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Expanding diversity of Acalyptratae (Diptera) in the Eocene Baltic amber forest: new species of *Acartophthalmites* (Clusiomitidae) and *Protanthomyza* (Protanthomyzidae stat. nov.)

JINDŘICH ROHÁČEK
Silesian Museum, Nádražní okruh 31, CZ-746 01 Opava, Czech Republic
rohacek@szm.cz; https://orcid.org/0000-0003-3311-2087

Abstract

Four new fossil species from two families of Acalyptratae (Diptera), all preserved in Baltic amber (Eocene, 48–34 Ma), are described: *Acartophthalmites bicolor* **sp. nov.**, *A. scotopteryx* **sp. nov.**, *A. striatus* **sp. nov.** (all Clusiomitidae), as well as *Protanthomyza chelicerata* **sp. nov.** (Protanthomyzidae). All new species are diagnosed, illustrated, and their relationships are discussed. Updated identification keys are provided. Based on newly acquired morphological data, the relationships of the subfamily Protanthomyzinae (formerly within Anthomyzidae) are revised. Since this fossil taxon is recognized as the sister group of Anthomyzidae (*s. str.*) (= without Protanthomyzinae) +Opomyzidae,, this group is elevated to the rank of a family, Protanthomyzidae **stat. nov.** The addition of four new species contributes to the knowledge of the diversity of Acalyptratae flies in the Eocene Baltic amber forest, even though they belong to extinct families.

Keywords: Clusiomitid flies, Protanthomyzid flies, four new species, taxonomy, morphology, relationships, keys, Tertiary

Introduction

Roháček *et al*. (2023) reviewed the current knowledge of Baltic amber Diptera Acalyptratae, including all recently described extinct families, viz. Hoffeinsmyiidae (Michelsen, 2009), Yantaromyiidae (Barták, 2019), Clusiomitidae (Roháček & Hoffeins, 2021) and Christelenkidae (Roháček *et al*., 2023). Since numerous unnamed fossil Acalyptratae taxa remain undescribed in collections, chiefly owing to activity of fly amber collectors, the diversity of this group in the so-called 'Baltic amber forest' is expected to continue growing. This study also contributes to a better understanding of the composition and species richness of the Acalyptratae fauna in this palaeohabitat. The Baltic amber forest evolved over *ca*. 10–15 million years during the Middle to Late Eocene, following the explosive radiation of vegetation initiated by the early Eocene warming maximum (*ca*. 49 Ma). This palaeohabitat was characterized not only by very rich plant communities but also by a diverse array of microhabitats with varying microclimatic conditions (Weitschat & Wichard, 2002; Weitschat, 2008; Kvaček, 2010; Szwedo, 2012; Słodkowska *et al*., 2013; Sadowski *et al*., 2020). Such a variable environment enabled the rapid diversification of insect fauna, including higher flies (Roháček *et al*., 2023).

The first part of this study focuses on three new species of the genus *Acartophthalmites* Hennig, 1965 belonging to the recently established family Clusiomitidae (Roháček & Hoffeins, 2021). This extinct family, known exclusively from Eocene Baltic amber, was revised by Roháček & Hoffeins (2021), who considered it closely related to Clusiidae. The family comprises two genera, *viz*., *Clusiomites* Roháček & Hoffeins, 2021 and *Acartophthalmites*. The genus *Clusiomites* includes only two known species: *C. clusioides* (Roháček, 2016) and *C. ornatus* Roháček & Hoffeins, 2021. The genus *Acartophthalmites* is more speciose, currently containing eight species: *A. crassipes* Roháček & Hoffeins, 2021, *A. luridus* Roháček & Hoffeins, 2021, *A. rugosus* Roháček & Hoffeins, 2021, *A. tertiaria* Hennig, 1965 (the type species), and *A. willii* Pérez-de la Fuente, Hoffeins & Roháček, 2018, along with three newly described species: *A. bicolor* **sp. nov.**, *A. scotopteryx* **sp. nov.**, and *A. striatus* **sp. nov.**

The second part of this study focuses on a new species of the genus *Protanthomyza* Hennig, 1965, which is also known exclusively from the Eocene. Most species have been found in Baltic amber, while one species originates from Bitterfeld amber (Roháček, 2013). Based on a single species, *P. collarti* Hennig,

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1965, Roháček (1998) established the separate subfamily Protanthomyzinae within the family Anthomyzidae. This classification of *Protanthomyza* has been followed to the present, with nearly a dozen species subsequently described (Roháček, 2006, 2013, 2020; Roháček & Hoffeins, 2020). However, the larger amount of known *Protanthomyza* species (including that described in this study), has allowed for a reassesment of morphological characters. The addition of newly revealed traits resulted in a revision of its relationships and classification: the subfamily Protanthomyzinae is now elevated to the family Protanthomyzidae, which is newly diagnosed. A total of 11 named species are now known within this family, all belonging to the genus *Protanthomyza*: *P. collarti* Hennig, 1965, *P. grimaldii* Roháček, 2020, *P. hennigi* Roháček, 2013, *P. hoffeinsorum* Roháček, 2013, *P. krylovi* Roháček, 2013, *P. loewi* Roháček, 2013, *P. meunieri* Roháček, 2013, *P. presli* Roháček, 2013, *P. ryszardi* Roháček & Hoffeins, 2020, *P. tschirnhausi* Roháček, 2013 plus *P. chelicerata* **sp. nov.** (described below).

Material and methods

Material

Four pieces of Baltic amber with inclusions (3 Clusiomitidae, 1 Protanthomyzidae) were studied. All samples were purchased from commercial sources in Lithuania and Poland, which obtained the material from Yantarny, Russia. Currently, these specimens are housed in the private collection of Christel and Hans Werner Hoffeins (Hamburg, Germany) (CCHH), but they will later be deposited in Senckenberg Deutsches Entomologisches Institut (SDEI), in Müncheberg, Germany.

Amber specimens

The above amber specimens containing Acalyptratae flies inclusions were prepared using the methods described by Tschirnhaus & Hoffeins (2009) and Hoffeins (2001). They were cut from original pieces, then ground and polished as close and parallel as possible to the frontal, dorsal and lateral sides of the fly specimen. These samples were subsequently embedded in artificial resin, then ground and polished again to secure their preservation and facilitate investigation.

Techniques of investigation

The amber inclusions were examined, drawn, and measured using two types of binocular stereoscopic microscopes (Reichert Austria Nr. 255799, Leica S9i). Photographic images were taken using either a Canon EOS 60D digital camera with a macro lens Canon MP-E 65 mm 1–5× or a Canon EOS 5D Mark III digital camera with a Nikon CFI Plan 4×/0.10NA 30 mm WD objective attached to a Canon EF 70–200mm f/4L USM zoom lens. The specimen photographed by means of the latter equipment was repositioned upwards between each exposure using a Cognisys StackShot Macro Rail and the final photograph was compiled from multiple layers (*ca*. 40) using Helicon Focus Pro 7.0.2. The final images were edited in Adobe Photoshop CS6. Other illustrations were drawn using the obtained 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/dm-cu : dm-cu (= ratio of length of section between r-m and dm-cu on discal cell : length of dm-cu) and index r-m/dm-cu : CuA_1 (= ratio of length of section between r-m and dm-cu on discal cell : length of apical portion of CuA_1).

Morphological terminology

Morphological terminology follows that used in Roháček (2006, 2009) and Roháček & Barber (2016), including terms of the male hypopygium, in continuity with Roháček (2013) and Roháček & Hoffeins (2021). The terminology of the male terminalia is based on the "hinge" hypothesis of the origin of the eremoneuran hypopygium, which was re-discovered and documented by Zatwarnicki (1996). Consequently, the following alterations of terms of the male genitalia (against those used by other hypotheses) need to be listed (term used here first): epandrium = periandrium, gonostylus = surstylus. Morphological terms of chaetotaxies of the thorax and head are illustrated in Figs 3A, B and 9A, those concerning wing venation in Figs 3F, 9D, and those of the male abdomen and terminalia in Fig. 4A–C, and 13A, B. The synonymous morphological terms for adult structures, along with their abbreviations as used in the most recent Manual of Afrotropical Diptera (Cumming & Wood, 2017) are given in parentheses in the list of abbreviations below.

Abbreviations of morphological terms used in text and/or figures

A_1—first anal vein (= anterior+posterior branch of cubital vein, CuA+CuP); A_2—second anal vein (= first branch of anal vein, A_1); ac—acrostichal (seta) (acr); ar—arista; avp—anteroventral process of epandrium; bm—basal medial cell; C—costa; ce—cercus; CuA_1—cubitus (= fourth branch of media, M_4); cup—posterior cubital cell; dc—dorsocentral (seta); dm—discal medial cell; dm-cu—discal medial-cubital (= discal medial, dm-m) cross-vein; dp—distiphallus; ep—epandrium; f_1, f_2,

f_3—fore, mid, hind femur; gs—gonostylus (= surstylus); ha—haltere; hu—humeral (= postpronotal, pprn) (seta); hum—humeral cross-vein; M—media (= first branch of media, M_1); mspl—mesopleural (= anepisternal, anepst) (seta); mt_2—mid basitarsus; npl—notopleural (seta); oc—ocellar (seta); ors—fronto-orbital (seta) (orb); pa—postalar (seta) (pal); pk—preapical kink; poc—postocular (setulae); ppl—propleural (= proepisternal+proepimeral, prepst+prepm) (seta); prs—presutural (= presutural intraalar, ial) (seta); prsc—prescutellar acrostichal (seta); pvt—postvertical (= postocellar, poc) (seta); R_1, R_{2+3}, R_{4+5}—1st, 2nd, 3rd branches of radius; r-m—radial-medial cross-vein; S1–S10—abdominal sterna; sa—supraalar (seta) (spal); sc—scutellar (seta) (sctl); Sc—subcosta; stpl—sternopleural (= katepisternal, kepst) (seta); T1–T10—abdominal terga; t_1, t_2, t_3—fore, mid, hind tibia; vi—vibrissa (vb); vte—outer vertical (seta) (o vt); vti—inner vertical (seta) (i vt).

Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Diptera Linnaeus, 1758
Acalyptratae Macquart, 1835
Family Clusiomitidae Roháček & Hoffeins, 2021
Genus *Acartophthalmites* Hennig, 1965

Type species. *Acartophthalmites tertiaria* Hennig, 1965; Baltic amber (Eocene); by original designation and monotypy.

***Acartophthalmites bicolor* sp. nov.**
(Figs 1–4)
http://zoobank.org/urn:lsid:zoobank.org:act:5CFBB846-A09B-4532-A30C-E4F60F8489A2

Type material. Holotype ♂, labelled: "Faszination Bernstein, Christel Hoffeins, Hans Werner Hoffeins" (framed on obverse), "1824-9 Diptera, Acalyptratae, Acartophthalmidae, Acartophthalmites ♂" (handwritten by C. Hoffeins, on reverse), "Baltic amber 40 mln years old, 41., 0.4 g, 18 × 7 × 4, Species Acalyptratae, B 3.4, rmvveta, www.ambertreasure4u.com" (printed, with some parts handwritten), "Russia: Kaliningrad Region, Baltic Sea coast, Yantarny" (printed) and "Holotypus ♂, *Acartophthalmites bicolor* sp.n., J. Roháček det. 2024" (red label), deposited in CCHH, no. 1824-9 [elongated block-shaped amber piece *ca.* 15.8 × 5.9 × 4.1 mm, embedded in polyester resin, size 15.8 × 7.5 × 6.3 mm, Fig. 1E]; syninclusions: pollen grains, dirt.

Etymology. The species is named "*bicolor*" (= bicolourous), a Latin adjective, owing to its distinctly bicolourous body, thorax in particular.

Diagnosis. A relatively slender species with bicolourous (dark brown and ochreous to yellow) body and unicolourous brown wings; frons surface smooth; frontal triangle small and short; orbit with additional microsetulae (only 2, very minute); scutum dorsally dark brown, laterally ochreous orange to yellow; thoracic pleuron dorsally with dark brown longitudinal band, ventrally yellow; 3 dc but the foremost small; prescutellar ac setae distinct, slightly beyond posterior dc; laterobasal sc distinctly shorter (0.7 times as long as) than apical sc; f_2 distinctly thicker and slightly longer than f_3; f_2 and also f_3 ventrally in distal fifth with short row(s) (two rows on f_2, one on f_3) of thicker short setae; t_2 with a long row of 10 erect posterior setae; Sc continuous; R_1 setulose; apical part of CuA_1 only 1.1 times as long as dm-cu.

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

Description. Male. A relatively slender species (Fig. 1A–C); total body length about 3.3 mm; body bicolourous, dorsally blackish brown to brown, ventrally ochreous to yellow, most distinctly on thoracic pleuron (Fig. 1A, C, D).

Head (Figs 2A–C, 3A, B) higher (1.35×) than long, slightly wider than thorax in dorsal view; occiput dorsally medially distinctly concave. Head pale brown anteriorly to dark brown posteriorly, occiput darkest; frons brown, anteriorly probably lighter; face pale brown, gena dirty yellow, postgena pale brown to brown. Frons relatively narrow, somewhat narrower than eye in dorsal view, slightly tapering anteriorly, smooth on surface. Orbit distinctly delimited and relatively broad, brown, darker posteriorly, paler anteriorly. Frontal triangle small and very narrow, with anterior corner acute and hardly reaching half of frons (Fig. 3A); ocellar triangle blackish, almost as wide as and about half length of frontal triangle, distinctly elevated; ocelli not enlarged. Frontal lunule not visible, probably small. Face very narrow, parafacialia distinct and wider than face below antennae. Postgena and adjacent part of occiput camparatively large (as in *A. crassipes*). Cephalic chaetotaxy (Fig. 3A, B): pvt relatively robust, about as long as vte, divergent and closely arising; vti strong and long (longest cephalic seta), twice (or more) as long as vte; oc relatively robust (about as long as foremost ors) and inserted between ocelli, slightly divergent and strongly proclinate; 3 reclinate ors becoming shorter anteriorly, hindmost ors longest and most robust (distinctly longer than vte); only 2 additional microsetulae (very minute, hardly discernible) on orbit, one each between ors; postocular setulae numerous, in 1 row dorsally at posterior eye margin but in 2 rows more ventrally plus some additional setulae scattered on adjacent medial part of occiput and postgena; postgena

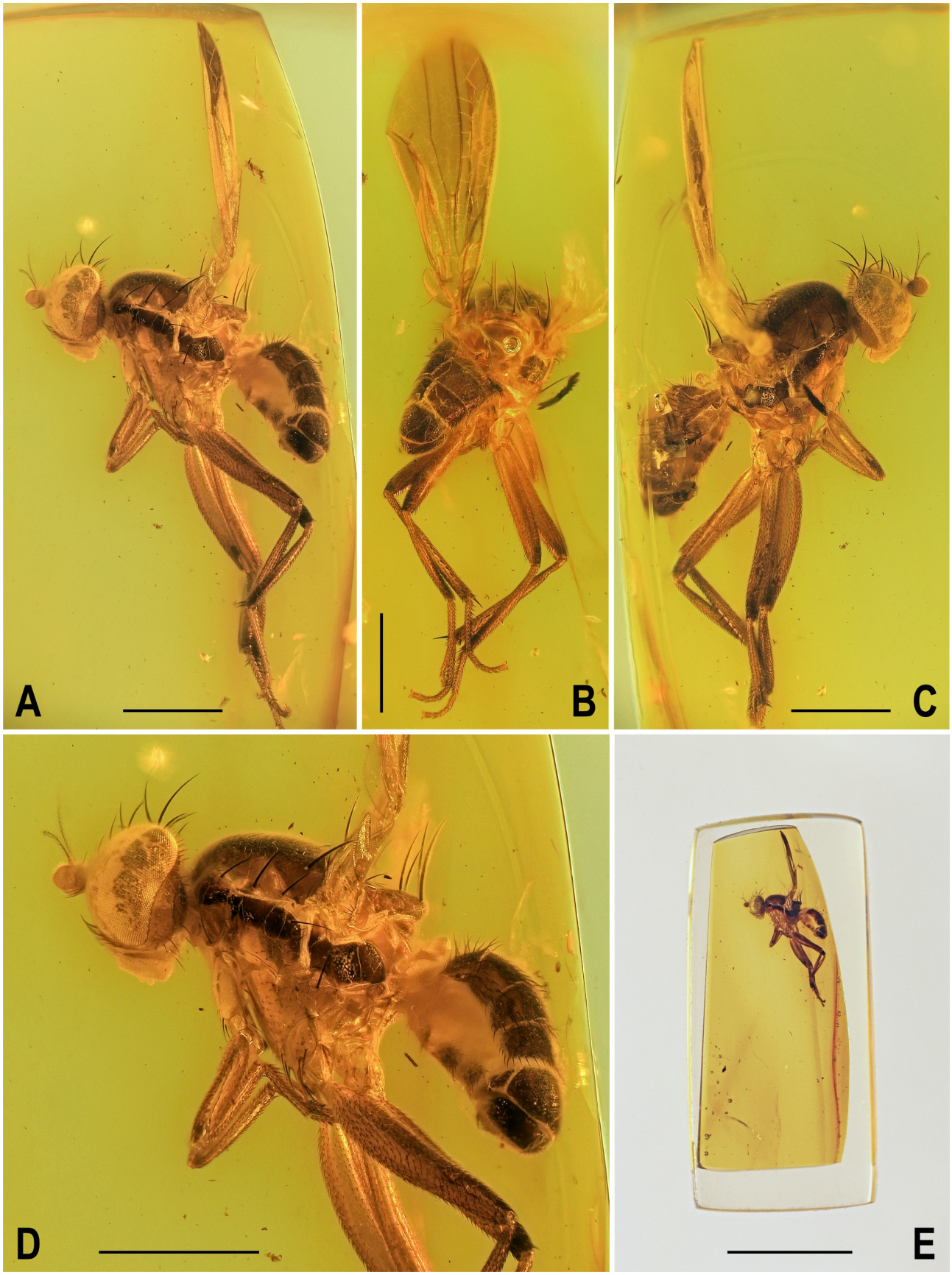

FIGURE 1. *Acartophthalmites bicolor* **sp. nov.**, holotype male (Baltic amber). **A**, Male, left laterally. **B**, Ditto, dorsocaudally. **C**, Ditto, right laterally. **D**, Male body, left laterally. **E**, whole amber sample (preparatum in polyester resin), in *situ*. Scale bars: 1 mm (**A**–**D**), 5 mm (**E**). Photographs by J. Roháček.

