

# The Jurassic Thrips *Liassothrips crassipes* (Martynov, 1927) and Its Taxonomic Position in the Order Thysanoptera (Insecta)

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Received October 10, 2006

**Abstract**—The Late Jurassic thrips *Liassothrips crassipes* (Martynov) is redescribed, and its taxonomic position discussed. It is shown that the male genitalia of *Liassothrips* are similar to the terebrantian type, while the female genitalia resemble the tubuliferan type. Therefore, the Liassothripidae shows the possible evolutionary pathway of tubuliferan thrips. *Liassothrips* is treated as the oldest known member of the suborder Tubulifera (previously known beginning from the Eocene), the ancestors of which belonged to the family Aeolothripidae (Terebrantia) rather than Thripidae.

**DOI:** 10.1134/S0031030108010073

**Key words:** Thrips, Thysanoptera, Late Jurassic.

## INTRODUCTION

The order Thysanoptera (= Thripida sensu stricto), fringe-winged insects or thrips, comprises about five thousand species of tiny insects, with diverse biology. Most species are plant cell-suckers, but predators and mycophages are also represented. The thrips life cycle is unusual, including two nymphal stages (active, wingless nymphs resembling adults, as is typical for hemimetabola), prepupa, and pupa (immobile and nonfeeding stages, with reduced external structures, as is typical for holometabola). The pupa is usually inside a cocoon produced by a second stage nymph. Tubuliferans have additional, second pupal stage (Moritz, 1989).

Most authors accept the system proposed by Priesner (1964) and divide the order Thysanoptera into two suborders, Terebrantia (oviparous thrips), less specialized anthophilous or predatory inhabitants of flowers and green parts of plants, and Tubulifera (tubuliferan thrips), which often live under bark or in leaf litter, feeding on fungal hyphae and spores.

There are different hypotheses concerning the relationships between the main groups of extant thrips. The hypothesis of tubuliferan ancestors of Terebrantia (Priesner, 1968) has not been supported by factual evidence. Some researchers have proposed independent evolution of both suborders from a common psocopteran ancestor (Ananthakrishnan, 1979). It is generally believed that Tubulifera evolved from certain thrips of the suborder Terebrantia (Stannard, 1968; Hennig, 1969; Schliephake, 1975).

At present, most authors follow Zherikhin (1980) and Vishnjakova (1981), that thrips are closely related to the extinct family Lophioneuridae, which displays a gradual transition from psocopterans to thrips. Some

authors include Lophioneuridae into the thrips order (= Thripida sensu lato) as a separate suborder (Zherikhin, 2002). In the present study, thrips are treated in the traditional, more restricted sense.

Triassic records (Grimaldi et al., 2004) are additional evidence of the close affinity of Lophioneuridae and true thrips. They agree with both the theory of the development of wing venation in thrips (Comstock, 1918) and the later hypothesis of Sharov (1972), which was based on single Jurassic thrips specimen in perfect condition. *Karataothrips jurassicus*, which was described by Sharov from the Upper Jurassic of the Karatau and placed in a new family, Karataothripidae. *Karataothrips* displays a venation pattern more similar to that of an aeolothripid than a lophioneurid. The hypothetical transitional form from Lophioneuridae to *Karataothrips* is very close to the condition seen in the Triassothripidae (Grimaldi et al., 2004). Certainly, this means the presence of a distinct evolutionary trend rather than a direct ancestor–descendant lineage.

In addition to *Karataothrips*, another thrips genus from the Jurassic of the Karatau has been described. Martynov (1927) named this genus and its new family *Mesothrips* and Mesothripidae, respectively; however, they were incompletely described. Subsequently, Priesner (1949) showed that *Mesothrips* was a junior homonym and proposed the replacement name *Liassothrips*. Priesner did not refer directly to material or provide additional description. Additional material has revealed the great phylogenetic importance of this insect, which demands its redescription.

The fossil remains of *Liassothrips crassipes* (Martynov, 1927) which are considered in this paper, come from the Karabastau Formation of the Upper Jurassic (Oxfordian–Kimmerigian) of the southern Karatau

Mountains (Kazakhstan). The geographical position and stratigraphy, paleoecology, fauna and flora of the locality are described in detail by Doludenko et al. (1990) and Kirichkova and Doludenko (1996). The first thrips were collected there by Martynov in 1925; additional material was collected by employees of the Laboratory of Arthropods of the Paleontological Institute of the Russian Academy of Sciences (PIN). A total of 92 specimens of *Liassothrips* have been collected, three of which are accompanied by counterparts; however, only 57 specimens are informative. All specimens studied are housed in the Laboratory of Arthropods of PIN.

