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New reduced-winged species of *Mumetopia*, with analysis of the relationships of this genus, *Chamaebosca* and allied genera (Diptera: Anthomyzidae)

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Abstract. Two new high-montane species of *Mumetopia* Melander, 1913 with strongly reduced and narrowed wings from Andean páramo ecosystem are described and illustrated, viz *M. messor* sp. nov. (Ecuador) and *M. taeniata* sp. nov. (Colombia). Owing to their striking external resemblance to brachypterous species of *Chamaebosca* Speiser, 1903 a cladistic analysis of the relationships of *Mumetopia*, *Chamaebosca*, *Stiphrosoma* Czerny, 1928, *Cercagnota* Roháček & Freidberg, 1993 and two unnamed Neotropical genera (Genus *B* and Genus *M*) is conducted based on selected morphological (mainly postabdominal and genitalic) characters. The phylogenetic hypothesis based on this analysis revealed that the current concept of the genus *Mumetopia* is polyphyletic because its two groups, viz. *Mumetopia* s. str. (= *M. occipitalis* group) and *M. nigrimana* group [the third species currently placed in *Mumetopia*, viz. *M. terminalis* (Loew, 1863) is not related to the group of genera under study] originate from different clades: *Mumetopia* s. str. is closely related to (unnamed) Genus *B* and also Genus *M*, while the sister-group of the *M. nigrimana* group proved to be the genus *Stiphrosoma*. The poorly known genus *Chamaebosca* seems to be somewhat intermediate between these two main branches but forms a sister-group to the clade Genus *M* + Genus *B* + *Mumetopia* s. str. The genus *Cercagnota* is postulated as a sister-group to all the remaining genera forming the *Chamaebosca* group of genera, the relationships of which seem to be well supported by a number of synapomorphies.

Taxonomy, phylogeny, new species, Diptera, Anthomyzidae, *Mumetopia*, *Chamaebosca* group of genera, New World

INTRODUCTION

Reduction or complete loss of wings is a phenomenon usually occurring in flies adapted to a terricolous way of life (Hackman 1964). This is also true for a few species of Anthomyzidae living near the ground in the tussocks, or near the bases, or in the litter below (mostly graminoid) plants. Within this family brachypterous forms have only been described in two genera, viz. *Stiphrosoma* Czerny, 1928 and *Chamaebosca* Speiser, 1903. In *Stiphrosoma* the brachyptery occurs (and often prevails) in three wing-polymorphic species, the Holarctic *S. sabulosum* (Haliday, 1837) and the Nearctic *S. artum* Roháček et Barber, 2005 and *S. hirtum* Roháček et Barber, 2005, all preferentially associated with grasses (see Roháček & Barber 2005). On the other hand, the biology of the short-winged species of *Chamaebosca* is unknown because descriptions of both these Chilean species, viz. *C. microptera* Speiser, 1903 and *C. cursor* (Kieffer, 1906), were based on holotypes. Moreover, only the male holotype of *C. microptera* has been traced and the genus and species redescribed based solely on this single specimen which remains the only one available for study (see Roháček 1998). In addition, there is one apterous, ant-mimicking species, *Apterosepsis basilewskyi* Richards, 1962 from Mt. Meru in Tanzania (known from only two females) confirmed as a member of Anthomyzidae only recently (Roháček 1998). Interestingly, all the genera discussed above involving species with reduced wings (including *Apterosepsis* Richards, 1962) are obviously related, cf. Roháček & Barber (2005) and Roháček (2006).

