hidden in shiny layers of air around an inclusion, particularly, when they are as fine and hair-like as in members of *Rohrthrips*. Furthermore, at present it is not clear if the length of these setae is subject to intraspecific variability as in extant fungivorous Tubulifera (Kobro & Rafoss 2006; Mound & Palmer 1983). On present knowledge, it seems advisable to avoid pronotal chaetotaxy as a main feature to identify Rohrthripidae at least at species level.

Wing veins. The most remarkable organs of these ancestral Tubulifera are their wings, showing some character states usually found in Terebrantia only. The presence of wing veins, and also their gradual reduction within Rohrthripidae and their absence in Phlaeothripidae, have been mentioned above. The factors causing this reduction, however, and the resulting benefits for these insects are not yet fully known. In flight, thrips are simply too slow to benefit from the usual aerodynamic forces and therefore they float in the viscosity of air (Nachtigall 2020). Like many other small insects, they use a particular flight mechanism to gain lift: the clap and fling motion (Santhanakrishnan *et al*. 2014). Miller & Pescin (2009) showed that the maximum drag force generated during fling can be significantly reduced by increasing the flexibility of the wings, in addition to improved net lift forces relative to rigid wings. This may answer the question of the benefits of reducing wing veins but leaves open why other thrips have retained them. The wings of Rohrthripidae have only longitudinal veins; the first vein is always furnished with setae, but the second, when developed, is setose only in some genera. With the exception of the distinctive terminal setae (eg in *Adstrictubothrips* **gen. n.** and *Sesquithrips* **gen. n.**), the venal setae, known as a stable character state in many terebrantian taxa (zur Strassen 2003), seem to be subject to intraspecific variation. Their number, length and position vary within those species for which more specimens are known or between males and females (eg *S. markpankowskii* **gen. et sp. n.**, *R. brachyvenis* **sp. n.** and *R. jiewenae*).

