

The pseudo-Gondwanan genus *Atlatlia* (Diptera: Dolichopodidae) from Australia, New Caledonia, and Baltic amber, with the description of two new genera

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ABSTRACT. The fly genus *Atlatlia* Bickel, 1986 (Diptera: Dolichopodidae: Medeterinae) is revised with additional new recent and fossil species, and now comprises two major species groups. The *Atlatlia grisea* group includes three recent species from Australia, *A. grisea* Bickel, 1986; *A. flaviseta* Bickel, 1986; and *A. isolata* sp. nov., three recent species from New Caledonia, *A. acra* sp. nov., *A. argenticoxa* sp. nov., and *A. cowanae* sp. nov., and three species from Baltic amber, *A. corynoura*, sp. nov., *A. electrica* sp. nov., and *A. licina*, sp. nov. The *Atlatlia ulrichi* group includes six species from Baltic amber, *A. angulicauda* sp. nov., *A. cryptica* sp. nov., *A. penicillata* sp. nov., *A. ramosa* sp. nov., *A. tonsa*, sp. nov., and *A. ulrichi* sp. nov. The genus *Kashubia* gen. nov., is described from Baltic amber with three species: *K. falcata*, sp. nov., *K. ornatipes* sp. nov., and *K. starki* sp. nov. The genus *Eridanomyia* gen. nov. is also described from Baltic amber with two species, *E. amica* sp. nov. and *E. conjugalis* sp. nov. Four of the newly described Baltic amber species also occur in Bitterfeld amber, suggesting their overall faunal similarity. The striking disjunction of the genus *Atlatlia* in both time and space, recent Australia and New Caledonia and Paleogene Baltic amber, suggests a once much wider distribution, possibly during Eocene “greenhouse earth” climatic conditions, with subsequent extinction leaving only a relict fauna in Australasia. With geological evidence suggesting New Caledonia was largely submerged in the early Paleogene and only emergent in the late Eocene, the New Caledonian *Atlatlia* fauna possibly originated by dispersal from Australia in the early to mid-Cenozoic.

Introduction

The genus *Atlatlia* (Diptera: Dolichopodidae: Medeterinae) was established for two newly discovered Australian species, *A. grisea*, collected on tree trunks in Ku-ring-gai Chase National Park, near Sydney, New South Wales, and *A. flaviseta* from Pemberton, Western Australia (Bickel, 1986). At the time, the genus was characterised by two striking synapomorphies, the total loss of posterior crossvein (crossvein dm-m) and the prolongation of the male abdominal peduncle (tergite and sternite 7) into a rod-like

extension for an apically positioned genitalic capsule or hypopygium (e.g., Figs 1a, 3a). A third Australian species and three additional species from New Caledonian were subsequently discovered along with additional records of the two described species.

Since *Atlatlia* was known only from Australasia and therefore of possible Gondwanan provenance, it was a surprise to find the genus present in Baltic amber, as identified by Hans Ulrich in Hoffeins and Hoffeins (2003). Amber is fossilised resin, primarily exuded from various tree species. When fresh resin is deposited in sediments, it loses

Keywords: Bitterfeld amber, *Kashubia* gen. nov., *Eridanomyia* gen. nov.

ZooBank registration: urn:lsid:zoobank.org:pub:B961B48C-9555-4D9A-ABB7-0EF6A9558C43

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Submitted: 27 September 2024 **Accepted:** 20 January 2025 **Published:** 7 May 2025 (in print and online simultaneously)

Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

Citation: Bickel, D. J. and J. Martin. 2025. The pseudo-Gondwanic genus *Atlatlia* (Diptera: Dolichopodidae) from Australia, New Caledonia, and Baltic amber, with the description of two new genera from Baltic amber. *Records of the Australian Museum* 77(2): 89–120. <https://doi.org/10.3853/j.2201-4349.77.2025.1907>

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its volatile components over time and becomes hardened into translucent amber. Any debris, plant structures or small arthropods that were initially trapped in the sticky resin are preserved as inclusions, often with fine morphological detail clearly visible. Baltic amber is the most abundant and best-known amber deposit and was derived from Eocene/Oligocene forests in what is present-day Scandinavia. Much of this amber was deposited by ancient river systems into sedimentary beds, which are eroded out by wave action under the Baltic Sea. Since amber is only slightly denser than sea water, pieces are often carried by currents and washed ashore, especially along the coasts of Poland, eastern Germany and the Baltic states. Bitterfeld amber, from deposits in Saxony-Anhalt, Germany, is considered contemporaneous in origin to the more extensive Baltic amber (Larsson, 1978; Weitschat & Wichard, 2002; Erichson & Weitschat, 2008).

This study arose when Hans Ulrich invited one of us (DJB) to study his extensive collection of Baltic amber Dolichopodidae. With augmentation from additional collections, a rich and disparate radiation of *Atlatlia* in Paleogene amber was discovered, strongly disjunct in time and space from the recent Australasian fauna. This paper describes new recent and Paleogene *Atlatlia* species along with a key to the entire genus, discussions of historical biogeography, and the description of two new related Baltic amber genera.

Methods

Material examined

During this study both recent and fossil material was examined, with the repositories of which are listed below. Most of the recent Australian material was collected by the senior author and is housed primarily at the Australian Museum in Sydney (AMS). The New Caledonian material was primarily collected from Malaise trap surveys by Jean Chazeau and associates, ORSTOM, Noumea (deposited MNHN), and by Evert Schlinger and associates (INHS).

The amber inclusions were from a wide range of collections, both institutional and private. The best amber inclusions in both clarity and species richness are found in private holdings. These were often “selected” for purchase based on their quality of preservation, as opposed to “unselected” inclusions of many museum collections obtained *en masse* and comprising many obscured specimens which are less useful for species-level diagnosis. We are grateful to have been given access to these private collections and for the trust shown by their owners in allowing their material to be studied offsite. Holotypes from private collections were deposited in the public institutions indicated as recommended by the ICZN (1999). The collections used and their text acronyms are listed below, along with the names of assisting curatorial staff.

a) Recent material.

AMS, Australian Museum, Sydney, NSW, Australia (David Britton); **ANIC**, Australian National Insect Collection, CSIRO, Canberra, ACT, Australia (Don Colless); **INHS**, Illinois Natural History Survey, Champaign, Illinois, U.S.A. (Colin Favret, Mike Irwin); **MNHN**, Museum national d’Histoire naturelle, Paris, France (Loïc Matile, Michel

Baylac); **MVM**, Museum of Victoria, Melbourne, Vic., Australia (Arturs Neboiss).

b) Amber material - Public Institutions

AMNH, American Museum of Natural History, New York City, NY, U.S.A. (David Grimaldi, Paul Nascimbene); **BMNH**, The Natural History Museum, London, England, U.K. (Andrew Ross, Claire Mellish); **GPIH**, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Hamburg Germany (Wolfgang Weitschat); **GPUG**, Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen Germany (Hans Jahnke, Mike Reich, Alexander Schmidt, Tanja Stegemann, Alexander Gehler); **MAGP**, Museum of Amber Inclusions, University of Gdansk, Gdansk Poland (Elżbieta Sontag, Ryszard Szadziewski, Jacek Szwed); **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. (Frank Carpenter, Phil Perkins, Ricardo Perez de la Fuente); **MHNN**, Musée d’Histoire Naturelle de Neuchâtel, Neuchâtel, Switzerland (Jean-Paul Haenni, Matthias Borer, Jessica Litman); **MZPW**, Muzeum Ziemi (Museum of the Earth), Warsaw, Poland (Barbara Kosmowska-Ceranowicz, Janusz Kupryjanowicz); **NCIR**, Skagen Ravnemuseum, Skagen, Denmark, subsequently transferred to ZMUC (Karin Nordmann); **SDEI**, Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; **SMF**, Senckenberg Museum und Forschungsinstitut, Frankfurt, Germany (Günther Bechly, Karin Wolf-Schwenninger, Frauke Stebner); **ZFMK**, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany, with the collection of Hans Ulrich. (Hans Ulrich, Netta Dorchin, Ximo Mengual); **ZMUC**, Zoologisch Museum, Universitets Copenhagen, Copenhagen, Denmark. (Stig Andersen, Lars Vilhelmsen).

c) Amber material - Private Collections

Ehlen, Holger. Germany; Eichmann, Friedhelm. Germany; Gröhn, Carsten. Glinde, Germany; Hoffeins, Christel & Hans-Werner. Hamburg, Germany (**CCHH**); Kernegger, Friedrich. Hamburg, Germany; Krummer, Hansjoachim. Greifswald, Germany; Stark, Andreas. Halle am Saale, Germany; Ulrich, Hans. Bonn, Germany (deposited ZFMK).

Specimen examination

Species were primarily defined on the basis of the male genitalic structure and male secondary sexual characters (MSSC). Photographs were taken by JM using a Leica M205A photomontage system. Body measurements and relative podomere ratios are as accurate as possible given distortion of the amber and the difficulty in seeing embedded structures in perpendicular view.

In describing the hypopygium, ‘dorsal’ and ‘ventral’ refer to morphological position prior to genitalic rotation and flexion. Therefore, in lateral view the hypandrium lies along the ventral surface, the surstyli are apical and the cercus is apical dorsal. Morphological terminology follows Cumming and Wood (2017). Features common to a group of species are listed in the introductory discussion and not repeated in descriptions unless needing clarification. Body length of males is measured from the base of the antennae to the tip of the seventh abdominal segment. Wing length is the distance from the wing base to apex, and wing width is measured from the junction of R₁ with the costa to the opposite side of

the wing, perpendicular to the wing's long axis. The CuAx ratio is the length of the dm-m crossvein/ distal section M₄. The position of features on elongate structures such as leg segments is given as a fraction of the total length, starting from the base. The relative lengths of the podomeres are representative ratios, not measurements, and are given for each leg in the following formula and punctuation: trochanter + femur; tibia; tarsomere 1/ 2/ 3/ 4/ 5. The following abbreviations and terms are used: MSSC - Male secondary sexual character(s); non-genitalic characters found only on male body; FSSC - Female secondary sexual character(s); non-genitalic characters found only on female body; I, II, III: pro-, meso-, metathoracic legs; C, coxa; T, tibia; F, femur; ac, acrostichal setae; ad, anterodorsal; av, anteroventral; dc, dorsocentral setae (a numbering system using subscripts indicates specific dc starting from the posterior end, thus dc₃ is the third seta anterior of the posteriormost seta); dv, dorsoventral; hm, postpronotal setae; npl, notopleural setae; pa, postalar setae; pd, posterodorsal; pm, presutural supra-alar setae; ppl, proepisternal setae; pv, posteroventral; sa, postsutural supra-alar setae; sr, presutural intra-alar setae; t, tarsus; t₁₋₅, tarsomeres 1 to 5; NP = National Park; SF = State Forest.

Stellate hairs (noted when present in amber pieces, e.g. Fig 11e) are commonly found in Baltic amber and are thought to be derived from protective scales on leaf buds and male inflorescences, possibly of the tree genus *Quercus* (Fagaceae). They are assumed to be seasonal indicators of spring and early summer growth, contemporaneous with seasonal exudations from associated resin-producing conifers (Larsson, 1978).

The acronym "BAM" followed by a number (e.g., "BAM-234") refers to a numbering system for photographs of Baltic amber inclusions. A complete database of these photos are held at AMS and relevant photos have been forwarded to collection curators. In citing specimen numbers, a simple number, e.g., "3 ♂, 2 ♀" implies three male and two female inclusions, each in a separate amber piece, whereas numbers in brackets, e.g., "[3 ♂, 2 ♀]" implies three male and two female inclusions together in the same amber piece.

Results

Taxonomy

Order Diptera Linnaeus, 1758

Family Dolichopodidae Latreille, 1809

Subfamily Medeterinae Lioy, 1864

Diagnosis. The Medeterinae are separated from all other dolichopodid subfamilies by the following combination of characters:

Head. Dorsal postcranium distinctly concave; vertex not excavated laterad of ocellar tubercle; scape without dorsal setae; arista generally apical, only rarely subapical.

Thorax. Posterior mesonotum strongly flattened and depressed, and distinct from curved anterior mesonotum; acrostichal setae usually biseriate although absent in some taxa; scutellum with two pairs of setae, even if lateral pair as tiny hairs.

Legs. Femora II and III almost always lacking anterior preapical seta; tibiae mostly bare of major setae.

Wings. Vein M₁ unbranched and without flexion (or *bosse alaire*) distad of dm-m crossvein.

Abdomen. Male hypopygium or genitalic capsule on peduncle formed by exerted haired sternite 7 and not enfolded by preceding abdominal segments; hypopygium with left lateral or left basal foramen.

Remarks. All taxa considered in this revision are assigned to the Medeterinae, a complex and diverse subfamily within the Dolichopodidae. Adults of many medeterine genera (along with other dolichopodid taxa) utilise tree trunks both as sites for mating and a source of soft-bodied invertebrate prey. This has led to their accidental entrapment in sticky tree resin, accounting for the diversity and relative abundance of dolichopodids in Cenozoic ambers.

Genus *Atlatlia* Bickel, 1986

Atlatlia Bickel, 1986: 165.

Type species. *Atlatlia grisea* Bickel, 1986, original designation.

Diagnosis. Small Medeterinae, mostly dark grey, with wing length <1.5 mm; male with head subcircular or slightly ovate in anterior view; male eye facets often enlarged anteroventrally (MSSC); scape and pedicel short, and postpedicel subrectangular, sometimes almost reniform on pedicel; arista apical; posterior mesonotum distinctly flattened; ac weak, in 3-4 irregularly pairs, or absent; 6 pairs dc; 1 pa; 2 sa; 2 sr; 1 hm; 1 pm; usually 2 npl, but sometimes only 1 npl present on the ventral margin of notopleuron; median scutellar setae strong with lateral scutellar setae reduced to weak hairs or absent; 2 short ppl just anterior to anterior spiracle; legs bare of major setae; vein R₁ terminating in basal third of costa; R₂₊₃ and R₄₊₅ diverging slightly towards apex (Fig. 1c-d); M₁ basally parallel with M₄ then bending anteriorly to converge toward R₄₊₅, and sometimes turning posteriorly to end at wing apex (MSSC); M₁ without flexion (= *bosse alaire* of Parent, 1938) in distal sector; crossvein dm-m absent; male abdominal segment 7 in the *grisea* group prolonged to form elongate hypopygial peduncle, with tergite and sternite displaced, tergite more basal and sternite more distal, adjoining left lateral sternite 8 covering hypopygial foramen; hypandrium basally fused to epandrium; surstylus elongate and bearing species-specific modified setae; cercus elongate and projecting in arc from hypopygium, and often with complex setation; female oviscapt (segment 9+10) ventrally deflexed, with elongate setae, and lacking peg-like acanthophorites (Fig. 4f-g).

Remarks. The genus *Atlatlia* is known from eastern and southwestern Australia, New Caledonia (Fig. 2f), and Paleogene Baltic and Bitterfeld amber. All members of the genus *Atlatlia* have lost the dm-m crossvein, a strong synapomorphy. The six extant Australasian species and three Paleogene species that comprise the *grisea* species group also have a prolonged sternite and tergite 7 (Figs 1a, 4a), a character initially thought to be characteristic of the entire genus. However, six Paleogene species (the *ulrichi* group) have a short segment 7. The loss of the dm-m crossvein is as a strong synapomorphy uniting both species groups as sister taxa in the same genus.

Based on personal observations (DJB) of the Australian species, *Atlatlia grisea* and *A. flaviseta*, these tiny flies rest primarily on smooth-barked *Eucalyptus* and *Angophora* trees, with head vertical and slightly leaning out from the trunk, in a manner similar to species of *Medetera* Fischer von Waldheim, 1819. Individuals move rapidly, in short quick flights to land vertically higher on the trunk and are soon out of sight. To the collector standing near the base of a tree, it is important to net or quickly place a tube over these fast-moving flies before they are out of reach, and patience is required. A more productive sampling methodology are tree trunk sticky traps (e.g., Bickel & Tasker, 2004) that passively collect both trunk-associated arthropods and drifting “aerial plankton” that accidentally land on them. Here the sticky trap adhesive can be considered analogous to sticky tree resins that are subsequently transformed into amber (also see Brues, 1933; Solórzano-Kraemer *et al.*, 2015).

Apart from the elongate postabdomen, basally swollen femora, and the modified venation found on some species the *Atlatlia grisea* group (Fig. 1), males display few distinctive secondary sexual characters. Most *Atlatlia* have a general sombre grey/ brown colouration, although the New Caledonian species have orientated silvery pruinosity on the coxae and femora. Although mating has not been observed in *Atlatlia*, it probably occurs in a manner similar to that seen in the genus *Medetera*, where the male approaches the female from behind, and thrusts its hypopygium far forward through its legs so that the tips of the surstyli can clasp the female’s abdomen. The elongate arm-like hypopygial peduncle found in the *Atlatlia grisea* group would enable males to thrust their hypopygium far forward. The male postabdomen of *A. grisea* (Fig. 1a) represents the most extreme development of the peduncle within the Dolichopodidae and probably the entire Diptera.

The following species are included in the genus *Atlatlia*:

I. *Atlatlia grisea* group

a. Recent Australian species

- Atlatlia flaviseta* Bickel, 1986: 169. Australia (WA).
- Atlatlia grisea* Bickel, 1986: 168. Australia (NSW, Qld, Vic).

Atlatlia isolata Bickel, sp. nov. Australia (NSW).

b. Recent New Caledonian species

- Atlatlia acra* Bickel, sp. nov. New Caledonia.
- Atlatlia argenticoxa* Bickel, sp. nov. New Caledonia.
- Atlatlia cowanae* Bickel, sp. nov. New Caledonia.

c. Paleogene species

Atlatlia corynoura Bickel, sp. nov. Baltic Region † (Eocene/ Oligocene).

Atlatlia electrica Bickel, sp. nov. Baltic & Bitterfeld Regions † (Eocene/ Oligocene).

Atlatlia licina Bickel, sp. nov. Baltic Region † (Eocene/ Oligocene).

II. Paleogene *Atlatlia ulrichi* group

Atlatlia angulicauda Bickel, sp. nov. Baltic Region † (Eocene/ Oligocene).

Atlatlia cryptica Bickel, sp. nov. Baltic Region † (Eocene/ Oligocene).

Atlatlia penicillata Bickel, sp. nov. Baltic Region † (Eocene/ Oligocene).

Atlatlia ramosa Bickel, sp. nov. Baltic Region † (Eocene/ Oligocene).

Atlatlia tonsa Bickel, sp. nov. Baltic Region † (Eocene/ Oligocene).

Atlatlia ulrichi Bickel, sp. nov. Baltic & Bitterfeld Regions † (Eocene/ Oligocene).

Key to males of Recent and Paleogene amber *Atlatlia* species (Diptera:

Dolichopodidae: Medeterinae)

This key includes both recent and extinct Paleogene species (†), and as such comprises a set of nested diagnoses for species in the genus.

