

Puyehuemyia chandleri, gen. nov., sp. nov.
(Diptera: Opetiidae): remnant of a
Cretaceous biota in Chile

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ABSTRACT

The first Opetiidae known from the Southern Hemisphere is described—*Puyehuemyia chandleri*, gen. nov., sp. nov.—based on a female specimen collected in Valdivian forest in the Province of Osorno, south Chile. The Palearctic species *Opetia nigra* Meigen was also studied, allowing detailed comparisons. Features of the antenna, mouthparts, wing, and terminalia allowed the issue of the position of the family within the Eremoneura to be revisited. The inclusion of Opetiidae in the Platypezoidea is corroborated, possibly in a clade also including Lonchopteridae and Phoridae. The 3-articled condition of the styluslike arista in *Puyehuemyia* corroborates the hypothesis that the 2-articled condition in *Opetia* is independently derived, as it is in the Empidoidea and many schizophorans. *Puyehuemyia chandleri* has female terminalia typical of parasitoid groups, as does *Opetia*, although their life history is not known. Described Platypezoidea Cretaceous amber fossils are reviewed, and *Lonchopterites* is considered to be sister to the crown group of Opetiidae. The presence of an Early Cretaceous biogeographical layer in the Valdivian forest, associated with plant and animals disjunct from New Zealand, and similar to the beech forests in the Northern Hemisphere, is discussed.

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INTRODUCTION

Publication of *Diptera of Patagonia and South Chile* between 1929 and 1951 by the British Museum (Natural History), mainly based on a large collection made by Francis W. Edwards and Raymond Cobertt Shannon, vividly illustrated the distinctive nature of the diversity of flies at the southern end of South America. Unlike the hyperdiverse fauna of the north and center of the continent, the assemblage of Chilean species was found to be substantially less diverse but to contain a significant number of flies related to species found in New Zealand and Australia. This resemblance, which we now consider to be the remnant of a southern Gondwanan fauna, extends across a number of groups of Diptera.

A field trip in January and February 2017 to Parque Nacional Puyehue in southern Chile made available a large number of phylogenetically interesting flies—including species of *Paracladura* Brunetti (Trichoceridae), *Canthyloscelis* Edwards (Canthyloscelidae), *Austroleptis* Hardy (Austroleptidae), *Gondwanamyia* Sinclair, Cumming, Brooks, Plant and Saigusa (Empidoidea), some rare syrphids, *Mayomyia* Malloch (Heleomyzidae), *Aenigmatomyia* Malloch (Pallopteridae), *Melanthomyza* Malloch (unplaced at the family level), and a number of other Malloch (1933) genera of acalyptrates, among many others. Most notably, the collection includes a species clearly associated with the extant but poorly known and phylogenetically intriguing family Opetiidae, making this the first known opetiid from the Southern Hemisphere.

The Opetiidae are a very small family of flies known so far from a single genus, *Opetia* Meigen, with one species described from Europe, *O. nigra* Meigen, and two from Japan, *O. alticola* Saigusa and *O. anomalipennis* Saigusa. Chandler (2001) revised the family in detail and discussed the complicated question of its position in the Platypezoidea and in the system of Eremoneura. The genus *Opetia* was originally part of the Platypezidae and assigned to a monotypic subfamily by Kessel and Maggioncalda (1968). Griffiths (1972), Hennig (1976), and Disney (1987) challenged its inclusion in the platypezids, while Cumming et al (1995) assigned it as sister to the remaining Cyclorrhapha. The family-group is attributed to Rondani (1856) and a separate family rank was admitted as desirable by Chandler (1981) and later used as such by Chvála (1981, 1983).

The systematic position of the Opetiidae within the Brachycera has been considered in detail by Cumming et al. (1995) and Chandler (1998, 2001) based on morphology. Cumming et al. (1995: 131, fig. 16) first showed that *Opetia* had circumversion, and Chandler (2001) agreed that the 360° rotation of the male terminalia and its deflection under the abdomen, a condition seen in *Opetia*, would support its placement in the Cyclorrhapha. Chandler (2001) mentioned the “empidiform” structure of the antenna in *Opetia*—a plesiomorphic condition within the Cyclorrhapha—as similar to that of Platypezidae, but stressed that *Opetia* differs from platypezids and all remaining Muscomorpha by having an antenna with a small basal aristomere (i.e., a 2-articled arista), a condition seen in Empidoidea (Cumming et al., 1995).

Wiegmann et al. (1993), also analyzing morphology, proposed the Opetiidae as the sister group to the remainder of the Cyclorrhapha. The 3-articled arista and the presence of three pigmented spermathecae in Cyclorrhapha were seen to be reversals of conditions seen in empidoids and *Opetia*. Cumming et al. (1995) arrived at similar conclusions. They proposed that the pres-

ence of an ejaculatory apodeme and a sperm pump detached from the base of the phallus would be apomorphies shared by all Cyclorrhapha and *Opetia*. These characters combine with others to support the placement of Opetiidae in the Cyclorrhapha. The presence of a phallapodeme, however, would be synapomorphic for all Cyclorrhapha exclusive of *Opetia*. The association of *Opetia* with Platypezidae was suggested by Chandler (2001) based on a combination of plesiomorphic and apomorphic characters. The condition of male eyes with enlarged upper facets and a notch at the eye margin at the level of the antenna is shared by *Opetia* and Platypezidae, as is the enlarged alula in the wing. These features are related to male swarming, which in Opetiidae and Platypezidae is synorchesic and associated with mating (Chandler, 2001). A similar condition is shared by many other Cyclorrhapha (McAlpine and Munroe, 1968), empidoidea and some lower Brachycera, associated with male aerial swarming but not related to mating. Chandler's (2001) conclusion was that the condition of three aristomeres and three spermathecae would be eremoneuran general features modified in the Empidoidea, rather than reversals at the base of the Cyclorrhapha.

In molecular phylogenies, the position of the Opetiidae within the Platypezoidea is well accepted. Wiegmann et al. (2011) proposed, using molecular and morphological evidence, that the Apystomyiidae instead is sister to the Cyclorrhapha, and Opetiidae is sister to a clade including Platypezidae, Ironomyiidae, and Phoridae. More recently, Tkoč et al. (2016) found *Opetia* joining *Microsania* Zetterstedt in a clade that is sister to the remaining Platypezidae (including *Melanderomyia* Kessel). Tkoč et al. (2016) used a limited-taxon sampling, including only *Sciadocera rufomaculata* White, *Megaselia scalaris* (Loew), and *Lonchoptera uniseta* Curran as outgroups. This limited sampling does not allow testing the monophyly of the Platypezoidea and gives only modest phylogenetic signal at the base of their ingroup, the Platypezidae; thus, the position of *Opetia* as sister of *Microsania* can be questioned.

This paper describes and illustrates the new genus and species found in southern Chile, considers the evidence that connects this genus with *Opetia* and with other platypezoids, and briefly addresses the biogeographical implications of relict taxa in Chile, many of which have connections with New Zealand.

MATERIAL AND METHODS

The material used in this study corresponds to a single female of the new taxon, belonging to the Museo Nacional de Historia Natural, Santiago, Chile (MNHN), as well as specimens of *Opetia nigra*, *Lonchoptera bifurcata* (Fallén), *Sciadocera rufomaculata*, *Archiphora patagonica* Schmitz, and some other platypezoid and nonplatypezoid species. Terminology for morphological characters basically follows McAlpine (1981), Chandler (2001), and Brown et al. (2015), except for the wing venation, following Wootton and Ennos (1989) and Saigusa (2006). The species being described is very delicate and seems to be extremely rare. We preferred to dry the specimen out of ethanol using the solvent hexamethyldisilazane (Brown, 1993), instead of disarticulating and slide-mounting the specimen. Consequently some of the details of mouthparts, ovipositor, and some other internal structures cannot be described in the same detail as in slide-mounted specimens.

Opetiidae Rondani, 1856

Puyehuemyia, new genus

Type species, *Puyehuemyia chandleri*, sp. nov.

DIAGNOSIS: Maxillary palpus small, 1-segmented, antennal pedicel widening to apex, first flagellomere slightly wider midway to apex, arista 3-articled. Only R_1 setose among wing veins, R_1 not curved anteriorly toward C at apex, C circumambient. Tibial spurs absent, hind tibia slightly sinuous. Scutum with only one pair of posterior dorsocentral setae, acrostical setae absent. Scutellum with four strong setae evenly spaced at discal margin. Female segments 5–8 telescoped, ending as a sclerotized, possibly parasitoid-type ovipositor, cercus probably absent.

COMMENTS: A generic status for this Chilean species seems well justified. Not only is the antenna strikingly different from *Opetia*, with a 3-articled stylus, but also there are features in the wing venation of *Puyehuemyia* that differentiates it from the remaining species of the family—particularly, the shape of Sc and R_1 , and the shape of the basal sector of Rs.

Puyehuemyia chandleri, new species

Figures 1–3, 12A

MATERIAL EXAMINED: Holotype, female, **Chile**, Osorno, Parque Nacional Puyehue, Termas Aguas Calientes, Sendero Rápido del Chanleufú, Malaise trap, Jan. 14–Feb. 3, 2017, D.S. Amorim and V.C. Silva, cols. (MNHN).

DIAGNOSIS: As stated for the genus.

FEMALE: Total body length, 2.5 mm (habitus, fig. 1A).

Head (fig. 1B, C): Blackish brown, rounded, eyes reddish, large, dichoptic, dorsal and ventral ommatidia of same size, eye entirely covered with pale ommatrichia. Labella cream yellow; maxillary palpus apparently 1-segmented, small, brownish, apically blunt, no apical sensory pit. Entire frons, occiput, and gena densely covered with setulae. Ocellar triangle clearly defined, ocelli of equal size, well separated. Frons with three well-developed fronto-orbital setae evenly spaced, anterior fronto-orbital and inner vertical slightly lateroclinate, mid and posterior fronto-orbitals inclinate; pair of reclinate strong ocellars, postocellars small. Eyes well separated dorsally at vertex and closely approximated ventrally, frons strongly triangular from a dorsal view. Antenna inserted at dorsal third of head, face slender, setose on ventral third, antennae close together. Antennal scape small, about half length of pedicel, with few setulae along distal margin; scape widening to apex, about one-half length of first flagellomere, with setae around distal half; first flagellomere wider midway to apex, with some scattered small setae on basal half, not produced at junction with arista or stylus; arista clearly with three slender articles of about equal length, texture similar to first flagellomere, covered with microtrichia, lacking setation. Face slender, brown, bare mesally, sparse setae on ventral third of parafacialia. Gena narrow, setose, with some stronger setae in irregular row.

