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A first survey of Cretaceous thrips from Burmese amber including the establishment of a new family of Tubulifera (Insecta: Thysanoptera)

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Abstract

Burmite, a Cretaceous amber coming from the north of Myanmar, is known to preserve a great diversity of fossil arthropods, particularly insects. Many inclusions of different taxa in several insect orders have been well analysed, but this is the first study focussed on the Thysanoptera found in Burmite. In the sub-order Terebrantia, family Merothripidae, *Myanmarothrips pankowskiorum* **gen. n., sp. n.** is recognized in various amber samples from a total of 34 females but only one male. In the sub-order Tubulifera, *Rohrthrips burmiticus* **sp. n.** is based on a single female with a tubular tenth abdominal segment. This is an exceptionally well-preserved specimen, and details of the mouth parts indicate that the gnathal apparatus of modern Tubulifera was already developed in the Cretaceous. Due to plesiomorphic characters with respect to extant Tubulifera, the genus *Rohrthrips* is transferred to Rohrthripidae **fam. n.,** and this family is clearly differentiated from extant Phlaeothripidae.

Key words: Burmite, Cenomanian, *Myanmarothrips* **gen. n.,** Merothripidae, new species, new genus, new family, Rohrthripidae **fam. n.**

Introduction

Burmese amber, often referred to as Burmite, is a fossil resin found in the north of Myanmar. It is primarily mined in the Hukawng Valley, Kachin State, specifically on Noije Bum, a hill near the Tanai Village that rises some 250m above a broad alluvial plain between the rivers Idi Hka and Nambyu Hku (26°21′33.41″N, 96°43′11.88″E) (Shi *et al.* 2012). The deposits containing the amber are volcanoclastic to mudstone. Zircons from these layers have been dated by U-Pb dating (Cruickshank & Ko 2003; Shi *et al.* 2012), resulting in an age of 98.8 ± 0.6 million years, i.e. Cenomanian (earliest Late Cretaceous).

For at least two millennia, Chinese people had primarily used Burmite for jewellery and carvings, for which this amber is ideally suited (Grimaldi 1996; Poinar *et al.* 2005). It is not brittle like Lebanese or other Cretaceous amber, but relatively hard (1.2 times harder than Baltic amber), receiving a glassy finish when polished (Koteja & Azar 2008; Shi *et al.* 2012). During the 20th Century, however, the demand for Burmite—and thus its mining—had declined and lapsed completely from just before the independence of Burma from Britain in 1947. It only rose again during the late 1990s when the scientific value of the fossil amber inclusions was realised. Since then, the worldwide scientific interest in this amber has skyrocketed, and hundreds of papers have been published in the last decade (Guo *et al.* 2017). Today, Burmite is known to preserve the most diverse palaeobiota among the world's major deposits of Cretaceous amber (Shi *et al.* 2012).

The largest portion of inclusions that have been studied from Burmite is represented by arthropods, comprising well more than 400 species of insects (Guo *et al.* 2017). Most have been associated with Diptera (118 species), Hymenoptera (73 species), Coleoptera (60 species), Hemiptera (52 species) and Neuroptera (33 species). Thysanoptera *sensu stricto* have not been studied yet. The single species mentioned by Guo *et al.* (2017), *Burmacypha longicornis* Zherikhin, had been described as a member of the Lophioneurinae (see Zherikhin 2000). At present the 'Lophioneurinae' are regarded as a paraphyletic group divided from the Thysanoptera *sensu stricto* and categorized in the order Lophioneurida Tillyard, which also includes the Moundthripidae Nel, Azar & Nel. As

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a consequence, the superorder Thripida Fallen is interpreted now to comprise (at least) three clades: the Panthysanoptera Nel, Azar, Prokop, Roques, Hodebert & Nel (including the Zoropsocidae Tillyard and the Thysanoptera *sensu stricto* Haliday), the Westphalothripidesidae Nel, Azar, Prokop, Roques, Hodebert & Nel (based on the Carboniferous genus *Westphalothripides* Nel, Azar, Prokop, Roques, Hodebert & Nel) and the Lophioneurida as mentioned above (Nel *et al.* 2014).

The Thysanoptera *sensu stricto*—also known as 'thrips'—are a monophyletic order (Moritz 2006), with more than 6,000 species classified into nine extant and four fossil families (Thrips Wiki 2018; Moundthripidae excluded, see above). Concerning extant species, Phlaeothripidae—mainly characterized by a tubular-formed tenth abdominal segment—is the largest family, with about 3,670 species in 460 genera (Thrips Wiki 2018). At present, this family is generally regarded as the sole member of the Thysanoptera suborder Tubulifera. However, fossils discussed below show plesiomorphic features lacking in modern Phlaeothripidae and thus require the establishment of a new family. As a consequence, Rohrthripidae **fam. n.** is proposed below as a new group of tubuliferan thrips. In general, species of Tubulifera differ greatly in structure from those of Terebrantia, the second suborder, but molecular evidence provided by Buckman *et al.* (2013) indicates that the Tubulifera and the Terebrantia are sister-groups. Terebrantia—mainly characterized by the presence of a distinct ovipositor in females—comprise all other (extant and fossil) families, but is suspected to be paraphyletic (Mound & Morris 2007). Table 1 shows the number of species within the families and suborders as well as chronological aspects.

