



Christelenkidae, a new extinct family based on a new taxon from Eocene Baltic amber (Diptera: Acalyptratae), with X-ray synchrotron microtomography imaging of its structures

Jindřich Roháček¹, Jörg U. Hammel², Viktor Baranov³

¹ Slezské zemské muzeum, Nádražní okruh 31, CZ-746 01 Opava, Czech Republic

² Helmholtz-Zentrum Geesthacht, Max-Planck-Straße 1, 21502 Geesthacht, Germany

³ Estación Biológica de Doñana-CSIC, Avd. Americo Vespucio 26, 41092 Sevilla, Spain

<https://zoobank.org/59920570-16FD-4897-BAA5-5272443A29F3>

Corresponding author: Jindřich Roháček (rohacek@szm.cz)

Received 03 February 2023

Accepted 25 April 2023

Published 25 May 2023

Academic Editors Bradley J. Sinclair, Mónica M. Solórzano-Kraemer

Citation: Roháček J, Hammel JU, Baranov V (2023) Christelenkidae, a new extinct family based on a new taxon from Eocene Baltic amber (Diptera: Acalyptratae), with X-ray synchrotron microtomography imaging of its structures. *Arthropod Systematics & Phylogeny* 81: 475–498. <https://doi.org/10.3897/asp.81.e101441>

Abstract

A new family of Diptera Acalyptratae, Christelenkidae Roháček **fam. nov.**, is established for *Christelenka multiplex* Roháček **gen. et sp. nov.**, an unusual extinct taxon described from a unique male specimen preserved in Baltic amber (Mid-late Eocene, ca 48–34 Ma). Apart from detailed examination by light microscopy and photography, the holotype of the new species has also been studied by means of X-ray synchrotron microtomography with the aim of obtaining additional morphological data for consideration of its relationships. Because of a very peculiar combination of morphological characters, the new family is tentatively considered a separate lineage of Acalyptratae having no apparent sister-group relationship with any of the known families. Its probable relationships to some families of Opomyzoidea and Ephydroidea are discussed.

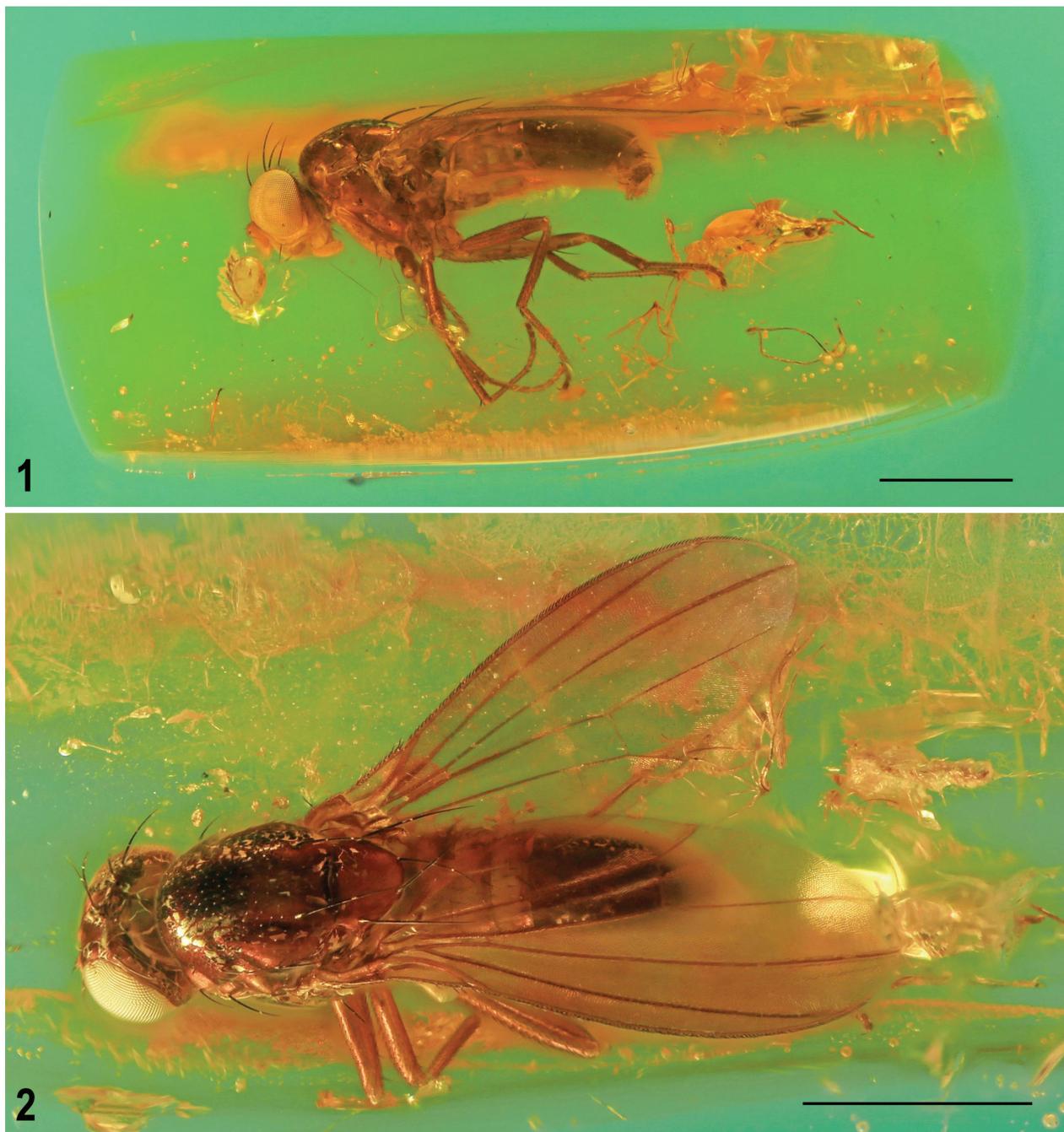
Keywords

Schizophora, new taxa, fossil true flies, morphology, taxonomy, relationships

1. Introduction

Schizophora is a section of true flies (Diptera) with about 80 member families. This monophyletic lineage comprises a huge number of species (over 50, 000), is very diverse and relatively recent in the geological record. Within the Schizophora, two formal groups of families are recognized: the paraphyletic Acalyptratae and the

monophyletic and younger Calyptratae (Wiegmann and Yeates 2017). The oldest reliable acalyptrate (and apparently also schizophoran) fossil records are known from Cambay amber from India (Early Eocene, ca 52 Ma, see Rust et al. 2010; Grimaldi and Singh 2012) and, particularly, from Baltic amber (also including Bitterfeld and



Figures 1, 2. *Christelenka multiplex* sp. nov., male holotype. **1** specimen in the whole amber preparatum, left laterally, with blue background; **2** whole specimen dorsally, with blue background. Scale bars: 1.0 mm. Photos by J. Roháček.

Rovno amber) (Mid-late Eocene, 48–34 Ma, cf. Hennig 1965, 1966, 1967, 1969, 1971, 1972; Tschirnhaus and Hoffeins 2009; Weitschat and Wichard 2010; Perkovsky et al. 2010). The oldest reliable record of Calyptratae, belonging to the family Anthomyiidae, also originates from Baltic amber (Michelsen 2000). It is peculiar that no representative of Acalyptratae has hitherto been found in older Tertiary amber from France: Oise (53 Ma, Nel and Brasero 2010), or in any of the late Cretaceous ambers (see e.g. McKellar and Wolfe 2010; Grimaldi and Nascimbene 2010). Given the unexpectedly large diversity of acalyprate families in Baltic amber, which is comparable to that of recent times or even higher (Tschirnhaus and Hoffeins 2009), it may be assumed that there was an

“explosive” radiation of Acalyptratae in the Mid to Late Eocene. Within this ~10–15 Myr long period, representatives of almost all currently known acalyprate families appeared in the so-called Baltic amber forest. This paleohabitat was characterized by authors including Weitschat and Wichard (2002), Weitschat (2008), Kvaček (2010), Szwedo (2012), Słodkowska et al. (2013) and Sadowski et al. (2020). The rapid diversification of higher flies was most likely connected with development of luxuriant vegetation in the Baltic area during the Early Eocene Climatic Optimum. The vegetation in the Baltic area had a tropical character in the early Eocene warming maximum (ca 49 Ma) that was subsequently changing to subtropical or warm-temperate as a result of gradual cooling towards

the end of the Eocene (Szwedo 2012; Słodkowska et al. 2013; Sadowski et al. 2020). Based on habitat and trophic demands of beetles (Coleoptera) recorded from Baltic amber, Alekseev and Alekseev (2016) characterized the Baltic amber forest as a thermophilic, humid-mixed forest similar to contemporary subtropical forests of eastern and southeastern Asia, but there were certainly also other forest types in the area formed in a warm-temperate climate (Sadowski et al. 2020).

In this context, it is not too surprising that new taxa of Acalypratae, often very odd, are still being discovered in Baltic amber. Intensive collecting of fly amber inclusions by Christel and Hans Werner Hoffeins, Michael von Tschirnhaus and other insect amber collectors has led to recent descriptions of a number of new genera and species of Acalypratae Diptera from Baltic amber (e.g. Hoffeins and Rung 2005; Woźnica 2006, 2007; Grimaldi 2008; Kotrba 2009; Grimaldi and Singh 2012; Hoffeins and Woźnica 2013; Roháček 2013, 2014, 2016, 2020; Pérez-de la Fuente et al. 2018; Roháček and Hoffeins 2020) including representatives of three new extinct families, viz. Hoffeinsmyiidae (Michelsen 2009), Yantaro-myiidae (Barták 2019) and Clusiomitidae (Roháček & Hoffeins 2021).

This study is aimed at description of a very peculiar Eocene (Baltic amber) taxon of “opomyzoid” appearance distinguished by an unusual combination of adult morphological characters that prevents its clear association with any of the known families of Acalypratae Diptera. Because some important structures of the ventral side of the postabdomen of this fly inclusion are obscured and, hence, invisible with an optical light microscope (cf. Fig. 1), X-ray synchrotron microtomography imaging techniques were used to reveal the morphology of some postabdominal sclerites and structures of the male terminalia.

Comparison of the resultant set of morphological characters of this new fossil taxon with those of other acalyprate families confirmed that it cannot be affiliated with any of them, and, therefore, it is described as a new genus and species belonging to a new family (see below).

2. Material and methods

2.1. Material

A single amber sample from the collection of Ch. & H.W. Hoffeins (Hamburg, Germany) has been examined (Figs 1, 2). It is now deposited in the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; SDEI.

2.2. Methods

2.2.1. Preparation of amber sample

The amber with the fly inclusion was prepared by H.W. Hoffeins following the methods described by Hoffeins

(2001) and von Tschirnhaus and Hoffeins (2009). It was cut, ground and polished as close and as parallel as possible to the frontal, dorsal and lateral sides of the fly; subsequently the preparatum was embedded in artificial resin (also ground and polished) in order to facilitate its stereoscopic study.

2.2.2. Techniques of microscopic investigation, photography and measurements

The amber specimen was observed, drawn and measured by means of two types of binocular stereoscopic microscopes (Reichert, Olympus). Drawings of legs were prepared on squared paper using a Reichert binocular microscope with an ocular screen. The whole specimen and its parts were photographed using a Canon EOS 5D Mark III digital camera, a Nikon CFI Plan 4×/0.10NA 30 mm WD or Nikon CFI Plan 10x/0.25NA 10.5 mm WD objective attached to a Canon EF 70–200 mm f/4L USM telephoto zoom lens. During photography, the specimen was repositioned upwards between each exposure using a Cognisys StackShot Macro Rail and the final photograph was compiled from 35 layers using Helicon Focus Pro 7.0.2. The final images (including also those obtained from synchrotron microtomography, see below) were edited in Adobe Photoshop CS6. Some illustrations were drawn using the resultant macrophotographs in which details were inked based on direct observation at higher magnification using a binocular microscope. Measurements: Six characteristics were measured – body length (measured from anterior margin of head to end of cercus, thus excluding the antenna), wing length (from wing base to wing tip), wing width (maximum width), index $Cs_3 : Cs_4$ (= ratio of length of 3rd costal sector : length of 4th costal sector), index $r-m\backslash dm-cu : dm-cu$ (= ratio of length of section between r-m and dm-cu on cell dm : length of dm-cu).

2.2.3. Techniques of X-ray synchrotron microtomography imaging

The specimen was scanned with the Imaging Beamline P05 (Greving et al. 2014; Wilde et al. 2016) operated by the Helmholtz-Zentrum Hereon at the PETRA III storage ring (Deutsches Elektronen Synchrotron – DESY, Hamburg, Germany), using a photon energy of 18 keV and a sample-to-detector distance of 100 mm. A series of projections was recorded with a custom developed 20 MP CMOS camera system with an effective pixel size of 1.28 μm (Lytaev et al. 2014). For each tomographic scan 3601 projections at equal intervals between 0 and π were recorded. Tomographic reconstruction was conducted by applying a transport of intensity phase retrieval approach and using the filtered back projection algorithm (FBP) carried out in a custom reconstruction pipeline using Matlab (Math-Works) and the Astra Toolbox (Moosmann et al. 2014; van Aarle et al. 2015, 2016). Raw projections were binned twice for further processing, resulting in an effective pixel size of the reconstructed

volume (voxel) of 2.56 μm . We have conducted a reconstruction of the scanned volumes with Drishti ver. 2.6.6 (Limaye 2012). To downscale the strain on the RAM and video card of the computer used, we have scaled down all the tiff images to 50% using the Fiji “scale” function (Schindelin et al. 2012). Downscaled stacks were then rendered into 3D volume in Drishti ver. 2.6.6 (Limaye 2012).

2.2.4. Morphological terminology

Terminology of morphological characters follows Roháček (2013) and Roháček and Hoffeins (2021) to be in continuation with recent studies of the senior author on fossil Anthomyzidae and Clusiomitidae. Terms of structures for the male terminalia are largely based on the “hinge” hypothesis for the origin of the eremoneuran hypopygium, re-discovered and documented by Zatwarnicki (1996) and, therefore, the terms derived from other hypotheses are listed below as synonyms to avoid any confusion. Morphological terms for structures of the male abdomen and terminalia are depicted in Figs 25, 27–30 and 35. Terminology used for wing veins and thoracic sclerites is traditional and, therefore, the synonymous morphological terms for these structures and/or their abbreviations used in the recent Manual of Afrotropical Diptera (Cumming and Wood 2017), are given in parentheses in the list of abbreviations below:

A₁ = anal vein (CuA+CuP), **ac** = acrostichal (setulae), **ar** = arista, **bm** = basal medial cell, **C** = costa, **ce** = cercus, **clp** = clypeus, **Cs₁**, **Cs₂**, **Cs₃**, **Cs₄** = 1st, 2nd, 3rd, 4th costal sector, **CuA₁** = cubitus (M₄), **cup** = posterior cubital cell (cua), **cx₁**, **cx₃** = fore, hind coxa, **dc** = dorsocentral setae, **dm** = discal medial cell, **dm-cu** = discal medial-cubital (posterior, dm-m) crossvein, **dp** = distiphallus, **ep** = epandrium (periandrium), **f₁**, **f₂**, **f₃** = fore, mid, hind femur, **gs** = gonostylus (surstylus), **ha** = haltere, **hu** = humeral (postpronotal) (seta), **hy** = hypandrium, **lab** = labellum, **M** = media (M₁), **ma** = medandrium (bacilliform sclerite, subepandrial sclerite, S10), **mspl** = mesopleural (anepisternal) (seta), **mt₃** = hind basitarsus, **npl** = notopleural (seta), **oc** = ocellar (seta), **ors** = fronto-orbital (seta), **pa** = postalar (seta), **pg** = postgonite, **plp** = palpus, **poc** = postocular setulae, **ppl** = propleural (proepisternal) (seta), **prs** = presutural (presutural intra-alar) (seta), **pvt** = postvertical (postocellar) (seta), **R₁** = 1st branch of radius, **R₂₊₃** = 2nd branch of radius, **R₄₊₅** = 3rd branch of radius, **r-m** = radial-medial (anterior) crossvein, **S1–S8** = abdominal sterna, **S7+S8** = synsternum 7+8, **sa** = supra-alar (seta), **sc** = scutellar (seta), **Sc** = subcosta, **scu** = scutellum, **ssc** = subscutellum, **stpl** = sternopleural (katepisternal) (seta), **T1–T6** = abdominal terga, **t₁**, **t₂**, **t₃** = fore, mid, hind tibia, **vi** = vibrissa, **vte** = outer vertical (seta), **vti** = inner vertical (seta).

