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Five new species of *Rohrthrips* (Thysanoptera: Rohrthripidae) from Burmese amber, and the evolution of Tubulifera wings

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Abstract

Rohrthripidae is a family of fossil thrips in the thysanopteran suborder Tubulifera. It includes a single genus, *Rohrthrips*, of which two species are previously known. Despite typical tubuliferan features, these thrips also show some terebrantian character states, particularly in the wings and antennae, and these are here interpreted as plesiomorphic. Five new species of these ancestral thrips are described from Burmese Cenomanian amber: *Rohrthrips breviceps* **sp. n.**, *Rohrthrips jiewenae* **sp. n.**, *Rohrthrips maryae* **sp. n.**, *Rohrthrips patrickmuelleri* **sp. n.** and *Rohrthrips schizovenatus* **sp. n.**. Structures on the wings support the conclusion that the wings of Tubulifera are homologous with those of Terebrantia. Syninclusions in the amber fragments provide evidence of the diet and habitats of these ancestral thrips.

Key words: Burmite, Cenomanian, new species, *Rohrthrips*, Rohrthripidae, Thysanoptera, Tubulifera, wing evolution

Introduction

Two suborders are recognised in the insect Order Thysanoptera, the Terebrantia and Tubulifera. Terebrantia includes more than 2,500 extant and 130 fossil species arranged in 12 families, whereas Tubulifera includes about 3,670 extant and 19 fossil species (ThripsWiki 2019; Ulitzka 2018a). Recognizing subgroups within Tubulifera, however, is exceptionally difficult because much of their diversification has involved the reduction or loss of characters, and homoplasy is evident (Mound & Marullo 1996). Thus, only one family, the Phlaeothripidae, has been generally accepted in the Tubulifera (Moritz 2006; ThripsWiki 2019). Recently, however, two extraordinary species of Tubulifera, fossils from the Cretaceous, have been described as representing a second family, the Rohrthripidae (Ulitzka 2018). Members of the Terebrantia and Tubulifera usually differ from each other considerably in structure (Bhatti 1988, 1998a, 2003; Ellington 1980; Moritz 2006; Mound 2009; Mound & Walker 1982; ThripsWiki 2019). However, the species of Rohrthripidae exhibit important tubuliferan character states (1–10 below) together with rather terebrantian features (11–15 below) that are interpreted as plesiomorphic (Nel *et al.* 2010; Ulitzka 2018a). At present, Rohrthripidae is characterized as follows: (1) abdominal segment X tubular; (2) segment X lacking a ventral longitudinal suture; (3) segment X bearing a terminal crown of anal setae; (4) male copulatory organs ventrally protrusible, covered by a subgenital plate; (5) abdomen broad at base; (6) abdominal pleurotergites spanning entire width of abdomen, laterally descending to meet the sternites (i.e. tergo-pleurotergal sutures not developed); (7) maxillary stylets usually elongate and extending deep into head capsule; (8) wing surface smooth, without microtrichia; (9) fore wing with fringe hairs on anterior and posterior margins nearly equal in length; (10) mid and hind tarsi two-segmented with hamus; (11) antennae 9-segmented; (12) abdominal sigmoid wing-retaining setae lacking; (13) fore wings with one or two well-developed longitudinal veins, first vein bearing setae; (14) fringe hairs on wings arising from sockets; (15) fore wing clavus with paired setiform processes at tip, and hind wing with basal recurved setae representing a wing coupling mechanism.

The establishment of Rohrthripidae was based on the above-mentioned plesiomorphic features with respect to extant Tubulifera, and the author specified it as a compromise between respecting strict phylogenetic principles and the practical manageability of classification (Ulitzka 2018a). Therefore, Rohrthripidae was defined neither as a stem group nor as an obligatory sister-group of Phlaeothripidae, but rather as one of many presumed branches of an

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early diversification. Rohrthripidae potentially is paraphyletic; however, its establishment complies with taxonomic claims *sensu* Hörandl & Stuessy (2010) and thus provides an elegant solution of differentiating these early ancestral Tubulifera without redefining the Phlaeothripidae.

Rohrthrips is the only genus in Rohrthripidae, and until the present study has included only two described species. The type species *R. libanicus* was described from Early Cretaceous (Neocomian) Lebanese amber (130–140 myr) and is considered the oldest known Tubulifera (Nel *et al.* 2010). Unfortunately, the pronotum of the holotype specimen is partly damaged and its head completely missing (Nel *et al.* 2010: 191, fig. 1). The second species, *R. burmiticus* Ulitzka, 2018, was described based on a male specimen from Burmese Late Cretaceous (Cenomanian) amber. Exceptionally well preserved, it clearly shows structures of the antennae and even of the inner mouthparts. *R. burmiticus* was differentiated from *R. libanicus* mainly due to the lack of a second longitudinal vein on the fore wings (Ulitzka 2018a).

The present study describes new fossil thrips species in the family Rohrthripidae. All are inclusions in Burmese amber coming from deposits in the north of Myanmar that have been dated to 98.8 ± 0.6 million years, i.e. Cenomanian (earliest Late Cretaceous) (Cruickshank & Ko 2003, Shi *et al.* 2012.). Some of the treated specimens show details allowing conclusions to be drawn on the evolution of wings among Tubulifera. The development of tubuliferan wings has been the subject of debate (Bhatti 1993, Mound & O'Neill 1974, Moritz 2006). Either the distal three quarters of the wings are a secondary development from a former micropterous condition (Mound & O'Neill 1974: 484) or the wings are fully homologous in both suborders (Bhatti 1998c). The new species described here indicate that *Rohrthrips* had reached a notable diversification during the Late Cretaceous. The study presented here strives to expand our knowledge of ancestral Tubulifera, including a better understanding of the diet and habitats of this remarkable group.

Material and methods

The Burmese amber inclusions discussed here are part of the author's Thysanoptera collection. The holotype female of *R. jiewenae* **sp. n.** has been given to the author by Yanzhen Zhao, Changsha, China; the holotype male of *R. maryae* **sp. n.** was a donation from Mary Pankowski, Rockville, Maryland, USA; the other inclusions have been generously donated by Patrick Müller, Käshofen, Germany, and detailed information on the fossils is included below. Numbers following a prefixed "MU-Fos-" refer to serial numbers in the author's collection. The holotype of *R. burmiticus* Ulitzka, 2018 (MU-Fos-53/1; SMF T 19282) has been re-examined for studies on its wing surface patterns and for comparison with the new species.