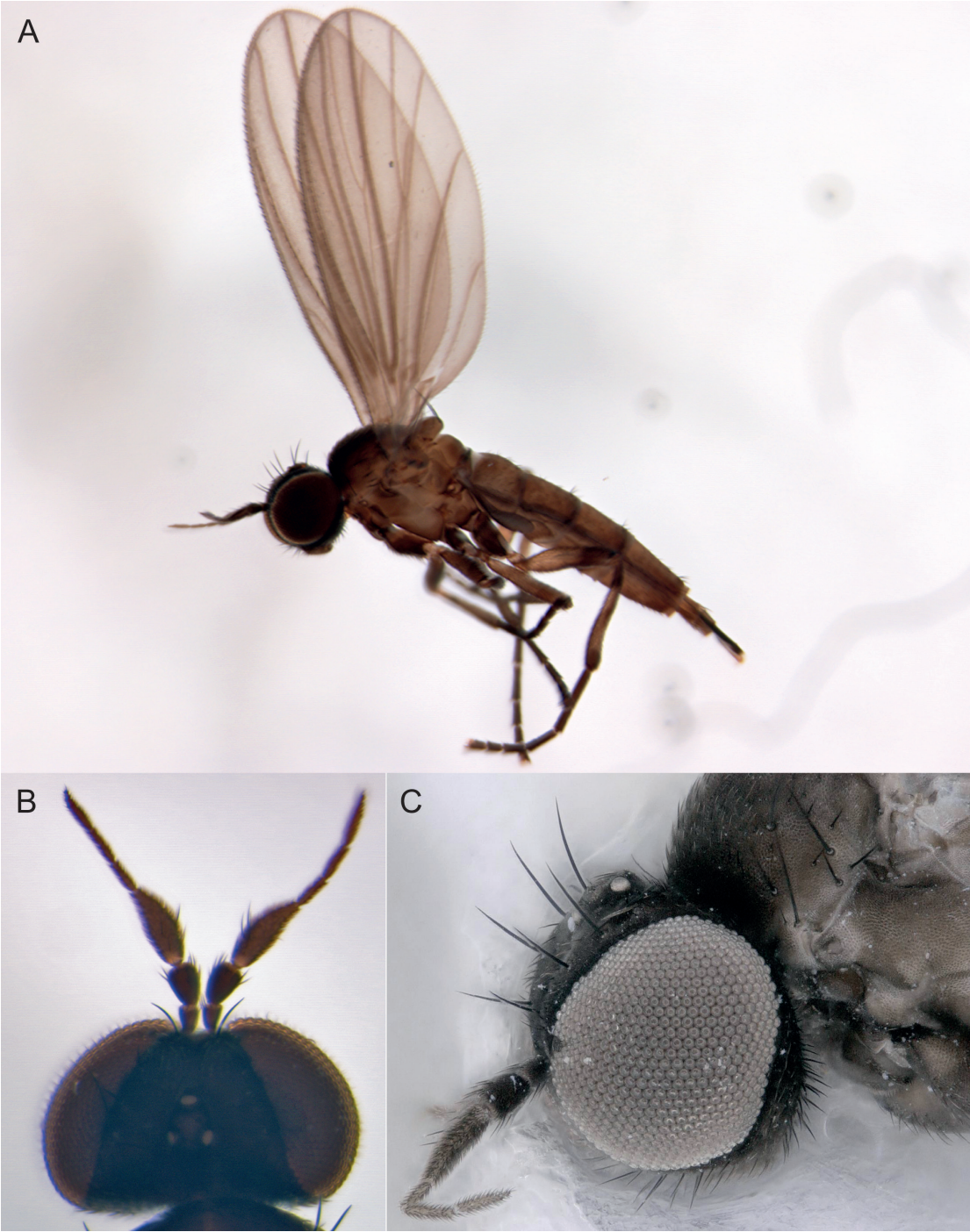


FIGURE 1. *Puehuemyia chandleri*, gen. nov, sp. nov., female holotype: **A**, habitus; **B**, head, dorsal view; **C**, head, lateral view.



FIGURE 2. *Puehuemyia chandleri*, gen. nov, sp. nov., female holotype: **A**, thorax, dorsal view; **B**, thorax, lateral view; **C**, wing. Black arrow points to the short displacement of the katepisternum under the mesepimeron, white arrows points to the partial suture between mesopleurotrochantin and meron. Abbreviations: **Anp**, anepisternum; **Ha**, haltere; **Ktp**, katepisternum; **Ltg**, laterotergite; **Mdt**, mediotergite; **Me**, meron; **Mes**, mesepimeron; **Pre**, proepimeron; **Prp**, proepisternum; **T1**, abdominal tergite 1; **S1**, abdominal sternite 1.

Thorax (fig. 2A, B): Cervical sclerite brown. Scutum dark brown anteriorly, gradually turning ochreous posteriorly; pair of dark brown stripes over undifferentiated dorsocentrals; one strong prescutellar dorsocentrals, no differentiated acrostichals. Two postpronotal setae, one strong and one minute; three strong presutural intraalars in irregular row; two large and three small notopleural setae; one strong supraalar. Scutellum ochreous, with apical pair of stronger, upcurved setae and pair of smaller, anteromarginal scutellars. Thoracic pleural sclerites not strongly sclerotized, ochreous, some areas brown or light brown on prosternum and proepim-

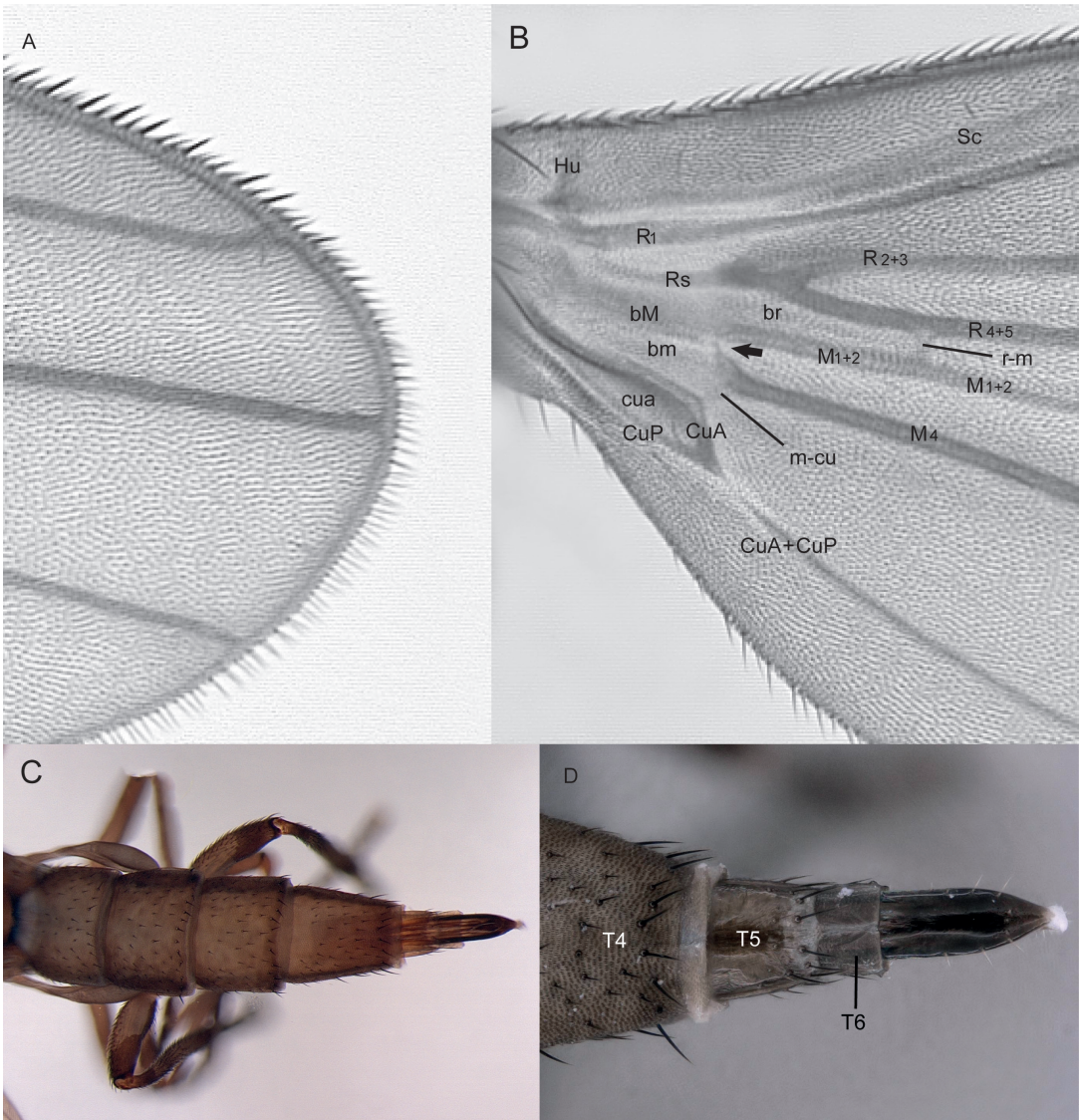


FIGURE 3. *Puehuemyia chandleri*, gen. nov., sp. nov., female holotype: **A**, wing tip; **B**, wing base—seta shows broken base of M4; **C**, abdomen, dorsal view; **D**, detail of terminalia, dorsal view. T4–6, abdominal tergites 4–6. Abbreviation of wing veins follows standard terminology.

eron, anteriorly and dorsoposteriorly on anepisternum, on ventral two-thirds of katepisternum, on dorsoanterior corner of meron, on metepisternum and on ventral margin of metepimeron, around posterior spiracle, mesially on mediotergite, and at contact between scutellum and mediotergite laterally (fig. 2A). Pleural sclerites entirely bare of setae, except ventral half of proepisternum. Anterior spiracle small, rounded, surrounded by membrane, placed dorsally to proepimeron. Prosternum V-shaped, bare, more sclerotized ventrally (fig. 2B). Propleural suture sigmoid, proepimeron entirely fused to katepisternum at posterior end. Anapleural suture depressed mesially. Anepisternum cleft dorsal opening bearing single elongated basalare.