3. Results

3.1. Christelenkidae Roháček, fam. nov.

<http://zoobank.org/AA3CA70D-2918-4836-AA9E-2CFE288B06DE>

Type genus. *Christelenka* gen. nov., designated here.

Diagnosis. Body: relatively slender and elongate, particularly the abdomen, ca 3 mm long (Figs 1–4). Head: Antenna exclinate (Figs 6, 9) and distinctly geniculate between pedicel and 1st flagellomere, the latter strongly decumbent (Figs 5, 8), discoidal but slightly elongate (somewhat longer than scape + pedicel); arista extremely dorsobasal; pedicel cap-like, with distal margin simple. Frontal triangle not developed; lunule absent (Figs 6, 9). Cephalic setae long but only present on posterior third of frons and on vertex (Figs 8–10); pvt small, convergent (crossed); vti by far the longest cephalic seta, upright and reclinate; vte strongly exclinate; oc upright to proclinate and divergent, longer than pvt; only 1 reclinate and slightly exclinate ors; frons in front of ors bare; vibrissa small but distinct, strongly medially curved; no genal seta or setulae. Thorax: with 1 postsutural dc, 1 prs, 1 sa, 1 pa, 2 sc (apical crossed, laterobasal the longest thoracic seta); 0 mspl, 1 stpl, 0 ppl. Mesonotum convex, somewhat hump-like; prosternum bare; mesopleuron with posterodorsal ridge developed (Fig. 14); subscutellum distinctly protruding (Fig. 17), metasternal area bare. Wing: with apex at end of R₄₊₅, somewhat pointed; membrane not distinctly patterned; C extending to apex of M, with 2 breaks (humeral and subcostal) proximally, and with uniform dark setulae (none spine-like) ending between apices of R₂₊₃ and R₄₊₅ (see Fig. 18); Sc basally distinct but distally fused with R₁, the latter without a preapical kink; no distinct humeral crossvein; cells dm, bm and cup complete; alula (not clearly visible) small and anal lobe well developed. Legs: cx₁ elongate (Fig. 13), and with 1 ventral seta in middle (Fig. 15); f₁ with 1 dorsal seta and an anteroventral ctenidium-like row of small blunt spines (Fig. 21); f₃ with 1 dorsal and 1 anteroventral seta (Fig. 23); all tibiae with 1 dorsal seta. Abdomen (of male) with unusual preabdominal sclerites: segments 1–4 with both terga and sterna short, while T5 and S5 are unusually strongly elongate (Figs 25, 28). Male postabdomen: T6 reduced (transversely band-like) but distinct and slightly asymmetrical; S6 of moderate length and symmetrical; T7 absent; S7+S8 fused to form a somewhat asymmetrical dorsal synsclerite with a pair of strong posterior setae. Male genitalia: epandrium arch-shaped, slightly asymmetrical and open ventrally (Figs 29, 30); cerci separate, large, inserted below large anal fissure; gonostyli



Figures 3, 4. *Christelenka multiplex* sp. nov., male holotype. **3** whole specimen, left laterally; **4** ditto, right laterally. Scale bars: 1.0 mm. Photos by J. Roháček.

somewhat asymmetrical, simple, elongate, tapered towards blunt apex, articulated with epandrium; hypandrium, short, obviously frame-shaped and symmetrical (Fig. 35); postgonites simple, elongate and pointed, symmetri-

cal; distal part of aedeagus (considered to be distiphallus) short, broad distally (Figs 32, 35).

For more detailed description see below under *Christelenka* gen.n.

3.2. *Christelenka Roháček, gen. nov.*

<http://zoobank.org/146B15DA-CF29-4E4C-BE91-DC-CCD07F6099>

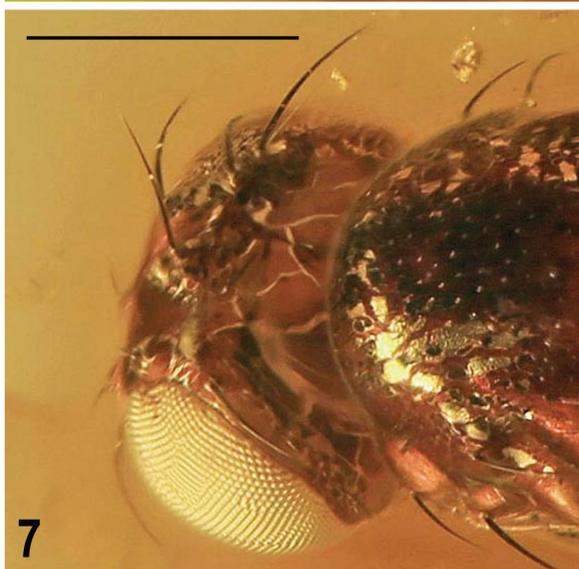
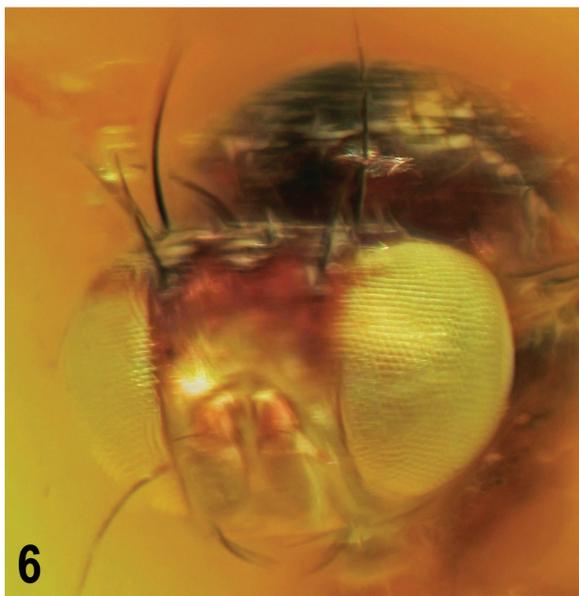
Type species. *Christelenka multiplex* sp. nov., designated here.

Diagnosis. Same as above for Christelenkidae fam. nov.

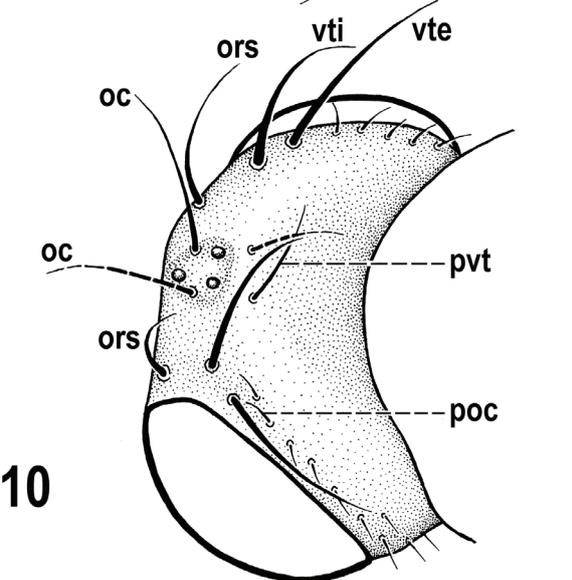
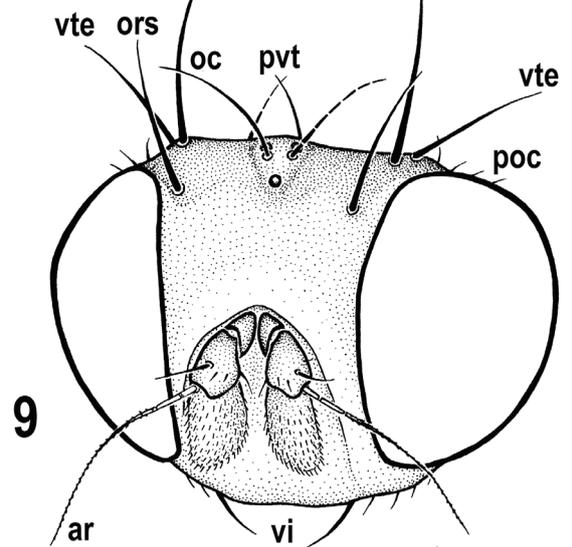
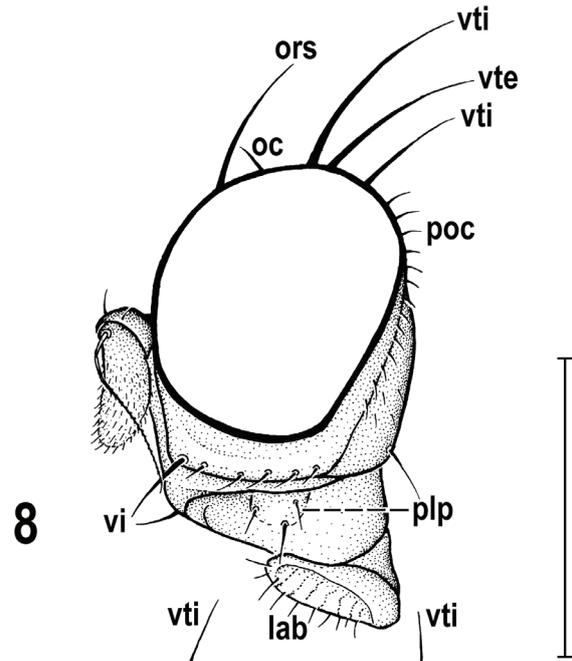
Description. Male. Small (body length ca 3 mm), largely dark brown, subshiny (Figs 1–4). — **Head:** (Figs 5–10) higher than long; occiput dorsally concave (Fig. 7). Frons (Figs 6, 9) moderately broad, hardly narrowed anteriorly, devoid of setae or microsetae in front of ors. Orbital plate very poorly delimited. Frontal triangle absent; ocellar triangle small and slightly elevated; ocelli small (Fig. 9); ptilinal suture distinct but lunule absent. Face (prae-frons) slightly concave, evenly sclerotized; gena distinct from postgena (Fig. 5). Cephalic macrosetae (Figs 8–10): pvt small, convergent (crossed); vti up-right, reclinate, subparallel (slightly inclinate), long; vte shorter, strongly exclinate; oc divergent, more upright than proclinate, situated within ocellar triangle; only 1 ors, slightly exclinate and reclinate, in posterior half of frons; vi present, curved medially (Figs 8, 9); subvibrissa and genal seta not developed. Postocular setulae in single long row; postgena with 1 distinct seta (Fig. 8); peristomal setulae sparse. Eye bare, convex, suboval (Figs 5, 6). Palpus rather slender (Figs 11, 12), with a few setulae (Fig. 8). Subcranial (oral) cavity relatively large (Figs 11, 12). Mouthparts with clypeus short and projecting little from oral cavity (Fig. 11) and labellum fleshy (Figs 8, 11, 12). Antenna (Figs 5, 6, 8, 9, 15) decumbent and geniculate between pedicel and 1st flagellomere. Pedicel cap-like, without dorsal seam or incision, with dorsal and lateral margins also simple, not projecting; 1st flagellomere suboval, laterally compressed (Figs 8, 9); arista dorsobasal, inserted extremely basally, very shortly pubescent (Figs 9, 15). — **Thorax:** with mesonotum distinctly convex, somewhat hump-like anterodorsally (cf. Figs 1, 3, 13, 14, 17). Humeral (postpronotal) callus and notopleural area more (postpronotum) or less protruding. Mesopleuron (anepisternum) with slightly elevated ridge at posterior margin dorsally; dorsal membranous part of pleural suture separating it from pteropleuron (anepimeron) enlarged. Scutellum large, broad, distinctly convex dorsally (cf. Figs 13, 17); subscutellum well developed (Fig. 15, 17). Metasternal area bare. Thoracic chaetotaxy (Figs 15, 16): 1 hu plus 6–8 microsetae on humeral callus; 2 npl; 1 prs; 1 sa; 1 pa; 1 postsutural dc, situated far behind level of sa; ac microsetae unordered, in about 6–8 incomplete rows; 2 sc, apical sc crossed, laterobasal sc longest and strongest of thoracic setae (Fig. 16); no ppl; no mesopleural (anepisternal) seta or setula; 1 (posterior) stpl; prosternum obviously bare. — **Wing:** (Figs 2, 18, 19) rather elongate, with apex somewhat pointed. C extended to apex of M but its last part (Cs₄) attenuated; C in Cs₂ and Cs₃, with dense uniform setulae ending in middle of Cs₃ (Fig. 18). Two costal breaks (smaller humeral,

larger subcostal) developed. Sc distinct but distally fused with R₁ but without preapical kink. Humeral crossvein not developed. R₁ short, robust and bare. R₂₊₃ long, subparallel with C, ending in C farther from wing apex than M. R₄₊₅ distally subparallel with M, ending in C at wing apex. Distal part of M terminally weakened and reaching wing margin (Fig. 19) (in right wing, cf. Fig. 18, M does not reach margin but considered anomalous). Discal (dm) cell elongate, distally widened; anterior crossvein (r-m) situated slightly beyond basal fourth of cell dm. Distal part of CuA₁ reaching wing margin; A₁ short, ending far from wing margin. Cells bm and cup closed. Anal lobe well developed. Alula (not clearly visible) small, narrow. Haltere (Figs 13, 15) relatively large. — **Legs:** relatively slender and long, fore leg shortest; cx₁ (Figs 3, 13, 15) distinctly elongate, with 1 seta in middle of ventral margin; f₁ with 1 enlarged posterodorsal subapical seta and 1 dorsal seta in anterior three-fifths (Figs 20, 21), with anteroventral ctenidium-like row of 8 small, very short blunt spines (Fig. 21); f₂ (Fig. 22) with row of 8 anterior setae becoming longer towards apex; f₃ with 2 strong setae (Fig. 23): longer anteroventral seta at distal third, and shorter dorsal seta at distal fourth. All tibiae (fore tibiae obscured) with 1 dorsal preapical seta; t₂ (Fig. 22) with 1 ventroapical seta, shorter than dorsal preapical seta; t₃ (Fig. 23) with dorsal preapical seta longer than on other tibiae. Claws on all tarsi well developed. — **Abdomen:** (Figs 24–28) slender, elongate. Preabdominal terga and sterna modified: T1 short (slightly shorter than T2), distinctly separated from T2; T2–T4 short (see also Fig. 17), transverse, subequal in length; T5 greatly elongated, somewhat enlarged, expanded lateroventrally (Figs 24–28). Preabdominal sterna S1–S4 short, total length subequal to total length of T1–T4 (cf. Figs 17, 25, 28); S1 (shortest), S2 (longer), S3 and S4 (longer and wider than S2); S5 very elongate (though shorter than T5) and narrow (Fig. 32). Pleural membrane of preabdominal segments reduced. — **Postabdomen:** (Figs 24–27, 29, 30, 32–35) more or less symmetrical. T6 seemingly absent (cf. Figs 29, 30) but forming short band-like sclerite hidden under enlarged T5 (cf. Figs 27, 32). S6 (Figs 25, 31–35) of moderate length, trapezoidal, symmetrical (Fig. 35). T7 absent. S7+S8 fused to form slightly asymmetrical dorsal saddle-shaped synsclerite bearing pair of robust dorsolateral setae. — **Genitalia:** Epandrium (Figs 25, 27, 29, 30) arch-shaped, open ventrally; anal fissure large (cf. Figs 34, 35). Cerci free, symmetrical, robust, situated below anal fissure (cf. Fig. 30). Gonostyli (Figs 27, 30, 32) simple, separate from epandrium but somewhat asymmetrical. Hypandrium relatively short, obviously frame-shaped (Figs 34, 35). Postgonite symmetrical, simply pointed and elongate with apex exceeding that of aedeagus (Figs 27, 30, 32–35). Distiphallus (?) short, relatively broad, especially distally (see Fig. 35). — **Female.** Unknown.