The fossils have been prepared according to Ulitzka (2015). To increase visibility during microscopic examination, however, the samples have been ground much thinner than outlined in this earlier description. MU-Fos-76/1, for example, was ground down to a thickness of 0.6mm to remove parts of a leaf that were hiding important features of the thrips fossil. 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 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/-, 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.

Suborder Tubulifera

Family Rohrthripidae Ulitzka 2018

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

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

Rohrthrips breviceps sp. n.

(Figs 1–2)

Male. Body slightly contracted; legs retracted under body; wings (except extreme base) missing as well as segments VII–IX of right antenna; tips of anal setae broken off; fore ocellus concealed by a bubble of air.

Colour (Fig. 1) uniformly dark brown including antennae and legs; all major setae dark.

Head (Fig.1) wider than long, with cheeks rounded behind eyes and converging slightly to base; cheeks lacking setae; one strong pair of long ocellar setae clearly visible close to base of antennae, projecting over apex of antennal segment I. Eyes not protruding over base of antennae, slightly prolonged ventrally. Hind ocelli close to compound eyes; far apart from each other. Vertex with two postocular setae far behind eyes. Antennae 9-segmented; segment I barrel-shaped; segment II basally with asymmetric pedicle, distally inverse cone-shaped; III–VII symmetrical, basally with a slender pedicel, then inverse conically shaped and tapering distally from level of sense cones; segment II apparently with a small distal sensorium (not clearly visible); sense cones short, their number difficult to assess but at least one inner and one outer on III, IV, V and one inner only on VI; segment IX style-shaped, at base much narrower than segment VIII distally. Mouth cone short, but rather pointed. Maxillary palps 2-segmented; labial palps not clearly assessable, very likely 2-segmented. Pronotum wider than long, trapezoidal; anteroangular, mediolateral and posteroangular setae long and pointed, anteromarginal and posteromarginal setae minute; epimeral setae long and pointed. Metanotum with a pair of fine setae far apart from the front margin of the plate. Mesopresternum (Fig. 2) complete and flat boat-shaped; trochantin (“meso-infrapreepisternum” in Bhatti 1988, p. 196; 1994, p. 108) clearly assessable as a separate sclerite; mesosternellum and metasternum fused. Fore wings torn off, their remnants on both sides recognizable including parts of the clavi, and on the left, the base of most likely one wing vein only. Fore legs with femora stout; fore tarsi with at least one tooth (its size/shape due to position of legs not clearly visible). 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 two (or three?) strong spines; mid and hind tarsi two-segmented, with hamus. Abdominal tergites with faint reticulate sculpture, without wing-retaining setae; lateral setae long (Fig. 1), pointed; setae s3 on V–VII longer than other lateral setae and conspicuously bent inwards. Abdominal segment I (pelta) not assessable; IX conical, with setae s3 long and protruding tube; sternite IX with subgenital plate. Abdominal segment X (tube) extended at base; basally reticulate sculptured and entirely furnished with tiny setae; apparently without campaniform sensilla; with terminal crown of anal setae.

Measurements. Male (in microns): Body, length 1245 (slightly contracted). Head, length 139; width 195. Eyes, dorsal length 63; ventral length 76; dorsal width 44. Hind ocelli, diameter 14; distance between the hind ocelli 71. Ocellar setae 43. Postocular setae 47. Prothorax, length 171; width 410; anteroangular setae about 20 (difficult to measure); mediolateral setae 63; posteroangular setae 100; epimeral setae 107. Pterothorax, largest width 403. Mesonotal lateral setae about 62; metanotal median setae 53. Abdomen, length 711 (slightly contracted); largest width 359 (segment II); segment X (tube), length 176; basal width 75. Setae s3 on tergite IX 240. Antennae, length 444; length (largest width) of segment I 40 (28), II 56 (26), III 71 (34), IV 68 (31), V 62 (25), VI 50 (22), VII 47 (19), VIII 34 (9), IX 16 (3). Sense cones, length of inner (outer) on segment III 12 (16), IV 16 (16), V 9 (11); VI 9 (–); basal width 3–4.

Material studied. Holotype male MU-Fos-81/1. Inclusion in Burmese amber donated to the author by Patrick Müller.

Syninclusions. Stellate hairs and small particles of plant detritus; asci and fungal spores, some spores attached to body setae of the thrips.

Etymology. The specific epithet *breviceps* comes from the Latin words *brevis*, meaning “short”, and *ceps*, meaning “head”. It refers to the conspicuously short head of this species.

Rohrthrips jiewenae sp. n.

(Fig. 3)

Female. Body slightly contracted; legs extended; right wings and left hind wing overlapping body, right fore wing spread to the side.

Colour (Fig. 3) dark brown including antennae and legs; all major setae and wing fringes dark; wing veins light brown but much darker at base; wing membrane shaded brownish.

Head mainly smooth, about as long as wide; slightly produced in front of anterior margin of eyes, with cheeks rounded behind eyes; cheeks lacking setae; one pair of long and strong ocellar setae close to base of antennae. Eyes not prolonged ventrally. Ocelli large; hind ocelli very close to compound eyes; far apart from each other. Vertex with two postocular setae far behind eyes. Antennae 9-segmented; segment I barrel-shaped; segment II basally bended outwards with a very short pedicle, then similar to III–VII asymmetrical inverse cone-shaped, distal margin inclined to the exterior side; VIII spindle-shaped; IX style-shaped. Segment II with a small distal sensorium; number of sense cones of the following segments difficult to assess (distorted) but at least one inner and one outer on III–V. Mouth cone short and rounded. Maxillary palps clearly 3-segmented. Pronotum about as long as wide, trapezoidal; mediolateral and posteroangular setae long and pointed, anteroangular setae as well as anteromarginal and posteromarginal setae minute. Anterior half of mesonotum sculptured coarsely reticulate; mesonotal setae not visible. Prosternal plates not assessable; mesosternellum and metasternum fused; sternacosta meeting each of the mesothoracic coxae with a conspicuous process. Fore wings (Fig. 3) becoming progressively larger in distal half; anterior vein complete, reaching costa near apex, bearing one median and two distal setae as well as one short basal seta located anteriorly to the vein; second vein not developed; membrane without microtrichia. Fringe cilia straight; arising from sockets; duplicated cilia present around apical margin of wing; clavus not clearly visible. Hind wings without microtrichia; without any veins; sockets of wing fringes smaller than on fore wing. Fore legs with femora stout; fore tarsi with a strong tooth and a very 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 smooth, without wing-retaining setae; lateral setae long but delicate, pointed; setae s3 on V–VII longer than other lateral setae, not conspicuously bent inwards as in other species. Abdominal segment I (pelta) not assessable; IX conical, with setae s3 very long, reaching tip of tube. Sternite IX with structures interpretable as gynosternal plates and fustis (cf. Bhatti 1998b). Abdominal segment X (tube) long and slightly extended at base; its sculpture not assessable; apparently without campaniform sensilla; with terminal crown of long anal setae.

