Modern thrips families Thripidae and Phlaeothripidae in Early Cretaceous amber (Insecta: Thysanoptera)

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Abstract. Two specimens of Thysanoptera with forked sensilla on third and fourth antennal segments were described from the Lebanese Neocomian and the Spanish Albian ambers, and attributed to the new genus *Tethysthrips* **n. gen.** in the family Thripidae Stevens 1829. One specimen with a tubular tenth abdominal segment was also discovered in the Lebanese Neocomian amber, and attributed to the new genus *Rohrthrips* **n. gen.** belonging to the family Phlaeothripidae Uzel 1895. Thripidae and Phlaeothripidae are nowadays the most species-rich families of Thysanoptera. The present discoveries of Early Cretaceous fossils show how diversified these families and thrips already were at that time. Moreover, this tubuliferan *Rohrthrips* specimen has plesiomorphies no longer present in the recent genera, in particular on the wings. Therefore it brings new insight in the evolution of Tubulifera.

Résumé. Thripidae et Phlaeothripidae, deux familles modernes de thrips dans l'ambre du Crétacé inférieur (Insecta : Thysanoptera). Deux spécimens de Thysanoptera portant des sensilles fourchues sur les troisièmes et quatrièmes segments antennaires ont été découverts dans les ambres du Néocomien du Liban et de l'Albien d'Espagne, et attribués à un nouveau genre *Tethysthrips* **n. gen.** dans la famille Thripidae Stevens 1829. Un spécimen présentant un dixième segment abdominal tubulaire a également été découvert dans l'ambre du Néocomien du Liban, et attribué au nouveau genre *Rohrthrips* **n. gen.** dans la famille Phlaeothripidae Uzel 1895. Thripidae et Phlaeothripidae sont aujourd'hui les familles de thrips les plus riches en espèces. La découverte de ces fossiles montre combien les Thysanoptera et ces familles étaient diversifiés au Crétacé inférieur. De plus, *Rohrthrips* présente des plésiomorphies qui ne sont plus observables dans les genres actuels, en particulier sur les ailes, et apporte de nouveaux éléments de compréhension de l'évolution des Tubulifera.

Keywords: *Tethysthrips* **n. gen.**; *Rohrthrips* **n. gen.**; new genus; new species; Neocomian; Albian.

The insect order Thysanoptera comprises nearly 6,000 known species (Mound 2007) distributed in nine extant families. The Phlaeothripidae Uzel 1895 is traditionally considered as the only family from the suborder Tubulifera. It is mainly characterized by the presence of a tubular tenth abdominal segment at the base of which is located the opening of the genital apparatus. Phlaeothripidae comprises about 3,500 described species (Mound & Morris 2007). The eight other extant families belong to what is traditionally considered as the other 'suborder' Terebrantia, however this group is suspected to be paraphyletic (Mound & Morris 2007). About 2,400 described species are distributed among Thripidae Stevens 1829 (85%), Aeolothripidae Uzel 1895 plus Melanthripidae Bagnall 1913 (10%), the remainder 5% being the

Stenurothripidae Bagnall 1929 (resurrected name in place of Adiheterothripidae, Peñalver & Nel, this issue), Fauriellidae Priesner 1949, Heterothripidae Bagnall 1912, Merothripidae Hood 1914, and Uzelothripidae 1952 (Moritz 2006).

History of Thysanoptera goes back to the Triassic (Triassothripidae Grimaldi & Shmakov 2004, oldest extinct described family, with representatives from Virginia and Kazakhstan), approximately 220 Myr old (Grimaldi *et al.* 2004). In particular, the Triassothripidae have wing venation 'intermediate' between living Aeolothripidae and the extinct, probably paraphyletic Lophioneuridae Tillyard 1921 (Permian to Cretaceous), the closest apparent relative to thrips (Grimaldi *et al.* 2004). These first Thysanoptera were preserved as compression fossils as were representatives of the extinct families Karataothripidae Sharov 1972 and Liassothripidae Priesner 1949 recorded from the Late Jurassic deposits of Karatau in Kazakhstan (Grimaldi *et al.* 2004). At that time Lophioneuridae are still more frequent in the fossil record and widespread

than Thysanoptera and no members of living thrips families are known to appear there (Zherikhin 2002). A decline of Lophioneuridae and their extinction occurred in Cretaceous, whereas Thysanoptera became more numerous (Zherikhin 2002).

From the Early Cretaceous Lebanese amber, Nel *et al.* (2007) described the extinct family Moundthripidae, presenting plesiomorphies for Thysanoptera that are present in "Lophioneuridae": prognathous mouthparts and wing venation, etc. Early Cretaceous is also the beginning of the history for extant Thysanoptera. From the deposits of Baisa (Transbaikalia), Shmakov