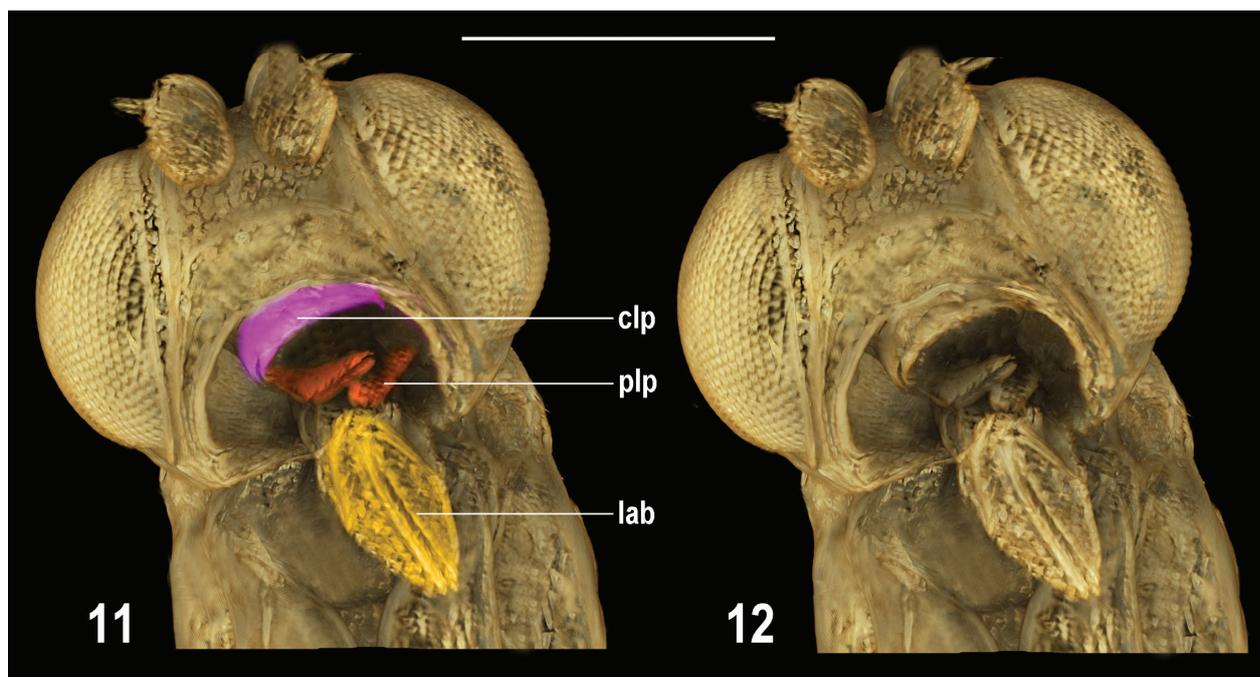
Etymology. The name of the genus is an abbreviated compound of the first names of two ladies, viz. Christe[l] + Lenka, playing important roles in the scientific career of the first author. It is dedicated to Christel Hoffeins



Figures 5–7. *Christelinka multiplex* sp. nov., male holotype. 5 head left laterally; 6 ditto, frontally; 7 ditto, laterocaudally. Scale bar: 0.5 mm. Photos by J. Roháček.



Figs 8–10. *Christelinka multiplex* sp. nov., male holotype, cephalic chaetotaxy. 8 head left laterally; 9 ditto, frontally; 10 ditto, laterocaudally. — Scale bar: 0.5 mm. For abbreviations see 2.2.4. Morphological terminology.



Figures 11, 12. *Christelenka multiplex* sp. nov., male holotype. **11** head frontoventrally, with some structures coloured; **12** ditto, without colours. Scale bar: 0.5 mm. For abbreviations see 2.2.4. Morphological terminology. Microtomograph image by V. Baranov.

(Hamburg, Germany) who discovered this amazing fly in Baltic amber, and to Lenka Roháčková, the wife of the first author, for her lifelong support and patience with his research in dipterology.

3.3. *Christelenka multiplex* Roháček, sp. nov.

<http://zoobank.org/CA2593AE-BC0B-4EFA-8E8A-55E300CF02B4>

Figs 1–35

Description. Male. Total body length 3.1 mm; general colour brown to dark brown, with some parts of head and abdomen lighter coloured (see below); thorax and abdominal terga probably subshiny to partly shiny (Figs 1–4). — **Head:** (Figs 5–10) about 1.3 times as high as long, dorsally very slightly wider than thorax. Dorsal part of occiput distinctly concave (Fig. 7). Head distinctly bicolourous, dorsally and posteriorly largely dark brown, anteriorly and ventrally orange ochreous to whitish yellow. Frons (Figs 6, 9) moderately broad, hardly tapered anteriorly, largely bare, dark brown behind apex of ocellar triangle and ors, reddish brown to orange ochreous in middle part and yellow to whitish yellow on crescent-shaped anterior margin surrounding bases of antennae. Orbital plate hardly delimited, slightly visible only at base of ors, dark brown behind latter, reddish brown to orange ochreous anteriorly, up to level of ptilinal fissure. Frontal triangle not developed. Ocellar triangle blackish brown, small, somewhat elongate, slightly protruded among ocelli. Ocelli small (Fig. 9). Lunule absent (or concealed within dorsal medial part of face). Face (prae-

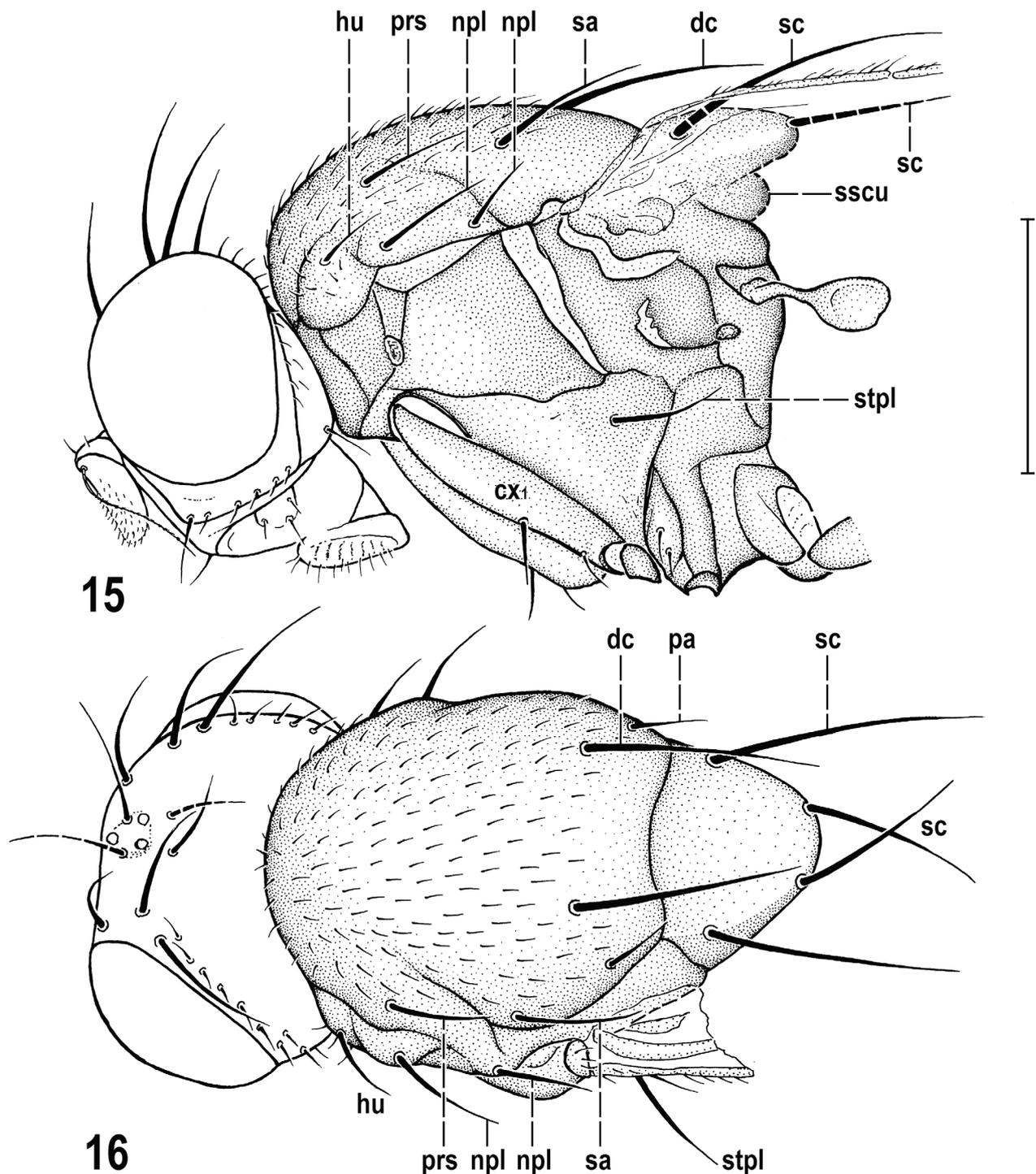
frons) slightly concave, yellow to yellowish white. Parafacialia and gena yellowish white, obviously whitish microtomentose; gena narrowly yellow-margined ventrally. Postgena darker yellow to ochreous, adjacent part of occiput brown, becoming darker dorsally (Fig. 5). Cephalic chaetotaxy (Figs 8–10): pvt relatively small, with apices crossed; vti long and strong (longest cephalic seta); vte shorter and weaker, about two-thirds length of vte; oc divergent, more upright than proclinate, relatively thin and short (shorter than ors), situated within ocellar triangle; only 1 (relatively robust) ors situated near level of anterior ocellus; no setae or setulae in large anterior part of frons; postocular setulae (13 or 14) in single long row behind posterior margin of eye, none of them enlarged but 1–2 most dorsal somewhat inclinate (see Figs 9, 10); a few additional setulae on adjacent lateral parts of occiput above postgena; postgena with 1 distinct posteroventral seta (Fig. 8); vi distinct though not very long, curved medially (Figs 8, 9); subvibrissa not developed; peristomal setulae fine, short and sparse (5 visible, Fig. 8); no genal seta. Eye relatively large, bare, strongly convex (Figs 5, 6), suboval, with straighter posteroventral margin; longest diameter slightly oblique, about 1.3 times as long as shortest diameter. Gena low but distinct; height about 0.17 times as long as shortest eye diameter (Fig. 8). Palpus poorly visible in light microscope (where seemingly short and robust, Fig. 8) but actually slender, somewhat twisted in microtomographs (Figs 11, 12), probably yellow, with a few fine black setulae (Fig. 8). Subcranial (oral) cavity relatively large (Figs 11, 12). Mouthparts yellow to pale yellow; clypeus short, narrow and projecting little from oral cavity (Fig. 11), labellum fleshy, finely pale setulose (Figs 8, 11, 12). Antenna (Figs 5, 6, 8, 9) strongly decumbent, geniculate between pedicel and 1st flagellomere, somewhat exclinate, relatively small. Scape



Figures 13, 14. *Christelenka multiplex* sp. nov., male holotype. **13** whole specimen, left laterally; **14** ditto, right laterally. Scale bar: 1.0 mm. Microtomograph images by V. Baranov.

and pedicel reddish brown, markedly darker than 1st flagellomere; pedicel with simple margin dorsally and laterally, with 1 longer but fine dorsal seta in addition to series

of very small marginal setulae; 1st flagellomere somewhat longer than scape and pedicel combined, yellow, elongate suboval, distinctly compressed laterally, very



Figures 15, 16. *Christelenka multiplex* sp. nov., male holotype, thoracic chaetotaxy. **15** thorax, left laterally; **16** ditto, dorsally. Scale bar: 0.5 mm. For abbreviations see 2.2.4. Morphological terminology.

finely pubescent (Figs 8, 9). Arista dorsobasal, inserted at posterior margin of 1st flagellomere, only about 1.8 times as long as antenna, completely brown, with two basal segments (aristomeres) elongate (not thickened); terminal section very shortly ciliate (pubescent), with longest cilia preapically (Figs 9, 15). — **Thorax:** very slightly narrower than head (Fig. 2), pale brown to blackish brown, darker and subshiny to shiny dorsally, paler laterally (Fig. 3). Mesonotum distinctly convex, somewhat hump-like anterodorsally (cf. Figs 1, 3, 13, 14, 17), blackish brown in anterior half and also laterally (outside of dc

lines) up to scutellum, light brown medially (between dc lines) in posterior half (see Fig. 2). Humeral (postpronotal) callus and notopleural area light brown and more (postpronotum) or less protruding; scutellum light brown (concolourous with posterior half of mesonotum), narrowly darkened only basolaterally, with suture between scutum and scutellum distinctly dark brown-margined (Fig. 3). Pleural part of thorax also somewhat variegated (Fig. 3): mesopleuron (anepisternum) light brown, with darkened area along dorsal margin; sternopleuron (katepisternum) also light brown, with darkened postero-