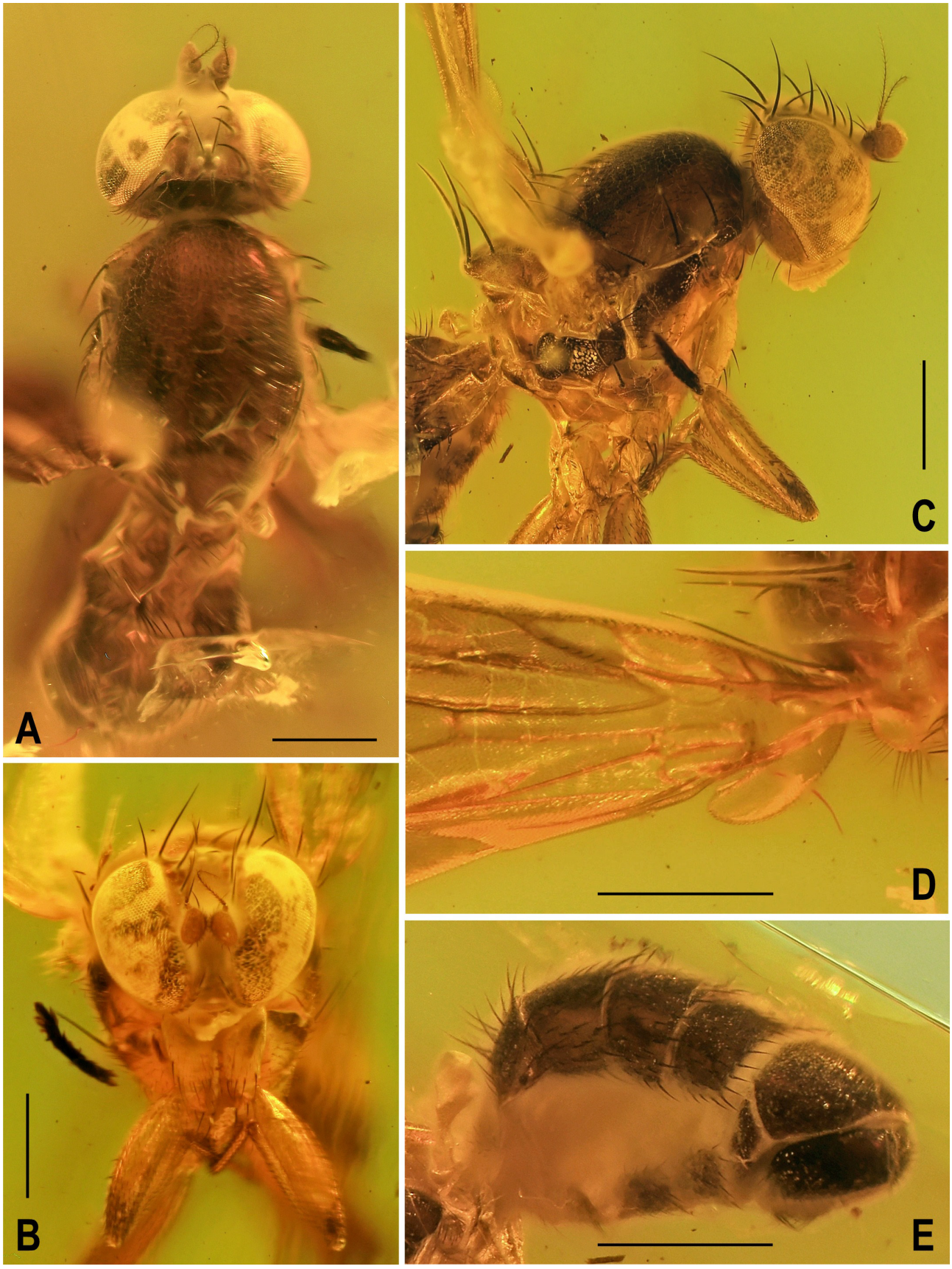

FIGURE 2. *Acartophthalmites bicolor* **sp. nov.**, holotype male (Baltic amber). **A**, Male body, dorsally. **B**, Head, frontally. **C**, Head and thorax, right laterally. **D**, Proximal part of left wing, dorsally. **E**, Abdomen, left laterally. Scale bars: 0.5 mm. Photographs by J. Roháček.

with 3 posteroventral setae (2 hindmost longer) in addition; vi relatively short but distinct, thicker and about twice or more longer than foremost peristomal setulae (vibrissae upcurved, convergent but their apices not meeting medially); no subvibrissa; peristomal setulae (except for foremost) small and fine, 6 or 7 visible on each side. Eye large, bare, convex, subovoid (with ventral part more narrowed and posterior margin excavated), having longest diameter *ca*. 1.6 times as long as shortest diameter. Gena very narrow, its height less than 0.1 times as long as shortest eye diameter. Palpus probably small, not visible. Mouthparts ochreous; clypeus small, narrow, pale brown; labella pale yellow, fleshy, finely, pale and short-haired. Antenna porrect (Figs 2C, 3B) and relatively small; scape (small, poorly visible) and pedicel pale brown; pedicel externo-laterally with anterior margin slightly convex, with one longer upright dorsal seta and 2 (1 longer and stronger) setae ventrally besides marginal and submarginal setulae; 1st flagellomere only slightly paler but distinctly longer than pedicel, suboval (about 1.3× higher than long), laterally compressed and suboval (slightly higher than long) in profile, very finely brownish pilose. Arista dorsobasal, relatively short, *ca*. 2.3 times as long as antenna, with shortly cylindrical ochreous basal segment and brown terminal section being moderately long-ciliate (Fig. 3B).

Thorax (Figs 1D, 2A, C, 3A). Slightly narrower than head, distinctly bicolourous, dark brown and yellow. Scutum dorsally dark brown, laterally with notopleural area and adjacent part of mesonotum (up to sa seta) ochreous orange (dorsally) to yellow (on notopleuron); also humeral callus (postpronotal lobe) bicolourous, anteriorly brown, posteriorly contrastingly yellow; scutellum and subscutellum brown; pleural part of thorax largely yellow but dorsally with dark brown band ranging from propleuron to katatergite of postnotum and covering dorsal half of propleuron and mesopleuron and entire pteropleuron and katatergite; anatergite ochreous yellow and contrasting with dark adjacent katatergite and meditergite of postnotum. Scutellum subtriangular with rounded apex, slightly convex dorsally; subscutellum well developed (see Fig. 1D). Thoracic chaetotaxy (Figs 1D, 2C, 3A): 1 hu (strong but slightly shorter than anterior npl) and about 10 microsetae on humeral callus; 2 npl, anterior longer and thicker than posterior; 1 robust sa, distinctly longer than anterior npl; 2 pa, anterior very long and strong (together with apical sc longest thoracic setae, posterior short and fine, about one-fourth of anterior; no prs; 3 dc (all postsutural) but foremost dc small and weak, about half length of middle dc, the latter somewhat shorter than posterior; hindmost dc relatively robust and about as long as laterobasal sc; 1 prescutellar medial ac (situated slightly beyond level of posterior dc) subequal in length and thickness to posterior pa; scutum otherwise with relatively dense microsetae; ac microsetae in about 10 irregular rows in front of suture but less posteriorly, reaching prescutellar ac setae); 2 strong sc (both unnaturally upright in holotype), apical about as long as anterior pa, laterobasal sc slightly thinner and about 0.7 times as long as apical sc; 1 relatively long but fine upcurved ppl; mesopleuron with one distinct mspl (as long as hu but thinner) in posterodorsal corner and numerous scattered microsetae in posterodorsal half of the sclerite, those situated at posterior margin being longer; sternopleuron with 1 long stpl (as long as mspl but more robust) and a number of microsetae scattered in posteroventral three-fourths of surface, and with 2 longer but fine setae on ventral corner of sternopleuron; prosternum bare.

Legs (Figs 1A, B, 3C–E). Somewhat variegated, with coxae, trochanters and tarsi ochreous yellow to yellow, while femora and tibiae are proximally pale (ochreous) and distally darkened (brown to dark brown on apex). Mid and hind legs markedly longer than fore legs. Femur and tibia of mid leg about 1.7 and 1.9 times as long as those of fore leg, respectively; f_2 (see Fig. 1C, D) distinctly thickened and slightly longer than f_3; cx_3 with distinct posteroventral process having blunt apex. f_1 with a short row of 5 inconspicuous (short and weak) posteroventral setae in distal fifth and with 3 short, widely separated, posterodorsal setae on distal half of femur; f_2 elongated and thickened, in proximal third broadest (about 1.7 times as thick as f_3 at this point) and gradually tapered distally where it is as wide as f_3; f_2 uniformly densely finely setulose but in distal fifth ventrally with 2 short rows of thicker short setae (6 in anteroventral, 8 in posteroventral row, Fig. 3D, E); also f_3 with a similar (posteroventral) row of 5 or 6 short thicker setae (Fig. 3E), otherwise uniformly setulose. t_1 finely setulose but with 1 small dorsal preapical seta and 1 yet shorter ventroapical setula (both shorter than longest ventral setulae on base of fore basitarsus). t_2 (apart from usual short setosity) with a long row of 10 erect posterior setae (those in middle third longest, Fig. 3C) in distal three-fifths, 1 very small dorsal preapical seta and 1 short robust ventroapical seta (as long as width of t_2) plus a group of 4 small but thick preapical (posterodorsal to ventral) setulae on apex (Fig. 3D); t_3 very slightly bent, without dorsopreapical seta, but with 2 similarly short (ventroapical and anteroapical) setae (Fig. 3E), otherwise uniformly setulose. Tarsi simple, slender; fore basitarsus with 2 or 3 longer setulae ventrobasally, other setulae short and dense; mid and hind basitarsus long (longer than rest of tarsus) and each with a row of thicker posteroventral erect setulae (those on mid basitarsus longer); claws small.

Wing (Figs 1B, 2D, 3F). Only left wing complete but folded in the holotype. Wing relatively narrow; veins

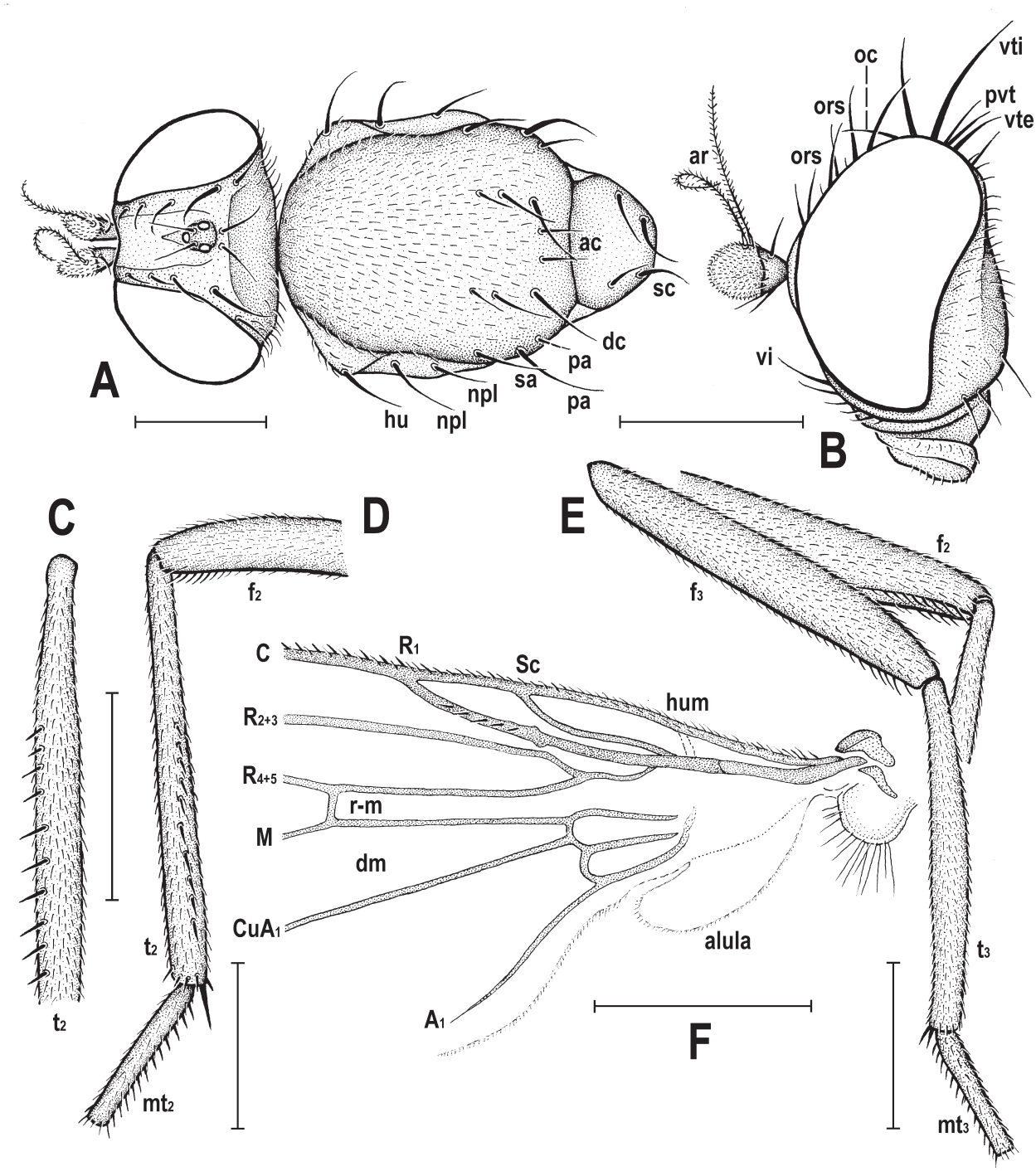

FIGURE 3. *Acartophthalmites bicolor* **sp. nov.**, holotype male (Baltic amber). **A**, Head and thorax, dorsally. **B**, Head, left laterally. **C**, Left mid tibia, subventrally. **D**, Left mid femur, tibia and basitarsus, posteriorly. **E**, Right mid femur and right hind femur, tibia and basitarsus, posteriorly. **F**, Proximal part of left wing, dorsally. Scale bars: 0.5 mm. For abbreviations see Material and methods.

brown; membrane uniformly brown. C strongly attenuated beyond R_{4+5} but reaching to M; C finely setulose, only basally with 1 longer seta and Cs_2 and basal fourth of Cs_3 with thicker (but not longer) sparse spine-like setulae in addition. No costal break. Sc well developed (Fig. 3F) and terminated in C distantly from apex of R_1. R_1 short, robust and with 5 distinct setulae (Fig. 3F), also preapical kink at the level of apex of Sc well developed. R_{2+3} long, almost straight in most of its length, only apically slightly upcurved to C and ending distinctly farther from wing apex than M. R_{4+5} shallowly bent posteriorly, distally straight and parallel with M and ending near wing apex. Distal

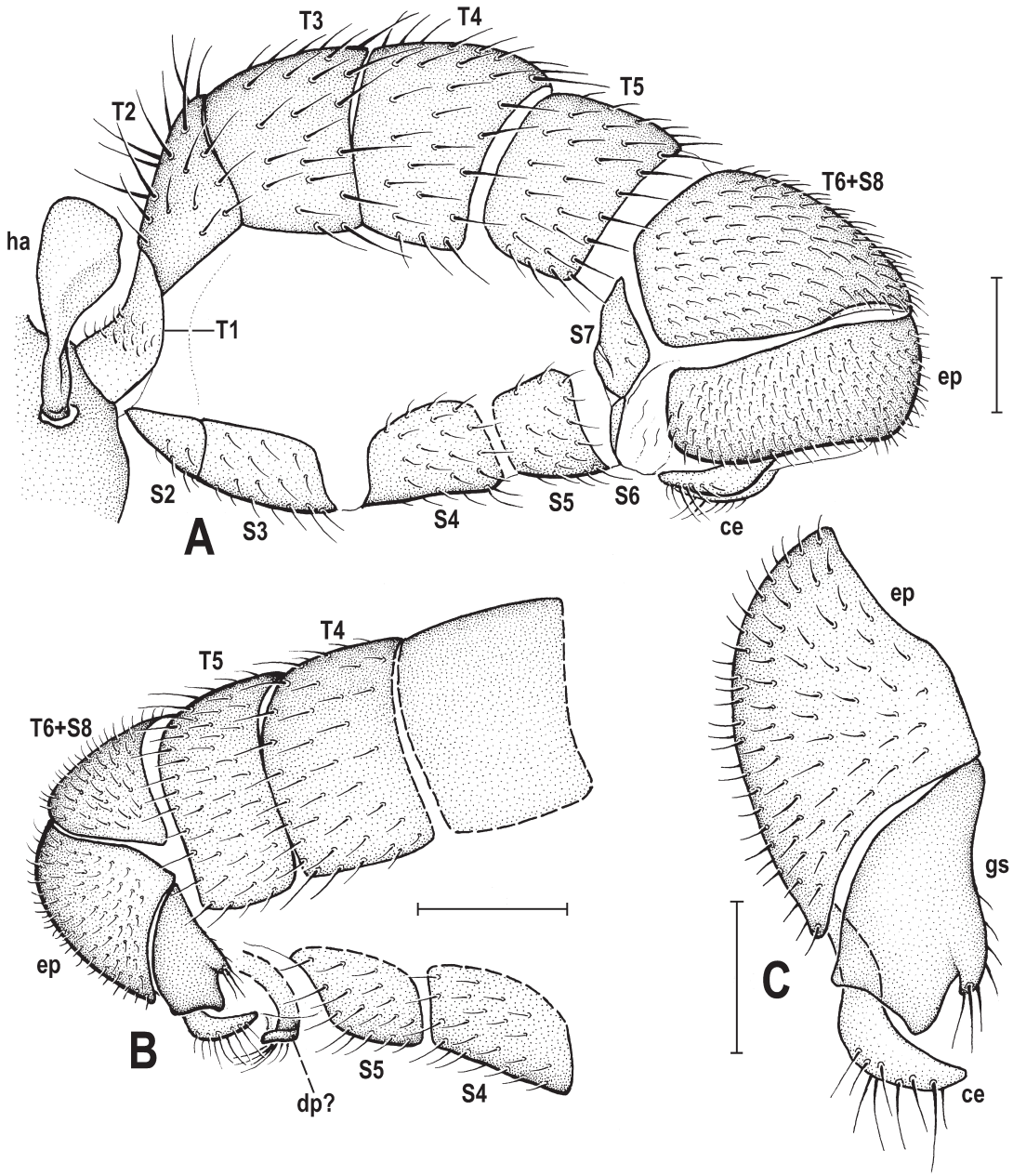

FIGURE 4. *Acartophthalmites bicolor* **sp. nov.**, holotype male (Baltic amber). **A**, Abdomen, left laterally. **B**, Abdomen, right laterally. **C**, male external genitalia, right laterally. Scale bars: 0.2 mm (**A**, **B**), 0.1 mm (**C**). For abbreviations see Material and methods.

part of M straight and reaching wing margin. Discal (dm) cell elongate and relatively narrow (particularly in basal third); anterior cross-vein (r-m) situated near the middle of cell. Distal part of CuA_1 short, only about 1.1 times as long as dm-cu and also reaching wing margin; A_1 long, slightly curved, and ending far from wing margin. Cells bm and cup closed. Anal lobe developed but its size not precisely recognized because twice folded (see Fig. 2D). Alula large and broad (Figs 2D, 3F). Wing measurements: length 3.18 mm, width 1.11 mm, Cs_3 : Cs_4 = 1.94, r-m/dm-cu : dm-cu = 2.38. Haltere (Figs 2E, 4A) relatively large, dirty whitish yellow, slightly darkened on knob.