Short dorsoposterior projection of katapisternum over meron. Katapisternum shield and meron shield well developed (respectively over mid- and hind legs). Meron more or less rectangular, reaching level of posterior spiracle, suture separating meron from mesepimeron and from metepisternum well marked. Partial suture of separation of mesopleurotrochantin and meron present. Limits of laterotergite from mesepimeron anteriorly and from mediotergite posteriorly well marked. Halter elongate, greyish, except lighter area basally; entirely bare of macrotrichia. Metanotum slender, but well characterized.

Legs delicate, coxae dark brown, densely setose anteriorly, remainder of legs brown with light brown areas. Tibial spurs absent on all legs, hind tibia distally with regular comb of longer setae. Tarsomeres gradually shorter, with no denticles or enlarged setae, no teeth on tarsal claws. Foretibia distally with inner, less well-sclerotized area covered with slightly stronger setae, and distal regular comb of elongate setae; mid- and hind tibiae with some more developed setae distally in more or less regular row.

Wing (fig. 2C): Length, 2.5 mm. Membrane light fumose brown, slightly darker along anterior margin, but without maculae. All wing veins bare of macrotrichia except R_1 with setae above along distal three-fourths. Hu present, well developed, Sc complete, reaching C at basal third of wing; R_1 long, gradually approaching C , reaching margin at distal three-fourths of wing; R_{2+3} long, reaching C close to wing tip, R_5 ending at wing tip (fig. 3A). C clearly circumambient. Transverse vein $r-m$ discrete, in basal fourth of wing; M_{1+2} (including sector basal to $r-m$) slightly longer than medial fork; M_4 thicker and more sclerotized than other posterior veins. Cells bm and br closed, crossvein $m-m+M_3$ (formerly $dm-Cu$) absent, very base of M_4 broken, $m-cu$ present, cell cua present, closed, $CuA+CuP$ reaching wing margin (fig. 3B).

Abdominal tergites and sternites light ochreous brown, darker along posterior margin (fig. 3C). No abdominal muscle plaques. Abdomen more or less flattened; segments 1–4 well developed, sternite 1 nearly unsclerotized, posterior border of sternites 2–3 with unsclerotized lunular area, tergites 1–4 sclerotized, with row of slightly more developed setae along posterior margin; segments 5–6 slender, weakly sclerotized, tergite 5 with row of setae along posterior margin, sternite 5 with scattered setae, segment 6 bare, segments 7–8 strongly modified to constitute well sclerotized, elongated ovipositor (fig. 3D). Cercus probably absent.

MALE: Unknown.

ETYMOLOGY: The generic epithet refers to the locality—Puyehue National Park, in southern Chile—where the holotype was collected. Puyehue is the name of one of the big lakes in Osorno Province. The park was created in 1941 just east of the lake. In the Mapudungum, or Mapuche language, *hue* means “place,” while *puye* is the common name of the galaxiine fish, *Galaxias maculatus* (Jenyns, 1842). The specific epithet honors Peter Chandler, who has a long and substantial contribution to dipterology in general and on platypezids and opetiids in particular, including his excellent review of the European Opetiidae and Platypezidae (Chandler, 2001).

DISTRIBUTION: This species is so far known only from the type locality, lowlands of Puyehue National Park. The vegetation is part of the Subantarctic Valdivian phytogeographic district (Gajardo, 1994), also known as Valdivian Forest. It is dominated by *Nothofagus dombeyi* Mirb.



FIGURE 4. Collecting site of *Puehuemyia chandleri*, gen. nov., sp. nov., with *Nothofagus dumbeyi* in the foreground.

Oerst., also having the characteristic Myrtaceae *Luma apiculata* (DC.) Burret, the conifer *Podocarpus nubigenus* Lindl. and other austral floral elements.

BIOLOGY: Not much can be said about the biology of this fly. It was collected with a Malaise trap in the lowlands (440 m) of a temperate rain forest, in a patch of primary forest recovering from previous anthropic influence, but still with large *Nothofagus* trees and a good amount of rotting wood and woodland detritus (fig. 4). The general structure of the environment where *P. chandleri* was collected is similar to the reports for *O. nigra* in Europe (e.g., Roháček and Ševčík, 2011; Tkoč and Roháček, 2014) and for the Japanese species of the genus (Saigusa, 1963). It is interesting to note that *O. nigra* adults have been reared from rotten *Fagus* wood (Speight et al., 1990; Chandler, 2001) and the larvae are still unknown. The sclerotized, piercing ovipositor of the females in *Opetia* species and in *P. chandleri* may suggest a parasitoid biology for the larvae, even though some tephritoids have a piercing oviscapt used to oviposit in fruits or stems. If this is correct, it would explain why the larvae have not been found although quite a number of adults have been reared from different localities.

COMMENTS: The spermathecae cannot be observed without dissection. In *Opetia* there is a single, unpigmented spermatheca (Sinclair and Cumming, 2006). It may be the case that the spermathecae is similar in *P. chandleri*. Additional specimens would allow dissection of specimens, clarifying several morphological features, including details of the maxillary palpus and ovipositor. There are some dimorphic features in *Opetia* that may well apply also to *Puyehueemyia*. Females of *Opetia* also have dichoptic eyes, with undifferentiated dorsal and ventral ommatidia, and the anal lobe is not developed in the wing. Male eyes of *Opetia nigra* (fig. 5A, C) are holoptic, the dorsal ommatidia are larger than the ventral ones, and the wing has a well-developed anal lobe.

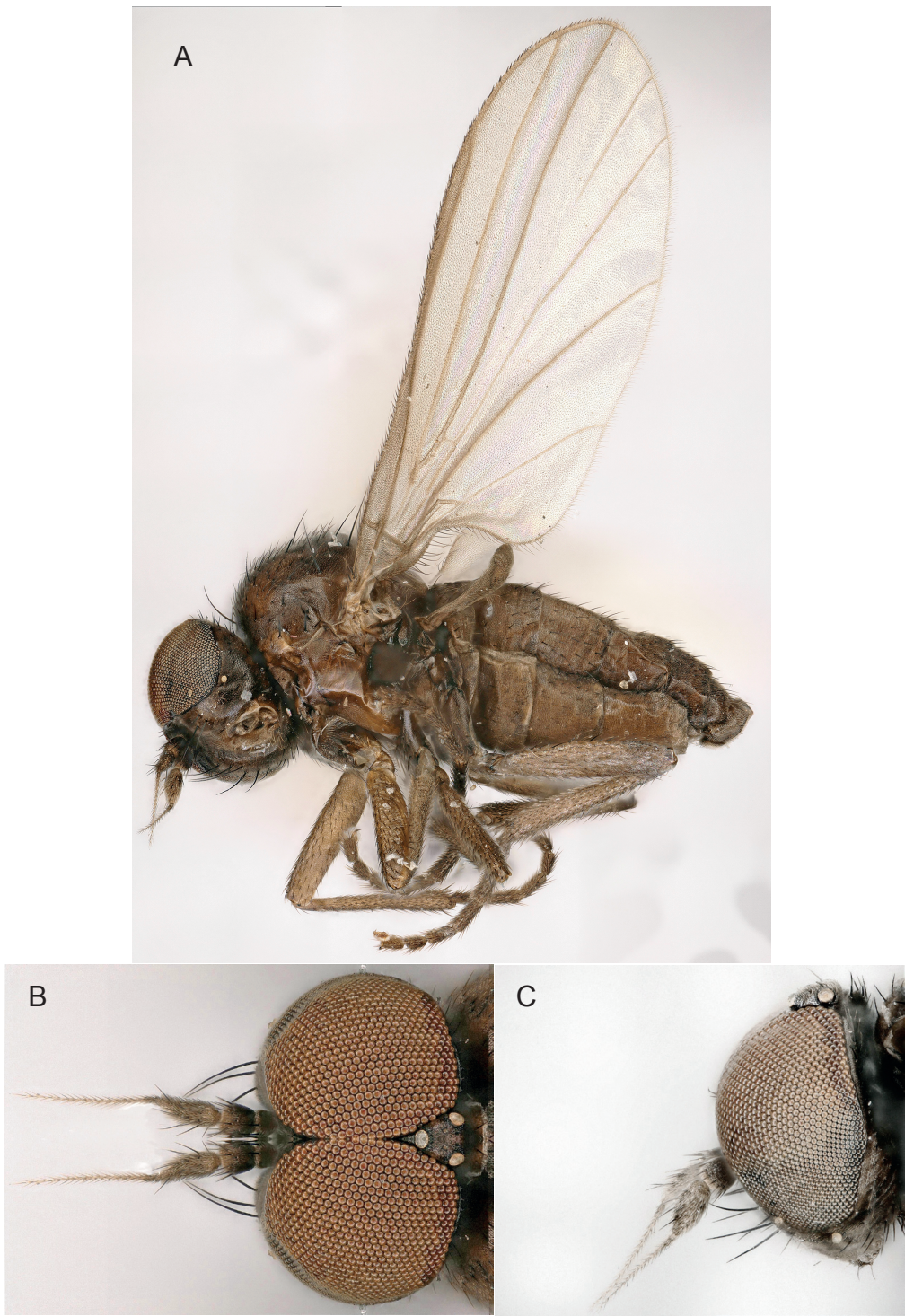


FIGURE 5. *Opetia nigra* Meigen, male: A, habitus; B, head, dorsal view; C, head, lateral view.