Measurements. Female (in microns): Body, length 1548. Head, length 166; width 176. Eyes, length 63; width 38. Ocelli, diameter 19; distance between the hind ocelli 47. Ocellar setae 37. Prothorax, length 239; width 365; posteroangular setae 76; mediolateral setae about 65 (not clearly visible); epimeral setae 120. Mesonotum, length 120; width not measurable. Pterothorax, largest width 347. Abdomen, length 911; largest width 490 (segment IV); segment X (tube), length 176; basal width 50. Setae s3 on tergite IX about 255. Antennae, length 334 (segments partially retracted); length (largest width) of segment I 50 (31), II 43 (31), III 50 (34), IV 40 (36), V 37 (28), VI 43 (19), VII 31 (16), VIII 31 (12), IX 9 (3). Sense cones, length of inner (outer) on segment III 6 (6), IV 9 (6), V 10 (–); basal width about 3–4. Fore wings, length 1196; largest width 225.

Material studied. Holotype female MU-Fos-89/1. Inclusion in Burmese amber, donated to the author by Yanzhen Zhao.

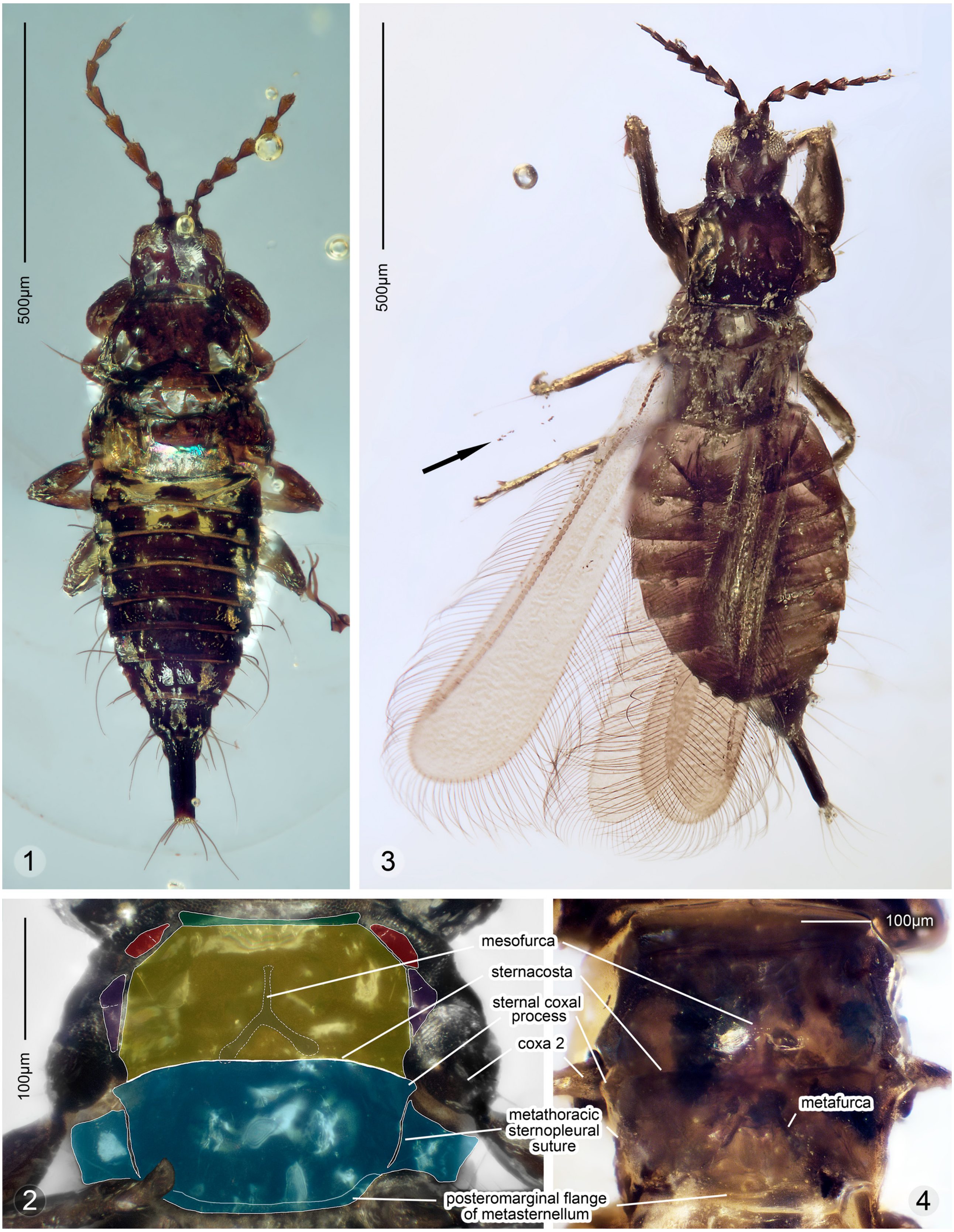
Syninclusions. Two midges and parts of a fly, one unknown insect larva and some fungal spores close to the thrips (Fig. 3).

Etymology. The species *R. jiewenae* is dedicated to Jiewen Zhao, granddaughter of Yanzhen Zhao who found the holotype female in a mine of the Hukawng Valley, Kachin State, Myanmar and donated it to the author.

Rohrthrips maryae sp. n.

(Figs 4–5)

Male. Body fully extended, slightly dorso-ventrally compressed; fore legs and left hind leg angled, other legs extended; left wings and right hind wing overlapping body, right fore wing slightly spread to the side.



FIGURES 1–4. *Rohrthrips* spp. *R. breviceps* **sp. n.** holotype male 1–2: **(1)** dorsal view; **(2)** pterothoracic sternal plates (green: mesopresternum, yellow: mesosternum, red: trochantin, violet: mesokatepisternum, blue: metasternum). **(3)** *R. jiewenae* **sp. n.** holotype female, dorsal view, indicated: fungal spores. **(4)** *R. maryae* **sp. n.** holotype male, pterothoracic sternal plates.

Colour (Fig. 5) brown including antennae and legs; head, pronotum and mesonotum as well as abdominal segments IX and X a shade darker; all major setae and wing fringes dark; wing veins brown, wing membrane shaded greyish-brown.