## SYSTEMATIC PALEONTOLOGY

Order Thysanoptera

Suborder Tubulifera

### Family Liassothripidae Priesner, 1949

*Mesothripidae*: Martynov, 1927, p. 768.

*Liassothripidae*: Priesner, 1949, p. 149.

Type genus. *Liassothrips* Priesner, 1949 (= *Mesothrips* Martynov, 1927, non Zimmerman, 1900) from the Upper Jurassic (Oxfordian–Kimmerigian) of the Karatau (Kazakhstan).

**D i a g n o s i s.** Antennae with strong secondary segmentation of last segment (divided into five rings). Piercing maxillary stylets, withdrawing deep into mouthcone. Wings without visible veins, broad, with rounded tips. Male genitalia located in last segment, as typical in Terebrantia. Pseudovirga very short. Last abdominal segment of females elongated tubular, with highly sclerotized fustis, as typical in Tubulifera.

**C o m p o s i t i o n.** Type genus.

**C o m p a r i s o n.** The family Liassothripidae differs from all other Tubulifera families in the structure of the male genitalia.

**O c c u r r e n c e.** Late Jurassic of Kazakhstan, Karatau locality (Galkino and Mikhailovka).

### Genus *Liassothrips* Priesner, 1949

*Mesothrips*: Martynov, 1927, p. 768 (nom. preocc., non *Mesothrips* Zimmermann, 1900).

*Liassothrips*: Priesner, 1949, p. 149.

Type species. *Mesothrips crassipes* Martynov, 1927.

**Description.** The head is longitudinally extended, with almost parallel sides. On the lateral side, the eyes reach posteriorly the midlength of the head. The antennal flagellum is eight-segmented, with a poorly developed stylus. Secondary segmentation of the last antennomere is well-pronounced, divided into five rings. The sensoria are flat (of aeolothripid or phloethripid type). The mouthcone is slightly asymmetrical, crosses the anterior margin of the prothorax and extends for a quarter of its length. The piercing maxillary stylets are broadly rounded at the base at rest.

The prothorax is transverse (especially in males) and trapezoidal. Its lateral margins curve slightly; the posterior corners project considerably laterally; a clear constriction is present between the prothorax and pterothorax. The furca is very broad, highly sclerotized, without a spinule. Its central part is shifted anteriorly, such that the furca curves posteriorly and is displaced to the posterior margin of the prothorax.

The pterothorax is longitudinally extended in males and slightly transverse in females, very highly sclerotized, with prominent sides. The wings are heteronomous, broad, with rounded tips. Fore wings and probably hind wings reach tergite 6. Venation is indiscernible or absent.

The fore femora are considerably thickened, almost high trapezoidal in shape and have a massive internal thorn on the frontal margin. Males have an apical thorn and probably the second internal thorn. The tibia is slender (9 : 1) in both sexes. The middle and hind femora and tibiae are slightly uniformly thickened, the tarsi are two-segmented (the tarsal formula is 2-2-2).

The dorsal side of the posterior margin of the last segment has a broad semicircular notch.

The aedeagus of the male genitalia is approximately as long as the parameres, and the phallosome and endotheca are separated by a shallow constriction. The phallobase is invisible. The pseudovirga is very short, genital appendages are located in the last segment.

In females, the last abdominal segment is elongated tubular, but a highly sclerotized fustis is located medially at segments 9–10. Segment 10 has two pairs of apical setae.

**Species composition.** Type species.

#### *Liassothrips crassipes* (Martynov, 1927)

*Mesothrips crassipes*: Martynov, 1927, p. 768, text-figs. 1 and 2.

