Redefining the Thripida (Insecta: Paraneoptera)

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The Thysanoptera (Paraneoptera) constitute a very diverse order of minute insects, characterized mainly by a ‘punch-and-suck’ mode of feeding due to a specialized asymmetrical gnathal apparatus with two maxillary stylets plus only one functional mandible. We have studied their fossil relatives from the Thripida family sensu Vishniakova (1981) and Zherikhin (2002), as revised by Nel et al. (2012a), in order to identify new morphological characters and help to polarize some of the characters present in the Thysanoptera. Here we present perfectly preserved specimens from the Middle Jurassic Daohugou beds of China, approximately 165 million years old, belonging to three new species and one new genus of Lophioneurida (Thripida): Lophiosina lini gen. et sp. nov., Undacypha bournieri sp. nov. and Undacypha kreiteri sp. nov. Precise analysis of the fossil heads revealed two ancestral mandibular sclerites that can still be found modified in the Recent thrips mouthcone, although in different ways in the two suborders of Thysanoptera, Terebrantia and Tubulifera. Their absence from the left side of the mouthcone of Terebrantia is a morphological apomorphy for this suborder. Studying fossils also allows us to inform the evolution of Thysanoptera in the deep past. Here we show that some of the characters usually thought to be apomorphies for Thysanoptera are instead apomorphies for all Thripida; this is the case for the typical gnathal apparatus but also for the eversible arolium and the fringe hairs. This leads us to redefine the Thysanoptera within the Thripida.

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Introduction

The paraneopteran Thysanoptera is a clade of about 6000 minute extant species (Mound 2012) that feed on pollen grains, plant tissues, fungi and/or small arthropods. Despite this great diversity, all thrips share a ‘punch-and-suck’ way of feeding that is linked to their original gnathal apparatus characterized by two maxillary stylets and only one functional mandible. The presence of two slender, long and independently movable maxillary laciniae, detached from stipes, is the rule in all Paraneoptera, with the exception that they are developed into stylets only in Hemiptera and Thysanoptera, but not in Psocodea (in Grimaldi et al. 2004). However, having only one mandible is particular to Thysanoptera. The developed left mandible is, in most cases, composed of an apical stylet attached to a basal tube-like section. The right mandible degenerates during embryogenesis through programmed cell-death (apoptosis) (Heming 1980; Moritz et al. 2006), and may be absent or reduced to the base of the mandible (Moritz 2006).

Due to their particularities, the head and gnathal apparatus of Thysanoptera have been much studied with regard to their anatomy and development (Reyne 1927; Risler 1957; Davies 1958; Mickoleit 1963; Heming 1978, 1980, 1993; Moritz 1982a, b, 1989). However, these studies could not be fully exploited using phylogenetic analyses due to a lack of knowledge regarding plesiomorphic character states, particularly as the available potential outgroups (Psocodea or Hemiptera) have very different mouthpart structures. Interestingly, some differences in head and gnathal apparatus have been noted within Thysanoptera between two suborders – Tubulifera and Terebrantia – considered since Haliday (1836). Following detailed studies devoted to establishing a clear relationship between these two suborders (for reviews see Mound et al. 1980; Bhatti, 1989; Moritz 1991; Mound & Morris 2007; Buckman et al. 2013), analyses based on cytologic plus ontogenetic characters (Moritz 1991) and the recent molecular phylogeny of Buckman et al. (2013) have supported the monophyly of Terebrantia and a sister relationship between the two suborders. Here we describe an apomorphy of the gnathal apparatus, also supporting the monophyly of Terebrantia, from studies based on new Middle Jurassic Chinese thripidan fossils belonging to the

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sister group of the thysanopteran lineage sensu stricto and so perfectly preserved that their head and gnathal apparatus are clearly interpretable.

The studied Chinese fossils allowed us to define the plasmomorphic states for characters other than those of the head and gnathal apparatus, revealing essential information for defining Thysanoptera within the Thripida. The studied fossils all belong to the superorder Thripida Fallen, 1814. This taxon was defined by Vishniakova (1981) and Zherikhin (2002) on the basis of the wing venation of the extinct Lophioneuridae Tillyard, 1921 (= Zoropsocinae + Lophioneurinae) and the Thysanoptera sensu stricto. However, also on the basis of the wing venation, Nel et al. (2012a) made major changes and divided the Thripida into at least three clades: Panthysanoptera Nel et al., 2012a (the possibly paraphyletic ‘Zoropsocinae’ restored to the Zoropsocidae, plus the Thysanoptera), Lophioneurida Tillyard, 1921 (the paraphyletic ‘Lophioneurinae’ plus the monophyletic Moundthripidae), and Westphalothripidesi-dae Nel et al., 2012a (based on the Carboniferous genus Westphalothripides Nel et al., 2012a). Following this new classification, the studied Chinese fossils are shown to belong to Lophioneurida.