- 1 Vertex not excavated laterad of ocellar tubercle, vein M₁ unbranched, posterior mesonotum flattened and slightly depressed and distinct from curved anterior mesonotum, antennal scape bare, femora II and III without strong anterior preapical setae, and tibiae II and III mostly bare of strong, dorsal posteranum concave strong setae. Subfamily Medeterinae 2
- Without this combination of characters other Dolichopodidae
- 2(1) Crossvein dm-m absent (*Atlatlia*) 3
- Crossvein dm-m distinctly present other genera of Medeterinae
- 3(2) Segment 7 (hypopygial peduncle) prolonged, with tergite being basal and sternite distal, with tergite and sternite connected by membrane (e.g., Fig. 4a–b), or fused (Fig. 1a, e); epandrium subrectangular in lateral view; vein M₁ often with elbow-shaped bend *grisea* group 4
- Segment 7 (hypopygial peduncle) short, concealed under tergite 6; epandrium basally spheroidal; vein M₁ with gentle bend (Figs 8–10) (Baltic & Bitterfeld amber)..... *ulrichi* group † 12

| | | |
|--------|---|----------------------------------|
| 4(3) | Recent species | 5 |
| — | Baltic and Bitterfeld amber species † | 10 |
| 5(4) | Vein M_1 with elbow-shaped bend before converging toward R_{4+5} (Figs 1c–d, 3a); body without silvery pruinosity; at least one femur basally swollen (Fig 3a) (Australia) | 6 |
| — | Vein M_1 with very gentle bend toward R_{4+5} (Figs 1f, 3c–d); legs often with silvery pruinosity; femora not basally swollen (New Caledonia) | 8 |
| 6(5) | Cercus broad and strongly curved, L-shaped, with some lateral setae and group of stronger blade-like setae; thoracic setae yellowish (Fig. 1e); (southwestern Australia) | <i>A. flaviseta</i> Bickel, 1986 |
| — | Cercus curved and digitiform; thoracic setae dark brown (eastern Australia) | 7 |
| 7(6) | Only femur III distinctly swollen; cercus (Fig. 2c) curved, lyriform with abundant dorsal and apical setae (Fig. 2a–c) | <i>A. isolata</i> sp. nov. |
| — | All femora basally swollen and tapering distally; cercus projecting laterally and distally, and bearing 3 distal blade-like setae, visible in ventral view (Fig. 1a–b) | <i>A. grisea</i> Bickel, 1986 |
| 8(5) | Coxae and legs mostly yellow; coxae and trochanters with orientated silvery pruinosity; small sized, wing < 1.2 mm; cercus broad, elongate distally with strong curved subapical seta, and other setae as figured (Figs 3d, 4d–e) | <i>A. argenticoxa</i> sp. nov. |
| — | Coxae and femora mostly dark brown; larger, wing > 1.4 mm | 9 |
| 9(8) | Coxa I with orientated silvery pruinosity; surstylus deeply cleft apically, cercus with large subrectangular base, and with deep bend from elongate arm arises in right angle to base, with three long dorsal setae near 2/3 (Figs 3b–c, 4a) | <i>A. acra</i> sp. nov. |
| — | Coxa I, distal anterior coxa II and anterior surfaces of all femora with orientated silvery pruinosity (MSSC); surstyli ventrally with narrow curved arm with distinctive elongate spatulate seta; cercus with narrow arm which expands apically into subtriangular crest (Figs 3e–f, 4b–c) | <i>A. cowanae</i> sp. nov. |
| 10(4) | Cercus bent at right angle near base to parallel bent surstylus, and with strong curved yellow seta at 2/3, and projecting well beyond hypandrium (Fig. 7c–d) | <i>A. licina</i> sp. nov. † |
| — | Cercus elongate and narrow, and bent or curved well beyond epandrial base | 11 |
| 11(10) | Cercus extending well beyond epandrium with gentle right angle bend and expanded apically with short setae (Fig. 5a–d) | <i>A. electrica</i> sp. nov. † |
| — | Cercus elongate and apically incurved (but not bent at right angle) and with expanded subapical apex bearing long setae and modified setae (Fig. 6a–d) | <i>A. corynoura</i> sp. nov. † |
| 12(3) | Surstylus with curved finger-like projection (Figs 8f, 10d) | 13 |
| — | Surstylus lacking finger-like projections | 14 |

- 13(12) Tibia III apically with curved anteroventral apical spinelike seta (MSSC); surstylus lobate with apical seta, and with median curved digitiform projection with apical seta; cerci elongate, narrow, forming lyriform crescent projecting laterad of distal epandrium (Fig. 8a–g) *A. ulrichi* sp. nov. †
- Tibia III apically unmodified; cercus elongate and narrow, extending well beyond epandrium, with 3 long curved apical setae (Fig. 10c–d) *A. ramosa* sp. nov. †
- 14(12) Surstylus and cercus both in a distinct right-angle bend, and the cercus bearing a tuft of short curved setae externally on the bend (Fig. 7a–b) *A. angulicauda* sp. nov. †
- Surstylus and cercus not in right-angle bend 15
- 15(14) Epandrium basally spheroidal but distally tapering; surstylus with elongate arm, cercus narrow and curved laterad of surstylus and extending beyond its apex, and with fine apical seta. (Fig. 9d–h) *A. cryptica* sp. nov. †
- Epandrium spheroidal and not tapering distally; surstylus and cercus otherwise 16
- 16(15) Cercus narrow and wire-like and surstylus blade-like (Fig. 9a–c) *A. tonsa* sp. nov. †
- Cercus elongate and with group of 4–5 curved apical to subapical setae subtended by apicoventral circular translucent cuticular projection (Fig. 10a–b) *A. penicillata* sp. nov. †

I. *Atlaltia grisea* group

The *Atlaltia grisea* group is characterised by an elongate hypopygial peduncle (Fig. 4a) comprising a prolonged segment 7, the tergite being basal, and the sternite distal (and connecting to the hypopygium with sternite 8, the cap-like covering over the hypopygial foramen). In some species (e.g., Fig. 4a–b), the tergite and sternite are separate and connected by membrane, while in other species (Fig. 1a, e) tergite and sternite 7 are partially to totally fused and forming a rod-like support for the hypopygium. The epandrium of the *grisea* group species is rather subrectangular and ovate in cross section. The cercus of the *grisea* group is often elongate and bowed in a broad U-shape, and bears modified setae.

This *Atlaltia grisea* species group includes both recent Australasian and fossil Paleogene species. The striking similarity between the Australian *A. grisea* (Fig. 3a) and the Baltic/Bitterfeld amber species *A. electrica* (Fig. 5a) is notable, and males of both species have all femora basally swollen (MSSC).

a. Recent Australian species

The three recent Australia species of the *grisea* group are associated with wet and dry sclerophyll forests of eastern and southwestern Australia. Males have an elbow-shaped bend on vein M₁, which is most strongly developed on the type species *Atlaltia grisea* (Fig. 1c).

Two of the species, the eastern Australian *A. grisea* and *A. isolata* have only one notopleural (npl) seta on the ventral margin of notopleuron; while all other *Atlaltia* species, including the Western Australian *A. flaviseta* have two notopleural setae, one on the ventral notopleural margin and the other positioned dorso-posteriorly.

Atlaltia grisea Bickel, 1986

Figs 1a–d, 2f, 3a, 4f–g

Atlaltia grisea Bickel, 1986: 168.

Type material. The male holotype of *Atlaltia grisea* was collected in Ku-ring-gai Chase NP near Sydney, New South Wales (ANIC, holotype 29-020654).

Additional material: Australia: **New South Wales:** Barrington Tops NP, Gloucester Tops, 32°04' S 151°34' E, 1280 m, 3.XII.1988, montane woodland, tree trunk; Barrington Tops NP, upper Williams River, 32°07' S 151°29' E, 550 m, 26.I.1987; Blue Mountains NP, Mt Banks, 33°35' S, 150°22' E, 28.XI.1984, dry sclerophyll forest, tree trunk; Ku-ring-gai Chase NP nr Mt Ku-ring-gai, 33° 40' 43" S, 151°7' 31" E, 5.I.1985, on *Eucalyptus haemastoma*, 23.XI.1996, 21.XII.1996, 5.IV.1997; Lorien Wildlife Refuge, 3km North of Lansdowne, 31° 45' S, 152° 32' E, 15–21.XI.1987, rainforest margin, Malaise trap, G. Williams (AMS); Myall Lakes NP, 32° 37' S, 152° 19' E, 50 m, on trunks *Angophora costata*, 24.XI.1987; Gibba Swamp at Putty Rd, 33°11' S, 150°41' E, 25.XI.2001, sticky trap on *Eucalyptus* sp.; Styx River SF, 30° 31' S, 152° 17' E, II.1990, canopy fog wet sclerophyll forest, R. Kitching; Styx River, 12 km S of Ebor, 17.X.1973, A. Neboiss (MVM); Deua NP, Wyanbene Caves Cpgd, 35° 45' 30" S, 149° 39' 30" E, 16.XII.2000; Carrai SF, various locales, 930–940 m, ~30°59' S 152°16' E, 1–16.I.1998, sticky traps variously on *E. cameronii*, *E. saligna*, *E. campanulata*, E. Tasker & P. German (AMS); Werrikimbe NP, various locales, 1025–1040 m, ~31°10' S 152°09' E, 1–7.XII.1997, 29.I–4.II.1998, sticky traps variously on *E. cameronii*, *E. saligna*, *E. nobilis*,

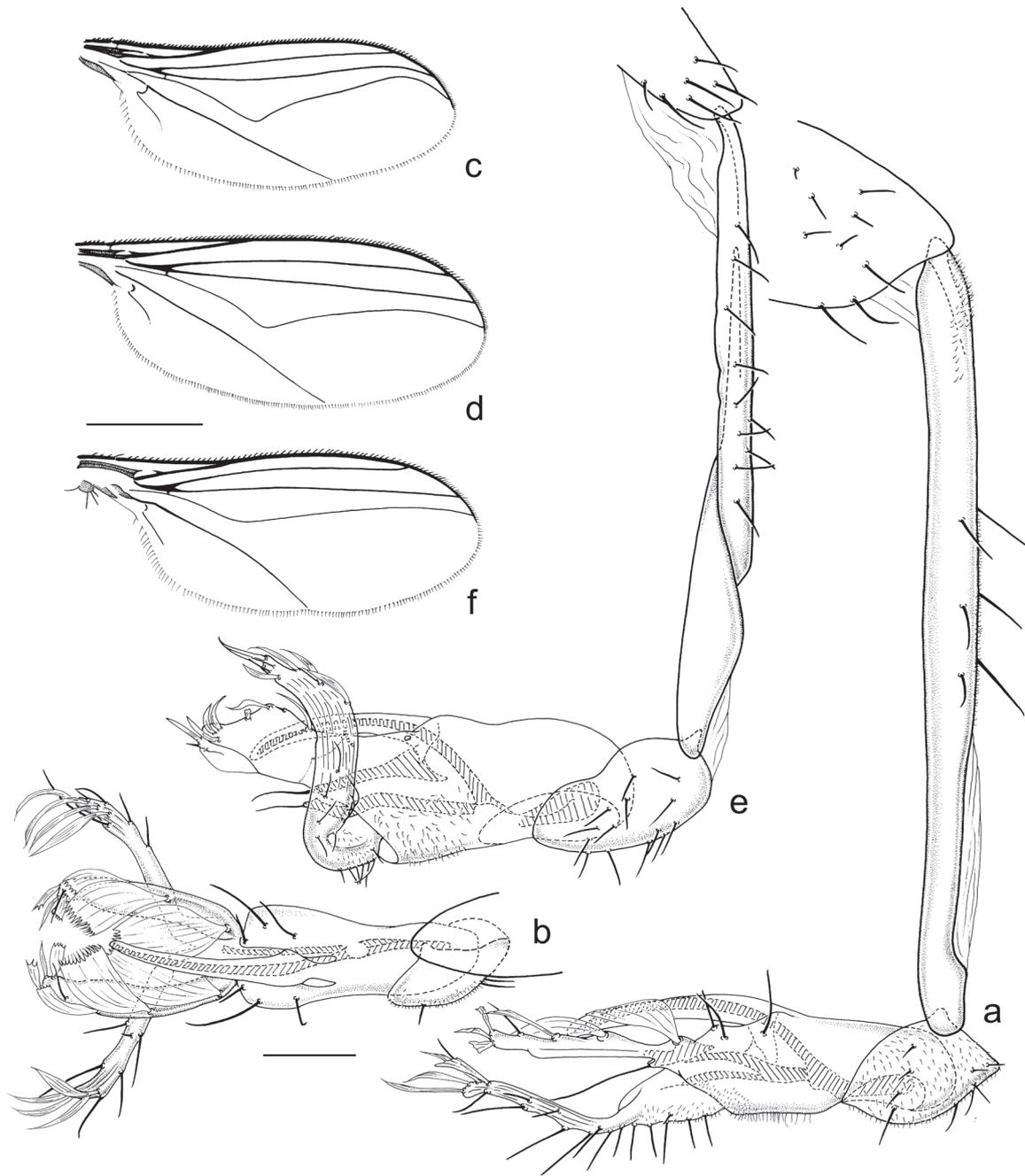


Figure 1. *Atlatlia grisea* Bickel: a, hypopygium and peduncle, left lateral; b, hypopygium, ventral; c, male wing; d, female wing. *A. flaviseta* Bickel: e, hypopygium and peduncle, left lateral. *A. cowanae* Bickel sp. nov.: f, male wing. Scale bars: Upper 0.5 mm; lower 0.1 mm.

E. viminalis, *E. campanulata*, *E. obliqua*, E. Tasker & P. German. (except where noted, all specimens collected by D. Bickel, AMS). **Queensland:** Carnarvon NP, Carnarvon Ck Gorge, 25°02' S, 148°13' E, 550 m, 28.XI.1992, on tree trunks, D. J. Bickel; Cooloola NP, 25°58' S, 153°09' E, 28.XI.1985, on trunks *Eucalyptus* spp.; Eurimbula NP, nr Miriam Vale, 24°11' S, 151°48' E, 3.X.1992, 30.X.1999, sandy coastal forest, tree trunk sticky trap, D. J. Bickel; Goodnight Scrub NP, 25°17' S, 151° 55' E, 28.X.1999, D.

Bickel. **Victoria:** Goonmirk Rd, nr Delegate River, 960 m, 16.I.1991, on trunk *E. nitens*, D.J. Bickel; Otway NP, Blanket Bay, 5.XII.1994, D. Bickel [all locales represented by males and deposited (AMS) unless otherwise noted].

Diagnosis. Male. Body length 1.8 mm; wing 1.6 x 0.5 mm.

Head. Vertex, frons, face, clypeus black with grey pruinosity; antennae black.

Thorax. Grey-black with metallic bronze reflections over ac band; with grey pruinosity; setae mostly dark brown

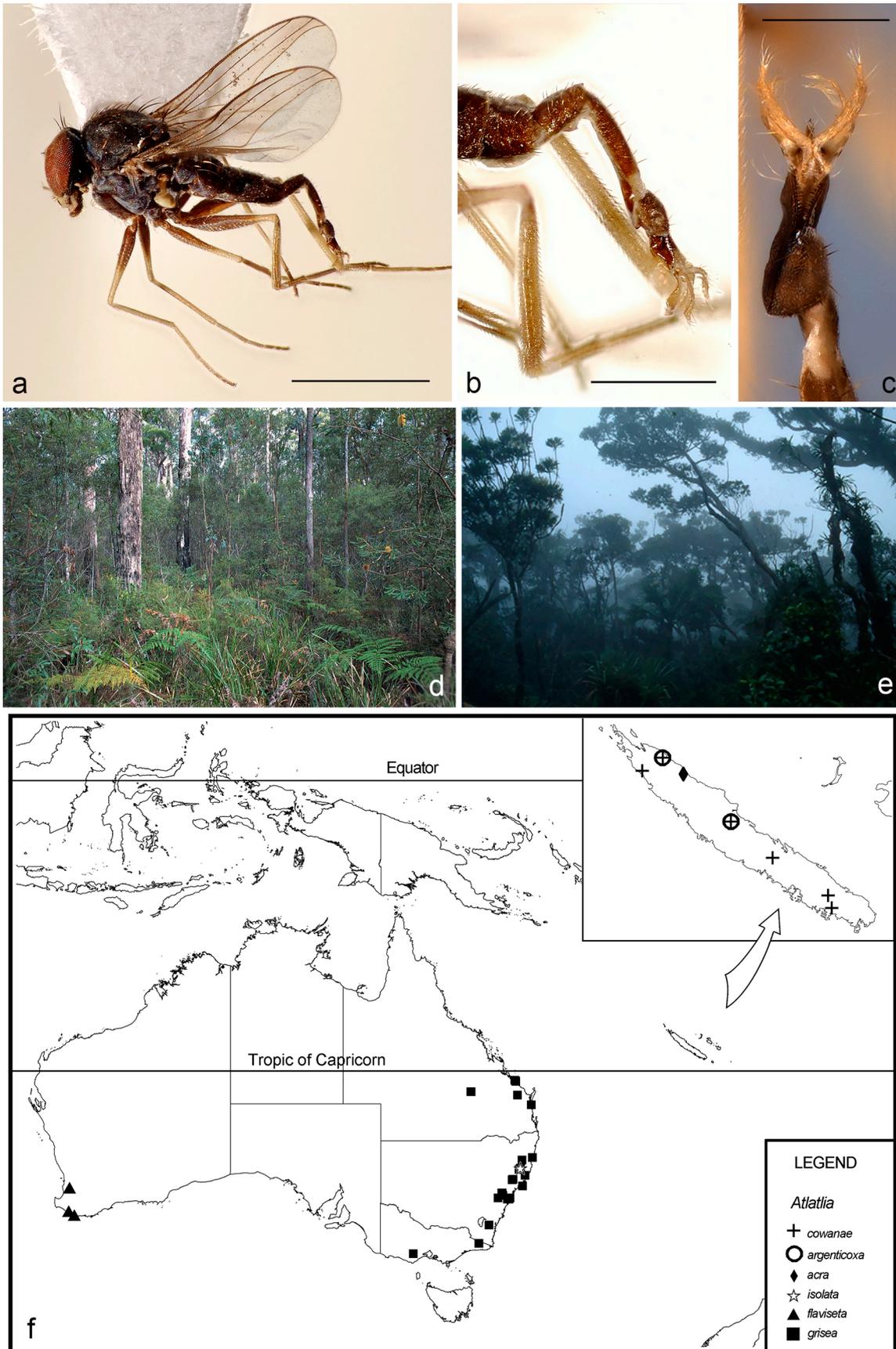


Figure 2. *Atlatia isolata* Bickel, sp. nov.: a, male habitus, left lateral; b, male postabdomen, left lateral; c, hypopygium, dorsal view. d, Werrikimbe NP, New South Wales, wet sclerophyll *Eucalyptus* forest, 950 m, habitat of both *A. grisea* and *A. isolata* (photo, P. German). e, Mt Panié, New Caledonia, *Agathis montana* forest, 1320 m, habitat of *A. acra*. f, Map of Australian and New Caledonian *Atlatia* spp. Scale bars: a, 1.0 mm; b, 0.5 mm; c, 0.2 mm.

