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A New Species of Eumanota Edwards (Diptera: Mycetophilidae: Manotine) from Colombia: Evidence for a Pseudogondwanan Pattern

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A new species of *Eumanota* Edwards (Diptera: Mycetophilidae: Manotine) from Colombia: evidence for a pseudogondwanan pattern

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ABSTRACT

Eumanota wolffae, sp. nov., is described from the high Andean forests of Colombia. This is the first Neotropical species of the clade of non-*Manota* genera of the mycetophilid subfamily Manotinae—to date known entirely from the Oriental and the northwestern Australasian regions, and in Baltic amber. With the other species of *Eumanota* Edwards, this species shares, among other features, a largely developed third maxillary palpomere, projecting beyond the base of fourth palpomere, with a wide sensorial pit, a flat inner face, and the last palpomere at least 4× the length of the fourth palpomere. The systematic position of the Colombian species within the Manotinae is addressed. The biogeographic significance of *Eumanota* in the Neotropical region is discussed, interpreted here as a concurrent incidence of a circumtropical pattern and Gondwanan distributions, in other words, a particular pattern of biogeographic pseudocongruence, referred to here as a "pseudogondwanan pattern." This pattern is associated with an early Cenozoic tropical biota over Laurasian terranes that expanded its distribution to the south (in the Americas, Africa, and Australasia), followed by large-scale extinction of Nearctic and Palearctic representatives due to global cooling in the Neogene. A discussion is provided about the correlation between these patterns and evidence of Late Cretaceous-Paleogene tropical floras over Laurasian terranes.

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INTRODUCTION

The Mycetophilidae subfamily Manotinae includes the Recent genera *Manota* Williston, *Paramanota* Tuomikoski, *Promanota* Tuomikoski, and *Eumanota* Edwards. All four genera have been shown to comprise a monophyletic group, the last three genera in a clade sister to *Manota* (Hippa et al., 2005, 2016; Ševčík et al., 2013).

Taxonomic knowledge of the world manotines has remarkably increased over the past 20 years. In the late 1990s there were less than 30 species of *Manota* described worldwide, two species of *Eumanota*, one species of *Paramanota*, and one of *Promanota*. We now have nearly 300 species of *Manota* (Kurina et al., 2018) and the number of species in the other genera have risen to 10 in *Eumanota*, nine in *Paramanota*, and two in *Promanota* (Hippa et al., 2017). The Cretaceous species described in *Alavamanota* Blagoderov and Arillo—*A. hispanica* Blagoderov and Arillo (2002), from Spain, and *A. burmitina* Blagoderov and Grimaldi (2004), from Myanmar—do not belong in a clade with *Eumanota*, *Paramanota*, and *Promanota* (Hippa et al., 2005).

The bulk of the diversity of the non-*Manota* genera of Manotinae is in the Oriental Region, with only three non-Oriental species in this group of genera: *Eumanota malukensis* Søli (2002), from the Molucca Islands, *E. jani* Papp (2004) from Papua New Guinea, and *Paramanota grandaeva* Hippa (2010) from the Baltic amber.

Fly diversity in Colombia is uniquely rich. There are tropical elements connecting Central America along the Pacific coast to the Chocó region, tropical elements with Amazonian connections east to the Andes, and the unique high-mountain Andean forests, as well as the paramo ecosystems. The high Andean forests are located at the top of the northern range of the Andes mountain system. The early stages of the Andean orogeny are Early Jurassic in age (Ramos, 2009), but the northernmost range of the Andes was formed as late as the Pleistocene (Hoorn et al., 2010).

These environments are subject to extreme climatic conditions, including intense solar radiation, strong winds, extensive cloudiness, and strong temperature fluctuations (with changes from "strong winter" to "intense summer" in a single day) (Rangel-Ch., 2000, 2005). No doubt a result of these physical regimes, the high Andean forests host a particular set of very localized, endemic species (Rangel-Ch., 2000). These ecosystems currently suffer drastic impact caused by anthropic activities. Due to the very restrict species ranges, this impact is rapidly leading to a great loss of biodiversity (Herzog et al., 2011).

Taxonomic and ecological studies of invertebrates inhabiting the paramos are scarce or nonexistent (for an overview, see Wolff et al., 2016). In what concerns Diptera diversity, the high Andean forest faunas combine some tropical Mesoamerican and Amazonian elements, but most frequently austral temperate and Nearctic components (Amorim and Pires, 1996; Oliveira et al., 2007; Amorim, 2009), producing not only a species-rich fauna but a phylogenetically diverse one as well.

Recent collecting in the high Andean forests of Colombia with Malaise traps produced an amazing diversity of fungus gnats. Among rather rare rangomaramids, ditomyiids, and various genera of mycetophilids, we found three males and a female of an undescribed species of *Eumanota*. This is the first non-*Manota* species of Manotinae known from the Americas. This

paper describes and illustrates this species, discusses the position of the species among the manotines, and discusses the evolutionary significance of the presence of this species in the Neotropical region.

Material and Methods

All specimens of the type series were collected with Malaise traps in the high Andean forest from the paramos of two sites, one in the municipality of Envigado and the other in Yarumal—both belonging to the Central Cordillera in the Department of Antioquia, Colombia. The male holotype and single male and female paratypes were deposited at the Colección de Entomología of the University of Antioquia (CEUA), and one male paratype was deposited at the Museu de Zoologia of the University of São Paulo (MZUSP). The male paratype housed at the CEUA was stored in 95% ethanol at –20°C for molecular studies.

The male paratype housed at MZUSP had the wings removed and was mounted on a permanent slide; the remainder of the specimen was treated with 10% KOH for about 10 minutes at 40°C to soften internal tissues. The specimen was then kept for 10–15 minutes in 100% glacial acetic acid, and mounted using Euparal on the same slide as the wing. Digital images were made with specimens in gel ethanol or after slide mounting. Photos were taken using a Leica DC 500 camera on a Leica M16 stereomicroscope. Stacking used Helicon Focus 6.7.1. Final photos were treated using Adobe Photoshop CC. Initial drawings of the male terminalia were made using a camera lucida on a compound microscope, vectorized with Adobe Illustrator CC. Photos of the complex male terminalia were taken in many different levels and stacking was made for particular ranges of focus, so individual inner sclerites could be visualized without blending with sclerites at other focus levels.

