

# On the systematic position of a highly derived amphiesmenopteran insect from Burmese amber (Insecta, Amphiesmenoptera)

Wolfram Mey,<sup>1\*</sup> Wilfried Wichard,<sup>2</sup> Emma Ross<sup>3</sup> and Andrew Ross<sup>3</sup>

<sup>1</sup> Museum für Naturkunde, Leibniz Institute of Evolution and Biodiversity Research at the Humboldt University, Invalidenstrasse 43, D-10115 Berlin, Germany.

Email: wolfram.mey@mfn-berlin.de

<sup>2</sup> University of Koeln, Institute of Biology, Gronewaldstrasse 2, D-50931 Koeln, Germany.

Email: Wichard@uni-koeln.de

<sup>3</sup> Department of Natural Sciences, National Museum of Scotland, Edinburgh, EH1 1JF, UK,

Email: A.Ross@nms.ac.uk

\*Corresponding author

**ABSTRACT:** A small fossil insect with scales on the wings and body was identified as a representative of Amphiesmenoptera from Burmese amber. The species is introduced here as *Tarachocelis microlepidopterella* (†). The insect is described in detail, and photos and line drawings are provided for wing venation, head, mouthparts, scales, legs and abdomen. All characters shared with primitive Lepidoptera and Trichoptera are symplesiomorphies or groundplan traits of Amphiesmenoptera. In addition, the Burmese fossil has a number of remarkable autapomorphies, giving it an appearance that deviates clearly from known families of Lepidoptera and Trichoptera. The species, representing a family of its own, Tarachocelidae, is considered a separate and unique taxon in the stem-group of Amphiesmenoptera and is provisionally placed as Amphiesmenoptera *incertae sedis*.\*

\*NB: See Note Added in Proof (Section 4).

**KEY WORDS:** Cretaceous, Lepidoptera, *microlepidopterella*, phylogeny, stem-group, *Tarachocelidae*, *Tarachocelis*, taxonomy, Trichoptera.

Amphiesmenoptera combines the orders Trichoptera and Lepidoptera. Dating analyses based on molecular chronograms across many Lepidoptera groups have yielded different results for the early divergence in Lepidoptera, spanning a period from 215 Mya (late Triassic) to 160 Mya (late Jurassic) (Regier *et al.* 2015). Importantly, the origin or time of the basal split of both orders cannot be determined with any better precision from the fossil record. The descriptions of Mesozoic fossils are almost always based on wing venation, a character insufficient to discriminate between ancestral Trichoptera and Lepidoptera. The oldest Lepidoptera species is thought to be *Archaeolepis mane* Whalley, 1985 from the Lower Lias (Sinemurian) of Dorset, England (Archaeolepididae) and two species from the Upper Lias (Toarcian) of Grimmen, NE Germany. The latter were tentatively assigned to Micropterigidae, suborder Zeugloptera (Ansorge 2002, 2003). The assignment of these Early Jurassic species to Lepidoptera is based solely on the observation of wing scales. In the absence of any other distinguishing characters, the presence of scales is regarded as the principal trait that defines Lepidoptera and separates the group from the remaining Amphiesmenoptera, including Trichoptera (Rasnitsyn & Quicke 2002).

The Burmese (= Myanmar) Amber Lepidoptera are known today from a few specimens preserved in collections from Europe and North America (Grimaldi *et al.* 2002; Grimaldi & Engel 2005; Ross *et al.* 2010; Sohn *et al.* 2012). However, only a single species has hitherto been formally described. This is *Micropterix pervetus* Cockerell, 1919, placed originally in Micropterigidae, but later transferred by Kristensen & Skalski (1998) to *incertae sedis*. This assignment appears to be unjustified in the light of new research results (Gibbs 2010; Gibbs & Kristensen 2011; Mey 2011).

Trichoptera species also are rare elements in Burmese amber (Ross *et al.* 2010). Botosaneanu (1981) discovered the first species and described it as *Burminoptila bemeneha* in the family Hydroptilidae. An additional five species were described by Wichard & Poinar (2005), Wichard *et al.* (2011) and Wichard & Wang (2016): *Palerasnitsynus ohlhoffi* (Psychomyiidae); *Wormaldia myanmari*; *W. cretacea*; *W. resina* (Philopotamidae); and *Neureclipsis burmanica* (Polycentropodidae).

