



# The blueprint of the Amphiesmenoptera – Tarachoptera, a new order of insects from Burmese amber (Insecta, Amphiesmenoptera)

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**Abstract.** Based on a total of 14 inclusions from Burmese amber the new insect order Tarachoptera is established. The family Tarachocelidae previously described from Burmese amber and then placed in Amphiesmenoptera incertae sedis is assigned to this new order. The genus *Kinitocelis* gen. nov. is established to accommodate three new fossil species: *K. hennigi* spec. nov., *K. divisinotata* spec. nov. and *K. brevicostata* spec. nov. The new genus differs from *Tarachocelis* gen. nov. by the absence of androconial scales on the wings and the loss of Cu2 in the forewings. The species are described in detail and the critical characters are illustrated by line drawings and photos. Both males and females were described. The species can be distinguished by traits in the wing venation. The new order Tarachoptera is placed in the superorder Amphiesmenoptera based on the presence of seven amphiesmenopteran apomorphies and nine tarachopteran apomorphies. Apomorphic characters of Trichoptera and Lepidoptera could not be disclosed, which suggests an independent origin and evolution from an amphiesmenopteran ancestor which was not the ancestor of the Trichoptera-Lepidoptera clade. The species of Tarachoptera are tiny insects with a wing span of 2.3–4.5 mm but highly specialized according to their aberrant morphology. Aspects of the presumed life history of the adults were deduced from some of the derived morphological traits that could be interpreted as adaptations to a highly structured micro-environment.

## 1 Introduction

Since 2009, we have had an enigmatic fossil insect from Burmese amber on our desk for study. The species was identified as being a representative of the Amphiesmenoptera, a superorder that contains the two orders Trichoptera and Lepidoptera. The term for the superorder was coined by Hennig (1969), who simultaneously provided a number of autapomorphic characters for this taxon. He also presented the first cladogram on the phylogeny of the Amphiesmenoptera in which he explained the differences between genuine and false stem-group members (Fig. 7). Kristensen (1984) added further autapomorphies and constructed a hypothesized groundplan for the Lepidoptera, which included 21 amphiesmenopteran autapomorphies. Although the fossil specimen was relatively well preserved with many characters visible, it could be assigned to neither the Trichoptera nor to the Lepidoptera. Only one autapomorphy is shared with Lepidoptera: the presence of scales on the wings. It is the most conspicuous and remarkable feature of the Lepidoptera and we were inclined to group the fossil species closer to the Lepidoptera than to the Trichoptera. However, the external morphology of the insect differs in nearly all aspects from Lepidoptera and we eventually came to the conclusion that it was best to treat this species as a member of a hitherto unknown lineage of the stem group of Trichoptera/Lepidoptera. The

species was recently described as *Tarachocelis microlepidopterella* Mey et al. (2017) and placed in the simultaneously established family Tarachocelidae of Amphiesmenoptera incertae sedis.

Shortly after completing the manuscript we received, to our surprise, additional inclusions of this Burmese amber insect. This new material was very welcome and enabled us to continue our study on this remarkable insect group. During the initial inspections it became obvious that the material contained males and females of at least three species which belong to Tarachocelidae but were not conspecific with the recently described *Tarachocelis microlepidopterella* in Mey et al. (2017). The fossils exhibited some new, previously unobservable characters and provided the first true indications for an estimation of the variability in morphological traits in this group. In a reassessment of the systematic position of Tarachocelidae we recognized the unusual morphology as significant and distinctive to consider the group as an order of its own. Here we describe this new fossil order of insects and give a discussion of the evidence which led us to establish this higher-rank taxon.

We have included in the present article a reduced version of the descriptions of Tarachocelidae and *Tarachocelis microlepidopterella* gen. nov. spec. nov. in order to avoid the establishments of nomina nuda. The detailed descriptions of the taxa are published in Mey et al. (2017).

## 2 Material and methods

Burmese amber has been recorded from the Shwebo, Thayetmyo, Pakokku, Magway, and Pegu districts in Myanmar (Ross et al., 2010). However, the only commercial source is the Hukawng Valley in Tanaing Township, Myitkyina District of Kachin State. The amber studied here is from an amber mine located near Noiye Bum Village, Tanaing Township (Kania et al., 2015). These deposits have been dated in detail by Shi et al. (2012). We tentatively follow the age determination as early Cenomanian ( $98.8 \pm 0.6$  million years) given by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Shi et al., 2012), but the geological age of Burmese amber should be slightly older than the zircon date (Ross, 2015).

The fossil specimens are embedded in small amber blocks cut out from larger Burmese amber pieces. Some adult insects are nearly completely preserved and often visible in ventral and dorsal view. The male genitalia are flattened. The hindwings are often partly covered by the somewhat distorted forewings. The head, thorax and abdomen show often signs of decomposition and maceration. Antennae and legs are often incomplete.

Photos were taken using a Leica stereomicroscope M 420 Apozoom in combination with a Canon EOS 600D, EOS utility software and the Zerene Stacker software or were taken with a Keyence VHX-900F digital microscope.

The fossils were examined under incident and transmitted light using a stereomicroscope (Leica MZ125). Line drawings were produced with a Leica camera lucida and digitally processed using Adobe Photoshop CS4. Measurements were made with the ocular micrometer of the stereomicroscope. The fossils will be embedded in rectangular pieces of artificial resin to make the inclusions more clearly visible and to ensure its durability.

Acronyms of depositories:

PM – collection of Patrick Müller;

WW – collection of Wilfried Wichard;

MfN – Museum of Natural History, Berlin;

NIGP – Nanjing Institute of Geology and Palaeontology, Nanjing.

## 3 Description of new taxa

**Tarachoptera**, ordo nov.

Type family: Tarachocelidae fam. nov. (Burmese amber)

Description (Figs. 1–14): Head flat, dorso-ventrally depressed, with coronal, frontal and frontogenal sulci present, one pair of elongate setose areas on vertex and frons, ocelli absent; antenna filiform, with barrel-like flagellomeres; anteclypeolabrum separated by horizontal furrow from frontoclypeus and kneed in frontal direction; mandibles vestigial; maxillary palpi very small, three-segmented, galea triangular; labial palpi long, porrect or ascending, three-segmented; cervix enlarged with laterocervicalia and additional pair of small cervical sclerites on dorsal side. Thoracal segments inclined frontad, pronotum flat, divided by membranous, transverse furrow into an anterior and posterior plate, both connected with lateropleuron small setose areas on lateral sides of pronotum. Wings homoneurous, with three radial veins forming a long radial cell closed apically by crossvein r1–r2; media unbranched, wing surface covered by small scales, which are spindle-shaped with acute or slightly rounded tips, hindwing and wing margin scales lanceolate and 2 times longer, but with only three to four primary ridges; veins devoid of hairs or scales; large and erect androconial scales on radial and medial veins of male fore- and hindwing present or absent. Hindwings incompletely covered by scales, smallest scales with a size of 28–35  $\mu\text{m}$  and more pigmented (darker) than other scales; all scales on the wings bent and slightly arched, which is in contrast to the flat scales of Lepidoptera; wing membrane on both wings densely covered by tubercles, giving the wings a granulate appearance; scales present on antennae, head, thorax and legs; legs slender, tibia of all legs without spurs, pretarsus with simple claws and pulvilli. Abdomen of male with sternal processes on segment IV–VI. Male genitalia small, retracted into segment IX, and covered dorsally

by single, long plate; segment IX with comb of spines on ventro-caudal margin. Female genitalia with paired or unpaired dorsal plate.

Diagnosis: The characters 21–29 in Figs. 4–9 discussed below are interpreted as apomorphies of the new order. Seven characters (1, 2, 4, 8, 9, 12, 13) were identified as amphiesmenopteran apomorphies (see discussion below). Three apomorphies of the Trichoptera/Lepidoptera clade (3, 6, 14) are in a plesiomorphic state, with the architecture of the prothorax as the most remarkable character (see Figs. 2, 9).

**Tarachocelidae** fam. nov.

(urn:lsid:zoobank.org:act:8C5E04FF-2B78-4BD4-A55F-2480D4BC90C9)

Type genus: *Tarachocelis* gen. nov.,

Description: Head elongate, mouthparts slightly hypognathous, vertex without setal warts, eyes oval, antenna filiform, maxillary palpi very short, three-segmented, of equal length, ciliated, last segment pointed; labial palpi long, three-segmented, all segments of about equal length, with long hairs, terminal segment with pointed apex; 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, pretarsus with slender ungues and stalked arolium, pulvilli 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; small jugum present, folded under base of wing, forewing with Sc a thin vein branched apically and with humeral (h) and subapical crossvein sc-r; radius divided into two thick veins, bearing broad, triangular, putative androconial scales on the underside of the wing, upper R vein unbranched (R1), lower R vein with two terminal branches R1 and R2 (or R2+3 and R3+4), ending on wing margin before and at apex respectively.

**Tarachocelis** gen. nov.

(urn:lsid:zoobank.org:act:BDE44937-0710-426A-B2A5-C4850CAFFF6A)

Type species: *T. microlepidopterella* spec. nov.

Gender: Female.

Etymology: The name is derived from the Greek *ταραχῆ* (*tarachi*), frightened, staggering, which concerns the presumed flight of the adults.