Morphological homology and terminology mainly follows Cumming and Wood (2009), Søli (1997), and Hippa et al. (2005), except for wing venation, which follows Cumming and Wood (2017), based on wing vein homology interpretation of Wootton and Ennos (1989) and Saigusa (2006).

We reran Hippa et al.'s (2005) phylogenetic analysis of the relationships among manotine genera only to verify the position of the new species in *Eumanota*, using the same dataset and all their terminals and *Eumanota wolffae*. Analyses were performed using TNT (Goloboff et al., 2008), with all characters unordered and equal weight and implied weighting with k = 3, 10000 trees retained in memory, random seed 0, 1000 replicates, and TBR saving 10 trees for interaction.

Eumanota Edwards, 1933

Eumanota Edwards, 1933: 231. Type species: *Eumanota leucura* Edwards, 1933, by original designation. Søli, 2002: 46-52, Papp, 2004: 228-232, Hippa et al., 2005: 410-414.

Amended Diagnosis (modified from Søli, 2002): A row of strong bristles around hind margin of eyes. Three ocelli in straight line, median ocellus about half the diameter of lateral ones. Four palpomeres visible; palpomere 1 lost or fused to palpomere 2; palpomere 3 large,

triangular, projected beyond insertion of palpomere 4, with a deep, conspicuous sensory pit; palpomere 5 from 4–6× longer than palpomere 4. Scutum densely clothed with minute setae, no defined acrostichals, a single row of dorsocentrals on posterior half, some stronger supra-alars. Basisternum shieldlike, with setae at least laterally. Anepisternum setose; mesepimeron bare; laterotergite ovate, bulging, setose; mediotergite, metepisternum, and metepimeron bare. Wing membrane either clear or darkened at distal half, at least posterior half with dorsal macrotrichia on membrane. C extends well beyond apex of R_5. Sc typically short, ending in bR; R_1 shorter or only slightly longer than r-m; r-m longitudinal. M_{1+2} less than half r-m length, basal most part of M_1 weakly sclerotized. M_4 separated from CuA at base of wing. Tibiae and tarsomeres with trichia arranged in regular rows. Spurs well developed.

COMMENTS. Some adjustment of the original diagnosis was necessary to include this new Neotropical species. Most features referred to as diagnostic for the Oriental/Australasian species of *Eumanota* (but not all) are also present in the Neotropical species (exceptions are discussed below). In *E. wolffae*, sp. nov., the hind tibia does not have a sensory groove and the female clearly has a two segmented cercus.

Eumanota wolffae, sp. nov.

Figures 1–5

Zoobank: urn:lsid:zoobank.org:pub:61CC009E-0407-48FD-8E10-D7B06CAB80A2.

MATERIAL EXAMINED: Holotype male, **Colombia**, Antioquia, Yarumal, Vereda El Respaldo, Farm La Maruja, 6°55′ 05″N, 75°24′48″W, Malaise trap, Bosque, 2,300 m, 15.Dec.2016, C.H.-Sepúlveda and J. Medina cols. (CEUA) (in ethanol). Paratypes. 1 male, same data as for holotype (CEUA); 1 female, Colombia, Antioquia, Envigado, Loma del Escobero, Parcelación Nubarrones, 6°13′97″N, 75°55′54″W, Malaise trap, Bosque, 29.Jan.–11.Feb.2017, M. Wolff and C. H.-Sepúlveda cols. (CEUA) (in ethanol); 1 male, Colombia, Antioquia, Envigado, Loma del Escobero, Parcelación Nubarrones, 06°08′23″N, 75°33′14″W, Malaise trap, Bosque, 25.Sept.–01. Oct.2017, M. Wolff and C. H-Sepúlveda cols. (MZUSP) (on a slide-mount).

DIAGNOSIS. Maculation on distal third of wing and over distal part of CuA (fig. 2E). Body mostly brown, with light brown to cream areas on sides of scutum, anterior half of thoracic pleura, coxae, and sternites 1–6. Female terminalia with two-segmented cercus (fig. 5A, B). Each gonocoxite with two distal projections, one lateral and one ventral, distal lateral projection with a megaseta on inner face; gonostylus small, well sclerotized, slightly asymmetric, tapering to apex, with an irregular indentation near tip, and a pair of straight megasetae on ventral face; gonocoxal bridge with setae; T9 with a pair of well-developed megasetae on inner face, tergite 9 elongate trapezoid; cercus projecting from distal margin of tergite 9 (figs. 3A, 4C).