(2009) describes the oldest members of the families Aeolothripidae and Thripidae. In about equivalent age Lebanese amber (125 Myr), zur Strassen (1973) created seven families synonymised by Bhatti (1979, 1986) with Stenurothripidae, except Jezzinothripidae placed into synonymy with Merothripidae. From mid-Cretaceous (Turonian) amber of New Jersey, Grimaldi *et al.* (2004) described a new Aeolothripidae. None of the Late Cretaceous Thysanoptera were described, but Stenurothripidae, Aeolothripidae, Thripidae, Heterothripidae, and Tubulifera seem to be present, in particular in Siberian (Azerbaidzhan) and Canadian
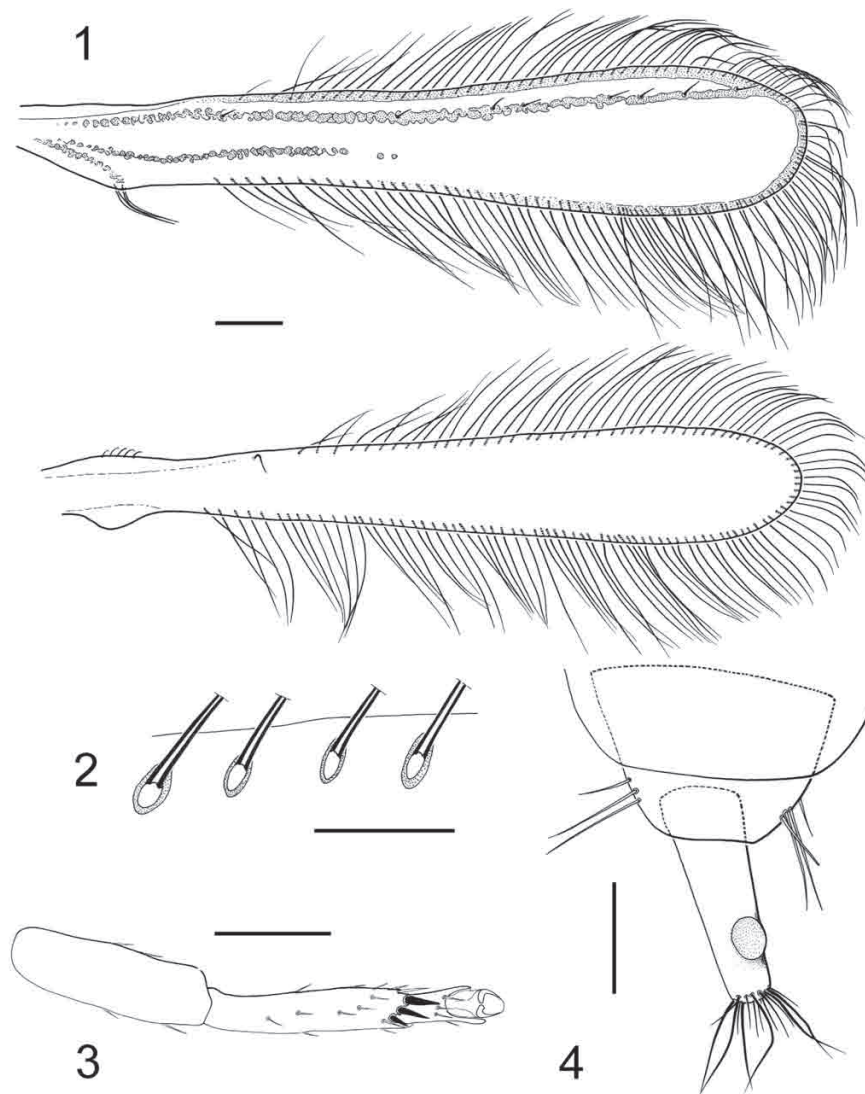

Figure 1
Camera lucida drawings of *Rohrthrips libanicus* **n. gen., n. sp.** (Phlaeothripidae); holotype 1217. **1,** Right fore and hind wings; **2,** Detail of the insertions of the fringe cilia at the mid length of the fore wing's anterior ridge in ventral view; **3,** Right hind leg in ventral view; **4,** Apex of the abdomen in ventral view. Drawings 1, 3 and 4 scale bars = 0.1 mm, drawing 2 scale bar = 0.05.

resins (after Zherikhin 2002; McKellar *et al.* 2008).

In both the Early Tertiary French and Baltic ambers, Phlaeothripidae, Aeolothripidae, Stenurothripidae, and Heterothripidae are common and diverse, however the dominant and most diverse family is Thripidae (Schliephake 2007; Nel pers. obs.). Virtually all of the Baltic amber thrips families and many of the genera are extant (Grimaldi *et al.* 2004).

Here we describe Early Cretaceous Lebanese and Spanish amber specimens that present the characteristics of Thripidae and Phlaeothripidae, and give new insights into the origins and evolution of these species-rich extant families.

Material and methods

The Lebanese material was prepared between two cover slips in Canada balsam medium as described by Azar *et al.* (2003). The Spanish material was prepared by removing the main part of surrounding amber in order to have the best visibility, and then it was mounted in Epoxy resin (EPO-TEK 301). Fossils were examined and measured using a binocular Olympus SZX9, an inverted compound microscope Olympus CK40, and direct microscope Leitz. Photographs were taken using digital cameras attached to a microscope Olympus BX51 and to microscope Olympus CK40. Some images were reconstructed using the computer software Combine Z5.

All measurements are in μm, length tL = total length of antenna; length s.am = length of pronotal anteromarginal seta; length s.pa = length of posteroangular setae.

Systematic palaeontology

Family Phlaeothripidae Uzel 1895

Genus *Rohrthrips* n. gen.

Type species. *Rohrthrips libanicus* **n. sp.**

Diagnosis. Fore wing becoming progressively larger in its distal third; no microtrichia visible; two longitudinal veins visible, first vein complete, reaching costa near apex, and bearing setae, second vein visible in proximal two-fifth of wing, without setae; fringe cilia arising from sockets; duplicated straight cilia all around margin of wing apex and in distal part of posterior margin; clavus with paired setiform processes at tip, one discal seta in proximal part. Hind wing without microtrichia, without vein, but with a clavus, basal series of five coupling setae not forked at tip; presence of a downwardly recurved (wing coupling) seta. Hind tarsi two-segmented, with a hamus on first tarsal segment; three ventral spines apically on tibia. No sigmoidal or inwardly recurved (wing retaining) setae on abdomen; abdominal segment X elongate tubular without median suture, with a crown of apical setae.

Etymology. Named after Rohr, German name for tube, and Thrips.

Rohrthrips libanicus n. sp.
(Figs 1, 4)

Material. Holotype specimen 1217 (incomplete, sex undetermined); Azar collection, provisionally deposited in the Muséum National d'Histoire Naturelle, Paris, France. The amber specimen from which derives the holotype also contains fungi.

Etymology. Named after Latin name for Lebanon.

Age and outcrop. Early Cretaceous, Neocomian, Hammana/Mdeirij, Caza Baabda (Baabda District), Mouhafazit Jabal Libnen (Governorate Mount Lebanon), Central Lebanon.

Diagnosis. As for genus.