DISCUSSION

PHYLOGENETIC POSITION OF *PUYEHUEMYIA* AND OF OPETIIDAE

The genus *Puyehuemyia* is monobasic and *P. chandleri* is the only species of the family known for the Southern Hemisphere and the New World. Its closer relationship with *Opetia*, i.e., its inclusion in the Opetiidae, is based on a number of derived similarities, not just plesiomorphies. Some plesiomorphic traits in *Puyehuemyia*—such as the long, complete Sc, the long R_1 and R_{2+3} , and the complete medial fork—are indeed shared with *Opetia*. Features such as the absence of crossvein dm-m, the very basal origin of Rs and of R_{2+3} , the long medial stem, and the small size and the basal position of cells br, bm, and cua are apomorphic features shared by *Puyehuemyia* with lonchopterids, sciadocerines, and euphorids (see Brown et al., 2015). A strong M_4 is shared by *Opetia* and *Puyehuemyia*, as well as the discrete r-m and the circumambient C (which is also known in the lonchopterids). A small maxillary palpus is widespread among the platypezoids, but the condition in *Opetia* is similar to that in *Puyehuemyia*. The reduced abdominal segments 5–7 and a piercing-type ovipositor are clearly shared by *P. chandleri* with *O. nigra* (Chandler, 2001) and *O. anomalipennis* (Saigusa, 1963) (female unknown in *O. alticola*).

The differences between the Chilean species and the Palearctic species are not enough to justify a separate family, but are certainly enough for a distinct genus. The dark brown or black color of *O. alticola* and *O. nigra* (fig. 5A) is not seen in *P. chandleri* (fig. 1A), which is grayish ochre to light brown. The antenna in the Chilean genus has meaningful dissimilarities with that of *Opetia*. The longer antennal pedicel in *Puyehuemyia*, widening to the apex (fig. 1B), diverges from the remaining opetiid species (fig. 5B, C). The shape of the first flagellomere in *Opetia* is slightly wider at the base and tapered to the apex; in *Puyehuemyia* the first flagellomere is slightly wider midway to the apex. As will be discussed below, the condition of a 3-articled arista in *Pueyhuemyia* is noticeably divergent from *Opetia*, and particularly meaningful to the understanding of the evolution of the antennae among the Eremoneura. The 3-articled arista is the plesiomorphic condition in Platypezoidea, and *Opetia* is well known for its 2-articled arista, with a short basal aristomere (fig. 5B, C). The wing in *Pueyhuemyia* has dorsal setation on R_1 (fig. 2C), while in *Opetia* all veins are entirely bare of macrochaetae (fig. 6C). Finally, *Opetia* has four pairs of well-developed dorsocentrals, though in irregular rows, reaching the anterior third of the scutum (fig. 6A), while in *Pueyhuemyia* there is a single pair of dorsocentrals at the distal fifth of the scutum (fig. 2A). The male of *P. chandleri* is unknown, so features of the male terminalia cannot be compared between the two genera at this time. Similarities of the antenna with the Atelestidae, in which the antenna has more a stylus than an arista, would be plesiomorphic.

The question of the 2-articled arista in *Opetia* is an old issue in the discussion of the position of *Opetia*. Other features, such as the rotation of the male terminalia, the three sclerotized spermathecae, and the ejaculatory apodeme and sperm pump detached from the base of the phallus, join the “problem” of the 2-articled arista to produce what Chandler (2001) referred to as an enigma—which is now clarified with the description of *Puyehuemyia*. A many-articled

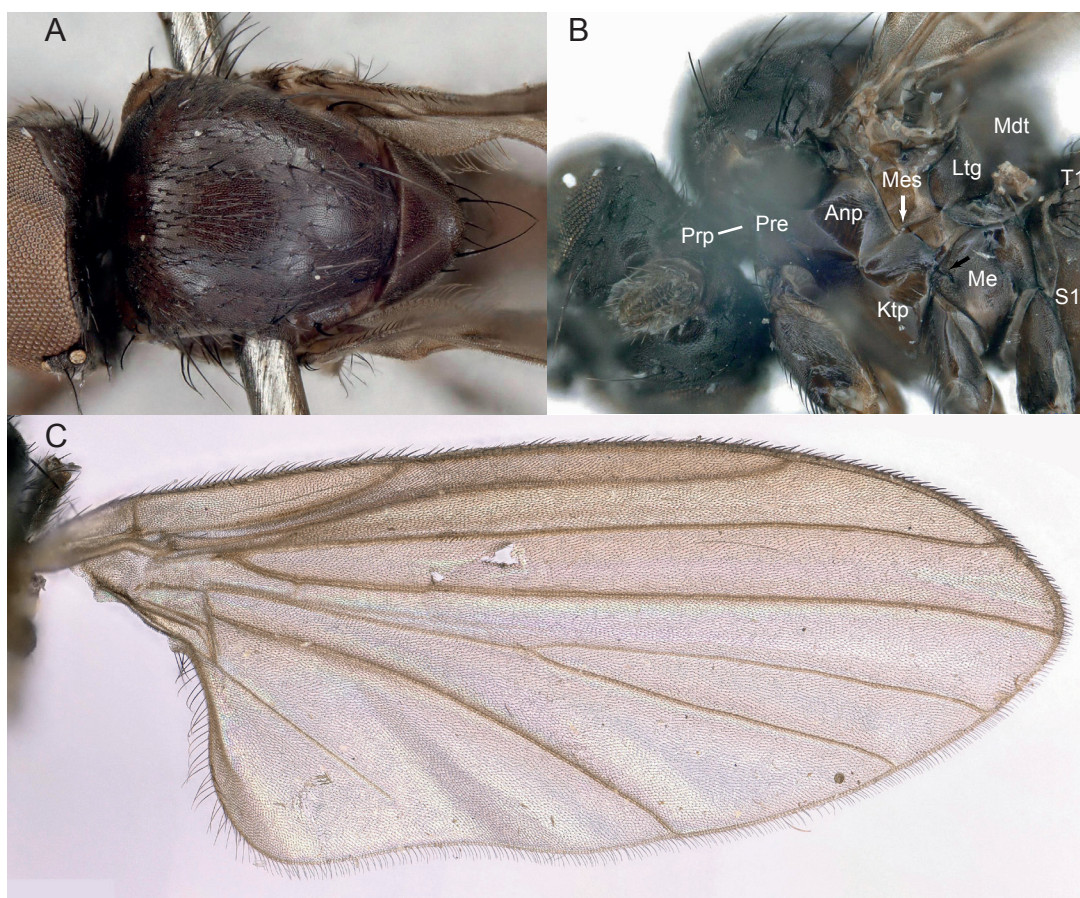


FIGURE 6. *Opetia nigra* Meigen, male: **A**, thorax, dorsal view; **B**, thorax, lateral view; **C**, wing. Black arrow points to the short displacement of the katepisternum under the mesepimeron, white arrows points to the partial suture between mesopleurotrochantin and meron.

arista is obviously the plesiomorphic condition for the antenna in flies, with many independent reductions. In the Stratiomyomorpha (James, 1981c; Woodley, 2009), the stylus has between five and eight flagellomeres, while in the Xylophagidae and in Xylomyidae its number varies between three and nine (James, 1981a, 1981b; Pechuman and Teskey, 1981; Webb, 1981; Stuckenberg, 1999). The Asilomorpha have a 2-articled stylus. The phylogenetic position of bombyliids, acrocerids, and nemestrinids relative to the asilomorphs and other higher brachycerans has been an issue, but the condition of the stylus in these families helps to clarify the discussion. The Nemestrinidae have a 3-articled stylus (Teskey, 1981), as do the Acroceridae (Schlinger, 1981). In the Bombyliidae this feature varies between one and three segments (Hall, 1981). Most Empidoidea have a 2-articled stylus. Cases of a 3-articled stylus in empidoidea are hypothesized to be secondary, since they are deeply nested inside the group—e.g., in the genera *Acarteroptera* and *Meghyperus*—with the possible exception of the Atelestidae.

In most syrphids, the arista has two segments (Vockeroth and Thompson, 1987), while the Pipunculidae have a 3-articled arista (Hardy, 1987). The question of the antennal arista in the

Schizophora is also complex. Both 2- and 3-articled conditions are present in various schizophoran families, although this information is not always clear. The 3-articled condition is known, among other families, in Micropezidae, Tanypezidae, Syringogastridae, Lonchaeidae, Ulidiidae, Pyrgotidae, Tephritidae, Richardiidae, in all Sciomyzoidea, all Lauxanioidea, Clusiidae, Agromyzidae, Heleomyzidae, Scatophagidae, Muscidae, Sarcophagidae, Tachinidae, and Calliphoridae. Inferences about the ground-plan condition at different levels within the brachycerans depend on optimization over a phylogeny—presently under heavy dispute. It is quite straightforward, however, independent of the disagreements about the phylogeny of the Muscomorpha, that the 3-articled arista is plesiomorphic and that reductions from three to two segments must have occurred many times independently in the group.

In the Platypezoidea, *Ironomyia*, *Lonchoptera*, most platypezids, and most phorids have 3-articled arista—phorids also have species with 2- and 1-articled arista (McAlpine, 2011). The Cretaceous amber platypezid *Electrosania cretica* Grimaldi and Cumming has a 2-articled arista (Grimaldi and Cumming, 1999). In other Cretaceous platypezids (some being described now, D. Grimaldi, personal commun.), ironomyiids, and sciadocerines, the arista is usually 3-articled. In this scenario the condition of the 3-articled arista in *Puyehuemyia* (fig. 2B, C) is instructive. It shares the plesiomorphic condition for most other Platypezoidea and elucidates that the 2-articled condition in *Opetia* is probably secondary. Indeed, the condition in *O. nigra*, with a first aristomere much shorter than the second, seems to be more modified than in *O. anomalipennis*, where the second aristomere is only slightly less than half the length of the third aristomere (see, e.g., Sinclair and Cumming, 2006: figs. 45–46). This scenario reinforces the opinion that the condition in acrocerids and nemestrinids, some bombyliids, most platypezids, pipunculids, and many schizophorans is indeed plesiomorphic, with independent reductions in the history of the Muscomorpha.