DESCRIPTION. Male: Wing length, 3.2 mm. Head (fig. 1A–D). Frons, face, and clypeus whitish yellow, occiput whitish yellow ventrally, darker toward vertex, dark brown at area of ocelli. Antennal scape and pedicel whitish yellow, flagellum light brownish yellow on first three flagellomeres, light brown on more distal flagellomeres. A crown of 8–10 black, long postocular bristles at each
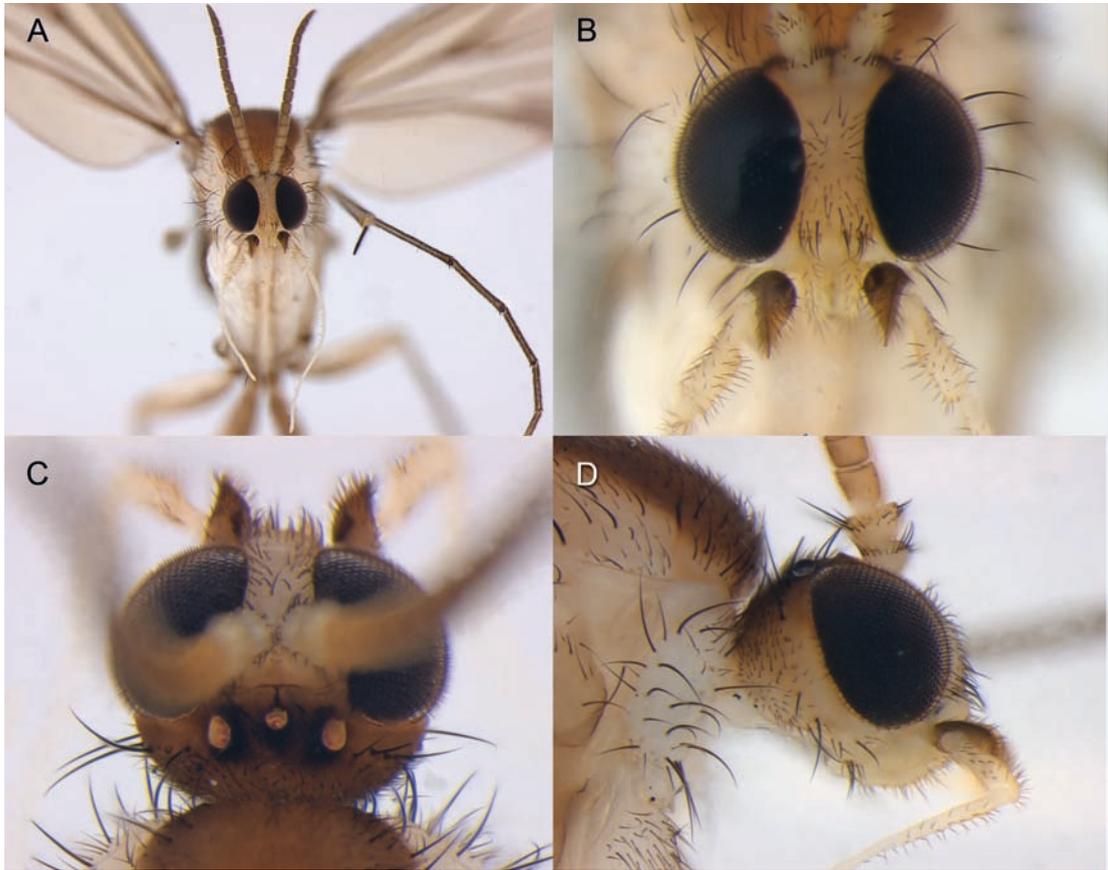
FIGURE 1. *Eumanota wolffae* male paratype: **A**, frontal view of head and thorax; **B**, head, frontal view; **C**, head, dorsal view; **D**, Head, lateral view.

side around eyes. Midocellus present, about half the width of lateral ocelli, ocelli in line, lateral ocelli closer to eye margin than its own width. No eye bridge, ommatotrichia present. Antennal scape and pedicel with a row of distal short, brown setae; first flagellomere 1.6× longer than wide, no black or stronger setae on any flagellomere. Fronto-clypeus 2.8× higher than wide, densely covered with blackish short setae, setation longer along ventral margin. Labella quite elongate, whitish yellow. Maxillary palpus with a small basal palpomere (either palpomere 1+2 or palpomere 2), palpomere 3 well developed, brownish, projecting over base of palpomere 4, a large, rounded sensory pit on inner basal fifth of palpomere; palpomere 4 whitish, distal two-thirds wider than basal third; palpomere 5 whitish, about 4× longer than palpomere 4.

Thorax (fig. 2A–C): Scutum largely brown, with a pair of whitish-yellowish bands along lateral margins. Scutellum brown dorsally, whitish-yellow along posterior margin. Basisternum well developed, shieldlike, with some lateral setae. Antepronotum, postpronotum, prosternum, and proepisternum whitish, proepimeron, dorsal part of anepisternum and of mesepimeron, metepisternum, and metepimeron light brownish yellow; ventral end of anepisternum, katepisternum, and ventral part of mesepimeron yellowish brown; laterotergite and mediotergite light
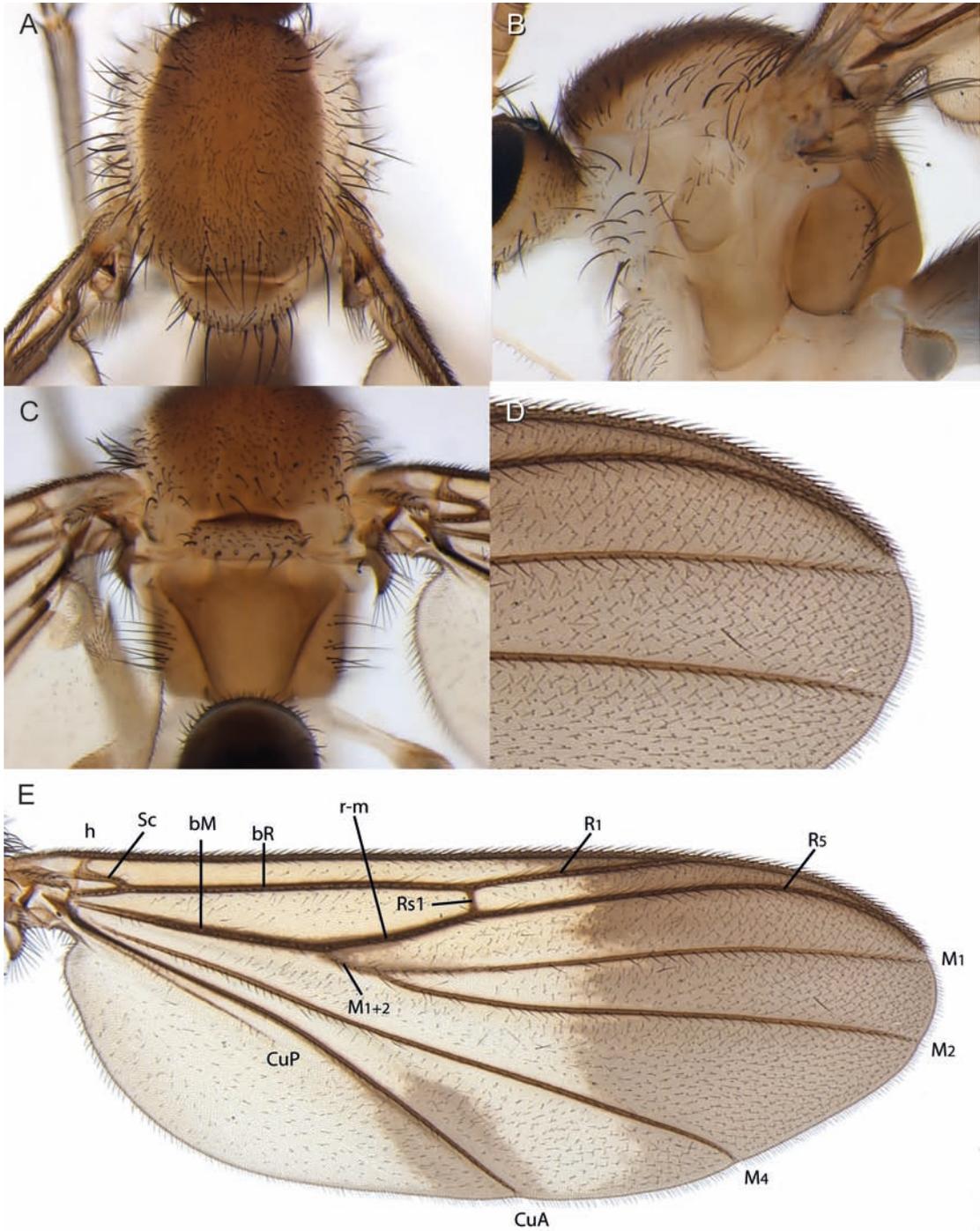
FIGURE 2. *Eumanota wolffae*, male paratype: **A**, thorax, dorsal view; **B**, thorax pleural, lateral view; **C,** thorax, posterior view; **D,** wing tip; **E,** full wing. Rs1, first sector of the radial sector.