Coevolution between insects and plants seems to have begun during the Devonian, providing a flora with ferns, clubmosses and horsetails. Molecular studies indicate an emergence of pterygote insects during the Mid-Devonian, 387 millions of years ago (Engel & Grimaldi 2004; Gaunt & Miles 2002). The first Thripida have been described from the early Permian (Zherikhin 2002). However, these represent—even if classified by the authors as 'Thysanoptera'—Lophioneuridae. Thus, these are separate from the direct line of thrips' ancestry, as is *Permothrips longipennis* Martynov, which is now considered a member of Sternorrhyncha (Sharov 1972, Grimaldi *et al.* 2004, see Table 1).

In our current state of knowledge, the history of Thysanoptera *sensu stricto* dates back to the Triassic. Two fossils from that era from Virginia and Kazakhstan—approximately 220 million years old—represent the oldest described family Triassothripidae Grimaldi & Shmakov. Their habitus makes them clearly attributable to Thysanoptera and their wing venation even indicates an intermediate position between Lophioneuridae and extant Aeolothripidae (Nel *et al.* 2010). During that period, as in the younger Jurassic deposits, Lophioneuridae are still more widespread and appear more frequently in fossil records. Members of extant thrips families are not known from these eras (Zherikhin 2002). The decline of Lophioneuridae and their extinction occurred during the Cretaceous, whereas the Early Cretaceous is the beginning of the history of extant Thysanoptera (Nel *et al.* 2010). Fossils described from this era or later are attributable for the most part to current and still existing thrips families (Table 1).

Cretaceous thrips have been found as inclusions in amber of various deposits, whereas all finds from prior eras were preserved exclusively as compression fossils. At present 14 species from Cretaceous amber have been described. In a first survey of Early (Hauterivian) Lebanese amber zur Strassen (1973) created seven families, of which six were subsequently synonymised by Bhatti (1979, 1986) with Stenurothripidae, and Jezzinothripidae was synonymised with Merothripidae. From Lebanese Neocomian amber Nel *et al.* (2010) described *Rohrthrips libanicus* (Rohrthripidae **fam. n.**) and *Tethysthrips libanicus* (Thripidae), as well as *T. hispanicus* from Albian amber from Spain. From Spanish amber of different Albian deposits came *Hispanothrips utrillensis* (Stenurothripidae), described by Peñalver & Nel (2010), as well as *Gymnopollisthrips major* and *G. minor* (Melanthripidae), described by Peñalver *et al.* (2012). The only species published from Mid-Cretaceous (Turonian) amber is *Cretothrips antiquus* (Aeolothripidae) from the Raritan Formation, New Jersey, USA (Grimaldi *et al.* 2004).

From Late Cretaceous ambers no Thysanoptera have, as yet, been described, even though inclusions clearly associated with living thrips families have been mentioned particularly in fossil resins from Siberia (Azerbaidzhan) and Canada (Zherikhin 2002; McKellar *et al.* 2008). Even though thrips are found quite commonly in Burmite samples, no species have been described from these specimens until now. The results presented here aim to fill this gap and to give a first impression of the startlingly different appearance of these species.

TABLE 1. Number of thrips species within the families and suborders. Numbers of fossils are arranged corresponding to the geological eras the species derive from. † indicates extinct families (adopted from ThripsWiki (2018) and amended). * *Permothrips longipennis* Martynov; according to Sharov (1972) not a thrips but a member of Archescytinidae (Sternorrhyncha). ** Amended according to Ulitzka (2017). *** Including the species described below.

	Extant	Paleogene	Cretaceous	Jurassic	Triassic	Permian
Terebrantia						
Aeolothripidae	207	12	2			1*
Fauriellidae	5					
† Hemithripidae		9				
Heterothripidae	89	4				
† Karataothripidae				1		
† Liassothripidae				1		
Melanthripidae	67	6**	2			
Merothripidae	16	4	2***			
Stenurothripidae	6	11	7			
Thripidae	2126	62	3			
† Triassothripidae					2	
Uzelothripidae	1	1				
Tubulifera						
Phlaeothripidae	3668	17				
† Rohrthripidae fam.n.			2***			

Material and methods

The present study deals with Burmese amber inclusions that are part of the author's Thysanoptera collection. All inclusions of *Myanmarothrips* **gen. n.** were generously donated to the author by Maximilian, Madeline and Mark Pankowski, Rockville, Maryland, USA; *Rohrthrips burmiticus* **sp. n.** was donated by Patrick Müller, Käshofen, Germany. More detailed information on the fossils is included in their descriptions below. Numbers following a prefixed "MU-Fos-" refer to serial numbers in the author's collection. All types are deposited in the collection of the Senckenbergische Naturforschende Gesellschaft, Frankfurt am Main, Germany (reference numbers are given below).