Head mainly smooth, faintly reticulate laterally; wider than long; produced in front of anterior margin of eyes, with cheeks slightly rounded behind eyes; cheeks lacking setae; one pair of long but very fine ocellar setae close to base of antennae. Eyes not prolonged ventrally. Hind ocelli conspicuously large; close to compound eyes; far apart from each other. Postocular setae broken off, their points of insertion visible far behind eyes. Antennae 9-segmented; segment I barrel-shaped; segment II basally asymmetric with a short pedicle; III–VI symmetrical and short, inverse conically shaped and tapering distally from level of sense cones, III with very slender pedicle; VII inverse cone-shaped; VIII spindle-shaped; IX style-shaped. Sensorium on segment II not visible; number of sense cones of the following segments difficult to assess (distorted) but at least one inner and one outer on III–VI. Mouth cone short and rounded. Palps not assessable. Pronotum broad, wider than long, trapezoidal; mediolateral and posteroangular setae long and pointed, anteromarginal and posteromarginal setae minute. Posterior half of mesonotum with scale-shaped sculpture; mesonotal setae lacking. Metanotum sculptured with fine longitudinal reticulations; setae not visible. Prosternum with fernal plates wider than long; basantra and mesopresternum not assessable; mesosternellum and metasternum fused; sternacosta meeting each of the mesothoracic coxae with a conspicuous process (Fig. 4). Fore wings becoming progressively larger in distal half (Fig. 5); anterior vein complete, reaching costa near apex, bearing one seta shortly before its distal end and one basal seta anteriorly to the vein; second vein not developed; membrane without microtrichia. Fringe cilia straight; arising from sockets; duplicated cilia present around apical margin of wing; clavus with paired setiform processes at tip. Hind wings without microtrichia; without any veins; base with recurved setae; sockets of wing fringes smaller than on fore wing. Fore legs with femora stout (Fig. 5); fore tarsi with two teeth. 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 covered by wings, for the most part not visible; lateral setae long, pointed; setae s3 on IV–VII longer than other lateral setae and conspicuously bent inwards. Abdominal segment I (pelta) broad basally, lateral parts not assessable; IX conical, with setae s3 long but not protruding tube; sternite IX with subgenital plate. Abdominal segment X (tube) conically extended at base; its sculpture not assessable; apparently without campaniform sensilla; with terminal crown of long anal setae.

Measurements. Male (in microns): Body, length 2173. Head, length 164; width 207. Eyes, length 80; width 44. Ocelli, diameter 30; distance between the hind ocelli 44. Ocellar setae 36. Prothorax, length 315; width 630; mediolateral setae 81; epimeral setae 126. Mesonotum, length 189; width 378. Pterothorax, largest width 519. Abdomen, length 1275; largest width 744 (segments III); segment X (tube), length 233; basal width 94. Setae s3 on tergite IX about 250. Antennae, length 409; length (largest width) of segment I 57 (32), II 63 (28), III 69 (41), IV 44 (38), V 44 (32), VI 44 (25), VII 38 (19), VIII 31 (9), IX 19 (6). Sense cones, length of inner (outer) on segment III – (19), IV 13 (19), V 22 (25), VI 19 (–), VII – (–); basal width 3–5. Fore wings, length 1331; largest width 337.

Material studied. Holotype male MU-Fos-88/1. Inclusion in Burmese amber, donated to the author by Mary Pankowski.

Syninclusions. Many tiny droplets.

Etymology. The species *R. maryae* is gratefully dedicated to Mary Pankowski for donating the holotype of this new species and for her valuable help with linguistic revisions to this paper.

***Rohrthrips patrickmuelleri* sp. n.**

(Figs 6–8)

Female. Body fully extended; pronotum basally slightly dented; basal abdominal segments difficult to assess due to shiny refraction; legs folded under body except right mid leg; fore wings overlapping hind wings.

Colour (Fig. 6) uniformly light brown including antennae and legs; all major setae and wing fringes dark; wing veins coloured pale greyish-brown, only a shade darker as wing membrane.

Head (Fig. 6) with reticulate sculpture particularly in the middle; about as long as wide and produced in front of anterior margin of eyes, with cheeks slightly rounded behind eyes; cheeks lacking setae; one pair of long but very fine ocellar setae close to base of antennae. Eyes not prolonged ventrally. Hind ocelli close to compound eyes;

far apart from each other. Vertex with postocular setae far behind eyes (left seta missing). Antennae 9-segmented; segment I barrel-shaped; segment II basally asymmetric without elongated pedicle; III–VIII symmetrical, inverse conically shaped and tapering distally from level of sense cones; sensorium on segment II not visible; number of sense cones of the following segments difficult to assess but at least one inner and one outer on III–VI and one outer only on VII; segment IX conically shaped, at base narrower than segment VIII distally. Mouth cone short and rounded. Maxillary palps 2-segmented; labial palps minute, not assessable. Pronotum wider than long, trapezoidal; posteroangular setae long and pointed, other pronotal setae not developed or missing; epimeral setae long and pointed. Metanotum with a pair of fine setae far apart from the front margin of the plate. Prosternum with fernal plates wider than long; basantra not visible (very likely not developed); mesopresternum complete, very flat boat-shaped; mesosternellum and metasternum fused. Fore wings (Fig. 6) becoming progressively larger in distal half; anterior vein complete, reaching costa near apex; bearing two distal setae and one basal seta located anteriorly to the vein; straight except for the short bending close to its tip; second vein not developed; membrane without microtrichia. Fringe cilia straight; arising from sockets; duplicated cilia present around apical margin of wing; clavus with paired setiform processes at tip. Hind wings at base clearly with microtrichia (Fig. 8); without any veins; base with recurved setae; sockets of wing fringes smaller as on fore wing (Fig. 7). Fore legs with femora stout; fore tarsi with two teeth. 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, much smaller on mid tibiae; mid and hind tarsi two-segmented, with hamus. Abdominal tergites faintly sculptured reticulate (partly visible only), without wing-retaining setae; lateral setae long, pointed; setae s3 on IV–VII longer than other lateral setae and conspicuously bent inwards (Fig. 6). Abdominal segment I (pelta) not assessable; IX conical, with setae s3 long and somewhat protruding tube; sternite IX with structures interpretable as gynosternal plates and fustis (cf. Bhatti 1998b). Abdominal segment X (tube) conically extended at base; its sculpture not assessable; apparently without campaniform sensilla; with terminal crown of long anal setae.