brown. Scutum with a regular row of moderately strong dorsocentrals, besides a very irregular row of long black supraalars, and a few prescutellars; no defined acrosticals. Anterior parapsidal suture short but well marked, ending outside row of dorsocentrals. Antepronotum and proepisternum with long, black setae; anepisternum with scattered short, brownish setae and a pair of longer setae on dorsoposterior margin; laterotergite with about 18 long, brownish setae; katepisternum, mesepimeron, metepisternum, and mediotergite bare. Mesepimeron not reaching ventral margin of thorax.

Legs: Foretibia with an anteroapical depression furred with setulae, no regular comb of setae. Front coxa whitish yellow, mid- and hind coxae light brownish yellow, with darker longitudinal areas. Front femur, tibia, and tarsus light brown; mid femur, tibia, and tarsus light yellowish brown, femur with a darker area ventrobasally, tarsus darker to apex; hind femur mostly light brown, lighter dorsodistally, tibia light brownish yellow, tarsus light brown. Front coxa entirely covered with short setae on anterior and lateral faces. Tibial spurs 1:2:2, mid and hind tibial spurs of about same length, about 3.8× longer than width of tibial apex. Tarsal claws with a long basal tooth.

Wing (fig. 2D–E): Membrane quite translucent on basal 3/5, distal 2/5 grayish brown, distal end of CuA also with a grayish-brown area, as well as membrane around M_{1+2} and distal end of r-m. Entire membrane densely covered with macrotrichia. All anterior and posterior veins with dorsal setae, including Sc, except for first sector of Rs. Sc clearly ending in bR. Rs originating at 0.6× wing length, transverse. R_1 quite long, about 1.4× r-m length, R_5 curved posteriorly on distal fourth, joining C in an acute angle, C extending beyond R_5, almost reaching M_1; r-m quite longitudinal, elongate, about 2.5× M_{1+2} length, anterior end of r-m apart from bR, hence br cell much wider medially; bM long, 1.7× r-m length, originating at level of h, very close to wing base; M_{1+2} weakly sclerotized, short, 2× length of first sector of Rs; basal tenth of M_1 dark, with setae, but not fully sclerotized as a vein; M_2 slightly curved anteriorly on basal third, with a quite unique shape; M_4 originating close to wing base, actually disconnected from other veins (with a very faint connection to CuA at base), with a gradual, discrete posterior curve along its length, with a slightly stronger curve at tip; CuA well sclerotized, with a stronger curve before level of proximal tip of r-m; CuP slightly sclerotized on basal half, entirely absent on distal half; no trace of A_1.

Abdomen: Tergite 1 dark brown, tergites 2–5 dark brown with some yellowish-brown basal areas, tergite 6 brown; sternites 1–6 yellowish; segments 7 and 8 brown. Tergite 8 slender, wide, extending laterally toward ventral side of abdomen, sternite 8 triangular and elongate, with seven distal setae.