Description: As described for the family.

Diagnosis: Males with presumed androconial scales on R and M veins on the underside of the forewings and on

the upper side of the hindwings. Membrane of forewing sparsely covered by spindle-shaped and piliform scales without perforations. Humeral vein in the forewing present and apical section of Cu2 in forewing absent.

*Tarachocelis microlepidopterella* spec. nov.

(urn:lsid:zoobank.org:act:2CADD125-72AA-4F9B-81B7-106B980B4C12)

(Figs. 13–14)

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

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 dorso-ventrally, 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; spurs and smaller spines absent on all tibiae, tarsal segments with terminal pair of ventral bristles; crossveins cu-r1 and r1-r2+3 present, the latter closing an elongate, triangular, radial cell; crossvein m-cu1a present; basal part of Cu2 fused with Cu1a+b; anal veins (A1 and A2) apparently with basal loop. Hindwing venation similar to forewing venation.

**Kinitocelis** gen. nov.

(urn:lsid:zoobank.org:act:22FA942B-37FA-4C47-932B-26519E0393A3)

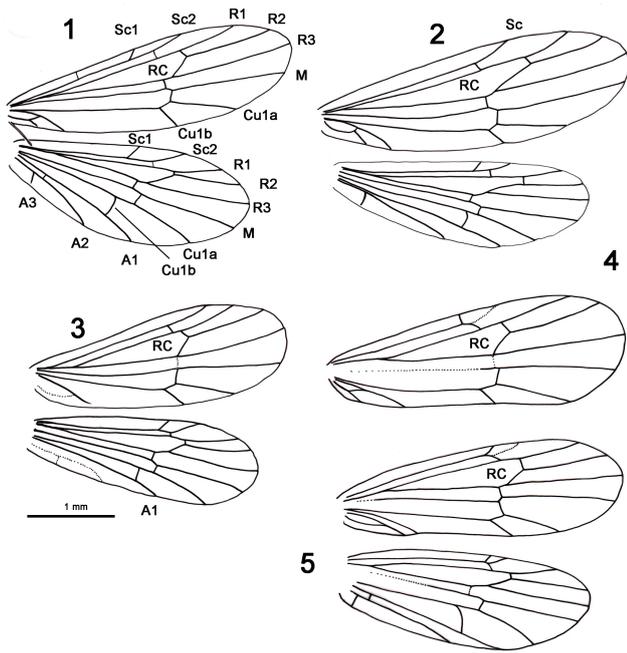
Type species: *K. hennigi* spec. nov.

Gender: Female.

Etymology: The name is derived from the Greek *kinitos*, agile, and *celis*, as a suffix of generic names.

Description: Small adult insects with 2.3–4.5 mm wing length, and 2.5–4.3 mm body length. Wings held above abdomen in a flat and overlapping mode.

Head: Elongate, moderately dorso-ventrally depressed, hypognathous, frons and vertex with semi-erect scales, eyes hemispherical, ocelli absent, antenna filiform, 20–26 barrel-shaped, scaled flagellomeres; head capsule with coronal and frontal sutures, fronto-genal sutures also present, anterior tentorial pits large, deep furrow between frontoclypeus and clypeolabrum, proximal part of clypeolabrum sclerotized, distal part membranous, mandibles vestigial, reduced to small, conical processes, lying laterally of clypeolabrum and obviously nonfunctional, galea of maxilla an enlarged, nearly triangular, flat lobe with a blade-like anterior margin, maxillary and labial palpi three-segmented and scaled, labial

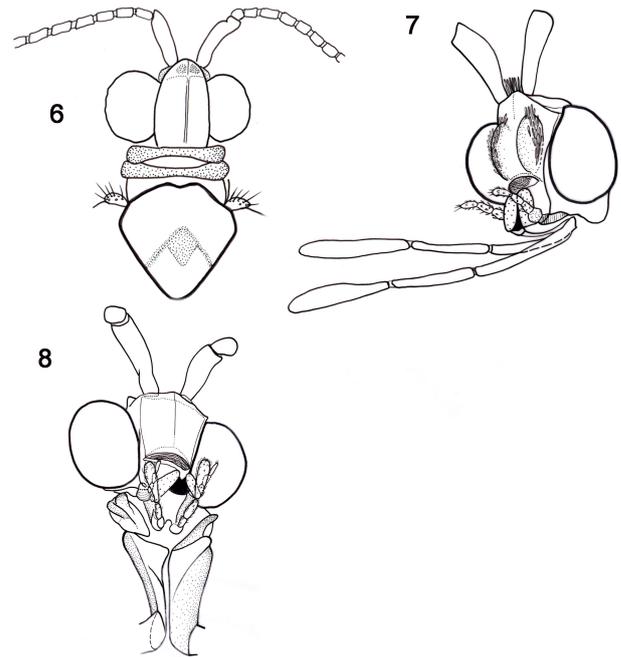


**Figure 1.** (1–5) Wing venation. (1) *Kinitocelis hennigi* spec. nov. (B113); RC – radial cell. (2) *Kinitocelis divisinotata* spec. nov. (B44). (3) *Kinitocelis divisinotata* spec. nov. (B67). (4) *Kinitocelis brevicostata* spec. nov. (BUB319). (5) *Kinitocelis brevicostata* spec. nov. (BUB399).

palpi much longer than the former, haustellum or proboscis absent.

**Thorax:** Thoracal segments inclined towards head, cervix extensible, laterocervical sclerite from broad base on episternum spanning to hind margin of head, pronotum seemingly divided transversally into an anterior and posterior notum, corner of anterior notum connected ventrally with episternum; fore- and hindwings translucent, of nearly the same length with rounded apices, humeral vein and pterostigma absent, jugal lobe transformed into rod-like appendage or absent, venation homoneurous concerning branching of R and M veins, three radial and a single, unbranched media present, forewing Sc with or without apical fork (Sc1 and Sc2), bases of R1+2 and R3 and crossvein r2–r3 forming radial cell (RZ); spindle-shaped scales and piliform or lanceolate scales on the wing membrane, the scales without perforations, some scattered scales also on the ventral side, hindwing scales and fringes mostly of the piliform type, hindwing without jugal lobe, Cu1b forming a false crossvein between Cu1a and A1, Cu2 absent; legs slender, epiphysis on foreleg absent, spurs and additional spines absent on tibiae, basal tarsomere nearly as long as remaining tarsal segments together, all tarsal segments with apical pair of short spines.

**Abdomen:** Female abdomen without sternal processes, male sternum of abdominal segment V with pair of short, lateral processes, segments VI–VII with small protuberances in shallow depressions on lateral sides.



**Figure 2.** (6–8) *Kinitocelis divisinotata* spec. nov.: (6) head and pronotum, dorsal; (7) head, latero-frontal; (8) head, ventro-frontal.

**Genitalia:** Male – dorsal part (uncus?) an elongate, roof-like plate, ventral part (vinculum?) with a bulbous, distal margin equipped with a transverse comb of about 15–20 stiff spines, valvae short, in vertical position, hardly protruding beyond comb of spines.

Females – dorsal part of final, abdominal segment produced distad with a pair of oval plates attached to the lateral sides, or with a single, apically rounded plate; ventral part broadly rounded bearing a large, triangular process in the middle, or without process, but with notched ventral margin.

**Diagnosis.** *Kinitocelis* gen. nov. can be separated from *Tarachocelis* gen. nov. by characters of wing venation: the humeral vein is absent, the radial and median veins are without enlarged, androconial scales and the postcubital vein (Cu2) has lost its free, apical section. An advanced character is the dense scaling on the forewings in contrast to the sparsely scaled wings of *Tarachocelis*.

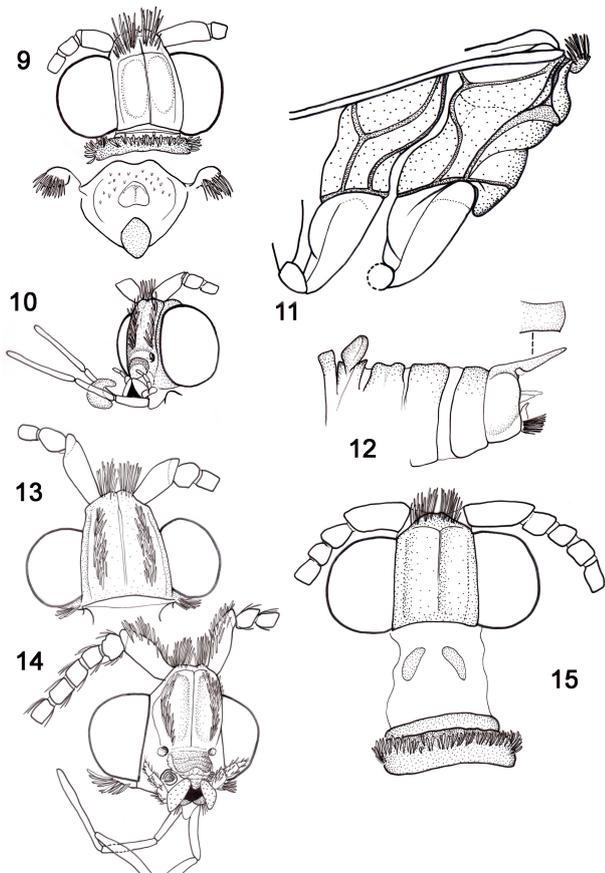
***Kinitocelis hennigi* spec. nov.**

(urn:lsid:zoobank.org:act:71B3ADEE-519A-4682-A105-F2180C539195)

(Figs. 1, 4(16–17), 8)

**Material:** Holotype ♀, B 113, deposited NIGP 164790

**Etymology:** Named in honor of Willi Hennig (1913–1976), in recognition of his ideas on the phylogeny of Ampiesmenoptera published in Hennig (1969).