Abdomen (Figs 2E, 4A, B). Slightly shorter than thorax, rather elongately pyriform than cylindrical (particularly in dorsal view, Fig. 2A). T1 pale ochreous, with short erect setulae on disc (Fig. 4A). All other preabdominal terga (T3–T5) dark brown and rather densely setose, with longest and thickest setae at posterior margins, only T2 with long and erect setae also proximally (Figs 2E, 4A). T1–T2 separation discernible, and terga also differing in colour. T2–T5 slightly bent laterally. T1 not shorter than T2; T3 and T4 longest, subequal in length; T5 somewhat shorter. Preabdominal sterna only visible in lateral view (Figs 2E, 4A, B), all distinctly paler than adjacent terga.

S1 lightest, S3–S5 becoming darker posteriorly, S5 pale brown. S2 short and probably narrowed anteriorly, S3 and S4 largest, transversely suboblong, S5 distinctly shorter than S4 and also T5, all these sterna sparsely, shortly and finely setose. Postabdomen (Fig. 4A, B) with all sclerites asymmetrical, dark brown to blackish, and most of them shortly densely setulose. T6 is considered (see Roháček & Hoffeins, 2021) as fused with S8 to form with it a large, long (almost twice longer than T5) and strongly asymmetrical (markedly larger on left side) dorsal synsclerite T6+S8 being all densely shortly setulose. S6 obviously small, very short, situated ventrally and on lelf laterally fused with S7; S7 forming a rhomboid sclerite on left laterally (Fig. 4A), very shortly and sparsely setulose while S6 is probably bare.

Genitalia. Epandrium (Fig. 4A–C) short and high, arch-shaped but somewhat asymmetrical (higher on left side), ventrally open and with anal fissure directed ventrally, blackish brown, with similarly dense short setosity as is that on T6+S8. Cerci yellow, relatively slender (Fig. 4C), somewhat asymmetrical and situated below anal fissure, each with fine (differently) curved setae along posterior margin (Fig. 4A). Only right gonostylus visible (Fig. 4B, C), relatively large, blackish brown, proximally as broad as epandrial length, distally slightly tapered and terminated by posterior bare corner and by short anterior setulose process bearing a few longer setulae on apex. Left gonostylus covered by milky coating and, therefore, its shape unrecognizable (*cf*. Fig. 4A). There is a slender blackish sclerite visible ventrally in front of cerci, probably representing apex of distiphallus (see Fig. 4B).

Female. Unknown.

Remarks. This new species is externally most similar to *A*. *willii*, *cf*. Pérez-de la Fuente *et al*. (2018) and Roháček & Hoffeins (2021). Both species are characterized by slender body (resembling those of *Clusiomites* species), relatively narrow wings, bicoloured (dark brown and ochreous) thorax and mid femur with enlarged ventral setae forming short rows distally. However, *A*. *bicolor* **sp. nov.** differs from *A*. *willii* by a number of both colour and structural characters: scutum with simple pattern (dorsally dark brown, only laterally ochreous); wing with uniformly brownish membrane (darkened along anterior margin in *A*. *willii*); eye more elongate; frons surface smooth (very finely rugose in *A*. *willii*), frontal triangle small but present (not developed in *A*. *willii*); 3 dc setae (2 dc in *A*. *willii*); ac microsetae less dense, with only *ca*. 10 rows on suture (in about 15 rows in *A. willii*); mid tibia with a row of 10 posterior setae (only 6 or 7 in *A*. *willii*). Also male cercus and gonostylus are probably different in both species if the original illustration of the male terminalia of *A*. *willii* by Hennig (1969: fig. 20, as *A*. *electrica*) is correct, *cf*. also Roháček & Hoffeins (2021: fig. 29B). There is another *Acartophthalmites* species with bicolourous thorax, *viz*., *A*. *striatus* **sp. nov.** (described below) but it is more dissimilar to *A*. *bicolor* **sp. nov.** due to more robust body; longitudinally striated frons, face, parafacialia and gena; scutum dorsally posteriorly pale brown and contrasting with blackish scutellum; only 2 dc and *ca*. 14 rows of ac microsetae on suture; mid and hind femora lacking enlarged ventral setae distally; mid tibia with a row of only 7 or 8 posterior setae; broader wing.

***Acartophthalmites scotopteryx* sp. nov.**

(Figs 5–7)

http://zoobank.org/urn:lsid:zoobank.org:act:6951B3DA-C835-4B8D-A4EF-40D70DADBFDF

Type material. Holotype ♂, labelled: "Faszination Bernstein, Christel Hoffeins, Hans Werner Hoffeins" (framed on obverse), "897-1 Acartophthalmidae, A. tertiaria" (handwritten by C. Hoffeins, on reverse), "Russia: Kaliningrad Region, Baltic Sea coast, Yantarny" (printed) and "Holotypus ♂, *Acartophthalmites scotopteryx* sp.n., J. Roháček det. 2024" (red label), deposited in CCHH, no. 897-1 [block-shaped amber piece *ca.* 12 × 11.7 × 3.4 mm, embedded in polyester resin, size 16 × 14.3 × 6 mm, see Fig. 5D]; syninclusions: plant remnants (cuticle with trichomes, stellate hairs and straight pointed trichomes), minute worm-like creatures (Nematoda?), dirt.

Etymology. The name "*scotopteryx*" (= dark wing, from Greek, noun in apposition) refers to dark brown wing membrane of the new species.

Diagnosis. Large (body length over 4 mm), blackish brown to brown species with unicolourous dark brown wings; frons surface smooth; frontal triangle small and very short, only reaching level of posterior ors; orbit with more additional microsetulae; scutum without contrasting pattern; 2 dc; prescutellar ac setae distinctly beyond posterior dc; ac microsetae dense, in 14–16 rows on suture; laterobasal sc distinctly shorter (0.7 times as long as) than apical sc; f_2 strongly swollen and slightly longer than f_3; t_2 with a long row of 10 erect posterior setae; t_2 with ventroapical seta short (shorter than width of tibia); Sc continuous; R_1 setulose; apical part of CuA_1 only as long as dm-cu. Haltere with brown stem and whitish knob.

Type locality and horizon. Russia: Kaliningrad region, Yantarny mine (formerly Palmnicken). Mid-late Eocene, 48–34 Ma.

Description. Male. Total body length about 4.4 mm (holotype). Body of the holotype is partly covered by a silvery air microlayer (Fig. 5A), partly by milky coating (Fig. 5B) and hence its colouration is rather obscured but general colour largely blackish brown to brown, including thoracic pleuron (see Fig. 6A).

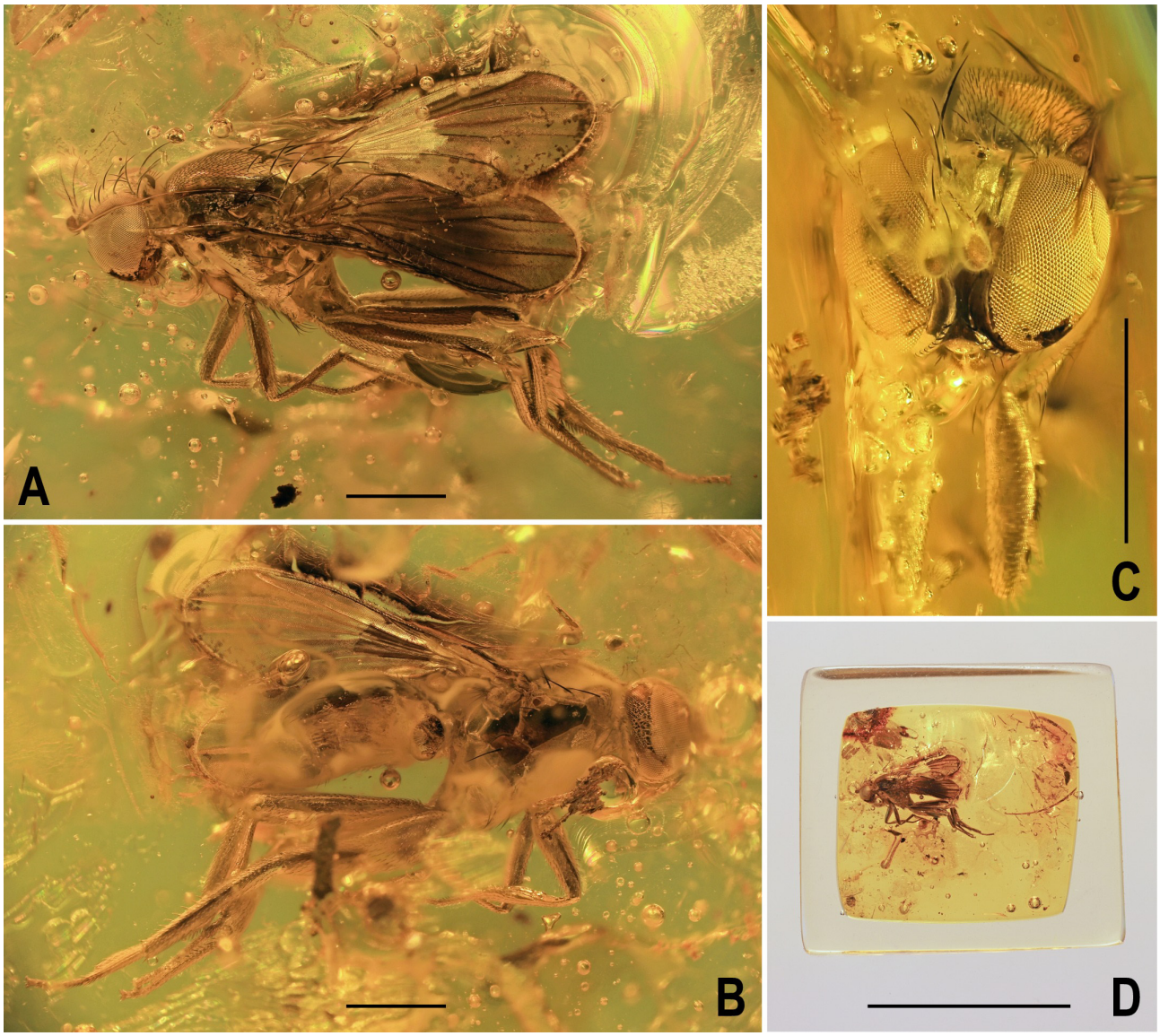

FIGURE 5. *Acartophthalmites scotopteryx* **sp. nov.**, holotype male (Baltic amber). **A**, Male, left laterally. **B**, Ditto, right laterally. **C**, Head, frontally. **D**, whole amber sample (preparatum in polyester resin), in situ. Scale bars: 1 mm (**A**–**C**), 10 mm (**D**). Photographs by J. Roháček.

Head (Figs 5C, 6A, 7A) somewhat higher than long and slightly wider than thorax in dorsal view; occiput dorsally distinctly concave. Head dark brown posteriorly and also anteriorly, occiput darkest; frons obviously dark brown to brown (seen at its anterior margin); face and (relatively broad) parafacialia brown dorsally, blackish brown ventrally; gena blackish brown, postgena brown. Frons narrow, distinctly narrower than eye in dorsal view, somewhat tapering anteriorly, smooth on surface. Orbit distinctly delimited by longitidinal stria, dark brown also anteriorly. Frontal triangle very small, short and narrow (not wider than ocellar triangle), with anterior corner acute and only reaching level of posterior ors (Fig. 7A); ocellar triangle blackish, more than half length of frontal triangle and distinctly protruding; ocelli large compared to entire ocellar triangle. Frontal lunule not visible in the male holotype. Face narrow, in the middle narrower than unusually broad parafacialia (Fig. 7A); gena low (narrow) but postgena and adjacent part of occiput large. Cephalic chaetotaxy (Figs 6A, 7A): pvt strong (as long as vte), divergent and inserted closely behind posterior ocelli; vti strong and long (by far the longest cephalic seta), more than twice as long as vte; oc thinner and slightly shorter than foremost ors and inserted between ocelli, divergent and proclinate; 3 strong reclinate ors becoming slightly shorter anteriorly, hindmost ors longest but not thicker than others (somewhat longer than vte); 5–7 additional microsetulae on orbit, 2 or more between each ors, 1–2 in front of anterior ors; postocular setulae relatively long, in 1 long row at posterior eye margin but in an additional

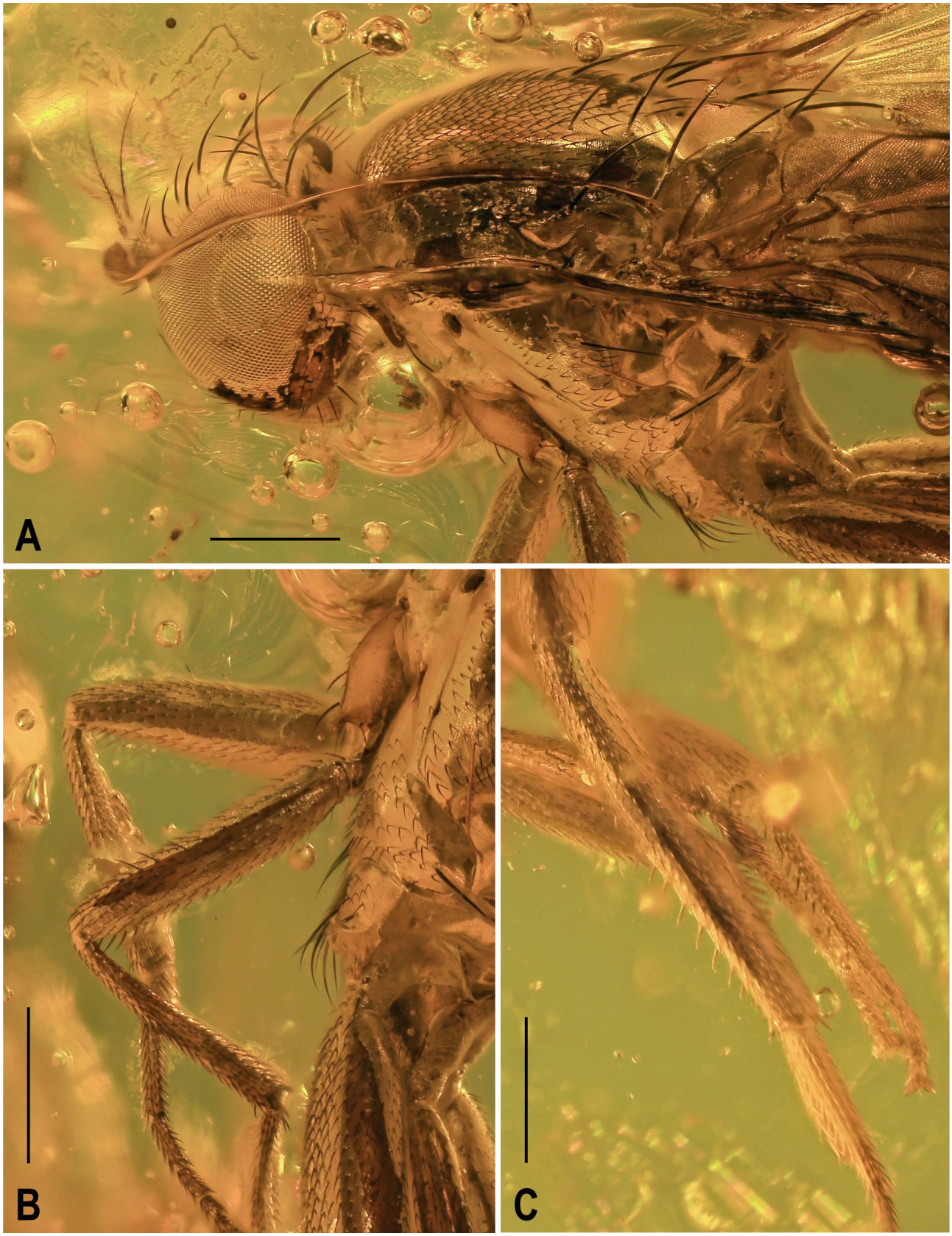

FIGURE 6. *Acartophthalmites scotopteryx* **sp. nov.**, holotype male (Baltic amber). **A**, Head and thorax, left laterally. **B**, Fore legs, left laterally. **C**, Right mid tibia and basitarsus, dorsally. Scale bars: 0.5 mm. Photographs by J. Roháček.