Material and methods

We examined 34 complete fossils from the Middle Jurassic Chinese Inner Mongolian Daohugou beds. The insects are fossilized in a very fine cinerite, with dorsal, ventral and even internal structures visible in many specimens. All specimens are housed in the Nanjing Institute of Geology and Palaeontology (NIGP). We also examined a new complete specimen (JEZ-F-9) of Moundthrips beatificus Nel et al., 2007 from the Lower Cretaceous of Wadi Jezzine, directly beneath the famous Jezzine Falls, in the Jezzine District of Southern Lebanon. Fossils were examined and measured using Olympus SZX7, Olympus (China) Co. and Nikon SMZ 1500, Nikon metrology Europe, N.V. stereomicroscopes or a Leitz direct microscope Leitz, Wetzlar, Germany; photographs were taken using an Olympus digital camera FE 5000. Some specimens of Recent taxa were prepared for scanning electron microscopy (SEM). The specimens were fixed in 70% ethanol, dehydrated in a graded ethanol series (70, 80, 90 and 100%), critical point-dried, and mounted on ionized gold plated brass. The SEM JEOL USA, Inc. images were taken with a JEOL JSM-6390/LGS microscope in the Electron Microscopy Unit of the Colegio de Postgraduados, Mexico.

Systematic palaeontology

**Thripida** Fallen, 1814

**Lophioneurida** Tillyard, 1921

*(sensu Nel et al. 2012a)*

**Genus Lophiosina** gen. nov.

**Type species.** *Lophiosina lini* sp. nov.

**Derivation of name.** Named after Sinica, Latin name for China, and Lophio for Lophioneuridae.

**Diagnosis.** Female last abdominal segments elongate, tergite X short and resembling a narrow ring opened ventrally, its length between one-fifth and one-sixth that of the ventral region of segment IX (Figs 1A, 2F); forewing without vein ScP; vein RA short, only slightly longer than R, i.e. vein R branching at length > one-third and ≤ one-half of R+RA length; vein RA simple; veins RP and M forked; vein M emerging from vein R; vein CuA distally simple; vein CuA emerging nearly perpendicular to fused veins R+M; vein CuP simple; one anal vein, and only one cross-vein between CuA and CuP (Fig. 1B–D); hind wing with vein RA present (Fig. 1E).

**Lophiosina lini** sp. nov.

*(Figs 1, 2)*

**Material.** Holotype: NIGP156160 (♀); paratypes: NIGP156161, NIGP156162, NIGP156163 (all ♀); three other specimens (all ♀).

**Type locality.** Daohugou beds, Inner Mongolia, China.

**Type horizon.** Middle Jurassic, approximately 165 Ma.

**Derivation of name.** The specific name *lini* is given in honour of Prof. Lin Qi-bin, a well-known specialist on fossil insects.

**Diagnosis.** As for genus.

**Description.** Holotype. Body 2247 μm long (Fig. 1B). Head 427 μm long, 225 μm wide at base of inside edges of eyes and 258 μm wide at beginning of mouthcone. Eyes 242 μm long and 79 μm wide. Antenna about 809 μm, with eight segments (Fig. 1F, G); antennal flagellomeres I 213 μm long for right one and 236 μm long for left one, 22 μm wide; at least one plate-like sensillum symmetrically at dorsal extremities on right and left flagellomeres I, one plate-like sensillum at dorsal extremity of right flagellomere II (Fig. 1F–H); also present dorsally on right flagellomere I of another specimen in lateral view (Fig. 11, J). Three ocelli on a prominence at base of cephalic capsule (paratype no. NIGP156161; Fig. 2A). Two large maxillary palps at each side of mouthcone, with four segments, segments III and IV jointed and forming a club (another specimen; Fig. 2B, C). Pronotum 157 μm long and 315 μm wide, with approximately the same quotes as mesonotum, 165 μm long and 315 μm wide. At least one tooth at top inner side of all tibiae (paratype no. NIGP156162 and another specimen; Fig. 2D, E). All tarsi two-segmented. Forewing 1966 μm long and 618 μm wide, ratio length / width = 3; veins RP 506 μm, RA 449 μm, and R 337 μm long. Ovipositor with two thin valvulae, attachment of valvulae with
valvifers highly developed and strong, and teeth poorly developed (Fig. 2F).

Genus **Undacypha** Vishniakova, 1981

**Junior synonyms.** **Undensis** Vishniakova, 1981; **Edgariekia** Jell & Duncan, 1986; **Beipiaopsocus** Hong, 1992 (nomen novum pro **Mesopsocus** Hong, 1983) (Hong 1983, 1992; Jell & Duncan 1986; Ansorge 1996; Jell 2004).

**Type species.** **Undacypha fumida** Vishniakova, 1981; Early Cretaceous, Siberia.

**Other species.** **Undacypha europaea** Ansorge, 1996 (Early Jurassic, Germany), **U. divaricatus** (Hong, 1983) (Jurassic, China), **U. longinervis** (Vishniakova, 1981) (Early Cretaceous, Siberia), **U. una** (Jell & Duncan, 1986) (Early Cretaceous, Australia), **U. bournieri** sp. nov., **U. kreiteri** sp. nov.

**Amended diagnosis.** Hind wing RA short; forewing without ScP; vein RA simple, long, i.e. vein R branching at a length < one-third of R+RA length; veins RP and M forked; vein M emerging from vein R; vein CuA distally simple; vein CuA emerging nearly perpendicular to fused veins R+M; vein CuP simple; one anal vein, and only one cross-vein between CuA and CuP (Figs 3A; 4A, B). Further differences to **Lophiosina** gen. nov. concern the female genitalia in the Daohugou material (**U. bournieri**...
sp. nov. and *U. kreiteri* sp. nov., see below): abdominal segment X long, ventrally only two to three times shorter than abdominal segment IX (Figs 3C, 4C).