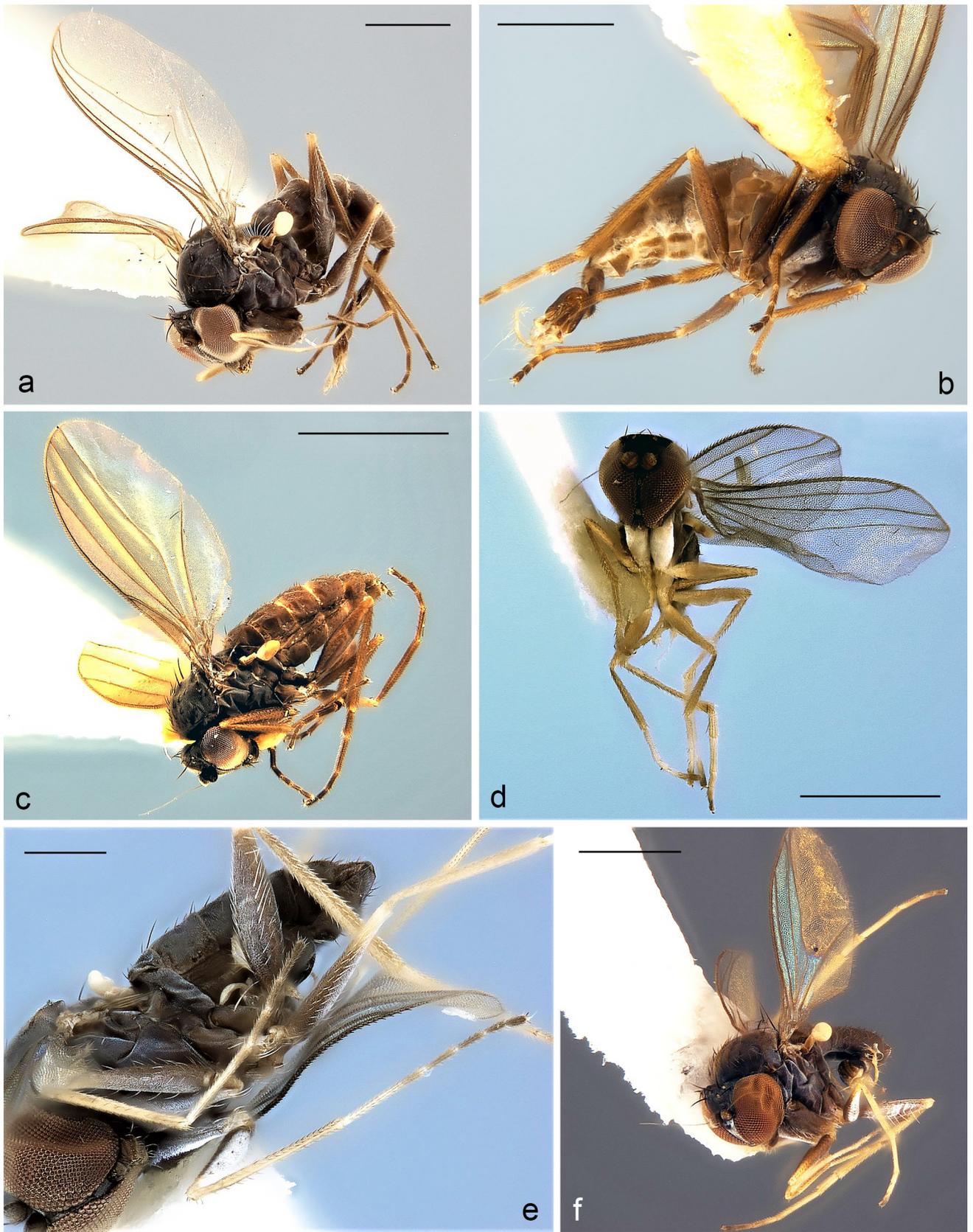


Figure 3. *Atlalia grisea* Bickel: a, male habitus, left lateral. *A. acra* Bickel, sp. nov.: b, male habitus, right ventral; c, female habitus, left lateral. *A. argenticoxa* Bickel, sp. nov.: d, male head and legs, anterior. *A. cowanae* Bickel, sp. nov.: e, male body and legs, left ventral; f, left anterior habitus. Scale bars: a, b, d, f = 0.5 mm; c = 1.0 mm; e = 0.2mm.

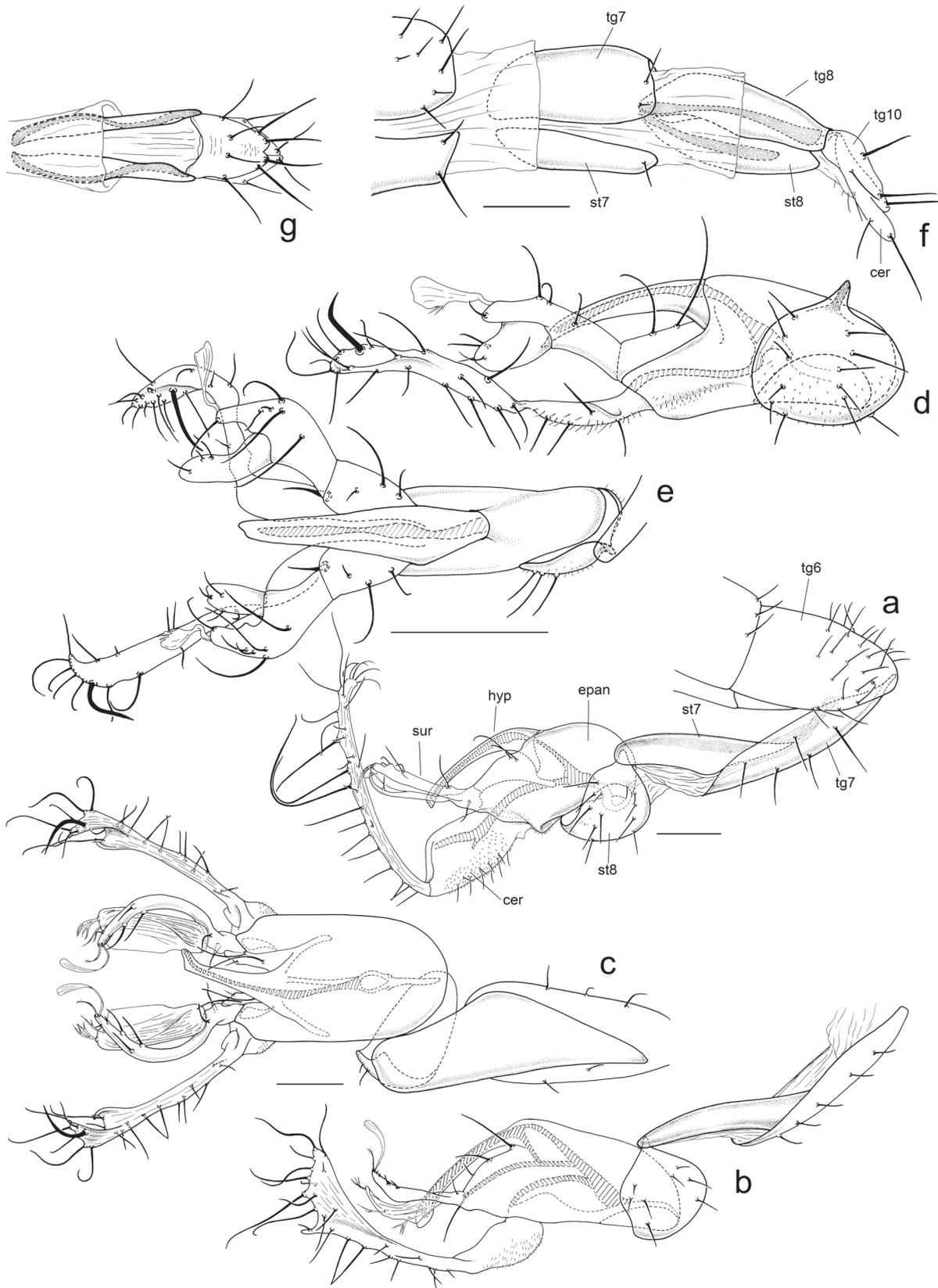


Figure 4. *Atlalia acra* Bickel, sp. nov.: a, hypopygium and peduncle, left lateral. *A. cowanae* Bickel, sp. nov.: b, hypopygium and peduncle, left lateral. c, hypopygium and peduncle, ventral. *A. argenticoxa* Bickel, sp. nov.: d, hypopygium, left lateral; e, hypopygium, ventral. *A. grisea* Bickel: f, female postabdomen, left lateral; g, female oviscapt, dorsal. Legend: cer, cercus; epan, epandrium; hyp, hypandrium; st7, st8, sternites 7, 8; sur, surstylus; tg6, tg7, tg8, tg10, tergites 6, 7, 8, 10. Scale bars: a, c, e, f = 0.1 mm.

although pa and posterior dc whitish; only 1 npl present on the ventral margin of notopleuron.

Legs: Coxae, femora mostly grey-black; distalmost femora yellow; tibiae, tarsi dark brown to black, although tibia I may appear yellowish; coxae I, II with yellowish anterior hairs, femora I, II, III basally swollen and tapering distally (MSSC).

Wings (Fig. 1c). Hyaline; vein M1 basally parallel with M4 but turning anteriorly to converge toward R₄₊₅ and then diverging subapically and turning posteriorly to end near wing apex (MSSC); lower calypter brown with fan of brown setae; halter stalk brown, club yellowish.

Abdomen. Grey-black with grey pruinosity; setae black; segment 7 (hypopygial peduncle) comprising mostly tergite, leaving only incurved ventral strip representing sternite, and bearing lateral setae; distal peduncle dorsally excavated on distal third (Fig. 1a–b); hypopygium elongate, subrectangular; hypopygial foramen left dorso-lateral, covered by a cap-like sternite 8; hypandrium fused to epandrium, immovable; aedeagus simple; epandrial seta near base of hypandrium; two epandrial lobe setae without peduncular bases but rest on epandrial surface; surstylus as elongate arm, ventral surface with two expanded fan-like setae; cercus arm-like, expanded basally, and projecting arc-like laterally and distally, and bearing 3 distal blade-like setae, visible in ventral view (Fig. 1b).

Female. Similar to male except where noted: face wider; femora not swollen; wing (Fig. 1d) wing vein M₁ gradually converging towards R₄₊₅, but two veins diverging slightly in distal fifth, and vein M₁ not strongly curved posteriorly; abdominal segment 8 with sclerotised internal supports (Fig. 4f–g); tergites 9+10 fused (not divided medially into hemitergites), with 4 apical setae, pair of strong lateral setae near base, and pair of strong medians; oviscapt ventrally deflexed in specimens.

Remarks. *Atlaltia grisea* occurs along the eastern Australian coast and ranges (Fig. 2f), south of the Tropic of Capricorn in Queensland to southern Victoria. During the warm and humid months of spring and early summer (October to January) in eastern New South Wales, adults are common on the tree trunks of large smooth-barked *Eucalyptus* and *Angophora* species, in both wet and dry sclerophyll forest habitats (e.g., Fig. 1d).

This species has the longest hypopygial peduncle (abdominal segment 7) of any *Atlaltia* species (and possibly all Diptera), approximately two-thirds the abdominal length, with tergite and sternite 7 almost completely fused to form a continuous rod (Fig. 1a). In other *Atlaltia* species, tergite and sternite 7 are prolonged but not as fused (e.g., Fig. 4a–b).

Atlaltia flaviseta Bickel, 1986

Figs 1e, 2f

Atlaltia flaviseta Bickel, 1986: 169.

Type material. This species was described from a single male collected near Pemberton, Western Australia (ANIC, holotype 29-020658).

Additional material. Australia: **Western Australia:** 2 ♂,

♀, Broke Inlet Rd, WNW of Walpole, 34° 59' S, 116° 35' E, 9–10.XI.1991, on trunk *Eucalyptus diversicolor*; 3 ♂, 3 ♀, Marradong Rd, 15km SE of Dwellingup, 32° 47' S, 116° 12' E, 31.X.1991, on trunk *E. wandoo*; 6 ♂, 4 ♀, Gardner River & Chesapeake Rd, 34° 39' S, 116° 7' E, 10.XI.1991, on trunk *E. diversicolor* (all collected by D. J. Bickel, AMS).

Diagnosis. Male. Body length 1.6 mm; wing 1.6 x 0.5 mm.

Head. Antennae dark brown.

Thorax: Grey-black with metallic bronze reflections over ac band, and with grey pruinosity; setae yellowish; two notopleural setae present.

Legs. All femora with basal two-thirds to three-quarters black with grey pruinosity, and distally yellow; all tibiae and basal tarsomeres yellow, and distal tarsomeres infuscated; all femora basally swollen, but not as strongly as in *A. grisea*.

Wings. Hyaline; M₁ basally parallel with M₄, but with gentle bend, to become subparallel with R₄₊₅ along its length and veins slightly diverge before wing apex (MSSC); lower calypter brown with fan of brown setae; halter stalk brown, club yellowish.

Abdomen. Grey-black with grey pruinosity; setae black; segment 7 (hypopygial peduncle) comprising an elongate tergite 7 with short setae, and shorter distal sternite, and tergite and sternite not fused (Fig. 1e); hypopygium subrectangular; hypopygial foramen left dorso-lateral, covered by a elongate cap-like sternite 8; surstylus broad, subrectangular, and ventral surface with curved blade-like seta, and with apical group of setae; cercus strongly curved L-shaped at base, and broad with some lateral setae and group of stronger apical blade-like setae.

Female. Similar to male except where noted: face wider; femora not swollen; vein M₁ with gentle bend (similar to Fig. 1f).

Remarks. *Atlaltia flaviseta* is known from the wet sclerophyll eucalypt forests of southwestern Western Australia, where it has been collected between October to December. It can be readily distinguished from the eastern Australian *A. grisea* and *A. isolata*, by the strong elbowed curve of the cercus (Fig. 1e) and the yellowish thoracic setae.

Atlaltia isolata Bickel, sp. nov.

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Fig. 2a–c, f

Type material: Holotype ♂, Australia: **New South Wales:** Werrikimbe NP, 31° 11' 56" S, 152° 10' 23" E, 1025 m, 1–7. XII.1997, sticky trap on trunk of *Eucalyptus campanulata*, E. Tasker & P. German (AMS, Holotype K.267849).

Description. Male. Body length 1.9 mm; wing 1.8 x 0.6 mm (Fig. 2a).

Head. Postcranium concave; single row of short postoculars, black dorsally and white ventrally, with dorsalmost postocular stronger than others; pair diverging ocellar setae; pair strong slightly converging verticals; vertex, frons, face, clypeus dark brown with grey pruinosity; face and clypeus narrow; fronto-clypeal suture complete; palp and proboscis brownish; palp with strong apical seta; antenna black; scape and pedicel short; postpedicel subrectangular; arista apical, about as long as head height.

Thorax. Dark metallic green-black; setae dark brown; posterior third of mesonotum flattened; somewhat oblong; ac short, 6 regular pairs to mesonotal depression; 6 dc, with posterior two bordering mesonotal depression stronger; 1 pa; 2 sa; 2 sr; 1 hm; 1 strong pm; only 1 npl present on the ventral margin of notopleuron; lateral scutellar seta about one quarter length of median scutellar seta.

Legs. Coxae, trochanters, FI to $\frac{1}{2}$, FII to $\frac{3}{4}$ and FIII to $\frac{4}{5}$ dark brown; distal femora, tibiae, and tarsi yellow, although distal tarsomeres slightly infuscated; CI with short lateral setae; CII with whitish anterior hairs; CIII with white lateral seta near $\frac{1}{2}$; I: 2.8; 2.3; 1.3/ 0.6/ 0.3/ 0.2/ 0.2; II: 2.3; 2.4; 1.4/ 0.6/ 0.4/ 0.2/ 0.3; III: 3.4; 3.7; 0.7/ 1.2/ 0.6/ 0.3/ 0.2; FII distinctly shorter than FI; FI & FII only slightly swollen, FIII swollen basally.

Wings. R_1 terminating in basal third of costa; R_{2+3} and R_{4+5} diverging slightly towards apex; M_1 basally parallel with M_4 , and with gentle bend to become closely subparallel with R_{4+5} and bending subapically slightly to join margin anteriorly of wing apex; crossvein dm-m absent; anal cell distinct, anal vein ending before wing margin; anal angle moderately developed; lower calypter white with fan of white setae; halter yellow.

Abdomen. Mostly dark brown with some grey pruinosity and with brownish vestiture; tergite 1 with row of long setae along posterior margin (Fig. 2b–c); segment 7 forming elongate peduncle for hypopygium, about twice length of epandrium; tergite 7 elongate with short setae and overlapping sternite 7 but not fused to it, distal peduncle somewhat membranous dorsally; epandrium elongate, subrectangular; hypopygial foramen left dorso-lateral, covered by a cap-like sternite 8; epandrial lobe setae without peduncular bases; surstylus expanded, spatulate with curved apical seta; cercus curved, lyriform (Fig. 2c) with abundant dorsal and apical setae.

Female. Unknown.

Remarks. *Atlatlia isolata* is described from a single male collected on a tree trunk sticky trap at 1025 m in montane wet sclerophyll forests in Werrikimbe National Park on the New South Wales northern tablelands (Fig. 2d). It can be separated from the sympatrically occurring *A. grisea* by the weak apical bend in vein M_1 , the only slightly swollen male femora I and II, and details of the hypopygial appendages. Also, *A. isolata* has a relatively short hypopygial peduncle (abdominal segment 7) in which sternite and tergite 7 are not strongly fused (Fig. 2b), a condition more like that of the three New Caledonian species (e.g., Fig. 4a–b) than that found in the sympatrically occurring *A. grisea*.

Etymology. The specific epithet *isolata* is from Latin and refers to the species being represented by a single specimen, by contrast with its common sympatric species, *Atlatlia grisea*.

b. Recent New Caledonian species

The New Caledonian *Atlatlia* species were collected entirely in Malaise traps stationed around Grande Terre (Fig. 2f). The three species appear to be a monophyletic assemblage within the *grisea* group, with the following characteristics: i) Males (sometimes females) have orientated silvery body pruinosity at least on the coxa I (Fig. 3b–f); ii) Vein M_1 has a very gentle bend (Fig. 1f), unlike the stronger distinct bend

found in some Australian species (Fig. 1c–d); iii) Tergite and sternite 7 are more freely articulated with each other (Fig. 4a) than in Australian species of the *grisea* group (Fig. 1a).

Atlatlia acra Bickel, sp. nov.

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Figs 1f, 2f, 3b–c, 4a

Type material: New Caledonia: **Province Nord:** Holotype ♂, paratypes 3 ♂, Mt Panié summit, 1628 m, Malaise trap, 5–16.XII.1990, Mission Panié, ORSTOM (MNHN; 2 ♂ paratypes AMS); paratypes ♂, 2 ♀, Mt Panié, east face, 1470 m, 5–16.XII.1990, Malaise trap (MNHN). Holotype registration number unavailable.