irregular row more ventrally; some erect additional setulae on adjacent medial part of occiput, one of them enlarged and longer than postgenal setae; postgena with 3 distinct posteroventral setae (hindmost longest); vi relatively short

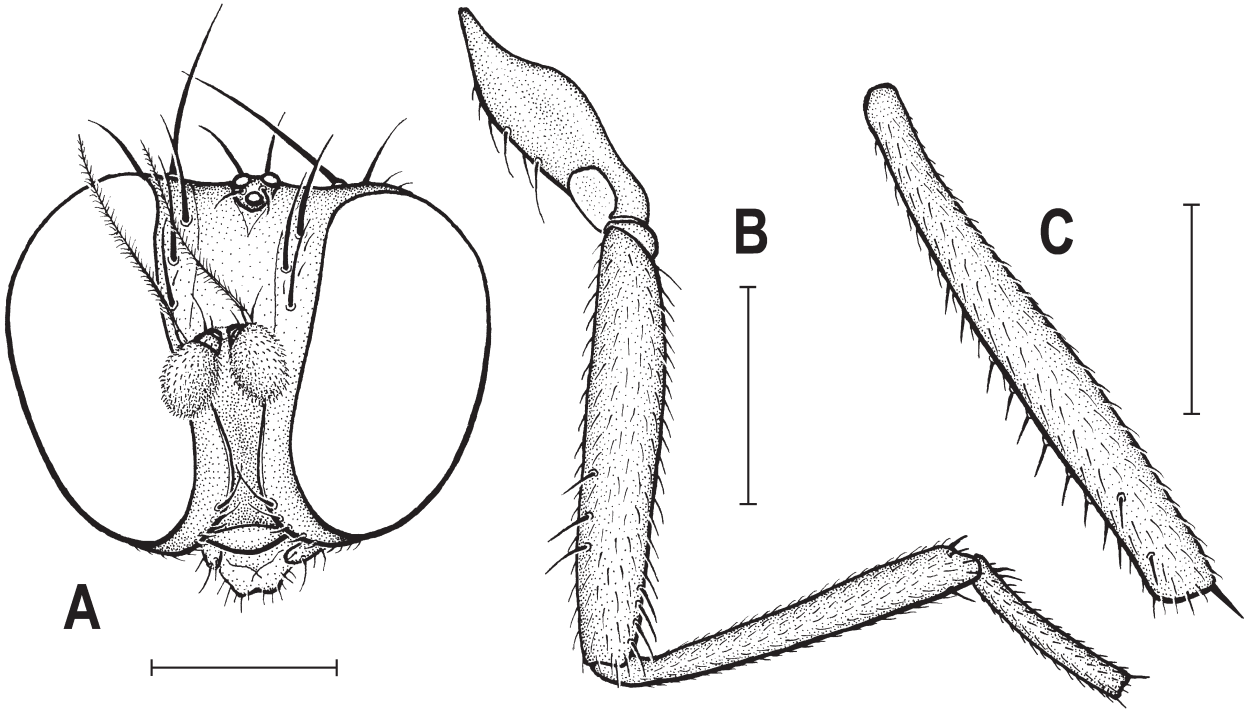

FIGURE 7. *Acartophthalmites scotopteryx* **sp. nov.**, holotype male (Baltic amber). **A**, Head, frontally. **B**, Left fore leg, posteriorly (segments 2–5 of tarsus omitted). **C**, Right mid tibia dorsally. Scale bars: 0.5 mm.

(shorter than foremost ors) but distinct (vibrissae incurved, with apices crossed medially, Fig. 7A); no subvibrissa but peristomal setulae relatively strong (6 or 7 visible), foremost about half length of vi. Eye large, bare, convex, broadly subovoid (with posterior margin almost straight), its longest diameter about 1.6 times as long as shortest diameter. Gena very narrow, its height only 0.07 times as long as shortest eye diameter. Palpus ochreous, small and short, with 1 longer black subapical setula and a few small setulae behind it. Mouthparts ochreous including small clypeus (Fig. 5C) contrasting with dark face; labella fleshy and finely, pale and relatively long-haired. Antenna porrect (Fig. 6A) and small; scape and pedicel brown; pedicel externo-laterally with anterior margin simply convex, with one longer seta dorsally and 2 finer setae ventrally apart from marginal and submarginal setulae; 1st flagellomere paler (ochreous) and only slightly longer than pedicel, laterally compressed and suboval (distinctly higher than long) in profile, finely whitish pilose on surface. Arista dorsobasal, longer than in *A. crassipes*, 2.9 times as long as antenna, with shortly cylindrical ochreous basal segment and dark brown terminal section being relatively long-ciliate (Fig. 7A).

Thorax (Figs 5A, B, 6A). Very slightly narrower than head, brown to dark brown. Scutum obviously entirely dark brown, including notopleural area; scutellum blackish brown, subscutellum not visible; pleural part of thorax dorsally darkest (blackish brown) and gradually becoming brown ventrally. Scutellum relatively large, subtriangular with rounded apex, almost flat dorsally. Thoracic chaetotaxy (Fig. 6A): 1 hu (strong and as long as anterior npl) and about 14 microsetae on humeral callus; 2 npl, anterior longer but not thicker than posterior; 1 robust sa, much longer than anterior npl; 2 pa, anterior very long and strong (only slightly shorter than apical sc), posterior fine and slightly less than half of anterior; no prs; 2 dc (both postsutural), anterior situated at level of sa and about three-fifths of length of posterior, posterior dc robust and as long as or longer than laterobasal sc; 1 microseta in front of anterior dc enalrged, twice longer than microsetae in front of it; 1 prescutellar medial ac (situated distinctly beyond level of posterior dc) distinct but shorter and thinner than posterior pa; scutum otherwise covered by very dense microsetae becoming distinctly smaller anteriorly; ac microsetae in about 14–16 rows in front of suture but less posteriorly (only 4 rows between posterior dc); 2 sc, both strong, apical very long and robust (longest thoracic seta), laterobasal sc slightly thinner and shorter (*ca*. 0.7 times as long as) apical sc; 1 long (as long as anterior dc) but fine upcurved ppl; mesopleuron with one distinct mspl (as long as hu but thinner) in posterodorsal corner and scattered (reletively numerous) microsetae in posterodorsal half of the sclerite, those at posterior margin distinctly longer; sternopleuron with one long (as long as mspl) stpl and numerous microsetae scattered over entire surface of sclerite, 2 or 3 longer but fine setae also on ventral corner of sternopleuron; prosternum bare.

Legs (Figs 6B, C, 7B, C). Brown to dark brown, with femora darkest, coxae and tarsi lighter. Mid and hind legs long and robust. Femur of mid leg about 1.6 times as long as that of fore leg; f_2 (see Fig. 5A, B) strongly thickened (as that of *A. crassipes*) but only slightly longer than f_3; cx_3 distally with small, finely setose posterior process (apex not precisely seen); f_1 (Figs 6B, 7B) with a short row of only 4 short posteroventral to ventral setae in distal fifth and with 3 short posterodorsal setae in row near distal third of femur; f_2 elongated and amplified, most swollen in proximal third (twice as thick as f_3 at this point, Fig. 5A), gradually tapered distally where only slightly thicker than f_3; both f_2 and f_3 rather uniformly densely finely setulose, also ventral setulae at distal end of femur only slightly longer than others; t_1 (Figs 6B, 7B) finely setulose but with 1 small dorsal preapical seta and also 1 similarly short ventroapical seta; t_2 (besides usual short setosity) with a long row of 10 erect posterior setae (those in the middle longest) in distal three-fifths, only 2 very small dorsal setae (one preapical, the other in distal fifth) and 1 short ventroapical seta (as long as longest seta in posterior row, Fig. 7C) plus 2–3 smaller and very short setae on apex near it; t_3 almost straight, without dorsopreapical seta, but with 1 short and small ventroapical (as long as that on f_2) and 2 smaller anteroapical setae, otherwise uniformly setulose. Tarsi simple, slender; fore basitarsus with 2 longer curved setulae ventrobasally (Fig. 7B), other setulae short and dense; mid and hind basitarsi long (longer than rest of tarsus) and each with a row of thicker posteroventral erect setulae (those on mid basitarsus more robust); claws small as usual.

Wing (Fig. 5A, B) relatively broad but distinctly narrower than that of *A. tertiaria*; veins brown; membrane uniformly dark brown. C strongly attenuated beyond R_{4+5} but reaching to M; C finely setulose but basally with 1 longer and thicker seta and Cs_2 and partly also Cs_3 (very proximally only) with sparse spine-like setulae in addition. No costal break. Sc distinct but pale and fine, developed also basally and ending in C far from apex of R_1. R_1 short, robust, dark and setulose in distal half (6 or 7 setulae recognized), with preapical kink well developed at the level of apex of Sc. R_{2+3} long, almost straight, only apically very slightly upcurved to C and ending markedly farther from wing apex than M. R_{4+5} shallowly but distinctly bent posteriorly, distally straightened and parallel with M, ending close to wing apex. Distal part of M almost straight and reaching wing margin. Discal (dm) cell elongated and rather narrow; anterior cross-vein (r-m) situated near the middle of cell. Distal part of CuA_1 short, about as long as dm-cu and terminating near wing margin; A_1 long, but ending far from wing margin. Cells bm and cup small, both completely closed. Anal lobe well developed. Alula large and broad. Wing measurements: length 3.37 mm, width 1.31 mm, $Cs_3 : Cs_4 = 1.68$, r-m/dm-cu : dm-cu = 2.35. Haltere bicolourous, with pale brown stem and dirty white knob.

Abdomen poorly visible due to milky coating and dorsal wing coverage. Subcylindrical and probably elongately ovoid in dorsal view, very slightly bent in lateral view (Fig. 5B). All preabdominal terga (partly visible right laterally) with relatively dense and short setae, the longest setae at posterior margins; setae on T1 and T2 somewhat erect. T1 brown, T2–T5 blackish brown. T1 and T2 obviously separated. T1 shorter than T2, T2–T5 subequal in length but T5 narrowed posteriorly. Preabdominal sterna not visible due to milky coating, only S5 partly discernible, brown and sparsely shortly setose. Postabdomen of the holotype obscured by heavy milky coating but T6+S8 clearly asymmetrical (with smaller part on left side) and very shortly setulose; other sclerites not visible.

Genitalia. Epandrium also obscured by milky coating (Fig. 5B) but relatively large, blackish brown, with anal fissure directed ventrally, and uniformly shortly setulose. No distinct appendages but fine setosity of cerci(?) is visible at ventral margin of epandrium.

Female. Unknown.

Remarks. *Acartophthalmites scotopteryx* **sp. nov.** and *A. crassipes* are similar in habitus and obviously most closely allied species distinguished by robust, uniformly blackish brown body and dark brown wings, strongly dilated mid femur (twice as thick as hind femur in proximal third) and mid tibia with a long row of 10–12 erect posterior setae. However, the new species, *A. scotopteryx* **sp. nov.** can be separated from *A. crassipes* by the distinctly shorter frontal triangle, wider parafacialia, longer arista, denser acrostichal microsetae (in 14–16 rows in front of suture), fore femur with 3 posterodorsal setae, shorter terminal section of CuA_1 and bicolourous halteres (see also the key below). *A. scotopteryx* **sp. nov.** also differs from *A. crassipes* in having the orbit with the 5–7 additional microsetulae, ratio $Cs_3 : Cs_4$ distinctly smaller (only *ca*. 1.7 versus *ca*. 2.1 in *A. crassipes*) and abdominal tergum T5 as long as T4. Unfortunately, structures of the male terminalia of both species cannot be compared because they remain undescribed in the new species (heavily obscured in the male holotype, *cf*. Fig. 5B).

***Acartophthalmites striatus* sp. nov.**

(Figs 8, 9)

http://zoobank.org/ urn:lsid:zoobank.org:act:50F77272-BD57-4D22-BD33-98749F1C1B00

Type material. Holotype male, labelled: "Faszination Bernstein, Christel Hoffeins, Hans Werner Hoffeins" (framed on obverse), "897-4 Acartophthalmidae, A. tertiaria" (handwritten by C. Hoffeins, on reverse),

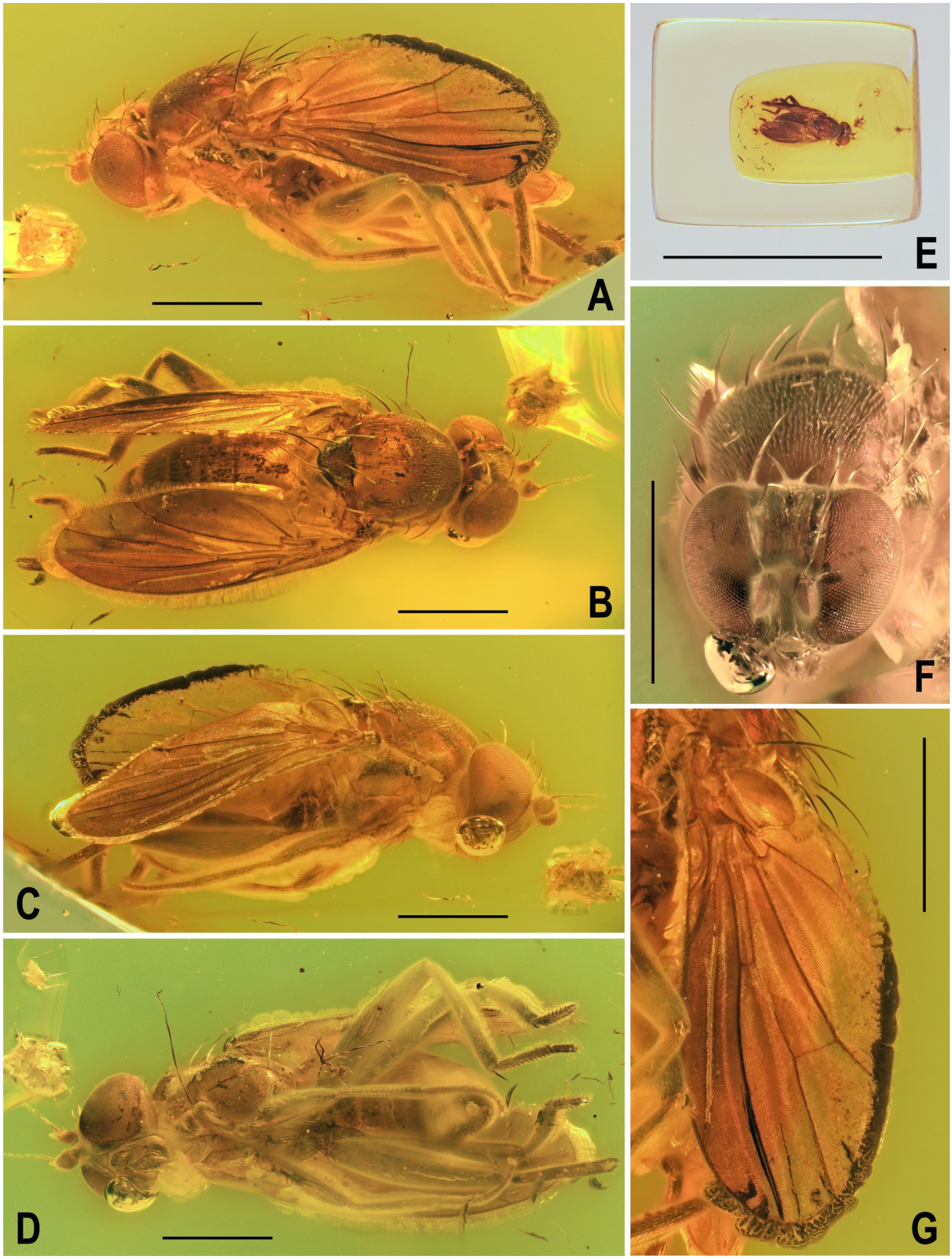

FIGURE 8. *Acartophthalmites striatus* **sp. nov.**, holotype male (Baltic amber). **A**, Male, left laterally. **B**, Ditto, dorsally. **C**, Ditto, right laterally. **D**, Ditto, ventrally. **E**, whole amber sample (preparatum in polyester resin), in situ. **F**, Head and thorax, frontally. **G**, Left wing, dorsally. Scale bars: 1 mm (**A**–**D**, **F**, **G**), 10 mm (**E**). Photographs by J. Roháček.

"Russia: Kaliningrad Region, Baltic Sea coast, Yantarny" (printed) and "Holotypus ♂, *Acartophthalmites striatus* sp.n., J. Roháček det. 2024" (red label), deposited in CCHH, no. 897-4 [block-shaped amber piece *ca*. 8.3 × 5.5 × 4.7 mm, embedded in polyester resin, size 12.4 × 9.7 × 7.6 mm, see Fig. 8E]; syninclusions: stellate hairs, small plant remnants, dirt impurities. The specimen has mid and hind tarsi incomplete, with distal parts more or less lost.

Etymology. The species is named "*striatus*" (= striated, from Latin, adjective) owing to its finely striated frons, face, parafacialia and gena.

Diagnosis. A robust, generally brown species with bicolourous (dark brown and pale brown) thorax and unicolourous dark brown wings; frons and also face very finely striated; frontal triangle short and very narrow; orbit with only 2 additional microsetulae; scutellum almost black and contrasting with pale brown posterior half of mesonotum; 2 dc; prescutellar ac setae slightly beyond posterior dc; laterobasal sc distinctly shorter (0.7 times as long as) than apical sc; f_2 strongly thickened and slightly longer than f_3; t_2 with a long row of only 7 or 8 erect posterior setae; Sc continuous; R_1 setulose; apical part of CuA_1 1.2 times as long as dm-cu.