Description. Head lacking; pronotum partly damaged, with one pair of long posteroangular setae (length 94), and two short pairs of posteromarginalis setae (length 8); epimeron bearing one pair of long setae (length 58). Pterothorax greatly damaged.

Fore wing 1032 long, becoming progressively larger in distal third (Figs 1.1, 4.1); no microtrichia visible; two visible longitudinal veins, first vein complete reaching costa near wing apex and bearing eight dispersed setae (Fig. 4.2), second vein visible in proximal two-fifth of wing, without setae; no setae along costal margin; fringe cilia nearly symmetrical, slightly shorter in anterior margin than in posterior margin, arising from sockets (Figs 1.2, 4.3); duplicated straight cilia all around apex margin and in distal part of posterior margin; clavus with paired setiform processes at tip, one discal seta in proximal part. Hind wing without microtrichia, without vein, but with a clavus bearing twelve small setae on proximal half of posterior margin; basal series of five coupling setae not forked at tip; presence of a downwardly recurved (wing coupling) seta.

Only one hind leg present; tarsi two-segmented, with a hamus on first tarsal segment; three ventral spines apically on tibia (Fig. 1.3).

Abdomen 960 long, 384 wide; no sigmoid or inwardly directed (wing retaining) setae; no tergo-pleurotergal sutures; segment X (length 160) elongate tubular without median suture, with a crown of apical setae, and bearing a swelling which may be a placoid sensilla on the ventral side (Figs 1.4, 4.4).

Discussion. The attribution of this fossil to the Phlaeothripidae is based on the presence of a tubular last abdominal segment without median suture and bearing an apical crown of setae. Moreover, in the preserved parts of the fossil, we can observe that *Rohrthrips* **n. gen.** shares with the other Tubulifera the absence of microtrichia on wings, a fore wing fringe with straight ciliae of nearly same length in anterior and posterior margins, a hind tarsus two-segmented with a hamus, and the sternal area of each abdominal segment spanning the entire width of abdomen (no tergo-pleurotergal sutures) (list of characters reviewed in Bhatti 1988).

However *Rohrthrips* **n. gen.** presents also several plesiomorphies particularly in wing characters, which is new because the wings of Phlaeothripidae are currently presented as exhibiting few of these (Mound *et al.* 1980).

The fore wings of recent Phlaeothripidae exhibit many apomorphies among which the followings: wing surface with no microtrichia, longitudinal veins absent and veinal setae absent (Mound *et al.* 1980). As comparison, *Rohrthrips* **n. gen.** has a fore wing without microtrichia but it differs from the other Tubulifera in the presence of two well defined longitudinal veins of which first vein bears setae. The only 'venation' so far hypothesed in the tubuliferan fore wing is few lacunae in the wing membrane and few setae in basal part of the wing (Bhatti 1991), but we can now ascertain that these are 'vestiges' of well-developed veins in the most basal representatives of this group. This character seen
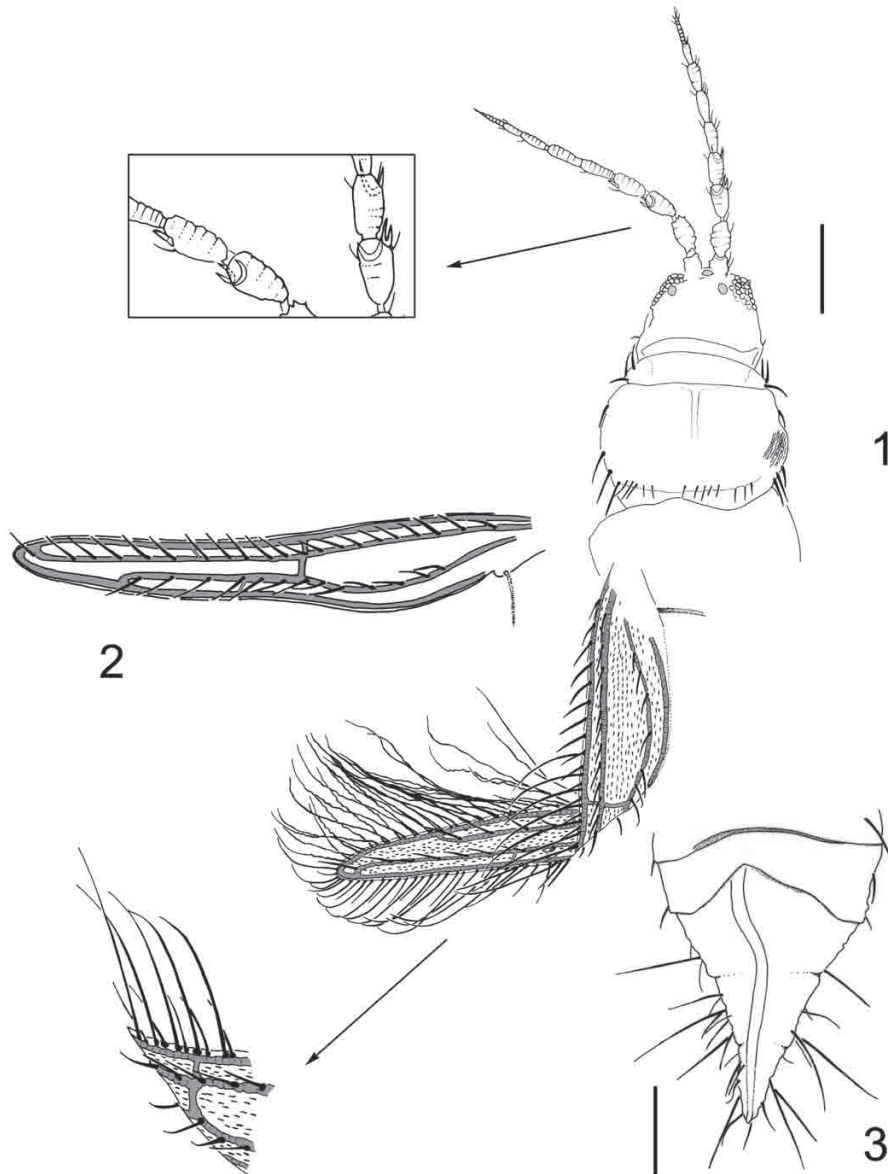