The present specimen from Burmese amber is relatively well preserved and allows the examination of important character complexes, which are not observable in compression fossils. The following description concentrates on characters which have diagnostic value and, thus, should provide the basis for a correct placement of the species into the contemporary system of Amphiesmenoptera. As a result, the species could be assigned neither to Trichoptera nor to Lepidoptera. Also, no closer affinity could be found to any of the extinct stem-group lineages of Amphiesmenoptera. The fossil is provisionally treated as Amphiesmenoptera *incertae sedis*.

## 1. Taxonomy

Amphiesmenoptera *incertae sedis*

Tarachocelidae Mey, Wichard, Müller & Wang, 2017 (†)  
(Figs 1–2)

**Type genus.** *Tarachocelis* Mey, Wichard, Müller & Wang, 2017.

**Description.** Small adult. Head elongate, mouthparts slightly hypognathous, vertex without setal warts, eyes oval, ocelli absent, antenna filiform, galea of maxilla unmodified, maxillary





**Figure 1** *Tarachocelis microlepidopterella*. Male in lateral view, forewing length 3 mm. Scale bar = 1 mm.

and labial palpi three-segmented with labial palpi longer than the former, haustellum or proboscis absent; fore- and hindwings of nearly the same length with rounded apices, pterostigma absent, venation homoneurous concerning branching of R and M veins, three radial and a single median vein present, forewing Sc with apical fork (Sc1 and Sc2), male with presumed androconial scales on R and M veins on both wings, spindle shaped scales and piliform scales without perforations on the wing membrane; hindwing without jugal lobe; epiphysis absent, spurs and additional spines absent; sternum of abdominal segment V with a pair of lateral processes probably serving as elevated openings for internal scent glands (Abbreviation of veins follows Scoble (1992)).

**Diagnosis.** Tarachocelidae can be separated from other non-glossatan, extant families of Lepidoptera by the presence of very small maxillary palpi composed of three segments, and by the presence of three-segmented labial palpi. The wing venation is clearly different from extinct and extant Lepidoptera families. In the fore- and hindwings, the radial veins consist of three branches; the medial vein (M) is unbranched and the postcubitus (Cu2) is basally fused with Cu1 and absent in the hindwing. In contrast, the basal clades of Lepidoptera have five radial veins, at least three median veins (except in Aenigmatineidae with M undivided in the forewing but divided in the hindwing (Kristensen *et al.* 2014)) and postcubitus present. In addition, the presumed androconial scales on the radial and medial veins on both wings, as in Tarachocelidae, are unknown in other extant families of ancestral Lepidoptera.

The family lacks ocelli, epiphysis and spurs on all legs, which are considered to be secondarily lost, if a closer relationship to Lepidoptera is taken into account. These three character states also separate Tarachocelidae from the other three non-glossatan families.

The absence of spurs and ocelli also distinguish the family from primitive and derived Trichoptera families. Additional distinguishing characters are the minute maxillary palpi, the distinctive wing venation and the presence of scales on the wings, thorax and head.

*Tarachocelis* Mey, Wichard, Müller & Wang, 2017(†)

**Type species.** *T. microlepidopterella* Mey, Wichard, Müller & Wang, 2017

**Gender.** Feminine.

**Etymology.** The name is derived from the Greek *ταραχή?* (tarachi), fluttering, which concerns the presumed flight of the adults.

**Description.** As described for the family.

*Tarachocelis microlepidopterella* Mey, Wichard, Müller & Wang, 2017 (†)  
(Plate 1)

Ross *et al.* 2010, p. 216, fig. 4C (as species of Trichoptera, Leptoceridae).