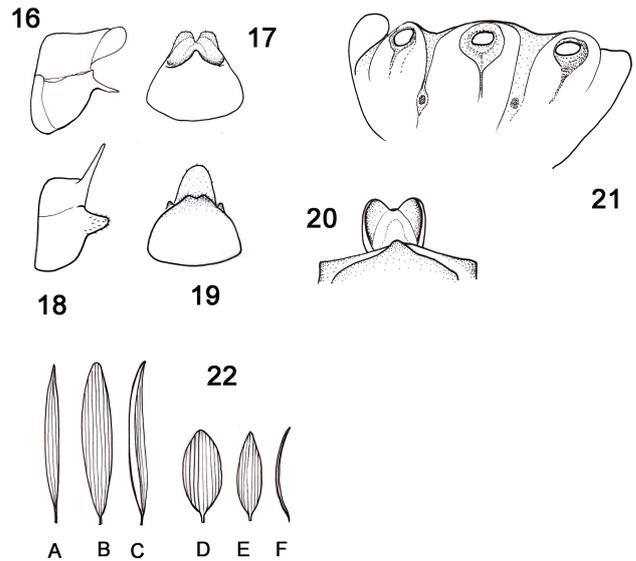


**Figure 3.** (9–14) *Kinitocelis brevicostata* spec. nov. (BUB319): (9) head and thorax, dorsal; (10) head, fronto-lateral; (11) pterothorax, lateral; (12) male abdomen with genitalia, lateral. *Kinitocelis brevicostata* spec. nov. (BUB399): (13) head, dorsal; (14) head, ventral. *Kinitocelis divisinotata* spec. nov. (BUB730): (15) head, dorsal.

**Description (holotype):** Length of forewing 2.9 mm; length of body 3.0 mm. Antenna with 21 flagellomeres; in forewing (Fig. 1(1)) subcosta apically furcate, right wing with a single costal crossvein, which is absent on left wing, distance between sc–r and r1–r2 is 2 times the length of the latter crossvein, A1 and A2 looping, jugum in form of a rod-like appendage; hindwings slightly broader than forewings, crossvein r1–r2 very short.

**Female genitalia (Fig. 4(16–17)):** Dorsal part of final abdominal segment produced distad with a pair of oval plates attached to the lateral sides, ventral part broadly rounded bearing a large, triangular process in the middle, directed distad.

**Diagnosis:** The species differs from all other species of the genus by the presence of an apically forked subcosta and the rod-like jugum of the forewing. The absence of the costal crossvein in one wing qualifies this character as regressive and of limited taxonomic significance.



**Figure 4.** (16–22) Female genitalia. (16–17) *Kinitocelis hennigi* spec. nov. (B113), lateral (16) and ventral (17). (18–19) *Kinitocelis divisinotata* spec. nov., lateral (18) and ventral (19). (20) *Kinitocelis brevicostata* spec. nov. (BUB399), ventral. (21) Male abdomen of *K. brevicostata* spec. nov., lateral view (B384). (22) Wing scales, dorsal side of *K. brevicostata* spec. nov. (BUB 843). Hindwing – A–B: dorsal side; C: lateral side. Forewing – D–E: dorsal side; F: lateral side.

***Kinitocelis divisinotata* spec. nov.**

(urn:lsid:zoobank.org:act:2DE92E61-C740-414E-8658-9DB441D79C55)

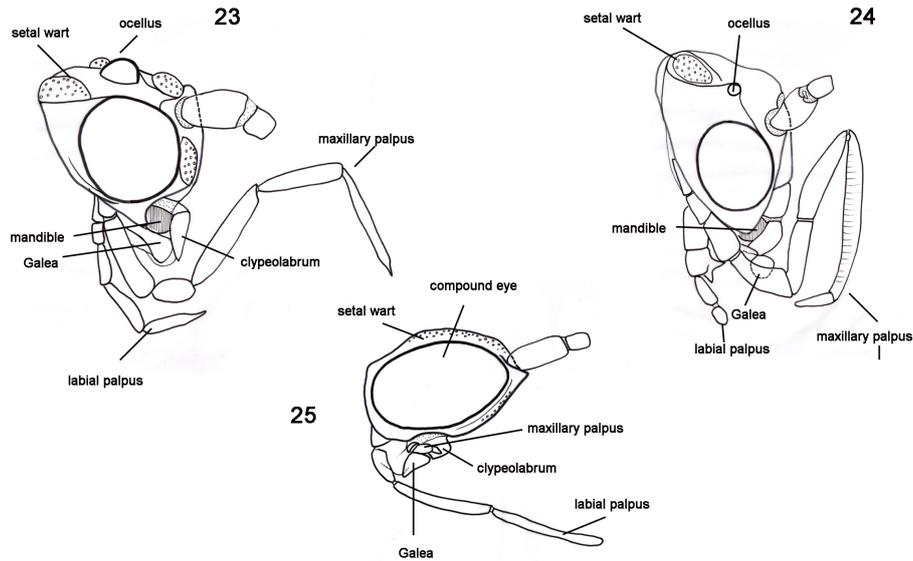
(Figs. 1(2–3), 2(6–8), 3(15), 4(18–19), 9)

**Material:** Holotype ♀, B 44x, deposited in NIGP **164789**

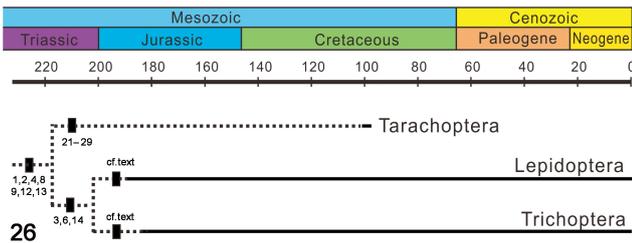
**Paratypes:** 1 ♀, BUB 773, deposited in PM; 1 ♂, BUB 730, deposited in MfN; 1 ♀, B 67 and 1 ♀, B 390 deposited in NIGP **164785**, NIGP **165287**

**Etymology:** The specific name refers to the seemingly split prototum in dorsal view.

**Description (holotype):** Length of forewing 3.5 mm; length of body 3.5 mm. Antenna with 22 flagellomeres; terminal segment of labial palpi thickened; pronotum divided into anterior and posterior plates by transverse fold, anterior plate connected ventrally with episternum; in forewing (Fig. 1(2–3)) subcosta simple, not forked, ending on wing margin before or after crossvein r1–r2; distance between sc–r and r1–r2 variable, 1 to 4 times the length of the latter crossvein, A1 and A2 looping, scales sparsely distributed on wing surface; hindwings as broad as forewings, crossvein r1–r2 as long as sc–r1.



**Figure 5.** (23–25) Head in lateral view (without flagellum). (23) *Rhyacophila sibirica* McLachlan, 1879; (24) *Micropterix calthella* (Linnaeus, 1758); (25) *Kinitocelis brevicostata* spec. nov. (BUB 319).



**Figure 6.** Cladogram of the phylogenetic relationship of Tarachoptera, Lepidoptera and Trichoptera (numbers correspond with those for synapomorphies and autapomorphies cited in the text).

Female genitalia (Fig. 4(18–19)): Dorsal part of final abdominal segment a single, elongate, oval plate, ventral part broadly rounded, upturned and notched in the middle.

Diagnosis: The club-shaped labial palpi, the female genitalia and the long apical section of the subcosta beyond crossvein sc–r are diagnostic for the species.

Remarks: The wing venation appears to be variable in the length of the radial cell (RZ). The positions of the crossveins are altered adequately. In Fig. 1(3) the aberrant wing venation of B 67 is depicted. It is left for future studies and more material to decide whether the forewing venation is indeed a variable character of *K. divisinotata* spec. nov. or a second species is involved.

*Kinitocelis brevicostata* spec. nov.