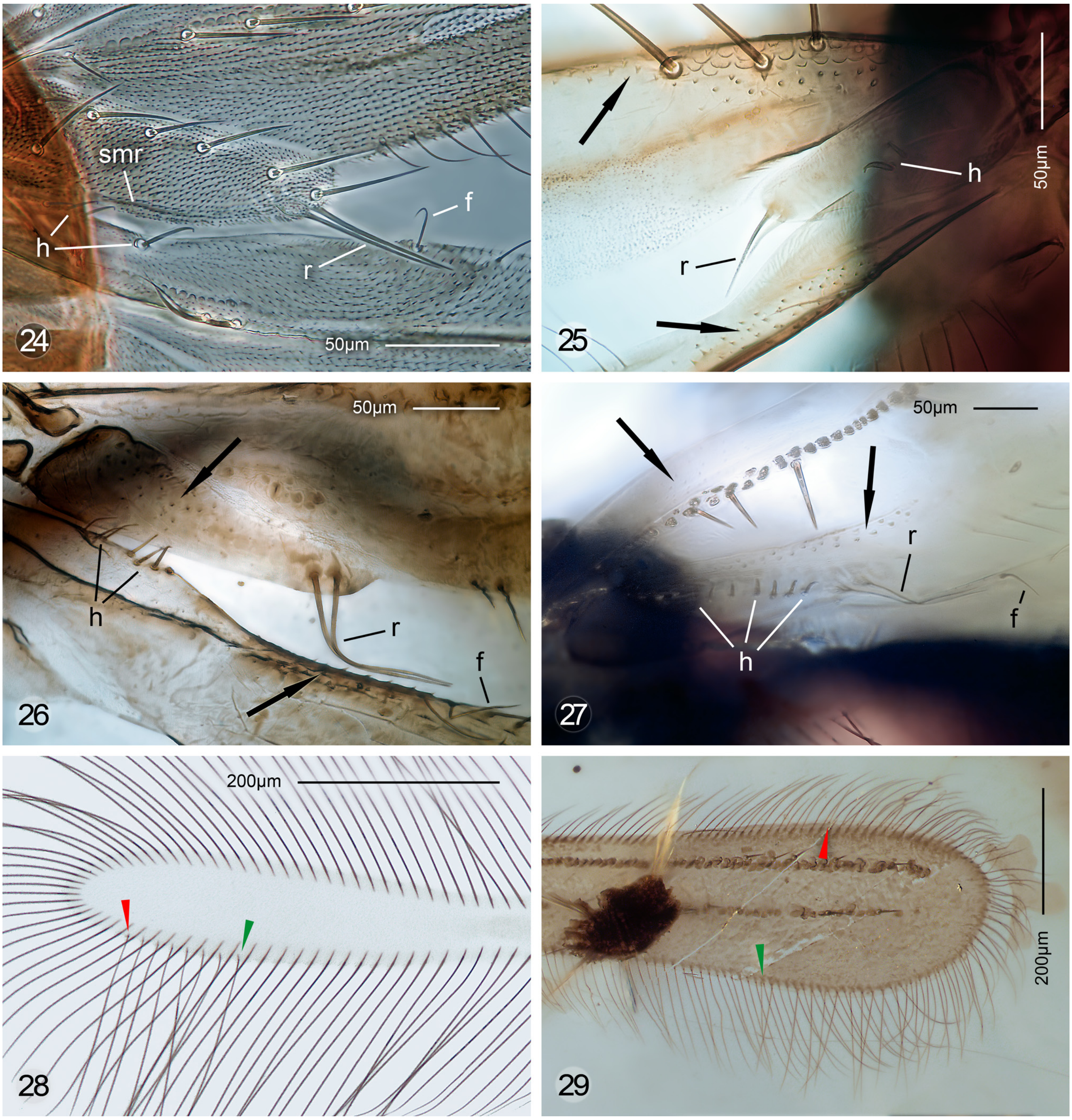
Wing membrane. The wing membrane in Rohrthripidae is lacking microtrichia, at least in all distal parts of the wings (eg Figs 7, 18). The membrane in this part shows characteristic primary surface pattern *sensu* Bhatti (1991) (see also Fig. 14 and Ulitzka 2019). However, at the wing base of some Rohrthripidae sparse microtrichia are present. This feature was first recognized in *R. patrickmuelleri* and described by Ulitzka (2019) as a "rudiment — or atavism (?)". In the present work, similar microtrichia have been found in *G. microcephalus* **gen. et sp. n.** (Fig. 26), *R. multihamuli* **sp. n.** (Fig. 27) and *R. rhamphorhynchus* **sp. n.** Comparative studies conducted with extant Tubulifera in this context yielded the surprising result that most species associated with Idolothripinae have scattered rudimentary microtrichia at their wing bases, eg *Anactinothrips* sp., *Dinothrips* sp. and *Elaphrothrips* sp. (Ulitzka unpublished; Fig. 25). These findings again emphasize that the wings of Tubulifera and Terebrantia are homologous organs (see Ulitzka 2019).

Wing cilia. The wing fringes in Rohrthripidae are straight and have a similar length on the fore and hind margin of the fore wing. They resemble those of Phlaeothripidae (see Bhatti 1993), but their base is different. In Phlaeothripidae, the fringes are embedded between the layers of the wing membrane (Fig. 28). In the descriptions of the first *Rohrthrips* fossils, it is stated that their wing cilia are attached on sockets, as in terebrantian thrips (Nel *et al.* 2010; Ulitzka 2018). In Terebrantia, the hinge-like morphology of these sockets provides a collapsible system allowing the fringes to be locked in two positions — one for flying and one for parking the wings (Ellington 1980). Ulitzka (2019), however, has expressed doubts that Rohrthripidae had collapsible fringe cilia. These doubts are corroborated by the present results: None of the fringes of the discussed fossils is snapped into a resting position and, moreover, in some of these species most fringes, although thickened at base, are embedded into the wing membrane, and thus remain immovable (eg Figs 2, 7). Still, the findings do not contradict the assumption that the bulges at the fringe bases in Rohrthripidae are derived from the hinge-like sockets of Terebrantia. However, this transition most likely did not occur in the Cretaceous, but in an earlier tubuliferan clade dating back further toward the Permian, when the Thysanoptera had diverged from their sister order Lophioneurida (see Ulitzka 2021a).