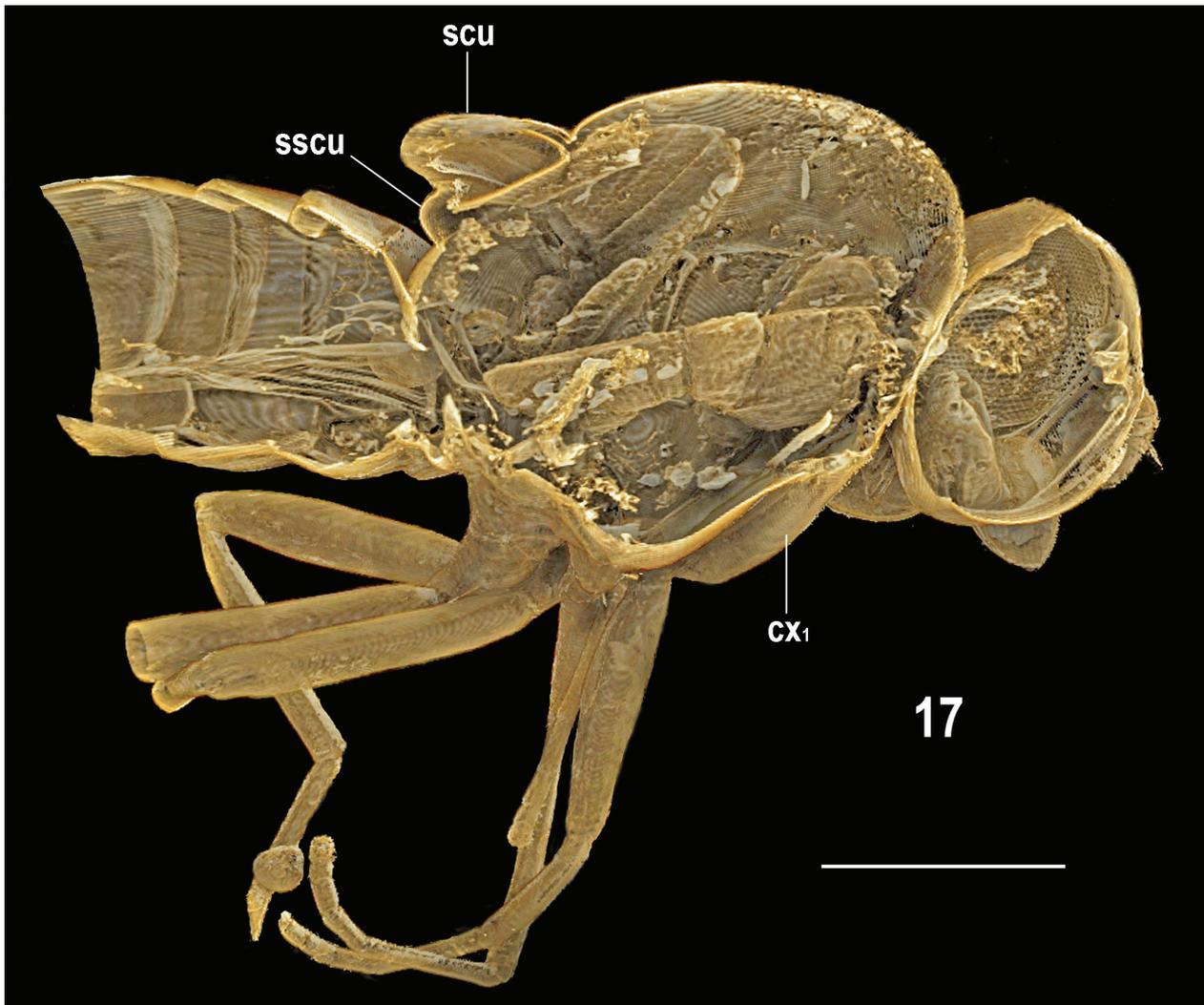
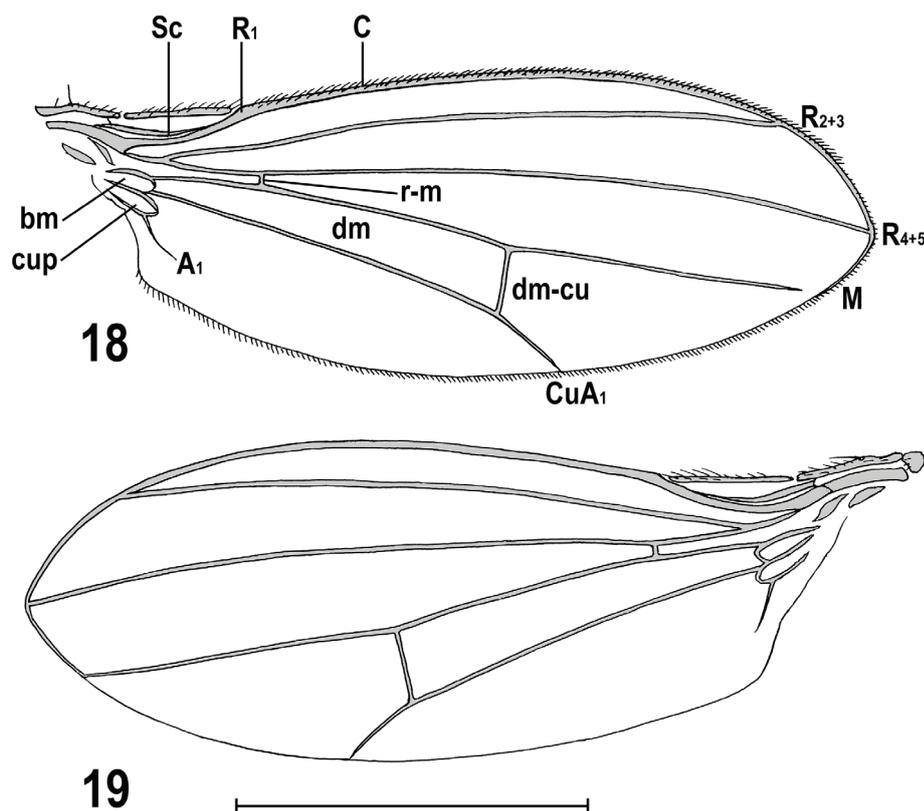


Figure 17. *Christelinka multiplex* sp. nov., male holotype, anterior part of body: sagittal section right laterally. Scale bar: 0.5 mm. For abbreviations see 2.2.4. Morphological terminology. Microtomograph image by V. Baranov.

dorsal corner; propleuron (proepimeron + proepisternum) and most of posterodorsal part of pleuron including metanotum (anatergite) and subscutellum dark brown. Mesopleuron with slightly elevated ridge at posterior margin; dorsal membranous part of pleural suture separating it from pteropleuron (anepimeron) enlarged. Scutellum large, broad, rounded subtrapezoidal, distinctly convex dorsally (cf. Figs 13, 15, 17); subscutellum also distinctly protruding as shown in microtomograph image (see Fig. 17). Metasternal area obviously lacking setae. Thoracic chaetotaxy (Figs 15, 16): 1 moderate hu (about as long as posterior npl) plus 6–8 microsetae on humeral callus); 2 npl (anterior relatively strong, distinctly longer than posterior); 1 distinct prs (as long as anterior npl); 1 long sa (slightly longer than anterior npl); 1 short and weak pa (smaller than hu); only 1 postsutural dc, very long and strong (almost as long as laterobasal sc), situated far behind level of sa; scutum otherwise covered by uniform, somewhat irregularly scattered microsetae; ac microsetae also unordered, in about 6–8 incomplete rows in front of suture, with only 4 ac microsetae posteriorly, between dc macrosetae (Fig. 16); 2 sc, apical strong and crossed, markedly shorter than laterobasal sc; latter longest and

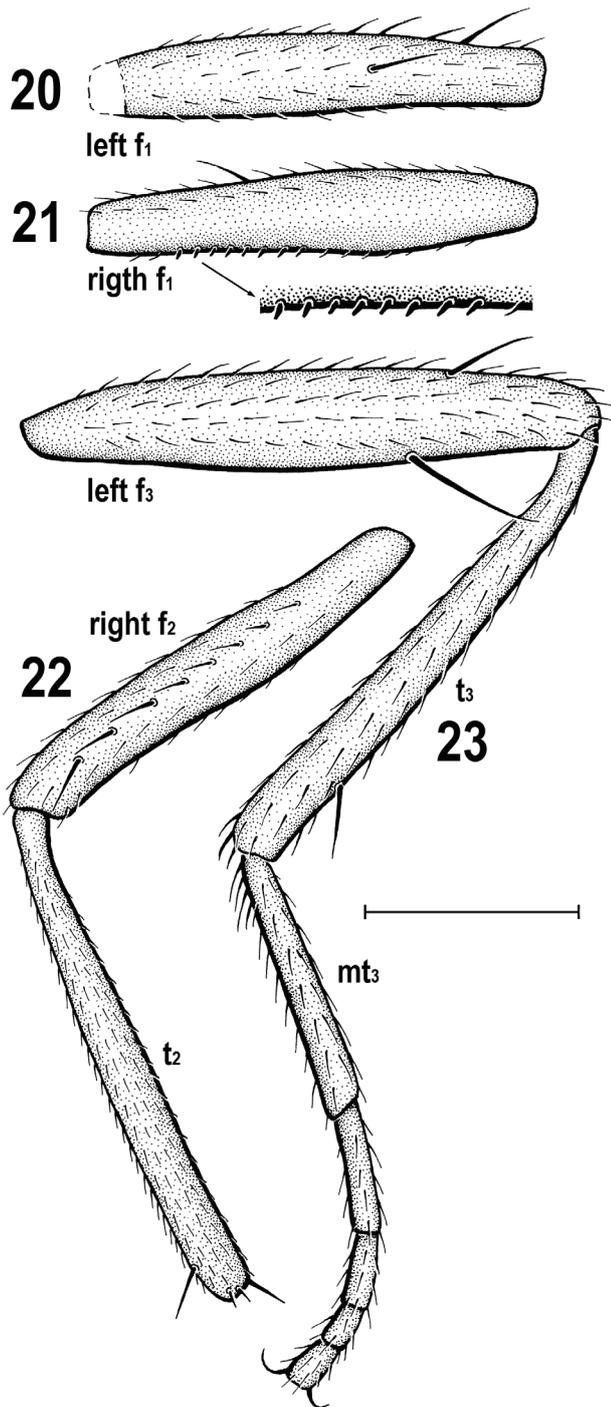
strongest thoracic seta (Fig. 16); no ppl observed; no mesopleural (anepisternal) seta or setula; sternopleuron (Fig. 15) with only 1 upcurved (posterior) stpl, about as long as anterior npl and a few, hardly visible, microsetae (1 dorsally, 3 or 4 on ventral corner of sclerite); prosternum obviously bare. — **Wing:** (Figs 2, 18, 19) rather elongate, with apex somewhat pointed at insertion of R_{4+5} , not rounded; veins pale brown, membrane brownish-tinged, most darkened in cell r_{2+3} (between R_{2+3} and C). C reaching apex of M but last segment (Cs_4) attenuated; C with uniform, very dense, dark setulae (except for longer seta basally, and somewhat enlarged setulae on Cs_1 , see Figs 18, 19) ending in middle of Cs_3 (see Fig. 18). Two costal breaks, smaller humeral and larger subcostal. Sc proximally distinct, distally attenuated and gradually fused with R_1 , without forming a preapical kink on the latter. Humeral crossvein not visible. R_1 short, robust and bare, slightly bent to C. R_{2+3} long, slightly curved, subparallel with C, apically straightened, ending in C distinctly farther from wing apex than vein M. R_{4+5} also shallowly but distinctly curved, distally subparallel with M, ending in C at wing apex. Distal part of M almost straight or indistinctly bent forward, distally attenuated, reaching (left



Figures 18, 19. *Christelenka multiplex* sp. nov., male holotype, wings. **18** right wing, dorsally; **19** left wing, dorsally. Scale bar: 1.0 mm. For abbreviations see 2.2.4. Morphological terminology.

wing, Fig. 19) or not reaching (right wing, Fig. 18) wing margin. Discal (dm) cell elongate, distally widened, with side veins slightly curved; upper distal corner obtuse-angled, lower distal corner acute-angled; anterior crossvein (r-m) situated slightly beyond basal fourth of cell dm. Distal part of CuA₁ slightly (about 1.2 times) longer than dm-cu crossvein and reaching wing margin; A₁ short, distally attenuated, ending far from wing margin. Cells bm and cup closed. Anal lobe distinct. Alula (not visible) probably small and narrow. Wing measurements: length 2.68 mm, width 0.99 mm, Cs₃ : Cs₄ = 1.69, r-m/dm-cu : dm-cu = 3.63. Haltere (Figs 13, 15) relatively large, with dirty yellow stem and whitish yellow knob. — **Legs:** largely pale brown to brown, femora darkest, coxae, tibiae and tarsi paler, cx₁ lightest. All legs relatively slender and long. Fore leg shortest but cx₁ (Figs 3, 13, 15) distinctly elongate, only slightly shorter than f₁, with 1 long seta in the middle of ventral margin. f₁ with distinct dorsal seta at anterior two-fifths (Figs 20, 21) and row of 4 long posteroventral setae on distal half, with last (preapical) distinctly longer; anteroventrally with row (ctenidium-like) of 8 small, very short blunt spines (Fig. 21) extending from midpoint of f₁ to distal fifth; f₂ (Fig. 22) longer than f₁, lacking distinct dorsal seta, with row of anterior (not posterior) setae becoming longer towards apex, with last (longest) seta at about distal sixth; f₃ with 1 longer anteroventral seta at distal third and 1 shorter dorsal seta at distal fourth (Fig. 23). Probably all tibiae with dorsal preapical seta, although not verified on t₁ (apex of tibia not visible in either fore leg); t₂ (Fig. 22) with 1 distinct but relatively short dorsal preapical seta, 1 slightly shorter ventroapical seta and 2 small anterior setulae on apex; t₃ (Fig. 23) with 1 dorsal preapical seta longer and more

distant from apex of tibia than that on t₂, with 1 or 2 small curved ventroapical setulae. Hind basitarsus (Fig. 23) with ventrobasal setulae somewhat enlarged; claws well developed. Other parts of femora, tibiae and tarsi uniformly shortly setulose. — **Abdomen:** (Figs 24–28) slender, elongate, unusually bicolourous, having anterior half pale and posterior half dark (see Figs 1, 3, 4). Preabdominal terga modified: T1 short (slightly shorter than T2), darker, narrower and distinctly separated from T2; T2–T4 short (see also Fig. 17), transverse, subequal in length, all unusually pale, translucent, silvery grey to whitish yellow and shiny and each sparsely but distinctly setose, with longest setae at posterior margins (Fig. 28); T5 enlarged, extremely elongate (Figs 24–28), longer than T1–T4 combined and also broad, expanded lateroventrally, brownish black, heavily sclerotized and sparsely finely setose. Preabdominal sterna pale-pigmented (cf. Fig. 3); S1–S4 short, combined length subequal to T1–T4 (cf. Figs 17, 25, 28); S1 and S2 ochreous brown, S3 and S4 dirty yellow; S1 (shortest) and S2 (longer than S1) with sparse and short setulae, S3 and S4 (both longer and wider than S2) with a few fine but longer setae (Fig. 28). Margins of S5 not recognizable, only some setae discernible in light microscope (Fig. 28); in microtomographs (Figs 25, 31, 32) S5 very elongate (though somewhat shorter than T5), narrow and probably pale-pigmented. Spiracles not visible in (reduced) pleural membrane nor at margins of terga. — **Postabdomen:** (Figs 24–27, 29, 30, 32–35) more or less symmetrical, with dorsal sclerites dark-pigmented. T6 seemingly absent (cf. Figs 29, 30) but recognized in microtomographs (Figs 27, 31, 32), forming short transversely band-like (probably bare) sclerite largely hidden under large T5, visible as narrow



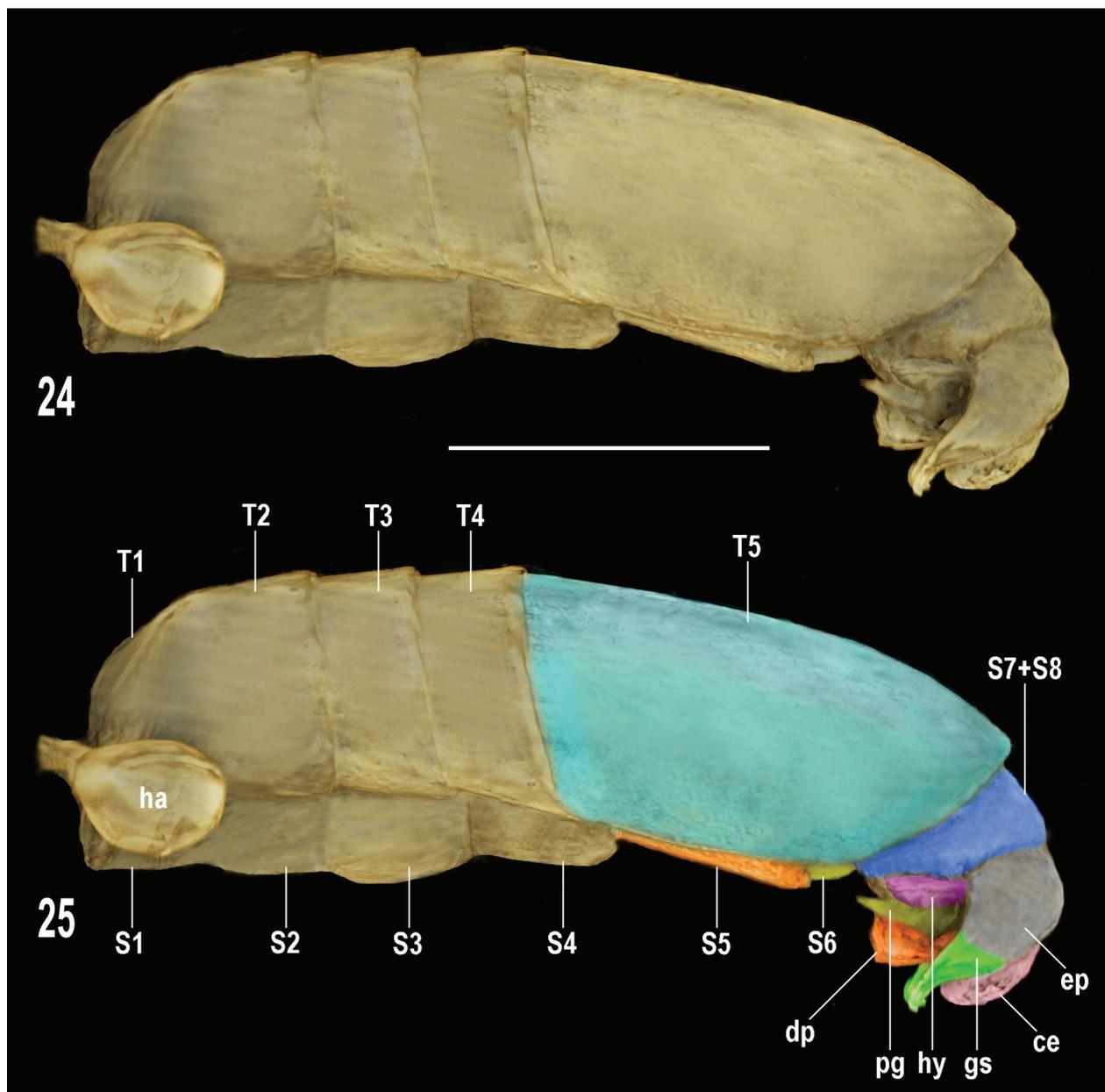
Figures 20–23. *Christelinka multiplex* sp. nov., male holotype, legs. **20** left fore femur, dorsally; **21** right fore femur, anteriorly; **22** right mid femur and tibia, anteriorly; **23** left hind femur, tibia and tarsus, anteriorly. Scale bar: 0.3 mm. For abbreviations see 2.2.4. Morphological terminology.