(urn:lsid:zoobank.org:act:B7D7B85C-630F-456D-B010-74B5E41DD76D)

(Figs. 1(4–5), 3(9–14), 4(20–21), 10–12)

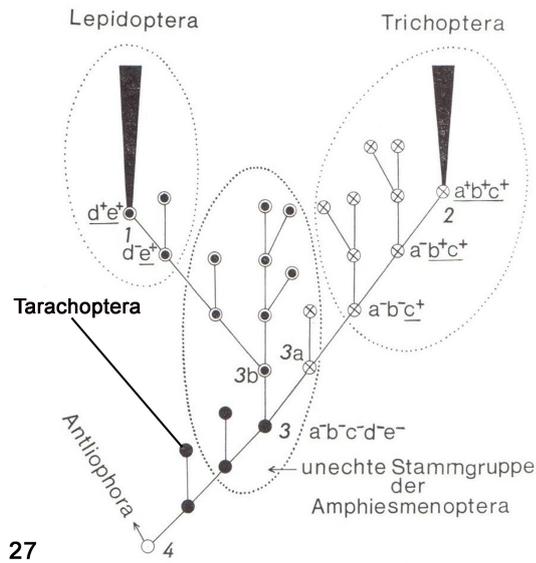
Material: Holotype ♀, BUB 399, deposited in MfN;

Paratypes: 1 ♂ BUB 319 PM, 1 ♂ B 307 WW, 1 ♂ 352 NIGP 164786, 1 ♀, B 371 NIGP 164787, 1 ♂, B 384 NIGP 164788, 1 ♂, BUB 843 PM, deposited NIGP, WW and PM.

Etymology: The specific name is composed of the Latin *brevis*, short, and *costa*, vein referring to the atrophied or weakly sclerotized apex of subcostal vein.

Description (holotype): Length of forewing 4.5 mm; length of body 4.3 mm. Antenna with 26 flagellomeres, the paratypes with 22–23 flagellomeres; erect piliform scales on frons arranged in two lines, right mandible a small, rounded cone sitting in a deep cavity close to the lateral side of clypeolabrum, segments of labial palpi sparsely scaled; in forewing (Fig. 1(4–5)) subcosta forked, both branches close together and weakly sclerotized, distance between sc–r and r1–r2 is the length of the latter crossvein, A2 and A3 looping, a small rod-like jugum present, scales densely distributed on wing surface; hindwings broad as forewings, only on costal area with dense scaling, crossvein r1–r2 shorter than sc–r1. Male abdomen with sternites V–VII enlarged dorsally and with a bulbous protuberance displaying a round orifice in a shallow depression.

Female genitalia (Fig. 4(20)): Dorsal part of abdominal segment with pair of oval plates, ventral part broadly rounded, upturned and notched in the middle.



**Figure 7.** Cladogram of Hennig (1969) on the presumed phylogeny of Amphiesmenoptera, illustrating the topographic differences between genuine and false (= unechte) stem groups. The cladogram still applies and the position of Tarachoptera is inserted, demonstrating its early branching from an amphiesmenopteran ancestor.

Additional characters provided by paratype specimens BUB 319:

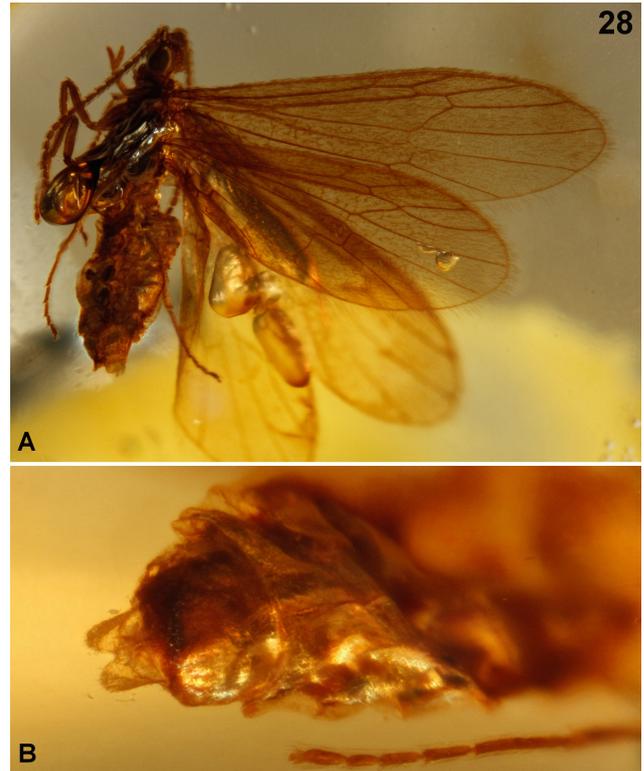
Male genitalia (Fig. 3(12)): Dorsal part of abdominal segment IX a flat, elongate plate with truncate apex, overarchng the genital cavity; ventral part with a short vinculum, and short vertical processes (? valvae); ventral hind margin of segment VIII with a comb of about 20 stiff spines, directed distad.

Diagnosis: The reduction of the apical section of the subcosta in both veins is a distinguishing character of the new species. The individuals of this species are slightly larger than the preceding species. There is some variation in the wing venation among the specimens, which is probably due to different embedding positions rendering direct comparisons and productions of corresponding illustrations difficult to make.

#### 4 Discussion

##### Amphiesmenopteran characters

Kristensen (1984) and Kristensen and Skalski (1998) summarized the autapomorphic characters of the superorder Amphiesmenoptera. In addition, Ivanov (2002) mentioned one trait (most of the forewing Sc branches lost) from his paleontological perspective. The presence of well-developed silk glands was found to be an embryological autapomorphy (Kobayashi and Ando, 1988). Of the 23 autapomorphies



**Figure 8.** *Kinitocelis hennigi* spec. nov., holotype ♀ (B113): (a) dorso-lateral view and (b) ventral side of tip of female abdomen.

identified at that time (1984–2002), 19 are adult and 3 are larval characters. Most of them have no relevance in the study of amber fossils, because they concern embryological, anatomical and cytological structures unobservable in inclusions. Characters of the exoskeleton can only be used for comparisons if well preserved and not covered by wings or other structures. None of the examined specimens displays the full set of the critical traits. Characters are well visible in one specimen but not in the other. The descriptions and discussions are based always on the individual that shows the character in the clearest way. The following characters in the sequence and numbering of Kristensen (1984) are applicable to Tarachoptera:

1. *Prelabium fused with hypopharynx.* This composite structure leads to the formation of the haustellum. The haustellum of primitive Trichoptera and of the aglossatan Lepidoptera families (Micropterigidae, Agathiphagidae, Heterobathmiidae) has a similar structure (see Kristensen and Nielsen, 1979). The fossil specimens do not show a clear haustellar lobe which allows a direct recognition of this autapomorphy, but in the holotypes of *K. divisinotata* spec. nov. and *K. brevicostata* spec. nov. the opening of the preoral cavity is visible, situated ventrally of the galea lobes (Figs. 2(7–8), 3(10, 14)). In extant Trichoptera the preoral cavity is filled with the eversible haustellum, in which no

space is left for a large opening or a large preoral cavity that can be seen from frontal view. As a consequence, an assumed haustellum of Tarachoptera must be a small organ too, similar to that of Micropterigidae. The preoral cavity appears to be large enough to provide space for something like an infrabuccal pouch in the hypopharynx, which plays a role in crushing food particles and which was considered by Kristensen (1984) as plesiomorphic for the Amphiesmenoptera or Panorpidia. However, the vestigial mandibles of Tarachoptera are obviously not moveable and thus unable to interact with an infrabuccal pouch. This function of the mandibles could have probably been adopted by the triangular galeas, which show blade-like ventro-median margins. If this is correct, the food particles were probably not pollen grains but something of a softer consistency like sporangia of lichens or fungi.

2. *Lower posterior corner of laterocervicale produced towards the prosternum.* The morphology of this cervical sclerite corresponds largely with the sclerites in extant Lepidoptera and Trichoptera. The cervix was observed in two fossil specimens (BUB 730, B 352) as a long, eversible organ with a pair of additional cervical sclerites or protuberances on the dorsal side (Fig. 3(15)). These sclerites are not known to occur in extant species of Trichoptera and Lepidoptera, but are present in distantly related orders like Homoptera, Zoraptera and Mantodea (Matsuda, 1970). The sclerites as supporting structures probably developed together with the elongated cervical membrane, which led to a greater movability of the head. The cervix and its dorsal, cervical sclerites seems to be an adaptation to an unknown foraging behavior and might have evolved independently from other lineages.

3. *Pronotum with paired setose warts.* In contrast to Trichoptera and Lepidoptera, which have vertically upright standing pronota with the warts in the middle, the pronotum of Tarachoptera is a flat plate, with setose parts on the lateral sides only, but without warts or distinct protuberances (Figs. 2(6), 3(9, 15)). In a number of Trichoptera families (e.g., Philopotamidae, Calocidae) the pronotum carries two pairs of setose warts, a condition which is considered a ground-plan character of Trichoptera (Ross, 1956). The pronotum in Tarachoptera is divided into anterior and posterior plates by a membranous fossa or fold (Fig. 2(6)). The plates can lie in the same plain or are angled on the transverse membrane. On the lateral sides, the pronotal plates seem to come close to the anepisternum and epimeron of the propleuron. Transverse sutures of the pronotum are described from Mecoptera (Matsuda, 1970). In the family Hepialidae (Lepidoptera) the pronotum includes an anterior dorsal plate (Nielsen and Kristensen, 1989) which could be interpreted as a remnant of a larger and transversely divided pronotum. However, the median sulcus of this anterior plate is not present in Tarachoptera, making homology of both structures doubtful.

The morphology of the pronotum in Tarachoptera differs considerably from Trichoptera/Lepidoptera and represents very probably the plesiomorphic state in Amphiesmenoptera, preserved in Tarachoptera.