Duplicated cilia. Duplicated cilia are developed on the fore wings of all (macropterous) species associated with Rohrthripidae; however, these cilia are arranged differently to Phlaeothripidae. The latter have duplicated cilia, when developed, exclusively along the distal part of the posterior wing margin, never on the fore margin (Fig. 28). In Rohrthripidae, duplicated cilia are present distally around the wing tip and at least single cilia on the anterior margin (Figs 2, 7, 10, 18, 22, 29). Furthermore, in Phlaeothripidae — except for *Lonchothrips* Hood) — duplicated cilia are attached at an angle at which they cross the normal wing fringes towards the body (Fig. 28). Except for *Gemineurothrips* **gen. n.** and *Paralleloalathrips* **gen. n.**, in Rohrthripidae the duplicated cilia run parallel to the normal fringes, causing just a denser setation in the distal part of the wing, particularly noticeable in *Rohrthrips* (Fig. 18). In some of the discussed thrips (eg in *Paralleloalathrips* **gen. n.**; Fig. 10), it becomes obvious that the duplicated cilia on the hind margin of the wings are arranged in a way where each forms a pair with a normal fringe. This situation corresponds to what is found usually in members of Terebrantia. Thus, this feature once indicates that the tubuliferan wings have evolved homologously to those of other Thysanoptera (see Ulitzka 2019). At present, no studies are available regarding the aerodynamic influence of these duplicated cilia, which, by the way, are a unique feature in thrips.

Wing coupling. The hamulo-frenate wing coupling type of terebrantian thrips is unique among extant insects (Bhatti 1993; Fig. 24). In Rohrthripidae, wing coupling is very similar and thus largely consistent with the descriptions provided by Bhatti (1975, 1988, 1993) for Terebrantia (see also Nel *et al.* 2010). However, Rohrthripidae in general have more hamuli (Figs 26, 27). On the wings of Phlaeothripidae, only the hamulate component is developed; the retinaculum is still evident but reduced and nonfunctional (Fig. 25). These thrips also have only a few (two to three) small hooks catching a ventral ridge of the fore wing clavus and, unlike in Rohrthripidae, these hooks are apically forked (Fig. 25; Bhatti 1993). Thus, Rohrthripidae in general have a coupling mechanism plesiomorphically present in non-tubuliferan Thysanoptera (Nel *et al.* 2010).

Wingless forms. Two species associated with Rohrthripidae have been described as apterous: *A. moralesi* and *R. pandemicus* **sp. n.** (Fig. 16). In the case of the former, however, it is not clear, and not discussed in the description, whether it is actually wingless or whether its wings are broken off, as in the holotype male of *R. breviceps* and another (unpublished) male in the author's collection identified as *R.* cf. *burmiticus* (MU-Fos-114/1; Fig. 30). *R. pandemicus* **sp. n.**, in contrast, is definitely apterous. Its pterothoracic nota differ from winged forms and, furthermore, its ocelli are lacking and the compound eyes are largely reduced. Similar features are generally known from apterous Phlaeothripidae (Okajima 2006; Schliephake & Klimt 1979). As mentioned in the description above, *R. pandemicus* **sp. n.** most likely represents just an apterous form of another *Rohrthrips* species. These thrips may have occurred in macropterous and apterous forms, as known from different fungivorous Tubulifera of the extant fauna. *Hoplothrips polysticti* (Morison) and *Hoplothrips carpathicus* Pelikán, for example, live on fungus infested logs, which provide habitat for several years until the next stage of decay is reached and the fungal flora changes. As long as foraging does not force them to relocate, they remain and reduce their wings to save energy, producing apterous and micropterous forms or macropterous ones that break their wings off (Kobro & Ulitzka 2021). Because members of *Rohrthrips* are considered fungivorous (Ulitzka 2019), a similar behaviour within this genus seems quite conceivable, including the possibility that the fossil specimens with broken-off wings may have removed them actively.