strip on right side of postabdomen (Fig. 32). S6 visible only in microtomographs (Figs 25, 31–35), of moderate length, trapezoidal, broader posteriorly where wider than long (Fig. 35). Slightly asymmetrical brown saddle-shaped sclerite dorsally (shorter on left side but reaching more ventrally, cf. Fig. 25 and Fig. 27) considered to be fusion of S7+S8; sclerite bears 1 strong dorsolateral seta on each side of posterior margin (Figs 3, 29, 30) and 1 or 2 short setae. — **Genitalia:** Epandrium (Figs 25, 27, 29,

30) simple, arch-shaped, open ventrally (Fig. 35), only slightly asymmetrical, with longer left side and a few small setae; anal fissure not clearly visible in light microscope but surely large (cf. Figs 34, 35). Cerci also large, symmetrical, free and projecting below anal fissure posterior to gonostyli (cf. Fig. 30); each cercus yellow, subconical with apex rounded, with (mainly posterior) fine, pale setae distinctly longer than setulae on gonostylus. Another medial sclerite situated between cerci (only visible in microtomograph image, Figs 34, 35) probably homologous to medandrium (= bacilliform sclerite, S10). Gonostyli (Figs 27, 30, 32) separate, yellow, elongate, somewhat asymmetrical. Left gonostylus (Figs 25, 30) more robust than right, elongate, wider proximally, gradually tapered distally; blunt apex slightly widened and bent posteriorly; right gonostylus (Figs 27, 29) of equal length to left, but slender (including apex) and distinctly curved; left gonostylus externally with a few small setae at anterior margin of proximal half and several fine pale-pigmented setulae on posterior margin of distal half (those on right gonostylus not seen). Internal genitalia: some indistinctly discernible sclerotized structures visible in front of external genitalia in light microscope (Figs 29, 30). More dorsal sclerite considered hypandrium, clearly frame-shaped in ventral view as shown in microtomograph images (Figs 34, 35). Paired and apparently symmetrical postgonites below hypandrium (Figs 27, 30, 32) – simple sclerites, situated dorsolaterally to distiphallus of aedeagus; each postgonite projecting anteriorly, acutely pointed and bare except for 2 preapical microsetulae (Fig. 30). Distiphallus (situated most ventrally) short, basally narrow, broad and dilated distally (see Fig. 35), of rather simple structure (appears more sclerotized dorsally and ventrally, see Fig. 30). Pair of slender tooth-like acutely pointed projections of uncertain homology (visible in microtomograph image of terminalia in ventral view, see “??” in Fig. 35) in front of apex of distiphallus appears derived from distal end of dorsal sclerite of distiphallus. — **Female.** Unknown.

Etymology. The name “multiplex” (Lat. adjective = various, manifold) refers to the unusual mixture of external characters of the new species precluding its association with any of the currently recognized families of Diptera Acalyptatae.

Comparative remarks. As remarked above, *Christelinka multiplex* sp. nov. at first glance looks like an opomyzoid fly, in external appearance most resembling some species of Opomyzidae, Anthomyzidae, Stenomicridae or Aulacigastridae (cf. images in Marshall 2012). However, it differs from any member of these families by a combination of its most diagnostic characters (see above under Christelinkidae) and can be immediately recognized by the bare forefrons, absence of the frontal triangle and lunule, a single posteriorly positioned ors, the extremely dorsobasal arista, the wing pointed at apex of R_{4+5} , a strong seta on fore coxa, peculiar chaetotaxy of the fore (with dorsal seta and an anteroventral row of small spines) and hind (with a dorsal and a longer anteroventral



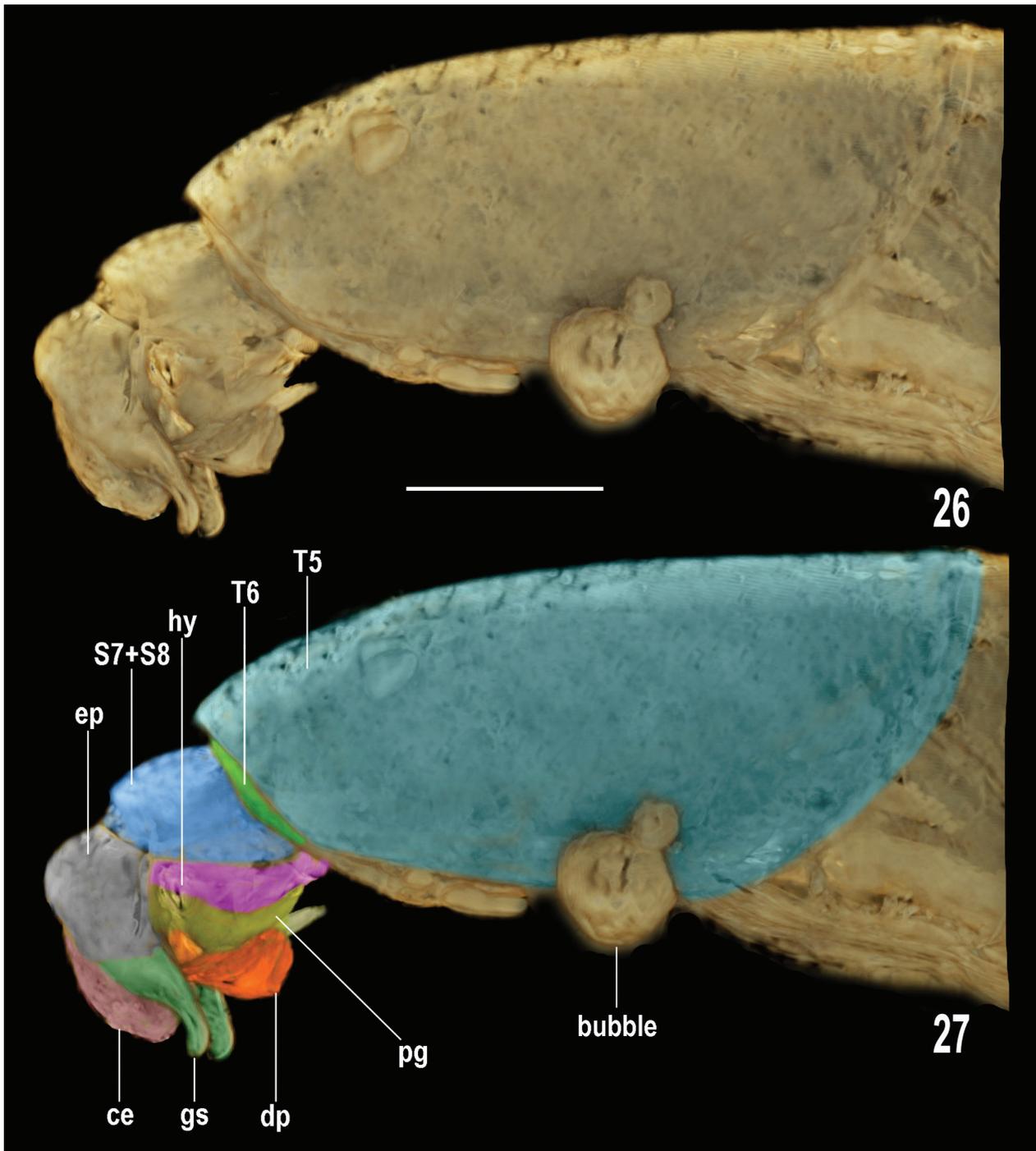
Figures 24, 25. *Christelenka multiplex* sp. nov., male holotype. **24** abdomen, left laterally; **25** ditto, with some structures coloured. Scale bar: 0.5 mm. For abbreviations see 2.2.4. Morphological terminology. Microtomograph image by V. Baranov.

seta) femur (see Figs 20, 21, 23), enlarged laterobasal and crossed apical sc setae, the enlarged and extremely elongate male T5 and S5 and the strong pair of setae on the dorsal pregenital synsclerite S7+S8.

Biology. The species was plausibly a member of the ancient dipterous community in the “Baltic amber forest”. This Eocene tropical to warm-temperate humid forest (Weitschat and Wichard 2010; Sadowski et al. 2020) covered most of northern Europe (from Fennoscandia to Ukraine) and evolved thanks to the very warm and humid climate during the Early Eocene Climatic Optimum (see Słodkowska et al. 2013), for more detail see Introduction. The presence of stellate trichomes of *Quercus* spp. in the amber sample (see Figs 3, 4) indicate occurrence of this fly in a warm-temperate type of forest (as characterized by Sadowski et al. 2020).

Type locality and horizon. Russia: Kaliningrad region, Yantarny mine. Mid-late Eocene, 48–34 Ma (cf. Seyfulah et al. 2018; Kasiński et al. 2020).

Type material. **Holotype** ♂ (inventory number Dip-00820), labelled: ‘Faszination Bernstein, Christel Hoffeins, Hans Werner Hoffeins’ (framed on obverse), ‘1818-3, Diptera: Acalypratae, cf. Anthomyzidae’ (handwritten by Ch. Hoffeins), ‘Baltic amber, Russia: Kaliningrad region, Yantarny’, ‘obtained in early 2017 from Marius Veta, owner of the amber company “AmberTreasure4u”, Lithuania’ and ‘HOLOTYPUS ♂, *Christelenka multiplex* sp.n., J. Roháček det. 2020’ (red label). The specimen is embedded in polyester resin, size of preparatum 10.4 × 6.6 × 5.9 mm, size of cut amber 7.5 × 4.5 × 3 mm (Fig. 1), deposited in SDEI. Syninclusions: only a few stellate hairs of various shapes.



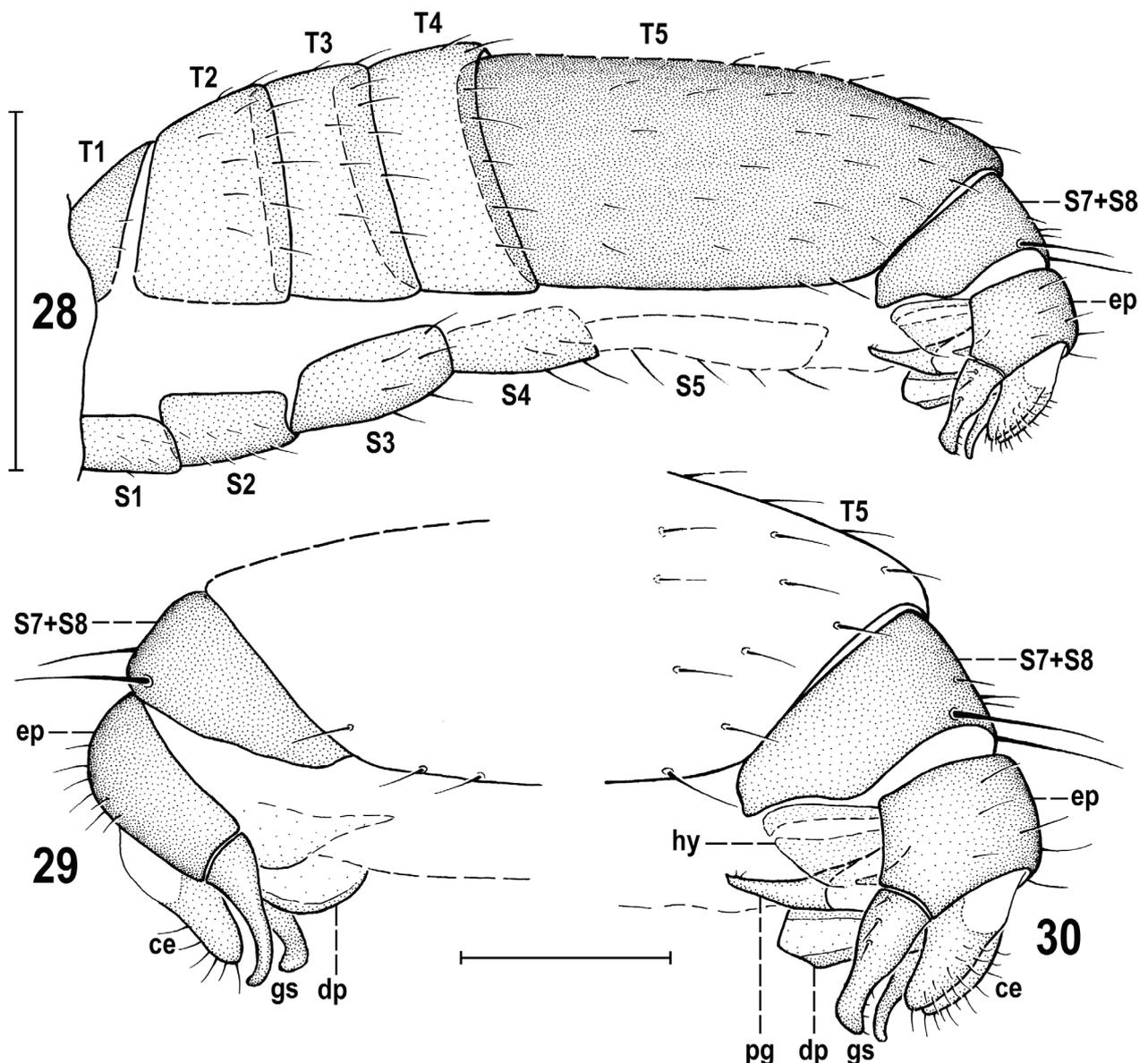
Figures 26, 27. *Christelinka multiplex* sp. nov., male holotype. **26** posterior half of abdomen, right laterally; **27** ditto, with some structures coloured. Scale bar: 0.2 mm. For abbreviations see 2.2.4. Morphological terminology. Microtomograph image by V. Baranov.

4. Discussion and conclusions

4.1. Affiliation of the new family

The placement of this new family in the current classification system of Schizophora proved to be rather difficult although Christelenkidae undoubtedly belongs to this group. As was found for the extinct families Hoffeinsmyiidae (Michelsen 2009) and Yantaromyiidae (Barták

2019), Christelenkidae also seems not to have an obvious sister-group family among the Diptera Acalypratae. The situation is also complicated by the fact that there is no accepted modern classification of families of Acalypratae. The only comprehensive system of Acalypratae Diptera (based on a phylogenetic hypothesis resulting from a manual analysis of morphological characters) remains that by McAlpine (1989). Although the most recent molecular and phylogenomic studies indicate that some groups (superfamilies and suprafamilies) recognized by



Figures 28–30. *Christelenka multiplex* sp. nov., male holotype, abdominal structures. **28** abdomen, left laterally; **29** postabdomen with terminalia, right laterally; **30** ditto, left laterally. Scale bars: 28 – 0.5 mm; others – 0.2 mm. For abbreviations see 2.2.4. Morphological terminology.