Measurements. Female (in microns): Body, length 1600. Head, length 202; width 200. Eyes, length 85; width 38. Hind ocelli, diameter 19; distance between the hind ocelli 50. Ocellar setae 32. Postocular setae 38. Prothorax, length 233; width 378; posteroangular setae 100; epimeral setae 107. Pterothorax, largest width 365. Metanotal median setae about 57. Abdomen, length 1000; largest width 461 (segments III–IV); segment X (tube), length 151; basal width 63. Setae s3 on tergite IX 220. Antennae, length 399; length (largest width) of segment I 40 (25), II 47 (34), III 62 (34), IV 47 (31), V 53 (31), VI 50 (28), VII 47 (22), VIII 34 (16), IX 19 (8). Sense cones, length of inner (outer) on segment III 20 (18), IV 22 (19), V 22 (25), VI 25 (19), VII – (16); basal width 4–5. Fore wings, length 1030; largest width 206.

Syninclusions. Remnants of another insect and a stellate trichome.

Etymology. The species *R. patrickmuelleri* is dedicated to Patrick Müller for his generous donations of Burmese amber thrips inclusions.

Rohrthrips schizovenatus sp. n.

(Figs 10–15)

Female. Body fully extended; head and various antennal segments deformed; right side of thorax slightly bent upwards and partly concealed by remnants of a leaf; body partially translucent showing many fungal spores inside the body (only visible using transmission light; fig. 15); right wings overlapping body, left wings spread; both fore legs and left hind leg folded under body.

Colour (Fig. 10) uniformly brown including legs, antennal segment I, II, VIII and IX; median antennal segments lighter at base; all major setae and wing fringes dark; wing veins uncoloured basally, darkened in the second third and distally broadened to a dark brown spot; wings shaded greyish.

Head crushed at the right anterior half and the left basal part, therefore its original shape difficult to assess; with reticulate sculpture; wider than long and produced in front of anterior margin of eyes; cheeks very likely slightly rounded behind eyes, without setae; ocellar setae broken off. Eyes large; ocelli not visible. Postocular setae missing, their points of insertion far behind eyes. Antennae 9-segmented; segment I long, barrel-shaped; segment II slightly asymmetric, inverse cone shaped; segments III-VIII inverse conically shaped; segment IX style-shaped, at base narrower than segment VIII distally; segment II with a structure interpretable as an apical sensorium;

segments III–VIII with long setae; a short sense cone visible on segment III and V. Pronotum crushed, trapezoidal; wider than long; anteroangular setae short, mediolateral setae and posteroangular setae long and pointed, other pronotal setae not developed or missing; epimeral setae rather short, strong and pointed. Pterothorax crushed and partly concealed by the remnants of a leave. Fore wings becoming progressively larger in distal half (Fig. 10); anterior vein distally split in two short branches reaching costa at about three quarters of the wings' length; each branch ending with a terminal seta (Fig. 11); vein furnished with 6 additional setae (basal setae located on the vein); second vein not developed; membrane without microtrichia. Fore wing clavus with paired setiform processes at tip. Hind wing without microtrichia and without any veins; base with recurved setae. Fore wing fringe cilia straight; arising from sockets (Fig. 13); duplicated cilia present around apical margin of wing (Fig. 13). Hind wing fringe cilia arising from sockets on the anterior margin, these sockets smaller as on fore wing; on hind margin fringes ingrained in the wing membrane without sockets (Fig. 12). Forelegs with femora stout; fore tarsi with teeth; a long seta visible dorsally on the right fore tibia; other setae lacking (broken off?). Mid and hind legs slender; femora with one long ventral and tibiae with one long dorsal seta; mid and hind tibiae terminally each with two visible spines, much smaller on mid tibiae; mid and hind tarsi two-segmented, with hamus. Abdomen without wing retaining setae; lateral setae long, pointed; setae s3 on III–VII longer than other lateral setae and conspicuously bent inwards (Fig. 10). Abdominal segment I (pelta) not assessable; VIII with a spiracle on each side close to the lateral margin of the tergum (Fig. 14); IX conical at base, distally tapering dome-shaped, with setae s3 long, but not protruding tube; sternite IX with structures interpretable as gynosternal plates and fustis (cf. Bhatti 1998b). Abdominal segment X (tube) long and slender, not extended at base (Fig. 10); sculptured reticulate; apparently without campaniform sensilla; with terminal crown of long anal setae.

Measurements. Female (in microns): Body, length 2188. Head, length 233; width about 245. Eyes, length 95; width 57. Prothorax, length about 265; width 410; anteroangular setae 14 (difficult to measure); mediolateral setae 69; posteroangular setae 126; epimeral setae 50. Pterothorax, largest width about 375 (compressed on the right). Abdomen, length 1372; largest width 510 (segments III); X (tube), length 343; basal width 67. Setae s3 on tergite IX 372. Antennae, length 471; length (largest width) of segment I 52 (28), II 68 (28), III 100 (37), IV 84 (31), V 62 (22), VI 50 (22), VII 28 (16), VIII 28 (9), IX 19 (5). Sense cones, length 16; basal width 4–5 (on segment III and V). Fore wings, length 1193; largest width 274. Wing vein, length 872 (measured from wing base).