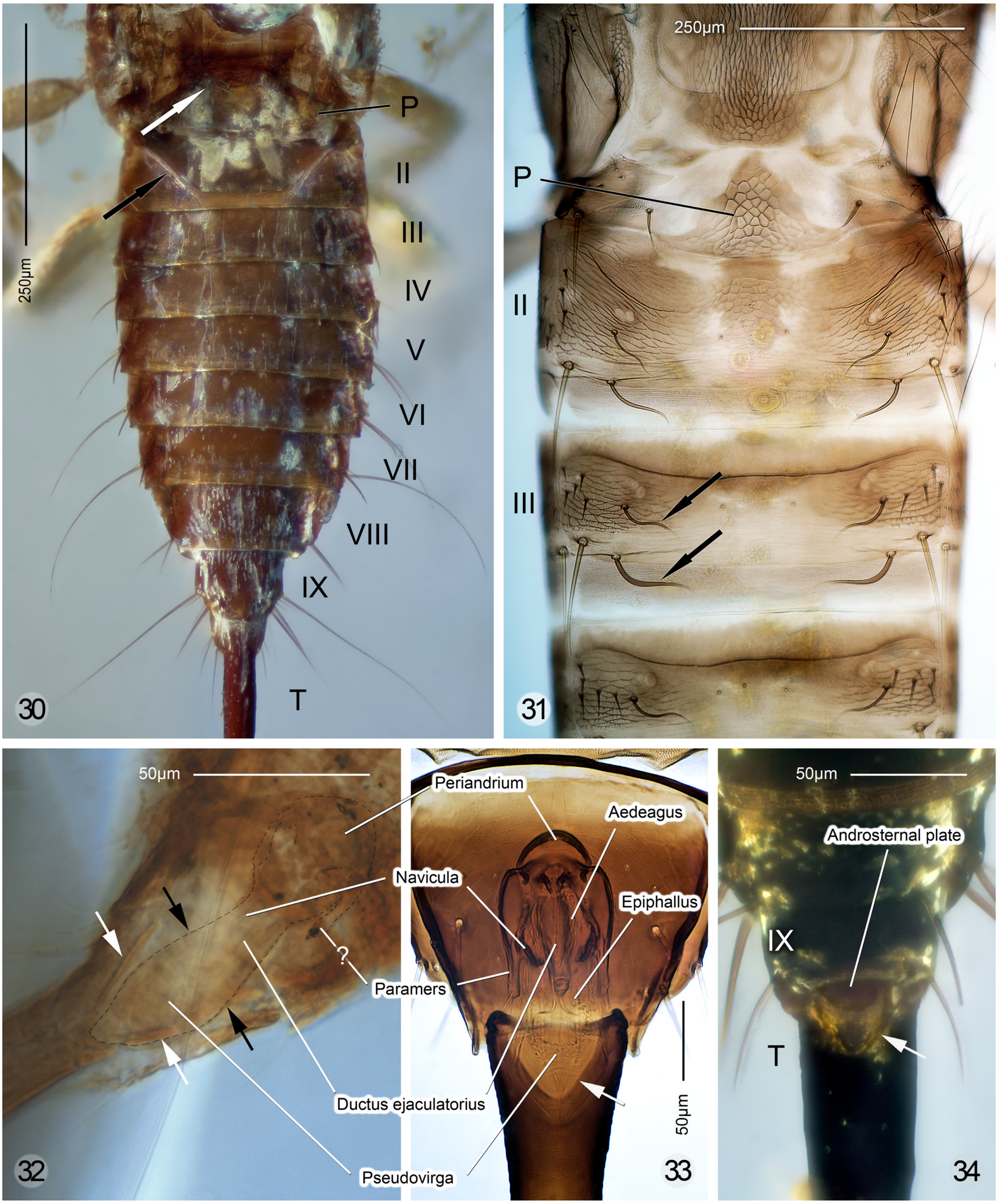


FIGURES 24–29. Thysanoptera wings. Wing coupling (f: frenulum, h: hamuli, r: retinaculum, smr: submarginal ridge, indicated: microtrichia) 24–27: **(24)** *Taeniothrips inconsequens* Uzel (Terebrantia: Thripidae); **(25)** *Elaphrothrips* cf. *costalimai* Hood (Tubulifera: Phlaeothripidae: Idolothripinae); **(26)** *Gemineurothrips microcephalus* **gen. et sp. n.** (Tubulifera: Rohrthripidae); **(27)** *Rohrthrips multihamuli* **sp. n.** (Tubulifera: Rohrthripidae). Tubulifera fore wing duplicated cilia (green to red arrow: area with duplicated cilia) 28–29: **(28)** *Haplothrips setiger* Priesner (Phlaeothripidae); **(29)** *Gemineurothrips microcephalus* **gen. et sp. n.** (Rohrthripidae).