Description. Male. Body length 1.6 mm; wing 1.5 x 0.5 mm.

Head. Postcranium concave; single row of short postoculars, black dorsally and white ventrally, with dorsal-most seta stronger than others; pair diverging ocellars; pair strong slightly converging verticals; vertex, frons, face, clypeus black with grey pruinosity; face and clypeus narrow; clypeus conformable with eye; fronto-clypeal suture complete; palp and proboscis brownish; eye facets slightly enlarged anteroventrally; antenna black; scape and pedicel short: postpedicel subrectangular; arista apical, slightly shorter than head height.

Thorax. Dark metallic brown-black; setae black; posterior third of mesonotum flattened; ac short, 5 pairs to mesonotal depression; 6 dc, with posterior two bordering mesonotal depression stronger; 1 pa; 2 sa; 2 sr; 1 hm; 1 pm; 2 npl; lateral scutellar seta weak, about one-quarter length of median seta; 2 ppl anteriorly of anterior spiracle.

Legs. Coxae, trochanters, and femora brown, but with apices of femora yellowish; tibiae and tarsi brownish, with distal tarsomeres slightly infuscated; CI and CII with short brownish setae; CIII with brownish lateral seta; CI covered with orientated silvery pruinosity (MSSC); femora not swollen; I: 2.2; 1.8; 0.9/ 0.4/ 0.3/ 0.2/ 0.2; FI with some short pv setae along distal half; II: 2.0; 2.1; 1.0/ 0.4/ 0.3/ 0.2/ 0.2; FII distinctly shorter than FI; III: 2.4; 2.9; 0.6/ 1.1/ 0.4/ 0.3/ 0.2.

Wings (Fig. 1f). R_1 terminating in basal third of costa; R_{2+3} and R_{4+5} diverging slightly towards apex; M_1 basally parallel with M_4 , and with gentle bend to become subparallel with R_{4+5} , to end just anteriorly of wing apex; crossvein dm-m absent; anal cell distinct, anal vein ending before wing margin; anal angle moderately developed; lower calypter white with fan of white setae; halter yellow.

Abdomen. Dark brown with some brown vestiture; tergite 1 with row of long setae along posterior margin; segment 7 forming elongate rod-like peduncle for hypopygium, about twice length of epandrium: tergite 7 elongate with short setae and overlapping sternite 7 but not fused to it, distal peduncle somewhat membranous dorsally; epandrium elongate, subrectangular; hypopygial foramen left dorso-lateral, covered by a cap-like sternite 8 (Fig. 4a); surstylus as elongate narrow arm, deeply cleft apically, with various normal setae and thickened apical seta as shown; cercus with large subrectangular base, and with geniculate bend from which elongate narrow arm (almost as long as epandrium + surstylus) arises in right angle to base, and with setae along

length, and with three very long dorsal setae near 2/3.

Female. Similar to male except where noted: face wider; coxa I brown, without silvery pruinosity; wing vein M_1 gradually converging towards R_{4+5} .

Remarks. *Atlatlia acra* is known from Malaise traps set at 1470 m and 1628 m near the summit of Mt Panié, New Caledonia. The trap at 1470 m. was in *Agathis montana* forest (Fig. 2e). The coxae are mostly brown, but in males, coxa I is covered with orientated silvery pruinosity. The elongate distal arm of the cercus is diagnostic.

Etymology. The specific epithet *acra* is from Greek, *akron*, meaning peak or summit, and refers to the collection of this species near the summit of Mt Panié, New Caledonia's highest mountain.

Atlatlia argenticoxa Bickel, sp. nov.

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Figs 2f, 3d, 4d–e

Type material: Holotype ♂, paratypes 16 ♂, 17 ♂, New Caledonia: **Province Nord**, Réserve spéciale de faune de l'Aoupinié, 21.157° S 165.323° E, 550 m, Malaise trap, 12–30.XI.2000, E. I. Schlinger, M. E. Irwin & L. J. Boutin (holotype, 2 ♂, 2 ♀ paratypes deposited MNHN; 2 ♂, 2 ♀ paratypes deposited AMS, remainder of paratypes in INHS); paratypes ♂, ♀, same but 30.XI–4. XII.2000 (INHS). Holotype registration number unavailable.

Additional material. New Caledonia: **Province Nord**, 2 ♀, Mt Mandjélia, 5 km WSW of Puébo, 20.397° S 164.528° E, 780 m, 2–13.XI.2000, Malaise trap, E. I. Schlinger & M. E. Irwin (AMS).

Description. Male. Body length 1.3 mm; wing 1.1 x 0.4 mm; similar to *A. acra* except as noted:

Head. Facets distinctly enlarged over most of the eye, and only small anterodorsal area with facets of normal size; scape and pedicel yellowish, and postpedicel brown; postpedicel subrectangular; arista apical, slightly shorter than head height.

Thorax. Brown with some grey pruinosity; scutellum yellow; setae brownish, except two posterior dc and scutellar setae whitish.

Legs. Coxae and remainder of legs mostly yellow, with distal tarsomeres slightly infuscated; vestiture yellowish; CI and with short anterior setae; all coxae and trochanters are covered by orientated silvery pruinosity, visible in anterior view, and especially intense on CI; CII with some short anterior setae; CIII with lateral seta; leg bare of major setae; femora not swollen; I: 1.4; 1.2; 0.7/0.3/0.3/0.1/0.2; II: 1.4; 1.2; 0.8/0.3/0.2/0.1/0.1; III: 1.6; 1.9; 0.4/0.6/0.4/0.2/0.1.

Abdomen. Dark brown with some yellowish vestiture; tergite 1 without row of long setae but only short vestiture; segment 7 forming elongate rod-like peduncle for hypopygium, about twice length of epandrium: tergite 7 elongate with short setae and overlapping sternite 7 but not fused to it, distal peduncle somewhat excavated dorsally; epandrium elongate, subrectangular; hypopygial foramen left dorso-lateral, covered by a cap-like sternite 8; epandrial seta relatively long, near base of hypandrium, external; setae of epandrial lobes without peduncular bases; surstylus fused

to epandrium, with no evidence of suture; surstylus rather broad and bent near base, with broad spatulate modified apical seta; cercus also broad and appearing constricted near 2/5, elongate distally with strong curved subapical seta, and other setae as figured.

Female. Similar to male except as noted: face and clypeus wider; eyes facets similar size; all coxae, and femoral bases also with orientated silvery pruinosity, especially visible in anterior view, and particularly intense on CI.

Remarks. *Atlatlia argenticoxa* is known from Malaise trap samples taken in November and December near Mt Aoupinié and Mt Mandjélia, Province Nord, New Caledonia. This species is quite small (male wing length 1.1 mm) and is distinguished in both sexes by the legs being entirely pale yellow, the scutellum yellow, and all coxae and trochanters are covered by orientated silvery pruinosity, especially visible in anterior view. The lateral scutellar setae are absent or represented only by tiny hairs, but the median scutellar setae are strong.

Etymology. The specific epithet *argenticoxa* is from Latin and refers to the oriented silvery pruinosity on the coxae of both sexes.

Atlatlia cowanae Bickel, sp. nov.

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Figs 1f, 2f, 3e–f, 4b–c

Type material. Holotype ♂, paratypes 3 ♂, 3 ♀, New Caledonia: **Province Nord**: Réserve spéciale de faune de l'Aoupinié, 21.157° S 165.323° E, 550 m, Malaise trap, 30.XI–4.XII.2000, M. E. Irwin & L. J. Boutin (holotype, paratypes ♂ and ♀ deposited MNHN); paratypes, 3 ♂, same but 30.XI–4.XII.2000 (INHS). Holotype registration number unavailable.

Additional material. New Caledonia: **Province Nord**: 4 ♂, E of Koumac, 20.553° S 164.291° E, 2–13.XI.2000, Malaise trap, D. W. Webb, E. I. Schlinger & M. E. Irwin (INHS); 12 ♂, ♀, Mt Mandjélia, 5 km WSW of Puébo, 20.397° S 164.528° E, 780 m, 2–13.XI.2000, 27.XI–8.XII.2000, Malaise trap, E. I. Schlinger & M. E. Irwin (INHS). **Province Sud**: 4 ♂, 2 ♀, Col d'Amieu, 7.5 km NW of Sarraméa, 303 m, 21.585° S 165.819° E, Malaisie trap, 9–14.XI.2000, 7–20. XII.2000, E. I. Schlinger & M. Irwin (INHS); 8 ♂, 7 ♀, Mt Koghis, 17 km NNE Noumea, 550 m, Malaise trap, 22.176° S 166.505° E, 13–16.XII.2000, M. Irwin & D. Webb (INHS); 3 ♂, Mt Ouin, 20 km from base of road to Mt Dzumac, 22.167° S, 166.428° E, 860 m; 2–11.XII.2000, Malaise trap, M. Irwin, E. I. Schlinger, & D. Webb; 10 ♂, 6 ♀, Vallée de Ni, 21° 59.591' S, 166° 30.172' E, 770 m, 18–23.XI.1998, Malaise trap, M. Irwin & D. Webb (deposited INHS, AMS, BPBM).

Description. Male. Body length 1.5–1.6 mm; wing 1.5 x 0.5 mm; similar to *A. acra* except as noted:

Head. Face and clypeus narrow, covered with grey/silvery pruinosity; clypeus conformable with eye, not projecting anteriorly; fronto-clypeal suture complete; anteroventral eye facets distinctly enlarged; palp and proboscis brownish; palp with apical seta; antenna dark brown; scape and pedicel short: postpedicel subrectangular; arista apical, slightly shorter than head height.

Thorax. Dark brown-black; setae black with brownish reflection; posterior third of mesonotum flattened; somewhat oblong.

Legs. Coxae mostly dark brown, but CI yellowish apically; trochanters also brownish; femora mostly dark brown, but distal third of FI and FII, and the distal eighth of FIII yellow; tibiae and tarsi yellow with distal tarsomeres slightly infuscated; CI with CII with short anterior whitish setae; CIII with white lateral seta; CI covered with bright silvery orientated pruinosity, visible in anterior view, also distal anterior CII, and anterior surfaces of all three femora also with silvery pruinosity (MSSC); femora not strongly swollen basally, but gradually tapering to apex; I: 2.7; 1.7; 1.2/ 0.6/ 0.4/ 0.3/ 0.2; II: 1.8; 1.7; 1.0/ 0.4/ 0.3/ 0.2/ 0.2; III: 2.3; 2.5; 0.7/ 1.0/ 0.6/ 0.4/ 0.3; FIII with 4-5 short white setae on anterior surface along distal two thirds (MSSC); III_{t2} distinctly longer than III_{t1}.

Abdomen. Dark brown with some yellowish vestiture; tergite 1 without row of long setae but only short vestiture; segment 7 forming elongate rod-like peduncle for hypopygium, epandrium: tergite 7 elongate with short setae and overlapping sternite 7 but sternite and tergite not fused; epandrium elongate, subrectangular; hypopygial foramen left dorsobasal and covered by a cap-like sternite 8 (Fig. 4b–c); hypandrium fused to epandrium, immovable; aedeagus simple; epandrial seta relatively long, near base of hypandrium; setae of epandrial lobes without peduncular bases; surstylus ventrally with narrow curved arm with distinctive elongate spatulate seta, and subtended dorsally by broad subrectangular projection (visible in Fig. 4c) which bear apical forked setae; cercus slightly thickened basally and with narrow arm and expanded apically into subrectangular crest and with setae as figured.

Female. Unknown.

Remarks. *Atlatlia cowanae* is the most widespread of the three New Caledonian species, known from locales throughout Grande Terre, at altitudes from 300–860 m. It is sympatric with *A. argenticoxa* at the type locale of both species, Mt Aoupinié. Male *A. cowanae* have striking orientated silvery pruinosity on the coxa and femora of all legs and it has a relatively short hypopygial peduncle.

Etymology. This species is named in honour of Sally Cowan, who assisted in the preparation and curation of the New Caledonian material from the Schlinger collections.

c. Paleogene species

Three species of the *Atlatlia grisea* group are known from Baltic amber and one of these also occurs in Bitterfeld amber. In addition to the three species treated below, a small-sized female *Atlatlia* sp., body length 0.8 mm and wing 1.0 x 0.5 mm (CCHH 1740/8), with vein dm-m absent, and vein M₁ curved, may represent an additional species.

Atlatlia electrica Bickel, sp. nov.

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Fig. 5a–d

Type material. Amber inclusions from the Baltic Region: Holotype ♂ (Coll. H. Ulrich, ZFMK; BAM-553); paratypes:

♂ (Coll. H. Ulrich, ZFMK, BAM-016); ♂ (BMNH, P.I. II554, BAM-253); paratypes [5 ♂] (Coll. C. Gröhn, #9539, BAM-293); paratype ♂ (Coll. Hoffeins, CCHH, 1454/9, BAM-341).

Other material. Amber inclusions from the Baltic Region: ♂ (Coll. Hoffeins, CCHH 1723/3); ♂ (Coll. Eichmann, #288). Amber inclusions from the Bitterfeld Region: [2 ♂ + *Medetera* sp.], (Krümmer Coll, # 5075, BAM-534).

Description. Male. Body length 1.6–1.7 mm; wing 1.4–1.5 x 0.5 mm (Fig. 5a–c).

Head. Head wider than high; postcranium concave; major setae black; single row of short postoculars; pair diverging ocellars; pair strong slightly converging verticals; vertex, frons, face, clypeus black with grey pruinosity; face and clypeus narrowed but distinctly separating eyes; clypeus conformable with eye, not projecting anteriorly; palp and proboscis brownish; palp with apical seta; eye facets more or less uniform; antenna black; scape and pedicel short; postpedicel subrectangular; arista apical, about as long as head height.

Thorax. Metallic dark brown; setae black; posterior third of mesonotum flattened; somewhat oblong; ac short, 9-10 regular pairs to mesonotal depression; 7-8 short dc, gradually increasing in size posteriorly, with two posteriormost (bordering mesonotal depression) stronger; 1 (pa, 2 sa, 2 sr; 1 hm; 1 strong pm; 2 npl, seta near ventral margin of notopleuron, and near middle of notopleuron; lateral scutellar seta about half length of median scutellar seta; short proepisternal seta present, anterior of anterior spiracle.

Legs. Coxae, trochanters and femora black to about 3/5; distal femora, tibiae, and tarsi yellow; setae and vestiture yellowish; CI and CII with short anterior hairs, CIII with strong lateral seta; legs without major setae, only short vestiture; I: 2.6; 2.5; 0.7/ 0.4/0.3/0.2/0.2; FI swollen in basal half, with distal half narrow (MSSC); II: 2.1; 2.0; 1.2/0.4/0.3/0.2/0.2; FII distinctly swollen in basal half, with distal half narrow and spindly (MSSC) III: 2.3; 2.6; 0.6/0.9/0.4/0.3/0.3; FIII slightly swollen basally and gradually tapering to apex; FIII with short av setae along distal two-thirds; in distal half; femora II, III tapering distally.

Wing. Hyaline; R₁ terminating in basal third of costa; R₂₊₃ and R₄₊₅ diverging slightly towards apex; M₁ basally diverging from R₄₊₅, then making elbowed bend and converging toward R₄₊₅, but near wing apex curving posteriorly to end in costa before wing apex; crossvein dm-m totally absent; M₄ extending to posterior wing margin; anal vein not reaching margin; halter yellow.

Abdomen. Tergites black and covered with short black vestiture; segment 7 forming elongate rod-like hypopygial peduncle, about as long as preceding two tergites, and comprising basal tergite overlapped by distal sternite; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium subrectangular; hypandrium elongate and projecting beyond epandrium; distal epandrium narrowing to form dorsal projection, from which arises strongly recurved U-shaped surstylus; cercus elongate and narrow, extending well beyond epandrium, distally curved into gentle right angle, and slightly expanded apically with some short modified setae.

Female. (Fig. 1d) Similar to male except where noted: face wider; femora not swollen; wing vein M₁ gradually



Figure 5. *Atlalia electrica* Bickel, sp. nov.: a, male, right lateral (BAM-253; BMNH); b, male head, thorax, and postabdomen, left lateral (BAM-293; Gröhn); c, male habitus, left lateral, Bitterfeld amber (BAM-534; Krummer); d, female, left lateral (BAM-050; MZPW). Scale bars: a = 1 mm; b = 0.2 mm; c = 0.5 mm; d = 1 mm.

converging towards R_{4+5} , but two veins diverging only slightly in distal fifth, and vein M_1 not curved posteriorly; fused segments 9+10 ventrally deflexed.

Remarks. *Atlalia electrica* is known from both Baltic and Bitterfeld amber (Fig. 5c). It displays a striking similarity to the recent Australian species *A. grisea* (cf. Fig. 5a with Fig. 3a). Although the surstylus of *A. electrica* is recurved, as in another Baltic amber species *A. licina*, it has a rather elongate curved cercus, unlike the sharply upturned cercus in *A. licina*. Stellate hairs have been found in the Baltic amber inclusions.

Etymology. The specific epithet *electrica* is derived from Latin name for amber, *electrum*.

Atlalia corynoura Bickel, sp. nov.

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Fig. 6a–d

Type material. Amber inclusions from the Baltic Region: [Holotype ♂ (figured in Fig. 6b–c), paratype ♂], (Coll. Hoffeins, CCHH #14541/5, to be deposited SDEI, BAM-342); paratype ♂, (#15614, MZPW).

Description. Male. Body length 1.6 mm; wing 1.5 x 0.5 mm (Fig. 6a–d); similar to *A. electrica* except as noted:

Legs. Coxae, trochanters and basal 3/5 of femora black; distal femora, tibiae, and tarsi yellow, with all tarsomere 5 brown; setae and vestiture yellowish; I: 2.3; 1.9; 0.9/ 0.5/ 0.3/ 0.2/ 0.3; FI only slightly swollen in basal half, with distal half narrower (MSSC); II: 2.1; 2.2; 0.1/ 0.4/ 0.3/ 0.2/ 0.2; FII distinctly swollen in basal half, with distal half narrow (MSSC) III: 2.6; 2.7; 0.5/ 1.0/ 0.4/ 0.3/ 0.3; FIII not swollen basally but gradually tapering to apex; FIII without short av setae.

Abdomen. Hypopygium dark brown with pale yellow surstylus and cercus; epandrium subrectangular; hypandrium elongate and projecting beyond epandrium; surstylus digitiform and angled ventrally toward apex of hypandrium; cercus elongate and narrow, extending well beyond epandrium, and apically incurved slightly (not bent at right angle) and with expanded subapical apex bearing long setae and thickened modified setae, and digitiform apex with long pale yellow external setae (Fig. 6c).

Female. Unknown.

Remarks. *Atlalia corynoura* is known from three males, and is close to *A. electrica*, the two species being readily separated by the respective diagnostic characteristics of the elongate cercus and the setation of its expanded apex.

Etymology. This specific epithet *corynoura* is from Greek, *koryne* for “club”, and *oura* for “tail”, a reference to the diagnostic apically clubbed cercus.