4. *Pterothoracic episterna with characteristic suture pattern.* The paracoxal sulcus and a short, ventrad running sulcus depicted by Kristensen (1984) are also present in Tarachoptera.

5. *Secondary furcal arms in pterothorax fused with posterior margin of corresponding epimera.* This autapomorphy becomes visible only by looking at the back sides of these segments. None of the available specimens allows this observation.

6. *Metathorax with a setose sclerite in the wing base membrane below/behind the subalare.* A setose sclerite is absent in this position, an observation possible only in specimen BUB 319 of *K. brevicostata*. However, the subalare in both thoracic segments is not discernable, but the dorsal side of the epimeron is unusually large and slightly concave (B 113).

7. *Pretarsus above the claws with a pseudempodium, a strong seta on a socket.* The pseudempodium is not clearly visible. Observing this character is further complicated by the presence of several setae arising from the dorsal side of the pretarsus.

8. *Wings with extensive covering of setae.* Setae are present on both the fore- and hindwings. They are dispersed randomly among the more numerous scales. Like in Lepidoptera and some Trichoptera the scales on the wings of Tarachoptera are modified setae. Their dorsal surface has 4–8 primary ridges without providing any visible perforations between ridges. They are spindle-shaped (like in Neopseustidae) and occur in different lengths (Fig. 4(22)). The forewing scales are smaller and more dense than their hindwing counterparts. The latter are somewhat elongate, with the longest comprising the fringes on the wing termen. The fringes of the anal hindwing margin are comprised of long hairs.

9. *Anal veins of the forewings apparently looping up into a double-Y configuration.* The anal veins of the forewing are amalgamated, but they differ in the studied specimens (Fig. 1). Apart from a double-Y form, a simple Y configuration is the dominant pattern, with or without a short, free apical piece of A3, which runs to the wing margin.

10. *One ventral neck muscle originating on the fore coxa;* 11. *conical furcopleural muscle in the mesothorax with broad end on the pleural ridge.* These anatomical characters are not observable in fossils, but could possibly be observed by using micro-CT scans.

12. *Presence of paired glands opening on sternum V.* Dorsal processes on the sternites of the abdominal segments are interpreted as being the location of gland openings. In Trichoptera similar sternal processes occur in several primitive families (e.g., Hydrobiosidae, Polycentropodidae) (Ivanov and Melnitsky, 2002; Djernaes, 2011). However, we cannot decide from the Tarachoptera fossils which segments are involved because intersegmental lines or depressions are obscured and a distinction between membranes and sclerites is not possible. Nevertheless, at least two segments have sternal processes, which points to the presence of more than one gland pair (Figs. 3(12), 4(21)). Only the males exhibit these sternal processes, a situation also found in Lepidoptera, Agathiphagidae (Djernaes and Kristensen, 2011).

13. *Male abdominal segment IX with tergum and sternum fused, forming a closed ring.* This character is present in the examined male specimens of Tarachoptera (Fig. 3(12)).

14. *Anterior margin of female segments VIII and IX with long, rod-like apodemes, accommodating the insertion of protractor/retractor muscles of the extensible oviscapt (= ovipositor).* The studied females of Tarachoptera do not possess papillae anales nor any elongated structures, which would imply the existence of an ovipositor (Fig. 4(16, 18)). If apodemes are present, they must be small and not of the long, rod-like shape as in extant Trichoptera and Lepidoptera. In Trichoptera vestiges of apodemes are retained in several families (e.g., Philopotamidae, Phryganeidae, Apataniidae), which are reason enough to consider the lack of these apodemes as secondary losses. This explanation is probably not applicable to the lacking apodemes in aglossatan Lepidoptera families (Micropterigidae, Heterobathmiidae) (Kristensen 1998) and in the primitive Hydrobiosidae of the Trichoptera. However, the ovipositor with long apodemes on segment VIII and IX is an ancestral character found in fossil specimens from the Upper Jurassic to Lower Cretaceous and was used to establish the extinct Lepidoptera family Eolepidopterigidae (Rasnitsyn, 1983).

Kristensen (1984) discussed a further five characters from visceral anatomy and cytology, including the female heterogamety as the classical synapomorphy, which are, however, of no relevance here.

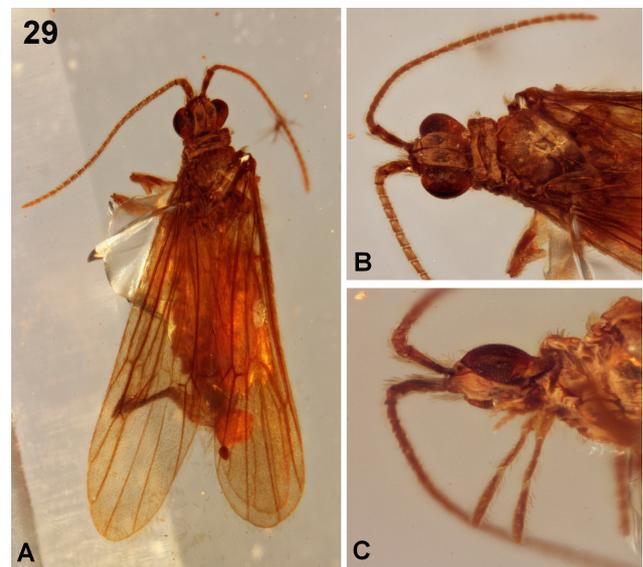
The results of the above discussion on the presence/absence of Amphiesmenopteran autapomorphies in Tarachoptera are summarized in Table 1. The numerals refer to character enumeration in the text.

### Autapomorphies of Lepidoptera

Kobayashi and Ando (1988) found three embryological traits which corroborate the monophyly of Lepidoptera. Kristensen and Skalski (1998) demonstrated the monophyly

**Table 1.** Seven characters are identified as being present, which clearly support the placement of Tarachoptera within the Amphiesmenoptera. Three characters were found to represent the plesiomorphic state, and two further ones remain unclear. The symplesiomorphies deserve further study, because they imply an advanced state in Trichoptera and Lepidoptera, and may provide additional synapomorphies for supporting the Trichoptera–Lepidoptera sister-group relationship.

Characters	Autapomorphies of Amphiesmenoptera		
	present	absent	undecided
1, 2, 4, 8, 9, 12, 13	3, 6, 14	5, 7	



**Figure 9.** *Kinitocelis divisinotata* spec. nov., holotype ♀ (B 44): (a) dorsal side of adult, (b) detail of thorax and head, and (c) detail of head and prothorax, ventrolateral.

of Lepidoptera through a suite of 26 synapomorphies. Most characters are found in adults, and a total of 17 concern the exoskeleton. Three of these characters can also be observed in Tarachoptera:

15. *Wings with covering of broad scales.* Fore- and hindwings in Tarachoptera bear scales which are sparsely or densely dispersed in a single layer with only a little overlap. Scales are also present on the underside of the wings, on the head, antenna, thorax, and legs. The wing vestiture, however, resembles the Lepidoptera vestiture only superficially. On closer inspection, the arrangement of scales and scale shape in Tarachoptera do not correspond with conditions in basal Lepidoptera (see Fig. 11e), but as demonstrated by Simonsen (2001) the evolution of wing vestiture is rather complex in basal Lepidoptera.

16. *Male gonopod (= valva) primarily undivided.* Only the tips of the male valvae are visible, barely protruding beyond the hind margins of segment IX (Fig. 3(12)). The valves are likely very small and without any hints of segmentation. This character was listed by Kristensen (1984) as a possible autapomorphy in contrast to the two-segmented gonopods of ancestral Trichoptera. In both orders, the gonopods in the basal lineages are usually large and protruding and serve as grasping organs. The gonopods in Tarachoptera differ clearly from such a structure. The assumed undivided gonopods is either a convergence or a symplesiomorphy at the Amphiesmenoptera level. In any case, the character does not support a relationship to Lepidoptera and Trichoptera.

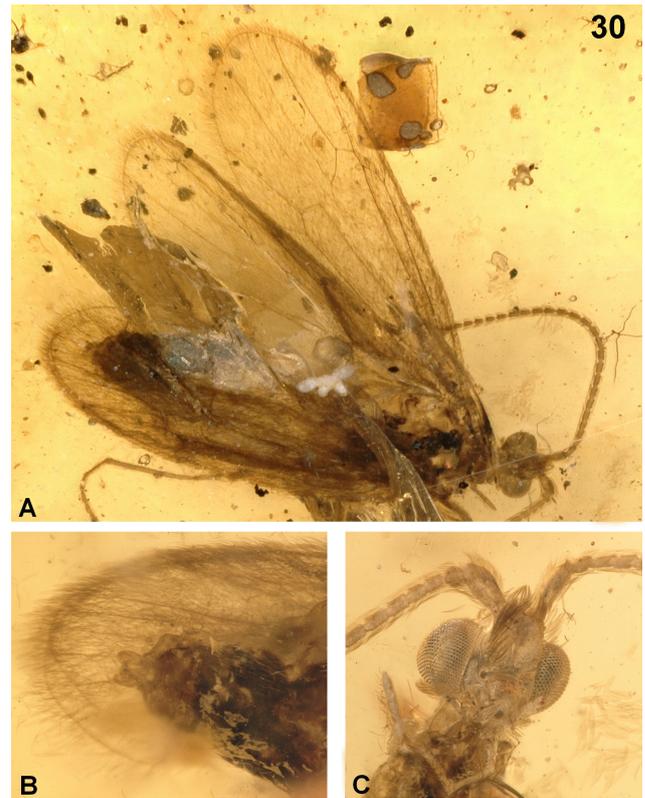
17. *Cerci lacking in both sexes.* This regressive character is probably of little significance. In Trichoptera it is present in female Annulipalpia and Spicipalpia but missing in almost all families of Integripalpia. The cerci are usually flanking the anal opening or are placed behind it, lying on a membranous short or telescoping segment X (ovipositor). A membranous terminal segment or ovipositor is not visible in Tarachoptera, and probably not present (Fig. 4(16, 17)). Even in a retracted position deep inside the genital–anal cavity of the abdomen, the tips of the papillae anales should be discernable at least.