To prepare the fossils for microscopic examination, and to prevent decomposition and oxidation of the amber, all samples have been ground into thin slices and conserved by embedding them in XOR-Crystal-Resin according to Ulitzka (2015b). The fossils were examined and measured using a Zeiss standard microscope with the following objectives: Zeiss Neofluar 6,3/0,20 160/-, Zeiss Plan 10/0,22 160/-, 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. Subsequently, details of the thrips inclusion were drawn using a Zeiss drawing tube attached to the microscope.

Sub-Order Terebrantia

Merothripidae Hood, 1914
Myanmarothrips gen. n.

Type species. *Myanmarothrips pankowskiorum* **sp. n.**

Diagnosis. Antennae (Fig. 3) 9-segmented with rings of short microtrichia on all segments; III with a circular sensorium, IV with a small transversely kidney-shaped sensorium; I–III distinctly stronger than distal segments. Fore wings (Fig. 7) distally narrowed to a softly pointed tip; longitudinal veins complete, with four cross-veins. Wing surface on fore wings covered with microtrichia; hind wings smooth, apart from some sparse microtrichia at extreme tip (Fig. 8). Head with long postocular setae directed backwards (Fig. 3). Pronotum studded with regular rows of marginal setae (similar to extant *Erotidothrips* Priesner; cf. Mound & O'Neill 1974); one pair of long posteroangular setae present. Fore femora stout in males and females (Fig. 4); tarsi two-segmented; fore tarsus without a hamus.

Etymology. Named after Myanmar, the amber's country of origin.

Discussion. Even though the antenna of *Myanmarothrips* **gen. n.** is not moniliform (cf. Bhatti 2006), the form of the antennal sensoria, the enlarged fore and hind femora as well as the shape of the wings with pointed tips and their venation characterized by the emergence of vein M distally to the fork RA–RP (cf. Nel *et al.* 2012) indicate that the new genus is attributable to Merothripidae. Species associated with this family have nine-segmented antennae, apart from members of *Merothrips* Hood, which have the two terminal segments fused (Mound & O'Neill 1974). The presence of nine antennal segments is a plesiomorphic character for all Thysanoptera (Mound *et al.* 1980). Merothripidae species are considered to have retained some of the ancestral character states of Thysanoptera, particularly the presence in females of a pair of lobes on the posterior margin of the seventh sternite (Ulitzka 2015a). These structures are considered to represent a reduced eighth sternite (Mound *et al.* 1980), and they are otherwise found only in species of Melanthripidae. In fossils, however, the abdomen is often constricted and thus this feature is hardly visible. In the new species described below it is not assessable.

Myanmarothrips **gen. n.** differs from *Jezzinothrips* zur Strassen at least in the shape of the antennae and the presence of microtrichia on the antennal segments. Furthermore, the wing-shape is clearly different (cf. zur Strassen 1973, p. 14, fig. 10). *Myanmarothrips* **gen. n.** is unusual in the presence of microtrichia only on the fore wings in contrast to a smooth hind wing membrane.

Myanmarothrips pankowskiorum sp. n.

(Figs 1–8)

Female: Colour uniformly dark brown including antennae and legs; all major setae dark as well as wing veins and fringes; fore wings (Fig. 7) shaded brownish, hind wings (Fig. 8) transparent.