Legs. The legs in adult Tubulifera, as in all Thysanoptera, consist of the typical six segments, i. e. coxa, trochanter, femur, tibia, tarsus and pretarsus (Bhatti 1998a; Okajima 2006). The fore tarsus in Tubulifera is always one-segmented and has a distinct tooth in many tubuliferan taxa, whereas the mid and hind tarsi are usually two-segmented but never have teeth. Furthermore, usually all tarsi bear a distal claw-like process, the hamus (pseudunguis); its absence is extremely rare (Bhatti 1998a). In *Rohrthrips*, as well as in the new genera described here, the hamus is present on all legs, but in *A. moralesi* the fore tarsus is "apparently without a claw-like process (hamus)" (Peñalver *et al.* 2022), possibly due to poor preservation (author's note). In females and males of *Rohrthrips*, as well as in the specimens associated with *Gemineurothrips* **gen. n.**, the fore tarsus has a large lateral tooth; furthermore, in both genera an inner and outer hamus are developed, corresponding to a hamus with bilateral pseudunguis *sensu* Bhatti (1998a, p. 256). On the mid and hind legs, the hamus has a single claw only. In males and females of *Paralleloalathrips* **gen. n.** and *Sesquithrips* **gen. n.**, a tarsal tooth at the fore legs is lacking (in *Adstrictubothrips* **gen. n.** not assessable) and the hamus (including fore legs) has one claw only. The fore tibiae in *Rohrthrips* are unarmed; subapical thorn-like setae, however, are present on the fore tibiae of *Gemineurothrips* **gen. n.** and *Paralleloalathrips* **gen. n.** Enlarged terminal spine-like setae also are present on the mid and hind tibiae in all genera except *Sesquithrips* **gen. n.**; their number, however, is not always clearly assessable. In *Rohrthrips*, all legs are furnished with two distinct long and hair-like setae, one dorsally on the tibiae and one ventrally on the femora. In other genera, similar setae are exclusively present on the tibiae and in *Gemineurothrips* **gen. n.** on the fore coxae (Fig. 36). In both genera, these setae appear to be a constant feature and may serve for their identification. In many Phlaeothripids, the fore legs, particularly the femora, are affected by sex and body size. The present results indicated that this may also be true for members of Rohrthripidae. Usually, specimens with a large body size or males, respectively, show enlarged femora.