Type locality and horizon. Russia: Kaliningrad region, Yantarny mine (formerly Palmnicken). Mid-late Eocene, 48–34 Ma.

Description. Male. Total body length about 3.6 mm (holotype); general colour dark to pale brown, with bicolourous (albeit less contrastingly than in *A. bicolor* **sp. nov.**) thorax (Fig. 8A, B).

Head (Figs 8A, B, F, 9A) higher than long and somewhat wider than thorax in dorsal view; occiput concave in dorsal half. Head brown anteriorly to dark brown posteriorly, occiput (dorsally) darkest; frons brown, darker posteriorly; also face and gena brown but postgena pale brown to ochreous. Frons relatively narrow, as wide as eye in dorsal view, slightly tapering anteriorly, and very densely finely striated (Fig. 9A). Orbit distinctly delimited because smooth on surface, light brown anteriorly, darkened posteriorly. Frontal triangle very small and narrow, with anterior corner acutely projecting but not reaching half of frons (only to level of middle ors); ocellar triangle dark brown, of the same width and about half length of frontal triangle, little protruding; ocelli of moderate size. Frontal lunule small and narrow, poorly visible due to milky coating. Face narrow, parafacialia distinct (relatively wide, Fig. 9A), both dark brown and very finely longitudinally striated. Gena very narrow, brown and also finely striated. Postgena and adjacent part of occiput relatively large and unusually pale ochreous. Cephalic chaetotaxy (Figs 8F, 9A): pvt strong (as long as vte), divergent and closely arising behind ocellar triangle; vti strong and long (longest cephalic seta), more than twice as long as vte; oc relatively robust (almost as long as pvt but thinner) and inserted between ocelli, divergent and proclinate; 3 reclinate ors, hindmost ors longest (longer than vte), other two subequal in length; distance between anterior and middle ors distinctly smaller than that between middle and posterior ors; only 2 additional microsetulae on orbit, one each between ors; postocular setulae in only 1 row at posterior eye margin and only several scattered setulae in ventral two thirds of occiput and on adjacent postgena; postgena with 3 longer but fine posteroventral setae (hindmost longest) in addition; vi relatively short and fine but thicker and about 1.3–1.5 times as long as foremost peristomal setulae; vibrissae strongly incurved, with apices crossed medially; no subvibrissa; 6 fine peristomal setulae becoming longer anteriorly, the foremost distinctly longer than others. Eye large, bare, convex, subovoid to almost semicircular, with posterior margin very slightly emarginated; its longest diameter about 1.4 times as long as shortest diameter. Gena very low, its height about 0.08 times as long as shortest eye diameter. Palpus pale ochreous, short and small, with series of black setulae on outer side. Mouthparts ochreous to brown; clypeus brown; labella pale brown, fleshy, finely whitish and relatively long-haired. Antenna porrect (Fig. 8C), relatively short, with all segments brown; pedicel externo-laterally with anterior margin somewhat convex, bearing 1 longer seta dorsally and 2 finer setae ventrally in addition to small submarginal setulae; 1st flagellomere hardly paler than and about 1.5 times as long as pedicel, laterally compressed and suboval (1.2× higher than long) in profile, all finely, densely and shortly whitish pilose. Arista dorsobasal, relatively short, about twice as long as antenna, with thicker, cylindrical and brown basal segment and dark brown (basally thickened) terminal section having moderately long ciliation.

Thorax (Fig. 8A–D). Somewhat narrower than head, bicolourous, pale brown to ochreous and blackish brown. Scutum bicolourous, having mesonotum laterally (including humeral callus and notopleural area) and in posterior half (gradually) pale brown, otherwise dark brown; scutellum almost black and contrasting with adjacent part of mesonotum; subscutellum possibly brown (poorly visible); pleural part of thorax dorsally with narrow blackish brown longitudinal band covering dorsal third of mesopleuron and most of pteropleuron; other parts of pleuron (and also entire postnotum) pale brown to ochreous. Scutellum relatively large, subtriangular with rounded apex (Fig. 8B) and flat dorsal surface. Thoracic chaetotaxy (Fig. 8A, B): 1 hu (strong but only slightly longer than posterior npl) and several (*ca*. 8) microsetae on humeral callus; 2 npl, anterior longer but not thicker than posterior; 1 robust sa, somewhat longer than posterior dc; 2 pa, anterior very long and strong (longest thoracic seta), posterior fine and about one-third of anterior; no prs; 2

dc (both postsutural), anterior situated at level of sa and about two-thirds of length of posterior, posterior dc robust but only as long as laterobasal sc; 1 microseta in front of anterior dc thickened and about twice longer than other dc microsetae; 1 prescutellar medial ac (situated slightly beyond level of posterior dc) subequal in length and thickness to posterior pa; mesonotum otherwise covered by dense uniform microsetae; ac microsetae in about 14 rows in front of suture but less posteriorly (only 4 rows reaching level of posterior dc); 2 sc, both strong, apical very long but slightly shorter than anterior pa, laterobasal sc slightly thinner and shorter (0.7 times as long as) than apical sc; 1 long (with apex reaching dorsal margin of propleuron) but fine upcurved ppl; mesopleuron with one distinct mspl (slightly shorter and thinner than hu) in posterodorsal corner and scattered (rather numerous) microsetae in posterodorsal half of the sclerite, 4 of them at posterior margin longer; sternopleuron with one long (longer than mspl) but fine stpl and a several microsetae scattered in posterior two-thirds of sclerite, 2 or 3 longer but fine setae also on ventral corner of sternopleuron; prosternum entirely bare.

Legs (Fig. 9B, C). Dark brown (mid and hind femora) to pale brown (tarsi, coxae); mid and hind legs long and robust, femora in particular. Femur of mid leg about 1.8 times as long as that of fore leg; f_2 (see Fig. 9B, C) strongly thickened and slightly longer than f_3; distal posterior process of cx_3 not visible (obscured) and, hence, undescribed; f_1 with a short row of 6 or 7 short posteroventral to ventral setae in distal fourth and with only 2 short posterodorsal setae in row near distal third of femur; f_2 in proximal third broadest (1.6 times as thick as f_3 at this point), gradually tapered distally where as wide as f_3; f_2 in distal sixth ventrally with 2 short rows of thicker but small setae (a few in anteroventral, 6 in posteroventral row) but these are less distinct (not visible in Fig. 9C) than those in *A. bicolor* **sp. nov.**; f_3 with similar but smaller setae in posteroventral row, otherwise uniformly setulose. t_1 finely setulose but with dorsal preapical pair of very small setae; t_2 (besides usual short setosity) with a long row of 7 or 8 erect posterior setae (those in the middle longest, Fig. 9C) in distal two-thirds, 2 very small dorsal setae (one preapical, the other in distal sixth, Fig. 9B) and 1 robust ventroapical seta (as long as tibial width) plus several small but thicker setulae at apex of tibia; t_3 very slightly bent, without dorsopreapical seta, but with 1 short ventroapical (only as long as width of hind basitarsus, Fig. 9C) and 1 much smaller anteroapical seta, otherwise uniformly setulose. Tarsi simple, slender; fore basitarsus with 2 longer fine setulae ventrobasally, other setulae short and dense; mid and hind basitarsi long (probably longer than rest of tarsus) and each with a row of thicker posteroventral erect setulae; claws small (preserved only on fore tarsus).

Wing (Figs 8G, 9D). Relatively broad but distinctly narrower than that of *A. tertiaria*; veins brown; membrane uniformly brown fumose. C attenuated beyond R_{4+5} but reaching to M; C finely setulose but basally with a usual pair of longer setae and Cs_2 and partly also Cs_3 (in basal fifth) with thicker (but not longer) sparse spine-like setulae in addition. No costal break. Sc distinct but fine, well developed also basally (where somewhat sinuated) and ending into C far from apex of R_1. R_1 short, robust, with 5 setulae dorsally (Fig. 9D) and with distinct preapical kink at the level of apex of Sc. R_{2+3} long, slightly sinuate, apically very slightly upcurved to C and ending distinctly farther from wing apex than M. R_{4+5} distinctly but shallowly bent posteriorly, distally subparallel with M and terminated near wing apex. Distal part of M almost straight and reaching wing margin. Discal (dm) cell elongated but not very narrow); anterior cross-vein (r-m) situated near the middle of cell. Distal part of CuA_1 about 1.2 times as long as dm-cu and almost reaching wing margin; A_1 relatively long, but ending far from wing margin. Cells bm and cup completely closed. Anal lobe well developed. Alula large and very broad (Fig. 8G). Wing measurements: length 2.98 mm, width 1.19 mm, $Cs_3 : Cs_4 = 1.95$, r-m/dm-cu : dm-cu = 2.36. Haltere unicolourous, pale brown.

Abdomen. Subcylindrical, elongately subovoid in dorsal view (only from dorsal and ventral side observable, see (Fig. 8B, D). All visible preabdominal terga rather densely and shortly setose, with longest setae at posterior margins; setae on T1 small, fine and partly erect; also T2 with several setae in the middle laterally distinctly erect. Anterior terga distinctly paler (T1 pale ochreous, T2 pale brown) than those more posterior (T3 brown, T4–T5 blackish brown). T1−T2 separation discernible. T1 somewhat longer than T2, T2–T4 subequal in length, T5 somewhat shorter than T4. T1–T3 becoming broader posteriorly (T3 widest), T4 and T5 narrower, T5 most tapered posteriorly. Preabdominal sterna only partly visible due to legs and milky coating of ventral side of abdomen. S2–S4 pale brown, relatively broad, with shorter and sparser setae than associated terga. S5 probably shorter and narrower than S4 but only its fine setosity visible in milky coating. Postabdomen largely not observable (Fig. 8A–D) but synsclerite T6+S8 long (markedly longer than T5), convex, blackish brown and very shortly setulose.

Genitalia. Epandrium (Fig. 8D) obscured by milky coating but blackish brown, short and high, open ventrally, with anal fissure distinctly directed ventrally and entirely shortly uniformly setulose. No appendages of terminalia (cerci, gonostyli) are visible in the holotype.

Female. Unknown.

Remarks. *Acartophthalmites striatus* **sp. nov.** most resembles *A. rugosus* because of sharing with the latter the

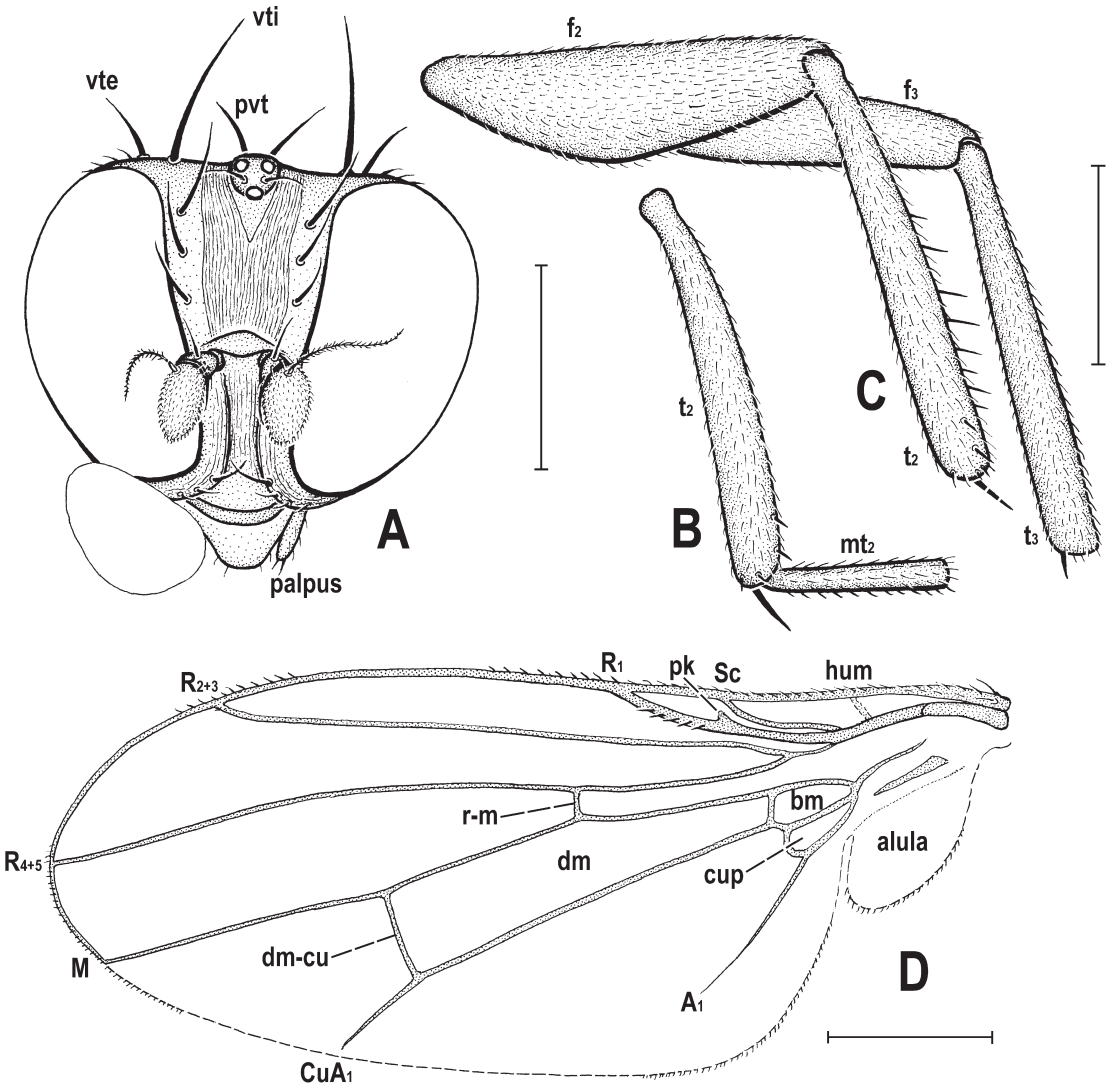

FIGURE 9. *Acartophthalmites striatus* **sp. nov.**, holotype male (Baltic amber). **A**, Head, frontally. **B**, Left mid tibia and basitarsus, anteriorly. **C**, Left mid and hind femora and tibiae, anterodorsally. **D**, Left wing, dorsally. Scale bars: 0.5 mm. For abbreviations see Material and methods.

longitudinally striated frons, additional microsetulae on orbit reduced in number, the unicolourous brown wings, only 2 dc, the prescutellar ac arising slightly beyond the level of posterior dc, t_2 with a row of only 7 or 8 erect posterior setae and similar wing venation including short apical part of CuA_1. On the other hand, the new species distinctly differs from *A. rugosus* in having the striation on frons very fine and also developed on face, parafacialia and gena; the lighter colouration of body including bicoloured thorax (mesonotum dark anteriorly and pale laterally and in posterior half contrasting with almost black scutellum) and pleuron (having dorsally blackish brown longitudinal band), the scutellum dorsally flattened, the acrostichal microsetae more densely arranged; the laterobasal sc only 0.7 times as long as apical sc; f_1 with only 2 short posterodorsal setae and R_{4+5} less (only shallowly) bent posteriorly in addition to a number of smaller differences (see description above). Unfortunately, structures of the male postabdomen and genitalia cannot be compared because they are not visible in the only specimen (holotype) examined. *Acartophthalmites striatus* **sp. nov.** can be easily separated from two other *Acartophthalmites* species with bicoloured thorax, *viz*. *A. willii* and *A. bicolor* **sp. nov.**, not only by its striated frons, face, parafacialia and gena but also by f_2 ventrally with short setae in distal row(s). In addition, *A. willii* is dissimilar by its thoracic and wing pattern, the latter being darkened along anterior margin (see Roháček & Hoffeins, 2021: fig. 28G). Similarly, *A. bicolor* **sp. nov.** also differs from *A. striatus* **sp. nov.** by dorsal thoracic pattern (scutellum

concolourous with mesonoum), by markedly wider frons and by a row of 10 posterior setae on mid tibia.