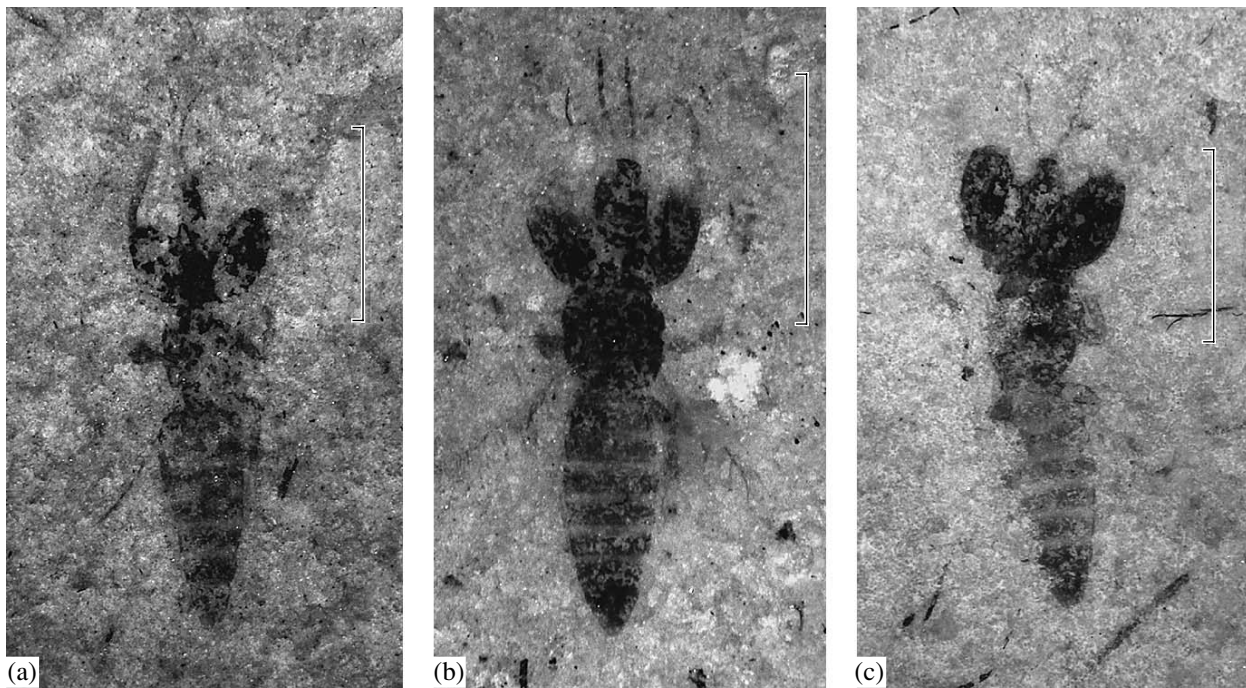
*Liassothrips crassipes*: Priesner, 1949, p. 149, text-fig. 38.

Lectotype. PIN, no. 2452/572 (571) (designated here).

**Description** (Figs. 1, 2). The head has weak transverse banding on the posterior side (specimen PIN, no. 2066/3622). The eyes are large, with many large facets and slight double notches on the ventral side; dorsally, they are rounded. The palps and mandibular stylet are indiscernible in the mouthcone.

The abdomen is elongated, all segments, except for the last two, are obviously transverse.

**Measurements**, mm and ratios, in males (female): total body length, 2.15–2.20 (1.93–2.04). Length-to-width ratio of: head, 1.10–1.14 (0.96–1.01); prothorax, 0.53–0.58 (0.80–0.84); pterothorax, 1.13–1.17 (0.92–0.97); fore wing, 9.10–9.17 (7.21–7.35); fore furca, 0.24–0.26 (0.29–0.31); abdominal segments: I, 0.38–0.40 (0.26–0.28); II, 0.21–0.25 (0.27–0.29); III, 0.27–0.30 (0.22–0.24); IV, 0.19–0.21 (0.24–0.27); V, 0.23–0.24 (0.29–0.32); VI, 0.27–0.28 (0.25–0.29); VII, 0.34–0.37 (0.31–0.32); VIII, 0.25–0.28



**Fig. 1.** *Liassothrips crassipes* (Martynov), appearance: (a) lectotype PIN, no. 2452/572, male; (b) specimen PIN, no. 2784/2207, female; and (c) specimen PIN, no. 2239/771, male. Scale bar, 1 mm.

(0.31–0.33); IX, 0.24–0.29 (0.68–0.71); X, 0.58–0.63 (3.91–3.95); femur: fore, 1.62–1.70 (1.67–1.72); middle, 5.09–5.14 (1.43–1.45); hind, 3.10–3.13 (2.28–2.40); tibia: fore, 8.93–8.97 (9.04–9.12); middle, 2.07–2.12 (1.81–1.84); hind, 4.73–4.77 (3.38–3.44). Ratio of hind margin fringe to fore (hind) wing width, 0.71–0.82 (0.72–0.86).