Head (Fig. 3) wider than long, constricted behind compound eyes but with cheeks swollen and roundly convergent to the base; cheeks irregularly furnished with small setae; with three pairs of ocellar setae (III anterior to the ocellar triangle). Eyes large, their front margin protruding over base of antennae, triangularly tapering on ventral side. Vertex with six postocular setae, s1 and s5 longer and stronger than the others, s6 in most specimens strongly curved inwards. Antennae (Fig. 3) with segments IV–IX distinctly more slender than basal segments; all segments with rings of microtrichia; III with a circular and IV with a tiny transversal and kidney-shaped distal sensorium. Mouth cone short; maxillary palps long, three-segmented; labial palps not visible. Pronotum (Fig. 3) wider than long; front margin with 14–16 setae directed anteriorly, lateral margins with about 10 setae; hind margin with about 30 setae directed posteriorly and with one pair of strong posteroangular setae; pronotal plate regularly covered with many discal setae. Mesonotum transversally striate with rows of microtrichia; metanotum—as far as assessable—reticulate. Mesothorax (mesopleura?) laterally with a pair of strong setae bent to the front (Fig. 2). Fore wings (Fig. 7) with microtrichia, distally softly pointed; with four cross veins clearly seen in one specimen (MU-Fos-62/3a); first vein bearing a row of about 20 setae, second vein bearing about 17 setae, posterior fringes straight; clavus with six marginal and one discal setae. Hind wings (Fig. 8) without any veins; membranous with some sparse microtrichia developed only around extreme tip. Legs covered with microtrichia; fore femora stout (Fig. 4); hind femora slightly enlarged (Fig. 4); tarsi 2-segmented. Abdominal tergites II–VII laterally with a row of posteromarginal setae that is less interrupted in the distal segments and finally closed to a continuous comb on tergite VIII (Fig. 4). Abdominal sternites II–VII with a complete row of many posteromarginal setae (about 30 on III); discal setae lacking. Abdominal segments IX and X conically shaped, with strong setae; X dorsolaterally with a pair of large trichobothria (Fig. 6).

Male MU-Fos-62/3b (Figs 5, 8). Similar to females in colour and shape, however smaller and rather slim; legs yellowish brown (possibly due to reflections in the amber). Abdomen slender; segment I much longer than in females and conically extended from its base; distal abdominal segments conically tapering; trichobothria on X lacking; genitals not visible.

Measurements. Female MU-Fos-62/1 (in microns): Body, length 1166 (abdomen slightly contracted). Head, length 113; width 183. Eyes, length 76, width 44. Hind ocelli, diameter 13; distance between the hind ocelli 34. Ocellar setae 3 40. Postocular setae s1 62, s5 62, s6 25. Maxillary palps, length 76. Pronotum, length 167; width 248; anterior marginal setae 22–24, lateral marginal setae 19–22, posterior marginal setae 30–34, posteroangular setae 93, discal setae 10–12. Pterothorax, largest width 265. Mesothoraxic lateral setae about 110 (difficult to measure due to their bend); mesonotal median setae 16. Abdomen, length 693; largest width 340 (segment V). Antennae, length 355; length (width) of segment I 25 (25), II 47 (25), III 65 (26), IV 68 (11), V 43 (11), VI 31 (9), VII 25 (9), VIII 22 (8), IX 28 (6). Fore wings, length 680; largest width 107; width at level of the r-m-cross vein 85.

The specimens differ greatly in their body size. The female MU-Fos-63/1 is much larger, reaching a body length of 1836 (fully distended); measurements are longer, respectively.

Male: Body, length 870. Head, length 113; width 126. Eyes, length 70, width 32. Longest postocular setae 50. Pronotum, length 124; width 180; posteroangular setae 74. Abdomen, length 465; largest width 130 (segment III); segment I, length 93. Antennae, length 305.

Material studied: Syntypes: Four females, MU-Fos-62/1 (Fig. 1), MU-Fos-62/2 (Fig. 4), MU-Fos-62/3a (Fig. 7), MU-Fos-63/1 (Figs 2, 3, 6), one male MU-Fos-62/3b (Figs 5, 8). All samples were purchased on eBay from two sellers ("the-past-experience": www.ebay.com/usr/the-past-experience, and "amber_resin_fossils": www.ebay.com/usr/amber_resin_fossils) by Maximilian, Madeline and Mark Pankowski and generously donated to the author. The origin of the amber is the north of Myanmar, as certified by the sellers. All five syntypes are deposited in the Senckenbergische Naturforschende Gesellschaft, Frankfurt am Main, Germany (SMF T 19277–19281). Specimens excluded from the syntypic series: 29 females in several amber pieces in collection Ulitzka.

Etymology. The species name '*pankowskiorum*' is gratefully dedicated to the Pankowski family for their donations of the Burmite samples.

Comments. Females of *M. pankowskiorum* **sp. n.** have been commonly found in many different samples of Burmese amber, often in high numbers. This abundance possibly could indicate a swarming behaviour, as seen in some extant thrips known as thunder flies (cf. Ulitzka 2018). At present the collection of the author includes 34 females of this species, however, only one single male. This result coincides with the sex ratio found in many field populations of extant thrips (Lewis 1973).

Sub-Order Tubulifera

Rohrthripidae fam. n.

Type genus. *Rohrthrips* Nel, Peñalver, Azar, Hodebert & Nel, 2010.