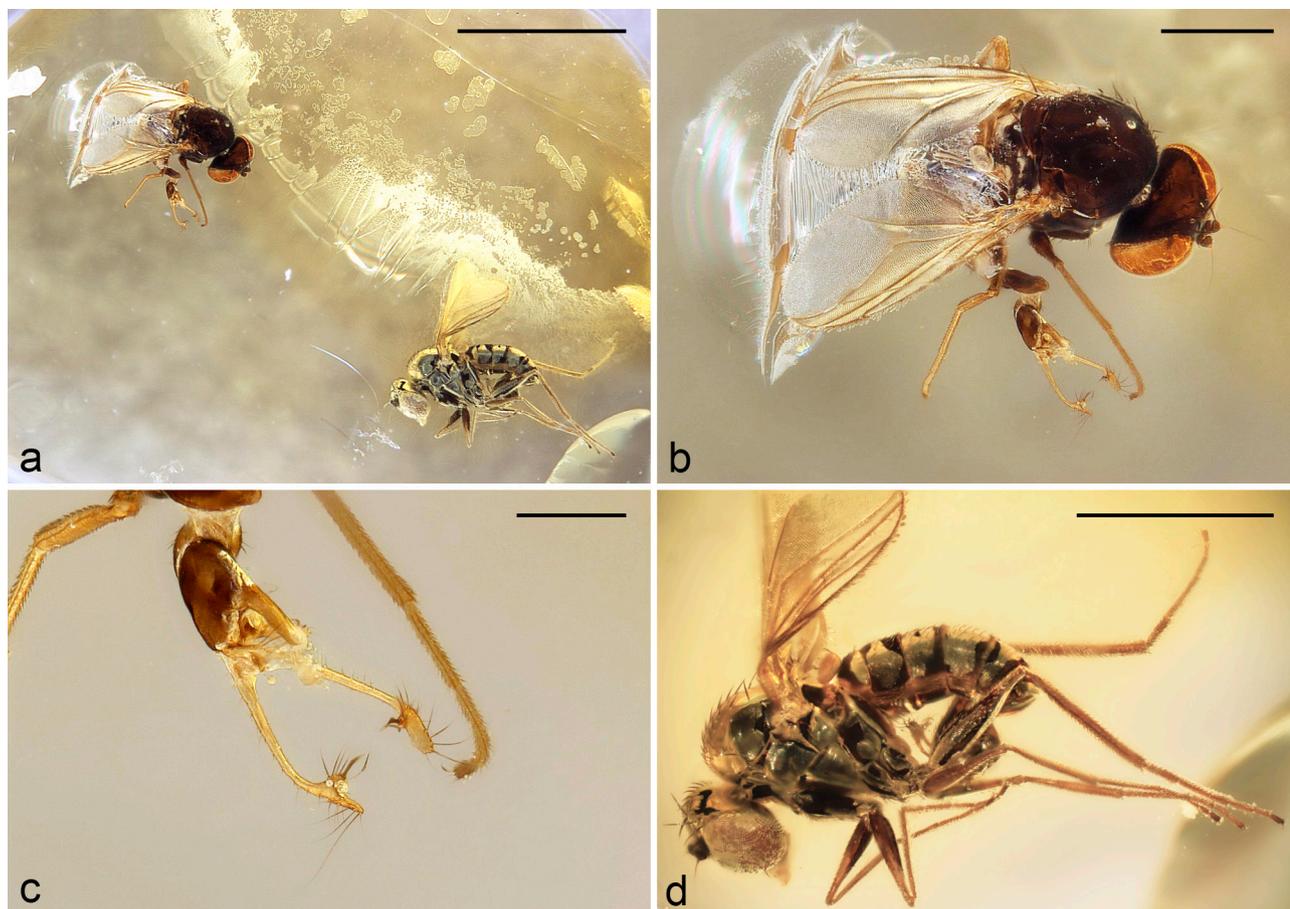


Figure 6. *Atlalia corynoura* Bickel, sp. nov.: a, two males, habitus; b, male habitus, right dorsolateral; c, male hypopygium, ventral view; d, male habitus, left lateral (BAM-342; CCHH) Scale bars: a = 2 mm, b = 0.5 mm; c = 0.2 mm; d = 1 mm.

***Atlaltia licina* Bickel, sp. nov.**

urn:lsid:zoobank.org:act:9FEF25BA-8BC1-49D6-AC52-4AF82A44699A

Fig. 7c–d

Type material. Amber inclusion from the Baltic Region: Holotype ♂ (Coll. Hoffeins, CCHH # 14541/1, deposited SDEI, BAM-340).

Additional material. Amber inclusion from the Baltic Region: ♂ (NCIR).

Description. Male. Body length 1.7 mm; wing: 1.4 x 0.6 mm (Fig. 7a–d); similar to *A. electrica* except as noted:

Legs. Coxae, trochanters, and femora to about 3/5 dark brown; distal femora, tibiae, and tarsi yellowish to yellow; setae and vestiture yellowish; CIII with strong lateral seta at 1/3; I: 1.8; 1.7; 0.8/0.3/0.3/0.2/0.2; FI swollen in basal half, with distal half narrowed (MSSC?); It₁ with 4–5 short erect ventral setulae (MSSC); II: 1.9; 1.6; 1.2/0.4/0.3/0.2/0.2; FII distinctly swollen in basal half, with distal half narrow and spindly (MSSC?); III: 2.3; 2.7; 0.6/0.9/0.4/0.3/0.3; FIII not swollen basally but gradually tapering to apex; FIII with very short apical ventral short apicoventral seta.

Abdomen. Tergites dark brown and covered with short brownish vestiture, segment 7 forming elongate rod-like hypopygial peduncle, about as long as preceding two tergites, and comprising basal tergite overlapped by distal sternite; sternite 8 ovate and covering left lateral hypopygial foramen;

(Fig. 7d) epandrium subtriangular and distally excavated; hypandrium elongate and projecting well beyond epandrium; surstylus elongate and recurved back onto epandrium, with some curved subapical setae; cercus elongate and bent at right angle near base to parallel bent surstylus, and with strong curved yellow seta at 2/3, and projecting well beyond hypandrium.

Female. Unknown.

Remarks. *Atlaltia licina* is known from a single male. Both the cercus and surstylus are basally bent at a right angle, with the cercus projecting well beyond the hypandrium, diagnostic characters for this species. Hoffeins and Hoffeins (2003, fig. 8) were the first to record *Atlaltia* in Baltic amber (identified by Hans Ulrich) and included a habitus photo of what is now the holotype of *A. licina*.

Etymology. The specific epithet is from Latin *licinus*, “bent” or “turned upwards”, in reference to the strong bend of both the cercus and surstylus.

II. Paleogene *Atlaltia ulrichi* group

The *Atlaltia ulrichi* group, by contrast with the *grisea* group, is characterised by a short hypopygial peduncle comprising a subrectangular tergite and sternite 7, and the peduncle is often concealed under tergite 6. Also, the epandrium of all included species is basally spheroidal in structure (Figs 7a–b, 8–10). The cercus of the *ulrichi* group, like that of the *grisea*

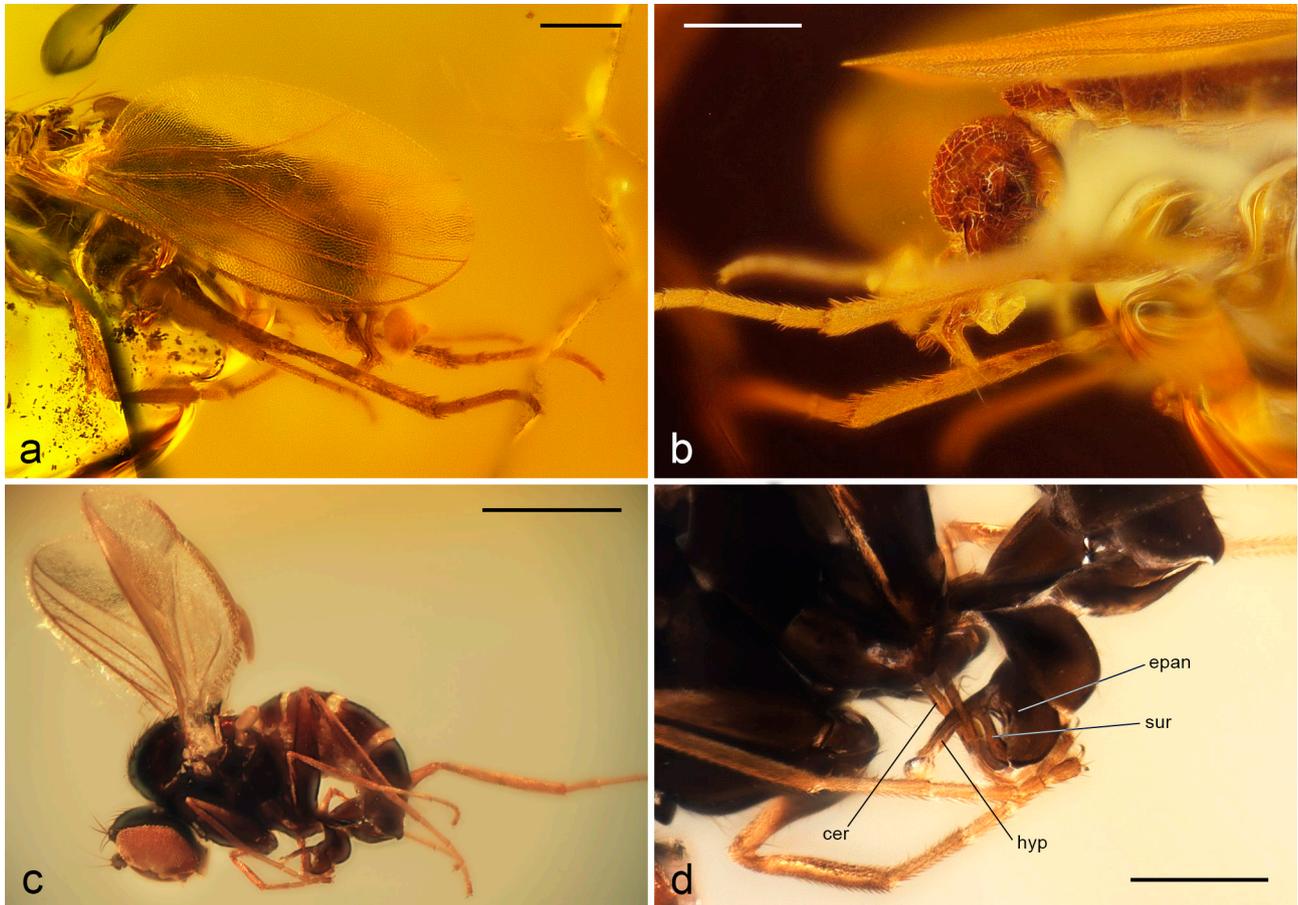


Figure 7. *Atlaltia angulicauda* Bickel, sp. nov.: a, male posterior body, left lateral; b, male genitalia, right lateral (BAM-452, CCHH). *A. licina* Bickel sp. nov.: c, male habitus, left lateral; d, male postabdomen, left lateral (BAM-340, CCHH). Legend: cer, cercus; epan, epandrium; hyp, hypandrium; sur, surstylus. Scale bars: a, b, d = 0.2 mm; c = 0.5 mm.

group is often bowed with modified setae. In comparison with the *grisea* group, the legs of the *ulrichi* group species appear relatively short, the male femora are never basally swollen, and vein M_1 has only a rather weak anterior bend beyond its divergence from vein M_4 .

Although the *Atlantia ulrichi* group is plesiomorphic with respect to the *grisea* group in having a short hypopygial peduncle, the rather swollen bulbous epandrium (Figs 8f, 9a, e, and 10c) of most species could be considered a synapomorphy for the group.

Atlantia ulrichi Bickel, sp. nov.

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Fig. 8a–g

Type material. Amber inclusions from the Baltic Region: Holotype ♂ (Coll. H. Ulrich, ZFMK; BAM-364); paratypes: ♂, (Coll. H. Ulrich, BAM-023; ZFMK); [♂ + ♂ *Argyra incyltus* (Meunier)] (CCHH, #1746, BAM-476); [8 ♂, 2 ♀, and ♂ *Medetera mustela* Meunier] (CCHH #1626/1, BAM 344); [2 ♂] (CCHH, #1022/1, BAM-363); 4 ♂, [2 ♂] (CCHH, 1802/7 #1022/1, #1746/8, #1729/5, BAM450); ♂, (NCIR); 3 ♂ (ZMUC; BAM-467, BAM-479), 2 ♂ (AMNH); ♂ (SMNS, #BB-2018-W, BAM-012).

Additional material. Amber inclusions from the Baltic Region: ♂ (GPUG, #5452; ♂ (Coll. Gröhn, #151); 2 ♂, 8 ♀ (MZPW; ♀, BAM-050); ♂, 3 ♀ (NCIR); 7 ♂, 4 ♀ (ZMUC); 2 ♂ (Coll. H. Ulrich, ZFMK); (4 ♂ + ♀) (AMNH); ♂, (MAGP, #554); 4 ♂ (Coll. Kernegger). Amber inclusions from the Bitterfeld Region. 4 ♂ (Krümmer Coll, # 5031); ♂ (Kutscher Coll. GPUG, BST.28553).

Description. Male. Body length 1.3–1.4 mm; wing 1.1 x 0.3 mm.

Head. Postcranium concave; setae yellowish; pair diverging ocellars; pair strong slightly converging verticals; vertex, frons, face, clypeus dark brown; face and clypeus wide; clypeus conformable with eye, not projecting anteriorly; fronto-clypeal suture complete; palp and proboscis brownish; eye facets relatively large, and larger anteriorly and dorsally; antenna dark brown; scape and pedicel short: postpedicel rounded subrectangular; arista apical, about as long as head height.

Thorax: dark brown; posterior third of mesonotum flattened; somewhat oblong; setae yellow; ac present as 8–9 regular pairs short setae extending anteriorly of mesonotal depression distinctly stronger; 1 pa, 2 sa, 2 sr, 1 hm, 1 strong pm, and 2 npl; median scutellar seta strong, lateral seta present as weak hair.

Legs. Coxae dark brown with remainder of legs yellowish, although slightly infuscated in some specimens; vestiture yellow; legs without major setae; femora not swollen; I: 1.1; 1.0; 0.5/ 0.2 /0.2/ 0.2/0.2; II: 1.2; 1.1; 0.4; 0.3/ 0.2/ 0.2/ 0.2; III: 1.6; 1.5; 0.3/ 0.6/ 0.4/ 0.3/ 0.2; TIII apically swollen, with curved anteroventral apical spinelike seta (MSSC), visible when TIII flexed (Fig. 8d).

Wing: Hyaline; R_1 terminating in basal third of costa; R_{2+3} and R_{4+5} diverging towards apex; M_1 basally diverging from R_{4+5} but parallel with M_4 , then making gentle anterior bend to become subparallel with R_{4+5} , but not diverging near wing apex; crossvein dm-m totally absent; M_4 extending to

posterior wing margin; anal angle weakly developed; lower calypter yellow with fan of yellow setae; halter yellow.

Abdomen: Tergites dark brown and covered with short yellow vestiture, no strong setae evident; segment 7 not visible, but not exerted; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium swollen and spheroidal, but tapering somewhat apically; epandrial lobe with incurved seta evident on ventroapical surface; surstylus lobate with apical seta, and with median curved digitiform projection with apical seta; cercus elongate, narrow, and curved out from epandrium, with both cerci together forming lyriiform crescent projecting laterad of distal epandrium (Fig. 8b, f–g).

Female. Similar to male except where noted: face wider; TIII not distally enlarged and without apical seta; venation similar.

Remarks. *Atlantia ulrichi* is a small-sized species that is quite common in Baltic amber collections, and it is also known from Bitterfeld amber. Stellate hairs are found as inclusions in many pieces. Males of *A. ulrichi* are unusual in having tibia III apically swollen with a curved anteroventral apical spine (MSSC) (Fig. 8d), and a character not found on the other five species in the *ulrichi* group. One male (ZMUC) is distinctly smaller (wing length = 0.9 mm) but the hypopygium is similar to that of larger sized specimens, and it occurs together with a normal-sized female in the same inclusion.

Etymology. The species is named in honour of Hans Ulrich, who encouraged my (DJB) study of amber and provided both hospitality and access to his superb collection of Baltic amber Dolichopodidae, now housed at the Museum Alexander Koenig, Bonn. I had known Hans primarily through personal meetings at entomological congresses and occasional correspondence. He wrote to ask me if I was interested in working on his collection of Baltic amber Dolichopodidae that he had privately purchased over the years from a dealer in Kaliningrad. The material had been selected for clarity and comprised some 700 inclusions. So in many respects, this current paper had its genesis as the result of his support.

Atlantia angulicauda Bickel, sp. nov.

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Fig. 7a–b

Type material. Amber Inclusion from the Baltic Region: Holotype ♂ (Coll. Hoffeins, CCHH-1723/9, deposited SDEI; BAM-452).

Description. Male. Body length 1.4 mm; wing 1.3 x 0.5 mm; similar to *A. ulrichi* except as noted:

Legs. Coxae and femora dark brown with distalmost FI and FII yellow; tibiae and tarsi mostly yellow; vestiture yellow; coxal setation obscured; I: 1.6; 1.3; 0.5/ 0.3 /0.2/ 0.2/0.2; II: 1.6; 1.2; 0.6; 0.3/ 0.3/ 0.2/ 0.2; III: 1.8; 1.5; 0.3/ 0.4/ 0.3/ 0.2/ 0.2; TIII without curved apical spinelike seta.

Wing. M basally diverging from R_{4+5} but parallel with M_4 , then making gentle bend anteriorly to become subparallel with R_{4+5} , but the two veins diverging slightly before wing apex, with M_1 ending in costa anteriorly of wing apex; anal angle weakly developed; lower calypter not visible; halter yellow.



Figure 8. *Atlalia ulrichi* Bickel sp. nov.: a, habitus, right lateral; b, hypopygium (BAM-161, ZFMK); c, habitus, frontal (BAM-023; ZFMK); d, apical hooked seta on male tibia III; e, habitus, right lateral; f, hypopygium, right lateral (BAM-450; CCHH); g, hypopygium, ventral (BAM-479; ZMUC). Legend: cer, cercus; sur, surstylus; sur proj, surstylar projection. Scale bars: a, c, e = 0.5 mm; b, d, f, g = 0.2 mm.

Abdomen. Tergites dark brown and covered with short yellow vestiture, no strong setae evident; segment 7 not visible; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium (Fig. 7b) swollen and spheroidal, but tapering somewhat apically; epandrial lobe not visible; surstylus not entirely visible but short and digitiform with distal right angle bend, and bearing pale apical setae; cercus with narrow and curved distally in right angle bend (in parallel with bend of surstylus) and bearing an external tuft of short curved setae at the bend.

Female. Unknown.

Remarks. *Atlalia angulicauda* is known from a single male specimen. It is readily recognised by the spheroidal epandrium with the subparallel surstylus and cercus, both in a distinct right-angle bend, and the cercus bearing a tuft of short curved setae externally on the bend.

Etymology. The specific epithet *angulicauda* is from Latin meaning “bent or angled tail” and refers to this species’ bent cercus and surstylus.