McAlpine (1989) may not be monophyletic (see Winkler et al. 2010; Wiegmann et al. 2011; Bayless et al. 2021), grouping of the acalyprate families in these studies is not consistent. Also, the attempt at producing a morphological hypothesis of the phylogeny of Diptera families by Lambkin et al. (2013) did not resolve the relationships within Acalypratae sufficiently to support a new classification. However, the monophyly of several (more or less distinct) superfamilies have been confirmed recently, re-classified and (sometimes) also re-diagnosed by morphological characters. Nerioidae and Diopsoidea belong to these groups, having their monophyly supported and taxonomic limits clarified by Lonsdale (2020) on the basis of a thorough phylogenetic morphological analysis. Also, Tephritoidea are (long recognized, see McAlpine (1989)) recognized as a monophyletic group, which was confirmed morphologically; e.g., by Korneyev (1999) and molecularly by Han & Ro (2016). In addition, the

monophyly and taxonomic limits of the Sciomyzoidea have been long recognized (see Tóthová et al. 2013), but the recent inclusion of Chamaemyiidae, Lauxaniidae and even Conopidae on the basis of phylogenomic data (Bayless et al. 2021) has put into question the morphological delimitation of this superfamily. Thus, Conopioidea and Lauxanioidea of McAlpine (1989) have now been included in the expanded concept of Sciomyzoidea by Bayless et al. (2021). Similarly, the monophyly of Carnoidea, analysed morphologically and re-defined by Buck (2006), has recently also been rejected by Bayless et al. (2021). Sphaeroceroidea (sensu McAlpine 1989) was also recognized as monophyletic (Bayless et al. 2021) but only when Mormotomyiidae is excluded; this enigmatic family has most recently been affiliated with the Ephydroidea (Winkler et al. 2022). Although there is no doubt that Ephydroidea is a monophyletic group (see McAlpine 1989), being also confirmed by the two most recent molecular

studies (Bayless et al. 2021; Winkler et al. 2022), the phylogenetic hypotheses proposed in these two studies differ significantly in recognition of the sister-group of Ephydroidea. From the above review, it is apparent that also among the superfamilies long considered monophyletic, the placement and relationships of certain families remain unstable and often recognized differently in hypotheses based on morphological and molecular data. While the classification and relationships of families affiliated by McAlpine (1989) in Sphaeroceroidea (= Heleomyzoidea) have been (partly) supported by Bayless et al. (2021), those of families formerly classified in Opomyzoidea, seem to be totally confusing when comparing results of the recent morphological (Lambkin et al. 2013; Lonsdale 2020) and molecular (Winkler et al. 2010; Wiegmann et al. 2011; Bayless et al. 2021) phylogenetic hypotheses. The only consensus of all these studies is that this superfamily is not monophyletic.

We assume that the precipitous radiation of acalyptrate families during a relatively short period in the Mid-late Eocene (see also Lonsdale 2020: 4, for more detail) could be the major reason for the difficulties in clarifying their phylogenetic relationships (both using morphological and molecular methods) and, subsequently, their unresolved systematic classification.

Comparing diagnostic features of Christelenkidae with sets of apomorphic characters defining superfamilies of Acalyptratae according to McAlpine (1989) with refinements added by more recent morphological studies (e.g. Korneyev 1999; Buck 2006; Tóthová et al. 2013; Lonsdale 2013, 2020; Lonsdale et al. 2010), we have reached the conclusion that this new fossil family is most probably allied with some families of the (polyphyletic) Opomyzoidea or the (monophyletic) Ephydroidea.

Following the list of characters and their polarities provided by Lonsdale (2020: 153–173) (with only a few of our own modifications), we have concluded that the majority of the above characters of Christelenkidae are plesiomorphic and only those listed below can be treated as apomorphic. Most of them are, however, homoplastic, occurring scattered in various superfamilies and families of Acalyptratae, so those unique or generally rare in Acalyptratae are marked “(U)” in the list below:

- (1) pedicel (more or less) cap-like
- (2) 1st flagellomere discoid and deflexed
- (3) arista extremely dorsobasal (U)
- (4) lunule absent (lost) (U)
- (5) occiput (at least dorsally) concave
- (6) pvt convergent
- (7) 1 ors
- (8) anterior half of frons bare (no microsetae) (U)
- (9) 0 ppl
- (10) 1 dc
- (11) 1 sa
- (12) 0 postsutural intra-alar
- (13) basal sc longer than apical
- (14) 0 msp1
- (15) 1 stpl
- (16) pleural suture widened dorsally
- (17) mesopleuron with elevated ridge at posterior margin
- (18) subscutellum contiguous with scutellum
- (19) wing apex pointed at end of R_{4+5}
- (20) C with humeral and subcostal breaks
- (21) Sc apically fused with R_1
- (22) CuA_1 reaching wing margin
- (23) cell cup closed, distally rounded
- (24) cx_1 with 1 distinct ventral seta in middle (U)
- (25) f_1 with 1 dorsal seta (U)
- (26) f_1 with anteroventral ctenidium-like series of short blunt spines
- (27) f_3 with 1 strong anteroventral and 1 distinct dorsal seta
- (28) t_2 with 1 ventroapical and 1 dorsopreapical seta
- (29) t_3 with 1 dorsal preapical seta
- (30) male T5 and S5 strongly prolonged (U)
- (31) male postabdomen more or less symmetrical
- (32) male S7+S8 completely fused, with pair strong dorsal setae (U)
- (33) epandrium slightly asymmetrical
- (34) gonostyli slightly asymmetrical
- (35) male cerci large, widely separate

Christelenkidae seem to share with Ephydroidea the following apomorphic characters: 1, 2, 5, 6, 14 (mesopleuron is entirely bare only in Drosophilidae, some Diastatidae and some Ephydriidae), 18, 19 (wing is only pointed in some Diastatidae and Camillidae), 20, 21, 22, 23 (not in Ephydriidae), 26 (ctenidium only present in Curtonotidae and Diastatidae), 28, 29, 31. Consequently, *Christelenka* resembles Ephydroidea (and particularly some Diastatidae: *Campichoeta* Macquart) in wing venation and (secondarily) symmetrical male postabdomen and terminalia. Notes: the humeral break is secondarily lost in *Campichoeta*; only in Curtonotidae f_3 is provided with 1 strong seta but it is anterodorsal (not dorsal); an anteroventral seta of f_3 is always absent in Ephydroidea. All these shared features occur as homoplasies frequently also elsewhere in Acalyptratae (see also below); none of them is a unique synapomorphy clearly demonstrating sister-group relationships of Christelenkidae and Ephydroidea or some of its families. It is clear that *Christelenka* cannot belong to Ephydroidea because it lacks important synapomorphies of the latter superfamily, such as: pedicel with dorsolateral seam (also occurring as homoplasies in some Tephritoidea, see Korneyev (1999) and Perisclididae, see below), one ors proclinate, C spinose, male S8 reduced or absent (cf. McAlpine 1989).

The comparison of Christelenkidae with Opomyzoidea (as delimited by McAlpine 1989) is more problematic because it is a very heterogeneous group, obviously polyphyletic in origin (first dismantled by Winkler et al. 2010), see above. Some of the characters used by McAlpine (1989) as synapomorphies to demonstrate monophyly of Opomyzoidea are obviously erroneously polarised or incorrectly selected. Therefore, the above set of putative apomorphies of Christelenkidae is compared rather with some families (recognized as most similar to *Christelenka*) placed historically in Opomyzoidea; of

course, without those already excluded from this superfamily, such as Acartophthalmidae (now in Carnoidea, see Buck 2006) and Fergusoninidae (now in Nerioida, see Lonsdale 2020). Also, several other families of Opomyzoidea markedly dissimilar to Christelenkidae are excluded from the considerations below. These include Clusiidae (recognized as the most basal lineage of Acalyptratae in a hypothesis by Lonsdale (2020)), the fossil Clusiomitidae (see Roháček & Hoffeins 2021), Agromyzidae (see Lonsdale 2021a) and Odiniidae. The latter two families were recognized as separate lineages distant from the Opomyzidae-Anthomyzidae pair which Lonsdale (2020) supported as the only families remaining in Opomyzoidea. However, it must be noted that also the relationship of this pair was doubted practically in all molecular studies treating both these families (Winkler et al. 2010; Wiegmann et al. 2011; Bayless et al. 2021). Further distinctly dissimilar and distantly related families hitherto placed tentatively in Opomyzoidea are Marginidae, Neminidae, Teratomyzidae, Asteiidae and Xenasteiidae. All these groups share with *Christelenka* only a few of the apomorphies listed above (and all these are widely homoplasious) but are characterized by a number of apomorphies specific to them but lacking in Christelenkidae.

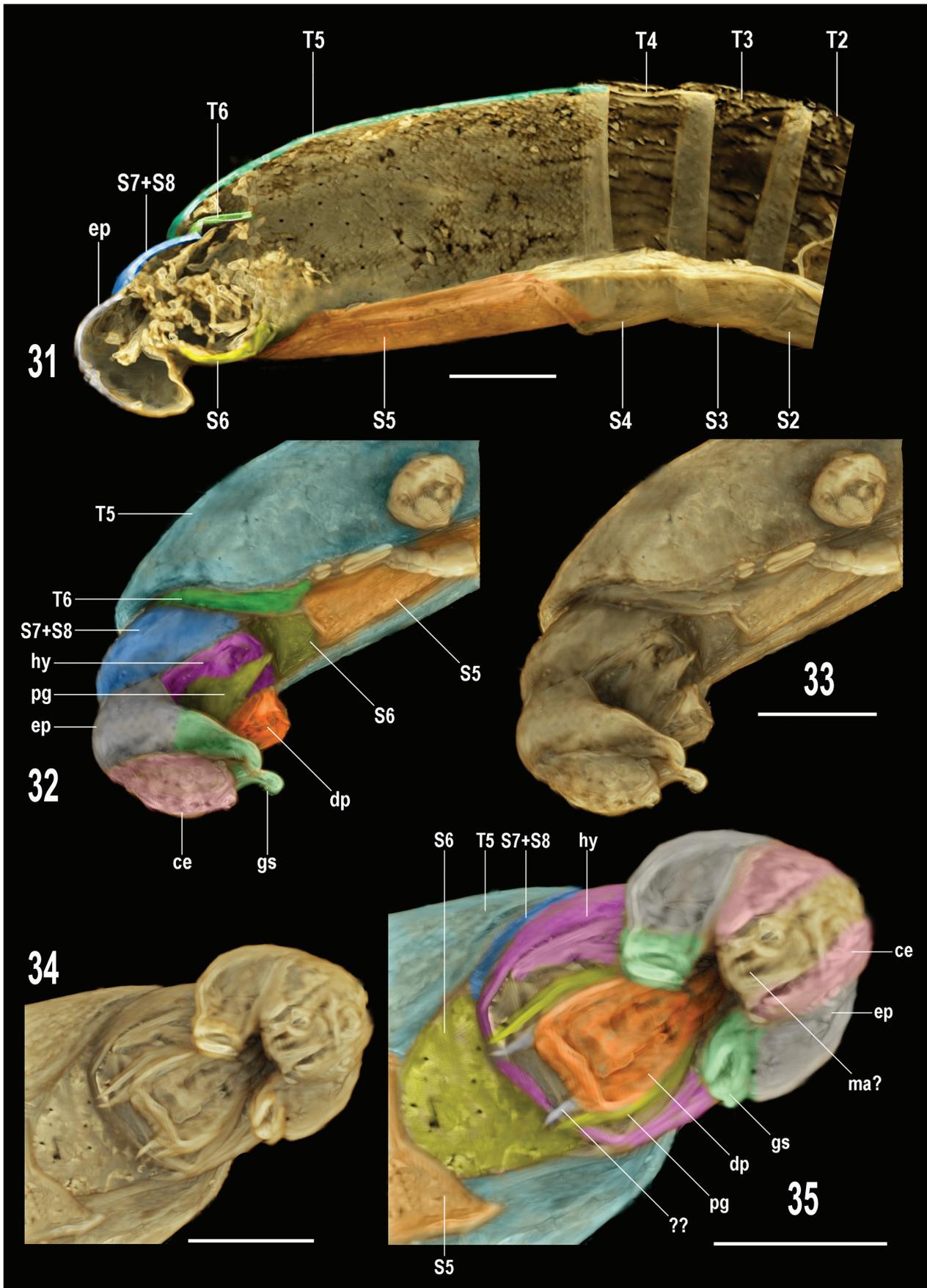
The Opomyzidae share with Christelenkidae the following apomorphies from the above list: 1, 2, 5, 6 (pvt are convergent only in the most archaic genus *Anomalochaeta* Frey, otherwise are absent), 7, 11, 12, 15, 17, 21 (or Sc distally reduced but forming preapical kink on R₁), 22, 23, 35. Opomyzidae resemble *Christelenka* mainly in shape of antennae (which, however, are not so divergent), reduced cephalic chaetotaxy, wing venation (but with humeral break absent). However, Opomyzidae differ principally from *Christelenka* in structures of the postabdomen (being asymmetrical = plesiomorphic) and external genitalia having gonostylus fused with epandrium, and some other apomorphic features, viz. face medially desclerotized, parafacialia silvery microtomentose, R₁ with preapical kink, vi absent, prosternum setulose (this really is an apomorphy of Opomyzidae not of Anthomyzidae as Lonsdale (2020) has in tree, fig. 424).

The Anthomyzidae also display considerable similarities to Christelenkidae. We have found shared apomorphies as follows: 1, 2, 5, 6, 7 (only in some genera of Anthomyzidae, otherwise 2 or 3 ors), 10 (also variable, 1–3 dc), 11 (sa rarely absent), 12, 14 (mspl setae are only present in the fossil Eocene subfamily Protanthomyzinae, see Roháček 2013), 15 (1 or 2 stpl), 17, 19 (angular wing apex only known in *Typhomyza* Roháček), 20 (humeral break only sometimes distinctly developed, often C is only attenuated there), 21 (but forming preapical kink on R₁), 22 (sometimes abbreviated), 23, 26 (ctenidium-like series of thickened setae is known in the genus *Barbarista* Roháček, see Roháček 2021: fig. 87:16). As for Opomyzidae, also Anthomyzidae have a markedly different, strongly asymmetrical (segments 6–8) male postabdomen. This condition of the postabdomen is considered plesiomorphic (Lonsdale 2020), but the construction of male internal genitalia (with complex folding apparatus between hypandrial and aedeagal complex) is autapomor-

phic for Anthomyzidae. Of the male terminalia only some structures are visible in *Christelenka* (Figs 28–35), which are generally short, broad, and symmetrical (hypandrium, distiphallus), thus markedly different from those in Anthomyzidae being elongate and slender, with asymmetrical and distally bifid distiphallus. Other apomorphies of Anthomyzidae (not found in *Christelenka*) include face medially desclerotized, parafacialia silvery microtomentose, preapical kink on R₁ (all shared with Opomyzidae) and the posteroventral (not anteroventral) “ctenidial spine” on fore femur (lost in some genera, see Roháček (1998, 2006)).

The family Neurochaetidae seems to share with Christelenkidae these apomorphies: 1, 2, 9, 10 (1 or 2 dc), 12, 14, 15 (1 or 2 stpl), 18, 27 (f₃ with only dorsal seta), 28. However, Neurochaetidae are distinguished by the peculiarly modified antenna with enlarged cap-like pedicel encompassing base of small 1st flagellomere, discrete orbital plate, enlarged frontal triangle, rich cephalic chaetotaxy (with proclinate anterior ors as in Aulacigastriidae and strong setosity of anterior portion of gena most resembling that in Periscelididae), highly modified dorsoventrally flattened thorax, prosternum narrowed (linear), subscutellum reduced, wing with cells bm, cup and also alula atrophied, postabdomen asymmetrical, epandrium flat and band-like, and distiphallus of aedeagus very long and at least partially coiled (McAlpine 1988; Lonsdale 2021b), thus markedly different from those of *Christelenka*. On the other hand, the broad sterna and reduced pleural membrane of preabdominal segments (treated as an autapomorphy of Neurochaetidae by McAlpine (1989) but not by Lonsdale (2020)) are reminiscent of those of *Christelenka* but preabdomen of the latter is not flattened, not to mention its peculiarly prolonged 6th segment.