In summary, we did not find any characters that support a sister-group relationship between Tarachoptera and Lepidoptera. The presence of wing scales is a shared character, but their different morphology suggests a different origin and makes it unlikely to assume common ancestry. A predisposition for the development of scales could be thought or held for the presence of an intrinsic trait in ancestral Amphiesmenoptera. The occurrence of wing scales in derived taxa of Trichoptera, unrelated to that of Lepidoptera, can be regarded as evidence of this predisposition.

### Autapomorphies of Trichoptera

Arguments for the monophyly of Trichoptera were first summarized by Ross (1956: 9), who provided nine adult characters. Weaver (1984) and Morse (1997: 434) added five further homologues supporting monophyly for Trichoptera. Kobayashi and Ando (1988) provided four embryological characters. Three morphological characters are applicable to Tarachoptera or deserve some notes:

18. *Modified haustellum.* The haustellum of Trichoptera is one of the main apomorphies of the order. It is a membranous, flexible organ, with a specialized fine structure on its surface that facilitates the uptake of fluid substances or small particles. In basal families the haustellum is small, with somewhat enlarged lateral sides (Klemm, 1966; Kubiak et al., 2015), whereas in families of Integripalpia the haustellum is a large, bulbous organ resembling a short proboscis.

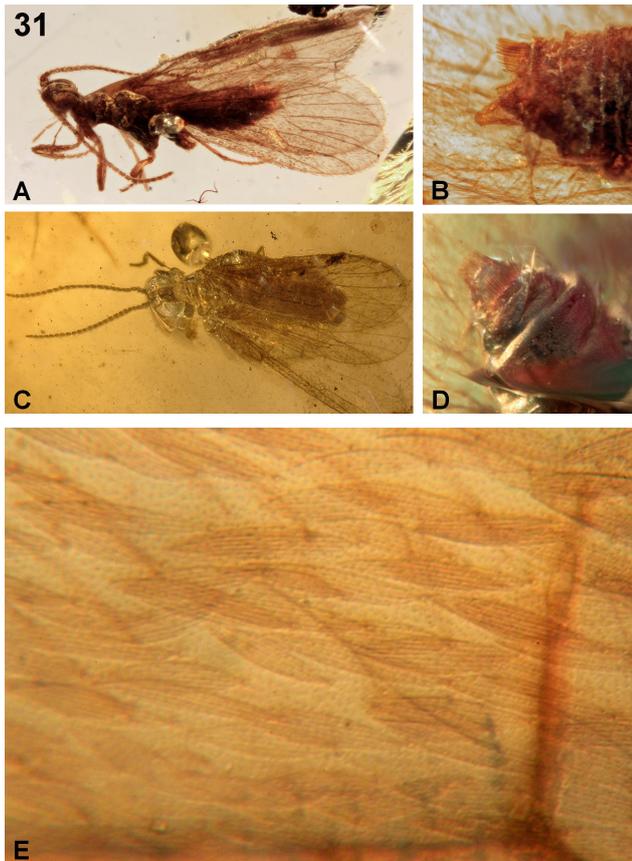


**Figure 10.** *Kinitocelis brevicostata* spec. nov., holotype ♀ (BUB399): (a) ventral view of adult, (b) ventral side of tip of female abdomen, and (c) head, ventral side.

As already mentioned in the discussion on character 1, a clearly developed haustellum is not discernible in Tarachoptera. It is probably in a primitive state, small and not visible externally, a situation also found in the non-glossatan Lepidoptera.

19. *Absence of adult mandibular articulations.* Sclerotized and functional mandibles are plesiomorphic groundplan characters of Ampiesmenoptera. They are retained in primitive Lepidoptera and have well-developed articulations with the head capsule. The mandibles of Trichoptera are non-functional (Klemm, 1966) and exhibit an array of different stages of reduction spanning from fully sclerotized ones lying beneath the anteclypeolabrum to small membranous lobes. The mandibles of Tarachoptera are also reduced; however, this reduction is more advanced and the remains of the mandibles appear as conical stumps in grooves beside the labrum (Fig. 3(14)).

20. *Nygma.* The presence of a single nygma (= corneus spot) in the base of apical cell 3 or fork 2 in the forewings is regarded a trichopteran synapomorphy. According to Kristensen (1984) nygmata occur in other holometabolous orders too, which makes this structure a plesiomorphy at the



**Figure 11.** *Kinitocelis brevicostata* spec. nov., paratype, ♂ (BUB 307): (a) dorso-lateral view of adult, (b) abdominal tip with comb of spines, ventro-lateral, (c) male adult in dorsal view (B 384), and (d) same specimen, abdominal tip, ventral view. (e) *Kinitocelis divisinotata* spec. nov., paratype ♀ (B67), scales on hindwing.

amphiesmenopteran level. The autapomorphic nature of the nygma in Trichoptera is the reduction from several to only one or two (e.g., Calamoceratidae). All examined specimens of Tarachoptera are without a nygma in the forewings.

There is no single autapomorphy which could serve as an argument for shifting the Tarachoptera into a closer relationship with Trichoptera. All shared characters are symplesiomorphies inherited from amphiesmenopteran ancestors.

#### Apomorphies of Tarachoptera, new order

21. *Dorso-ventral depression of the head capsule.* All insect orders can usually be defined by characteristic head morphology in combination with the architecture of the mouth parts. In Fig. 5(23–25) the heads of the two basalmost families of Trichoptera (Rhyacophilidae) and Lepidoptera (Micropterigidae) are depicted and grouped together with the head of Tarachoptera. (BUB 319). The most striking features are the compound eyes, which are comparatively

large and oval, resulting probably from the flattening of the head capsule. The vertex is likewise a flat plate with a pair of elongate setal warts. The frons is also flat, not protruding, and the mouthparts are situated more basad which gives the head a pronounced, hypognathous appearance. This configuration of the head capsule differs strongly from the heads of basal Trichoptera and Lepidoptera, and differs also from the head morphology of other holometabolous orders. The dorso-ventrally flattened head with oval eyes is here interpreted as an apomorphy of the Tarachoptera.

22. *Ocelli absent.* This is a regressive character which cannot easily be ascribed to the groundplan of Tarachoptera. The groundplan of Lepidoptera is without the single, frontal ocellus, and in Trichoptera three large ocelli are present. In many primitive and derived families of both orders the ocelli are reduced in size and can be completely absent.

23. *Angled position of the anteclypeolabrum.* The anteclypeolabrum with a sclerotized proximal and membranous apical part present in most Trichoptera (Kubiak et al., 2015) is also present in Tarachoptera and Lepidoptera. However, at the horizontal furrow between frontopostclypeus and anteclypeolabrum, the latter is bent frontad nearly at a right angle forming a protruding, thick process (Fig. 5(25)). In basal Lepidoptera and Trichoptera the clypeus and labrum are not angled here, and the labrum is a simple linear prolongation of the frons.

24. *Triangular galea.* The basal sclerites of the maxilla are not visible. The distal parts consist of the three-segmented maxillary palpi and a triangular lobe, which is here interpreted as the galea (= outer endite). The inner endite of the stipes, the lacinia, is not visible. In Trichoptera both endites can form a composite structure (the galeolacinia of Kubiak et al., 2015). The galea is a flat plate of triangular shape and seems to have a thin, blade-like anterior margin. It is regarded as autapomorphy of the Tarachoptera.

25. *Maxillary palpi reduced.* Maxillary palpi with five segments and being much longer than the labial palpi with three segments are the ancestral character state in Trichoptera and Lepidoptera (Fig. 5(23–25)). It is retained at least in the females of Trichoptera and in the basal families of Lepidoptera. In advanced families of this order the maxillary palpi are gradually reduced from five, long segments to a complete absence while simultaneously the labial palpi become larger and more prominent, leading to a similar configuration to Tarachoptera palpi. This character, the form of the palpi, has evolved independently in Exoporia and in monotrystian heteroneuran families like Prodoxidae and Palaephatidae (Lepidoptera), but here the lepidopteran proboscis was already in existence (Davis, 1986, 1998), and the reduction of the maxillary palpi seems to be a convergence which must have occurred several times.