The two anthomyzid species with vestigial wings described below were discovered in the alpine zone of Andean ranges and are externally highly similar to brachypterous species of *Chamaebosca*. Because the only known representatives of *Chamaebosca* (see above) were described from Chile, these new species were originally regarded to belong to this genus. Their detailed study, however, revealed they are undoubtedly members of *Mumetopia* Melander, 1913 because their postabdominal structures closely resemble those of *M. occipitalis* Melander, 1913, the type species of the latter genus. This finding raised a problem with interpreting the relationships of the genera *Mumetopia* and *Chamaebosca*. Roháček & Barber (2005) and Roháček (2006) recognized their affinity to *Stiphrosoma* and *Cercagnota* Roháček et Freidberg, 1993 and also mentioned the existence of further unnamed Neotropical groups that likely originated from the same clade but did not study their interrelationships. To gain a more accurate image of the phylogeny of these genera, a cladistic analysis has been performed based on the original examination of a number of species (most of them unnamed – see in "Material and Methods" below) of *Mumetopia* and two undescribed genera (called Genus *B* and Genus *M* by Barber & Roháček, in prep.) and on morphological data for *Cercagnota*, *Stiphrosoma* and *Chamaebosca* adapted from Roháček (1998, 2006) and Roháček & Barber (2005). The phylogenetic hypothesis obtained from this analysis (presented below) is rather surprising and will have a significant impact on the generic classification of the New World Anthomyzidae belonging to this clade. It should be noted that the genus *Mumetopia* currently contains three described species: *M. occipitalis* Melander, 1913 (the type species), *M. nigrimana* (Coquillett, 1900), and *M. terminalis* (Loew, 1863), see Sabrosky (1965), Roháček (1998). However, the latter species is not congeneric with either of these two species and is unrelated to any other group under study here. Its correct generic affiliation and relationships will be the subject of a subsequent study.

MATERIAL AND METHODS

The material examined is deposited in institutional collections as follows: CASC – California Academy of Sciences, Department of Entomology, San Francisco, CA, U.S.A.; CNCI – Canadian National Collection of Insects, Biodiversity (Entomology) and Integrated Pest Management, Ottawa, Ontario, Canada; DEBU – University of Guelph – Insect Collection, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada; INBC – Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica; LEMQ – Lyman Entomological Museum, McGill University, Macdonald Campus, Ste.-Anne-de-Bellevue, QC, Canada; QCAZ – Pontificia Universidad Catolica del Ecuador, Catholic Zoology Museum, Quito, Ecuador; SMOC – Silesian Museum, Opava, Czech Republic; USNM – National Museum of Natural History, Smithsonian Institution, Department of Entomology, Washington, DC, U.S.A.; ZSMC – Zoologische Staatsammlung München, München, Germany.

Besides the type material of the new species listed under their descriptions below, a number of additional species (and specimens) have been examined to obtain character data for the cladistic analysis: 2 unnamed species of the Genus *B*, both from Chile: Juan Fernández Is., Robinson Crusoe I. (DEBU); 6 unnamed species of the Genus *M*, viz. sp. #1 from Argentina: Tucuman (CNCI), sp. #2 from Chile: Nuble (CASC), sp. #3 from Ecuador: Pichincha (CNCI), sp. #4 from Peru: Ollantaytambe (ZSMC), sp. #5 from Argentina: prov. Neoquén, Lago Mascardi (ZSMC) and sp. #6 from Argentina, 53 km W Buenos Aires (ZSMC); *Mumetopia occipitalis* Melander, 1913 from Canada: Ontario, Manitoulin I. (DEBU); 2 unnamed species of the *Mumetopia occipitalis*-group, viz. sp. #1 from Ecuador: Galapagos Is., Isla St. Cruz (CNCI, LEMQ) and sp. #2 from Ecuador: Galapagos Is., Isla Isabela (CNCI); *Mumetopia nigrimana* (Coquillett, 1900) from Dominica: W.I., Clarke Hall Est. (USNM); 8 unnamed species of the *Mumetopia nigrimana*-group, viz. sp. #1 from

Table 1. Data matrix of character states in the taxa of the investigated group of genera.
0 = presumed plesiomorphic condition; 1, 2 = apomorphic conditions; ? = missing data; – = character not applicable; grey highlighted = presupposed state of characters in unknown females of *Chamaebosca*.

taxon \ character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercagnota	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	1	–	0	0	0	0	0	0	0	1
Stiphrosoma	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	1	0
Mumetopia nigrimana group	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	0
Chamaebosca	?	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	?	?	?	1	1	0
Genus *M*	2	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	1	1	0
Genus *B*	2	1	1	1	1	1	1	1	2	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	1	1	0
Mumetopia s. str.	2	0	0	1	1	1	1	1	2	1	0	0	1	1	0	0	1	0	0	1	1	1	1	0	1	1	0

Costa Rica: Est. Cuericí (INBC), sp. #2 from Ecuador: Napo Prov., Rio Pisque (DEBU), sp. #3 from Ecuador: Cuenca (CNCI), sp. #4 from Ecuador: Napo Prov., Rio Pisque (DEBU), sp. #5 from Venezuela: Mérida (DEBU), sp. #6 from Costa Rica: Santo Domingo (DEBU); sp. #7 from Venezuela: Mérida (DEBU) and sp. #8 from both Costa Rica: Cartago and Venezuela: Mérida (DEBU). The two unnamed groups (genera) are provisionally referred to as Genus *B* and Genus *M* following Barber & Roháček (in prep.) where they are characterized in a key. Character data for the other analysed genera were obtained from Roháček (1998 – *Chamaebosca*), Roháček & Barber (2005 – *Stiphrosoma*) and Roháček (2006 – *Cercagnota*). Abdomens of a number of specimens were detached and genitalia dissected. After examination, all dissected parts were put into plastic tubes containing glycerine and pinned below the respective specimens; this is indicated by the abbreviation "genit. prep." in the text.