An updated key to identification of species of the genus *Acartophthalmites*

1 Frons dark brown and coarsely (Roháček & Hoffeins, 2021: fig. 20A) or finely (Fig. 9A) striated along frontal triangle 2

- Frons dark brown to yellowish orange with smooth or only very finely transversely rugose surface (Figs 3A, 7A; Roháček & Hoffeins, 2021: figs.16B, 28A).....3

2 (1) Frons coarsely longitudinally striated (Roháček & Hoffeins, 2021: fig. 20A); face, parafacialia and gena smooth. Laterobasal sc almost as long as apical sc. Scutum unicolourous dark brown, not patterned (Roháček & Hoffeins, 2021: fig. 19D). R_{4+5} distinctly recurved in basal half (Roháček & Hoffeins, 2021: fig. 19F) ..... *A. rugosus*

- Frons and also face, parafacialia and gena longitudinally finely striated (Fig. 9A). Laterobasal sc distinctly shorter (0.7 times as long as) than apical sc. Scutum with scutellum almost black and contrasting with pale brown posterior half of mesonotum (Fig. 8B). R_{4+5} very slightly bent in basal half (Fig. 9D) ..... *A. striatus* **sp. nov.**

3 (2) 1st flagellomere small, not longer or higher than pedicel (Roháček & Hoffeins, 2021: fig. 26B). Anterior pa as long as sa; 3 dc, middle as long as posterior dc (Roháček & Hoffeins, 2021: fig. 26F). Wing broad, with R_{4+5} strongly downcurved in basal half and CuA_1 distinctly longer than dm-cu (Roháček & Hoffeins, 2021: fig. 26I) .... *A. tertiaria*

- 1st flagellomere larger, usually longer and always higher than pedicel; anterior pa distinctly longer than sa (Roháček & Hoffeins, 2021: figs 16A, 28B); 2 or 3 dc, the middle (or the anterior if only 2 dc) markedly shorter than posterior dc (Fig. 3A; Roháček & Hoffeins, 2021: fig. 16A); wing more elongate (Fig. 8G; Roháček & Hoffeins, 2021: figs 17B, 28G) with R_{4+5} less downcurved in basal half; CuA_1 at most slightly longer than dm-cu.....4

4 (3) Thorax with dark brown and ochreous pattern, both on scutum and pleuron (Figs 1D, 2C; Roháček & Hoffeins, 2021: fig. 28B). f_2 ventrally with short distal row(s) of thicker setae (Fig. 3F); f_2 distinctly (about 1.6 ×) but not strongly thicker than f_3 (Fig. 1B; Roháček & Hoffeins, 2021: fig. 27A).....5

- Thoracic scutum and pleuron more or less unicolorous, without distinct pattern (Fig. Roháček & Hoffeins, 2021: figs 10C, 14F); f_2 ventrally simply finely setulose (or with a few slightly longer setulae) and markedly thicker than f_3 (twice as thick as f_3 in proximal third, Fig. 5A; Roháček & Hoffeins, 2021: fig. 11B).....6

5 (4) Wing elongated and darkened along anterior margin (Roháček & Hoffeins, 2021: fig. 28G). Frontal triangle not delimited and frons very finely transversely rugose (Roháček & Hoffeins 2021: fig. 28A). Only 2 dc setae. t_2 with a row of 6 or 7 erect posterior setae (Roháček & Hoffeins 2021: fig. 28A) ..... *A. willii*

- Wing also elongated but unicolourous brown (Fig. 1B). Frontal triangle present but small and frons smooth on surface (Fig. 3A). 3 dc setae (Fig. 3A); t_2 with a row of 10 erect posterior setae (Fig. 3C, D)..... *A. bicolor* **sp. nov.**

6 (5) Body pale ochreous to orange-ochreous, with pale ochreous-brown wings (Roháček & Hoffeins, 2021: fig. 14A); oc very small (Roháček & Hoffeins, 2021: fig. 16B); t_2 with a row of 8 or 9 relatively short erect posterior setae; t_3 distinctly bent (Roháček & Hoffeins, 2021: fig. 16D)..... *A. luridus*

- Body blackish brown, with dark brown wings (Fig. 5A; Roháček & Hoffeins, 2021: fig 10A); oc variable; t_2 with a long row of 10–12 relatively strong erect posterior setae (Fig. 7C; Roháček & Hoffeins, 2021: fig. 10D); t_3 indistinctly bent (Roháček & Hoffeins, 2021: fig. 2F)..... 7

7 (6) Frontal triangle longer, reaching in front of posterior ors; parafacialia narrow; arista short, only 2–2.1 times as long as antenna (Roháček & Hoffeins, 2021: fig. 11A). Acrostichal microsetae in about 10 rows in front of suture. f_1 with only 2 posterodorsal setae near distal third of femur. Distal part of CuA_1 about 1.3 times as long as dm-cu. Haltere unicolourous, brown ..... *A. crassipes*

- Frontal triangle very small, only reaching level of posterior ors; parafacialia broad; arista longer, *ca*. 2.9 times as long as antenna (Fig. 7A). Acrostichal microsetae denser, in 14–16 rows in front of suture. f_1 with 3 posterodorsal setae (Figs 6B, 7B) in short row near distal third of femur. Distal part of CuA_1 only as long as dm-cu. Haltere bicolourous, with brownish stem and dirty white knob..... ..... *A. scotopteryx* **sp. nov.**

Family Protanthomyzidae Roháček, 1998 stat. nov.

Protanthomyzinae Roháček, 1998: 170.

Protanthomyzinae Roháček, 2006: 33; 2013: 434.

Type genus. *Protanthomyza* Hennig, 1965: 169, by original designation.

Diagnosis (revised and updated)**.** Head with large, strongly convex eyes having longest diameter vertical or slightly oblique; eye bare; frons narrow; frontal triangle small (short) or not differentiated; ocellar triangle protruding, ocelli comparatively large; frontal lunule relatively large (long) but narrow; face relatively narrow because of dilated parafacialia; antenna porrect (never geniculate between pedicel and 1st flagellomere) but more or less bent ventrally; pedicel simple, not capiform; arista dorsobasal, shortly ciliate to bare; palpus slender, with several setae. Cephalic chaetotaxy complete: pvt convergent to crossed; vti, vte and oc long; ocellar triangle with microsetulae; 3 reclinate ors; postocular setulae numerous, dorsally in 2 rows; vi about as long as anterior ors but subvibrissa absent; postgena with 1 or 2 longer setae besides setulae. Thoracic chaetotaxy rich: 1 hu, 2 npl, 1 prs, 1 sa, 2 pa, 2–4 dc (all postsutural), 1 long prescutellar ac seta, 2 long sc, 2 distinct ppl, mesopleuron with numerous setulae and 2 or 3 longer setae, 1 long and (sometimes) 1 short stpl. f_1 with or without ctenidial spine; f_2 with 2 or 3 erect anterior setae near middle; t_2 always with ventroapical seta; no dorsal preapical seta on tibiae. Wing relatively broad, unicolourous, never patterned. C not interrupted but distinctly attenuated at apex of Sc, uniformly densely setulose (without spinulae) between apices of R_1 and M; Sc distinct but in distal half to sixth usually attached to and apically fused to R_1 to form a small preapical kink on R_1. R_{4+5} apically straight or slightly recurved. Terminal part of CuA_1 relatively long and almost reaching wing margin. Both A_1 and A_2

developed, terminating far from wing margin. Alar lobe and alula distinct although small. Abdomen relatively short and broad. Preabdominal terga (= T1–T5) wide, transverse but not reaching far on lateral side of abdomen so that pleural membrane is large; preabdominal sterna (= S1–S6) moderately narrow (more so in female) but well sclerotized and pigmented. Male S6–S7 bare, short, asymmetrical and displaced on left side of postabdomen. Male S8 large, dorsal and (more or less) symmetrical. Epandrium always with peculiar anteroventral digitiform to hook-like projection (= surstylus) on each side and with 2–3 pairs of long and strong dorsobasal setae. Gonostylus discrete, relatively small but often longer than anteroventral process of epandrium, more or less pointed. Male cercus discrete, situated in anal fissure of epandrium, slender to small, with a few longer setae. Aedeagal complex with simple, short and robust distiphallus (see Roháček & Hoffeins, 2020: fig. 5C). Female postabdomen relatively short and broad (Roháček, 2013: figs 8A, 9C, G). Female T6 and S6 resembling T5 and S5 respectively but smaller. Female T7 more or less extended laterally, often almost meeting with margins of S7, the latter transverse but unmodified; T8 and S8 markedly smaller than T7 and S7, both pale-pigmented and sparsely finely setose; T10 very small, pale, plate-shaped, with a pair of longer setae (sometimes with a few setulae in addition); S10 smaller than T10, pale, with a few small setulae. Female cercus (Fig. 6C) elongate, with 2 or 3 longer slightly sinuous setae (1 apical, others dorso- and/or ventropreapical) besides short setulae.

Discussion. Roháček (1998) established the subfamily Protanthomyzinae for a single fossil genus and species, *Protanthomyza collarti* Hennig, 1965. This classification was subsequently maintained as such when additional species of the genus *Protanthomyza* Hennig, 1965 were discovered (see Roháček, 2013, 2020; Roháček & Hoffeins, 2020). Until now, Protanthomyzidae has been treated as the sister group of all remaining Anthomyzidae, including the fossil genera *Grimalantha* Roháček, 1998 (Dominican amber), *Lacrimyza* Roháček, 2013 (Balic amber) and *Reliquantha eocena* Roháček, 2014 (Baltic amber), all grouped within the subfamily Anthomyzinae Czerny, 1903 (= Anthomyzinae Frey, 1921 in Roháček, 1998). In this broad concept, Anthomyzidae (comprising these two subfamilies) was considered the sister group of Opomyzidae (Roháček, 1998: 170, 2006: 28).

However, the recently obtained morphological data from studies of additional fossil species of *Protanthomyza* described from Baltic amber by Roháček (2020), Roháček & Hoffeins (2020), and in this study (see above) demonstrate that the previous classification and proposed relationship of *Protanthomyza* are incorrect. The group previously classified as Protanthomyzinae in fact possesses several plesiomorphies not found in either Opomyzidae or Anthomyzidae (*s. str.*), *viz*., the porrect antenna; thoracic mesopleuron with 2 or 3 strong setae; relatively broad, never patterned wing, lacking a distinct subcostal break (at most with an attenuation at apex of R_1); presence of both A_1 and A_2; a short and simple distiphallus, and aedeagal complex plausibly without a folding apparatus; a short and broad female postabdomen; unmodified, short, and transverse female T7 and S7. Additionally, some characters previously considered synapomorphies of Protanthomyzinae+Anthomyzinae have not been confirmed in Protanthomyzinae. Specifically, phallapodeme lacks a ventral fulcrum (= aedeagal guide), and the distiphallus is not terminally bifid in the latter group. The ctenidial spine on the fore femur, formerly considered a synapomorphic character of Protanthomyzinae+Anthomyzinae, is now more probably a synapomorphy of these groups along with Opomyzidae. However, it was secondarily lost in the majority of *Protanthomyza* species (see below for the identification key), in more than half of the genera of Anthomyzinae (including all fossil genera and species), and in all currently known genera of Opomyzidae. Based on these findings, it is suggested that fossil Protanthomyzinae should be treated as the sister group to Anthomyzidae (*s. str.*)+Opomyzidae and, consequently, is elevated here to family status as Protanthomyzidae. Apart from the plesiomorphies listed above, members of this group also retain several other ancestral features, some of which are shared with Opomyzidae, such as numerous postocular setulae and a setulose mesopleuron. Although all three families, Protanthomyzidae, Anthomyzidae and Opomyzidae, share synapomorphies already listed by Roháček (1998, 2006), one of them should be commented upon, viz., the preapical kink formed by the fusion of the terminal part of Sc and R_1. In the new species described below, the most ancestral formation of Sc was observed (see Fig. 12E), in which Sc remains free up to its end, where it fuses with both C and R_1 without forming the characteristic kink. This fact supports the basal position of Protanthomyzidae relative to the other two families. On the other hand, the monophyly of Protanthomyzidae is well-supported by several distinct synapomorphies, including: f_2 with 2 or 3 erect anterior setae near middle; epandrium with 2–3 pairs of long and strong dorsobasal setae; and particularly, the unusual anteroventral digitiform to hook-like projection. This projection, in my opinion, is homologous with the surstylus of Periscelididae (see Roháček & Andrade, 2017; Roháček, 2022) and possibly also of Aulacigastridae (*e.g.*, Rung & Mathis, 2011), but not with surstylus *auctt*. = gonostylus in other Acalyptratae.

The sister-group relationship between Anthomyzidae (*s. str.*) and Opomyzidae is supported by the following synapomorphies: antenna more or less geniculate between pedicel and first flagellomere; thoracic mesopleuron with

at most 1 macroseta; wing narrow, often with a reduced anal lobe and frequently patterned membrane; subcostal break present; vein A_2 absent and A_1 more abbreviated; aedeagal complex with folding apparatus and distiphallus slender, elongated and often bifid (in Anthomyzidae); female postabdomen elongated and slender; female T7 and, particularly, S7 often species-specifically modified. The close relationship between Anthomyzidae and Opomyzidae has also been recently confirmed by a morphological analysis made by Lonsdale (2020).

Genus *Protanthomyza* Hennig, 1965

Type species. *Protanthomyza collarti* Hennig, 1965; Baltic amber (Eocene); by monotypy.

***Protanthomyza chelicerata* sp. nov.**
(Figs 10–13)
http://zoobank.org/ urn:lsid:zoobank.org:act:3431D2B1-B516-442C-A99B-0224EAE620FF

Type material. Holotype ♂ labelled "Faszination Bernstein, Christel Hoffeins, Hans Werner Hoffeins" (framed on obverse), "1828-14 Diptera, Acalyptratae, Anthomyzidae ♂, ? Nematoda" (pencil handwritten by C. Hoffeins, on reverse), "Baltic amber 40 mln years old, 14.2, 2 g, 32 × 17 × 7, Species Acalyptratae, B2.6, rmvveta, www-ambertreasure4u.com" (partly printed, rest handwritten), "Russia: Kaliningrad Region, Baltic Sea coast, Yantarny" (printed) and "Holotypus ♂, *Protanthomyza chelicerata* sp.n., J. Roháček det. 2024" (red label), deposited in CCHH, no. 1828-14 [block-shaped amber piece *ca*. 10.1 × 6.2 × 5.4 mm, embedded in polyester resin, size 13.9 × 9.2 × 6.9 mm, see Fig. 10E], cut from larger (32 × 17 × 7 mm) rounded flat piece of amber; syninclusions: minute worm-like creatures (Nematoda?), dirt.

Etymology. This new species is named "*chelicerata*" (noun in apposition) for its male terminalia in lateral view (Figs 11C, 13B) closely resembling the uncate chelicera of solifuges (Solifugae).

Diagnosis. Unusually pale (orange ochreous to brown) species. Ocellar triangle delimited by a line; frontal triangle developed but very short and narrow; 1st antennal flagellomere normal, not enlarged; arista virtually bare; vibrissa well developed; eye large; 2 ppl setae but only anterior long; 4 postsutural dc macrosetae; f_1 without a ctenidial spine; male pregenital sternum (S5) medially with a brush of dense setulae; epandrium normal (not tapered posteriorly), with long, hook-like curved anteroventral process; gonostylus slender, also hook-like curved but apically not acutely pointed.

Type locality and horizon. Russia: Kaliningrad region, Yantarny mine (formerly Palmnicken). Mid-late Eocene, 48–34 Ma.

Description. Male (Fig. 10A–D). Total body length *ca*. 2.78 mm; general colour orange ochreous to brown including head and extremities.

Head (Figs 11A, B, 12A, B) somewhat higher than long, anteriorly very little protruding in front of eye margin, rounded (Fig. 12B). Occiput very slightly concave only dorsally, brown to dark brown. Frons narrow (Figs 11A, 12A) but hardly tapered anteriorly, orange brown (thus contrasting with occiput). Frontal triangle delimited, short (hardly reaching to half of frons) and very narrow (not wider than ocellar triangle), with acutely pointed anterior corner (Fig. 12A) and dull in contrast to adjacent silky parts of frons; ocellar triangle slightly darker than frontal triangle, relatively large (wider than one third of frons), somewhat protruding and delimited by marginal line. Ocelli moderate in size (*cf*. Fig 12A). Orbit yellowish ochreous, thus lighter than frons medially but with similarly silky surface. Frontal lunule large and long, orange ochreous but at ptilinal suture darker hemmed. Face and parafacialia yellowish, both narrowly brownish margined. Gena and postgena orange ochreous to yellow as are also mouthparts: clypeus orange ochreous but with ventral margin narrowly darkened; palpus orange, rest (including labellum) pale yellow. Cephalic chaetotaxy (Fig. 12A, B): pvt short, only about half length of foremost ors, strongly convergent but with apices not meeting medially; vti and vte subequal, longest of cephalic setae; vti distinctly inclinate, vte strongly exclinate; 3 distinct ors, all more or less reclinate, posterior and middle ors slightly longer than anterior ors but distinctly shorter (0.6 ×) than vte; oc as long as but slightly thinner than posterior ors, proclinate and distinctly divergent, arising inside ocellar triangle (Fig. 12A); anterior half of frons with 7 pairs of distinct (relatively long) microsetae in front of frontal triangle and with 2 microsetae also between ors setae (Fig. 12A); vi well developed, somewhat shorter than anterior ors and about 3 times as long as foremost peristomal setula; no subvibrissa; 7 small and weak proclinate peristomals; postocular setulae dorsally in two rows as usual, with a few setulae in inner row dorsally; outer row of postoculars long, reaching below ventral eye margin and with 2 or 3 dorsal setulae markedly enlarged (Fig. 12A); postgena posteroventrally with 2 or 3 distinct but fine setae, posterior slightly longer. Palpus slender and long, slightly bent, with a series of fine setulae ventrally, 2 or 3 longer (Fig. 12B). Mouthparts exposed in holotype, relatively small, largely pale ochreous; clypeus darkest (pale brown), labellum whitish yellow, fleshy. Eye bare, very large (Fig. 11B), covering most of side of head (as in *P. ryszardi* or *P. tschirnhausi*), strongly convex, broadly suboval, anteriorly rounded, with only posterior margin straighter; its longest diameter nearly vertical and about 1.2