The family Periscelididae is treated here in the narrowed concept (= Periscelidinae of Rung & Mathis 2021b), thus excluding genera affiliated to the family Stenomicridae (for review see Roháček 2011). Periscelididae seems to share more apomorphies with Christelenkidae than Stenomicridae and, therefore, only this family is compared with *Christelenka* here. The shared apomorphies are as follows: 1, 2, 5, 7, 11, 12, 14 (but often with setulae at the posterior margin of mesopleuron), 17, 31. Although the secondarily symmetrical postabdomen can be seen in both groups, that of Periscelididae differs by a large T6 and large, entirely symmetrical dorsal pregenital synsclerite probably formed by fusion of T7, S7 and S8 (Roháček & Andrade 2017). Periscelididae is also distinguished in having pedicel with distinct dorsal seam (as in Ephydroidea), arista pectinate, oc arising outside ocellar triangle, gena anteriorly strongly setose (as in Neurochaetidae), C without breaks and ending at apex of R₄₊₅, and, most significantly, by uniquely formed male genitalia having reduced to absent gonostylus, ventrally positioned elongate cerci and, particularly, the extremely expanded (larger than entire external genitalia) pocket-shaped phallopodeme (see Roháček & Andrade 2017). Although the male genitalia are not precisely visible in *Christelenka*, it is clear that they are wholly different from those of Periscelididae.



Figures 31–35. *Christelenka multiplex* sp. nov., male holotype, abdominal structures. **31** abdomen (without 1st segment), sagittal section right laterally, with some structures coloured; **32** posterior end of abdomen, right ventrolaterally, with structures coloured; **33** ditto, without colours; **34** posterior end of abdomen, ventrally; **35** ditto, enlarged and coloured. Scale bars: 0.2 mm. For abbreviations see 2.2.4. Morphological terminology. Microtomograph images by V. Baranov.

Species of the family Aulacigastridae resemble externally Christelenkidae but the shared apomorphies are only a few: 5, 8, 9, 11, 12, 18, 21 (sometimes forming a kink on R_1), 22, 31. As above, almost all these apomorphies are widely homoplasious in Acalypratae. We would like to remark on character 8 (anterior half of frons bare). The frons of Aulacigastridae is bare (without setulae) anteriorly but the strong proclinate-inclinate (anterior) ors usually arises in anterior half of frons. This distinctive ors seta, the strongly reduced or absent oc, the absent pvt and true vibrissa are the most distinct differences in cephalic chaetotaxy against Christelenkidae. The symmetrical postabdomen (character 31) is shared by both families but in Aulacigastridae there is a large pregenital sclerite (fusion of T6 and S6 according to Rung & Mathis (2021a: fig. 88:6), but obviously also integrating S7 and S8, cf. Rung et al. (2005)) forming almost complete (ventrally shortened, asymmetrical and narrowly open) ring. This synsclerite can be considered an autapomorphy of Aulacigastridae. The external male genitalia are also very distinctive in Aulacigastridae because a true gonostylus is lacking and the epandrium is provided with a rigid posteroventral process on each side (erroneously treated as surstylus by authors, see Rung & Mathis (2021a)), thus they are quite dissimilar to those of *Christelenka*.

4.2. Most significant apomorphies of Christelenkidae (same numbering as in above list)

(3) Arista extremely dorsobasal. The ancestral condition is surely an apical arista on a porrect antenna (as known in Phoroidea). In Schizophora, the dorsal or dorsobasal position of the arista should be considered a synapomorphy of this group and the (uncommonly occurring) apical arista in some of its families as a reversal. Therefore, we believe that its shifting extremely basally, just at the distal margin of the pedicel (Figs 8, 9) in *Christelenka*, is secondary and hence an apomorphic condition, unusual in Acalypratae.

(4) Frontal lunule absent (lost) (Figs 6, 9). The lunule is a synapomorphy of the Schizophora (McAlpine (1989: 1423) but its reduction occurs commonly among families of Acalypratae. However, in these cases some remnant of the lunule (often depressed and sunken into a small medial fissure) are preserved. The condition found in *Christelenka* is considered unusual because the lunule disappeared entirely and only a ptilinal suture can be seen above bases of antennae.

(8) Anterior half of frons bare (also microsetae absent, Fig. 9). At least microsetae (but usually also anterior ors macrosetae) are present on the forefrons of the majority of Acalypratae. Glabrous (entirely bare) anterior half of frons is rare because microsetae are present also in families with reduced cephalic chaetotaxies (such as Micropezidae, Psilidae, Piophilidae, Sepsidae, etc.). Bare forefrons can be seen; e.g., in some Conopidae, Ulidiidae

(*Physiphora* Fallén), Chamaemyiidae (some *Leucopis* Meigen), Celyphidae, Asteiidae (*Leiomyza* Macquart). Within Opomyzoidea (and also Ephydroidea) this condition is extremely rare.

(13) Laterobasal sc longer than the crossed apical sc (Fig. 16). Apical sc are often crossed but normally longer than laterobasal sc. The above combination is rare in Acalypratae (known in some Tephritidae and in Diastatidae: *Diastata* species, where apical sc are, however, upright) and are unknown in families historically placed in Opomyzoidea.

(19) Wing with apex somewhat pointed at end of R_{4+5} (Figs 18, 19). Apically pointed wings are known mainly in some Ephydroidea (Camillidae, Diastatidae: *Camipichoeta*) but also in some species of other groups of Acalypratae, viz. Fergusoninidae (see Lonsdale 2020: figs 192, 411), Teratomyzidae (cf. Papp 2011; Rodrigues et al. 2016) and also in *Typhamyza bifasciata* (Wood) from the family Anthomyzidae (see Roháček 1992, 2006). It can perhaps be considered a putative apomorphy indicating relationships of Christelenkidae to Ephydroidea.

(24) cx_1 elongate and with 1 distinct ventral seta in middle (Figs 3, 15). Elongated cx_1 is not common in Acalypratae but the presence of a single strong medial ventral seta is quite unusual and probably unique character.

(25, 26) f_1 with an anteroventral ctenidium-like series of small spines and 1 dorsal seta (Figs 20, 21). This chaetotaxy of the fore femur seems to be unique. The row of small anteroventral spines seems to be homologous with a series of dense, thickened setae or spines called a ctenidium e.g. in Lauxaniidae (*Homoneura* Wulp), Diastatidae, Curtonotidae, Sepsidae (*Nemopoda* Robineau-Desvoidy). It was also found in *Marshallya platythorax* Roháček (Roháček 2018: fig. 27) and in species of *Barbarista* Roháček belonging to Anthomyzidae (Roháček 2021: fig. 16). These ctenidium-like spines or spiniform setae are anteroventral, and therefore, not homologous with the posteroventral “ctenidial spine” in Anthomyzidae. In all the above cases, however, the dorsal seta is absent. The presence of the dorsal seta on f_1 is considered an unusual and distinct apomorphy of *Christelenka*.

(27) f_3 with 1 anteroventral and 1 distinct dorsal seta (Fig. 23). This combination is also considered unusual in Acalypratae. Both these setae can be seen in some Palloptera, with addition to 1 or 2 anterodorsal setae, although all are situated more distally (McAlpine 1987) than those in *Christelenka*. The presence of a strong anteroventral seta or setae on f_3 is more common, similarly as is the occurrence of anterodorsal setae, or both in combination. A distinct truly dorsal seta of f_3 seems to be rare, known in some representatives of Neurochaetidae (Lonsdale 2021).

(30) T5 and S5 enlarged and very elongate (Figs 24–28). This character has hitherto been unknown in the majori-

ty of families of Acalyptratae. The only exception is the markedly elongated 5th abdominal segment in males of the genus *Protearomyia* McAlpine (see MacGowan & Rotheray 2008; MacGowan 2014) belonging to the unrelated Lonchaeidae (superfamily Tephritoidea).

(32) Male S7+S8 completely fused, with a pair of strong dorsal setae. Surprisingly, a similar pair of robust setae at the posterior margin of S8 is (only) known in Cypselosomatidae and Pseudopomyzidae (see Lonsdale 2020: figs 216, 217) belonging to Nerioidea.

5. Conclusion

The peculiar mixture of characters apomorphic for the Christelenkidae and, particularly, those considered almost unique or rarely occurring in Acalyptratae, indicate that although this new group seems to have an affinity with some groups of the Ephydroidea (Diastatidae in particular) and Opomyzoidea (sensu McAlpine 1989) (mainly Opomyzidae and Anthomyzidae), it cannot be related to any of them. This is also demonstrated by the fact that the apomorphic characters shared with these taxa are relatively few in number and, moreover, known to occur as scattered homoplasies not only among other families of Opomyzoidea but also in evidently unrelated groups of Acalyptratae. Therefore, it is suggested that the Christelenkidae could be tentatively considered a separate lineage of Acalyptratae possibly related to Opomyzoidea sensu Lonsdale (2020) (= Opomyzidae + Anthomyzidae) or to Ephydroidea, having no apparent sister-group relationship with any of the currently recognized families of these groups.

6. Competing interests

The authors have declared that no competing interests exist.

7. Acknowledgements

First of all, we would like to thank Mrs Christel Hoffeins (Hamburg, Germany) for the discovery of this peculiar fossil taxon in Baltic amber, for making it available for study and for valuable comments on earlier drafts of the manuscript. We are grateful to Mr. Marius Veta (Palanga, Lithuania), owner of the amber company “Ambertreasure4u” from whom the specimen was purchased, for his continuing support with Baltic amber Diptera and especially acalyptrates. Our sincere gratitude is also expressed to Miroslav Barták (Praha, Czech Republic) and the late László Papp (Budapest, Hungary) for discussion on establishing a new family of Acalyptratae and its relationships. Kevin N. Barber (Sault Ste. Marie, Ontario, Canada) and Peter Chandler (Melksham, England, U. K.) are acknowledged for all their improvements and language corrections in the manuscript. Owen Lonsdale (Ottawa, Ontario, Canada) is thanked for his critical review of the submitted version of the manuscript. The senior author’s research on amber fossil acalyptrate flies was

supported by the Ministry of Culture of the Czech Republic with institutional financing of long-term conceptual development of the research institution (the Silesian Museum, MK000100595). Viktor Baranov’s work is funded by the State Agency of Innovation, within the Ramon y Cajal Program, grant number RYC2021-032144-I. Scanning of the specimen was supported by the DESY Block Allocation Group project “Scanning the past – Reconstructing the diversity in million years old fossil amber specimens using SR μ CT” at PETRA III.

8. References

- Aarle W van, Palenstijn WJ, De Beenhouwer J, Altantzis T, Bals S, Batenburg KJ, Sijbers J (2015) The ASTRA Toolbox: A platform for advanced algorithm development in electron tomography. *Ultramicroscopy* 157: 35–47. <https://doi.org/10.1016/j.ultramicro.2015.05.002>
- Aarle W van, Palenstijn WJ, Cant J, Janssens E, Bleichrodt F, Dabravolski A, De Beenhouwer J, Batenburg KJ, Sijbers J (2016) Fast and flexible X-ray tomography using the ASTRA toolbox. *Optics Express* 24: 25129–25147. <https://doi.org/10.1364/OE.24.025129>
- Alekseev VI, Alekseev PI (2016) New approaches for reconstruction of the ecosystem of an Eocene amber forest. *Biology Bulletin* 43: 75–86. <https://link.springer.com/article/10.1134/S1062359016010027>
- Barták M (2019) Yantaromyiidae, a new family of Diptera (Brachycera: Schizophora) from Tertiary Baltic amber and X-ray synchrotron microtomography imaging of its structures. *Journal of Systematic Palaeontology* 18: 187–195.
- Bayless KM, Trautwein MD, Meusemann K, Shin S, Petersen M, Donath A, Podsiadlowski L, Mayer C, Niehuis O, Peters RS, Meier R, Kutty SN, Liu S, Zhou X, Misof B, Yeates DK, Weigmann BM (2021) Beyond *Drosophila*: resolving the rapid radiation of schizophoran flies with phylotranscriptomics. *BMC Biology* 19(23): 1–17. <https://doi.org/10.1186/s12915-020-00944-8>
- Buck M (2006) A new family and genus of acalyptrate flies from the Neotropical region, with a phylogenetic analysis of Carnoidea family relationships (Diptera, Schizophora). *Systematic Entomology* 31: 377–404.
- Cumming JM, Wood DM (2017) 2. Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Vol. 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria, 89–133.
- Greving I, Wilde F, Ogurreck M, Herzen J, Hammel JU, Hipp A, Friedrich F, Lottermoser L, Dose T, Burmester H, Müller M, Beckmann F (2014). P05 imaging beamline at PETRA III: first results. In: Stock SR (Ed.) *Developments in X-Ray Tomography IX*. Proceedings of the Society of Photo-Optical Instrumentation Engineers (SPIE), 9212: 921200. <https://doi.org/10.1117/12.2061768>
- Grimaldi DA (2008) A stalk-eyed ephydroid fly from the Eocene (Diptera: Ephydroidea: Camillidae). *Proceedings of the Entomological Society of Washington* 110: 543–550.
- Grimaldi D, Nascimbene PC (2010) Raritan (New Jersey) amber. In: Penney D. (Ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, UK, 167–191.
- Grimaldi DA, Singh H (2012) The extinct genus *Pareuthychaeta* in Eocene ambers (Diptera: Schizophora: Ephydroidea). *The Canadian Entomologist* 144(1): 17–28.
- Han H-Y, Ro K-E (2016) Molecular phylogeny of the superfamily Tephritoidea (Insecta: Diptera) reanalysed based on expanded taxon