Abdomen. When at rest, the wings of all Thysanoptera are folded back over their abdomen. However, in all members of Terebrantia they lie parallel one beside the other, whereas they overlap in Phlaeothripidae. The wings of the latter are usually held in place by distinct recurved sigmoid wing retaining setae (Fig. 31; see also Bhatti 1988, p. 205 Fig. 19) and these setae are only lacking in *Lonchothrips* and *Chirothripoides* Bagnall (Bhatti 1998). Unlike in Phlaeothripidae, the abdominal tergites of all examined specimens associated with Rohrthripidae lack wing retaining setae. Moreover, in *G. microcephalus* **gen. et sp. n.** one of the females obviously has its wings closed over the abdomen in parking position, indicating that the wings lie parallel at rest, similar as in Terebrantia (Fig. 3). The protection of these sometimes large but delicate organs may have been of particular concern for these thrips and raises the question of how the wings were attached at rest. The posterior abdominal segments of *Gemineurothrips* **gen. n.** and *Rohrthrips* are furnished with exceptionally long and recurved lateral setae, which are directed slightly upwards (Fig. 30). These setae may certainly have helped to retain the broad wings of these thrips. A further distinctive structure found in *Paralleloalathrips* **gen. n.** and in all macropterous specimens of *Rohrthrips* (not assessable in *R. libanicus*; P. Nel, pers. comm. 2021) may have supported wing retaining: a pair of dorsolateral grooves on abdominal tergite II (Figs 11, 30). Within Phlaeothripidae similar structures are found exclusively in extant species of *Dactylothrips* Bagnall and in *Parahoplothrips nicolaji* Schliephake from Eocene Baltic amber; however, these thrips have grooves on tergites II–VII and located differently (see Crespi, Morris & Mound 2004; Schliephake 2003; Ulitzka 2022). Similar structures are also known from members of the terebrantian genus *Aulacothrips* Hood (see Cavalleri *et al.* 2012, p. 65 Fig. 8). In *Paralleloalathrips* **gen. n.** and *Rohrthrips* the grooves are distinctly slanting inwards towards the posterior margin of the tergite (Figs 11, 30). Three-dimensional observation with a stereo microscope revealed that the median plate is recessed between these grooves, resulting in protruding ridges laterally. These ridges might have supported holding the wings at rest. The function of the grooves found in *Dactylothrips* and *Parahoplothrips* is unknown; however, there is reason to assume that they are also part of a wing retaining system: ridges, tubercles or sigmoid setae to hold the wings are formed from the inner margin of the lateral plates (eg Crespi, Morris & Mound 2004, p. 178 Figs 162–164; Ulitzka 2022, Fig. 2). Abdominal tergum I may be described as a broad pelta in all specimens where assessable (Figs 11, 30), i. e., it is not formed by sclerotization of the entire tergum, but of its median division, the tergite (see Bhatti 1998b, 1998d). In all members of Rohrthripidae, abdominal segment X is tubular in both sexes (ventrally not split in females). Campaniform sensilla, which are present in most Phlaeothripids, have so far only been recognized in *S. markpankowskii* **gen. et sp. n.** (Fig. 21); as described above for the sensillum on antennal segment II, they may be present in other specimens but remain hidden due to fossilisation.

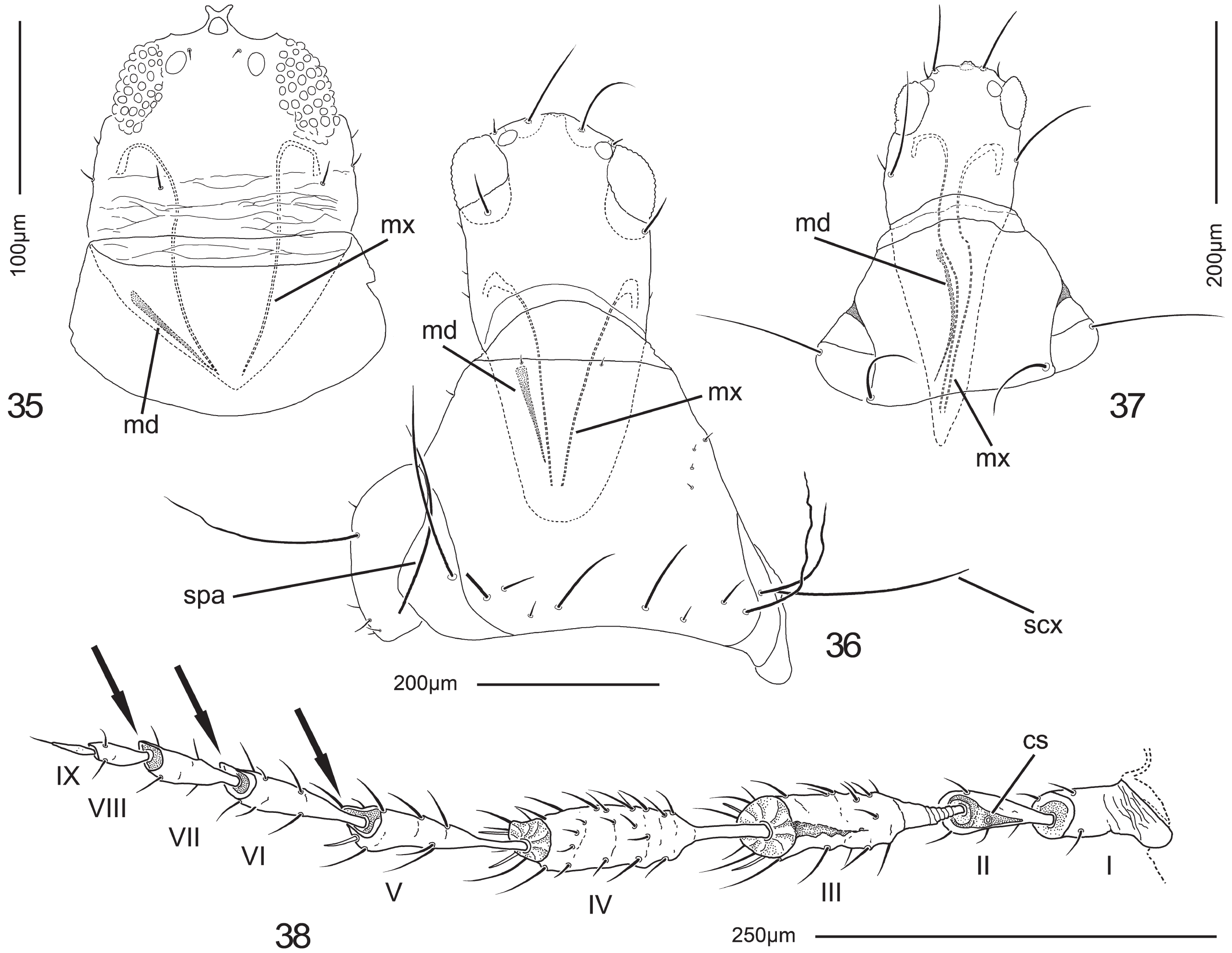
Sex-specific features. Recognizing the sex of Tubulifera in amber fossils is not always easy. Usually, only genital features of the exoskeleton are preserved. The most striking feature to differentiate males and females is the ventral fore margin of the tube. In males it is recessed, whereas females lack such an emargination. In males of Phlaeothripidae this recess is also found (Fig. 33). It is rounded in most species (eg *Haplothrips* Amyot & Serville; see Priesner 1968, p. 17 Fig. 17), but triangular in others (see Fig. 33), and occluded by a separate plate of the exocuticula, the androsternal plate (Bhatti 1988; this plate is also known as *operculum* or *lingula*, respectively; see Priesner 1965; 1968). In males of Rohrthripidae, the emargination is triangularly pointed, and usually the tip of the androsternal plate that projects beyond the base of the tube is well assessable (Fig. 34). This is where the phallus emerges for mating; it protrudes between the androsternal plate and the recessed anterior emargination of the tube.