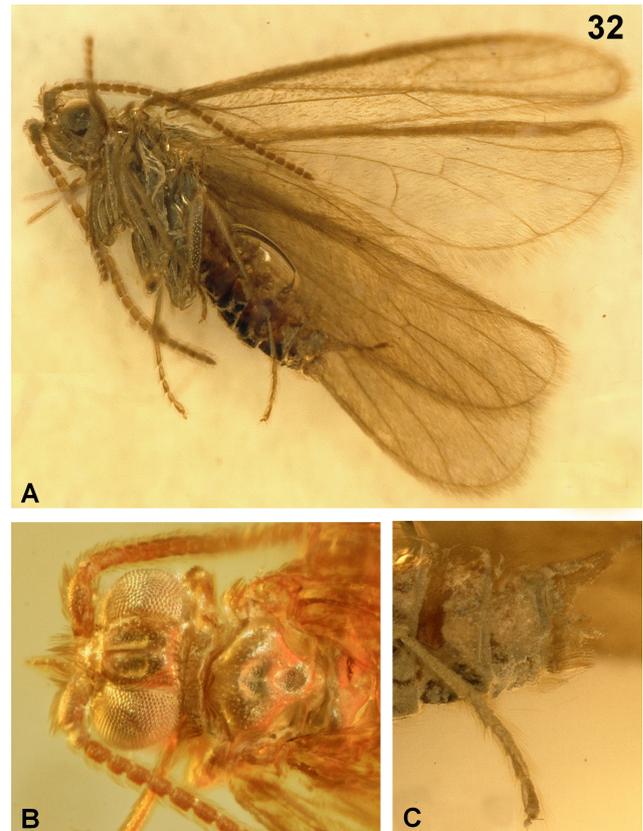
26. *Elongate cervix with dorsal sclerites.* Usually, the membrane between head and prothorax is short and stabilized by the laterocervicalia. In Tarachoptera the cervix is longer and has developed an additional pair of dorsal sclerites, which are hitherto not observed in Lepidoptera/Trichoptera (see character 2).

27. *Tibial spurs absent on all legs.* This strange character is known from specialized species in Psychidae and in Hepialidae (Lepidoptera), but as far as we know it is not described from a Trichoptera taxon. The existence of spurs is a plesiomorphy of the Holometabola and certainly belongs to the groundplan of Amphiesmenoptera. Its complete absence in Tarachoptera is rather unusual and raises questions about the function and adaptive value of spurs in insects. According to Burrows and Dorosenko (2015) spurs are involved in the jumping abilities of adult insects, which do not possess a catapulting mechanism. Jumping is not only a process of rapid movements to escape predators or to bridge space but is also involved in the start of flight. Spurs are needed to enable rapid movements of both the middle and hind legs, providing propulsion that launches winged adult moths into the air. The absence of spurs in combination with a weak wing coupling mechanism appears to be a strong argument for the assumption of a restricted flight ability of the Tarachoptera species.

28. *Radial system of both wings with three branches forming a radial cell.* This is a unique character in the wing venation which does not occur in extant Trichoptera/Lepidoptera. In checking the huge record of illustrations of fossil wings (e.g., Handlirsch, 1906; Kozlov, 1988; Kuznetsov, 1941; Rodendorf, 1962; Tindale, 1980) not a single species was found with radial veins reduced to three branches in the fore- or hindwings. Also, the unbranched media is a further apomorphic trait which contributes to the strange and unique wing venation of Tarachoptera. In Lepidoptera, a simple, undivided medial vein was observed only in the primitive family Aenigmatineidae (Kristensen et al., 2014).

29. *Wing scales.* The scales of primitive Lepidoptera are mostly of the solid type, i.e., without a lumen and perforations, a type 1 bilayer scale covering and primary ridges extending beyond apical scale margin (Simonsen, 2001). The scales of Tarachoptera are also without perforations, but somewhat smaller with smooth apical margins. All scales on wing surface are bent and slightly arched with the concave side facing wing membrane (Figs. 5(25), 11). The scales are of a single type and are arranged in a single layer with little overlapping.

The different morphology and arrangement of the Tarachoptera scales is no evidence of a different origin but suggests a different development which does not indicate a close relationship to Lepidoptera. The scales have obviously



**Figure 12.** *Kinitocelis brevicostata* spec. nov., paratype ♂ (BUB319): (a) ventro-lateral view of adult, (b) head and thorax, dorsal, and (c) abdominal tip and hind tarsus, ventro-lateral view.

evolved independently in the two orders from an amphiesmenopteran ancestor with hairs or setae present on the wings. In Trichoptera scales on the forewings are observed in several genera of more derived families (e.g., Lepidostomatidae, Calocidae, Leptoceridae). Scale-like hairs may also occur on maxillary palpi, the head or the thorax, but usually in small arrangements or as singletons. In contrast to Lepidoptera scales the longitudinal ridges of caddisfly scales lack flutes. It therefore seems likely that scales have arisen independently in these two orders (Huxley and Barnard, 1988: 310). The basalmost families of Trichoptera (Spicipalpia) do not have proper scales on the wing membrane, not exceeding minute scales in the form of androconinal organs or thickened hairs present in species of Hydroptilidae and Glossosomatidae.

There are some further characters which seem to be promising candidates for adding to the list of apomorphies, e.g., the tegulae, the jugum on the forewings, the female and male genitalia and the pleuronota of the pterothorax. The detailed observation of these characters is obscured by position and preservation of the insect within the inclusions available for study at the moment. The morphology of the first and second abdominal segments should also bear valuable traits

for phylogenetic considerations. This character complex is regrettably unobservable in all examined specimens. Future investigations employing micro-CT imagery might provide more insights whether these characters may serve as autapomorphies.

### Phylogeny of Tarachoptera

The Tarachoptera is the first group of fossil Amphiesmenoptera for which we have a more comprehensive set of data compared to other fossil taxa where just wings are available. The external morphology of head, thorax and abdomen could be studied in detail, of course with the restrictions inclusions in amber usually provide. The fossils were compared with extant species of Trichoptera and Lepidoptera. We have excluded from the analysis the extinct taxa such as Protomeropina and Prorhyacophilidae because they provide with the wing venation only a single character type which is uninformative at this taxonomic level (see discussion above). Their inclusion would weaken the strength of the cladogram by the inadequate or unbalanced number of compared characters.

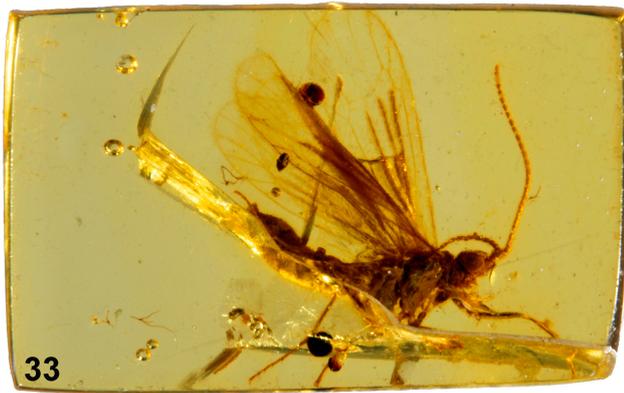
The monophyly of the order is based on the presence of nine derived characters of the adult stage (21–29). Most of these characters are of a regressive nature (22, 25, 27–28) or can be regarded as adaptations to foraging behavior of the adults (21, 23–24, 26). This array of characters is typical for taxa which are highly specialized and adapted to peculiar habitats. There are numerous examples in Trichoptera and Lepidoptera of aberrant species with many derived characters which render the systematic/phylogenetic placement difficult. We have the impression that the species of Tarachoptera follow this pattern qualifying the whole order as a very specialized lineage which evolved from an amphiesmenopteran ancestor independently from the stem-group ancestor of the Trichoptera/Lepidoptera clade (Fig. 6). The age of the Tarachoptera fossils in Burmese amber is about 100 Ma (Ross et al., 2010). Burmese amber is known to contain species of Micropterigidae and glossatan moths (Lepidoptera) (Cockerell, 1919; Grimaldi and Engel, 2005; Ross et al., 2010) and Trichoptera of the families Hydroptilidae, Philopotamidae, Polycentropodidae, Psychomyiidae and Odontoceridae (Botosaneanu, 1981; Wichard and Poinar, 2005; Wichard et al., 2011; Wichard and Wang, 2016a, b). These families take a basal position in the phylogeny of the order (Holzenthal et al., 2007) (Concerning the glossatan moths of Lepidoptera we are unable to assign any of the Burmese fossils we have seen to an extant family). As contemporaries of the same geographical area they appear to stand in strong contrast to the very advanced species of Tarachoptera. This led us to conclude that the group had already undergone a long time of evolution from an ancestor which lived in the Jurassic, probably even earlier.