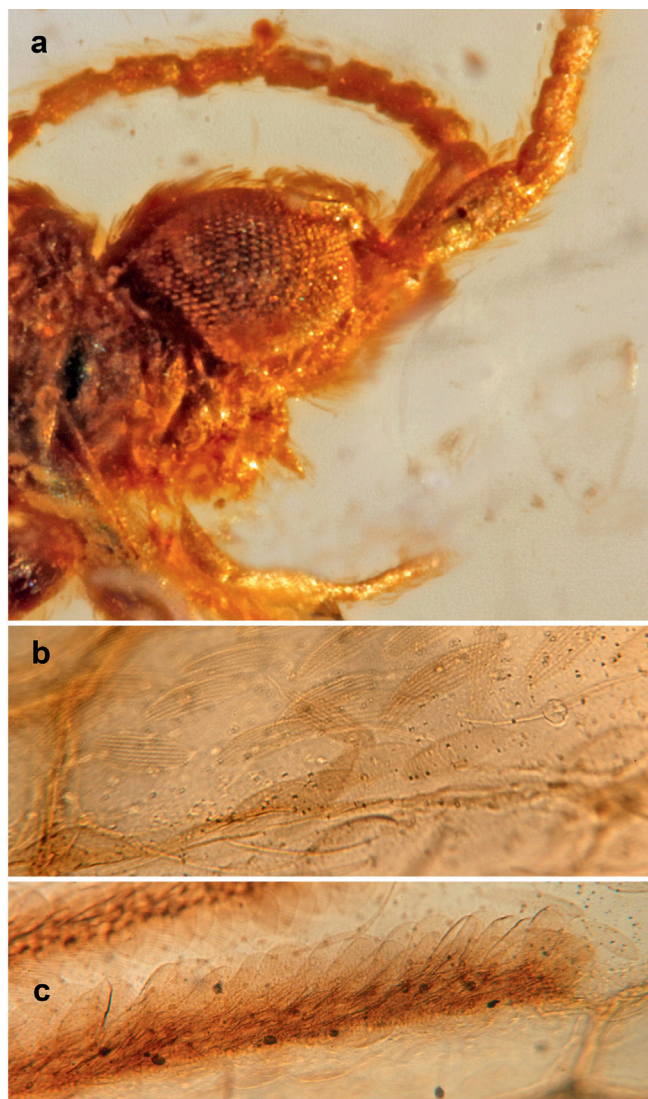
**Material.** Holotype male, Burmese Amber, S. Anderson Coll. (No. 47), Reg. No. G2010.20.36, National Museums Scotland, Edinburgh.

**Preservation.** The fossil is embedded in a rectangular block cut out from a larger amber piece. The adult insect is nearly completely preserved and clearly visible from a lateral view. The hindwings are partly covered by the somewhat distorted forewings. Some of the legs or parts of legs are missing. The head, thorax and forelegs show signs of decomposition or fragmentation.

**Etymology.** The name refers to the general similarity of the insect to various microlepidopteran species.

**Description.** Length of forewing 3 mm, length of hindwing 2.9 mm; head elongate and somewhat flattened dorsoventrally, with erect scales on vertex and frons; eyes oval, not rounded, hemispherical, ocelli absent; scape and pedicel together as long as eye diameter, scaled dorsally, 23 barrel-shaped flagellomeres present, basal segments (1–8) with scales, subsequent segments unscaled, each flagellomere with short cilia, evenly distributed over the entire length; maxillary palpi very short, three-segmented, of equal length, ciliated, last segment pointed; labial palpi





**Figure 2** *Tarachocelis microlepidopterella*: (a) head in lateral view; (b) piliform scales on the wing membrane; (c) androconial scales on R and M veins.

long, three-segmented, all segments of about equal length, with long hairs, terminal segment with pointed apex; mandibles not visible; labrum large, produced medially as a quadroangular and voluminous organ, not set as a prolongation of the clypeus but protruding by nearly 30° from the clypeus; pilifers absent; maxilla minus maxillary palpi with two terminal, membranous lobes (galea and lacinia?); haustellum, if present, very small.

Foretibia without epiphysis and spurs, spurs and smaller spines absent on all tibiae, tarsal segments with terminal pair of ventral bristles; pretarsus with slender ungues and stalked arolium, pulvilli absent, pseudempodium not visible. Wings with rounded apices, forewings sparsely scaled in costal and discoidal area, not arranged in two layers, small jugum present, folded under base of wing (see Plate 1, fig. 4 for wing venation); forewing with Sc a thin vein branched apically and with humeral (h) and subapical cross-vein sc-r; radius divided into two, thick veins, bearing broad, triangular, putative androconial scales on the underside of the wing, upper R vein unbranched, lower R vein with two terminal branches (R2 + 3 and R4 + 5), ending on wing margin before and at apex respectively; cross-veins cu-r1 and r1-r2 + 3 present, the latter closes an elongate, triangular, discoidal cell (Trichoptera terminology), or accessory cell (Lepidoptera terminology); median vein undivided, basal stem with broad, triangular scales on the underside;

cross-vein m-cula present; basal part of Cu2 fused with Cu1a + b; anal veins (A1 and A2) apparently with basal loop. Hindwing venation similar to that of forewing, but broad, triangular scales on upper sides of R1, R2 + 3 + 4 + 5 and M veins; Cu2 absent, three anal veins present, not looping at base.