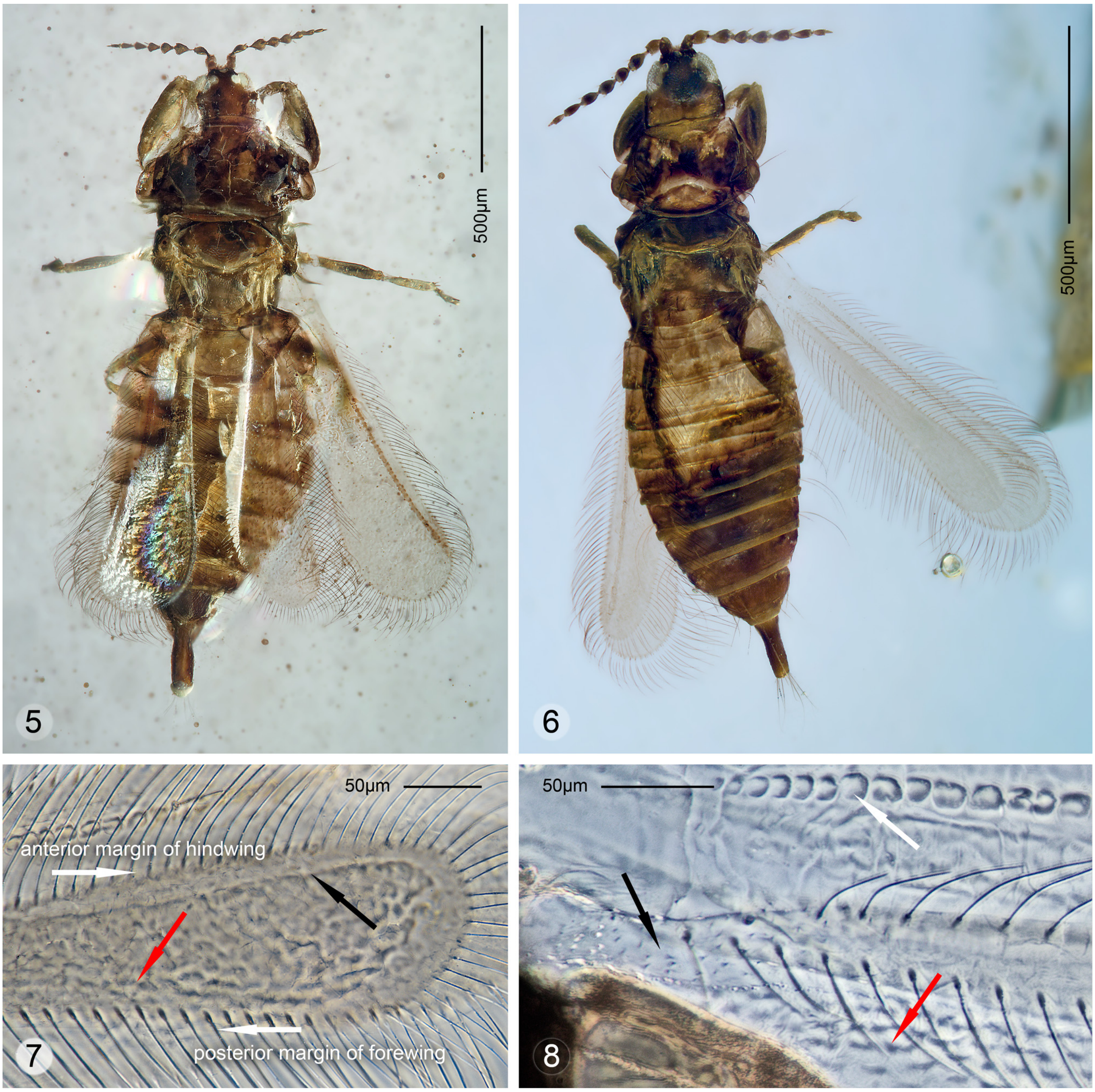
Material studied. Holotype female MU-Fos-76/1. Inclusion in Burmese amber, donated to the author by Patrick Müller.

Syninclusions. Remnants of a beetle and a springtail; detritus including small coprolites and parts of plants like stellate hairs, fibres and fragments of leaves. Many fungal spores inside the body of the thrips (Fig. 15).

Etymology. The specific epithet *schizovenatus* comes from the Greek word *σχίζω (skhízō),* meaning "to split", and the Latin word *venatus* meaning "with veins". It refers to the wing vein of this species, which is distally divided into two short branches.

Key to the species of *Rohrthrips* from Cretaceous amber

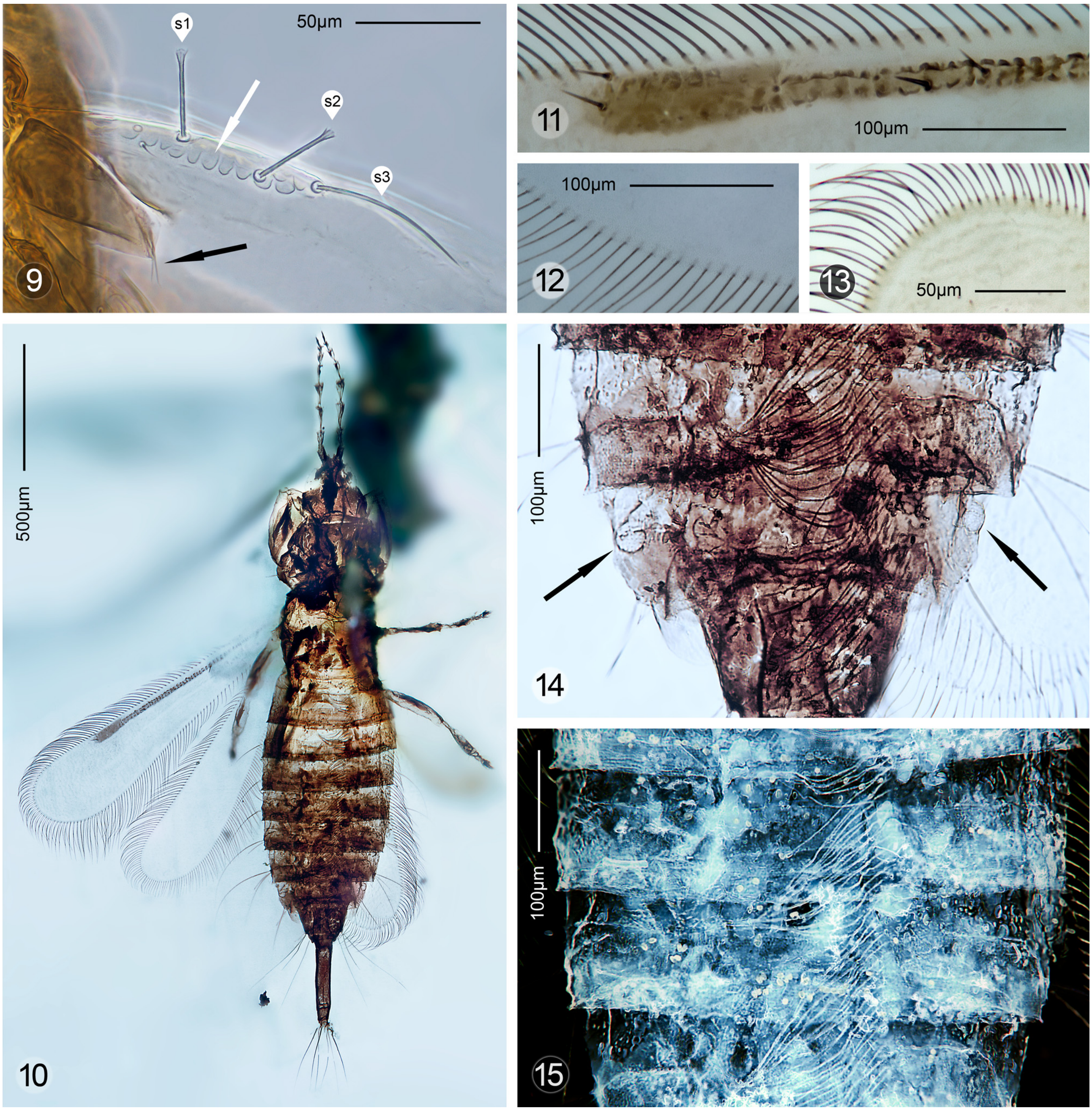
1. From Lebanese amber; fore wings with two veins . . . . *R. libanicus*
- From Burmese amber; fore wings with one vein 2
2. Tube short and bulky (length: basal width about 2.3–2.5) 3
- Tube long and slender (length: basal width about 3.5–5.1) 5
3. Head very short, about 1.4 times wider than long; antennal length about 0.3 of body length; small species (body length < 1.3mm). . . . . *R. breviceps*
- Head longer; larger species (body length > 1.5mm) 4
4. Head about 1.25 times wider than long; wing vein distally dark; very large species (body length over 2.1mm) . . . . . *R. maryae*
- Head about as long as wide; wing vein pale along entire length; smaller species (body length about 1.6mm). . . . . *R. patrickmuelleri*
5. Head clearly longer than wide; epimeral setae very long (> 170) . . . . *R. burmiticus*
- Head wider than long; epimeral setae shorter (< 120) 6
6. First vein short, hardly reaching last quarter of fore wing, apically split, with two terminal setae; tube very long and slender (length/basal width about 5.1); antennal segment III conspicuously long (about 100); very large species (body length over 2.1mm) . . . . *R. schizovenatus*
- First vein longer, reaching costa close to apex of fore wing, not diverged into two branches; tube and antennal segment III shorter; smaller species (body length about 1.5mm). . . . . *R. jiewenae*