Terminalia (figs. 3A, B, 4A–D): Terminalia slightly elongate, gonocoxites (gc) at least 2× as long as wide, mesial fusion reaching distal margin with no suture, mediodistally with a short posterior incision with indented margin; distal end of gonocoxites with a distal lateral projection (glp) extending beyond insertion of gonostylus (gs) and an additional more mesial oblique projection (gmp) as long as lateral ones; gonocoxites with a large modified seta directed inward (gci) at inner face of tip of each lateral projection, besides a regular, elongate distal seta at tip of external face of lateral projection (gcd) and additional shorter setae on external face. Gono-
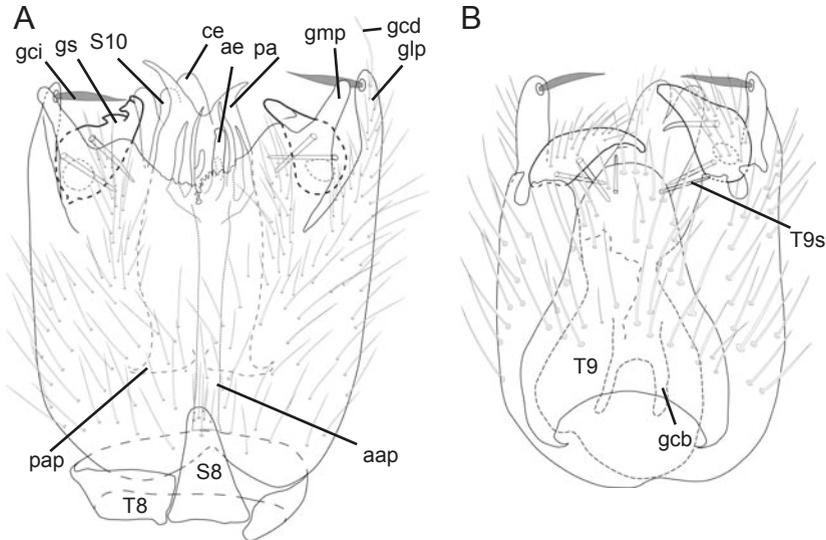
FIGURE 3. *Eumanota wolffae*, male paratype: **A**, ventral view; **B**, dorsal view. Abbreviations: **aap**, aedeagal apodeme; **ae,** aedeagus; **ce,** cercus; **gcb,** gonocoxal bridge; **gcd,** gonocoxal distal setae on lateral projection; **gci,** gonocoxal inner seta on latera projection; **glp,** gonocoxite lateral projection; **gmp,** gonocoxitemesal projection; **gs,** gonostylus; **pa,** paramere; **pap,** parameral apodeme; **S8, S10,** sternites 8, 10; **T8,** tergite 8; **T9,** tergite 9; **T9s,** differentiated seta of tergite 9.

stylus well sclerotized, slightly asymmetrical, shorter than gonocoxite projections, displaced to a quite dorsal position at terminalia, bearing two long, strong straight setae at ventral face, distal end with irregular indentation. Aedeagus (ae) present as a long, straight, well-sclerotized medial sclerite with two pairs of distal lateral projections and an additional medial projection bearing gonopore at tip, aedeagal apodeme (aap) reaching anterior end of terminalia; paramere (pa) with a pair of anterior apodemes, each with a short lateral, curved extension (pap), medially fused on distal half dorsal to aedeagus, with a slightly asymmetrical pair of distal projections curved outward extending beyond tip of aedeagus, and a pair of short, well-sclerotized elongate projections adjacent to aedeagus. Tergite 9 (T9) trapezoid, elongate, wider at base than distally, with curved distal margin, bearing at inner face a pair of distal, long, differentiated setae (T9s). Gonocoxal bridge (gcb) with setae at its distal and inner margins, gonocoxal apodemes elongate, close together anteriorly. Cerci (ce) projecting beyond distal margin of tergite 9, covered with elongate setae and elongate microtrichia, sternite 10 (S10) quite well developed, triangular, with long, straight setae.

Female (paratype): As male, except as follows. Wing: Length, 3.5 mm. Thorax: Pleural sclerites light brown. Abdomen: Segments light brown, segments 2–5 with yellowish-brown areas, all tergites and sternites setose. Tergite 7 much wider than long, sternite 7 slightly projected medially over base of tergite 8. Terminalia (fig. 5A, B): Sternite 8 elongate, with a pair of wide bare, basal lobes, each with a short distal projection with some few dark setae. Tergite 8 wide, short, with a row of setae along posterior margin, a laterodistal lobe quite ventrally bearing some few setae. Tergite 9 extending posteriorly at each lateral end, with some few setae.
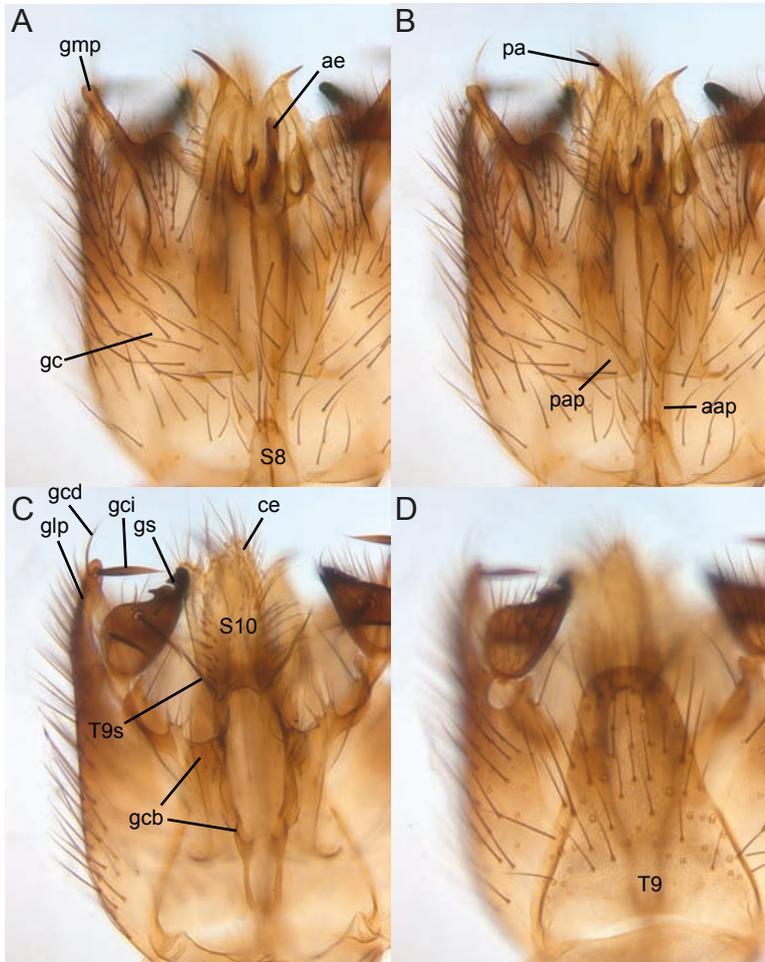
FIGURE 4. *Eumanota wolffae*, male paratype: **A**, ventral view at level of syngonocoxite; **B**, ventral view at level of parameres; **C,** ventral view at level of gonostylus and gonocoxal bridge; **D,** Ventral view at level of tergite 9. Abbreviations: **gc,** gonocoxite; for others, see figure 3.