***Atlaltia tonsa* Bickel, sp. nov.**

urn:lsid:zoobank.org:act:8295CAF7-8B5D-4294-823B-2E2C6AAE9D0E

Fig. 9a–c

Type material. Amber Inclusion from the Baltic Region: Holotype ♂ (Coll. Hoffeins, CCHH 1727/7, deposited SDEI; BAM-475).

Description. Male. Body length 1.3 mm; wing 1.1 x 0.5 mm (Fig. 9a–c); similar to *A. ulrichi* except as noted:

Thorax. Dark brown; 5 dc present, with two posterior setae distinctly stronger; median scutellar setae strong, other thoracic setae obscured.

Legs. Coxae and femora mostly dark brown, femora II and III with yellow “knees”; tibiae I and II yellow with TIII yellowish; tarsi yellowish; vestiture yellow; I: 1.3; 1.0; 0.5/ 0.2 /0.2/ 0.1/0.2; II: 1.3; 1.2; 0.6; 0.3/ 0.2/ 0.2/ 0.3; III: 1.5; 1.4; 0.3/ 0.5/ 0.3/ 0.2/ 0.2; TIII without curved apical spinelike seta.

Wing: Vein M_1 basally diverging from R_{4+5} but parallel with M_4 , then making gentle bend to become subparallel with R_{4+5} , with M_1 ending in costa anterior of wing apex; lower calypter and halter not visible.

Abdomen. Tergites dark brown and covered with short yellow vestiture, no strong tergal setae evident; segment 7 not visible; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium (Fig. 9c) swollen and spheroidal, but tapering somewhat apically; epandrial lobe as short projection on epandrial margin; surstylus elongate and blade-like, with elongate digitiform projection arising medially and projecting beyond hypopygium; cercus elongate narrow, similar to thick wire subtending surstylus, and without evident setae.

Female. Unknown.

Remarks. *Atlaltia tonsa* is known from a single male and can be identified by the blade-like surstylus and the elongate wire-like cercus.

Etymology. The specific epithet *tonsa* is from Latin for “oar” and refers to the blade-like male surstylus, similar to the blade of an oar.

***Atlaltia cryptica* Bickel, sp. nov.**

urn:lsid:zoobank.org:act:70FD45C9-19D5-41ED-B60A-8041C8181C7E

Fig. 9d–h

Type material. Amber inclusion from the Baltic Region: Holotype ♂ (Coll. Hoffeins, CCHH-1746/10, deposited SDEI; BAM-476).

Description. Male. Body length 1.1 mm; wing 1.1 x 0.4 mm (BAM-476); similar to *A. ulrichi* except as noted:

Head. (Fig. 9h). Postcranium concave; scape and pedicel short; postpedicel rounded subrectangular; arista apical.

Thorax. Median scutellar seta strong, lateral seta not evident.

Legs. Coxae and femora dark brown with tibiae and tarsi brown; vestiture yellow; coxal setation obscured; I: 1.2; 1.0; 0.4/ 0.3 /0.2/ 0.2/0.2; II: 1.3; 1.1; 0.5; 0.4/ 0.2/ 0.2/ 0.2; III: 1.4; 1.2; 0.2/ 0.5/ 0.2/ 0.1/ 0.1; TIII without curved apical spinelike seta.

Wing: Vein M_1 basally diverging from R_{4+5} but parallel with M_4 , then making gentle bend anteriorly to become subparallel with R_{4+5} , but the two veins diverging slightly before wing apex, with M_1 ending in costa anterior of wing apex; anal angle weakly developed; lower calypter not visible; halter yellow.

Abdomen. Tergites dark brown and covered with short yellow vestiture, no strong tergal setae evident; segment 7 not visible; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium swollen and spheroidal, but strongly tapering distally; epandrial lobe not visible; surstylus wide basally and forming tapering triangle with elongate median arm extending beyond triangle, and slightly clavate apically with short setae; cercus as thin arm curved laterad of surstylus and extending beyond apex of surstylus, and with fine apical seta.

Female. Unknown.

Remarks. *Atlaltia cryptica* is known from a single male. It is relatively small-sized and can be recognised by the spheroidal but distally tapering epandrium with a triangular tapering surstylus subtended by a median arm, and a long narrow cercus curving laterad of the epandrium (Fig. 9f). Stellate hairs are present in the amber piece.

Etymology. The specific epithet *cryptica* is from Greek meaning “hidden” or “secret” and refers to it being a single specimen among a group of inclusions I had initially sorted as *Atlaltia ulrichi*.

***Atlaltia penicillata* Bickel, sp. nov.**

urn:lsid:zoobank.org:act:D7800B9A-3893-4263-AC9C-DEF0DD2B4488

Fig. 10a–b

Type material. Amber inclusion from the Baltic Region: Holotype ♂ (Coll. Hoffeins, CCHH-1626/2, deposited SDEI; BAM-481).

Description. Male. Body length 1.4 mm; wing 1.2 x 0.5 mm (Fig. 10a–b); similar to *A. ulrichi* except as noted:

Thorax. Median scutellar seta strong, lateral scutellar seta not evident.

Legs. Coxae and femora brown; tibiae and tarsi yellowish; vestiture yellow; I: 1.3; 1.0; 0.6/ 0.3 /0.3/ 0.2/0.2; II: 1.6; 1.3; 0.7; 0.3/ 0.3/ 0.2/ 0.2; III: 1.8; 1.6; 0.3/ 0.5/ 0.3/ 0.2/ 0.2; TIII slightly expanded distally, with curved anteroventral apical spinelike seta (MSSC).

Wing. R_{2+3} and R_{4+5} subparallel towards distal costa but diverging towards apex; M_1 basally diverging from R_{4+5} but parallel with M_4 , then making gentle bend to turn anteriorly and becoming subparallel with R_{4+5} , but the two veins diverging slightly with near wing apex, with M_1 ending in costa anterior of wing apex; lower calypter not visible; halter yellow.

Abdomen. Tergites dark brown and covered with short yellow vestiture; segment 7 not visible; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium swollen and spheroidal, but tapering somewhat apically; surstylus curved, elongate with apical seta and with dorsobasal incurved digitiform projection; cercus elongate and with group of 4-5 curved yellow apical to subapical setae subtended by apicoventral circular translucent cuticular



Figure 9. *Atlatlia tonsa* Bickel, sp. nov.: a, habitus, left lateral; b, habitus, right lateral; c, male postabdomen, right lateral (BAM-475; GPIH). *A. cryptica* Bickel, sp. nov.: d, habitus, right lateral; e, hypopygium, right lateral; f, hypopygium, left lateral; g, hypopygium, dorsal; h, male head, left dorsal (BAM-476; CCHH). Scale bars: a, b, d = 0.5 mm; c, f, f, g, h = 0.2 mm.

projection (Fig. 10b).

Female. Unknown.

Remarks. *Atlatlia penicillata* is known from a single male inclusion and can be identified by the group of yellow hairs and circular cuticular projection at the apex of the elongate cercus. Similar to *A. ramosa*, the surstylus also has a curved-finger like projection near the base of the surstylus. Stellate hairs are present in the amber piece.

Etymology. The specific epithet *penicillata* is from Latin for “brush” or “tuft”, in reference to the group of yellow hairs at the apex of the cercus.

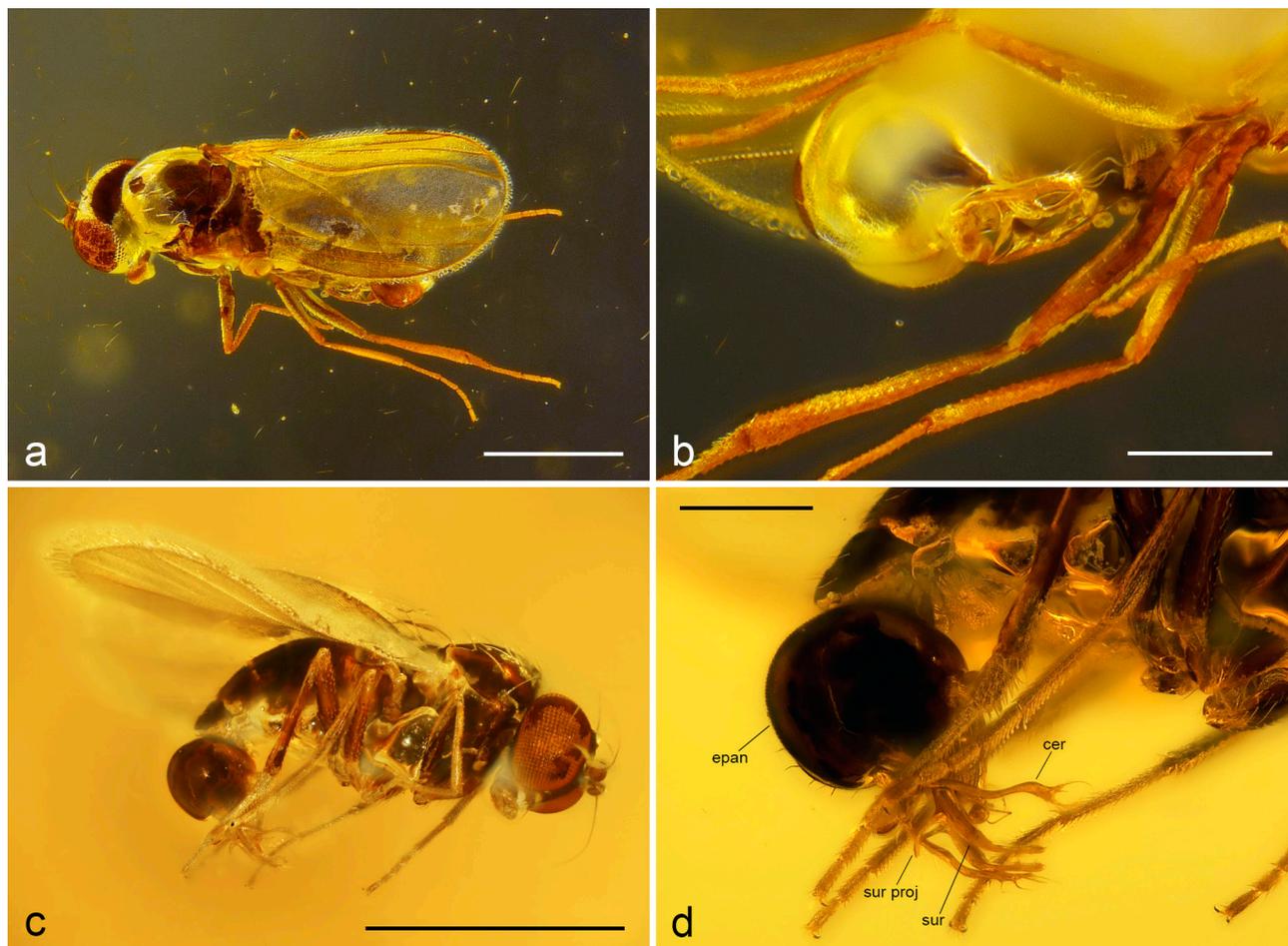


Figure 10. *Atlaltia penicillata* Bickel, sp. nov.: a, male habitus, dorsal; b, hypopygium, right dorsal (BAM-481; CCHH). *Atlaltia ramosa* Bickel, sp. nov.: c, habitus right lateral; d, hypopygium, right lateral (BAM-024; ZFMK). Legend: cer, cercus; epan, epandrium; sur, surstylus; sur proj, surstylar projection. Scale bars: a = 0.5 mm; b, d = 0.2 mm; c = 1mm.

Atlaltia ramosa Bickel, sp. nov.

urn:lsid:zoobank.org:act:B9FD2728-8044-418F-A8BA-8E3327C60C2E

Fig. 10c–d

Type material. Amber inclusion from the Baltic Region. Holotype ♂ (Coll. H. Ulrich, ZFMK, BAM-024).

Description. Male. Body length 1.4 mm; wing 1.4 x 0.6 mm (Fig. 10c); similar to *A. ulrichi* except as noted:

Thorax. Median scutellar seta strong, lateral scutellar setae absent.

Legs. Coxae and femora dark brown; TI and TII yellowish, TIII brown; tarsus I and II yellow, tarsus III distinctly white (MSSC); vestiture yellow; I: 1.8; 1.3; 0.6/ 0.3 /0.3/ 0.2/0.2; II: 1.8; 1.7; 0.7; 0.3/ 0.3/ 0.2/ 0.2; III: 2.1; 1.8; 0.3/ 0.5/ 0.3/ 0.3/ 0.2; TIII slightly expanded distally but without curved apical spinelike seta.

Wing. R_{2+3} and R_{4+5} subparallel towards distal costa; diverging towards apex; M_1 basally diverging from R_{4+5} but parallel with M_4 , then making gentle bend to turn anteriorly and become subparallel with R_{4+5} , but the two veins diverging slightly with near wing apex, with M_1 ending in costa anterior of wing apex; lower calypter not visible; halter yellow.

Abdomen. Tergites dark brown and covered with short yellow vestiture; strong tergal setae not evident; segment 7 not visible; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium swollen and spheroidal,

but tapering somewhat apically (Fig. 10d); epandrial lobe with incurved seta evident on ventroapical surface; surstylus elongate and tapering, and curved medially in gentle L-shape with apical seta, and with dorsobasal curved digitiform projection; cercus elongate and narrow, extending well beyond epandrium, with 3 long curved apical setae.

Female. Unknown.

Remarks. *Atlaltia ramosa* can be identified by the curved-finger like projection of the surstylus and the curved apical setae at the apex of the cercus.

Etymology. The specific epithet *ramosa* is Latin for “branch,” and refers to the curved finger-like projection branching off the surstylus.

New genera from Baltic Amber

The following two new genera of Medeterinae, *Kashubia* and *Eridanomyia*, are known only from Paleogene Baltic/Bitterfeld amber. Similar to the genus *Atlaltia*, both have wing vein M_1 closely parallel with vein R_{4+5} , with the two veins aligned behind the costa along the distal half of the wing. By contrast, both new genera have have crossvein dm-m, a plesiomorphic character for most dolichopodid genera. (e.g., see Figs 11g, 12d).

Of the two genera, *Kashubia* shares with *Atlatlia* the putative apomorphies of having having the epandrium somewhat flattened, and with often elongate lyriform cerci (Figs 11c, 11f, 12c) that are curved outwards and rather weakly setose. Therefore *Kashubia* might be considered the sister group of *Atlatlia* that retains the plesiomorphic complete crossvein dm-m. By contrast, *Eridanomyia* has a more cylindrical epandrium and short subtriangular or lobate cecus (Figs 12f, 13d), characteristic of many genera in the subfamily Medeterinae.

Genus *Kashubia* Bickel, gen. nov.

urn:lsid:zoobank.org:act:BB00A9A2-E129-4E32-97E7-4D61735B5623

Type species: *Kashubia starki* Bickel, sp. nov., here designated.

Etymology: *Kashubia* is a region in eastern Pomerania that includes Gdansk. It was originally inhabited by the Slavic Kashubian people and includes some of the richest Baltic amber deposits. The gender is feminine.

Diagnosis. Small Medeterinae, mostly dark grey, with wing length <1.7 mm; head wider than high; male eye facets only slightly enlarged anteriorly; postpedicel subrectangular, almost reniform on scape; arista apical; posterior mesonotum distinctly flattened; ac weak, in 3-4 irregularly pairs, or absent; 5-6 pairs dc; 1 pa seta; 2 sa setae; 2 sr setae; 1 hm seta; 1 pm seta; 2 npl setae; median scutellar strong with lateral scutellar setae reduced to weak hairs; 2 short ppl setae anterior of anterior spiracle; legs bare of major setae, but male *K. ornatipes* with modified femur and tibia I (MSSC); vein R_1 joining margin in basal third of costa; R_{2+3} and R_{4+5} diverging slightly towards apex; M_1 basally parallel with M_4 , but beyond dm-m closely subparallel to R_{4+5} almost to apex, not diverging distally, and with M_1 joining margin just anterior of apex; crossvein dm-m distinctly present; male tergite and sternite 7 not prolonged, forming short hypopygial peduncle; epandrium tapering subrectangular; hypandrium trough-like, fused at base to epandrium; cerci flattened and elongated and together appearing lyriform or harp shaped.

Remarks. The genus *Kashubia* comprises three Baltic amber species, two of which also occur in Bitterfeld amber. *Kashubia* species have a flattened and lyriform cercus, elongate and curved away from the hypopygium, and rather bare of vestiture. The genus shares with *Atlatlia* in having vein M_1 beyond the dm-m crossvein curving to approaching R_{4+5} and becoming closely subparallel in distal half of the wing. In having this venation, along with the flattened and lyriform cerci, *Kashubia* could be considered the stem group from which *Atlatlia* rose.

The following species are included in *Kashubia*:

Kashubia falcata Bickel, sp. nov. Baltic & Bitterfeld Regions † (Eocene/Oligocene).

Kashubia ornatipes Bickel, sp. nov. Baltic & Bitterfeld Regions † (Eocene/Oligocene).

Kashubia starki Bickel, sp. nov. Baltic Region † (Eocene/Oligocene).

Kashubia starki Bickel, sp. nov.

urn:lsid:zoobank.org:act:72F8238C-73B9-4ACA-8A1B-0ED5043124CF

Fig. 11a–d

Type material. Amber inclusions from the Baltic Region. Holotype ♂ (Coll. H. Ulrich, BAM-109); paratypes: 4 ♂, [♂, ♀] (Coll. H. Ulrich, ZFMK; photos BAM-106, BAM-110, BAM-433, BAM-446); ♂, (MZPW, #15337, BAM-017); 2 ♂, [3 ♂] (Coll. Hoffeins, CCHH, #162616 BAM-345, # 1646/7, 1646/9); ♂ (Coll. A. Stark, Halle am Saale); ♂ (ZMUC, BAM-005); ♂, ♀, (NCIR); ♂ (Be 1255, SMF).

Additional material. Amber inclusions from the Baltic Region: ♂ (BMNH, In 22142); probable ♀ (MZPW, # 15606).

Diagnosis. *Kashubia starki* has striking cerci, which in ventral view appear lyriform or harp-shaped (Fig. 11c), and the surstylus has a distinct apicoventral seta.

Description. Male. Body length 1.6-1.7 mm; wing 1.6 x 0.5 mm (Fig. 11a–d).

Head. Head distinctly wider than high, and tapering ventrally in anterior view; postcranium concave; major setae brownish; single row of short postoculars; pair strong diverging ocellars; pair strong slightly converging verticals; vertex, frons, face, clypeus black with grey pruinosity; face and clypeus distinctly separating eyes; clypeus conformable with eye, not projecting anteriorly; palp and proboscis brownish; palp with apical seta; eye facets only slightly enlarged anteriorly; antenna dark brown; scape and pedicel short; postpedicel rounded subrectangular, almost reniform; arista dorsoapical, about as long as head height; ventral postcranium without field of setae.