FIGURES 5–8. *Rohrthrips* spp. **(5)** *R. maryae* **sp. n.** holotype male, dorsal view. *R. patrickmuelleri* **sp. n.** holotype female 6–8: **(6)** dorsal view; **(7)** surface pattern of wings (phase contrast), indicated red: longitudinally orientated surface pattern, indicated black: submarginal ridge; **(8)** basal part of wings (phase contrast), indicated white: wing vein, indicated red: longitudinally orientated surface pattern, indicated black: microtrichia.

Annotation

Another new species of *Rohrthrips* had been recognized in a photo taken by Yanzhen Zhao and presented to the author by Mary Pankowski. A description of the new species was planned as part of the present study. However, the amber—a donation from Mary Pankowski—was mailed from China, then rejected by German Customs and sent back to the sender. On the way back, unfortunately, it was lost. The missing species is rather large with long antennae and a long and slender tube. It has a pale (possibly translucent) vein on the fore wings, which meets the costa near the wing apex in a conspicuously longitudinal brown spot.



FIGURES 9–15. FIGURE 9. *Haplothrips haideeae* Mound & Minaei (Phlaeothripidae), wing base, s1–s3: subbasal wing setae, indicated white: wing vein, indicated black: rudiment of paired setiform process. **FIGURES 10–15.** *R. schizovenatus* **sp. n.** holotype female: **(10)** dorsal view; **(11)** distal part of wing vein; **(12)** posterior margin of hind wing (fringes embedded in wing membrane); **(13)** distal margin of fore wing (fringes on sockets); **(14)** position of spiracles on segment VIII (indicated black); **(15)** fungal spores (light yellowish dots) inside the body (inverted transmission light image).

Differential diagnosis

Rohrthrips species from Burmese amber differ from *R. libanicus* from Lebanese amber in having only one vein developed on the fore wing. For *R. breviceps* this character state may be questionable because only basal parts of the wings are preserved in the holotype specimen. This species, however, differs from *R. libanicus* in having much longer epimeral setae, and a heavier tube (Fig. 1). Concerning shape and length-width ratio of their tubes, *Rohrthrips* species from Burmese amber may be classified into two groups. The first group contains species with a short and bulky tube (length-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-width ratio 3.5–5.1): *R. burmiticus*, *R. jiewenae* and *R. schizovenatus*. In the first group *R. breviceps* may be distinguished by its conspicuously short head (Fig. 1). 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* (Fig. 6), and in *R. maryae,* the head, which is also wider than long (Fig. 5). 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 (Fig. 6). In contrast the vein is dark brown in the distal two thirds and curved forwards from the middle of its length in *R. maryae* (Fig. 5). 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. burmiticus* differs from other species in having much longer epimeral setae and particularly by its head, which is much longer than wide. *R. schizovenatus*, finally, differs from all other species by its striking long and slender body and its slim tube (Fig. 10). Furthermore, this species is unique in having short wing veins that are forked into two small branches distally (Fig. 11).

At present, the distinctive character states justify establishing a new species for each specimen of the studied *Rohrthrips*. Nevertheless, it should be noted that these fossil thrips most likely were feeding on fungal spores (see below) and that modern forms of fungivorous Tubulifera commonly appear polymorphic (Mound & Marullo 1996; Mound & Palmer 1983). Therefore, further findings possibly may reveal within-species variation or polyphenism and thus lead to a different classification.

Conclusion

Rohrthripidae had been defined as a basal group of Tubulifera that merges typical tubuliferan character states with rather terebrantian features interpreted as plesiomorphic. These plesiomorphies refer particularly to the wings and antennae, whereas the attributes of the body are morphologically rather similar to those of modern Phlaeothripidae. The descriptions above indicate further typically tubuliferan characteristics. In *R. breviceps*, *R. maryae,* and *R. patrickmuelleri,* the sternal sclerites of the thorax are well preserved and reveal that the mesosternellum and metasternum are fused to one single plate (Figs 2 and 4). Furthermore, the sternacosta meets each of the mesothoracic coxae with a short sternal coxal process (c.f. Bhatti 2003, p. 44, fig.1). In *R. breviceps*, moreover, the trochantin (“meso-infrapre-episternum” in Bhatti 1988, p. 196; 1994, p. 108) is visible as a prominent demarcated sclerite (Fig. 2). According to Bhatti (2003), these features are highly conserved character states in Tubulifera, as is the position of the spiracles on abdominal segment VIII located close to the lateral margin of the tergum, which is clearly visible in *R. schizovenatus* (Fig. 14) and *R. jiewenae*.