The evolution of the thoracic pleural sclerites in Phoridae has been addressed in great detail in Brown et al. (2015). Thoracic pleural sclerites show a number of different modifications along the evolution of phorids, particularly in the size and position of the meron relatively to the mesepimeron. The condition seen in sciadocerines is relatively plesiomorphic within the phorids, in many senses similar to the condition in Platypezidae or even outside the Platypezoidea. The condition in *Lonchoptera* is highly distinctive, apparently with a dorsoposterior displacement of the posterior spiracle, stretching the shape of the meron. In *Puyehuemyia* the shape of the katepisternum is puzzling, since it only slightly projects posteriorly over the meron. The considerable projection of the katepisternum over the meron is widespread in brachycerans, seen, e.g., in Therevidae, schizophorans, Platypezidae, Lonchopteridae, and Phoridae (see Brown et al., 2015: figs. 1–4). In this sense, the short katepisternum in *Puyehuemyia*, also seen in *Opetia* (seta respectively in figs. 2B and 6B), should be seen as apomorphic in relation to the condition in platypezids or sciadocerines. On the other hand, the size and placement of the anterior spiracle relative to the anepisternum and to the proepimeron, and the elongated shape of the anterior basallare, at the dorsoposterior corner of the anepisternum, show considerable similarity with the pattern seen in other nonphorid platypezoids, corroborating its inclusion in the clade. The shape of the mesopleurotrochantin in *Puyehuemyia* (fig. 6B), with an incom-

plete suture separating it from meron, is similar to *Opetia* (fig. 6B), but also to other platypezids (Brown et al., 2015: fig. 2), when comparing the complete mesopleurotrochantin, e.g., in *Therevidae* (Brown et al., 2015: fig. 1). Another helpful feature in this context concerns the abdominal plaques seen in tergites and sternites of different fly families. These structures have been found in all nematoceran clades, besides basal brachycerans (including Empidoidea), assumed to be the site of attachment of muscles used by the pupa for abdominal movements and for eclosion of the adult (Stoffolano et al., 1988). These structures are missing in all Cyclorrhapha (including *Opetia*), which does not have mobile pupae (Wiegmann et al., 1993, Cumming et al., 1995, Sinclair and Cumming, 2006), and are not seen as well in *Puyehuemyia*.

A long Sc, reaching at least the middle of the wing, is the plesiomorphic condition in Brachycera, also seen in some platypezid genera (fig. 8A), as well as in *Ironomyia* (fig. 8B). In *Lonchoptera* (fig. 8C), *Opetia* (fig. 6C), and in most phorids, Sc does not reach the middle of the wing. A reduction of Sc also has occurred independently within the Platypezidae. The evolution of the length of R_1 is slightly different: a strong reduction occurred independently in *Lonchoptera* and in the Euphorida (Brown et al., 2015). The only noticeable change in R_{2+3} in platypezoids is, by contrast, the extension of the vein in *Lonchoptera*, ending close to the wing tip. The extension of R_{4+5} shows no significant changes in the Platypezoidea except for the major reduction (with various stages) that has occurred in the evolution of the Phoridae. The extension of the costa has some variation. In different species of Platypezidae (fig. 8A) C reaches M_1 . Sinclair and Cumming (2006) infer that the circumambient costa would be the ground-plan condition within the Empidoidea, with many changes within the clade, stating that this feature is variable and hard to code. For the time being, it is difficult to say whether the condition in *Opetia* and *Puyehuemyia* is homolog to that of empidooids, or whether it is a secondary development within the Platypezoidea. A reduction of the costa to R_{4+5} is shared by *Ironomyia* and nearly all phorids. The condition in *Lonchoptera* is puzzling, since there is a wide costa clearly extending to R_{4+5} , but a slender circumambient costa along the posterior margin of the wing.

The origin of Rs in all platypezoids seems to be closer to the wing base than in most empidooids (fig. 7C), maybe with the exception of the Dolichopodidae (fig. 7D), and other cyclorhaphans (fig. 9B–C). This feature, however, is hard to quantify and to transform into an objective character. The displacement to the base of the fork between R_1 and Rs may have occurred in parallel with the displacement of the closed posterior cells to the base of the wing (see below). The transverse vein r-m is conservative in the Platypezoidea. It acquires a longitudinal position in *Lonchoptera* and is lost in the Euphorida (r-m is tiny in *Sciadocera*, but still present). Perhaps the position of r-m is slightly more displaced to the base in the platypezoids, but the differences are subtle and this is a variable feature. In *Lonchoptera* and sciadocerines the origin of r-m at Rs is much closer to the fork of the radial sector, i.e., the origin of R_{2+3} . The medial fork appears to have undergone different changes in the evolution of the Platypezoidea. In *Platypezina* the medial fork is at the level of m-m+ M_3 . Other platypezids have a complete loss of M_2 (as in *Agathomyia* and *Callomyia*) or displacement of the medial fork close to the tip of the wing (as in *Lindneromyia*, in which M_2 does not reach the wing margin). The medial fork in *Lonchoptera*

is possibly at its plesiomorphic position, slightly beyond the middle of the wing, as is also seen in *Opetia* and in *Puyehuemyia*. The main difference of the medial fork in Opetiidae and Lonchopteridae, when compared with *Ironomyia* or the platypezids, is that the distal crossvein (that closes the discal-medial cell) is clearly absent. Surprisingly in Sciadocerinae (fig. 13) there is a tiny dm cell near the base of the wing, with the crossvein still present. The displacement of the closed posterior wing cells—d, br, bm, and cua—to a basal position in the wing and their reduction in size in higher platypezoids is one of the most characteristic features of a clade including Opetiidae (fig. 12A–B), Lonchopteridae (fig. 11B), and Phoridae (fig. 13). These cells are considerably larger in *Ironomyia* (fig. 8B) and all platypezid genera (e.g., fig. 8A)—and even larger in some empidoids (fig. 10B) or pipunculids (fig. 9B), and schizophorans (fig. 9C).

As mentioned above, a relatively wide M_4 is a newly proposed synapomorphy of the Opetiidae (figs. 2C, 6C). The fusion of CuA and CuP is apomorphic in all Eremoneura (with parallel developments in other brachycerans, as in some asilids, acrocerids, etc.). An elongated cell cua is the plesiomorphic condition shared, for example, by brachystomatids, pipunculids, and conopids (fig. 7A–C, 9B–C). The reduction of the size of cell cua has occurred independently at different times. In all Platypezoidea, cell cua is relatively short, but the condition in Platypezidae and *Ironomyia* is plesiomorphic when compared to that in Lonchopteridae, Opetiidae, and Phoridae, all of which have a very small cell cua. Different clades within the empidoids and the schizophorans developed an incomplete CuA+CuP, not reaching the wing margin. Within the Platypezoidea, only *Opetia* males (complete in females, fig. 2C) and some few phorids have an incomplete CuA+CuP.

An additional source of information in the discussion about the placement of *Puyehuemyia* and the position of the Opetiidae is the structure of abdominal segments—at this stage applicable only to females. Platypezids, ironomyids, and lonchopterids have a regular number of well-developed abdominal segments, i.e., from 1–7. Chandler (2001: 19) describes the female abdomen of *Opetia* as with “segments 1–3 normal, 4 at least a little longer than 3 (...) and 5 shorter,” with tergum and sternum fused basally, the remaining segments fused into the ovipositor, “strongly chitinised.” This condition, which is unique in the Platypezoidea (with some possible exceptions among strongly modified phorids), is extremely similar to that seen in *Puyehuemyia* (fig. 3C, D).

The set of features seen in *Puyehuemyia*, hence, supports the hypothesis (Chandler, 2001; Wiegmann et al., 2011) that the Opetiidae belongs to the Platypezoidea Cyclorrhapha. The 2-articled condition of the stylus in *Opetia* is a secondary, independent reduction, while the wing venation suggests a close connection of the Opetiidae with the higher Platypezoidea—all of which with cells small cells br, bm, and cua, displaced toward to wing base.

FOSSILS ASSOCIATED WITH THE OPETIIDAE

Evenhuis (1994) compiled five Mesozoic fossils in the world catalog of fossil Diptera assigned to Opetiidae: *Palaeopetia* Zhang, *Pseudopetia* Zhang, *Mesopetia* Zhang, *Lithopetia* Zhang—*Sinolestia* Hong and Wang was later considered a junior synonym of *Palaeopetia*—and