Figure 2
Camera lucida drawings of female *Tethysthrips hispanicus* **n. gen., n. sp.** (Thripidae); holotype ES-07-11. **1,** Head and thorax in dorsal view, showing left fore wing and detail of the cross-veins (inset: detail of the elongate and forked sensilla of antennal segments III and IV); **2,** Left fore wing reconstruction; **3,** Apex of the abdomen in ventral view. Scale bars = 0.1 mm.

in our fossil is a thysanopteran plesiomorphy (Mound *et al.* 1980). In phlaeothripids the bases of the fringe cilia on wings differ from those of all other Thysanoptera in that they do not arise from sockets but are immovably embedded in the wing membrane (Bhatti 1988). But in *Rohrthrips* **n. gen.** these fringe cilia do arise from sockets. Without the possibility to make more precise examination, we are unable to distinguish between structures of sockets in *Rohrthrips* **n. gen.** and those present in all non-tubuliferan Thysanoptera. In the later, sockets are well seen by surface scanning electron microscopy (Moritz 2006). They allow the cilia to be locked in two positions, one for flight and one for rest. When not in use, cilia may be locked in closed position which prevents entanglement between the wings (Ellington 1980). In Phlaeothripidae, the wings normally overlap the abdomen at rest so that a similar problem of entanglement is avoided (Ellington 1980), and also wings are held between paired sigmoid setae of abdominal segments (Bhatti 1988). We could note that no setae putatively implicated in retaining wings were present on the abdomen of *Rohrthrips* **n. gen.**

The wing coupling mechanism differs between the recent Phlaeothripidae and the other Thysanoptera in that Tubulifera usually lack a U-shaped recurved seta on the hind wing and therefore only relies on the hamuli, the basal marginal setae on the hind wing catching on a submarginal ridge on the clavus of fore wing (Bhatti 1988). But *Rohrthrips* **n. gen.** bears a seta recurved downwardly and in good place to hold the apical setiform processes of clavus. Therefore *Rohrthrips* **n. gen.** presents the wing coupling mechanism plesiomorphically present in non-tubuliferan Thysanoptera.

With all this information, it appears that Mound & O'Neill (1974)'s statement that 'the distal three-quarters of the wing membrane in the Phlaeothripidae is a secondary development … and not strictly homologous with the wing of the rest of Thysanoptera' is erroneous. Indeed, the Tubulifera *Rohrthrips* **n. gen.** presents in its wings numerous plesiomorphies shared by non-tubuliferan Thysanoptera, and it is more likely that the tubuliferan wing structures developed later in the tubuliferan clade: reduction of wing venation, etc.

Family Thripidae Stevens 1829

Genus *Tethysthrips* n. gen.

Type species. *Tethysthrips hispanicus* **n. sp.**, other species *Tethysthrips libanicus* **n. sp.**

Diagnosis. Female characters only. Antenna nine-segmented, with segment IX clearly subdivided; presence of annulae and microtrichia on all antennal segments; segments III and IV with clearly emergent forked trichome (III with two and IV with one); two segments at least on fore- and hind-tarsus; fore tarsus without a claw-like process (hamus); fore wing distally narrow; longitudinal veins complete, four cross-veins; posterior fore wing fringe cilia undulate; one longitudinal vein on hind wing; abdominal pleurites present; a well developed saw-like ovipositor directed downwards.

Etymology. Named after Tethys, for the Cretaceous ocean between Spain and Lebanon, and Thrips.

Tethysthrips hispanicus n. sp. (Figs 2, 5)

2009 'thysanopteran specimen'; Najarro *et al.*; fig. 12A.

Material. Holotype specimen ES-07-11 (complete female; it was found in an amber mass with a ceratopogonid dipteran of the genus *Archiaustroconops*, ES-08-6, as syninclusion), stored provisionally at the Museo Geominero (IGME), Madrid, Spain.

Etymology. Named after Hispania, Latin name for Spain.

Age and outcrop. Early Cretaceous, early Albian in Las Peñosas Fm. Amber outcrop from El Soplao territory in northwestern Cantabria (near the village of Rábago), Spain (see Najarro *et al.* 2009).

Diagnosis. As for genus.

Description. Body length 1088 (Figs 5.1, 5.2). Antenna nine-segmented (Fig. 2.1), segment IX with seven subdivisions (Fig. 5.3); presence of annulae and microtrichia on all antennal segments; segments III and IV elongate, cylindrical; sensoria of antennal segments III and IV elongate and forked (Fig. 5.4); tL 315; lengths of segments: I 20, II 43, III 40, IV 40, V 40, VI 40, VII 34, VIII 23, IX 33; head circa 115 long, 135 wide; ocelli present ; ocellar setae not visible (but absence impossible to establish); maxillary palps three-segmented, 45 long.

Pronotum broadly rectangular with a longitudinal median furrow, visible near anterior margin (Fig. 2.1), 165 long, 210 wide, with anterior margin 155 wide; three pairs of very long posteroangular setae (Fig. 2.1), s.pa 69 (largest); three antero-angular setae and one rather long lateral setae, but shorter than the posteroangular setae, s.am 28; nine pairs of postero-marginal setae estimated.

Fore wing progressively narrowed at apex (Figs 2.1, 2.2), 600 long, circa 70 wide at mid-length, with microtrichia; posterior fringe cilia undulate (Fig. 5.5); two complete main longitudinal veins, one cross-vein between them at basal third, plus above it one clearly visible cross-vein, between anterior vein and anterior wing margin (Figs 2.1, 2.2); two less sclerotized cross-veins toward the apex, one between anterior vein and anterior wing margin, and the other one between posterior vein and posterior wing margin (Figs 2.1, 2.2); anterior vein with 21 visible setae, posterior vein with 13 setae distributed both distally and proximally to the cross-vein between longitudinal veins; posterior vein ending 125 basal of wing apex, anterior vein ending very close to wing apex (Figs 2.1, 2.2, 5.5).