Thorax. Dark brown; setae brown with yellowish reflections; posterior third of mesonotum flattened, somewhat oblong; ac short, 5-6 irregular pairs to mesonotal depression; 5 dc, gradually increasing in size posteriorly; 1 pa, 2 sa, 2 sr, 1 hm; 1 strong pm, 2 npl; lateral scutellar seta weak, about one quarter length of median scutellar seta.

Legs. Coxae, and femora mostly brown; tibiae and tarsi yellowish; vestiture yellow; CI and CII with short anterior hairs, CIII with lateral seta at 1/3; I: 2.3; 1.9; 0.7/0.3/0.3/0.2/0.2; leg I without major setae; II: 2.2; 2.1; 1.0/0.7/0.4/0.3/0.2; FII gently tapering; TII with distinct anterior seta near 1/4, and with short apical anterior, av, and pv setae; III: 2.3; 2.8; 0.6/1.0/0.5/0.3/0.3; FIII gently tapering; TIII with some short dorsal setae and short apical ventral seta.

Wings. R_1 joining margin in basal third of costa; R_{2+3} and R_{4+5} diverging slightly towards apex; M_1 basally parallel with M_4 , but beyond dm-m closely subparallel to R_{4+5} almost to apex, not diverging distally, and with M_1 joining margin just anterior of apex; crossvein dm-m present; CuAx ratio: 0.2; anal angle weakly developed; lower calypter with fan of pale yellow setae; halter yellow.

Abdomen. Tergites dark brown and covered with short yellowish vestiture; tergite 1 with posterior row of short yellow setae; segment 7 short, with tergite and sternite more or less opposed; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium tapering subrectangular; hypandrium trough-like, extending almost to apex of surstylus; single fused epandrial lobe present at base of surstylus with basal collar and bearing apparently single

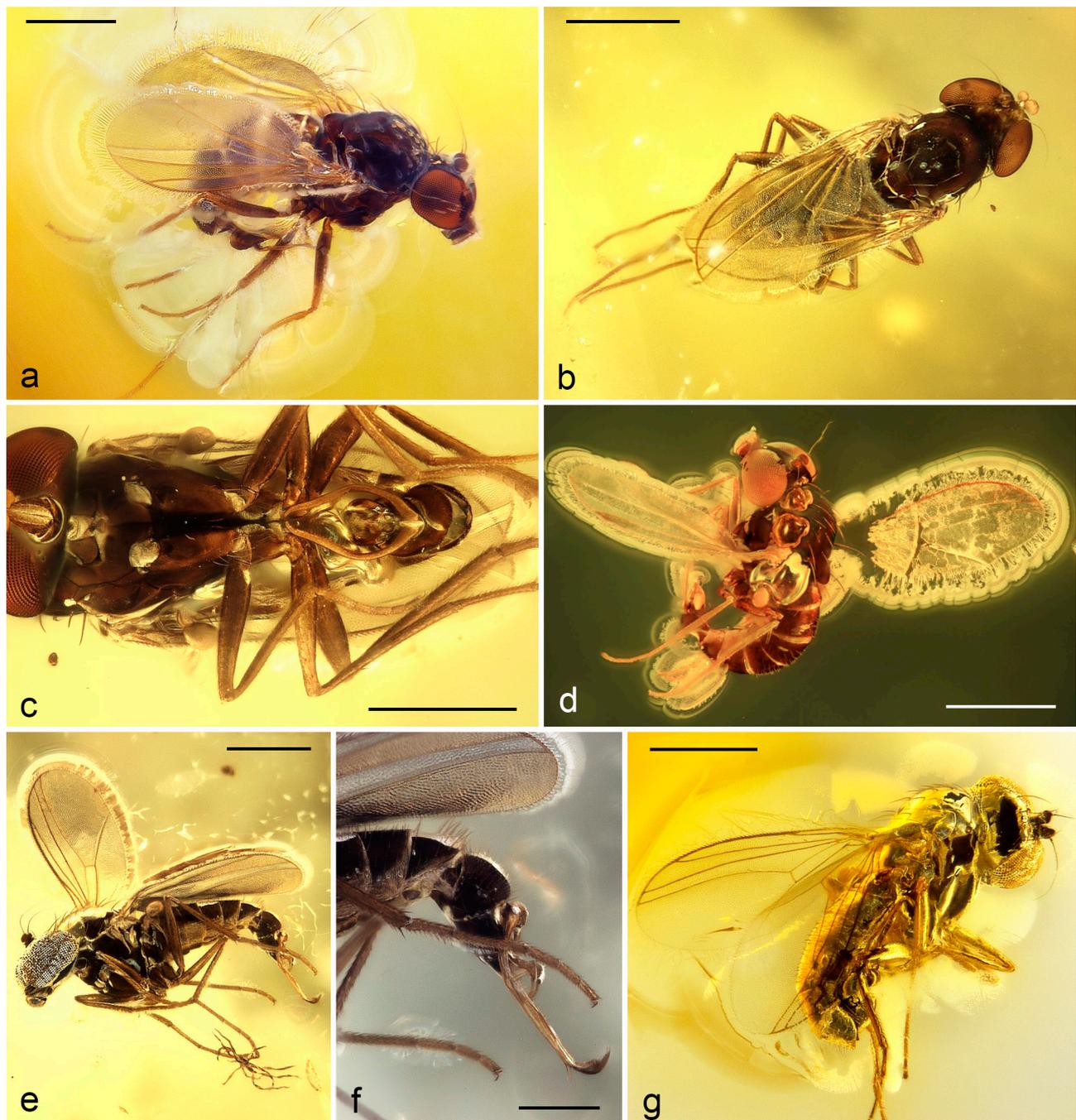


Figure 11. *Kashubia starki* Bickel, sp. nov.: a, male habitus, right lateral (BAM-106; ZFMK); b, male, dorsal; c, habitus, ventral (BAM-109; ZFMK); d, habitus, left dorsal (BAM-345; CCHH). *Kashubia falcata* Bickel, sp. nov. e, male habitus, left lateral; f, hypopygium (BAM-451; CCHH); g, male, right lateral – note right wing aberration (BAM-554; CCHH). Scale bars: a, b, c, d, e, g = 0.5 mm; f = 0.2mm.

long apical seta; surstylus as elongate arm with long thickened curved apicoventral seta; cercus (Fig. 11c) curved and elongate, flattened with some fine pale hairs along inner margin, and cerci together appear lyriform, laterally expanded at base and gradually converging distally to reach base of CIII.

Female. Similar to male except face and clypeus distinctly wider.

Remarks. *Kashubia starki* is known from a number of Baltic amber inclusions. It has striking cerci, which in ventral view appear lyriform or harp-shaped (Fig. 11c). As well,

it is distinctly larger than the other two *Kashubia* species. Stellate hairs are included in several pieces.

Etymology. This species is named in honour of Andreas Stark, who helped found and publish the journal *Studia Dipterologica*, and who loaned an amber inclusion of this species.

***Kashubia falcata* Bickel, sp. nov.**

urn:lsid:zoobank.org:act:2AB3976A-C240-45CB-A6DB-9D8B5E97CB85

Fig. 11e–g

Type material. Amber inclusions from the Baltic Region. Holotype ♂ (Coll. Hoffeins, CCHH, deposited SDEI, #1729/4, BAM-451); paratype ♂ (ZMUC, BAM-315).

Additional material. Amber inclusions from the Baltic Region. [2 ♂] (Coll. Hoffeins, CCHH, #275/5, BAM-554). Amber inclusions from the Bitterfeld Region: 3 ♂ (Coll. Ehlen, # 105, 306, 829).

Diagnosis. *Kashubia falcata* has the cercus distinctly hook-shaped with some distinct outer subapical setae (Fig. 11f) and with a distinctly geniculate surstylus.

Description. Male. Body length 1.5 mm; wing 1.3 x 0.4 mm (Fig. 11e); similar to *K. starki* except as noted:

Legs. Coxae dark brown; femora brownish basally, becoming yellow on distal quarter; tibiae and tarsi yellowish; setae and vestiture yellow; CI and CII with short anterior hairs, CIII with lateral seta at 1/2, subtended basally by shorter seta; I: 1.8; 1.6; 0.7/0.3/0.2/0.2/ 0.2; leg I without major setae; II: 1.7; 1.8; 0.9/0.5/0.3/0.2/ 0.2; TII without major setae; III: 2.0; 2.2; 0.4/0.8/ 0.4/0.3/0.2; FIII gently tapering; TIII with some short dorsal setae and short apical ventral seta.

Wings. R₂₊₃ and R₄₊₅ diverging slightly towards apex; M₁ basally parallel with M₄, but beyond dm-m closely subparallel to R₄₊₅ almost to apex, not diverging distally, and with M₁ joining margin just anterior of apex; crossvein dm-m present; CuAx ratio: 0.2.

Abdomen. Tergites dark brown and covered with short yellowish vestiture; tergite 1 with posterior row of short yellow setae; segment 7 short, with tergite and sternite more or less opposed; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium (Fig. 11g) tapering subrectangular; surstylus geniculate, with distinct right angle bend, with external seta at bend, and with distal surstylus medially directed and digitiform; cercus basally curved, elongate and flattened, lyriform, with pair internal setae at 1/3, and apically incurved, almost hook-like, and with 2 distinct subapical external setae before apical bend, and with some short weak apical setae.

Female. Unknown.

Remarks. *Kashubia falcata* is known from both Baltic and Bitterfeld amber. It is close to the slightly larger *K. starki*, and the two species differ primarily in the shape of the elongate cercus, which is distinctly hook-shaped with some distinct outer subapical setae in *K. falcata* (Fig. 11f), but flattened and lyriform, without distinct subapical setae in *K. starki* (Fig. 11c). As well, *K. falcata* has a distinctly geniculate surstylus and has veins R₄₊₅ and M becoming closely subparallel beyond the dm-m crossvein. Stellate hairs are present in one of the Baltic amber pieces. Of interest is the aberrant venation in Fig. 11g, where the left wing is normal and the right wing has crossvein dm-m making an angled bend to join vein M₁ near 2/3, creating a long acute angle in wing cell dm.

Etymology. The specific epithet *falcata* is from Latin for “sickle-shaped” and refers to the curved hooked cercus of this species.

***Kashubia ornatipes* Bickel, sp. nov.**

urn:lsid:zoobank.org:act:7A3C8DA5-9CAC-43EB-9F5D-B6BFBACB99CA

Fig. 12a–c

Type material. Amber inclusions from the Baltic Region. Holotype ♂ (MHNN 1732, achat S. Podenas, BAM-366); paratypes: ♂ (Coll. C. Gröhn, #5727, BAM-447); 2 ♂ (Coll. Hoffeins, CCHH, #1740/6; #274/4, BAM-551).

Additional material. Amber inclusion from the Bitterfeld Region. ♂ (Kutscher Coll. GPU, BST.28550).

Diagnosis. *Kashubia ornatipes* has a distinctive, a ventral swelling with pale yellow setae on tibia I and two ventral projections along the distal third of femur I. The cerci are laterally bowed and horseshoe-shaped.

Description. Male. Body length 1.5 mm; wing 1.4 x 0.6 mm (Fig. 12a); similar to *K. starki* except as noted:

Legs. Coxae, and femora mostly dark brown, but femoral knees yellow; tibiae and tarsi yellowish; setae and vestiture yellow; CI and CII with short anterior hairs, CIII with lateral seta at 1/3; I: 1.8; 1.5; 0.3/0.2/0.2/0.2/ 0.3 (Fig. 12b); FI with rounded ventral projections at 2/3 and 5/6 (MSSC); TI with ventral swelling from 1/3 to 2/3 with 7–8 pale yellow ventral setae (MSSC); It₁ slightly thickened (MSSC); II: 2.1; 2.0; 0.9/0.6/0.3/0.2/ 0.2; III: 2.0; 2.3; 0.4/0.8/ 0.3/0.2/0.2; legs II and III bare of significant setae or modifications.

Wing. Relatively broad; R₂₊₃ and R₄₊₅ diverging slightly towards apex; M₁ diverging from R₄₊₅ basally, but gradually approaching R₄₊₅ beyond dm-m, to become almost subparallel, and diverging slightly from R₄₊₅ subapically to join margin just anterior of apex; CuAx ratio: 0.3.

Abdomen. Tergites dark brown and covered with short yellowish vestiture; tergite 1 with posterior row of short yellow setae; segment 7 with short tergite and sternite; sternite 8 ovate and covering left lateral hypopygial foramen; epandrium tapering subrectangular; hypandrium, epandrial lobe and surstylus not clearly visible; cercus in ventral view with short curved narrow median arm arising from base, and with slightly flattened curved outer arm with pale hairs along inner margin, and ending at level of surstylus, two arms forming broad horseshoe shape in ventral view (Fig. 12c).

Female. Unknown.

Remarks. *Kashubia ornatipes* is known from both Baltic and Bitterfeld amber. It has a distinctive modification (MSSC) of the male foreleg, where tibia I has a ventral swelling with pale yellow setae, and femur I has two distinct ventral projections along the distal third. The cerci are laterally bowed and horseshoe-shaped (Fig. 12 c). Stellate hairs are present in one of the Baltic amber pieces.

Etymology. This specific epithet *ornatipes* is from Latin and means “ornamented leg” in reference to the modified male leg I of this species.

***Eridanomyia* Bickel, gen. nov.**

urn:lsid:zoobank.org:act:A27DCE76-DE31-44D1-8BDA-2DD615DF9FF9

Type species: *Eridanomyia conjugalis* Bickel, sp. nov., here designated.



Figure 12. *Kashubia ornatipes* Bickel, sp. nov.: a, male habitus, right ventral; b, ventral, enlargement, note leg I (BAM-366; MHNN); c, hypopygium, dorsal (BAM-447; Gröhn). *Eridanomyia amica* Bickel, sp. nov.: d, habitus, right lateral; e, habitus, left lateral; f, male postabdomen, right lateral (BAM-507; GPIH). Scale bars: a, d, e = 1 mm; b = 0.5 mm; c, f = 0.2 mm.

Etymology: *Eridanomyia* is derived from Eridanos, the name of a river in classical Greece, the setting for the story of Phaethon, the boy who attempted to drive the chariot of his father, the sun god Helios. His inability to control the chariot caused so much chaos that Zeus killed him with a lightning bolt and he fell flaming into the river. His sisters, the Heliades, wept for Phaethon and being deities, they shed golden tears which were transformed into amber. Appropriately, “Eridanos” is also the name given to the

ancient river system that drained the Eocene Baltic amber forests. The suffix *-myia* is Greek for “fly.” The gender is feminine.

Diagnosis. Small Medeterinae, with wing length <1.6 mm; head wider than high; face and clypeus distinctly separating eyes; eye facets uniform; postpedicel rounded subtriangular, arista apical; 5-6 irregular pairs ac; 5-6 pairs dc; 1 pa seta; 2 sa setae; 2 sr setae; 1 hm seta; 1 pm seta; 2 npl setae;

median scutellar strong with lateral scutellar setae short; legs bare of major setae; R_{2+3} and R_{4+5} diverging slightly towards apex; M_1 slightly diverging from R_{4+5} basally, but beyond dm-m approaching R_{4+5} so that veins become closely subparallel to diverge just before apex, with both R_{4+5} and M_1 joining margin anterior of apex; crossvein dm-m distinctly present; male tergite and sternite 7 not prolonged, forming short hypopygial peduncle; epandrium subrectangular; hypandrium trough-like, fused at base to epandrium; surstylus with short straight digitiform ventral arm and curved subequal dorsal arm; cercus short, subtriangular with short ventral projection.

Remarks. The genus *Eridanomyia* comprises two Baltic amber species. Both species have cylindrical epandrium and a short subtriangular cercus. The genus shares with both *Atlaltia* and *Kashubia* in having vein M_1 beyond the dm-m crossvein curving to approaching R_{4+5} and becoming closely subparallel in distal half of the wing.

The following two species are included in *Eridanomyia*:

Eridanomyia amica Bickel, sp. nov. Baltic Region † (Eocene/Oligocene).

Eridanomyia conjugalis Bickel, sp. nov. Baltic Region † (Eocene/Oligocene).

Eridanomyia conjugalis Bickel, sp. nov.

urn:lsid:zoobank.org:act:1A4CEFB9-A3E3-405F-A36B-6D784C232E69

Fig. 13a–f

Type material: Amber inclusions from the Baltic Region. Holotype ♂ (ZFMK, BAM-354); paratypes: ♂ (ZFMK, photo BAM-107); [2 ♂] (MZPW, #14849, photo BAM-018); paratypes [♂ & ♀, in copula] (CCHH, 275-8, photo BAM-559).

Diagnosis. *Eridanomyia conjugalis* has the male surstylus apically indented with short dorsal and ventral arms, and the cercus with a ventral projection.

Description. Male. Body length 1.4 mm; wing 1.2 x 0.6 mm.

Head. Subcircular in anterior view, but distinctly wider than high; postcranium concave; major setae black; single row of short postoculars; pair strong diverging ocellars; pair strong slightly converging verticals; vertex, frons, face, clypeus black with grey pruinosity; face and clypeus distinctly separating eyes; palp brown; palp with apical seta; eye facets uniform; proboscis dark brown; antenna dark brown; scape and pedicel short; postpedicel rounded subtriangular, arista apical, about as long as head height.

Thorax. Relatively broad, not elongated; dark brown with metallic reflections; setae black; posterior third of mesonotum flattened; somewhat oblong; 5-6 irregular pairs of short ac; 5 dc, gradually increasing in size posteriorly, 1 pa, 2 sa, 2 sr, 1 hm; 1 pm; 2 npl; median scutellar setae strong, lateral setae short.

Legs. Coxae, and femora mostly dark brown; setae black; tibiae and tarsi brownish; CI and CII with short anterior hairs, CIII with lateral seta at 1/3; I: 1.4; 1.3; 0.7/0.3/0.3/0.2/ 0.3; leg I without major setae; II: 1.9; 1.7; 0.8/0.4/0.3/0.2/ 0.2; TII bare except with short apical anterior, av, and pv setae; III: 2.2; 2.5; 0.4/0.7/ 0.3/0.3/0.2; TIII with row of short spaced dorsal setae, and with short apical ventral seta.

Wing. Hyaline; R_{2+3} and R_{4+5} diverging slightly towards

apex, with R_{2+3} joining costa at 5/6; M_1 slightly diverging from R_{4+5} basally, but beyond dm-m approaching R_{4+5} so veins become closely subparallel to diverge just before apex, with both R_{4+5} and M_1 joining margin anterior of apex; crossvein dm-m distinctly present; CuAx ratio: 0.2; anal angle weakly developed; lower calypter with fan of black setae; halter brown.

Abdomen. Tergites dark brown and covered with short brownish vestiture; tergite 1 with posterior row of short setae; segment 7 short; sternite 8 ovate and covering left lateral hypopygial foramen; hypopygium mostly dark brown; epandrium subrectangular and distally truncated; hypandrium as short narrow hood projecting outwards along ventral epandrial surface; epandrial lobe present at base of surstylus with basal collar and bearing apparently single long apical seta; surstylus apically indented with short digitiform ventral arm and subequal dorsal arms; cercus short, subtriangular with short ventral projection.

Female. Obscured.