**Remarks.** Diagnostic characters are particularly well-pronounced in the following specimens: flagellum (PIN, no. 2239/813), last antennomere (PIN, no. 2066/3612), mouthcone (PIN, no. 2997/4160), maxillary stylets (PIN, no. 2997/4183), prothorax (PIN, no. 2784/2209), fore furca (PIN, no. 2239/765), pterothorax (PIN, no. 2066/3612), fore femora (PIN, no. 2997/5025), tibia (PIN, no. 2239/764), notch in the last segment (PIN, no. 2452/66), male genitalia (PIN, no. 2239/780), and female genitalia (PIN, no. 2784/2207).

The proportions of antennal segments are not provided because of poor preservation in all specimens.

**Material.** The type series (PIN, nos. 2452/66, 2452/571 (572), 2452/585) consist of poorly preserved specimens. The holotype was not designated by the author. A lectotype (PIN, no. 2452/572) is designated here. In addition to the type series, the collection includes 88 specimens collected later (PIN, nos. 2066/3611–3626, 3628, 3629, 3631–3633; 2239/756–760, 762–781, 813; 2554/1077, 1082; 2784/2207–2209, 2268, 2269; 2904/665, 666, 1729; 2997/4158–4180, 4183, 5025–5031). Specimens 2239/771, 2452/585, and 2784/2207 are particularly well-preserved, providing additional morphological information.

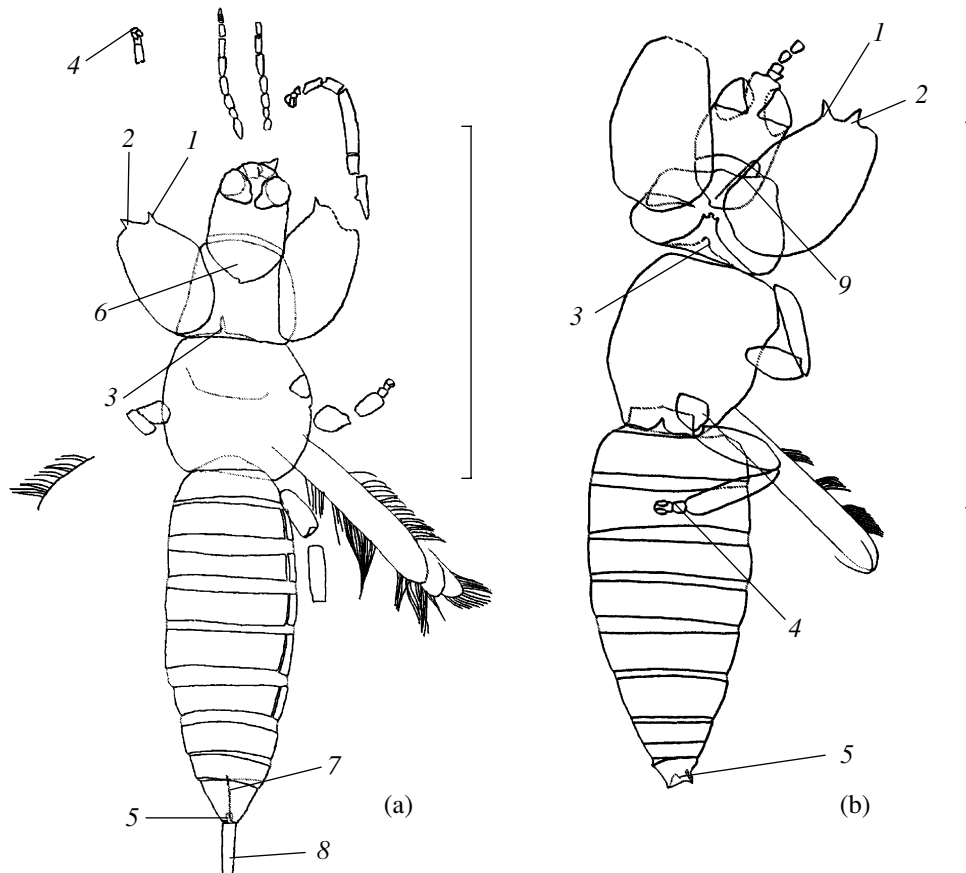
#### LIASSOTHRIPS MORPHOLOGY

**Antennae** of *Liassothrips* have secondary segmentation of the last antennomere; it is divided into five rings. Secondary segmentation is also characteristic of some thrips from the Cretaceous Lebanese amber, which have from six to nine secondary rings (zur Strassen, 1973). Among Recent Thysanoptera, this modification is usual for some members of the family Phloeothripidae (for example, *Neosmerinothrips*), although they have at most three rings in the last antennomere. This feature of Jurassic and Cretaceous thrips is probably a primitive character.