Tergite 10 short, slightly projected laterally, with some few, weaker setae. Sternite 10 elongate, wider at base, with rounded tip, covered with setae. First segment of cercus longer than second; second segment lobose, wider than long, apically rounded, setose.

ETYMOLOGY: The species epithet is named to honor of Marta Wolff, one of Colombia's outstanding woman scientists, who has dedicated her career to the knowledge of the insect fauna of Colombia, particularly fly diversity. She also coordinates the larger project studying the Diptera fauna of the high Andean forests of Colombia, including the paramos, and took part in the hard fieldwork underlying the project.

BIOLOGY: The project on the high Andean forests includes collecting fungi for to rear adult mycetophilids in the lab. Adults of *E. wolffae*, however, have so far not been obtained from fungi. There is no information, hence, on the biology of this species except the kind of environment in which they were collected, the high Andean forests on Colombia (fig. 6).
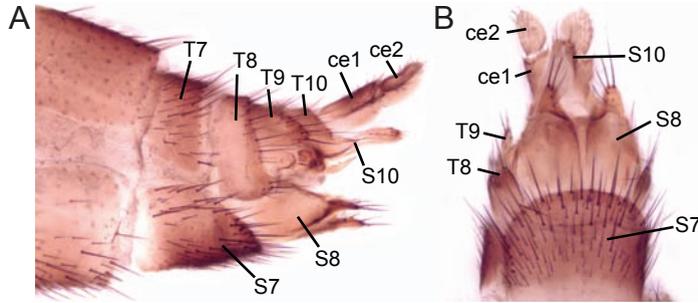
FIGURE 5. *Eumanota wolffae*, female paratype: **A**, lateral view; **B**, ventral view. Abbreviations: **ce1, ce2,** cercus segments 1–2; **S7–10,** sternites 7–10; **T7–10,** tergites 7–10.

COMMENTS: Males and females of *E. wolffae* are identical to each other in general body color, including the wing pattern. The male terminalia of *E. wolffae* is very complex, and has some distinctive features compared to the Oriental/Australasian species of *Eumanota*. The gonocoxites are fused all the way to the distal margin of the syngonocoxites, with no medial suture except for a short, irregular distal incision (fig. 3A). The gonocoxites ventrally have a pair of more mesal projections at the distal margin and a pair of distal lateral projections both extending beyond the base of the gonostylus (fig. 4A, C). Each lateral projection of the gonocoxite bears a single, very distinctive distal megaseta on the inner face (figs. 3A, B, 4C), unique in the genus. The aedeagus is complex, with a long, straight apodeme that almost reaches the anterior end of the terminalia and a medial tubular distal structure bearing a terminal opening (figs. 3A, 4A, B). The parameres have a pair of typical distal outward projections (figs. 3A, 4B). The general shape of tergite 9 (fig. 4B, D) is very similar to that found in the Oriental species, but there is a pair of strong setae at the inner face of tergite 9, absent in other species of the genus. The well-sclerotized gonostylus (figs. 3A, B, 4C) has a unique shape, not only due to the two or three distal indentations, but to the pair of strong setae directed ventrally.

DISCUSSION

PHYLOGENETIC POSITION OF *EUMANOTA WOLFFAE* IN THE MANOTINAE

The genus *Eumanota* was originally described by Edwards (1933) based on two species from Borneo. Søli (2002) added three species to the genus, two from Thailand and one from the Maluku Islands. Papp (2004) described two species, one from Taiwan and one from Papua New Guinea, while Hippa et al. (2005) described one species from Myanmar and one species from Sumatra, Indonesia, referring to an additional species from Pahang, in Malaysia, known from a single female that they did not formally describe.

Our phylogenetic analysis of the Hippa et al.'s (2005) dataset including *E. wolffae* showed that this Neotropical species groups with the remaining species of the genus. We had nine shortest trees under equal-weight analysis, in which all Hippa et al.'s (2005) main conclusions for the manotines were exactly recovered: Manotinae monophyletic, *Manota* sister of the clade of the remaining genera, *Paramanota* sister to (*Promanota + Eumanota*),

FIGURE 6. High Andean forest environment in Loma del Escobero, Envigado, Departamento de Antioquia, Colombia, where *Eumanota wolffae* was collected.

all genera monophyletic. In other words, the addition of a new species did not reveal any manotine rogue taxa and confirmed from a phylogenetic perspective that the new Colombian species belongs to *Eumanota*.

Biogeographical Patterns and Explanations

The genus *Manota* is well known for its worldwide distribution, with about 300 described species (and maybe at least the equal number awaits to be described) from all biogeographical regions (Kurina et al., 2018). This is one of the genera considered by Bickel (2009) to be "open ended." The other three manotine genera compose together a clade that has comparatively few species, with considerably limited distribution, basically centered in the Oriental region. The northern range of this clade reaches Taiwan, while its eastern extension goes through the Maluku Islands to reach Papua New Guinea. The description of a species of *Paramanota* from Baltic amber (Hippa, 2010) enlarged the known distribution range of the clade and bridges the Oriental fauna of non-*Manota* manotines with *Eumanota wolffae* in Colombia.

Eumanota wolffae in South America geographically overlaps with other temperate sciaroid genera in the high Andean forests, either with austral or Nearctic connections. Our study of this fauna has so far revealed, e.g., a species of the rangomaramid genus *Eratomyia* Amorim and

Rindal (Amorim and Falaschi, 2010)—sister to the genus *Chiletricha* Chandler (Amorim and Rindal, 2007)—and the mycetophilid genera *Paraleia* Tonnoir (Oliveira and Amorim, 2012), *Duretophragma* Borkent, *Aneura* Marshall, *Neaphelomera* Miller, etc. Some of these sciaroid genera are known from southern Chile, Australia, and New Zealand.