FIGURES 30–34. Abdomen of Tubulifera. Tergites (P: pelta, T: tube, II–IX: abdominal segments number) 30–31: **(30)** *Rohrthrips* c.f. *burmiticus* male (MU-Fos-114/1), wings broken off (remains indicated white), indicated black: dorsolateral grooves on tergum II; **(31)** *Gynaikothrips uzeli* (Zimmermann) female, indicated: wing retaining sigmoid setae. Distal sternites of males, indicated white: edge of pointed emargination at base of tube 32–34: **(32)** *Alavathrips moralesi* reinterpreted from Peñalver *et al*. (2022, p. 5 Figs 3c), indicated black and dashed redrawn: phallus (designated "ovipositor" in Peñalver *et al*. 2022); **(33)** *Holothrips schaubergeri* (Priesner); **(34)** *Rohrthrips breviceps* holotype male (T: tube; IX: hypandrium, sternite IX).

Sternite IX of males is a complete plate, the hypandrium (Fig. 34), and is consistent with descriptions for Phlaeothripids (Bhatti 1988; Priesner 1968). In females, the genital plates are also very similar in Rohrthripidae and Phlaeothripidae, but difficult to recognize in fossils. Sternite IX is divided into a basal subgenital plate and a pair of lateral gynosternal plates bordering an unpaired ovipositor. In some fossils, needle-like acicula at the anterior margin of the gynosternal plates are recognisable as well as a weak fustis, both described as attachments of muscles of the female reproductive system (see Bhatti 1998b).