Another tubuliferan feature that has not been studied so far in Rohrthripidae is the surface pattern of the wings (c.f. Bhatti 1991, 1998c). These structures usually remain hidden in (extant) slide-mounted samples due to the refractive index of the mounting media being nearly equal to that of the wing membrane. Viewing these delicate sculptures requires a special preparation technique (i.e. Exsur Technique; c.f. Bhatti 1991, 1998c) that reveals “primary surface patterns” showing tiny lines, wrinkles, asperae, granulations or tubercles on both pairs of the wings (not to be confused with a reticulate pattern seen on the wings of some genera like extant *Stictothrips* Hood, 1925) and “secondary surface patterns” like humps or elongated bulges and ridges particularly along the fore wings. The primary surface pattern functionally is interpreted as imparting rigidity to the thin tubuliferan wing membrane. According to Bhatti (1991), it is species-specific and hence of taxonomic importance. In Terebrantia it is not developed; their wing membrane is stretched between the veins and may obtain additional strengthening by the pubescence with microtrichia. In amber inclusions of Tubulifera, fossilisation sometimes allows the primary surface pattern to be viewed (c.f. Ulitzka 2018b, fig. 1). In this case, the refractive effect probably is caused by separation of the wing membrane from its surrounding matrix or by a thin layer of embedded air around the wing surface. Concerning *Rohrthrips*, phase contrast examination shows primary surface patterns of wrinkled surface projections in *R. burmiticus* (in all parts of the wings), *R. maryae* (in all parts of the wings), *R. jiewenae* (on the left fore wing), *R. schizovenatus* (at the tip of the left fore wing) and *R. patrickmuelleri* (particularly on the hind wing where the wings overlap; fig. 7). Furthermore, in the latter species longitudinal striae towards the wing base are visible on the posterior part of the hind wings (Figs 7 and 8). *R. patrickmuelleri* also shows a structure interpretable as an anterior "submarginal ridge" (Fig. 7). Further secondary surface patterns *sensu* Bhatti (1991), however, are not recognizable. These structures have been considered as wing veins (Bhatti 1991, 1994, 1998c) or as stabilizing bends and foldings of the wing membrane (Moritz 2006). Concerning *Rohrthrips*, they may be redundant due to the rigidity provided by the wing vein(s).

The wing structures found in Rohrthripidae contradict the suggestion that the distal three-quarters of the tubuliferan wing is a secondary development of a micropterous condition (Mound & O'Neill 1974, Moritz 2006) and "not directly homologous with the wings found in the rest of the Thysanoptera" (Mound *et al.* 1980, p. 118). Concerning the wing veins, the findings instead lead to the conclusion that the short basal vein present in (almost all) macropterous Phlaeothripidae (Fig. 9) is a plesiomorphic feature that resulted from the reduction of a former well-developed longitudinal first vein of ancestral Tubulifera. Thus, the subbasal setae s1–s3 (Fig. 9) may be interpreted as wing setae that simply were moved towards the base within this process. The similar microscopic sculpture of the first vein in Rohrthripidae and of the basal vein in Phlaeothripidae may substantiate this hypothesis (c.f. figs 8 and 9). In fact, various other features of the modern tubuliferan wing seem to have developed similarly, i.e. plesiotypically and by reduction of ancestral character states, becoming visible in Rohrthripidae as kind of evolutionary intermediate stages. The fore wing clavus of *Rohrthrips*, for example, still bears paired setiform processes at its tip and the hind wing a basal recurved seta representing a functional coupling mechanism similar to that of Terebrantia. In contrast, the wing coupling in Phlaeothripidae is of the hamulate type only, with a few (two to three) small hooks along the anterior margin at the base of the hind wing catching a ventral ridge of the clavus of the fore wing (Bhatti 1998a). The former paired setiform processes, however, are still present in Phlaeothripidae as a small—and most likely functionless — rudiment apically at the fore wing clavus (Fig. 9). Furthermore, the wing fringes in Terebrantia arise from sockets providing a collapsible system for the fringes to be locked in two positions—one for flying and one for parking the wings (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). In Rohrthripidae the wing fringes clearly arise from sockets; however, there is reason to doubt their function as part of a collapsible system. In contrast to amber inclusions of Terebrantia, which often show fringes lying in both positions (c.f. Ulitzka 2017, p. 208, fig. 7, p. 210, fig. 14; Ulitzka 2018, p. figs 5, 7), none of the fringes of any *Rohrthrips* fossil is snapped into resting position or at the least kinked at its socket. Furthermore, not all of these sockets are placed at the extreme edge of the wing (as in fig. 13); some clearly are recessed into the wing membrane and therefore, the relevant fringes definitely remain immovable (Figs 8 and 11; Nel *et al.* (2010) p. 155, fig. 2). In *R. schizovenatus*, moreover, the fringes of the posterior margin of the hind wings do not even arise from sockets, but are deeply embedded in the membrane similarly to those of Phlaeothripidae (Fig. 12). The present findings may indicate that the sockets have been modified, recessed and reduced from an ancestral form, and that the collapsible fringe system was given up in Rohrthripidae. Whether this is related to a particular wing position at rest must remain an open question; none of the fossils allows a reliable conclusion on how the wings were parked. In this context, the situation found in *R. maryae* and *R. schizovenatus*, at least, indicates that the long recurved lateral body setae may have had a similar function of retaining the wings as the sigmoid abdominal setae in Phlaeothripidae (c.f. right wings of *R. schizovenatus*, fig. 13; Bhatti 1988, p. 205, fig. 19). Another feature to be considered in the context of reduction is the structure of the wing membrane. In Tubulifera it differs conspicuously from that of other Thysanoptera in lacking surface microtrichia (Mound & O'Neill 1974). In the main, this applies to both Phlaeothripidae and Rohrthripidae, with one exception: *R. patrickmuelleri* shows some sparse microtrichia at the base of the hind wings (Fig. 8). This rudiment—or atavism (?)—is an important finding, which indicates that the membranous tubuliferan wings derive from a pubescent ancestral form. All things considered, the present results refute the belief that the tubuliferan wings—or even parts of them—are neogenic. Definitively, these organs are homologous to those of other Thysanoptera. However, they are characterized by plesiotypic ancestral character states, which have been reduced or even completely receded.

The present findings, moreover, permit conclusions on the diet of *Rohrthrips* and hence—albeit limited—on the habitats of these thrips. Nel *et al.* (2010) had already mentioned the presence of fungi in the amber matrix of *R. libanicus. libanicus*. In the present study some fungal spores have been recognized close to *R. jiewenae* (Fig. 3) and attached to the body of *R. breviceps* as well as spores and some asci in the streak this specimen left by movements in the resin. In *R. schizovenatus* it is even more evident that these thrips were closely associated with fungi:

Examinations using transmission light reveal that the inside of the body of the holotype specimen is covered with fungal spores (Fig. 14), which only could have been ingested as food. This suggests *Rohrthrips* fed on spores, similar to extant Idolothripinae (Mound & Palmer 1983). As a consequence, the hitherto known species of *Rohrthrips* must have lived in habitats providing suitable fungal spores, with dead branches or leaf litter. This conclusion corresponds with the concept suggested for ancestral Tubulifera as insects having cryptozoic habits and seeking fungal hyphae and spores (Bhatti 1993)—the "Prototubuliferon".

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