Diagnosis. The fossils attributed below to this new family share many features with species of Phlaeothripidae. Both have abdominal segment X tubiform, unforked antennal sense cones and wing membranes without microtrichia. However, other character states are plesiomorphic with respect to extant or younger fossil (e.g. Eocenic) Tubulifera or they are known in a similar form from Terebrantia. The Rohrthripidae is diagnosed as a group of Cretaceous Tubulifera with nine-segmented antennae; fore wings with one or two longitudinal veins, and the first vein bearing setae; wing fringes arising from sockets; fore wing clavus with paired setiform processes at the tip; hind wing bearing basal recurved setae representing a wing coupling mechanism similar to that of Terebrantia.

Etymology. Named after '*Rohr*', German name for tube, and '*-thripidae'*, the usual term for a family of Thysanoptera.

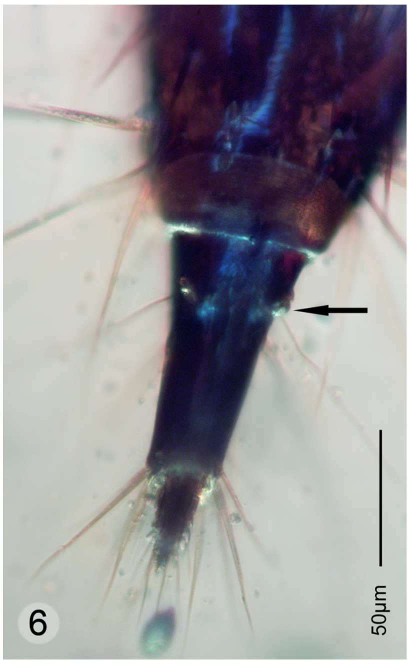

500µm
1


500µm
2


200µm
3


500µm
4


500µm
5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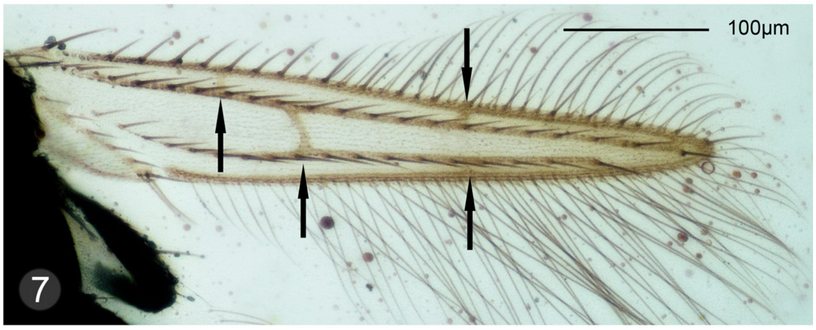
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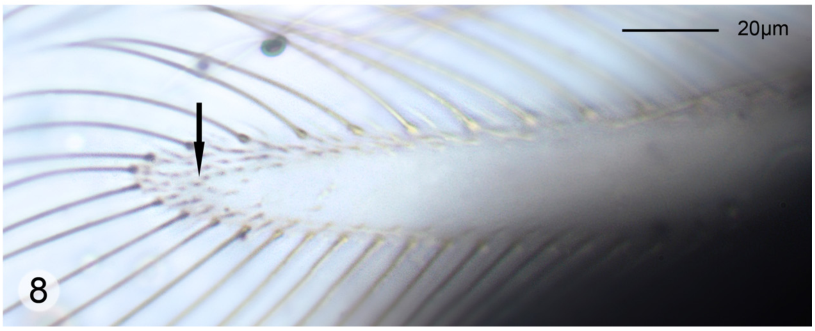
7


20µm
8

FIGURES 1–8. *Myanmarothrips pankowskiorum* **gen. n., sp. n. (1)** female (MU-Fos-62/1), dorsal view; **(2)** female (MU-Fos-63/1), dorsal view; **(3)** female (MU-Fos-63/1), head and prothorax; **(4)** female (MU-Fos-62/2), lateral view; **(5)** male (MU-Fos-62/3b), dorsal view; **(6)** female (MU-Fos-63/1), trichobothria on abdominal tergite X (indicated); **(7)** fore wing (MU-Fos-62/3a), cross veins (indicated); **(8)** hind wing (MU-Fos-62/3b), membrane smooth with microthrichia present only at tip (indicated).