Hind wing narrow, circa 555 long, 44 wide, with microtrichia on membrane and fringe undulate, one longitudinal vein that does not reach the wing apex.

Fore tarsus without a distal hamus; no tooth on inner margin of fore tibia; fore femur incrassate; at least fore and hind tarsi two-segmented; fore leg 335 long (femur 128 long, 58 wide; tibia 135 long, 33 wide; tarsi 47 long and arolium 25 long).

Abdomen with apex slender (Figs 2.3, 5.6); pleurites present; approximate length of sternite VIII 88, IX 125, X 168; segment X with five pairs of long and strong setae and around seven pairs of shorter setae (largest pair 120 long); segment IX anteriorly curved, with two pairs of short lateral setae, shorter than those of segment X; sclerotized ovipositor present, but its curvature not discernable, circa 290 long.
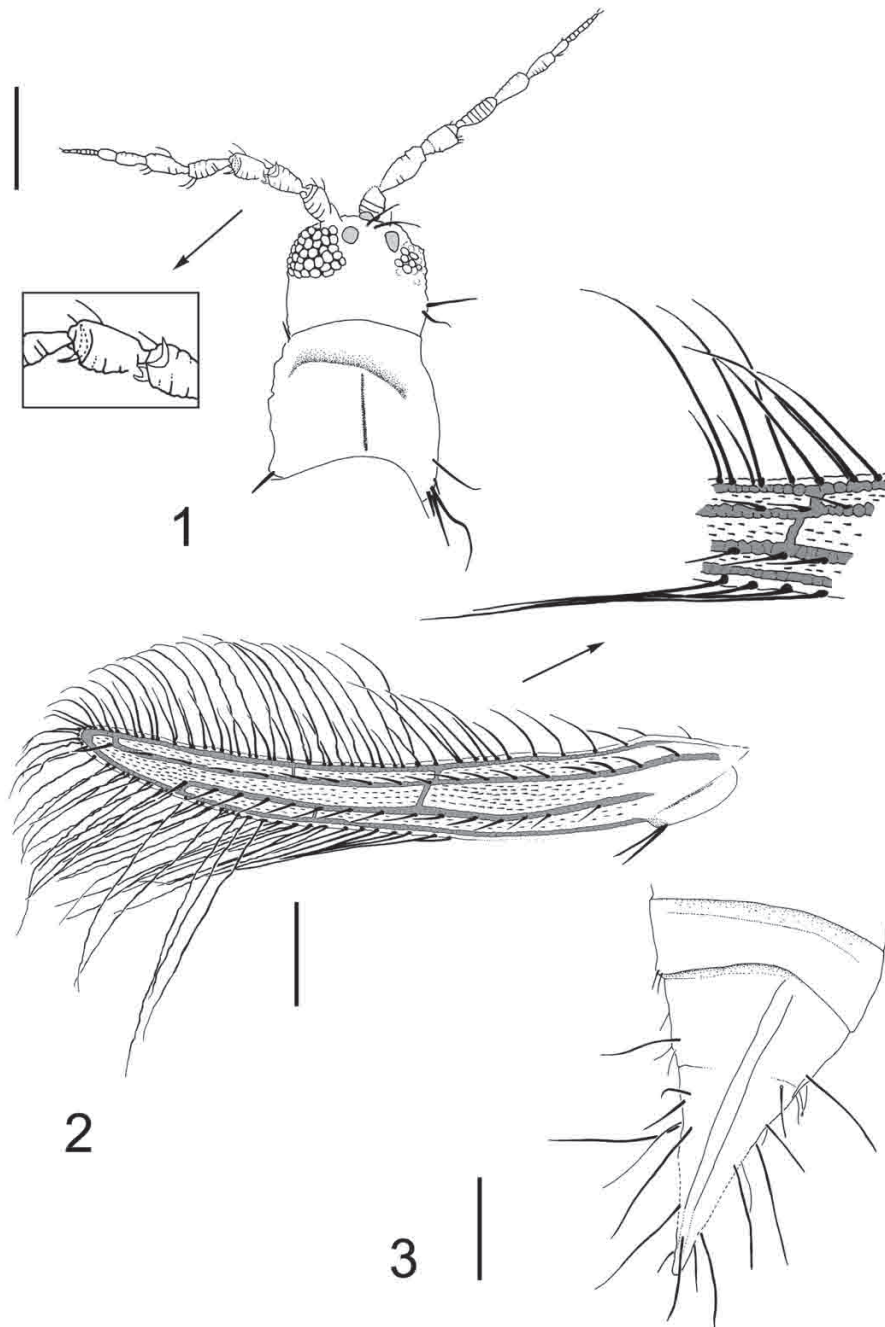

Figure 3
Camera lucida drawings of female *Tethysthrips libanicus* **n. gen., n. sp.** (Thripidae); holotype 97A. **1,** Head and thorax in dorsal view (inset: detail of the elongate and forked sensilla of antennal segments III and IV); **2,** Left fore wing with detail of most sclerotized cross-veins; **3,** Apex of the abdomen in ventral view. Scale bars = 0.1 mm.

Tethysthrips libanicus n. sp.
(Figs 3, 5.7)

Material. Holotype specimen 97A (complete female), Azar collection, provisionally stored at the Muséum National d'Histoire Naturelle, Paris, France.

Etymology. Named after Libanon, Latin name for Lebanon.

Age and outcrop. Early Cretaceous, Neocomian, Hammana/ Mdeirij, Caza Baabda (Baabda District), Mouhafazit Jabal Libnen (Governorate Mount Lebanon), Central Lebanon.