The antennae are divided into ten segments. A similar situation is observed in Aeolothripidae and Phloeothripidae, but has not been recorded in Thripidae.

The supposition of the presence of aeolothripid or phloeothripid sensorium types in *Liassothrips* is based on the comparison with thrips of similar preservation from the Lower Cretaceous Baisa locality. Thripidae from Baisa, which dominate in the thrips assemblage, have prominent sensoria typical of this family, even in less preserved specimens. No prominent sensoria have been recorded in *Liassothrips*.

**Mouthcone** extends for a quarter of the prothorax length. The piercing maxillary stylets are slender, broadly curve at the base at rest. In extant thrips, this shape of stylets means that they can be withdrawn deep into the head capsule. Among living taxa, this stylet type is only known in the suborder Tubulifera (Stannard, 1968; Mound and Palmer, 1983), i.e., it is a syn-



**Fig. 2.** *Liassothrips crassipes* (Martynov), structural details: (a) specimen PIN, no. 2784/2207, female; (b) specimen PIN, no. 2239/771. Designations: (1) internal thorn; (2) external thorn; (3) furca; (4) tarsus; (5) dorsal slit; (6) mouthcone; (7) fustis; (8) tube; and (9) maxillary stylet. Scale bar, 1 mm.

pomorphy shared with Tubulifera. Maxillary palps are indiscernible.

**Fore furca** is almost as broad as the prothorax. This condition is probably accounted for by the strengthened prothoracic musculature; in addition, a broader furca provides attachment for more muscles. However, in extant thrips, including Tubulifera with the same development of the fore femora, the prothoracic sternite is divided into several sclerites, and no traces of furca are observed (Stannard, 1968). The fore furca of extant Terebrantia is usually well developed.

**Fore legs** of *Liassothrips* have a massive femur, resembling that of many Tubulifera, for example, from the subfamily Idolothripinae (Mound, 1971); in extant Terebrantia, such femora are unknown. The fore femur of Jurassic thrips has a massive thorn on the internal side of the anterior margin, another taxonomically significant character of several groups of Tubulifera. Among extant Tubulifera, such a thorn is typical for tropical taxa (Stannard, 1957) and has not been recorded in Terebrantia.

Many specimens have an apical thorn and, occasionally, one more (proximal) internal thorn, which are not

restricted to certain systematic groups, but occur relatively frequently in Tubulifera.

The function the thin, weak tibia (which is not adapted for heavy loading), which is nine times as long as wide, remains uncertain. The fore femur is not drop-shaped (this could have been attributed to the need for attachment of additional muscles), but high-trapezoidal. It is possible to propose that this shape is optimal to endure a heavy load on the anterointernal thorn, as is characteristic of many living Tubulifera, which however have short, jagged tibiae slightly curved internally.

In spite of distinct similarity in the structure of fore legs in *Liassothrips* and Tubulifera, the modification of legs in these groups could have developed independently, although these changes could have follow from the same prerequisites. The Jurassic thrips has a fore furca, which is absent from extant taxa. This difference is related to differences in the arrangement and function of the prothoracic musculature; consequently, similarity in general appearance does not necessarily imply similar functions. Thus, the similarity in fore legs does not necessarily mean close relationships between Liassothripidae and living Tubulifera.

**Wings** are broad, with rounded tips. The same shape is characteristic of the majority of representatives of the family Aeolothripidae (Terebrantia); the wings always have six (two longitudinal and four transverse) or seven veins (with an additional transverse vein). However, some extant genera of Tubulifera have wings of the same shape, but lacking veins. It is generally accepted that the broad wings developed secondarily in Tubulifera. The same point of view was proposed with reference to the wings of Aeolothripidae (Mound and O'Neil, 1974). Unfortunately, it is impossible to use venation of *Liassothrips* for understanding its relationships with other thrips families because of weak development or complete reduction of veins (they are absent from all specimens, even if the marginal fringe is well-preserved).

The family is similar to extant and most extinct thrips in the length of the fringe at the posterior margin of the fore wings; however, it differs essentially from Karataothripidae. The Karataothripidae were probably a blind lineage of Thysanoptera (Grimaldi et al., 2004).