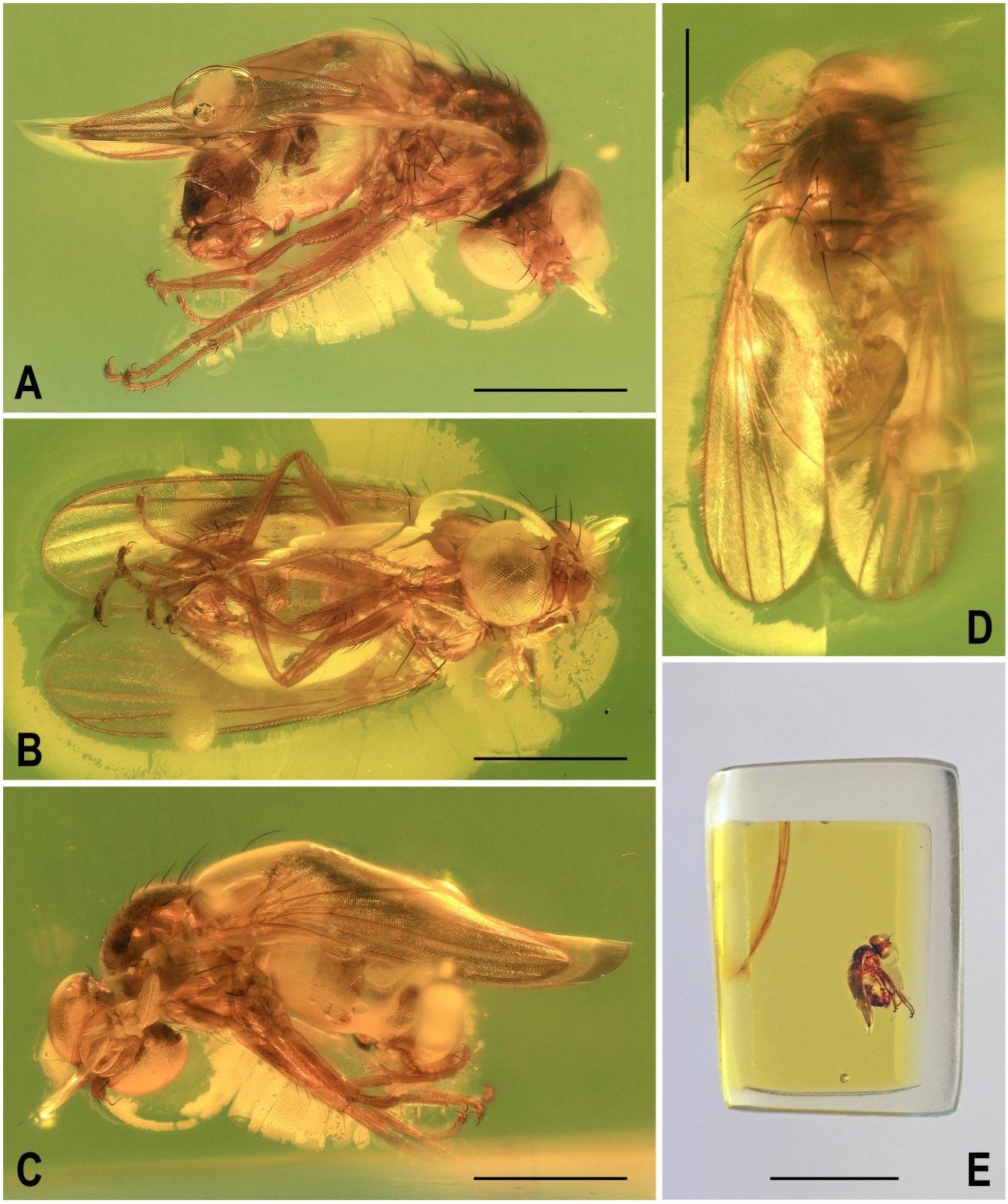

FIGURE 10. *Protanthomyza chelicerata* **sp. nov.**, holotype male (Baltic amber). **A**, Male, right laterally; **B**, Ditto, ventrally. **C**, Ditto, left laterally. **D**, Ditto, dorsally. **E**, whole amber sample (preparatum in polyester resin), in situ. Scale bars: 1 mm (**A**–**D**), 5 mm (**E**). Photographs by J. Roháček.

times as long as the shortest. Gena very narrow, narrowed due to enlarged eyes, with shortest height 0.03–0.04 times as long as shortest eye diameter. Antenna medium-sized, generally porrect (not geniculate) but directed ventrally (see Figs 11B, 12B) and entirely orange ochreous. Pedicel subconical, markedly shorter than 1st flagellomere, with 1 long dorsal seta and several microsetae; 1st flagellomere suboval, more elongate than in relatives (1.6× longer

than broad), laterally compressed, very shortly, densely and dark pilose; arista about 1.7 times as long as antenna, entirely bare (Fig. 12B) and having 2 basal segments somewhat dilated, both bare.

Thorax (Fig. 10A, C, D) distinctly narrower than head, all orange brown, subshining. Mesonotum markedly convex (Fig. 10C); scutellum also convex dorsally and separated from mesonotum by deep suture. Scutellum rounded trapezoidal, about twice wider than long; subscutellum developed but short. Thoracic chaetotaxy (see Figs 10A, D, 11E): 1 short hu (only half length of anterior npl) and a few on humeral callus (= postpronotal lobe); 2 npl, anterior much (almost 2×) longer than posterior; 1 distinct (exclinate) prs (longer than posterior but shorter than anterior npl); 1 long sa; 2 pa, external very long (longer than sa), internal shorter (about half length of external pa); 4 distinct postsutural dc becoming shorter anteriorly, the hindmost longest (as long as or longer than external pa); ac microsetae relatively sparse, in 6 or 7 irregular rows on suture, in 4 rows more posteriorly, medial ac rows reaching level of posterior dc; medial prescutellar ac macrosetae well developed but not long

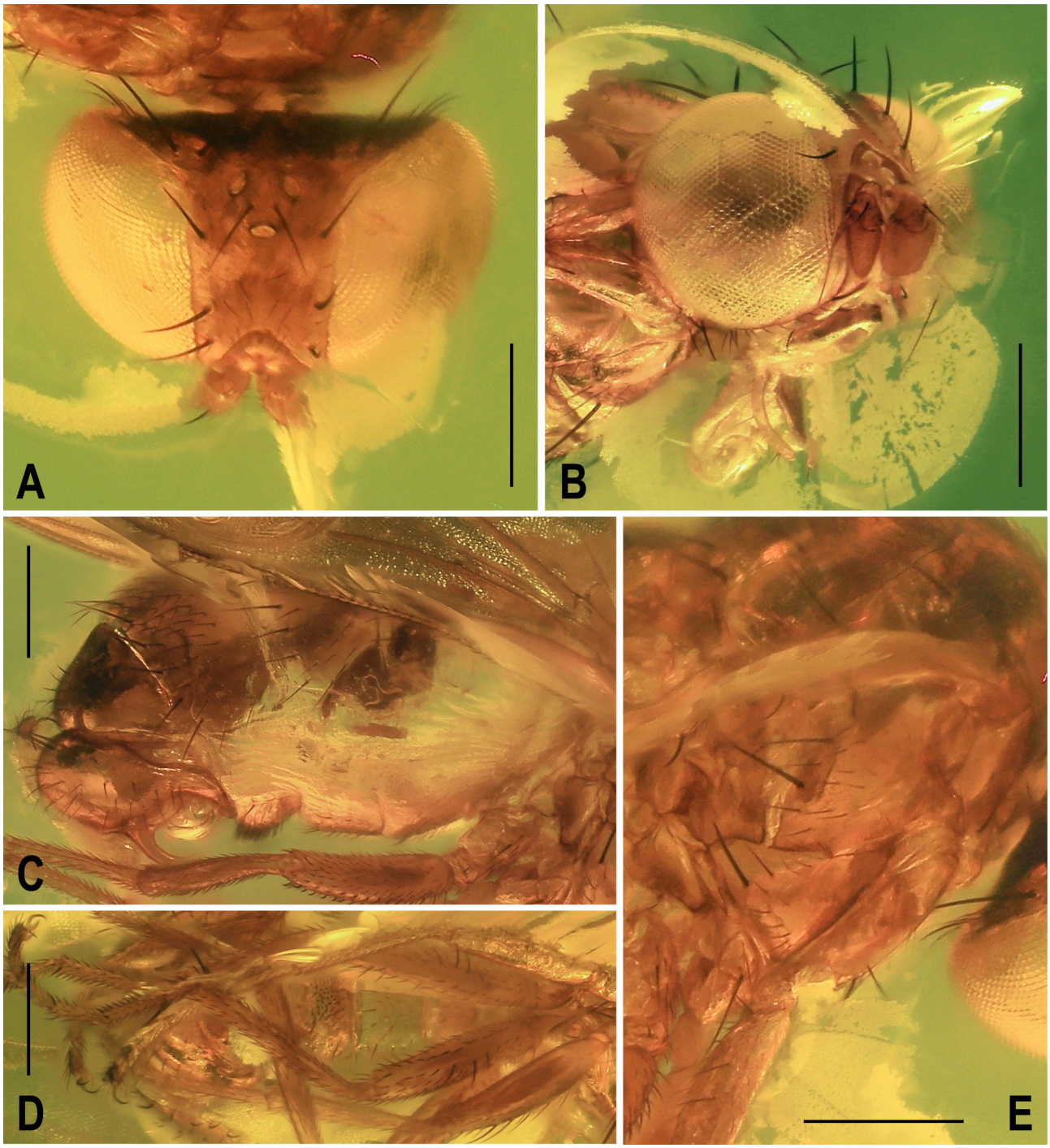

FIGURE 11. *Protanthomyza chelicerata* **sp. nov.**, holotype male (Baltic amber). **A**, Head, dorsally. **B**, Head, right frontolaterally. **C**, Abdomen, right laterally. **D**, Ditto, ventrally. **E**, Thoracic pleuron, right laterally. Scale bars: 0.3 mm. Photographs by J. Roháček.

(distinctly shorter than sa); 2 sc, laterobasal short (as long as prescutellar ac), apical very long (longest thoracic seta); no additional setulae on scutellum; 2 distinct but fine upcurved ppl, anterior as long as hu but thinner, posterior only half length of anterior and hair-like. Mesopleuron and sternopleuron with chaetotaxy resembling that of most other *Protanthomyza* species: 3 long mspl (1 dorsal upcurved and shortest, 1 posterodorsal and 1 posterior longest (see Figs 11E, 12C) and over 20 setulae (more than in relatives) scattered over almost entire surface of mesopleuron; 1 long posterior stpl and 1 shorter and finer stpl in front of it (Fig. 12C) and about 14 setulae mainly in posterior half of sternopleuron; other more posterior sclerites of pleural part of thorax and also prosternum bare.

Legs orange brown, femora only slightly darker. f_1 (Fig. 12D) lacking ctenidial spine and with a row of 5 or 6 sparsely arranged posterodorsal setae (foremost longest); setae in posteroventral row shorter, finer and more numerous (7 or 8), densely arranged in distal half of femur. f_2 with 3 or 4 anterior setae in middle third (Fig. 13C), otherwise shortly setulose as also is f_3. t_2 (Fig. 13C) with distinct ventroapical seta (as long as maximum width of tibia) and 3 short and small (2 anteroapical, 1

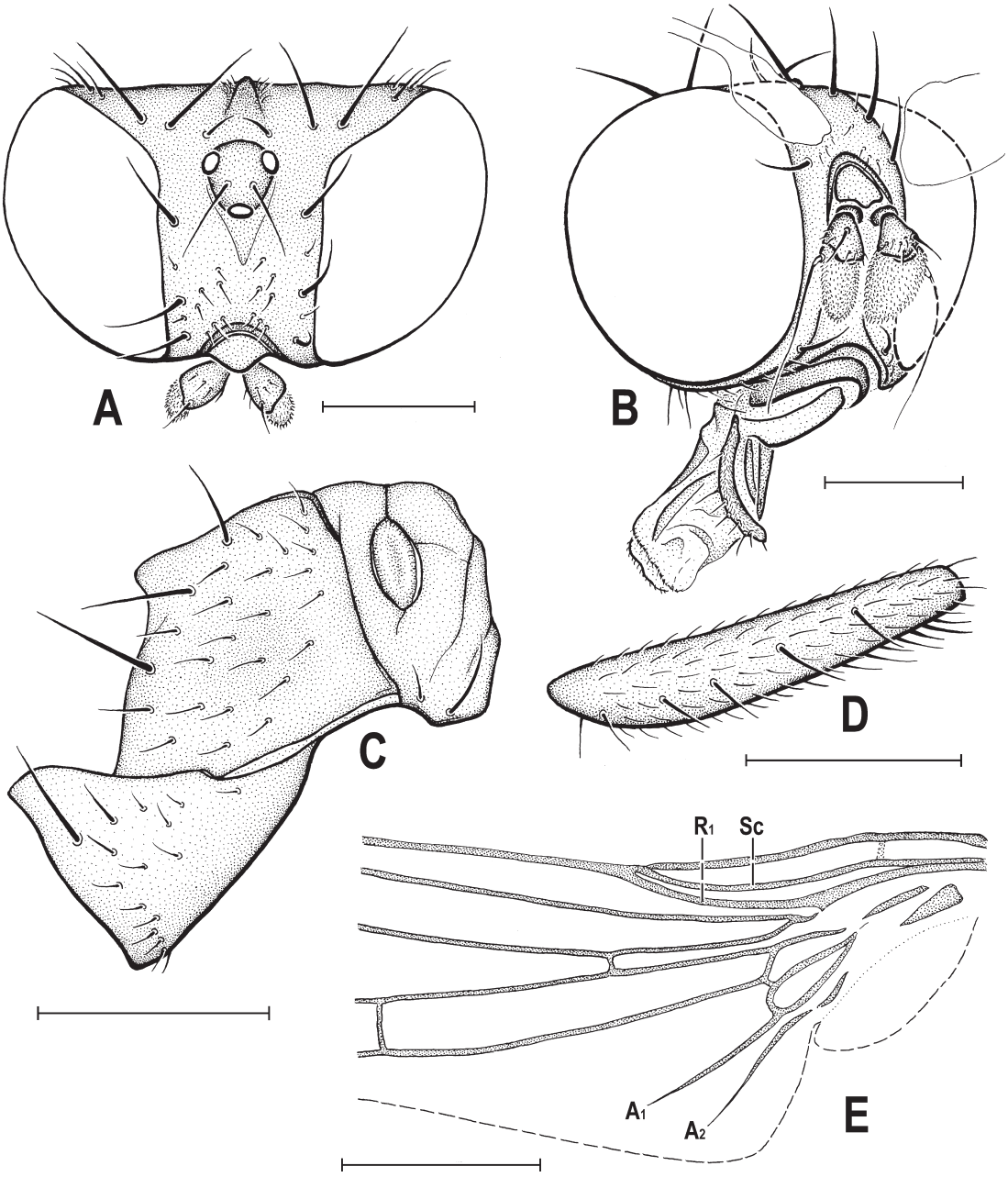

FIGURE 12. *Protanthomyza chelicerata* **sp. nov.**, holotype male (Baltic amber). **A**, Head, dorsally (aristae omitted). **B**, Head, right frontolaterally. **C**, Propleuron, mesopleuron and sternopleuron, right laterally. **D**, Right fore femur, posterodorsally. **E**, Base of left wing, dorsally (setosity omitted). Scale bars: 0.3 mm (**A**–**D**), 0.5 mm (**E**). For abbreviations see Material and methods.

posteroapical) setae on apex; t_1, t_3 and all tarsi simply setulose but mid basitarsus (Fig. 13C, mt_2) with 1 or 2 ventrobasal setulae somewhat longer than other setulae on tarsus; claws relatively long.

Wing not precisely visible in either view (see Fig. 10A–D), hence some features have not been described. Wing somewhat shorter than body, moderately narrow, widest at distal third; veins pale brown to light ochreous, membrane unicolorous, pale brown tinged; C pale brown, with subcostal break poorly visible (Fig. 12E); without attenuation or break at humeral cross-vein. C extended to apex of M but terminally attenuated and lightened, basally with 1 longer seta and with fine dense setulae on Cs_1, more densely uniformly short setulose on Cs_2 and finely and short pilose more distally (on Cs_3 and Cs_4); Sc well developed, separate along its entire length, only very apically fused both with R_1 and C so that no preapical kink is developed (see Fig. 12E); R_1 short but distally only slightly wider than Sc, distally fused with both Sc and C; R_{2+3} long, unusually straight, with apex hardly upcurved to C; R_{4+5} very slightly recurved in distal half, divergent from R_{2+3} and apically slightly convergent with M; M distally almost straight. Discal (dm) cell relatively long, narrow proximally and distinctly widened distally (not so in Fig. 12E where wing is oblique in distal half), with anterior outer corner rectangular and posterior outer corner slightly acute-angled; r-m situated at about basal two-fifths of dm cell; dm-cu straight; apical portion of CuA_1 distinctly (1.9 times) longer than dm-cu and almost reaching wing margin; A_1 relatively long but ending far from wing margin; A_2 well developed, almost as long as A_1 (see Fig. 12E) but ending at same distance from wing margin; alula relatively large but narrow (Fig. 12E). Wing measurements: length 2.50 mm, width 0.83 mm, Cs_3 : Cs_4 = 1.35, r-m/dm-cu : dm-cu = 2.90, r-m/dm-cu : CuA_1 = 1.53. Haltere with stem ochreous, knob brown and relatively large.

Abdomen (Figs 11C, D, 13A, C) short and robust compared to thorax. Proximal part of abdomen obscured by large air bubble, therefore undescribed. Preabdominal terga T4 and T5 darker (orange brown), but T3 pale ochreous at least in anterior half as probably also are T1+2. T3–T5 with relatively sparse and fine setae, only those at posterior margins long and strong (twice longer than others, see Figs 11C, 13A); T3 obviously shorter than T4; T4 and T5 largest, subequal in length (Fig. 13A). Preabdominal sterna (S2–S5) partly visible on right side in the holotype (Figs 11C, 13A) and also ventrally (Figs 11D, 13C), all distinctly smaller and narrower than associated terga, pale ochreous and becoming wider posteriorly; S4 longest but narrower than S5; S5 widest and most transverse (Fig. 13C), much shorter than adjacent T5 and also S4, darker (orange brown) and somewhat bulging ventrally (Fig. 13A). S3 and S4 sparsely shortly setulose, S5 peculiar in having medially a dense brush of short setulae (Fig. 13A, C), laterally sparsely setulose.

Postabdomen. T6 absent. S6, S7 and S8 fused to form pregenital synsclerite (as in relatives). S6+S7 only poorly visible on left side of postabdomen, small and short, strongly asymmetrical and projecting ventrally; S8 relatively long (almost as long as T5 but markedly narrower), more symmetrical, situated dorsally (Figs 11C, 13A), orange brown as T5, with small setae in posterior half dorsally.