It seems quite unlikely, however, that the connection of the Colombian species of *Eumanota* to the Oriental species of the genus could be through the southern end of South America and Australia. A post-Gondwanan direct connection between southern South America and Australia was predicted by Amorim et al. (2009) and demonstrated to have persisted until about 40 million years ago (Mya) by Almeida et al. (2012), later corroborated with a study on scionine tabanids (Lessard et al., 2013). Data from mammals points to the separation between South America and Antarctica at the early Eocene (Lawver et al., 2011) and between Australia and East Antarctica between the late Paleocene and the Eocene (Reguero et al., 2014; Lawver et al., 2011). There are, however, no non-*Manota* manotine taxa known from Chile or other Andean areas south of Colombia, neither from New Zealand or Australia. We discard, hence, a scenario in which *Eumanota* belongs to the same biogeographic layer as the fungus-gnat genus *Paraleia* (Oliveira and Amorim, 2012), the colletid bees (Almeida et al., 2012), or the scionine tabanids (Lessard et al., 2013).

It is worth noting that most species of *Eumanota* occur at higher areas along its range in the Oriental/Australasian regions, between 700 and 2000 m (with the single exception of *E. racola* Søli, collected close to sea level in Koh Ra, an island in Thailand). These records agree with the presence of *E. wolffae* in high Andean forests, at 2300 m, not in lower altitudes in Colombia. If the connection between *E. wolffae* with other species of the genus is not through the austral fauna, it should be through the Palearctic-Nearctic regions. Indeed, the high Andes temperate Colombian fungus-gnat fauna also includes typical Nearctic components, such as *Cordyla* Meigen (Kurina and Oliveira, 2015) and *Docosia* Winnertz (Oliveira and Amorim, 2011). This overlap of faunas presents a striking case of a biogeographical node in the sense of Croizat (1964), with the confluence of tropical Neotropical and austral Neotropical and Nearctic elements at the same site (Oliveira et al., 2007).

Animal and plant groups connecting the Neotropics to taxa with typically Oriental distribution, such as *Eumanota*, can be often also found in the Afrotropical region, composing a "circumtropical" pattern. Most of the taxa with this kind of distribution, however, are too recent to be truly Gondwanan in origin. This coincidence between circumtropical distribution and Gondwanan pattern is better explained as pseudocongruence (Donoghue and Moore, 2003). Amorim (2010) referred to this particular pattern as "pseudogondwanan," a more parsimonious explanation that dismisses either transoceanic dispersal or a Gondwanan origin.

There is important evidence that the southern margin of Laurasia (including what is now the Oriental region) had a tropical biota in the early Cenozoic (e.g., Paleogene). A widespread tropical flora and fauna over Laurasian terranes has been referred to as the "boreotropics" (e.g., Lavin and Luckow, 1993). Cretaceous floras were far from being dominated by angiosperm forests, the diversification and dominance of dicots at that time being mostly based on ruderals (Wing and Boucher, 1998). Johnson and Ellis (2002) proposed that angiosperm tropical forests

as we know would be an early Paleogene development, but Davis et al. (2005) provide divergence-time models that suggest that closed-canopy tropical rainforests may have existed before the K-T boundary, in the Albian or the Cenomanian.

In the early Paleocene, there were tropical forests in Colorado (Johnson and Elis, 2002) and Eocene temperatures in North America were about 10° C higher than today (Fricke and Wing, 2004). Greenhouse conditions were also widespread in Europe (Schwarz, 1997). From a floristic point of view, Burnham and Johnson (2004) indicated that Neotropical rainforests were either rare or equivocal before the Paleocene, while there is evidence of Paleocene rainforest in North America. Herngreen and Dueñas Jimenez (1990), nevertheless, demonstrate a core angiosperm flora in the African–South American (ASA) Albian-Cenomanian province, demonstrated to extend to China and Papua–New Guinea. Robust evidence for angiosperm tropical rainforest in Africa is Late Eocene to Late Oligocene, less than 40 Mya (Jacobs, 2004). Diversification of modern tropical rainforest angiosperm clades in South America actually may have begun in the Paleocene (Burnham and Johnson, 2004). This builds in a scenario for the evolution of a tropical biota in the Neotropics very different from the idea of a widely distributed tropical biota inherited from the Gondwana.

Pseudocongruent patterns are actually generated by geographical expansion of biotas followed by differential extinction. Pseudogondwanan patterns were, hence, produced by faunistic exchange of elements of a tropical Laurasian biota between Europe and Africa, between North America and the Neotropics, and between the Oriental and the Australasian regions, followed by widespread extinction of these tropical elements in the Nearctic and Palearctic regions due to global cooling in the Neogene. A rather naïve view of long isolation between North and South America until the Pliocene, for example, seems to be gradually replaced by a model with "a series of collisions of island arcs and oceanic plateaus—the Proto-Antilles—from the Early Cretaceous to the middle Miocene as a result of interaction with the Caribbean plate" (Ramos, 2009: 31). This means that there was plenty of opportunity for reciprocal biotic exchange between North and South America since the Cretaceous, despite the long-held view by vertebrate workers about the significance of the Pliocene connection through the Isthmus of Panama. Because of different dispersal abilities of these Laurasian tropical elements in the northern hemisphere to the south and of different extinction rates, taxonomic groups show final worldwide patterns that disagree in details.

In terms of insect fossil evidence, Baltic amber elements testify to the connections of the Eocene European fauna with Recent Oriental diversity. Engel (2001: 5) states that the Baltic amber bees are generally related to "groups currently inhabiting sub-Saharan Africa and Southeast Asia, a biogeographic pattern common to many Baltic amber groups." The Early Eocene Cambay amber fossil deposits in India share elements with the Baltic amber fauna and corroborates the view of a continuous Oriental-Palearctic fauna in the Paleogene (Rust et al., 2010). Moreover, the Cambay amber was formed by dipterocarps, which today are the predominant trees of Southeast Asian rainforests, thus indicating this type of forest is at least 50 Mya.