- sampling and sequence data. *Journal of Zoological Systematics and Evolutionary Research* 54(4): 276–288
- Hennig W (1965) Die Acalypratae des Baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipteren-Gruppe. *Stuttgarter Beiträge für Naturkunde* 145: 1–215.
- Hennig W (1966) Conopidae im Baltischen Bernstein (Diptera, Cyclorrhapha). *Stuttgarter Beiträge für Naturkunde* 154: 1–24.
- Hennig W (1967) Neue Acalypratae aus dem Baltischen Bernstein (Diptera: Cyclorrhapha). *Stuttgarter Beiträge für Naturkunde* 175: 1–27.
- Hennig W (1969) Neue Übersicht über die aus dem Baltischen Bernstein bekannten Acalypratae (Diptera: Cyclorrhapha). *Stuttgarter Beiträge für Naturkunde* 209: 1–42.
- Hennig W (1971) Die Familien Pseudopomyzidae und Milichiidae im Baltischen Bernstein. *Stuttgarter Beiträge für Naturkunde* 233: 1–16.
- Hennig W (1972) Beiträge zur Kenntnis der rezenten und fossilen Carnidae, mit besonderer Berücksichtigung einer neuen Gattung aus Chile (Diptera: Cyclorrhapha). *Stuttgarter Beiträge für Naturkunde* 240: 1–20.
- Hoffeins HW (2001) On the preparation and conservation of amber inclusions in artificial resin. *Polskie Pismo Entomologiczne* 70: 215–219.
- Hoffeins C, Rung A (2005) *Procyamops succini*, a new genus and species of Periscelididae (Diptera, Brachycera) from Baltic amber (Tertiary, Eocene). *Studia dipterologica* 12(1): 23–27.
- Hoffeins C., Woźnica A.J. 2013. Description of a new species *Eopseudomyza szadziewskii* sp. n. and redescription of *E. kuehnei* Hennig, 1971 from Eocene Baltic amber (Diptera: Pseudopomyzidae). *Polskie Pismo Entomologiczne* 82: 317–325.
- Kasiński JR, Kramarska R, Słodkowska B, Sivkov V, Piwocki M (2020) Paleocene and Eocene deposits on the eastern margin of the Gulf of Gdańsk (Yantarny P-1 bore hole, Kaliningrad region, Russia). *Geological Quarterly* 64: 29–53. <https://doi.org/10.7306/gq.1513>
- Korneyev VA (1999) Phylogenetic relationships among the families of the superfamily Tephritoidea. In: Aluja M, Norrbom AL (Eds), *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*. CRC Press, Boca Raton, FL, 3–22.
- Kotrba M (2009) *Prospyracephala kernegeri* spec. nov. (Diptera, Diopsidae) – a new stalk-eyed fly from Baltic amber. *Spixiana* 32(2): 187–192.
- Kvaček Z (2010) Forest flora and vegetation of the European early Palaeogene – a review. *Bulletin of Geosciences* 85: 63–76. http://www.geology.cz/bulletin/fulltext/1146_kvacek.pdf
- Lambkin CL, Sinclair BJ, Pape T, Coutney GW, Skevington JH, Meier R, Yeates DK, Blagoderov V, Wiegmann BM (2013) The phylogenetic relationships among infraorders and superfamilies of Diptera based on morphological evidence. *Systematic Entomology* 38: 164–179.
- Limaye A (2012) Drishti: a volume exploration and presentation tool. In: Stock SR (Ed.) *Developments in X-ray Tomography VIII*. Proceedings of the Society of Photo-Optical Instrumentation Engineers (SPIE), 8506: 85060X. <https://doi.org/10.1117/12.935640>
- Lonsdale O (2013) Review of the families Tanypezidae and Strongylophthalmyiidae, with a revision of Neotanypeza Hendel (Diptera: Schizophora). *Smithsonian Contributions to Zoology* 641: 1–60.
- Lonsdale O (2020) Family groups of Diopsoidea and Neriioidea (Diptera: Schizophora) – definition, history and relationships. *Zootaxa* 4735(1): 1–177.
- Lonsdale O (2021a) Manual of North American Agromyzidae (Diptera, Schizophora), with revision of the fauna of the “Delmarva” states. *ZooKeys* 1051: 1–481. <https://doi.org/10.3897/zookeys.1051.64603>
- Lonsdale O (2021b) 90. Neurochaetidae (Upside-down Flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Vol. 3. Brachycera—Cyclorrhapha, excluding Calypratae. Suricata 8. South African National Biodiversity Institute, Pretoria, 1971–1979.
- Lonsdale O, Marshall SA, Fu J, Wiegmann B. (2010) Phylogenetic analysis of the druid flies (Diptera: Schizophora: Clusiidae) based on morphological and molecular data. *Insect Systematics & Evolution* 41: 231–274.
- Lytaev P, Hipp A, Lottermoser L, Herzen J, Greving I, Khokhriakov I, Meyer-Loges S, Plewka J, Burmester J, Caselle M, Vogelgesang M, Chilingaryan S, Kopmann A, Balzer M, Schreyer A, Beckmann F (2014) Characterization of the CCD and CMOS cameras for grating-based phase-contrast tomography. In: Stock SR (Ed.) *Developments in X-Ray Tomography IX*. Proceedings of the Society of Photo-Optical Instrumentation Engineers (SPIE), 9212: 921218. <https://doi.org/10.1117/12.2061389>
- MacGowan I (2014) Three new species of *Protearomyia* McAlpine, 1962 (Diptera: Lonchaeidae) with a key to males of the Palearctic species. *Zootaxa* 3796(2): 337–348.
- MacGowan I, Rotheray G (2008). *British Lonchaeidae*. Diptera Cyclorrhapha, Acalypratae. Handbooks for the Identification of British Insects. Vol. 10, Pt. 15, Royal Entomological Society, St. Albans and Field Studies Council, Shrewsbury, U.K., 142 pp.
- Marshall SA (2012) Flies. The natural history and diversity of Diptera. Firefly Books Ltd, Richmond Hill & Buffalo, 616 pp.
- McAlpine DK (1988): Studies in upside-down flies (Diptera: Neurochaetidae). Part I. Systematics and phylogeny. *Proceedings of the Linnean Society of New South Wales* 110: 31–58.
- McAlpine JF (1987) 68. Pallopteridae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (Eds) *Manual of Nearctic Diptera*. Agriculture Canada Monograph No. 28, Vol. 2. Minister of Supply and Services Canada, Ottawa, 839–843.
- McAlpine JF (1989) 116. Phylogeny and classification of the Muscomorpha. In: McAlpine JF, Wood DM (Eds) *Manual of Nearctic Diptera*. Agriculture Canada Monograph No. 32, Vol. 3. Minister of Supply and Services Canada, Ottawa, 1397–1518.
- McKellar RC, Wolfe AP (2010) Chapter 9. Canadian amber. In: Penney D (Ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, UK, 149–165.
- Michelsen V (2000) Oldest authentic record of a fossil calyprate fly (Diptera): a species of Anthomyiidae from early Coenozoic Baltic amber. *Studia dipterologica* 7: 11–18.
- Michelsen V (2009) Hoffsmyiidae, a new extinct family of Schizophora (Diptera) in Baltic amber. *Studia dipterologica* 15(2008): 211–222.
- Moosmann J, Ershov A, Weinhardt V, Baumbach T, Prasad MS, LaBonne C, Xiao X, Kashef J, Hoffmann R (2014) Time-lapse X-ray phase-contrast microtomography for in vivo imaging and analysis of morphogenesis. *Nature Protocols* 9: 294–304. <https://doi.org/10.1038/nprot.2014.033>
- Nel A, Brasero N (2010) Chapter 8. Oise Amber. In: Penney D (Ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, UK, 137–148.
- Papp L (2011) Oriental Teratomyzidae (Diptera: Schizophora). *Zootaxa* 2916: 1–34.

- Pérez-de la Fuente R, Hoffeins C, Roháček J (2018) A new Acartophthalmites Hennig from Eocene Baltic amber (Diptera, Acalypratae). *ZooKeys* 737: 125–139. <https://doi.org/10.3897/zookeys.737.20639>
- Perkovsky EE, Zosimovich VZ, Vlaskin AP (2010) Chapter 7. Rovno Amber. In: Penney D (Ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, UK, 116–136.
- Rodrigues JPV, Pereira-Colavite A, Mello RL (2016) Catalogue of the Teratomyzidae (Diptera, Opomyzoidea) of the World. *Zootaxa* 4205(3): 275–285.
- Roháček J (1992) *Typhomyza* gen. n. for *Anthomyza bifasciata* Wood, with description of immature stages (Diptera, Anthomyzidae). *Bollettino del Museo Regionale di Scienze Naturali (Torino)* 10: 187–207.
- Roháček J (1998) Taxonomic limits, phylogeny and higher classification of Anthomyzidae (Diptera), with special regard to fossil record. *European Journal of Entomology* 95: 141–177.
- Roháček J (2006) A monograph of Palaearctic Anthomyzidae (Diptera) Part 1. *Časopis Slezského Zemského Muzea, Opava (A)* 55 (supplement 1): 1–328.
- Roháček J (2011) Taxonomy of *Stenomicroa cogani*, with description of *S. gracilior* from Turkey and comparative morphology of terminalia in Stenomicroidae. *Acta Entomologica Musei Nationalis Pragae* 51(2): 697–722.
- Roháček J (2013) New amber fossil Anthomyzidae (Diptera): an unexpected Eocene diversity. *Journal of Systematic Palaeontology* 11(4): 431–473.
- Roháček J (2014) *Reliquantha eocena* sp. nov., first tertiary representative of an extant genus of Anthomyzidae (Diptera). *Acta Entomologica Musei Nationalis Pragae* 54(2): 773–784.
- Roháček J (2016) The second species of Acartophthalmites from Baltic amber (Eocene), with notes on the relationships of the genus (Diptera: Acalypratae). *Acta Entomologica Musei Nationalis Pragae* 56(1): 409–422.
- Roháček J (2018) First Anthomyzidae (Diptera) from China: a new genus, six new species and new records. *Acta Entomologica Musei Nationalis Pragae* 58: 35–76. <https://doi.org/10.2478/aemnp-2018-0007>
- Roháček J (2020) *Protanthomyza grimaldii* sp. nov., a further member of the extinct subfamily Protanthomyzinae (Diptera, Anthomyzidae) from Baltic amber. *ZooKeys* 973: 1–15. <https://doi.org/10.3897/zookeys.973.51435>
- Roháček J (2021) 87. Anthomyzidae (Anthomyzid Flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Vol. 3. Brachycera—Cyclorhapha, excluding Calypratae. Suricata 8. South African National Biodiversity Institute, Pretoria, 1939–1956.
- Roháček J., Andrade R (2017) *Periscelis fugax* sp. nov., an overlooked European species of Periscelididae (Diptera), with notes on the morphology and terminology of terminalia. *Acta Entomologica Musei Nationalis Pragae* 57(1): 229–251.
- Roháček J, Hoffeins C (2020) *Protanthomyza ryszardi* sp. nov., another Eocene species of †Protanthomyzinae (Diptera: Anthomyzidae) from Baltic amber. *Palaeontology* 3(5): 473–482. <https://doi.org/10.11646/palaeontology.3.5.5>
- Roháček J, Hoffeins C (2021) Clusiomitidae, a new family of Eocene fossil Acalypratae, with revision of *Acartophthalmites* Hennig and *Clusiomites* gen. nov. (Diptera). *Insects* 12(12), 1123: 1–52. <https://doi.org/10.3390/insects12121123>
- Rung A, Mathis WN (2021a) 88. Aulacigastridae (Sap Flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Vol. 3. Brachycera—Cyclorhapha, excluding Calypratae. Suricata 8. South African National Biodiversity Institute, Pretoria, 1957–1962.
- Rung A, Mathis WN (2021b) 91. Periscelididae (Dwarf Flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Vol. 3. Brachycera—Cyclorhapha, excluding Calypratae. Suricata 8. South African National Biodiversity Institute, Pretoria, 1981–1987.
- Rung A, Mathis WN, Papp L (2005) *Curiosimusca*, gen. nov., and three new species in the family Aulacigastridae from the Oriental Region (Diptera: Opomyzoidea). *Zootaxa* 1009: 21–36.
- Rust J, Singh H, Rana RS, McCanna T, Singh L, Anderson K, Sarkare N, Nascimbene PC, Stebner F, Thomas JC, Solorzano Kraemer M, Williams CJ, Engel MS, Sahni A, Grimaldi D (2010) Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proceedings of the National Academy of Sciences of the United States of America* 107: 18360–18365.
- Sadowski E-M, Schmidt AR, Denk T (2020) Staminate inflorescences with in situ pollen from Eocene Baltic amber reveal high diversity in Fagaceae (oak family). *Willdenowia* 50: 405–517. <https://doi.org/10.3372/wi.50.50303>
- Seyfollah LJ, Beimforde C, Dal Corso J, Perrichot V, Rikkinen J, Schmidt AR (2018) Production and preservation of resins—past and present. *Biological Reviews* 93: 1684–1714. <https://doi.org/10.1111/brv.12414>
- Schindelin J, Arganda-Carreras I, Frise E, Kaynig E, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, Tinevez JY, White DJ, Hartenstein V, Eliceiri K, Tomancak P, Cardonaet A (2012) Fiji: an open-source platform for biological-image analysis. *Nature Methods* 9: 676–682. <https://doi.org/10.1038/nmeth.2019>
- Słodkowska B, Kramarska R, Kasiński JR (2013) The Eocene Climatic Optimum and the formation of the Baltic amber deposits. In: Kosmowska-Ceranowicz B, Gierlowski W, Sontag E (Eds) *The international amber researcher symposium Amber. Deposits—collections—the market*. Gdańsk (Poland), 22–23.03.2013. Gdańsk International Fair Co. Amberif, Gdańsk, 28–32.
- Szwedo J (2012) Life in the Eocene forests. In: Pytlos R, Szadziński R, Zbierska E, Adamska G, Dmowska A (Eds) *World Amber Council Seminar. Gdańsk the World Amber Capital, Gdańsk (Poland)*, May 18–19.2012., Mayor's Office for City Promotion, City Hall of Gdańsk, Gdańsk, 56–70.
- Tóthová A, Rozkošný R, Knutson L, Kutty SN, Wiegmann BM, Meier R. (2013) A phylogenetic analysis of Sciomyzidae (Diptera) and some related genera. *Cladistics* 29(4): 404–415. <https://doi.org/10.1111/cla.12002>
- Tschirnhaus M von, Hoffeins C (2009) Fossil flies in Baltic amber—insight in the diversity of Tertiary Acalypratae (Diptera, Schizophora), with new morphological characters and a key based on 1,000 collected inclusions. *Denisia* 26: 171–212.
- Weitschat W (2008) Bitterfelder und Baltischer Bernstein aus Paläoklimatischer und Paläontologischer Sicht. In: Rascher J, Wimmer R, Krumbiegel G, Schmiedel S (Eds) *Bitterfelder Bernstein versus Baltischer Bernstein: Hypothesen, Fakten, Fragen. II. Bitterfelder Bernsteinkolloquium. Exkursionsführer der Deutschen Gesellschaft für Geowissenschaften* 236. Mecke Druck und Verlag, Duderstadt, 88–97.
- Weitschat W, Wichard W (2002) *Atlas of Plants and Animals in Baltic Amber*. Dr. Friedrich Pfeil Verlag, Munich, Germany, 256 pp.
- Weitschat W, Wichard W (2010) Chapter 6. Baltic amber. In: Penney D. (Ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, UK, 80–115.

- Wiegmann BM, Trautwein MD, Winkler IS, Barr NB, Kim J-W, Lambkin C, Bertone MA, Cassel BK, Bayless KM, Heimberg AM, Wheeler BM, Peterson KJ, Pape T, Sinclair BJ, Skevington JH, Blagoderov V, Caravas J, Kuttly SN, Schmidt-Ott U, Kampmeier GE, Thompson FC, Grimaldi DA, Beckenbach AT, Courtney GW, Friedrich M, Meier R, Yeates DK (2011) Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences* 108: 5690–5695.
- Wiegmann BM, Yeates DK (2017) 11. Phylogeny of Diptera. In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Vol. 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria, 253–265.
- Wilde F, Ogurreck M, Greving I, Hammel JU, Beckmann F, Hipp A, Lottermoser L, Khokhriakov I, Lytaev P, Dose T, Burmester H, Müller M, Schreyer A (2016) MicroCT at the imaging beamline P05 at PETRA III. In: Shen Q, Nelson C (Eds) *Proceedings of the 12th International Conference on Synchrotron Radiation Instrumentation – SRI2015*, 1741:030035. <https://doi.org/10.1063/1.4952858>
- Winkler IS, Rung A, Scheffer SJ (2010) Hennig’s orphans revisited: Testing morphological hypotheses in the “Opomyzoidea” (Diptera: Schizophora). *Molecular Phylogenetics and Evolution* 54: 746–762.
- Winkler IS, Kirk-Spriggs AH, Bayless KM, Soghigian J, Meier R, Pape T, Yeates DK, Carvalho AB, Copeland RS, Wiegmann BM (2022) Phylogenetic resolution of the fly superfamily Ephydroidea – Molecular systematics of the enigmatic and diverse relatives of Drosophilidae. *PLoS ONE* 17(10): e0274292. <https://doi.org/10.1371/journal.pone.0274292>
- Woźnica AJ (2006) *Protoorbella hoffeinsorum* gen. and sp. nov., a new heleomyzid genus and species of the tribe Orbellini Gorodkov from Baltic amber (Diptera, Heleomyzidae). *Annales Zoologici, Warszawa* 56(1): 147–151.
- Woźnica AJ (2007) *Balticoleria michaeli*, gen. et spec. nov. from Eocene Baltic amber (Diptera, Heleomyzidae). *Genus (Suppl.)* 14: 83–88.
- Zatwarnicki T (1996) A new reconstruction of the origin of eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus* 7(1): 103–175.