Abdomen unscaled, sterna IV to V with elongate appendages directed dorsad, forming apically broad processes surpassing the dorsal surface of the abdomen and probably serving as openings of abdominal glands in sternum V. Male genitalia forming a wide cavity between a protruding, process on dorsal side (segment IX or X) and a similar process (segment IX) on ventral side, flat and rounded superior appendages present, inferior appendages or valvae not visible, if present, retracted into segment IX.

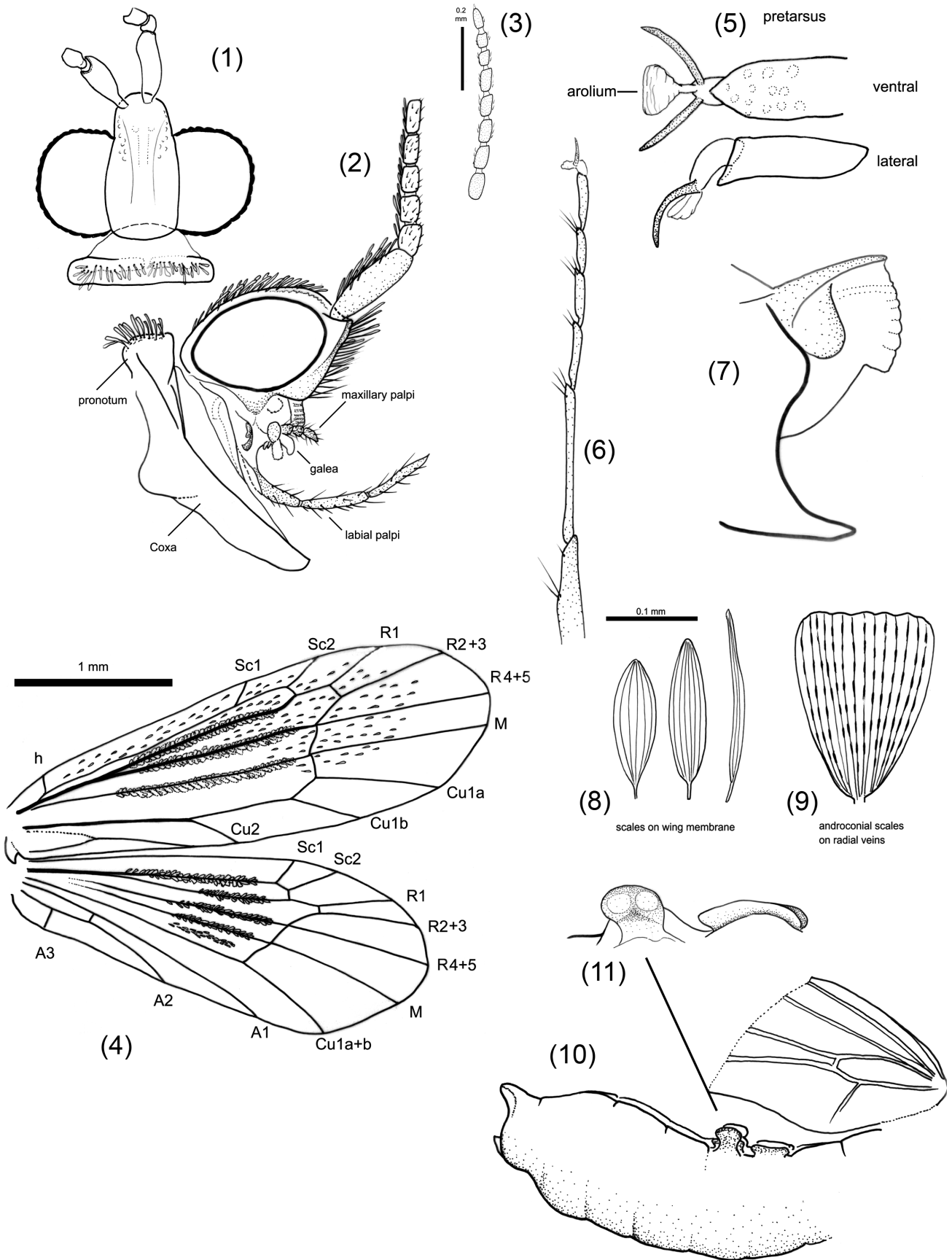
## 2. Systematic position

The species represents a hitherto unknown evolutionary lineage which is associated with the Amphiesmenoptera. Autapomorphies of the Amphiesmenoptera are described in Kristensen (1984). He listed 21 characters which are the synapomorphies of the Trichoptera + Lepidoptera. Of these, 11 morphological features are applicable to well-preserved fossil imagines. The following five characters are exhibited by the species:

- lower posterior corner of laterocervicale produced towards the prosternum;
- wings with extensive covering of setae/scales;
- anal veins of the forewings apparently upwardly looping;
- presence of a paired gland opening on sternum V;
- male genital segment IX forming a closed ring.

The most striking apomorphy of Lepidoptera is the dense covering of the wings with small, flattened scales. In contrast, Trichoptera wings such as Lepidostomatidae, Calocidae and Leptoceridae. It therefore seems likely that scales have arisen independently in these two orders (Huxley & Barnard 1988). The basal-most families of Trichoptera (Spicipalpia) do not have scales on the wing membrane, at least not exceeding the minute scales forming androconial organs present in species of Hydroptilidae. The scales of Lepidoptera are very diverse in morphology and in their arrangement on the wings (Simonsen 2001). The non-glossatan families have scales without perforations, which is probably the plesiomorphic character state in Lepidoptera. The scales of *Tarachocelis microlepidopterella* are also without visible pores. The scales are not confined to the wings, but are also dispersed on the thorax, head and antennae. This extensive covering with scales would suggest that *T. microlepidopterella* is more likely to belong to Lepidoptera rather than to Trichoptera. Also, the maxillary and labial palpi of the mouthparts are more similar to those of Lepidoptera, the