Discussion. Recognizing subgroups within Tubulifera is exceptionally difficult because much of their diversification has involved the reduction or loss of characters, and homoplasy is evident (Mound & Marullo 1996). As a consequence, extant Tubulifera are usually classified in a single family, the Phlaeothripidae. The new family is based on the genus *Rohrthrips* that was established for the species *libanicus* based on a single specimen from Lebanese amber (Nel *et al.* 2010) with the pronotum partly damaged and the head completely missing (cf. Nel *et al.* 2010 p. 191, Fig. 1). The specimen is considered the oldest known Tubulifera, and its attribution to Phlaeothripidae was based mainly on the presence of a tubular last abdominal segment lacking a median suture and bearing a terminal crown of anal setae (Nel *et al.* 2010). Moreover, it shares other features of Phlaeothripidae as listed in detail by Bhatti (1988). However, *Rohrthrips* also shows thysanopteran plesiomorphies, particularly in its wings. *R. libanicus* has two longitudinal veins on the fore wing (Fig. 13), and the new species described below has a single vein, whereas wing veins are consistently lacking in Phlaeothripidae. Furthermore, the fringe cilia arise from sockets as in Terebrantia. The function of this feature as part of a collapsible system allowing the fringes to be locked in two positions—one for flight and one for parking the wings—has been discussed extensively by Ellington (1980). This has been interpreted as preventing the fringes from tangling when the wings lie parallel at rest over the abdomen. In Phlaeothripidae, the wings overlap on the abdomen when not in use, thus a similar parking problem does not arise. Their fringes are embedded immovably between the cuticular layers of the wing (Bhatti 1988). Finally, the fore wing clavus of *Rohrthrips* bears paired setiform processes at its tip and the hind wing a basal recurved seta (Fig. 10) interpreted as a coupling mechanism similar to that of Terebrantia (Nel *et al.* 2010).

Nel *at al.* (2010) referred to *R. libanicus* as 'a milestone in the evolution of tubuliferan thrips'. *Rohrthrips burmiticus* **sp. n.** described below certainly has a similar status, due to its excellent conservation of the head and particularly of the mouthparts (Fig. 12), and these structures allow an appropriate association of the genus. Moreover, they reveal that the gnathal apparatus of modern Tubulifera was already developed in the Cretaceous—in a form very similar to that found today in species of the *Hoplothrips* linage. In contrast, the head of *R. burmiticus* **sp. n** bears nine-segmented antennae**,** another plesiomorphy that has not previously been seen in Tubulifera (cf. Mound *et al.* 1980) (Fig. 11).

Establishing Rohrthripidae may be interpreted as a compromise between respecting strict phylogenetic principles and the practical manageability of classification. The establishment of this new family clearly differentiates these early ancestral Tubulifera from extant Phlaeothripidae. Rohrthripidae probably is not likely to be the sister-group of Phlaeothripidae but rather is part of an early diversification demanding, nevertheless, definition and diagnosis.

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

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

Rohrthrips burmiticus sp. n.

(Figs 9–12)

Male: Colour (Fig. 9) uniformly dark brown including antennae and legs; all major setae dark as well as wing veins and fringes; wings shaded greyish-brown.

Head (Fig. 12) with reticulate sculpture at base; longer than wide, with cheeks rounded behind eyes and converging slightly to base; cheeks lacking setae; ocellar setae difficult to assess, one strong pair clearly visible close to base of antennae. Eyes large, their front margin protruding over base of antennae, not prolonged ventrally. Hind ocelli close to compound eyes; far apart from each other. Vertex with two postocular setae far behind eyes. Antennae (Fig. 11) 9-segmented; segments III–VII inverse conically shaped and tapering distally from level of sense cones; segment II apically with a circular sensorium; number of sense cones of the following segments difficult to assess but at least two on III, IV and V; segment IX broadly joined to VIII. Mouth cone ophistognathus; short but pointed; clypeal suture clearly asymmetric. Maxillary palps with two apical setae; short and very likely 2-

segmented; labial palps not visible. Maxillary stylets (Fig. 12) slender, deeply retracted into head capsule, extending to base of compound eyes, close together and parallel medially; maxillary bridge not developed. Left mandible strong; right mandible degenerate (a shaded structure possibly its remnant). Pronotum (Figs 9, 12) wider than long, trapezoidal; pronotal chaetotaxy not assessable; epimeral setae long and pointed. Pterothorax as well as basal abdominal segments dented and partly concealed. Fore wings (Fig. 9) becoming progressively larger in distal third; anterior vein complete, reaching costa near apex and bearing setae; second vein not developed, reduced to a faint basal shading; membrane without microtrichia. Fringe cilia straight; arising from sockets (Fig. 10); duplicated cilia present around margin of wing apex and on distal part of posterior margin; sub-basal wing setae at anterior margin lacking; clavus with paired setiform processes at tip (Fig. 10). Hind wing without microtrichia and without any veins; base with recurved setae. Fore legs (Figs 9, 12) with femora stout; fore tarsi with a large tooth. Mid and hind legs slender; all tibiae with one long dorsal seta (Fig. 9); mid and hind tibiae terminally each with one strong spine; mid and hind tarsi two-segmented. Abdominal tergites without wing-retaining setae; lateral setae long and pointed. Abdominal segment IX conical, sternite with clearly visible subgenital plate. Abdominal segment X elongated tubular, with terminal crown of anal setae (Fig. 9).