Remarks. *Eridanomyia conjugalis* is known from four amber pieces, including a pair *in copulo*.

The piece includes stellate hairs.

Etymology. This specific epithet *conjugalis* is from Latin meaning “pertaining to marriage,” since one of the amber inclusions (Fig. 13f) had a male and female joined *in copulo*.

Eridanomyia amica Bickel, sp. nov.

urn:lsid:zoobank.org:act:A4B6CEBD-077B-4DD5-BEFB-00AF1502AE70

Fig. 12d–f

Type material. Amber inclusion from the Baltic Region. Holotype ♂ (Coll. C. Gröhn # 8307, deposited GPIH, photo BAM-507).

Diagnosis. The venation has veins R_{4+5} and M_1 closely subparallel beyond the dm-m crossvein. The surstylus has a short straight digitiform ventral arm and curved subequal dorsal arm and the cercus is short, tapering subtriangular, with short setae.

Description. Male. Body length 1.8 mm; wing 1.5 x 0.5 mm (Photo BAM-507); similar to *E. conjugalis* except as noted:

Thorax. Median scutellar setae strong, laterals apparently absent.

Legs. Coxae and remainder of legs mostly dark brown; CI and CII with short anterior hairs, CIII with lateral seta at 1/3; I: 2.3; 2.1; 1.0/0.8/0.5/0.2/ 0.2; leg I without major setae; II: 2.4; 2.3; 1.2/0.6/0.5/0.3/ 0.2; FII with weak subapical pv seta; TII bare except with short apical anterior, av, and pv setae; III: 2.7; 2.8; 0.6/1.2/ 0.7/0.5/0.3; TIII with row of short spaced dorsal setae, and with short apical ventral seta.

Wing. CuAx ratio: 0.3; anal angle weakly developed; lower calypter with fan of pale yellow setae; halter yellow.

Abdomen. Tergites dark brown and covered with short brownish vestiture; tergite 1 with posterior row of short setae; segment 7 short; sternite 8 ovate and covering left lateral hypopygial foramen; hypopygium mostly dark brown; epandrium large, subrectangular; hypandrium as short narrow hood; epandrial lobe present at base of surstylus with basal collar and bearing apparently single long apical

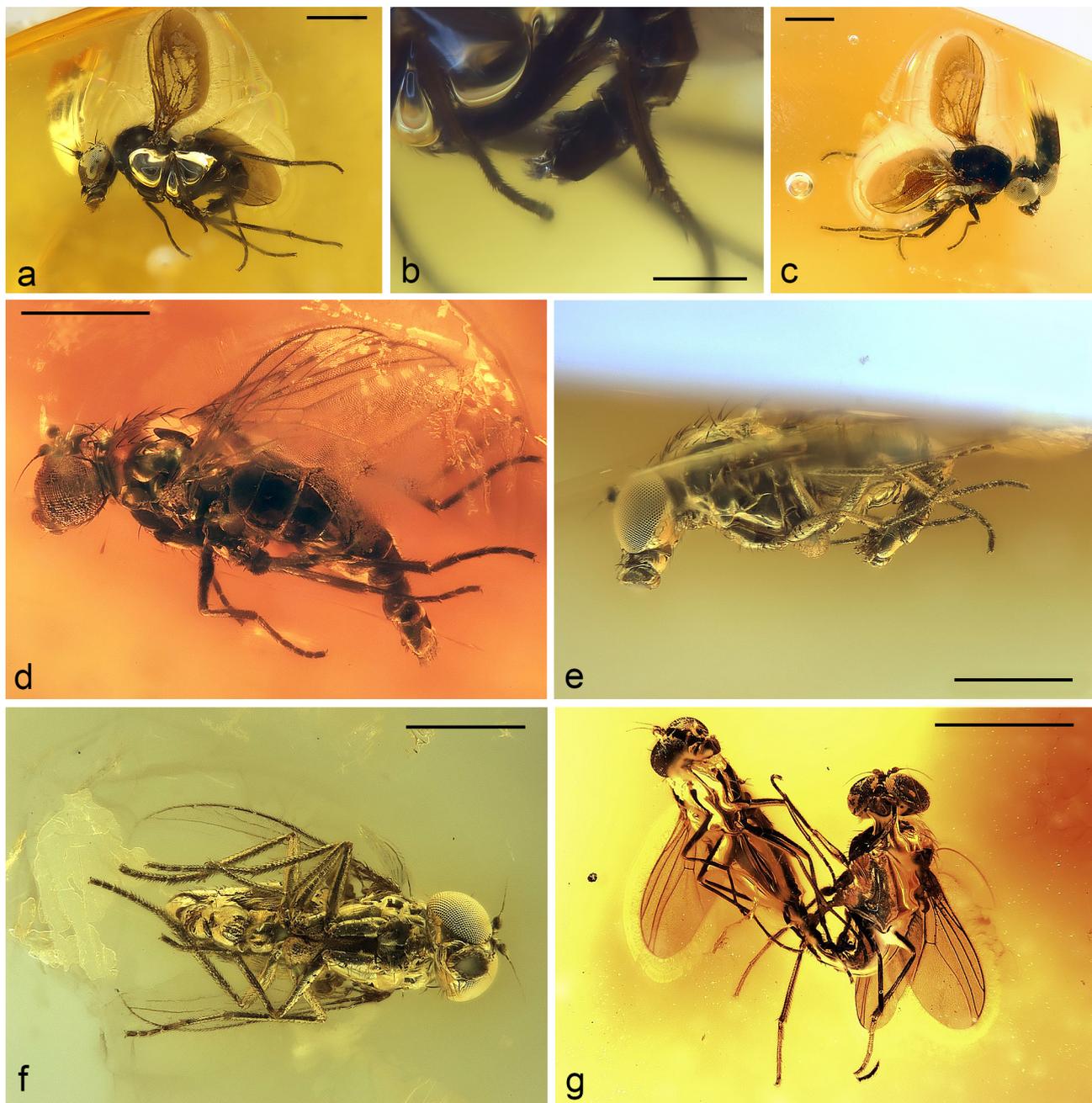


Figure 13. *Eridanomyia conjugalis* Bickel, sp. nov.: a, male habitus, left lateral; b, male postabdomen, left lateral (BAM-107; ZFMK); c, male habitus, left lateral; d, male postabdomen, left lateral; e, habitus, ventral (BAM-354; ZFMK); f, pair *in copulo* (BAM-559; CCHH). Scale bars: a, b, c, d, e = 0.5 mm; b, = 0.2 mm; f, = 1mm.

seta; surstylus with short straight digitiform ventral arm and curved subequal dorsal arm; cercus short, tapering subtriangular, with short setae.

Female. Unknown.

Remarks. *Eridanomyia amica* is known from a single male that has a Ptiliidae beetle syninclusion (Fig. 12d–e).

Etymology. This specific epithet *amica* is from Latin meaning “friend,” in reference to the ptiliid beetle “friend” included in the same amber piece.

Dicussion

Morphological considerations

Atlatlia and the two newly described genera, *Kashubia* and *Eridanomyia*, have morphological features that require further discussion.

1. *Loss of crossvein dm-m.* The total loss of crossvein dm-m is the strong defining synapomorphy of *Atlatlia*, found in both the *grisea* and *ulrichi* species groups. The only other dolichopodid genus that shows such crossvein loss is the Old World genus *Cryptophleps* Lichtwardt (subfamily Diaphorinae) where most described species totally lack dm-m, but some show the crossvein as a trace (Bickel, 2005).

Also of note, the Parathalassiinae genus *Chimerothalassius* Shamshev & Grootaert (2003) also lost this crossvein, although this is part of the basal sister group to the remainder of the Dolichopodidae, and not Dolichopodidae *s.s.* Since almost all other dolichopodid genera and most Diptera have this crossvein as part of the venational ground plan, it is not clear if its loss has any adaptive character, or how it might affect wing flexion during flight.

2. *Elongate hypopygial peduncle (segment 7)*. An external male peduncle, comprising tergite and sternite of segment 7 and supporting an exerted male genital capsule or hypopygium (the epandrium and appendages of Fig. 4a), is a major trend within the Dolichopodidae. It evolved independently in various subfamilies, especially the Sciapodinae, Dolichopodinae, and Medeterinae. In some *Atlatlia* species, the hypopygial peduncle has become greatly prolonged, initially with tergite and sternite 7 becoming prolonged (e.g., Fig. 4a–b), then more elongated but with tergite and sternite 7 still separate, as in *A. flaviseta* (Fig. 1e), and then the most extreme development, tergite and sternite 7 are totally fused into a long rod, as in *A. grisea* (Fig. 1a). This elongate arm-like hypopygial peduncle found in the *Atlatlia grisea* group would enable males to thrust their hypopygium far forward during mating, and that of *A. grisea* represents the most extreme development of the hypopygial peduncle within the Dolichopodidae and probably the entire Diptera.

3. *Male secondary sexual characters*. Dolichopodidae are noted for the range of often elaborate male secondary sexual characters (MSSC), the non-genitalic modifications on the male body that are absent on females, and which are assumed to enable conspecific mate recognition during courtship. These include flag-like flattening of the arista and tarsomeres, modified setae, prolongation and deformation of podomeres, orientated silvery pruinosity, and deformation of wings.

a. Although the subfamily Medeterinae usually display limited development of MSSC in comparison to other dolichopodid subfamilies, the strongly swollen basal male femora in some recent and in amber species of the *grisea* group, the Australian *A. grisea* (Fig. 3a) and the Baltic/Bitterfeld amber species *A. electrica* (Figs 5a–b) is notable.

b. Males of New Caledonian *Atlatlia* species (and sometimes to a less degree females) have orientated silvery body pruinosity on the coxa I (Figs 3d–f).

c. Males of *Atlatlia ulrichi* have tibia III apically swollen with a curved anteroventral apical spine (Fig. 8d).

Amber and bionomics of the Medeterinae

Being located in Europe, Baltic amber and its included biota have received much scientific attention, generating a large associated literature, both technical and semi-popular (e.g., Larsson, 1978; Weitschat & Wichard, 2002; Erichson & Weitschat, 2008; also discussion in Szwed & Sontag, 2009). Dolichopodidae are abundant as Baltic amber inclusions since adults of many genera favour tree trunks both as lekking sites to find mates and places to hunt for soft-bodied invertebrate prey. This facilitates their accidental entrapment in resin and ultimate diagenesis as amber fossils. It is important to remember that the Dolichopodidae *sensu stricto* (i.e. without the basal subfamilies Microphorinae and Parathalassiinae) are unknown from Cretaceous ambers (D. Grimaldi, *pers. comm.*) and appear to have undergone an

explosive radiation in the early Cenozoic, producing a rich and disparate fauna by Baltic amber time (Lim *et al.*, 2010).

The dolichopodid subfamily Medeterinae is well-known for tree trunk associations. Indeed, many recent species in the type genus *Medetera* (also in Baltic amber) are known to lay their eggs at the entrance of bark beetle galleries (Curculionidae: Scolytinae), attracted by bark beetle aggregation pheromones, and their larvae enter the galleries to prey on the beetle larvae (e.g., Hulcr *et al.*, 2005). *Medetera* itself has a long evolutionary history, and in addition to amber faunas (Evenhuis, 2014), the recent fauna is near cosmopolitan in distribution with some 317 species listed for the genus (Yang *et al.*, 2006), but many more await description. For example, from an elevational Malaise trap transect on Doi Inthanon, the highest mountain in Thailand, 35 morphospecies of *Medetera* were collected, only two of which could be associated with described species (Plant *et al.*, 2019). The Baltic amber Medeterinae are diverse and more taxa await description (also see Grichanov, 2023).

Faunal relationship of Baltic and Bitterfeld amber

Based on similar age, amber chemistry and included arthropod assemblages, some workers (Weitschat, 2008; Szwed & Sontag, 2013) consider both the widespread Baltic amber and the more restricted Bitterfeld (Saxonian) amber of northern Germany to have been derived from the same forest ecosystem that persisted for some ten million years in what is now Scandinavia. However, Wolfe *et al.* (2016), citing distinct differences in hydrogen isotopes, claim there is a clear differentiation in amber provenance, reflecting separate northern (Baltic) and southern (Bitterfeld) origins along the margins of a Paleogene North Sea. They suggest that although the two deposits are geologically distinct in origin, their faunal similarities are the result of being contemporaneous in time. The present work supports the faunal similarity of the two ambers. Although we have seen limited Bitterfeld material in comparison to Baltic, four of the 14 Baltic amber species treated here, *Atlatlia electrica*, *A. ulrichi*, *Kashubia falcata*, and *K. ornatipes* also occur in Bitterfeld amber, further highlighting the closeness of the two faunas.

Historical stasis and disjunction in the *Atlatlia grisea* group

The genus *Atlatlia* is a radiation that appears strongly disjunct in both time and space: the Eocene/Oligocene of the Baltic/Bitterfeld Region and recent Australia and New Caledonia. The two faunas are so close that I regard the *grisea* species group as being a valid monophyletic grouping for both the recent and Paleogene faunas. Indeed, comparing the common eastern Australian *Atlatlia grisea* (Fig. 3a) with the Baltic amber *A. electrica* (Fig. 5a), one might imagine the two species occurring sympatrically.

Insect genera in a wide range of families can display remarkable disjunctions in both time and space, often with minimal morphological divergence between amber and recent specimens (Grimaldi & Engel, 2005). In the Diptera, for example, the diverse family Ceratopogonidae (biting midges) have a rich fossil record in amber starting from the Lower Cretaceous. They often are well-preserved and

abundant as amber inclusions, allowing them to be compared in detail with recent taxa. The genus *Austroconops* Wirth & Lee, 1958 comprises seven amber species from the Lower Cretaceous of Lebanon, Spain and Myanmar and the Upper Cretaceous of France and Siberia, and two extant species in Western Australia (Szadziewski, 2008). The genus *Meunierohalea* Szadziewski has four Baltic amber species, two species from Indian Eocene Cambay amber and one extant species in northeastern Queensland. However, the recent discovery of *Meunierohalea* in Eocene Anglesy amber from Victoria, Australia, a region once attached to subpolar Antarctica during Eocene “greenhouse earth” climatic conditions (Peñalver *et al.*, 2022), suggests this genus was widespread, possibly near cosmopolitan during the early Paleogene but now has only a relictual occurrence in northern Australia. In this light, the original distribution of *Atlatlia* was undoubtedly much wider but remains unknown. Hence the term “pseudo-Gondwanan” for the genus, found today only in southeastern and southwestern Australia and New Caledonia. This might have been considered a relictual distribution within the ancestral Gondwanan supercontinent comprising the southern hemisphere landmasses and India. However, the presence of *Atlatlia* in Baltic amber suggests a much different historical and biogeographic scenario.

World paleogeographic maps for the early Eocene (55 mya, near the time of Baltic amber production), show Australia and ancestral New Caledonia entirely south of 30°S and near Antarctica (see Markwick, 2021). At the time, Australia was even further away from the Baltic region than it is today and was close to South America via an ice-free Antarctica. However, climatic conditions were much different then, especially with the Paleocene–Eocene Thermal Maximum (PETM) around 55 mya. This relatively brief period (some 200, 000 years) of intense warming produced a “greenhouse earth,” with a 5–8 °C global average temperature rise and massive input of carbon into the ocean and atmosphere (McInerney & Wing, 2011). The PETM may have facilitated widespread dispersal of many insect taxa which otherwise would have been blocked by climatic barriers. However, the disjunction of *Atlatlia* remains somewhat puzzling. Why is the genus not found in other regions? Although relatively small, *Atlatlia* is readily identifiable, and it could possibly occur in other Cenozoic ambers, or be extant in other zoogeographic regions. And the genus is not uncommon —*A. grisea*, for example, is easily found in late spring to early summer (October to January) resting on smooth-barked eucalypts in southeastern Australia. Many more such insect genera of restricted recent provenance are possible relicts of a once much wider distribution in time and space.

The Australian and New Caledonian *Atlatlia* faunas

The historical biogeography of the unusually rich New Caledonian biota has been the subject of considerable debate (e.g., Grandcolas *et al.*, 2008; Heads, 2019, 2023; Malem *et al.*, 2023). Previously, the main island (Grande Terre) was presumed to be a Gondwanan fragment supporting a unique biota of vicariant origin, a view supported by the presence of primitive angiosperms such as Amborellaceae, a rich flora of southern hemisphere conifers, and other endemic taxa. However, recent geological evidence suggests that New

Caledonia was submerged during the Palaeocene and was not emergent until the late Eocene–early Oligocene, when its ultramafic covered lithosphere was uplifted. Thus, many workers consider the New Caledonian biota to be the result of post-Eocene transoceanic dispersal, following the geological emergence, and this view is increasingly supported by various taxonomic studies (Malem *et al.*, 2023). However, Giribet and Baker (2019) discussed the presence on New Caledonia of “paleoendemic” ground dwelling invertebrate taxa of limited salt-water dispersal capability. They suggest such taxa may have survived on now vanished islands that would have served as biotic refugia and steppingstones for colonisation. Heads (2019, 2023) supports the view that New Caledonia was never fully submerged and its biota survived on terranes near the tectonic plate margins.

The presence of *Atlatlia* on New Caledonia contributes little to the New Caledonian submersion debate. First, there is no evidence of Dolichopodidae *sensu stricto* (i.e., without the basal Microphorinae clade) being present during the Cretaceous, so the genus is unlikely to have been present on pre-submersion New Caledonia. Second, trans-oceanic waif dispersal is not uncommon in the family Dolichopodidae (including subfamily Medeterinae)—in Micronesia, for example, some species occur on both high islands and isolated atolls across vast areas of ocean (Bickel 1994, 1997). Therefore, ancestral New Caledonian *Atlatlia* species could possibly have dispersed from Australia. Other dolichopodid genera with an exclusive Australia–New Caledonia distribution that also might have dispersed from Australia to an emergent late Paleogene New Caledonia include *Kowmungia* Bickel, 1987, with undescribed New Caledonian species), *Antyx* Meuffels & Grootaert, 1991 (Bickel, 1999), and *Pindaia* Bickel, 2014.

ACKNOWLEDGEMENTS. DJB thanks Jean Chazeau, ORSTOM, Noumea, New Caledonia for providing facilities and enabling participation in the 1990 Mission Panié. Travel support for a 2008 trip to museums in Germany was provided by the Australian Museum Trust. The late Hans Ulrich (Bonn, Germany) provided hospitality and encouragement. Both Christel and Hans-Werner Hoffeins and Carsten and Jutta Gröhn graciously provided hospitality and access to their extensive personal Baltic amber collections. We thank the respective curators of institutional collections and especially the owners of private collections for the loan of their specimens (see listing under “Material and Methods”). Hannah Mathews drew and inked the figures of recent taxa. Melissa Graf and Natalie Tees assisted with plate preparation. Elizabeth Tasker and Pavel German maintained tree trunk sticky traps on the Carrai and Werrikimbe plateaus of northern New South Wales in conjunction with their small mammal surveys, and Pavel German provided the habitat photograph of Figure 2d. Two anonymous referees provided helpful comments.

Conflict of Interest. Both authors declare that they have no conflict of interest.

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