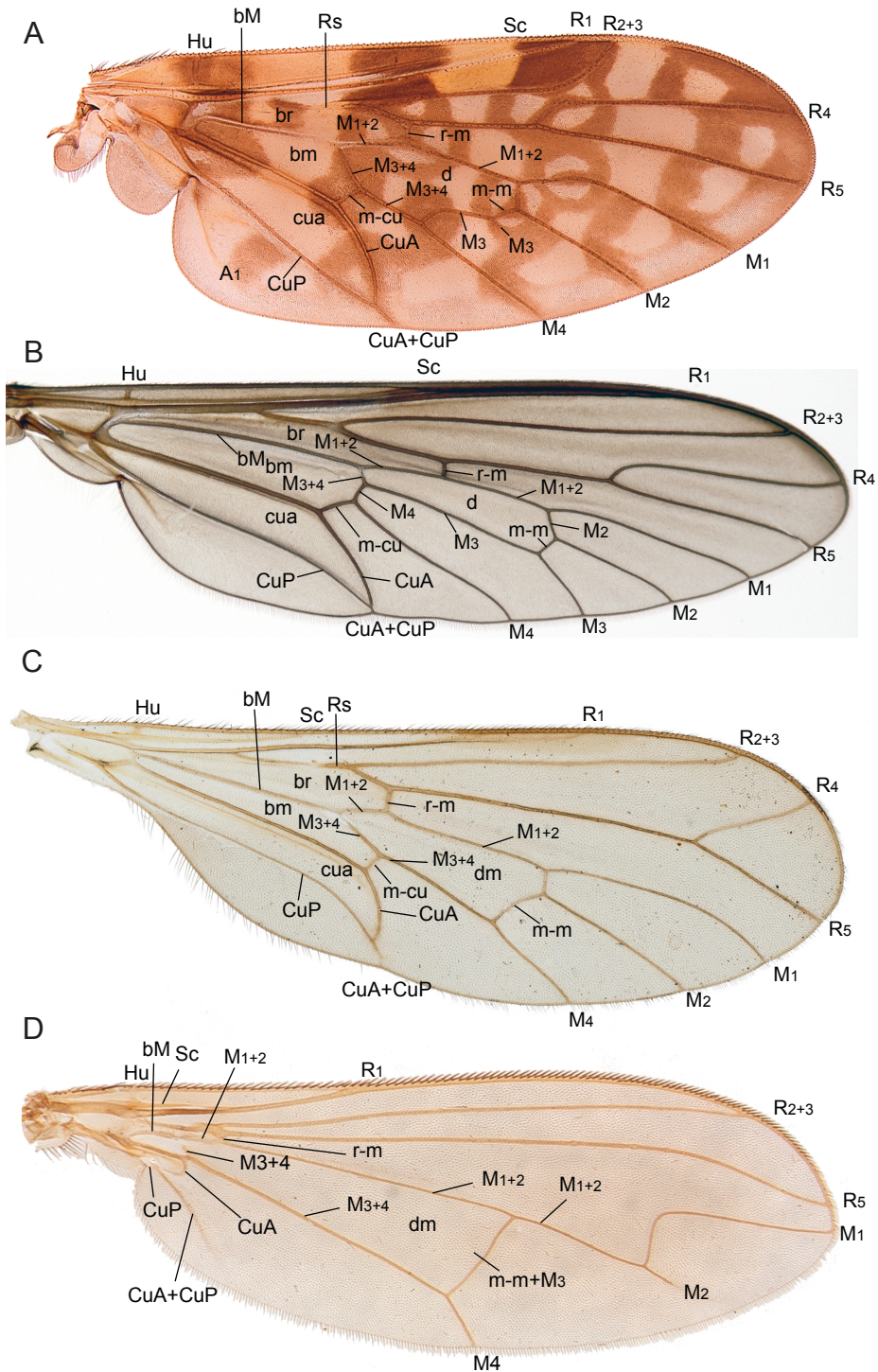


FIGURE 7. Wing of brachyceran families: **A**, *Austroleptis* sp. (Austroleptidae); **B**, *Holcocephala calva* (Loew 1872) (Asilidae) (photo kindly provided by Torsten Dikow); **C**, *Brachystoma* sp. (Brachystomatidae); **D**, *Amblypsilopus* sp. (Dolichopodidae).

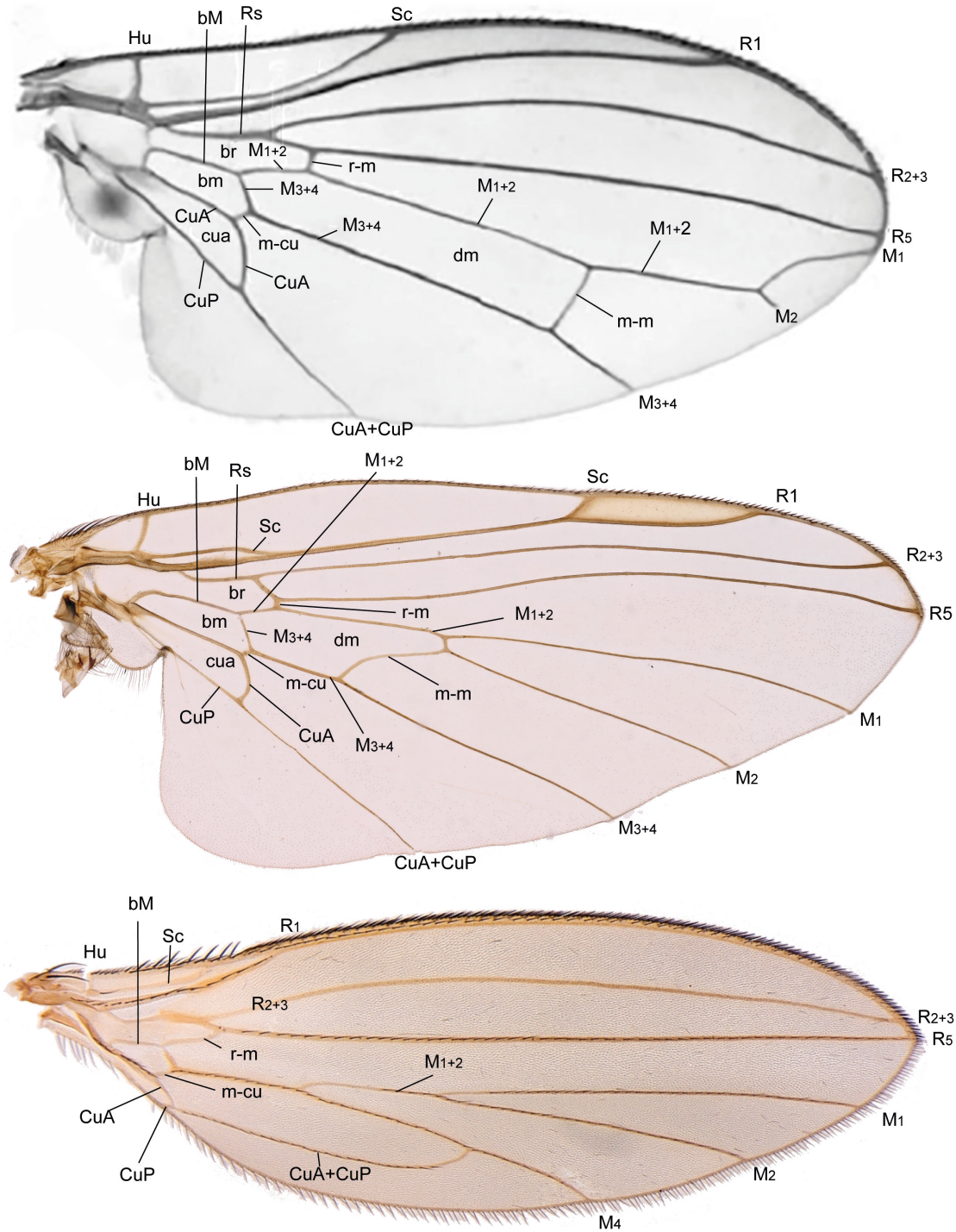


FIGURE 8. Wing of brachyceran families: **A**, *Lindneromyia* sp. (Platypezidae); **B**, *Ironomyia* sp. (Ironomyiidae); **C**, *Lonchoptera bifurcata* Fallén (Lonchopteridae).

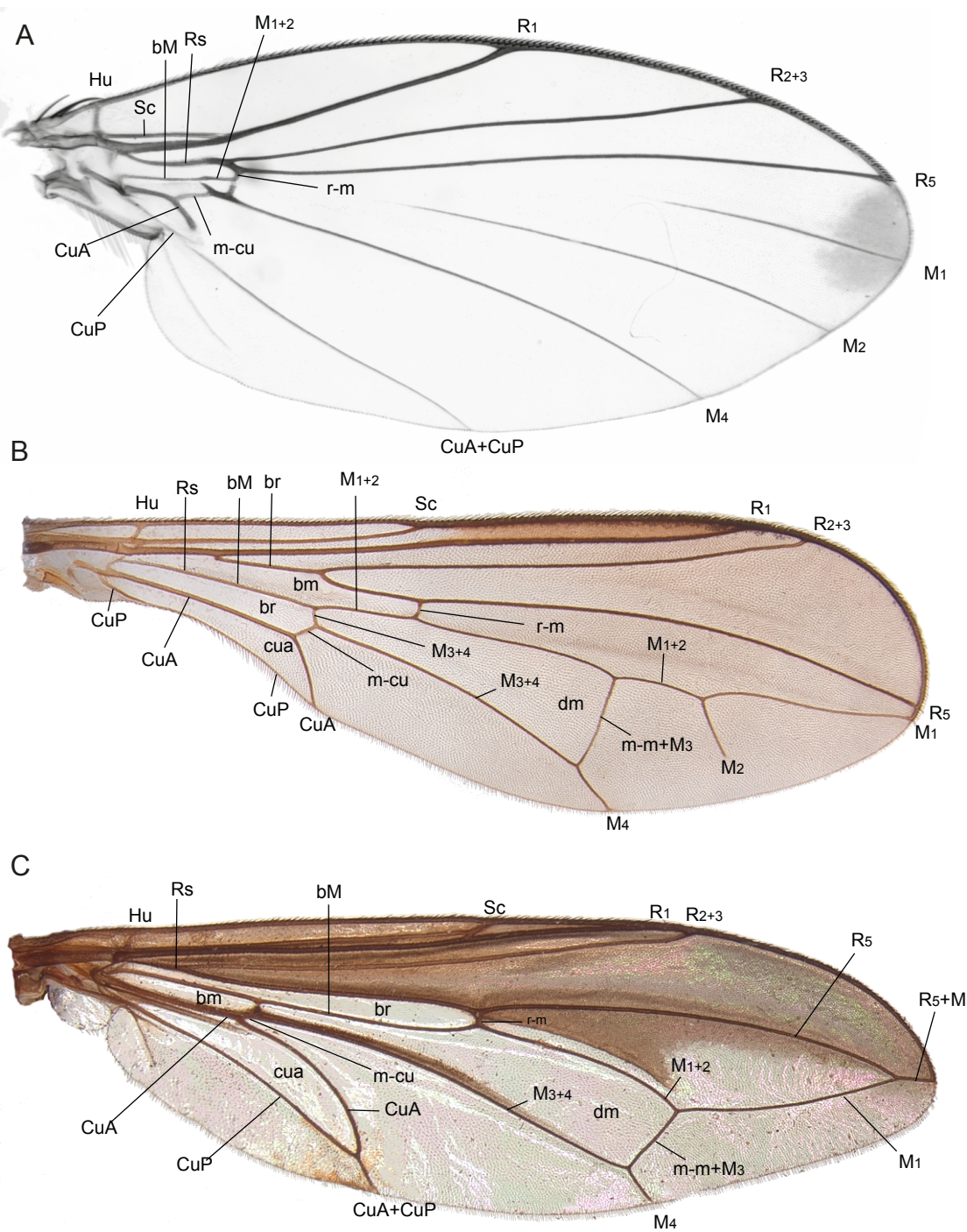


FIGURE 9. Wing of brachyceran families: **A**, *Sciadocera rufomaculata* (White 1916) (Phoridae); **B**, *Protonephrocerus* sp. (Pipunculidae); **C**, *Physoconops* sp. (Conopidae).