**Undacypha bournieri** sp. nov.

(Fig. 3)

**Material.** Holotype: NIGP156164 (♀); paratypes: NIGP156165; NIGP156166 (both ♀); and 6 other specimens (all ♀).

**Type locality.** Daohugou beds, Inner Mongolia, China.

**Type horizon.** Middle Jurassic, approximately 165 Ma.

**Derivation of name.** The specific name *bournieri* is given in honour of Prof. Alexandre Bournier, well-known specialist on Thysanoptera, and whose collection is housed in the MNHN, Paris, France.

**Diagnosis.** Differences with *Undacypha kreiteri* (see below). Ratio of tergites IX/X between 2 and 2.2 (Fig. 3C); foreleg tibia not long, with a ratio tibia/femora between 1.2 and 1 (Fig. 3D, E). Differences with other *Undacypha* species are indicated in Table 1.

**Description.** Holotype. Body 2489 μm long (from base of antennae; Fig. 3D). Head 260 μm long (to base of antennae). Eyes 215 μm long. Antennae not well preserved, appear to be eight-segmented on two other specimens. Pronotum 161 μm long, a little shorter than mesonotum, 182 μm long; pleurite well-separated from tergal pronotum; pleural suture very visible, completely separating epimeron and episternum (paratype NIGP156165; Fig. 3E). At least one tooth at top inner side of foreleg tibia; all tarsi two-segmented (paratype NIGP156165; Fig. 3E). Left forewing 2311 μm long and 645 μm wide; veins RP 804 μm, RA 753 μm, and R 333 μm long. Stout setae very visible on forewing veins (Fig. 3A). Long setae present although very faint on wing margins (Fig. 3A).

**Undacypha kreiteri** sp. nov.

(Fig. 4)

**Material.** Holotype: NIGP156167 (♀) ventral view; paratypes: NIGP156168, NIGP156169 (both ♀); 6 other specimens (all ♀).

**Type locality.** Daohugou beds, Inner Mongolia, China.

**Type horizon.** Middle Jurassic, approximately 165 Ma.

**Derivation of name.** The specific name *kreiteri* is given in honour of Prof. Serge Kreiter thanks to whom Prof. Alexandre Bournier’s Thysanoptera collection is housed in the MNHN, Paris, France.

**Diagnosis.** Differences with *Undacypha bournieri*. Ratio of tergite IX/X between 2.9 and 3.1 (Fig. 4C); foreleg tibia long, with a ratio tibia/femora between 1.5 and 1.7 (Fig. 4D). Differences with other *Undacypha* species are indicated in Table 1.
Description. Holotype (ventral view). Body 3020 μm long from base of antennae (Fig. 4A). Antenna about 1307 μm long, apparently eight-segmented. Pronotum short (paratype NIGP156169; Fig. 4E). Foreleg tibia long, with a ratio tibia/femora of 1.6 (Fig. 4D). Forewing 3076 μm long and 1108 μm wide; veins RP 1077 μm, RA 1046 μm, and R 385 μm long. Ovipositor directed upwards (paratype NIGP156165; Fig 4E).

Discussion. We attribute these new fossils to the Thripida and in particular to Lophioneurida on the basis of their wing venations, i.e. for Thripida: a simple vein ScP when present, vein RA simple, veins RP and M forked, vein M emerging from vein R, vein CuA distally simple (CuA no longer visible as an independent vein in Thysanoptera), vein CuP simple, one anal vein. The character ‘vein CuA simple’ (e.g. not distally forked) is the unique wing venation synapomorphy of Thripida (Nel et al. 2012a, b). Within Thripida, we interpret the origin of the forewing vein CuA in accordance with our previous work (Nel et al. 2012a, b), and observe that the Chinese fossil specimens display the synapomorphy of Lophioneurida with vein CuA emerging nearly perpendicular to fused veins R+M (Nel et al. 2012b).

Vein setae and long hairs are visible on the wing margins of several Chinese fossil specimens but only one such specimen is illustrated here (Fig. 3A). These have never been described in other Lophioneurida. In contrast,
setae on the main veins have been considered as present in Zoropsocidae and Thysanoptera (Vishniakova 1981). Long fringe hairs are movable structures that can be lost during the process of fossilization; they are very delicate, making them difficult to observe, and have not previously been described in Thripida other than Thysanoptera. Although we had not observed these hairs in the previously described specimens of *Moundthrips beatificus* (Nel et al. 2007), they are present in a new specimen shown here (Fig. 5A–C). Fringe hairs were not detailed in our previous publication on *Westphalothripides oudardi* (Nel et al. 2012b) but they are present (Fig. 5D, E).