Genitalia. Epandrium (Fig. 13A, B, ep) orange-brown, medium long, thus much shorter and not tapered posteriorly as that of *P. grimaldii*; right anterior margin of epandrium (Fig. 13A) modified, thickened, with small anterodorsal process and anteroventral window; anteroventral process of epandrium (= surstylus) strong, long as in *P. krylovi* (*cf.* Roháček, 2013: fig. 6B), but somewhat hook-like, bent posteriorly and distally tapered (see Fig. 13B, avp) but not acutely pointed. Epandrium anterodorsally with the usual 3 pairs of long erect setae (the most lateral shortest), otherwise shortly and finely setose (Fig. 13B). Anal fissure invisible. Cercus partly visible on only right side (Fig. 13B), small (about third length of gonostylus), pale ochreous and very sparsely shortly setulose. Gonostylus (Fig. 13A, B, gs) concolourous with epandrium, long, slender and hook-like, bent anteriorly but not acutely pointed and entirely bare in contrast to those of *P. ryszardi* (see Roháček & Hoffeins, 2020: fig. 5C) and *P. hoffeinsorum* (cf. Roháček, 2013: fig. 4E, G, H). No structures of internal genitalia (aedeagal complex) can be seen in male holotype.

Female. Unknown.

Remarks. Ten named species were previously known in the Eocene fossil genus *Protanthomyza* (Roháček, 2013, 2020; Roháček & Hoffeins, 2020), all recorded from Baltic and/or Bitterfeld amber. The new, eleventh species, *Protanthomyza chelicerata* **sp. nov.**, belongs to a group of taxa without a ctenidial spine on the fore femur, which also includes *P. hennigi* Roháček, 2013, *P. grimaldii* Roháček, 2020, *P. krylovi* Roháček, 2013, *P. loewi* Roháček, 2013, *P. presli* Roháček, 2013, and *P. ryszardi* Roháček & Hoffeins, 2020. Due to its bare arista, the ocellar triangle delimited by a groove or line, and the presence of 3–4 dc setae, *P. chelicerata* **sp. nov.** seems to be particularly allied to *P. grimaldii* and *P. ryszardi*. Roháček & Hoffeins (2020) considered these two species to be closely related due to their similar fusion of Sc and R_1, the shape of dm cell, the same mid leg chaetotaxy, and, particularly, a similarly formed anteroventral process of the epandrium (see Roháček, 2020: fig. 9; Roháček &

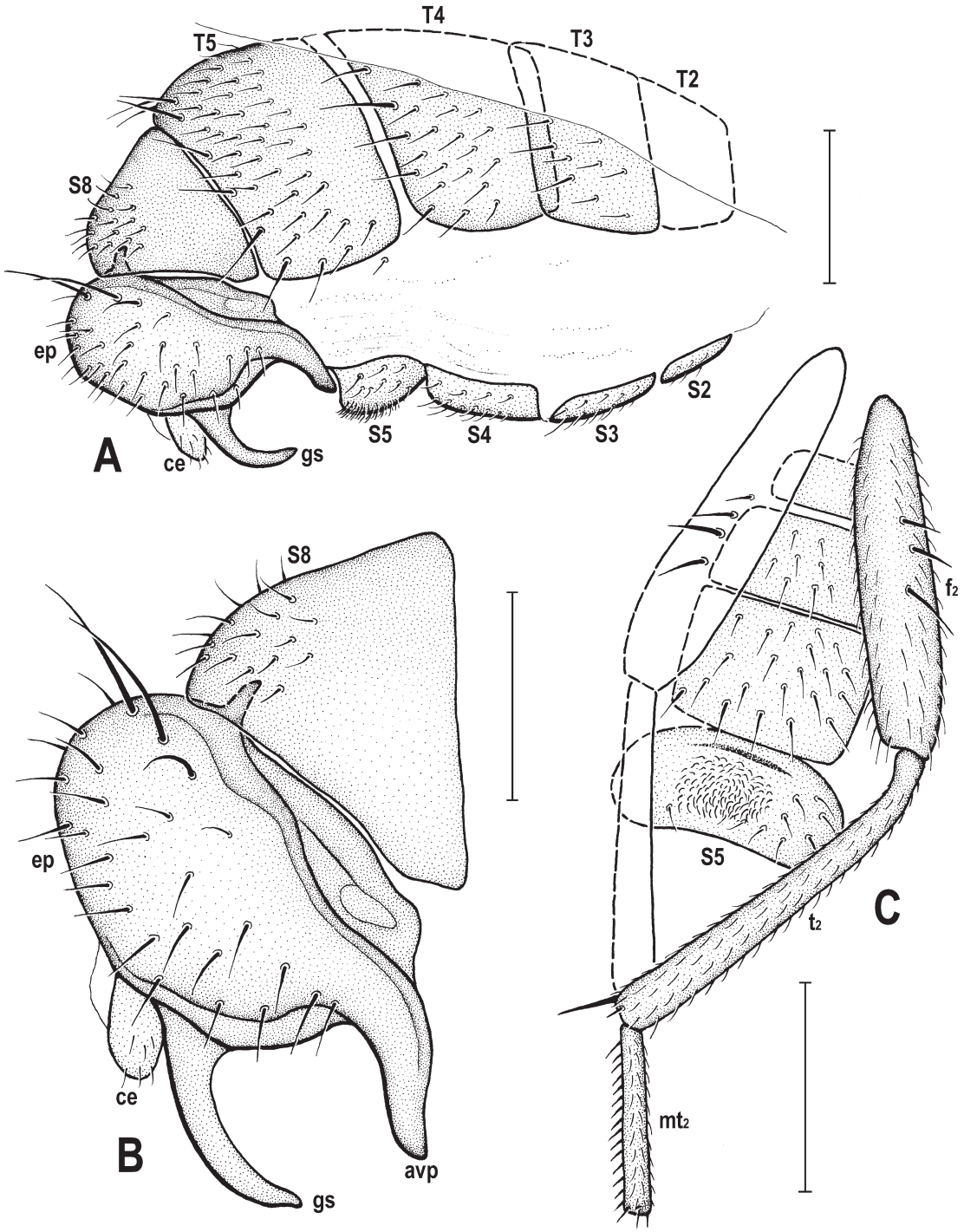

FIGURE 13. *Protanthomyza chelicerata* **sp. nov.**, holotype male (Baltic amber). **A**, Abdomen, right laterally. **B**, Male S8 and external genitalia, right laterally. **C**, Mid legs (partly) and abdominal sterna, ventrally (setosity partly omitted). Scale bars: 0.3 mm (**A**, **C**), 0.2 mm (**B**). For abbreviations see Material and methods.

Hoffeins, 2020: fig. 5C). However, *P. chelicerata* **sp. nov.** distinctly differs from these species (and other species of the genus) by its unusual Sc, which runs free up to C where it fuses with R_1 without forming a preapical kink (see Fig. 12E). It also has male pregenital sternum (S5) with a medial brush of dense setulae, as well as a uniquely formed (long, relatively slender, and hook-like curved) anteroventral process (surstylus) of the epandrium. Since the publication of the key to *Protanthomyza* (Roháček, 2013: 439–442), three additional species have been discovered. Therefore, the posterior part of the key (starting from couplet 5) is updated below.

Key to *Protanthomyza* species lacking ctenidial spine on fore femur

5 (1) Only 2 dc setae; ac microsetae relatively sparse, in 6 rows on suture (Roháček, 2013: fig. 6E). f_1 with only 1 long and thicker seta in posterodorsal row (Roháček, 2013: fig. 6D).....6

- At least 3 dc setae; ac microsetae dense, in 8 or more rows on suture. f_1 with 2 or more long and thicker setae in posterodorsal row (Roháček, 2013: fig. 8C; Fig. 7B).....7

6 (5) Ocellar triangle not separated by line or groove; pvt not crossed. Prescutellar ac longer than anterior dc. Epandrium with strong, slightly sinuous and distally somewhat dilated anteroventral process; gonostylus haunch-shaped, with acute apex (Roháček, 2013: fig. 6B). Female T6 with sparse and short setae (Roháček, 2013: fig. 6C).....*P. krylovi*

- Ocellar triangle distinctly delimited by marginal groove-like line; pvt crossed. Prescutellar ac not longer than anterior dc ..... *P.* sp. *cf. krylovi*

7 (5) Antenna large, its length almost as long as half height of head; arista completely bare (Roháček, 2013: figs 7C, 8B). Face, parafacialia, gena, palpus and 1st antennal flagellomere yellow to ochreous-yellow. Female abdomen elongate, relatively slender (Roháček, 2013: figs 7B, 8A); postabdomen with relatively long T7 and small pale-pigmented T8 and S8 (Roháček, 2013: fig. 8A). Male unknown ..... *P. loewi*

- Antenna small, distinctly shorter than one-third of head height. Arista bare or shortly ciliate. Face, parafacialia, gena, palpus and 1st antennal flagellomere variable in colour, yellow to black.....8

8 (7) Arista bare or nearly so.....9

- Arista shortly but distinctly ciliate.....11

9 (8) Body largely orange brown, antenna orange ochreous, face and parafacialia yellowish, narrowly brown margined. Sc free up to C where it is fused with R_1 without forming a preapical kink (Fig. 12E). Mesopleuron (apart from 3 posterior setae) with setulae scattered over almost entire surface (Fig. 12C). Male S5 medially with a dense brush of short setulae (Fig. 13A, C). Anteroventral process of epandrium long, relatively slender and hook-like curved and gonostylus dark, concolourous with epandrium, long, slender and curved anteriorly but not acutely pointed and bare (Fig. 13A, B). Female unknown.....
.....*P. chelicerata* **sp. nov.**

- Body dark brown to blackish; antenna, face and parafacialia variable (yellowish ochreous to dark brown). Sc distally fused with R_1 forming on it a preapical kink (Roháček, 2020: fig. 6). Mesopleuron (apart from 3 posterior setae) with setulae largely in posterodorsal half of surface (Roháček, 2020: fig. 7). Male S5 simply and sparsely setose (Roháček & Hoffeins, 2020: fig. 5C). Anteroventral process of epandrium hook-like but short and robust (Roháček, 2020: fig. 9; Roháček & Hoffeins, 2020: fig. 5C)..... 10

10 (9) Antenna with 1st flagellomere pale brown or ochreous in contrast to dark brown pedicel. Frontal triangle not developed (Roháček, 2020: fig. 4). Only anterior ppl long (Roháček, 2020: fig. 4). Wing distinctly broader and dm cell shorter and wider distally (Roháček, 2020: fig. 10). Epandrium elongate and tapered posteriorly (Roháček, 2020: fig. 9). Female with S6, S5 and S4) broad, all more or less not transverse (Roháček, 2020: fig. 13)....*P. grimaldii*

- Antenna unicolourous brown. Frontal triangle distinctly delimited by silvery microtomentose pattern (Roháček & Hoffeins, 2020: figs 3B, 4A). Both ppl setae long. Wing narrow, more elongate and dm cell narrower, less widened distally (Roháček & Hoffeins, 2020: figs 2A, 4C). Epandrium of normal length, little tapered posteriorly and gonostylus pale-pigmented, slender, curved anteriorly and acutely pointed (Roháček & Hoffeins, 2020: fig. 4C). Female abdomen with S6, S5 (and probably also S4) narrow, not transverse (Roháček & Hoffeins, 2020: fig. 4E) .....*P. ryszardi*

11 (8) 3 dc setae. Mouthparts (Roháček, 2013: figs 2C, 7A) very long, almost twice as long as head height, when exposed. Mesopleuron with sparse setulae (Roháček, 2013: fig. 2D). Apical portion of CuA_1 as long as distance between r-m and dm-cu (Roháček, 2013: fig. 7A). Epandrium relatively short and high, with very long (3 pairs) dorsobasal setae, small S-shaped anteroventral process and distinctive gonostylus (widest in its middle) (Roháček, 2013: fig. 2E). Female unknown .....*P. hennigi*

- 4 dc setae. Mouthparts markedly shorter (Roháček, 2013: fig. 10D). Mesopleuron with numerous setulae (Roháček, 2013: fig. 9D). Apical portion of CuA_1 much shorter (about 0.6 times as long as) than distance between r-m and dm-cu (Roháček, 2013: fig. 10D). Female abdomen short and broad, with short and strongly transverse T7 (Roháček, 2013: fig. 9G). Male unknown .....*P. presli*

Discussion

Diversity of Clusiomitidae and Protanthomyzidae in the Baltic amber forest

Already Roháček & Hoffeins (2021) stated that at least 10 species of Clusiomitidae were found in just 26 amber pieces. Of these, seven species were named by Hennig (1965), Roháček (2016), Pérez-de la Fuente *et al*. (2018), and Roháček & Hoffeins (2021), while the remaining three are described in this paper. However, these are not the only species recognized in this series of amber samples. There are three additional species that cannot be associated with any of the described taxa, including one unusual specimen that may even belong to a different genus. Unfortunately, these fossils are in poor condition, making their description impossible. Nevertheless, the high species-to-sample ratio (when every second sample is containing a different species) suggests that Clusiomitidae may have been higly diverse in the Baltic amber forest.

The diversity of the newly established family Protanthomyzidae appears to be quite similar. Initially, when Roháček (2013) discussed the species richness of Anthomyzidae, which at that time included species of the genus *Protanthomyza* within the subfamily Protanthomyzinae, a total of 11 species of Anthomyzidae (*s*. *lat*.) were found in just 15 amber samples. Using rarefaction analysis, he concluded that Anthomyzidae (including Protanthomyzinae) must have been more diverse in the Baltic amber forest than they are today in the whole of Europe (see Roháček, 2013: 470). Focusing only on Protanthomyzidae from this study, a total of nine species of *Protanthomyza* (one unnamed) were recognized in 12 amber pieces. Subsequently, three more

amber samples containing *Protanthomyza* flies were found, yielding two additional species (see Roháček, 2020; Roháček & Hoffeins, 2020; present paper). Thus, a total of 11 species of Protanthomyzidae have hitherto been found in 15 amber samples. This fact indicates that Protanthomyzidae were even more diverse in the Baltic amber forest than Clusiomitidae.

The diversity of Acalyptratae families in the Baltic amber forest was also unusually high. Representatatives of most families known from Europe have been recorded in this palaeohabitat, including Anthomyzidae, Asteiidae, Aulacigastridae, Camillidae, Campichoetidae, Carnidae, Chamaemyiidae, Chloropidae, Clusiidae, Conopidae, Chyromyidae, Cryptochaetidae, Curtonotidae, Diopsidae, Drosophilidae, Dryomyzidae, Heleomyzidae, Lauxaniidae, Megamerinidae, Micropezidae, Milichiidae, Odiniidae, Pallopteridae, Periscelididae, Pseudopomyzidae, Psilidae, Pyrgotidae, Sciomyzidae, Sepsidae, and also extra-European Cypselosomatidae, Natalimizidae, Neurochaetidae (see Hennig, 1965, 1966, 1967, 1969, 1971, 1972; Haenni, 2003; Hoffeins & Rung, 2005; Woźnica, 2006, 2007, 2019; Grimaldi, 2008; Grimaldi & Singh, 2012; Tschirnhaus & Hoffeins, 2009; Hoffeins & Woźnica, 2013; Roháček, 2013, 2014). In addition, six extinct families have so far been identified exclusively from Baltic amber: Proneottiophilidae (Hennig, 1969), Protanthomyzidae (Roháček, 1998, see above), Hoffeinsmyiidae (Michelsen, 2009), Yantaromyiidae (Barták, 2019), Clusiomitidae (Roháček & Hoffeins, 2021), and Christelenkidae (Roháček *et al*., 2023). It is worth nothing that several more Acalyptratae families were likely present in the Baltic amber forest and are expected to be discovered in future. Among the most probable candidates are Agromyzidae (known from Tertiary compression fossils, see Evenhuis, 1994) and Sphaeroceridae (previously recorded as *Borborus* sp. from Baltic amber by Helm, 1896: 233, but this has yet to be confirmed).

Habitat association of fossil species of Clusiomitidae and Protanthomyzidae

The occurrence of Clusiomitidae in the Baltic amber forest was first discussed by Roháček & Hoffeins (2021). Their probable relationship with the saproxylic Clusiidae indicates that members of Clusiomitidae can be associated with a similar habitat—rotting dead trees in a humid forest environment. Plant syninclusions (various remnants, pollen grains, and frequent stellate hairs) found in all examined specimens, including those of three species decribed above, do not contradict this assumption. Also the recorded animal syninclusions of two species (Roháček & Hoffeins, 2021) support this association. These include representatives of Diptera (Keroplatidae, Cecidomyiidae, Sciaridae), Coleoptera (Latridiidae), Hymenoptera (Scelionidae), and Hemiptera (Coccoidea), all of which are commonly associated with decaying wood in forest.

Determining the habitat of Protanthomyzidae (all belonging to the genus *Protanthomyza*) is more challenging. Based on the rarity of Anthomyzidae *s. lat*. (*i.e*., including also *Protanthomyza* species) among Diptera inclusions, Roháček (2013) suggested that they were more likely associated with low herbaceous vegetation (such as in forest undergrowth, littoral habitats *etc*.) rather than directly with trees. This assumption seems particularly plausible for true Anthomyzidae (species of *Lacrimyza* and *Reliquantha*). The extant species, *Reliquantha variipes* Roháček, 2013, was reared in England by Smith (2017) from dead wood taken from the rot hole of a sycamore (*Acer pseudoplatanus*) together with several other saproxylic flies. This finding suggests that also some (more primitive) modern Anthomyzidae may have saproxylic larvae. As *Protanthomyza* species have no extant relatives, their habitat affinity remains uncertain. However, insect syninclusions found with *P. hoffeinsorum* Roháček, 2013 (Thysanoptera, Diptera: Chironomidae), *P. krylovi* (Diptera: Dolichopodidae, Phoridae, Chironomidae, Sciaridae, Proneottiophilidae?, Chloropidae?) and *P. grimaldii* (Diptera: Empididae: *Rhamphomyia* sp., Mycetophilidae, Simuliidae, Chironomidae; fragments of Trichoptera, Coleoptera and Araneae) (Roháček, 2013, 2020) suggest that these species may have lived within the herbaceous layer of the forest.

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