Diagnosis. Differences between *Tethysthrips hispanicus* n. sp. and *T. libanicus* n. sp. are very few: presence of 18 setae on anterior longitudinal vein of fore wing in *Tethysthrips libanicus* instead of 21 in *Tethysthrips hispanicus*; presence of 15 setae on posterior longitudinal vein in *Tethysthrips libanicus* instead of 13 in *Tethysthrips hispanicus*; body length slightly larger in *Tethysthrips libanicus* than in *Tethysthrips hispanicus*.

Description. Female characters only. See that of *Tethysthrips hispanicus*. Body length 1268 (Fig. 5.7). Antenna nine-segmented (Fig. 3.1), segment IX with seven subdivisions; tL 330; lengths of segments: I 25, II 30, III 53, IV 40, V 47, VI 43, VII 32, VIII 21, IX 37; head 118 long, 140 wide; maxillary palps three-segmented.

Pronotum broadly rectangular with a longitudinal median furrow (Fig. 3.1), 115 long, 160 wide, with anterior margin 130 wide; metathoracic sterno-pleural sutures well developed; three pairs of very long posteroangular setae, s.pa 80 (largest); difficult to see lateral and postero-marginal setae, but there is a seta in the third anterior like in *T. hispanicus*.

Fore wing progressively narrowed at apex (Fig. 3.2), 661 long, 72 wide at cross-vein, with microtrichia; posterior fringe cilia undulate; two complete main longitudinal veins, one cross-vein between them at basal third slightly inclined towards wing apex, plus above it one clearly visible cross-vein, between anterior vein and anterior wing margin (Fig. 3.2); two less sclerotized cross-veins toward the apex, one between anterior vein and anterior wing margin, and the other one between posterior vein and posterior wing margin (Fig. 3.2); anterior vein with 18 visible setae, posterior vein with 15 setae distributed both distally and proximally to the cross-vein between longitudinal veins; posterior vein ending 115 basal of wing apex, anterior vein ending very close to wing apex.

Hind wing narrow, circa 665 long, 49 wide in the distal third, with microtrichia on membrane and posterior fringe cilia undulate, one longitudinal vein not reaching wing apex.

Fore tarsus without a hamus; no tooth on inner margin of fore tibia; tarsi two-segmented; fore tibia 128 long, mid femur 115 long, mid tibia 108 long, mid tarsus 34 long, mid arolium 23 long, hind femur 160 long, hind tibia 143 long.

Abdomen with apex slender (Fig. 3.3); four pairs of postero-marginal setae visible on sternites VI and VII at least, one close to lateral side and three close to median line; pleurites present; approximate length of sternite VIII 65, IX 100, X 205; segment X with the same ornamentation of setae as in *Tethysthrips hispanicus*, viz. five pairs of long and strong setae and around seven pairs of shorter setae (largest pair 140 long); segment IX with two pairs of short lateral setae, shorter than those of segment X; sclerotized ovipositor present, directed downwards, shorter than abdomen, circa 265 long.

Discussion. The attribution of these Spanish and Lebanese thrips to the same genus is supported by their nearly identical habitus. The presence of clearly forked and long trichomes on antennal segments III and IV is an apomorphic character proper to the 'most higher Thripidae' (Mound *et al.* 1980). Only Thripidae and recent Phlaeothripidae have slender, emergent trichomes on antennal segments III and IV (Mound *et al.* 1980). *Tethysthrips* shares with the other Thripidae (but not exclusively with this family) the well-developed down curved ovipositor (as can be seen in the Lebanese specimen), the narrow fore wing, the presence of well defined abdominal pleurites (as in the majority of Thripidae after Schliephake & Klimt 1979), and the absence of hamus on fore tarsi.

Nevertheless, *Tethysthrips* **n. gen.** has some characters that are currently considered as plesiomorphic for a Thripidae. The presence of nine antennal segments is a plesiomorphic character for all Thysanoptera (Mound *et al.* 1980), but one of the most evident apomorphies in Thripidae is the reduction in the number of antennal segment from "9 segments, all separated", to "8 segments or less, if 9 segments than terminal broadly joined" (in Palmer & Mound 1985). Therefore the antenna of *Tethysthrips* **n. gen.** is quite unusual for a Thripidae in two ways: it bears nine segments and segments VII–IX are longer than VI and well separated. This feature has only been described in *Psydrothrips* Palmer & Mound 1985 which represents one recent genus out of the 17 genera of Thripidae bearing nine-segmented antenna (Palmer & Mound 1985). Multiple division of the terminal antennal segment has been found in some other fossils from various other families (in Mound *et al.* 1980) and is probably homoplasic. As far as fore wings are concerned, presence of complete fore wing longitudinal veins and presence of cross-veins as observed in *Tethysthrips* **n. gen.** are considered plesiomorphic characters for all Thysanoptera (Mound *et al.* 1980), while in Thripidae, the basal part of the posterior longitudinal vein is rarely present (for example it is present in *Eremiothrips* Priesner 1950) and two cross-veins are also rarely present. The tarsi are two-segmented in basal thysanopteran families, but in most Thripidae they have been reduced to one segment on all legs (Mound *et al.* 1980). In that case also, it appears that *Tethysthrips* **n. gen.** has retained a plesiomorphic condition. Abdominal tergo-pleural sutures are well-developed in *Tethysthrips* **n. gen.**, which is considered as plesiomorphic for Thysanoptera (Mound *et al.* 1980), but in higher Thripidae, as in Heterothripidae and Phlaeothripidae, the tergites and pleurotergites are completely fused.