Vishniakova (1981, fig. 48) figured the Cretaceous lophioneuridan *Jantardachus* with arolia in both deflated and expanded positions. Paratype specimen 503C of *Moundthrips beatificus* also shows deflated or expanded arolia (Fig. 6A–C). Two strongly sclerotized structures are present in the pretarsus, similar to the claws of modern thrips larvae (Fig. 6B–D, F). A sclerotized single structure is present at the base of the claws, in the same position as the unguifer of modern Thysanoptera (Fig. 6B, F). An unguitractor plate extends into an unguitractor apodeme, which continues proximally as a broad and hollow strand towards the base of the tibia (Fig. 6A, D, E). In the apex of the tibia, the unguitractor apodeme enlarges into an apical fork (Fig. 6E). Such a feature can also be observed in larvae of Recent Thysanoptera (Fig. 6F; Heming 1972, fig. 2A). In thysanopteran adults the unguitractor apodeme is also enlarged at this position but not in the same way (Heming 1971, figs 1–5); in Recent Thysanoptera this so-called apodeme ‘head’ has an important function in the retraction mechanism of the arolium and claws (Heming

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**Figure 4.** *Undacypha kreiteri* sp. nov. **A–D**, holotype, NIGP156167, ventral view; **A**, general habitus in ventral view also showing veins of right hind wing; **B**, left forewing; **C**, last abdominal segments showing a ratio of tergites IX/X of about 3; **D**, right foreleg with tibia/femora ratio of about 1.6. **E**, paratype, NIGP156169, general habitus in lateral view showing ovipositor directed upwards. Scale bar: 1 mm (A, E), 500 μm (B, D); 100 μm (C).

**Table 1.** Differences in forewing venation amongst species of *Undacypha*. Character 1: posterior branch of M ending on posterior margin of wing or at tornus (0); on distal margin of wing (1). Character 2: fork of RP opposite apex of RA (0); distal of apex of RA (1). Character 3: fork of M opposite apex of RA (0); distal of apex of RA (1). Character 4: space between branches of M very deep (0); less deep (1). Character 5: wing length 2.5 mm or less (0); more than 2.5 mm long (1).

| Character 1 | Character 2 | Character 3 | Character 4 | Character 5 |
|------------|------------|------------|------------|------------|
| U. fumida  | 0          | 1          | 1          | 1          | 0          |
| U. europaea| 0          | 1          | 1          | 1          | 0          |
| U. divaricatus| 1         | 0          | 0          | 0          | 1          |
| U. longinervis| 1         | 0          | 1          | 0          | 0          |
| U. una     | 0          | 0          | 1          | 0          | 0          |
| U. bournieri| 1          | 0          | 1          | 1          | 0          |
| U. kreiteri| 0          | 1          | 1          | 1          | 1          |
U. longinervis and close to the Mesozoic genus proportions of forewing RA and R. The latter brings them in the shape of the female genitalia and the Lophiosina from Karataocypha only slightly longer than R. However, and from type material of forewing Sc, the same as our fossils from Daohugou. The Undacypha has a short transverse hind wing RA and no (1996) also revised the type material, indicating that cus Vishniakova, 1981 (Cretaceous), i.e. vein RA short, cus Karatavocypha nal description in which the genus name is also written 1981 (Jurassic; note a mistake in the spelling in the origi-
zone showing base of setae at wing margin. Focus on boxed zone showing long setae; arrows indicate two regions where fringe setae are visible; Moundthrips beatificus, focus on boxed m (A), 1 mm (D).

Figure 5. Fringe setae present in Moundthrips beatificus and Westphalothripides oudardi. A–C, Moundthrips beatificus; A, arrows indicate two regions where fringe setae are visible; B, focus on boxed zone showing long setae; C, focus on boxed zone showing base of setae at wing margin. D, E, holotype of Westphalothripides oudardi; D, whole wing with the zone of fringe setae in box; E, focus on boxed zone, arrows indicate parallel setae. Scale bars: 200 μm (A), 1 mm (D).

1971, p. 99). We cannot know whether the enlarged apical fork seen in Moundthrips has the same function. The same zigzag claw structures are present in the Chinese material (see Fig. 6G).

Note that Nel et al. (2007) made an error of interpreta-
tion of the tarsal structures of Moundthrips – they mistook the second tarsomere for the pretarsus, while this insect has two tarsomeres similar to the modern Thysanoptera, with the second tarsomere being longer than first.

Lophiosina gen. nov. shares the same pattern of forewing radial venation with Karataocypha Vishniakova, 1981 (Jurassic; note a mistake in the spelling in the original description in which the genus name is also written Karataocypha, Vishniakova 1981, p. 58) and Jantaradacu cus Vishniakova, 1981 (Cretaceous), i.e. vein RA short, only slightly longer than R. However, Lophiosina differs from Karataocypha in the absence of Sc in the forewing, and from Jantaradacus by the presence of a hind wing RA.

The two other species from Daohugou differ from Lophiosina in the shape of the female genitalia and the proportions of forewing RA and R. The latter brings them close to the Mesozoic genus Undacypha Vishniakova, 1981, with which Undensis, Edgariekia and Beipiaopso- cus (Ansome 1996) were later synonymized. Ansome (1996) also revised the type material, indicating that Undacypha has a short transverse hind wing RA and no forewing Sc, the same as our fossils from Daohugou. The type material of U. fumida, U. europaea, U. divaricatus, U. longinervis and U. una are all in poor condition, difficult to compare with the Daohugou fossils. In particular, their female genital structures are poorly preserved or not preserved at all. Only the wings can be compared to those of our fossils (Table 1), allowing us to define the two species described herein.