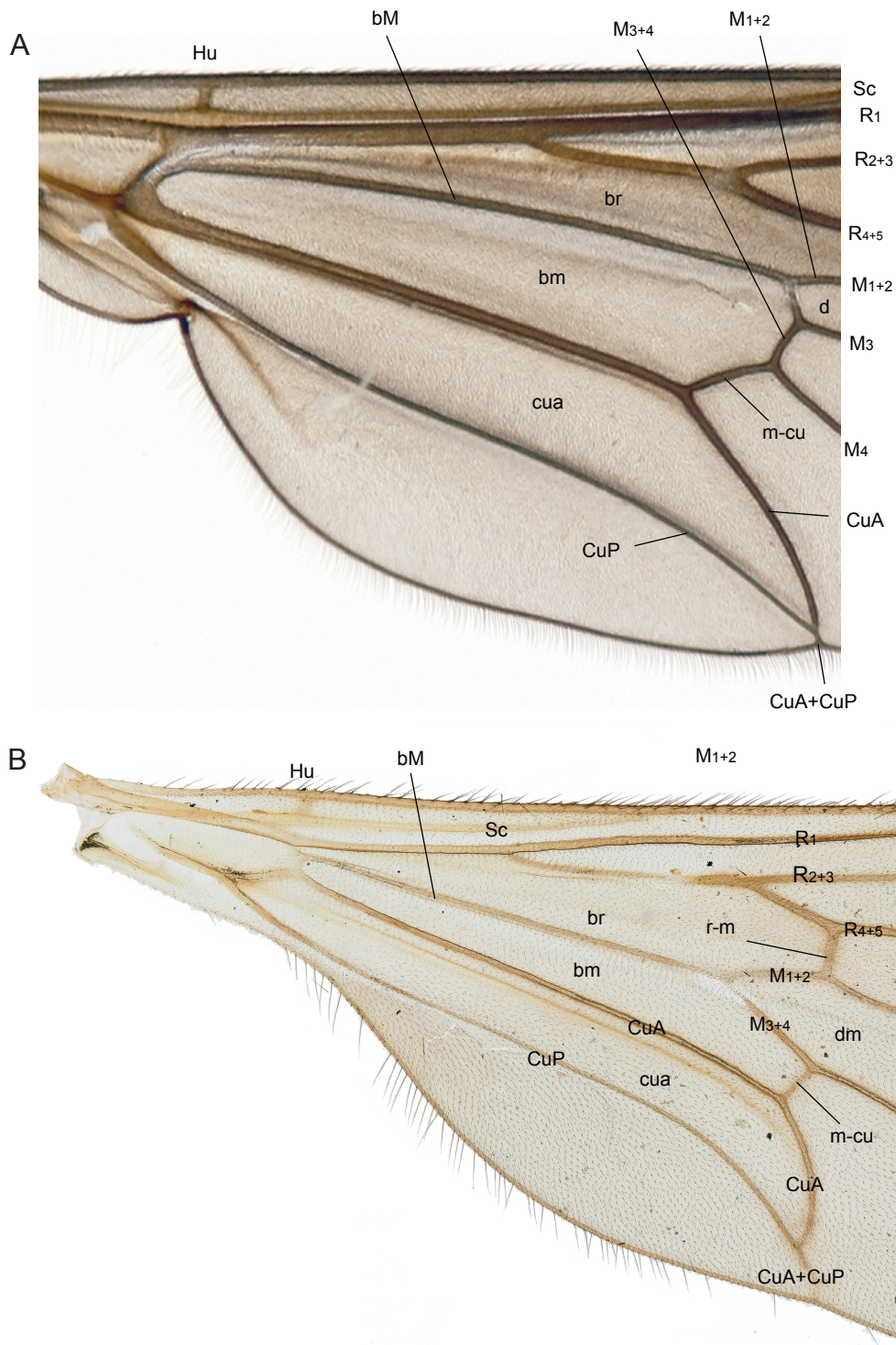


FIGURE 10. Detail of venation at base of wing of Muscomorpha families: **A**, *Holcocephala calva* (Loew 1872) (Asilidae; photo, Torsten Dikow); **B**, *Brachystoma* sp. (Brachystomatidae).

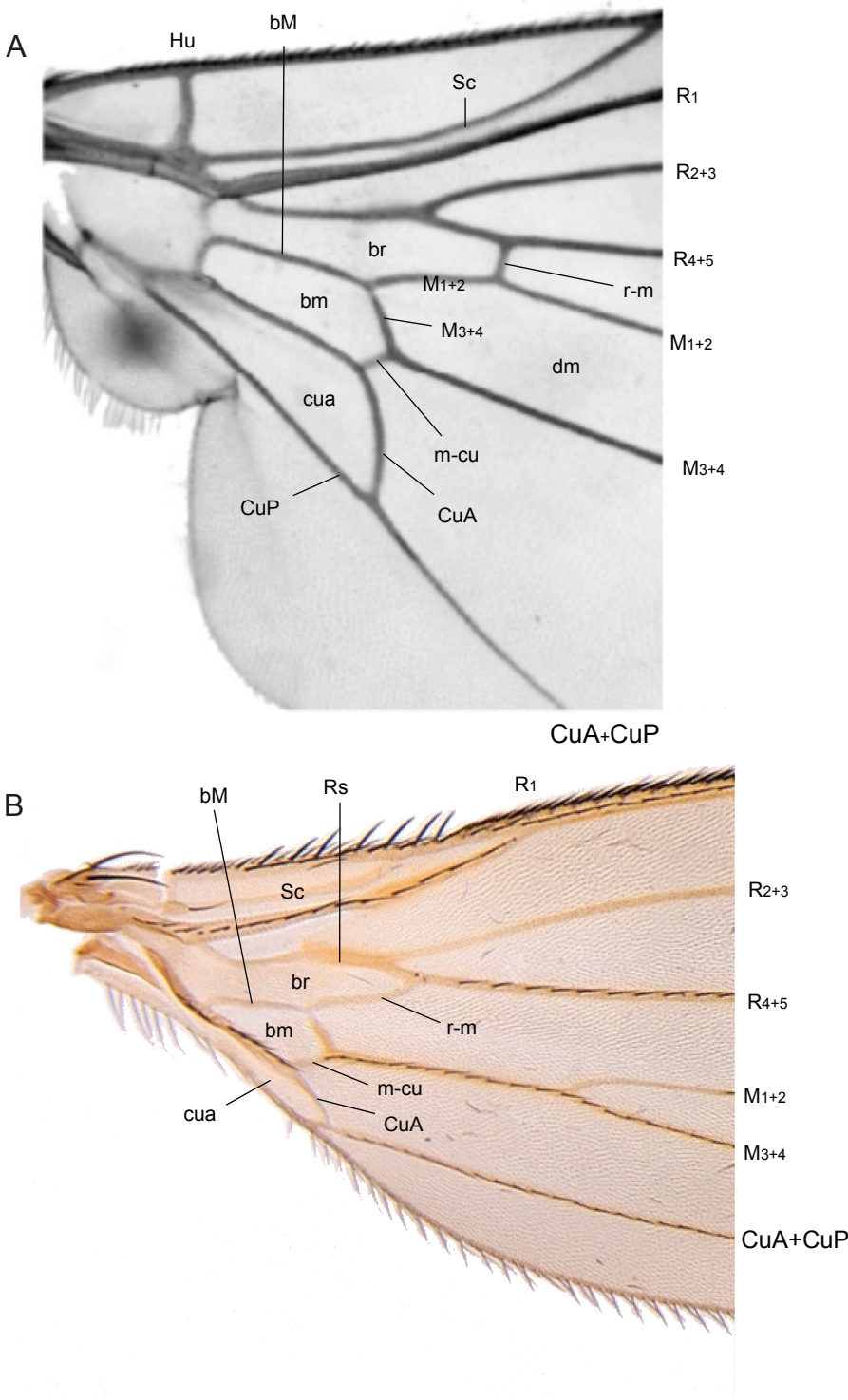


FIGURE 11. Detail of venation at base of wing of Muscomorpha families: **A**, *Lindneromyia* sp. (Platypezidae); **B**, *Lonchoptera bifurcata* Fallén.

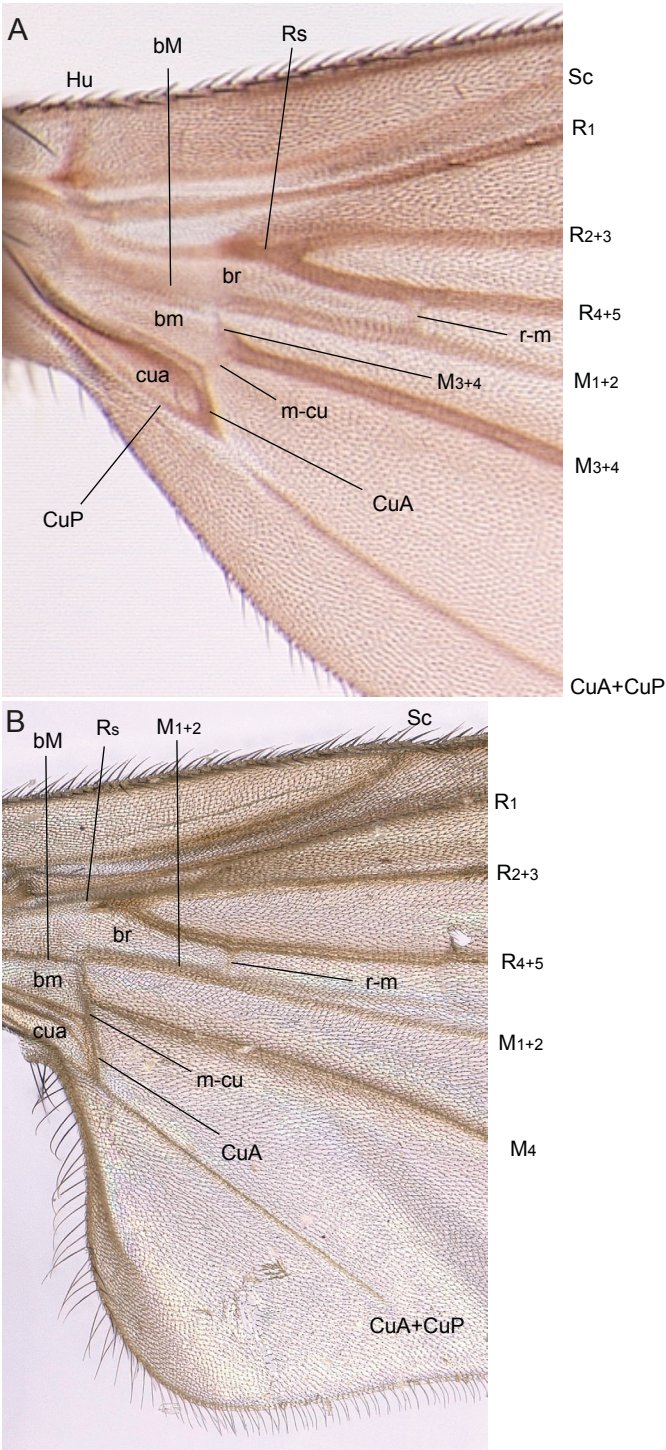


FIGURE 12. Detail of venation at base of wing of Muscomorpha families: **A**, *Puyehuemyia chandleri*, gen. nov., sp. nov.; **B**, *Opetia nigra* Meigen.