Morphological terminology follows that used in Roháček (2006) including terms of the male hypopygium. The "hinge" hypothesis of the origin of the eremoneuran hypopygium, re-discovered and documented by Zatwarnicki (1996), has been accepted and, therefore, the following alterations of terms of the male genitalia need to be listed (new term first): ejacapodeme = ejaculatory apodeme, epandrium = periandrium, medandrium = intraperiandrial sclerite, phallapodeme = aedeagal apodeme, transandrium = posterior hypandrial bridge. Morphological terms of the male genitalia are displayed in Figs 2–8, of the female postabdomen and genitalia in Figs 9–16.

Taxon sampling and characters. Seven genus-group taxa were included in the cladistic analysis. Because the sister-group taxon of the analysed genera is unknown, the outgroup is defined as a hypothetical taxon accumulating plesiomorphic states of characters used in the analysis. The choice of the seven ingroup taxa was based on the preliminary studies of their relationships (see Roháček & Barber 2005; Roháček 2006). For character descriptions see the chapter "Phylogeny of the *Chamaebosca* group of genera" below; their coding is given in Table 1 and was based on examination or descriptions of 1 species of *Cercagnota*, 18 species of *Stiphrosoma*, 9 species of the *Mumetopia nigrimana* group, 1 species of *Chamaebosca*, 6 species of the Genus *M*, 2 species of the Genus *B* and 5 species of *Mumetopia* s. str.

Phylogenetic analysis. The 27 selected characters (25 binary and 2 multi-state) were all equally weighted; the multi-state characters were treated as unordered (Fitch optimization). Inapplicable characters were coded as "–", and unknown character states as "?". The parsimony analysis was performed in NONA 2.0 (Goloboff 1999) run with WinClada ver. 1.00.08 (Nixon 2002). Ambiguous optimizations were disallowed and ambiguous characters were optimized using DELTRAN and ACCTRAN. The tree search has been performed by means of the heuristic algorithm "multiple tbr+tbr" with settings "maximum trees to hold" = 10000, "number of replications" = 100, "starting trees per replication" = 10.

Abbreviations of morphological terms used in text and/or figures

A_1 – anal vein
ac – acrostichal (seta)
afa – aedeagal part of folding apparatus
bm – basal membrane
C – costa
ce – cercus
cp – caudal process of transandrium
cs – connecting sclerite
Cs_3, Cs_4 – 3rd, 4th costal section
CuA_1 – cubitus
cup – posterior cubital cell
dc – dorsocentral (seta)
dm – discal medial cell
dm-cu – discal medial-cubital (= posterior, t_p) cross-vein
ea – ejacapodeme
ep – epandrium
f – filum of distiphallus
f_1, f_2, f_3 – fore, mid, hind femur
fc – fulcrum of phallapodeme
gs – gonostylus

hl – hypandrial lobe
hu – humeral (= postpronotal) (seta)
hy – hypandrium
is – internal sclerite(s)
M – media
ma – medandrium
npl – notopleural (seta)
oc – ocellar (seta)
ors – orbital (seta)
pa – postalar (seta)
pg – postgonite
pha – phallapodeme
pp – phallophore
ppl – propleural (= proepisternal) (seta)
prg – pregonite
prs – presutural (seta)
pvt – postvertical (seta)
R_1, R_{2+3}, R_{4+5} – 1st, 2nd, 3rd branches of radius
r-m – radial-medial (= anterior, t_a) cross-vein
s – saccus of distiphallus
S1–S10 – abdominal sterna
sa – supraalar (seta)
sc – scutellar (seta)
Sc – subcosta
stpl – sternopleural (= katepisternal) (seta)
T1–T10 – abdominal terga
t_1, t_2, t_3 – fore, mid, hind tibia
ta – transandrium
vi – vibrissa
vr – ventral receptacle
vte – outer vertical (seta)
vti – inner vertical (seta)