The phylogenetic sequence for the three orders of Amphiesmenoptera in the cladogram in Fig. 6 has been ar-

ranged according to the synapomorphic characters discussed and enumerated in the text. Tarachoptera is obviously neither an early offshoot of the Lepidoptera branch nor a lineage of the stem group of Trichoptera. It is probably the first genuine taxon of a number of amphiesmenopteran clades which are known by fossil wings only (included in Protomeropina). The Tarachoptera very probably represents an evolutionary line which branched off from the lineage of the Trichoptera/Lepidoptera ancestor long before the split into the two extant orders had occurred. The two genera of Tarachoptera, *Tarachocelis* gen. nov. and *Kinitocelis* gen. nov., appear to be crown groups of this order that have achieved a high level of morphological specialization in the adult stage, which is probably a reflection of an adaptation to a particular habitat or environment. The Tarachoptera obviously went extinct. Their specialization was probably one of the reasons for its disappearance, though we do not know the habits and morphology of the larvae. The concurrently living species of Micropterigidae with their completely scaled wings were detritus (larvae) and pollen feeders (adults) using functional mandibles. This primitive feeding type survived and thereby conserved the scaly vestiture of body and wings, which became the prominent morphological character in the later radiation of the Lepidoptera. The scales of Tarachoptera obviously developed before the scales of the Lepidoptera were “invented”. It is like a blueprint of a character which developed its high adaptive value and significance during the evolution and subsequent radiation of the Lepidoptera, one of the most successful insect orders in terms of species numbers and ecological adaptations in all biomes of the globe.

### The fossil record

The fossil record of Trichoptera and Lepidoptera differs fundamentally. Nearly all fossils of the Amphiesmenoptera, prior to the basal split into Trichoptera and Lepidoptera, were assigned to Trichoptera (Rasnitsyn and Quicke, 2002; Sohn et al., 2012). The extinct taxa were summarized in the suborders Protomeropina and Paratrachoptera and in the families Necrotauliidae Handlirsch, 1906 and Prorhyacophilidae Rieck, 1955. They were not established as monophyletic entities and represent paraphyletic assemblages (Schlüter, 1997) which are not included in the global treatment of Trichoptera (Holzenthal et al., 2011). Most of them belong to lineages of the stem group of Amphiesmenoptera and only a few may be considered as stem-group members of Trichoptera. The Trichoptera contain seven extinct families which are assigned to inclusive taxa of existing suborders or superfamilies. There are no fossil families in the ancestral Rhyacophiloidea, Hydroptiloidea and Glossosomatoidea. All fossils associated with Trichoptera have a wing venation with four to five radial and at least three medial veins. The basal cell (= discoidal cell, DZ) is enclosed by veins of the radial sector (R2+3 and R4+5) and closed apically by r3–r4. These venation features are in striking contrast to Tarachoptera,



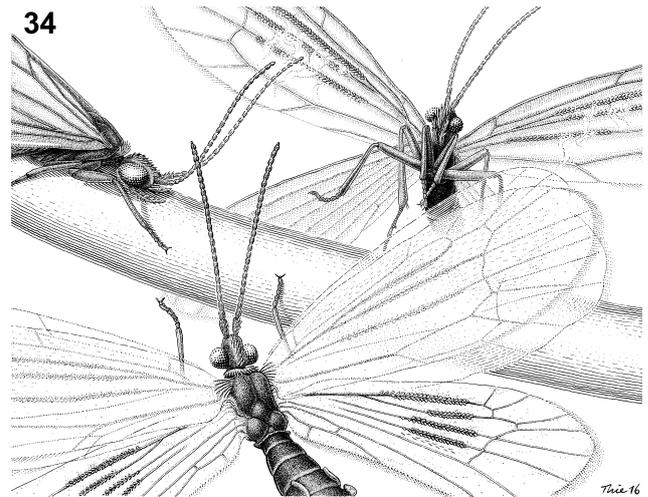
**Figure 13.** *Tarachocelis microlepidopterella* spec. nov., holotype, ♂, lateral view.

whose species have only three radial and one medial cell in both wings. The anterior and posterior margin of the basal cell (= radial cell, RZ) is formed by R1 and R3 and closed anteriorly by r1–r2. The peculiar venation of Tarachoptera is an autapomorphy of the order and appears to be a highly derived character, which was already present in the Cretaceous, at a time when all Trichoptera and most Lepidoptera fossils had a wing venation similar to Micropterigidae.

In addition to the occurrence of an epiphysis on the foretibia, the recognition of fossil Lepidoptera depends on the presence of wing scales. It is the most conspicuous and diagnostic groundplan autapomorphy currently recognized for the Lepidoptera (Kristensen and Skalski, 1998). All fossil families were assigned to the stem group of Lepidoptera with Archaeolepidae, Eolepidopterigidae, Mesokristenseniidae and Ascololepidopterigidae described from the Mesozoic (Zhang et al., 2013). For the Eolepidopterigidae the suborder Eolepidopterigina was established (Rasnitsyn, 1983). As discussed above for the Trichoptera, the wing venation bears no resemblance to Tarachoptera, and wings of fossil Lepidoptera are nearly indistinguishable from Trichoptera (Kristensen, 1984). With the discovery of the scale bearing Tarachocelidae fam. nov., the only family of Tarachoptera, we have to concede that wing scales did not appear for the first time with the advent of the Lepidoptera but have evolved independently in earlier lineages within Amphiesmenoptera.

#### Aspects of the life history of Tarachoptera derived from morphological traits

In general habitus the species of Tarachoptera bear an external resemblance to members of the Trichoptera family Hydroptilidae and Lepidoptera families Heterobathmiidae and Acanthopteroctetidae. These families belong to the ancestral or primitive taxa in each order (Holzenthal et al., 2011; Regier et al., 2015). All species of these families have small to minute adults and are usually without striking wing patterns or colorful markings. The presence of small-sized



**Figure 14.** Life reconstruction of males of *Tarachocelis microlepidopterella* spec. nov. performing actions to attract a female or to push away competing males (illustration by O. Thie).

adults seems to be a shared feature in the evolution and early radiation of both orders. The species of Tarachoptera are also tiny insects. An advantage of being small is the use and occupation of a wide array of microhabitats in a small area. In Lepidoptera the larvae of the smallest species are endophagous and live as leaf, stem, bark, or seed miners. In Trichoptera, the larvae of Hydroptilidae are algal feeders in lenitic and lotic aquatic environments. The females dive into the water in search of oviposition sites. The hairy surface prevents the wings from becoming wet and enables the females to display repetitive diving and flying unless a suitable place is found (Siltalai, 1906: 28). Scaled wings are certainly not an adaptation to an aquatic environment in general. In assuming that wing scales are a morphological feature and adaptation of a terrestrial lifestyle, the Tarachoptera were probably also terrestrial insects. The small size of the imagines is suggestive for assuming that their larvae were endophagous. Leaf mining of larvae is an ancient feeding type documented from compression fossils from the Upper Jurassic and Cretaceous to Oligocene. Leaf mines of the gallery type were found in fossil leaves of several plant families, and were assigned to Lepidoptera families Nepticulidae, Bucculatricidae, and Gracillariidae (Labandeira et al., 1994; Rozeffelds, 1988; Opler, 1982). The association with these families is more or less tentative and, in essence, an extrapolation from present-day mine morphology of known host and mining species. We will probably never know the mines of Tarachoptera species, if they were indeed miners. But the existence of this group in the Cretaceous provides a new candidate among mine producers, which further undermines the validity of identification of fossil mines.

The adult morphology of the studied species of Tarachoptera provides some interesting characters, which might be adaptations to a special lifestyle. The dorso-ventrally de-

pressed head in combination with the probably flatly appressed wings in their resting position suggests a dwelling of the imagines in narrow shelters like crevices, fissures, cracks in bark or in curled leaves. Judging from the mouthparts, the species were not predators but phytophagous insects. External feeding on plant material can be excluded because the adults do not have functional mandibles and are incapable of biting and chewing. With regard to the small size of the species the food material must have been in the form of small particles or fluid substances. In the inclusion BUB 319 the labial palpi are holding a small, rounded particle which was perhaps cracked by the pressure of the labial palpi. If this is not an artifact, the particle is of particular interest. Unfortunately, the margins are smooth and the surface does not offer any microstructures. The question regarding the kind of food remains unanswered, but the position of the labial palps holding the small grain is an indication of highly mobile labial palpi and their possible function in the uptake of food. In the Micropterigidae, the adults feed on pollen grains, which are gathered by the grasping action of the maxillary palpi and transported by the galeae into the preoral cavity and hypopharynx, where they are crushed by the movements of the mandibles (Hannemann, 1956). In Tarachoptera a similar combined action between labial palps and the galea pair seems to be a possible mechanism for the uptake of food.

The absence of spurs on the tibia of all legs is an autapomorphy of the Tarachoptera (see discussion of character 27). Without spurs the insects were probably not able to perform rapid jumps. However, the presumed habit of the adults, described above, does not necessitate jumping abilities. Moreover, as sedentary dwellers in these microhabitats the inclination to fly should have been reduced.

The presence of enlarged, androconial scales (Fig. 13) on fore- and hindwing veins in *Tarachocelis microlepidoptera* spec. nov. opens another aspect in the life history of the new order. The scales were probably connected with glandular cells aggregated along the veins. Males release scent or pheromones when the females are nearby to stimulate the females for mating. Since the sex scales are on the underside of the forewings and upper sides on the hindwings, the display of these organs and dissemination of scent should have been performed during a specific courtship ritual. The release of scent probably happened on an exposed or otherwise suitable place and attracted females and males. Like at a tournament ground, the males were competing with each other for females in a certain courtship ritual. The life reconstruction in Fig. 14 illustrates such an aggregation of males of *T. microlepidoptera* spec. nov.

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prepared and provided the fossils for investigation and commented on the manuscript.

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