For the remainder of the body, the new Chinese fossils exhibit the general habitus of previously described Lophioneurida and Zoropsocidae (Vishniakova 1981; Zherikhin 2002; Nel et al. 2012a).

Two other points worth noting are that no Zoropsocidae have been found in this collection, and also that all speci-
mens examined are female. In Recent Thysanoptera, females often predominate in natural populations. Different reasons have been evoked for this: in many species the reproduction is parthenogenetic, in some species fewer males occur when it is warmer, in others males are flight-
less, and also females often live longer than males, show broader dispersion, and have periods of great abundance (Lewis 1973; Moritz 2006).

Head of Lophiosina lini

The cephalic capsule is schematically a little smaller than a quarter of a sphere (Fig. 7A, B), poorly developed in the posterior part behind the proximal limits of the two large protruding compound eyes situated laterally (Figs 1B, 2A, 7A). In the anterior section, the antennal bases are well separated, situated in an inner position relative to the eyes, and also very close to the mouthparts (Figs 1B, F, 2A, 7A). The antennae are filiform, with the scape inserted in a large membranous socket (Figs 1F, 7A); the pedicel is longer than the scape but distinctly shorter than the first flagellomere, the flagellum is very elongate with all flagellomeres elongate and rather similar in diameter; flagellomere I is the longest, those following become progressively shorter; the last flagellomeres are clearly distinct from one another (Fig. 1F, G). The gnathal complex is cone-shaped, in a hypognathous, or slightly prognathous, position, clearly visible on non-deformed speci-
mens fossilized in lateral view (Fig. 7A, B).

In order to describe the gnathal complex more precisely and to interpret the nature of the structures of the head of Lophiosina lini, we compared the extended heads of the specimens of L. lini fossilized in dorsal view showing the dorsal parts of the mouthcone, with ventral views of the heads of extant Thysanoptera. In these latter insects, the dorsal view of the mouthcone is visible in this position due to its hypo- to opisthognathous position (Fig. 7C, D).

In Lophiosina lini, the following sclerotized pieces rep-

1. The epipharyngial sclerite with the epipharynx apodeme and the hypopharyngeal sclerite; these are identical in L. lini and in modern Thysanoptera and
form the respective upper and lower sclerites of the cibarium or ‘sucking pump’ (Fig. 8A, B; Online Supplementary Material). The upper epipharyngial sclerite is an elastic roof that can be drawn upwards by contraction of dilator muscles that attach to the epipharyngial sclerotized apodeme, creating a vacuum that allows fluids to be sucked up.

2. The structure named ‘Tragarm des Pharynx’ by Reyne (1927) is another landmark. At the right side of the thysanopteran mouthcone, the absence of the mandibular stylet leads to the sclerotization of the adjacent edges of the labrum and maxillary stipites which finally fuse to form a direct link to the lateral hypopharyngial margin of the cibarium (Reyne 1927). All of these structures are heavily sclerotized in Thysanoptera (Fig. 8A) and are also clearly visible in *L. lini* (Fig. 8B; Online Supplementary Material).

3. On the opposite side, to the left of the thysanopteran mouthcone, the ‘Tragarm des Pharynx’ does not exist because the mandible is normally developed and the edges of the labrum and maxillary stipites join with the epipharynx and the hypopharynx to form a mandibular guide for the long stylet-like part of the mandible (Fig. 8C). In *L. lini* the left mandibular guide is clearly visible, and without doubt the ‘Tragarm des Pharynx’ structure is not present on the left side (Fig. 8B; Online Supplementary Material).

Due to the landmarks described above, we can locate the labrum on the head of *L. lini* (Fig. 9B) that covers the region of the cibarium. At the proximal limit of the labrum is a membranous region that separates it from the frons and corresponds to the thysanopteran anteclypeus (Fig. 9). In this membranous area two triangular sclerites
occupy the left and right sides (Fig. 9). Because of their position between the labrum and the frons and within the membranous region, they correspond to the thysanopteran mandibular sclerites (see Discussion). The clypeofrons is the region situated between the antennal bases and extending backward to the vertex. The vertex is the most dorsal and proximal region of the cephalic capsule and it usually bears the ocelli. In \textit{L. lini} the three ocelli are situated close to the occipital ridge (Fig. 2A). The maxillary palps emerge at the lateroproximal edges of the labrum (Fig. 9B) and the labial palps appear faintly in the distal region of the mouthcone in Fig. 9B (see also Online Supplementary Material).

**Discussion**

**Interpretation of the head of \textit{Lophiosina lini}**

**General anatomy.** Major differences distinguish the head of \textit{Lophiosina lini} from the extant Thysanoptera. The lophioneuridan \textit{L. lini} has a cephalic capsule a little smaller than a quarter of a sphere (Fig. 7A, B), while Thysanoptera have a large cephalic capsule shaped into a sugarloaf with a forward-directed vertex (Fig. 7C, D). The two antennae are wide apart in \textit{L. lini} and close to the base of the mouthcone, whereas in thrips they are situated at the top of the sugarloaf, very close together in an inner position relative to the eyes (compare Fig. 7A, B with 7C, D), away from the base of the mouthcone. The morphologically anterior face of \textit{L. lini} is in quite a normal anterior position, whereas it is anatomically in a ventral position in Thysanoptera. The larger clypeofrons of Thysanoptera has pushed the mouthcone ventrally, more or less backward in a hypo- to opisthognathous position, while the latter is hypognathous or slightly prognathous in \textit{L. lini}. The maxillary palps of \textit{L. lini} are large and club-shaped, which is unknown in Thysanoptera.