Measurements. Male (in microns): Body, length 1480 (slightly contracted). Head, length 227; width 201. Eyes, length 107, width 50. Hind ocelli, diameter 19; distance between the hind ocelli 57. Ocellar setae 44. Postocular setae 38. Prothorax, length 258; width 441; epimeral setae 176. Abdomen, length 888 (slightly contracted); largest width 391 (segment IV); segment X (tube), length 189; basal width 50. Antennae, length 422; length (largest width) of segment I 37 (31) [deformed], II 65 (34), III 71 (37), IV 56 (37), V 53 (34), VI 43 (28), VII 50 (22), VIII 31 (16), IX 16 (6). Sense cones, length of inner (outer) on segment III 19 (16), IV 19 (22), V 16 (22); basal width 5–6. Fore wings, length about 1200; largest width 245.

Material studied. Holotype male MU-Fos-53/1 (Fig. 9). Inclusion in Burmese amber, donated to the author by Patrick Müller. Holotype deposited in the Senckenbergische Naturforschende Gesellschaft, Frankfurt am Main, Germany (SMF T 19282).

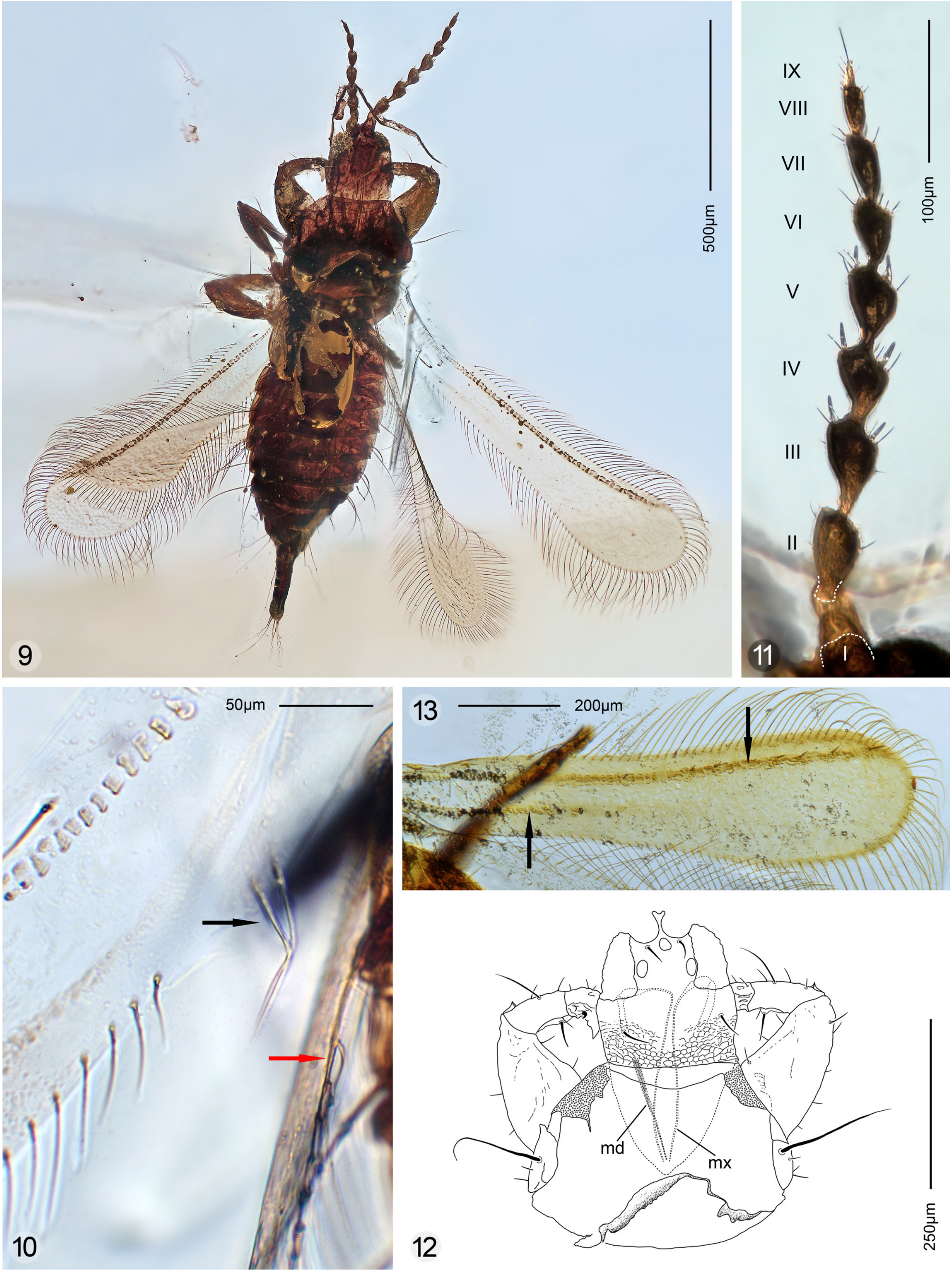
Etymology. The specific epithet '*burmiticus*' refers to the occurrence of the fossil in Burmite.