In *A. moralesi* even parts of the internal reproductive organs are preserved, but these are interpreted differently in the present work than in the original description (compare Figs 32, 33). The holotype of *A. moralesi* was considered a female; Peñalver *et al.* (2022) characterize the tube as "having in its ventral side a long and broad proximal aperture acuminate distally". They interpret this "as an early stage of closure of the abdominal segment X . . . (which) most likely corresponds to a plesiomorphic character state, as the Terebrantia and the representative of the stem group of the modern Thysanoptera have opened abdominal segment X" (Peñalver *et al.* 2022, p. 6). However, what the authors describe is actually the triangular, pointed emargination at the base of the tube discussed above, the most characteristic feature of males. Moreover, the phallus is clearly recognizable, but it had been misinterpreted as an ovipositor (Fig. 32). It is remarkably well preserved and even shows details like the periandrium, the paramers, navicula, as well as the ductus ejaculatorius. As an inevitable consequence, the holotype of *A. moralesi* is here recognised as a male. From this fact, the considerations regarding *A. moralesi* as "more inclusive than *Rohrthrips* in the tubuliferan lineage" due to the "basally open abdominal segment X" are invalid (Peñalver *et al.*, p. 6).



FIGURES 35–38. Line drawings of Rohrthripidae. Head, mouthparts and prothorax (md: mandibula, mx: maxillary stylets) 35–37: **(35)** *Adstrictubothrips mirapterus* **gen. et sp. n.** holotype female; **(36)** *Gemineurothrips peculiaris* **gen. et sp. n.** holotype (spa: posteroangular setae, left broken off and lying close to coxa; scx: coxal setae); **(37)** *Rohrthrips rhamphorhynchus* **sp. n.** holotype. **(38)** *Rohrthrips multihamuli* **sp. n.** holotype; left antenna, segment numbers in Roman numerals, indicated: ventral projections on segments V–VII (cs: campaniform sensillum, uncolored trichomes indicate presumptive sense cones).

Conclusions

With each fossil added, an increasingly complete mosaic of knowledge about these ancestral Tubulifera slowly emerges, including insights into their outer and inner morphology, their diet and even their habitats. The findings presented here add some stable character states, which can help identify and classify these species as well as future finds, and they indicate that Rohrthripidae had reached remarkable diversity during the Late Cretaceous. Their origin, therefore, is certainly much further back, perhaps in the Late Jurassic. But it still remains an open question when the evolutionary lineages within Thysanoptera gave rise to the Tubulifera.

Synonymy of Rohrthripidae and Phlaeothripidae is not supported here, even if Rohrthripidae is potentially paraphyletic. In future studies, the wing retaining setae as a salient feature of macropterous Phlaeothripidae should be considered carefully, as they may turn out as the hitherto missing autapomorphy. Taking this in account, however, would result in splitting of at the least *Lonchothrips* and *Chirothripoides* (due to the lack of these sigmoid setae) from Phlaeothripidae into separate families, and thus unnecessarily complicate taxonomy within the Tubulifera (see also Bhatti 1998b, 2003).

Acknowledgements

Some results of this paper were presented at the 6th Symposium on Palaearctic Thysanoptera in Zamárdi, Hungary. First of all, therefore, I would like to express my sincere gratitude to all colleagues who have contributed by discussing the presented results. A very special thanks goes to Patrick Müller, Käshofen, Germany for his generous donations of a large number of amber thrips, including the type specimens of *Adstrictubothrips mirapterus*, *Gemineurothrips microcephalus*, *G. peculiaris*, *Paralleloalathrips bivenatus*, *Rohrthrips brachyvenis*, *R. breviceps*, *R. multihamuli*, *R. pandemicus*, *R. rhamphorhynchus* and *Sesquithrips rostratus*. I am also very grateful to Mark Pankowski, Rockville, Maryland, USA for the donations of the male of *R. jiewenae* and the holotype female of *S. markpankowskii*, and for the continuous support of my work on fossil thrips. Moreover, I thank him and his son Max Pankowski for the linguistic revision of this paper. I also wish to express sincere thanks to Laurence A. Mound, CSIRO, Canberra, Australia for numerous discussions inspiring this work. I thank Andrea Hastenpflug-Vesmanis, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany for sending slides of *Lonchothrips* and *Chirothripoides*, and I thank Patricia Nel, Muséum National d'Histoire Naturelle, Paris, France for detailed information on *R. libanicus* and high-resolution pictures of this species. Furthermore, I am grateful to the two anonymous referees for their help and advice in improving this paper.

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