**Mandibles and mouthcone.** Despite the external dissimilarities, the heads of \textit{Lophiosina lini} and Thysanoptera share a particular cone-shaped gnathal complex. Moreover, the mouthcone of \textit{L. lini} contains some sclerotized and therefore very visible features characteristic of the Thysanoptera (see Fig. 8; Online Supplementary Material): (1) the sclerites forming the cibarium are easily visible and identical to those of Recent taxa; (2) the right side of the mouthcone also shows the ‘Tragarm des Pharynx’ typical of thrips, i.e. the sclerotized link between the cibarium and the labrum ridge, itself fused with the maxillary stipites (Reyne 1927); (3) the left mandibular guide is present in \textit{L. lini} while no such structure is present on the right side of the mouthcone.
In Recent thrips, the specialized ‘Tragarm des Pharynx’ and the absence of the right mandibular guide are obviously linked to the absence of the right mandible, while the left mandibular guide is linked to the presence of a stylet-like left mandible (Moritz 1982a, 1989). The presence of the same structures in Lophiosina lini strongly supports the hypothesis that its left mandible is stylet-like and its right mandible is absent (Fig. 8; Online Supplementary Material). The asymmetrical mouthcone that characterizes Thysanoptera is therefore present in L. lini. We previously deduced that Lophioneurida and Panthysanoptera share this mandibular asymmetry by applying this attribute to thripidan phylogeny, and also by studying the Cretaceous Moundthrips which has no right mandible, a stylet-like left mandible and two long maxillary stylets (Nel et al. 2007, 2012b).

Anteclypeus. Between the mouthcone and the cephalic capsule, a membranous anteclypeus is present in Lophiosina lini as it is in Thysanoptera (Fig. 9). Inside this membranous region, two triangular sclerites occupy the left and right halves in L. lini, just proximal to the labrum (Fig. 9B; Online Supplementary Material). These structures have never been described in this configuration for modern Thysanoptera and their homologues have yet to be determined. A very similar arrangement of a triangular sclerotized structure that lies in exactly the same position at the right side of the membranous anteclypeus is present in some families of Terebrantia and Tubulifera (Figs 9A, 10). Such a triangular sclerite has already been figured fused with the remnant of the right mandible in Aeolothrips fasciatus (L., 1758) (Mickoleit 1963) and A. intermedius Bagnall, 1934 (Fig. 10A, modified from Moritz 1982a), but never named; it is also clearly visible in Aeolothrips romanruizi Ruiz-De La Cruz et al., 2013 (Fig. 10B, C), in the Melanthripidae Cranothrips vesper Mound, 1972 (Fig. 9A), and also in the Heterothripidae Heterothrips borinquen Hood, 1915 (Fig. 10D). In Tubulifera such a structure is seen in many species at the right side of the mouthcone (Bhatti 1998; Fig. 10E, F). Using comparative anatomy, the position of the right triangular sclerite in L. lini and the Thysanoptera indicates an identity of a similar nature.

In Lophiosina lini, the left and right triangular sclerites are symmetrically disposed. In Terebrantia, this structure does not exist at the left side of the mouthcone, which has a normally developed mandible (Fig. 10A–D). However, the situation is different in Tubulifera. At the left side of the mouthcone of Tubulifera we can observe a sclerotized structure that is not triangular but lies in the exact position of the triangular sclerites of L. lini (Fig. 10E, F), i.e. in

**Figure 9.** Comparison of the structure of the head of Lophiosina lini sp. nov. with Recent Thysanoptera. A, head of Cranothrips vesper in ventral view. B, head of Lophiosina lini sp. nov. in dorsal view. Arrows without captions indicate mandibular sclerites.

**Figure 10.** Detailed structure of mandibular sclerites in Thysanoptera. A, drawing after Moritz (1982a) of ventral aspect of head in Aeolothrips intermedius (a lateral view is in Fig. 7D). B, C, ventral views of head of Aeolothrips romanruizi; B, under optical microscopy; C, under SEM. D, ventral view of head of Heterothrips borinquen. E, F, ventral views of head of Preeriella jacottia (lateral view is in Fig. 7C); E, drawing; F, optical microscopy. Scale bars: 50 μm.
the anteclypeus proximally to the labrum and sometimes in a proximal left indentation of the labrum, also figured in the literature (Reyne 1927; Mickoleit 1963; Heming 1993; Bhatti 1998). We surmise that the position of these left sclerites in L. lini and Tubulifera also indicates their identity, i.e. the left triangular sclerite of L. lini is still present in Tubulifera but absent in Terebrantia. This left tubuliferan sclerotized structure has been named ‘mandibular sclerite’ by Bhatti (1998) and we propose to keep this denomination for the triangular structures discovered in Lophiosina and found also in Recent Thysanoptera. Although we use the denomination ‘mandibular sclerite’ of Bhatti (1998), we do not think this sclerotized structure is part of the mandible. Rather, we follow Reyne (1927) who discussed the fact that the left mandibular sclerite appearing on the surface in Tubulifera seemed to have integrated foreign elements not formed by the mandible histoblast. Hence we hypothesize that the left mandibular sclerite in Tubulifera is an independent structure fused to the base of the left mandible. Fusion of mandibular sclerite with mandible seems also to be the case for the right mandibular sclerite of Terebrantia because it is figured fused with, but distinct from, the right mandibular remnant by Mickoleit (1963) and Moritz (1982a).