former being much smaller than the latter. Nevertheless, the primitive Lepidoptera have long, five-segmented maxillary palpi; but in all more advanced groups, these palpi become reduced or disappear entirely. The size decrease of the palpi appears to be the result of an intrinsic, general tendency in Lepidoptera. In Trichoptera, the maxillary palpi are always the prominent appendages of the mouthparts, whereas the labial palpi remain small.

In Lepidoptera, the Micropterigidae, together with the extant Agathiphagidae and Heterobathmiidae, are the basal-most groups of extant Lepidoptera (= non-glossatan moths). Their systematic position is based on several apomorphies and groundplan characters, which were documented morphologically in detail by Kristensen (1984, 1998, 2003) and Kristensen & Nielsen (1979, 1982). In a recent molecular phylogeny for the non-ditrysian lineages of Lepidoptera, their basal-most



**Plate 1** Morphological characters of *Tarachocelis microlepidopterella*: (1) head, dorsal view; (2) head and prothorax, lateral view; (3) apical segments of antenna; (4) wing venation (reconstructed from folded position); (5) pretarsus, ventral and lateral views; (6) hind leg; (7) tip of abdomen, lateral view; (8) scales of forewing membrane; (9) androconial scales on R and M veins; (10) abdomen in lateral view; (11) dorsal processes of segments IV and V (enlarged).



position was confirmed (Regier *et al.* 2015), although the precise topological relationship between them remains somewhat doubtful. In contrast to the rest of the Lepidoptera, the adult moths of this clade retained moveable mandibles and undifferentiated maxillae.

Mandibles are not visible in the fossil species, but this character is scarcely observable in amber, attributable to their usually folded formation below the labrum. Even in species of Micropterigidae from Baltic or Bitterfeld amber, which do have mandibles, as well as in freshly pinned specimens of *Micropterix*, the mandibles are difficult to observe. It seems very likely that the species has mandibles. As to the maxillae, the second distinguishing character, they are clearly not elongated. The galea is a small and rounded lobe, which is the plesiomorphic condition in Holometabola. As for the independent origin of wing scales, the galea in Trichoptera had the potential to develop into a proboscis or proboscis-like structure, such as in species of Dipseudopsidae.