Discussion. Many features of *R. burmiticus* **sp. n.** correspond clearly to those of *R. libanicus*, particularly with regard to the plesiomorphic characters of the wings mentioned above. The new species, however, has only one vein developed on the fore wings (Fig. 9). Furthermore, it has only one ventral spine on the apex of the hind tibiae, whereas *R. libanicus* has three (cf. Nel *et al.* 2010, p. 155, fig. 3). Establishing a new genus based on these differences was rejected. Further findings that allow comparing the head structures of both species may lead to another classification.

Assuming the loss of the wing veins as an apomorphy in the evolution of Tubulifera (Mound *et al.* 2010), *R. burmiticus* from the late Cretaceous might be interpreted as more modern than its Mid-Cretaceous sister species (cf. figs 9 and 13). Its phylogenetic position as a direct ancestor of recent Phlaeothripidae or as an evolutionary dead end remains undetermined.

Conclusion

Modern Thysanoptera are likely to have evolved in the Lower Cretaceous. During the later periods of this era, they not only had diversified greatly but were widespread over the supercontinents of Gondwana and Laurasia. Their wide distribution is evident from the presence of fossils in deposits far apart from each other (Nel *et al.* 2010). Inclusions attributable to recent families of Terebrantia have been described from Early and Mid-Cretaceous amber (Grimaldi *et al.* 2004, Nel *et al.* 2010, Peñalver & Nel 2010, Peñalver *et al.* 2012, zur Strassen 1973), thus the occurrence of related specimens in the younger Burmite was likely to be assumed. However, it was surprising to find one species, *Myanmarothrips pankowskiorum*, in striking abundance and in many different amber samples. Small insects like thrips may have been captured in the sticky resin mainly due to their flight activity. A swarming behaviour known from certain extant thrips could be a plausible reason for the striking occurrence of *M. pankowskiorum*. Unfortunately, no syninclusions giving further hints on the behaviour or ecology of this species could be recognized. Extant species of Merothripidae are fungus-feeding; whether this applies also to *M. pankowskiorum* must remain open. Even though *M. pankowskiorum* clearly could be attributed to the Merothripidae, it presents character states that have not been recognized before and that are difficult to interpret, such as the presence of microtrichia only on the forewings. These microstructures are generally interpreted as promoting droplet shedding from the wings (Polet *et al.* 2015); there seems no obvious reason for their absence on the hind wings.



FIGURES 9–13. FIGURES 9–12. *Rohrthrips burmiticus* **sp. n.**, holotype male (MU-Fos-53/1). **(9)** dorsal view; **(10)** coupling mechanism of the wings, fore wing clavus with paired setiform processus (black arrow), hindwing with basal recurved seta (red arrow); **(11)** right antenna (segments I and II reconstructed); **(12)** head and prothorax (md: left mandible, mx: maxillary stylets). **FIGURE 13.** *Rohrthrips libanicus*, holotype, right fore wing with two veins (indicated).

Moreover, the present study demonstrates the presence of ancestral Tubulifera, as previously found in Mid-Cretaceous Lebanese amber (Nel *et al.* 2010). Defined mainly by thysanopteran plesiomorphies, these thrips are recognized here as members of Rohrthripidae, a new family of Tubulifera. Tubuliferan fossils from later eras, e.g. Eocenic ambers, all show synapomorphies of extant Phlaeothripidae. Thus, the evolution of Tubulifera must have happened earlier, very likely during the Cretaceous (Nel *et al.* 2010). This process probably produced much diversity, with most species wiped out again later—as in all groups of organisms. Recent Phlaeothripids, therefore, seem to represent just a few long branches that once came out of this 'bush' of diversity long ago. In the phylogeny of Tubulifera the ancestral characters of Rohrthripidae suggest a rather basal position for this group. But occurrence of these fossils in Lebanese as well as in Burmese amber show that they lived in habitats far apart from each other, implying that their roots may reach back much farther. Shmakov (2008) proposed an interpretation of *Liassothrips crassipes* (Martynov) as a possible step in the evolution of tubuliferan thrips during the Jurassic. His interpretation, however, seems doubtful in terms of evolutionary development and functional morphology as comprehensively stated by Nel *et al.* (2010).

Thrips fossils from Burmite will most likely not be able to help solve the mystery of the origin of Tubulifera. However, they surely will present valuable information on the phylogeny and evolution of modern Thysanoptera.

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