Among recent thrips, the **tarsal formula** (2-2-2) is only typical for Terebrantia. Extant Tubulifera are usually characterized by formulas 1-2-1 and 1-2-2 (Stannard, 1957). Thus, the most complete tarsal composition of *Liassothrips* is the most primitive condition of thrips; therefore, it is not surprising that Jurassic Thysanoptera displays this condition. Cretaceous thrips from the Lebanese amber show the same formula (the tarsal segmentation of Triassothripidae and Karataothripidae remains unknown).

**Male external genitalia** have very short pseudovirga, as is typical for Terebrantia (Matsuda, 1976). Note that the genitalia of *Liassothrips* are located in the last segment (as is typical for living Terebrantia) instead of the penultimate segment (as is typical for Tubulifera). These characters of *Liassothrips* are undoubtedly symplesiomorphies.

The female genitalia also show synapomorphy shared with Tubulifera. They are similar in structure to other members of the order. Distinctive features are the relatively long fustis and very weakly sclerotized tube (segment 10).

Both sexes have a broadly rounded concavity on the dorsal side of the posterior margin of the last segment. Extant Tubulifera lack this structure, although many Terebrantia have a distinct dorsal slit in the same position. Its function is uncertain. The same structure was probably present in *Liassothrips*, although its shape is unusual. This presumable synapomorphy shared with Terebrantia seems a weak point, because homology of the structures discussed is not evident.

## DISCUSSION

Thus, *Liassothrips* shows a combination of characters unique not only to the thrips families, but also to suborders in the traditionally accepted composition.

The family is similar to Terebrantia in the tarsal formula and male genitalia and to Tubulifera in the structure of maxillary stylets and female genitalia. Of these features, the characters of Tubulifera seem to be more significant taxonomically. *Liassothrips* is similar to Terebrantia mostly in plesiomorphic features and to Tubulifera, only in apomorphic; this suggests monophyly with Tubulifera.

It is significant that, in several characters (the number of antennomeres and the shape of sensoria and wings), two families, Aeolothripidae (which is presumably ancestral to all extant thrips families, and probably appeared in the Middle Jurassic) and Phloeothripidae (which is presumably the most specialized and youngest thrips group, known beginning from the Eocene), show great similarity. This similarity along with morphological similarity of Liassothripidae and Phloeothripidae suggest that true Tubulifera evolved from a group closely related to Liassothripidae or from this family in the Late Jurassic; this shifts greatly the moment of appearance of Tubulifera.

During a revision of all Mesozoic Thysanoptera housed in PIN, Tubulifera (except for Liassothripidae) were not found. The rarity of Jurassic and Cretaceous Tubulifera compared to Terebrantia is probably attributable to the following:

(1) Identification of early Tubulifera is difficult, if they had a weakly sclerotized and hardly discernible tube, as in *Liassothrips*, because the female tube is the main diagnostic character of Tubulifera.

(2) At present, the Phloeothripidae are subordinate relative to other thrips families; this probably follows from their feeding specialization, consumption of fungal hyphae and spores. Attempts at transition to anthophagy, predation, or feeding on plant sap were successful in relatively small number of species. Therefore, they mostly inhabit humus, leaf litter, bark, and decaying wood. Tubulifera are inferior to Terebrantia in flying ability (because of differences in the wings), phloeothripids are mostly larger and include many wingless species. Therefore, they have a lesser chance of becoming fossils, because of less opportunity than flying taxa to move out of the colony or forage on plants; winged taxa are often carried on by the wind. Certainly, some Tubulifera could have dropped into the water from branches; however, this situation (dwelling on plants just near burial places) probably occurred much rarely. Note that brachypterous or apterous Thysanoptera have not been recorded in the fossil state, except for preserved in amber. Thrips could have become trapped in amber not only after flight but also after moving up or down a tree stem; therefore, the probability of finding the poorly flying Tubulifera in amber is much higher.

## CONCLUSIONS

The family Liassothripidae combines the following characters: the symplesiomorphies shared with Tere-

brantia are the tarsal formula and male genitalia; the synapomorphies shared with Tubulifera are the shape of maxillary stylets, the structure of fore legs and female genitalia; the synapomorphy shared with Terebrantia is dorsal concavity (slit). The results obtained suggest the assignment of Liassothripidae to the suborder Tubulifera.

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