The Cambay amber fauna actually fills in a gap in our knowledge of "pseudogondwanan patterns." Stebner et al. (2017) described three species belonging to three different genera of the

sciaroid fly family Lygistorrhinidae in Cambay amber. Members of this fly sciaroid family are known from tropical to temperate warm forests (Grimaldi and Blagoderov, 2001), with the core of its present diversity in the Oriental region, with additional members in western Africa, in the Nearctics, and the Neotropical region. Fossils of Lygistorrhinidae are known from the Cretaceous in amber from Lebanon (Blagoderov and Grimaldi, 2004), Myanmar (Blagoderov and Grimaldi, 2004), Taimyr (Blagoderov and Grimaldi, 2004), and Canada (Blagoderov and Grimaldi, 2004), followed by Eocene amber from Cambay (Stebner et al., 2017), Oise (Blagoderov et al., 2010), and the Baltic region (Meunier, 1904), and Oligocene-Miocene Dominican amber (Grund, 2012). As mentioned by Stebner et al. (2017), "[t]he discovery of a diverse assemblage of Lygistorrhinidae in Cambay amber reinforces the reconstruction of a tropical palaeoenvironment."

Such Asian-Palearctic connection can be also seen in other Diptera families. In the Phoridae genera *Diplonevra* Lioy (Brown, 1999) or *Anevrina* Lioy (Brown, 2013), for example, there are known cases of shared Baltic amber/Oriental and Baltic amber/Palearctic-Oriental elements. There are other similar cases of pseudogondwanan patterns in insects. Among the fungus gnats, for example, the macrocerine tribe Robsonomyiini of the Keroplatidae is composed of five genera, with its present diversity known basically from the Oriental region, but present as well in Baltic amber, Madagascar, and North America (table 1), besides three undescribed Neotropical species, from Panama and from the Brazilian Amazon (Falaschi and Amorim, in prep.). In the case of this keroplatid clade, the huge worldwide genus *Macrocera* Meigen would be evolutionarily comparable in the Macrocerinae to what *Manota* is in the Manotinae and to the widespread genus *Lygistorrhina* Skuse in the Lygistorrhinidae. The recent species of the Xyphocentronidae (Trichoptera) compose a clear Neotropical-Afrotropical-Oriental distribution pattern (Schmid, 1982).

CONCLUSIONS

General patterns in biogeography reveal much more about biotic evolution than do individual histories. A pseudogondwanan pattern—not old enough to be explained by true Gondwanan origin, not recent enough to demand transoceanic dispersal—was shown here with evidence from different groups of flies, an explanation expected to also apply to other groups of insects, angiosperms, vertebrates, etc. Evidence favoring this hypothesis—i.e., that most "circumtropical patterns" either are not Gondwanan in origin or they originated through transoceanic dispersal—comes from different groups of animals and plants. Evidence for a "boreotropics" in the Paleocene has been documented in the literature, but this is the first time that this pattern is suggested to be the source of present circumtropical distributions. Data from phylogenetic reconstruction, biogeographical patterns, associated fossils, and age of clade divergence in different animal and plant groups will be particularly helpful to detail the history of this Laurasian tropical environment with southern biotic extensions.

The Oriental-Neotropical distribution pattern known for *Eumanota*, with the description here of *E. wolffae* from Colombia, implies a widely distributed tropical Laurasian fauna and flora, now largely extinct in the Palearctic and Nearctic regions. In the case of the clade com-

TABLE 1. Distribution of recent Sciaroidea genera of the Mycetophilidae subfamily Manotinae, the Keroplatidae macrocerine tribe Robsonomyiini, and of the family Lygistorrhinidae.

Mycetophilidae Manotine	
Eumanota Edwards	Sumatra, Borneo, Myanmar, Maluku Utara (Indonesia), Thailand, Papua–New Guinea, Taiwan, Malaysia, South America
Paramanota Tuomikoski	Malaysia, Myanmar, Sumatra, Brunei, Taiwan, Thailand, Baltic amber
Promanota Tuomikoski	Myanmar, Taiwan
Keroplatidae Macrocerinae Robsonomyiini	
Calusamyia Coher	Florida, USA
Kelneria Matile	Baltic amber
Langkawiana Ševčík	Malaysia
Micrepimera Matile	Christmas Ids, Madagascar, and Vietnam
Robsonomyia Matile andVockeroth	Western North America
Srilankana Matile	Sri Lanka
Undescribed genus	Panama, Brazil (Amazonas)
Lygistorrhinidae	
Asiorrhina Blagoderov, Hippa, and Ševčík	Sri Lanka, Malaysia
Blagorrhina Hippa, Mattsson, and Vilkamaa	Malaysia
Indorrhina Stebner & Grimaldi	Cambay amber
Gracillorrhina Hippa, Mattsson and Vilkamaa	Malaysia
Labellorrhina Hippa, Mattsson and Vilkamaa	Brunei/Malaysia
Loyugesa Grimaldi and Blagoderov	Vietnam
Lygistorrhina Skuse	*Worldwid*e, Cambay amber, Dominican amber
Matileola Papp	*Taiwa*n
Palaeognoriste Meunier	*Baltic* amber, Cambay amber
Parisognoriste Blagoderov, Hippa, and Nel	Paris amber
Seguyola Matile	*C*ameroun, Gabon, Uganda, Tanzania, Kenya, Zaïre, Central African Republic, Comoros Islands

posed by (*Paramanota* (*Promanota* + *Eumanota*)), all Nearctic and Palearctic elements are presumably extinct (with a remnant preserved in Baltic amber), with no known Afrotropical extensions. The fact that the South American species is not sister to the entire set of manotine genera indicates that there was diversification of the clade before expansion of this clade reached South America.

This entire set of evidence suggests that the recent Oriental tropical biota is not an isolated "source" fauna and flora for the world tropics, but rather the remnant of an earlier, widespread and diversified tropical biota extending through large parts of the northern hemisphere. This discovery emphasizes the extremely urgent need to protect the Colombian high Andean forests and the paramos, maybe some of the most threatened, phylogenetically diverse ecosystems in the world.

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