The origin of the mandibular sclerites remains to be determined. However, the triangular mandibular sclerites of Thripida may lend support to an existing hypothesis of a composite origin for the anteclypeus. Indeed Bitsch (1973) hypothesized that the median part of the insect anteclypeus is of clypeal origin while the lateral parts (paracylpeus) are of genal origin. This hypothesis is linked to the dicondylar mandible of insects. While the secondary condyle is traditionally considered to be on the lateral part of the insect clypeus, Bitsch (1973) made the assumption that this lateral part would be of a different origin than the rest of the clypeus, more precisely that it would be originating from a mandibular subgenal lobe. In the case of Aeolothrips (Terebrantia), the right mandibular sclerite is laterally fused to the anteclypeus but is distinctively sclerotized rather than being membranous, as is the case for the anteclypeus (Fig. 10C). The distinctive anteclypeus of Thripida, with a membranous median part and two lateral mandibular sclerites to which the mandibles are attached, thus supports Bitsch’s hypothesis of a composite origin of the insects anteclypeus.

**Apomorphies for Terebrantia**

The external presence of mandibular sclerites of the mouthcone must be considered as a plesiomorphy for Thysanoptera within Thripida as they are present in Thysanoptera and Lophiosina lini. This suggests that the presence of the left mandibular sclerite at the surface of the head of many Tubulifera is indeed a plesiomorphy, as stated by Bhatti (1998). Bhatti (1998) also showed that its ‘absence’ in some Tubulifera is probably not real but is due to an amalgamation of the labromaxillary complex (including this sclerite) with the cranium and must therefore be considered as a derived condition. Hence the character ‘absence of the left mandibular sclerite’ shared by all Terebrantia is a synapomorphy of this group. This morphological apomorphy supporting the monophyly of Terebrantia also supports the currently available molecular phylogeny (Buckman et al. 2013), and adds to the apomorphies of Terebrantia, which are defined on cytological and ontogenetic data (Fig. 11): sperm without acrosome (Paccagnini et al. 2010), and the embryo with katatrepsis without rotation (Moritz 1988).

**Apomorphies for Thysanoptera within Thripida and Paraneoptera**

Thysanoptera are generally distinguished from the other Paraneoptera by the following characters: single, unpaired left mandibular stylet; an eversible arolium; structural sclerites at the base of the forewing; reduction of abdominal spiracles to two pairs on segments one and eight; neo-panoistic ovarioles; and tri-flagellated early spermatid cell. These characters are irrespective of the chosen outgroup, Psocoptera or Hemiptera (Mound et al. 1980; Moritz 1991, 2006; Bhatti 1998; Yoshizawa & Saigusa 2001; Mound & Morris 2007; Paccagnini et al. 2010). In actual fact, it is not legitimate to compare Thysanoptera directly with the other Paraneoptera, but better to give apomorphies for Thripida within Paraneoptera and for Thysanoptera within Thripida (Fig. 11).

We demonstrate here that all Thripida share an asymmetrical mouthcone, consequently with a single, unpaired left mandibular stylet (inference obtained by morpho-anatomical comparison between Recent and fossil taxa). Previously we showed by phylogenetic inference that they also have piercing lacinal stylets, following the direct observation of these in the fossil Moundthrips (Nel et al. 2012b). Vishniakova (1981, fig. 48) has shown that the Cretaceous thripidan Jantardachus had eversible arolium. Identical observations in the paratype of Moundthrips confirm by phylogenetic inference that lophioneuridans have an eversible arolium (Fig. 6). We also show here that all Thripida share the long fringe hairs (a character independently evolved in many small flying insects, e.g. chalcidoid wasps, ptiliid beetles). We can also add the character ‘vein CuA without branches (CuA not visible in Thysanoptera) in the forewing’ from previous work (Nel et al. 2012b). We have previously demonstrated that the character ‘vein CuA simple’ (e.g. not distally forked) is an important wing venation synapomorphy of Thripida (Nel et al. 2012a, b). Nevertheless, all characters not linked to the forewing are of unknown state in the most basal thripidan lineage Westphalothripidesidae. From the characters listed above for Thysanoptera, only some
apomorphies remain and concern the ovarioles, the sperm, and the base of the wing. From the present study we can now deduce new characters on the body. The antennae of Thysanoptera are very close together and both antennal sulci encounter the median almost together, while in Lophiosina, Undacypa, as well as in other fossil Panthysanoptera and Lophioneurida, which have been figured previously (Vishniakova 1981; Zherikhin 2002; Nel et al. 2012a), they are widely separated. The pronotum of Thysanoptera is broad and always as long as or longer than the mesonotum; it is much larger than in Lophiosina, Undacypa, as well as in other Panthysanoptera and Lophioneurida which have been figured previously (Vishniakova 1981; Zherikhin 2002; Nel et al. 2012a). From previous studies (Nel et al. 2012b), we can add some thysanopteran apomorphies concerning the forewing, namely ‘complete loss of an independent vein CuA’, and ‘vein RA reduced and resembling a cross-vein’. However, in one previous study the fringe setae were also validated as being an apomorphy for true Thysanoptera (Nel et al. 2012b), though we have shown here that this is not the case.