Conclusion

The oldest records of the extant families of Thysanoptera date from the Early Cretaceous and concern the basal families Stenurothripidae (cf. Peñalver & Nel this issue), plus Aeolothripidae and the most derived family Thripidae (Shmakov 2009). The placement into synonymy of Jezzinothripidae zur Strassen 1973 with Merothripidae by Bhatti (1979, 1986) would need further study because reasons for it were not given. It may be because of the absence of microtrichia on the wing surface (zur Strassen 1973), however this never appeared as an apomorphy of the Merothripidae. The specimens we describe herein show that at that time, the thysanopteran diversification was greater than what was previously supposed. Fossil Thripidae were present in Lebanese and Spanish amber of about the same age as the Baisa deposit, which shows how wide spread this family already was, suggesting a greater antiquity. Moreover, we could demonstrate that the Phlaeothripidae were also already surely present. Shmakov (2008) proposed an interpretation of *Liassothrips crassipes* (Martynov 1927), single member of the family Liassothripidae, making it a possible step in the evolution of the tubuliferan thrips. However, Shmakov (2008) indicated that 'the male genitalia of *Liassothrips* are similar to the terebrantian type, while the female genitalia resemble the tubuliferan type', with in particular, no tube for male and one for female. This assumption seems doubtful in terms of evolutionary development and functional morphology. Moreover, no tube is visible on the photography presented, and 'relatively long fustis' of figure 2 in Shmakov (2008) may perhaps be interpreted as a weak ovipositor.
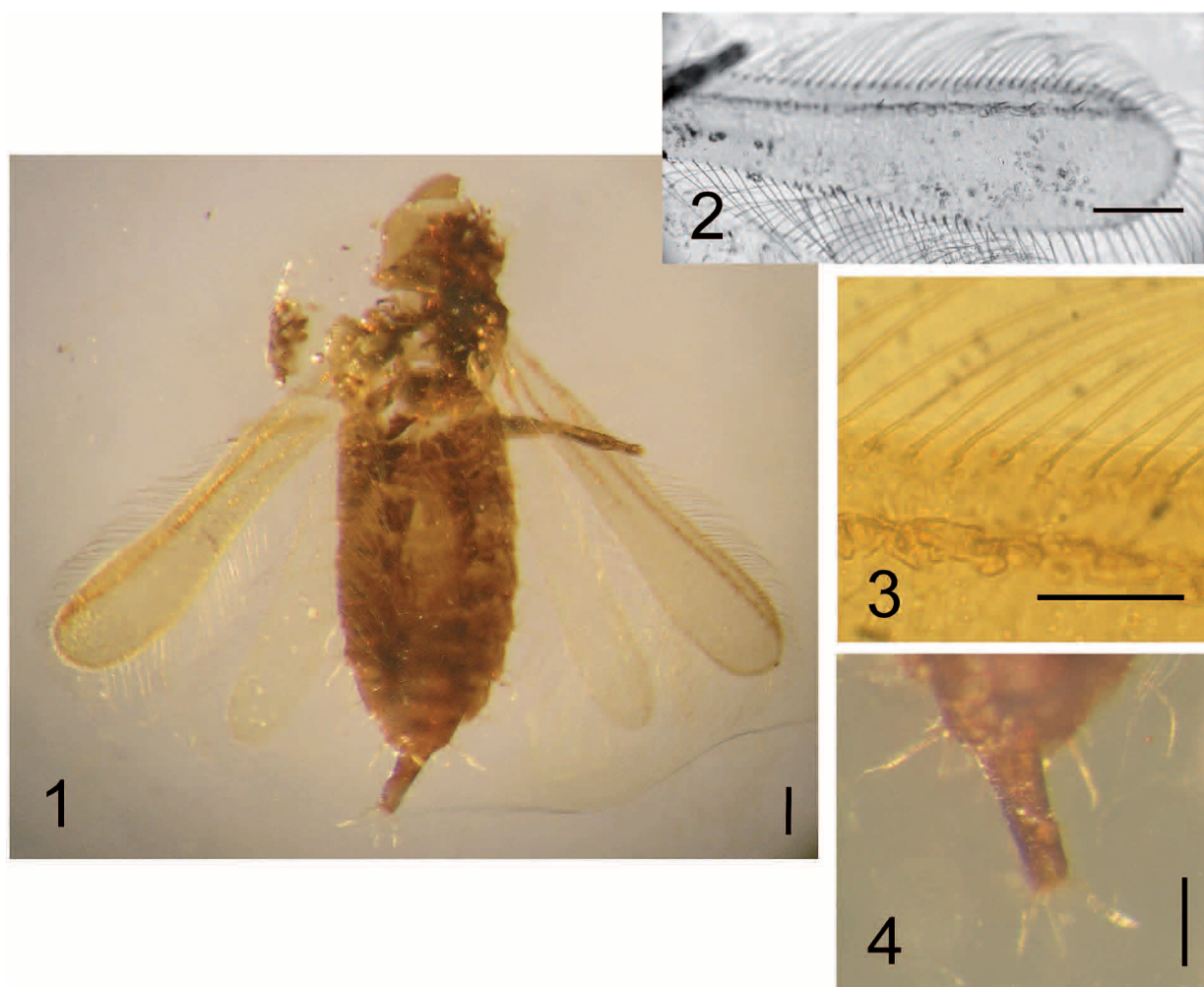