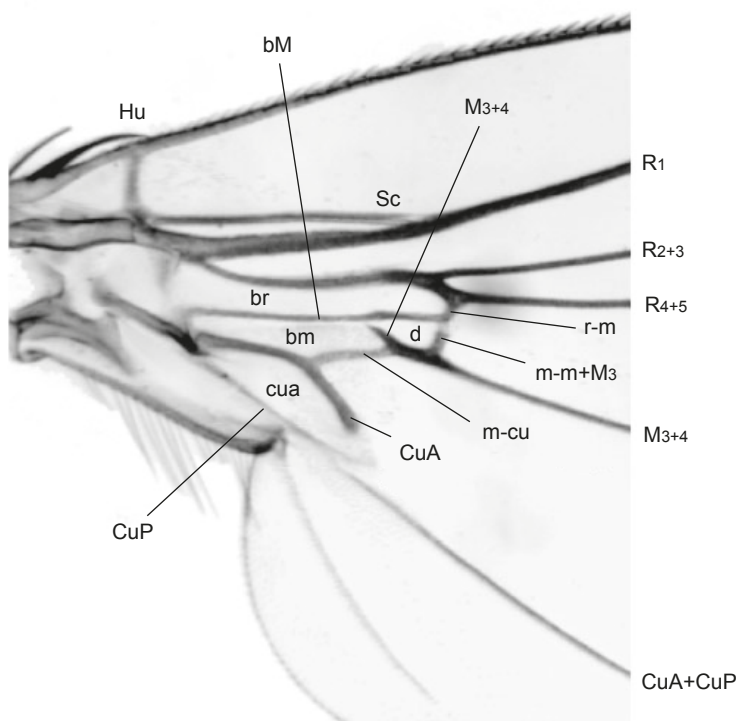


FIGURE 13. Detail of venation at base of wing of Muscomorpha families: *Sciadocera rufomaculata* (White 1916).

their position was later discussed by Chandler (2001). He assumed that *Pseudopetia* Zhang belongs to the Rhagionidae, while *Mesopetia* Zhang could belong to Platypezidae. *Palaeopetia* Zhang was suggested by Mostovski (1996) to be related to the Ironomyiidae. *Lithopetia* Zhang also does not fit with other opetiids. The long medial fork and the origin of R_{2+3} distant from the wing base clearly separates it from the Opetiidae crown group, as well as from the stem group. Zhang's (1987: fig. 5B) illustration of the wing is not very clear, because of a leg over the wing, but cell *cua* seems to be too long to fit into the clade including Opetiidae, Lonchopteridae, and Phoridae. *Lithopetia* might belong in Platypezoidea, but more certainty depends on the reexamining the holotype for a better understanding of the wing venation. Being a Jurassic fossil, it would be understandable if it fits slightly lower in the platypezoid phylogeny.

The Cretaceous New Jersey amber fossil *Electrosania* Grimaldi and Cumming was questionably assigned to the Platypezidae. Chandler (2001) agreed with its inclusion in the Platypezidae, observing that it "has a thoracic chaetotaxy and arista structure as in Opetiidae." The distal medial fork with an incomplete M_2 in *Electrosania* is a unique synapomorphy of a subgroup of Platypezidae. The setation of the scutum, as in *Puyehuemyia*, is a plesiomorphic trait, while the condition of two aristomeres in *Electrosania* is most certainly only an additional case of independent shift from three to two articles in the arista within the platypezoids. The results here help to fully support Grimaldi and Cumming's (1999) and Chandler's (2001) association

of *Electrosania* to the platypezids. More recently, Coram et al. (2000) described *Opetiala* from the Purbeck Limestone Early Cretaceous. The wing has a closed discal cell and there is no medial fork. It is beyond the scope of this paper to determine its position within the platypezoids, but *Opetiala* does not belong to the crown of Opetiidae or to its stem.

A relevant addition to the discussion of platypezoid fossils concerns the Neocomian early Cretaceous Lebanon amber *Lonchopterites prisca* Grimaldi and Cumming. Sc and R_1 in this fossil are shorter (apomorphic traits) than in the crown species of Opetiidae. R_{2+3} and R_{4+5} diverging at the very base of the wing, the shape of the medial fork, the absence of a closed discal cell, and the fact that cells bm, br, and cua are not at a more distal position in the wing—not represented in the original illustration (Grimaldi and Cumming, 1999: fig. 53)—produce a wing pattern like that of *Opetia*. Some features typical to the Lonchopteridae—the basal fusion of M_{1+2} to M_4 , the displacement of R_{2+3} to the tip of the wing, and the strong reduction in the length of Sc and R—are not present and *Lonchopterites* does not properly fit into crown-group Lonchopteridae. Moreover, the antenna has a basal flagellomere widening midway to the apex and the arista has a terminal position with two aristomeres—features that we can better understand in light of the information brought up by *Puyehuemyia*. There is no other group within the eremoneurans with such a combination of features. In fact, Grimaldi and Cumming (1999) specifically discuss the similarities of *Lonchopterites* with *Opetia*. Nevertheless, the acute apex of the wing, vein C ending at R_{4+5} (instead of circumambient), the bristly legs, a well-developed vibrissa, and robust head setae led them to suggest *Lonchopterites* to be a stem-group lonchopterid. Some features listed as present in the fossil and absent in *Opetia* are actually observable in *Puyehuemyia*, including the spinulose costa and R_{4+5} longitudinally bisecting the wing. On the other hand, the abdomen of the female holotype has a “generalized structure, with small pair of terminal cerci closely adpressed to apex of abdomen” (Grimaldi and Cumming, 1999: 84) and the wing has a well-developed anal lobe in the female. These are plesiomorphic conditions compared to the recent species of Opetiidae of the genera *Opetia* and *Puyehuemyia*. This combination of features suggests that *Lonchopterites* would be a good candidate to be sister to the clade with the recent members of the family.

BIOGEOGRAPHICAL AND EVOLUTIONARY IMPLICATIONS

Anyone who might have sorted a Malaise trap sample from the southern island of New Zealand may have noticed the similarity of the final list of sampled families with the list of Cretaceous amber flies—basically species that belong to families that go “up” in the fly phylogeny to the phorids. Only a few schizophorans come into the traps. Malaise trap samples from southern Chile lowland temperate rainforests are similar, though the number of schizophorans may be slightly higher. Austral nonschizophoran elements shared by New Zealand and Chile include, for example, the ditomyiid genus *Nervijuncta* Marshall (also present in southern Brazil), the canthyloscelid genus *Canthyloscelis*, ceratomerines empodoids and the sciadocerine phorids *Sciadocera rufomaculata* (New Zealand and Australia) and *Archiphora patagonica* (Chile). The empidoid *Gondwanamyia*, though quite derived, also has one species known from Puyehue National Park and one

species known from New Zealand (Sinclair et al., 2016). *Canthyloscelis*, *Gondwanamyia*, and *Archiphora* Schmitz were all collected at the collecting site of *Puyehuemysia*. There are a considerable number of other austral connections in tipulomorphs, bibionomorphs, and other flies, as well as in various insects (reviewed in Grimaldi and Engel, 2005).

Dominant floral elements in these forests, including certain clades of bryophytes, ferns, conifers, and early angiosperms, are well documented as fossils in Antarctica (Cantrill and Poole, 2005). Cases of disjunctions between Chile and Australia already include a number of modern elements, i.e., the schizophoran families Paraleucopidae, Pseudopomyzidae, Pallopteridae, Teratomyzidae, Helosciomyzidae, Helcomyzidae, and the quite diversified (and possibly paraphyletic) Heleomyzidae. This means that the shared elements between Chile and New Zealand are phylogenetically more restricted than those between Chile and Australia, i.e., probably limited to the fly diversity at the time of detachment between New Zealand and the rest of southern Gondwana.

Edwards (1929) based on extensive collecting in Chile already assumed a land connection between South America, New Zealand, and Australia, and in a period with limited information on geology, paleoclimatology, and phylogeny of flies, Hennig (1966) tried to explain the elements shared between these three areas. More recently, Almeida et al. (2012) demonstrated that the latest cladogeneses between South American and Australian elements of colletid bees occurred about 30 million years ago. This was later corroborated with results in scionini tabanid evolution (Lessard et al., 2013).

The fact that *Opetia* has been reared from rotting *Fagus* wood logs and that *Puyehuemysia* has been found in the Valdivian forest in Chile, dominated by *Nothofagus*, is also noteworthy. *Fagus* and *Nothofagus* are not sister genera, but belong to the same clade Fagales (Hilu et al., 2003). The age estimated for the cladogenesis separating the clades including Fagaceae and Nothofagaceae is close to 120 m.y. (Sauquet et al., 2012), which is about Aptian age. The divergence age for the Cyclorrhapha has been suggested to be about 150 m.y. (Wiegmann et al., 2011). This is also compatible with the age of the Lebanon amber fossil *Lonchopterites*, from the Neocomian. The combination of the data seen here including fossils, age of divergence of Cyclorrhapha and of Fagales, geology of the southern terranes of Gondwana, and biogeography suggests that the lowland temperate rain forest biota in Chile that includes *Puyehuemysia* belongs to a biogeographical layer (in the sense of Amorim et al., 2009) that typically encompasses the fly diversification that originated prior to the large schizophoran diversification. If the reasoning is correct we may still expect more cases of unnoticed higher brachyceran relicts in austral lowland forests in Chile and/or New Zealand, perhaps even species that would fit at the stem of the Schizophora. As in any case of negative evidence, this can be checked only with intense collecting in these environments.

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