Conclusions

Because of the similarities in mouth pieces within Thripida (except perhaps Westphalothripidesidae) and the known sucking habit of all Thysanoptera, we can infer a sucking feeding habit for Lophioneurida and Zoropsocidae and thereby confirm the assumption of Zherikhin (2002). However, major differences in head and even pronotum have occurred during the evolution to Thysanoptera. In Thysanoptera, the clypeal region is very developed and represents the main part of the ventral side of the head (Davies 1958). This feature is frequent in Recent sucking insects because the clypeal region is the part to which the dilator muscles of the sucking pump are attached. The pronotum has also been modified in Thysanoptera, being larger than that of Lophioneurida, and this can also be linked to feeding. Indeed, in thrips the prothorax plus head constitute a functional unit involved in punching and the forelegs afford a tripod-like structure with the mouthcone (Moritz 1989). All of these characters have appeared either as adaptations in the evolution of the usual feeding source of thrips, or as adaptations to feeding on new food source(s). Grinfel’d (1959) hypothesized that the particular asymmetrical mouthparts of Thysanoptera evolved as an adaptation to sucking pollen, assuming that a single mandible must be more efficient for piercing such small and resistant food. Because Thripida share the same piercing mouth pieces lacking the right mandible (although unknown in Westphalothripidesidae), the hypothesis of Grinfel’d may in fact be valid for Thripida (with or without Westphalothripidesidae) rather than Thysanoptera. Pollen is a nutritious food source but is mostly exploited by insects in the form of whole grains. Piercing the grain is known for insects of the order Thysanoptera. Pollen is a nutritious food source but is mostly exploited by insects in the form of whole grains. Piercing the grain is known for insects of the order Thysanoptera. Pollen is a nutritious food source but is mostly exploited by insects in the form of whole grains. Piercing the grain is known for insects of the order Thysanoptera. Pollen is a nutritious food source but is mostly exploited by insects in the form of whole grains. Piercing the grain is known for insects of the order Thysanoptera. Pollen is a nutritious food source but is mostly exploited by insects in the form of whole grains.

Figure 11. Phylogenetic hypothesis based on morphology. Apomorphies are as follows (see Discussion for explanations). Not represented on the graph are paraneopteran apomorphies: legs with three or fewer tarsomeres; cerri lost; ganglia in abdomen fused into one large mass; maxillary laciniae slender, long, detached from stipites; postclypeus large, with large cibarial dilator muscles (Grimaldi & Engel 2005). Thripida: 1, left mandibular stylet, right one lost; 2, piercing lacinial stylets; 3, pretarsus with eversible arolium; 4, claws reduced in adults; 5, wings with fringe of long setae; 6, forewing with CuA simple, no ‘aerola postica’ (CuA not visible in Thysanoptera). Westphalothripidesidae: 7, forewing vein CuA with no sigmoid curve and ‘aerola postica’ (CuA not visible in Thysanoptera). Terebrantia: 24, reduced tentorium; 25, ovipositor katatrepsis without rotation; 23, absence of left mandibular sclerites at the base of the forewing; 22, piercing lacinial stylets; 19, epiproct and paraproct not differentiated; 20, wings at rest overlapping along the dorsum. Terebrantia: 21, sperm structure without acrosome; 22, embryo with katatrepsis without rotation; 23, absence of left mandibular sclerite. Inside Terebrantia: 24, reduced tentorium; 25, ovipositor straight or curved downwards; 26, forewing: emergence of vein M distally to fork RA-RP.
wells appear capable of resisting considerable force and this may have driven natural selection to modify the mouthparts of these insects to improve the efficiency of their piercing ability.

There is some indirect evidence for pierced plant spores from Permian noeggerathialean cones; Wang et al. (2009) attributed the piercings to Thripida as no other Permian group of insects is known to have a similar mouthpart adaptation. These pierced spores have a circular hole 40–60 μm in diameter, while Recent thrips make holes 2–10 μm in diameter (Heming 1993), but some Palaeozoic Thripida are seven to 13 times as large as Recent thrips, compatible with the sizes observed in these Permian holes. Thysanoptera appeared in the fossil record during the Triassic, with pronotum, wings, antennae, and in particular the head modified in several ways compared to their ancestors, although to what extent it was in response to a modified diet is unclear. At the present day, feeding on pollen is common for numerous species of Thysanoptera (Kirk 1984), but feeding on leaf and flower tissues, or fungi, is also very frequent. Mound et al. (1980) suggested that Thysanoptera were primitively fungivorous, and in this hypothesis eating fungi may have been the selective pressure. However, it is also known that the appearance of Thysanoptera in the Triassic corresponds with the appearance and diversification of plants with smooth and broad leaves; the oldest broad angiosperm-like fossil leaves are known from the same outcrop as Triassothrips (Cornet 1989, 1993). These may have afforded Thripida another nutritional resource and one may also consider the possibility that true Thysanoptera evolved alongside such plants and later with true angiosperms.

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Supplemental material

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