If the correct position of Tarachocelidae is within the lineages of extant Lepidoptera, then the family should be placed in the grade affiliated with the non-glossatan families mentioned above. This clade is accorded superfamily rank (Regier *et al.* 2015). It cannot, however, be included in any of the above subgroups, mainly because of the very aberrant wing venation, unusual head structure and unique mouthparts (see diagnosis of family). What remains to be evaluated is whether the family can be associated with one of the fossil families described in Lepidoptera or Trichoptera. The genera and families of Mesozoic Lepidoptera are summarised in Zhang *et al.* (2013). In addition to the Micropterigidae, there are four families that have been assigned to Lepidoptera: Archaeolepidae; Eolepidopterigidae; Mesokristenseniidae; and Ascololepidopterigidae. Concerning the Eolepidopterigidae, the suborder Eolepidopterigina was established (Rasnitsyn 1983). The monophyly and suitability of this family and suborder was questioned by Kristensen & Skalski (1998), because of the presence of an extensible ovipositor in females with apophyses anteriores, presented as a diagnostic character and which, in fact, is a synapomorphy of Trichoptera and Lepidoptera. This character, however, is absent in females of Micropterigidae and extant Heterobathmiidae and is, therefore, of some taxonomic value. The other families are treated as suborder *incertae sedis* (Huang *et al.* 2010; Zhang *et al.* 2013).

Adult characters supporting these families are few and of variable significance. They are based principally on wing venation and spurs or spines of the legs. In general, the fore- and hindwing venation is of the micropterigid type, which is also expressed in the ancestral trichopteran family Rhyacophilidae. Differences are often small and concern the presence or absence of a single vein, a fork or a cross-vein (see Schachat & Gibbs 2016). In this respect, all fossil lepidopteran families are alike. When compared with Tarachocelidae, the morphological gap is evidently immense. The venation of this is of a different type, with only three radial veins and a single median vein, carrying putative androconial scales on the underside (forewing) and upper side (hindwing) in the male. The species is obviously not an ancestral form, but represents a highly derived evolutionary lineage probably originating prior to the split of Amphiesmenoptera into Trichoptera and Lepidoptera. No synapomorphies with any of the fossil families already described in Lepidoptera or in Trichoptera could be identified in addition to the above mentioned amphiesmenopteran characters. Therefore, the establishment of the family in Amphiesmenoptera *incertae sedis* seems to be justified. This placement, outside Lepidoptera, implies an independent and multiple evolution of wing scales in primitive Amphiesmenoptera. Currently, there

is no evidence of scales present in other stem-group taxa of Amphiesmenoptera.

Tarachocelidae is the first family in the fossil record of Amphiesmenoptera, from which we now have good knowledge of characters other than wings and legs and traces of body features. Unfortunately, the taxon is based on a single specimen. We anticipate that additional material of this novel family will be detected in new Burmese amber material when it becomes available for scientific study in the future. Further specimens of Tarachocelidae are necessary to corroborate the presented results and to resolve the systematic position of the new family.

With an age of 99 Ma, Burmese amber is of Early Cretaceous origin (Cenomanian). At that time, the evolution of the Lepidoptera, based on the fossil record, had been underway for about 50 Mya (Whalley 1978). The extant family Micropterigidae was already in existence. The advanced and derived morphology of Tarachocelidae is suggestive of a similar or even an older age for the origin of this group.

### 3. Acknowledgements

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Our colleague J. Dunlop corrected the English text of the first draft, and Renate Heinrich (Berlin) checked the derivation of the names from the Greek language. C. C. Labandeira and an unknown reviewer are thanked for providing corrections and remarks. The first author received financial support from the Museum für Naturkunde, Berlin towards attending the conference, which is gratefully acknowledged.

### 4. Note added in Proof

This current paper was accepted and in press before another paper, describing additional taxa, was submitted by the senior authors (Mey *et al.* 2017). The second paper was quickly accepted and ready for publication. However, the publication of the family, genus and species names would have resulted in *nomen nuda*; thus, brief descriptions were included in the second paper to validate the names. This current paper has been altered to include the correct authorships of the taxa and the additional reference. It is regretted that the senior authors did not include the junior authors in the second paper; however, according to the International Code of Zoological Nomenclature, the first authorship to be published is correct.

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