Figure 4
Rohrthrips libanicus **n. gen., n. sp.** (Phlaeothripidae); holotype 1217. **1,** Dorsal habitus; **2,** Detail of some setae on the first vein of the right fore wing; **3,** Detail of the insertions of the fringe cilia at the mid length of the fore wing in ventral view; **4,** Apex of the abdomen in ventral view. Images 1 and 4 scale bars = 0.1 mm, images 2 and 3 scale bars = 0.05 mm. Image 1 was made with integrated consecutive pictures taken at successive focal planes.
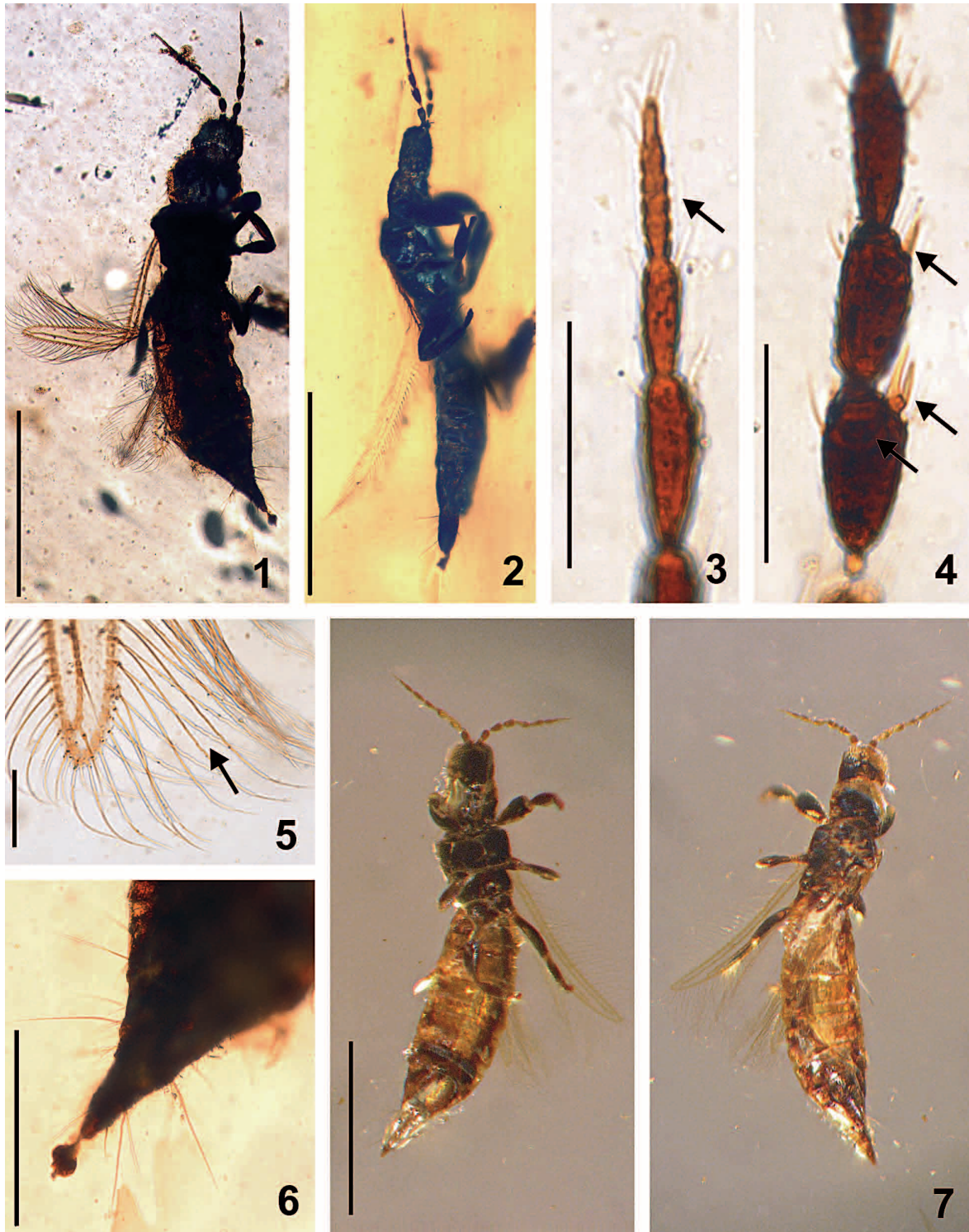
Figure 5

Females of *Tethysthrips* **n. gen.** (Thripidae); Images 1 to 6 are of *Tethysthrips hispanicus* **n. gen., n. sp.,** holotype ES-07-11. **1,** Dorsal habitus; **2,** Lateral habitus; **3,** Detail of the antennal segment IX showing seven subdivisions; **4,** Detail of the elongate and forked sensilla (arrows) of antennal segments III and IV; **5,** Detail of the fore wing apex showing the distal part of one longitudinal vein and the undulate fringe (arrow); **6,** Apex of the abdomen in ventral view; **7,** Dorsal and ventral habitus of *Tethysthrips libanicus* **n. gen., n. sp.** (Thripidae); holotype 97A. Images 1, 2 and 7 scale bars = 0.5 mm, images 3-5 scale bars = 0.05 mm, image 6 scale bar = 0.2 mm. Images 1-5 and 7 were made with integrated consecutive pictures taken at successive focal planes.

We confirm here the assumption by Grimaldi & Engel (2005), whereby 'Like Psocoptera in Cretaceous ambers, eventual study of many more Lebanese amber thrips and ones in other Cretaceous ambers will be exceptionally important for understanding the origins and evolution of modern families'. Many living insect families extend to the Cretaceous about 120 Myr ago (Grimaldi & Engel 2005) and Thysanoptera do not make exception to it. Most important implications for description of fossils concern contribution to the evolutionary history of taxa and elucidation of relationships among extant taxa. *Tethysthrips* **n. gen.** shows many plesiomorphies for Thysanoptera and these are still observed and recognized as such in few recent thripid genera. *Rohrthrips* **n. gen.** presents many plesiomorphies never observed in other Phlaeothripidae. Therefore *Rohrthrips* **n. gen.** gives a milestone in the evolution of tubuliferan thrips. The second accurate oldest Tubulifera is an undescribed fossil from the Early Eocene amber of France, which presents all the synapomorphies of the recent Phlaeothripidae (Nel, pers. obs.). Thus the evolution of Tubulifera probably took place during the Cretaceous. On the other hand, *Rohrthrips* **n. gen.** possesses no apomorphy shared with another non-tubuliferan family and does not help to solve the uncertainty concerning the phylogenetic affinities of the Tubulifera. Indeed the relationship of the Tubulifera to the rest of Thysanoptera is equivocal (Mound & Morris 2007), the Tubulifera being either the sister-group of the rest of Thysanoptera, or the sister-group of a thripid subgroup (Mound *et al.* 1980). It is nevertheless a fact that *Rohrthrips* **n. gen.** is an important fossil in the tubuliferan history, as it gives arguments against a neogenic origin of the tubuliferan wing and constitutes a good example showing that ignoring fossils seriously compromises our understanding of insect evolution. We can expect that any new Early Cretaceous Tubulifera may give useful discoveries for the comprehension of the relationships with other Thysanoptera.

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