TAXONOMY

Mumetopia messor **sp. nov.**
(Figs 1–19)

Type material. Holotype male labelled: "ECU: Carchi, Páramo El Angel, 17.3 km NW El Angel, 3400 m, pan traps among Espeletia, 1–3 Nov 1999, S. A. Marshall, debu00112525" (DEBU, intact). Paratypes: ECUADOR: same data as for holotype, 3 females, debu00112501, debu00112532 and debu00112576 (DEBU, SMOC, 2 females with genit. prep., female debu00112501 with left wing removed and preserved in glycerine mount together with postabdomen); same, but 18.2 km NW El Angel, 3400 m, aspirated under dead *Puya* stems, 3.xi.1999, 1 male, debu00112782 (SMOC, left wing removed and preserved in glycerine mount together with genit. prep.), 1 female, debu00112770 (QCAZ, intact), all S. A. Marshall leg.; same locality as for holotype, litter under dead *Espeletia*, 31.x.1999, 1 female, debu00111100, R. Andersson leg. (QCAZ, headless).

Etymology. The name "messor" (= L. reaper, cutter with scythe) refers to the scythe-shaped wing of this terricolous species with reduced wings.

Description. **Male**. Total body length 1.82–2.02 mm; brown to dark brown, relatively shiny; only parafacialia, gena and legs partly yellow (Figs 1, 17). Head very slightly higher than long, mostly dark brown. Frons with blackish brown stripes between frontal triangle and orbits, the latter distinctly lighter brown than other parts of frons. Frontal triangle large, almost reaching anterior margin of frons, sparsely greyish brown microtomentose including ocellar triangle, but with bare shiny spots in posterior corners on both sides of ocellar triangle; lunule very reduced, brown. Orbit also partly bare and more shining. Occiput dark brown, sparsely dark grey microtomentose (less so and hence more shining above foramen). Face brown (paler dorsally, darker ventrally) and sparsely silvery grey microtomentose. Parafacialia and dorsal stripe in anterior half of gena yellow and densely silvery microtomentose; ventral part and posterior half of gena (and postgena) dark brown, sparsely microtomentose and shining. Mouthparts brown including palpus, proboscis somewhat paler. Cephalic chaetotaxy: pvt small and very weak, convergent to parallel; vte, vti, oc and posterior ors subequal, long (longest of cephalic setae) and moderately robust or posterior ors sometimes slightly shorter; 2 strong ors, but anterior markedly shorter (one-third to slightly more than half length of) than posterior; 0–1 microsetula in front of anterior ors; at most 1 pair of minute medial microsetulae just in front of anterior frontal margin; vi shorter than posterior ors but longer than anterior ors; subvibrissa up to two-thirds of vi length but weaker; usually 4 short peristomal setae and some small setae also on postgena; postocular microsetulae minute, sparse, in single row. Eye very shortly and sparsely pilose, suboval; its longest (oblique) diameter about 1.4 times as long as shortest; smallest genal height 0.13–0.15 times as long as shortest eye diameter. Palpus with several ventral setulae in addition to usual preapical seta. Antenna geniculate, with scape and pedicel dark brown; 1st flagellomere pale brown, usually with anterodorsal corner (around base of arista) darkened; apex of 1st flagellomere with whitish cilia twice longer than those of arista. Arista about 2.0 times as long as antenna, dark brown and very shortly ciliate.

Thorax small, reduced due to reduction of wing muscles, considerably narrower than head. Mesonotum largely dark brown, only sutures between pleural sclerites, humerus (= postpronotum) and (sometimes) notopleural area pale brown to ochreous. Mesonotum very sparsely brownish grey microtomentose and shining; pleural part of thorax with denser microtomentum and subshiny. Thoracic chaetotaxy: 1 relatively small hu (as long as or shorter than posterior npl); 2 npl, anterior very long (as long as apical sc), posterior short and upcurved; prs reduced to microseta; sa absent; pa about as long as posterior npl; 2 strong posterior dc, anterior long (but shorter than large anterior npl), posterior dc longest of thoracic setae (markedly longer than apical sc); only 1–2 dc microsetae in front of anterior dc; ac microsetae in only 2 (medial) short rows, usually reaching slightly beyond anterior dc; 2 sc, basal very short and weak, apical sc long but shorter

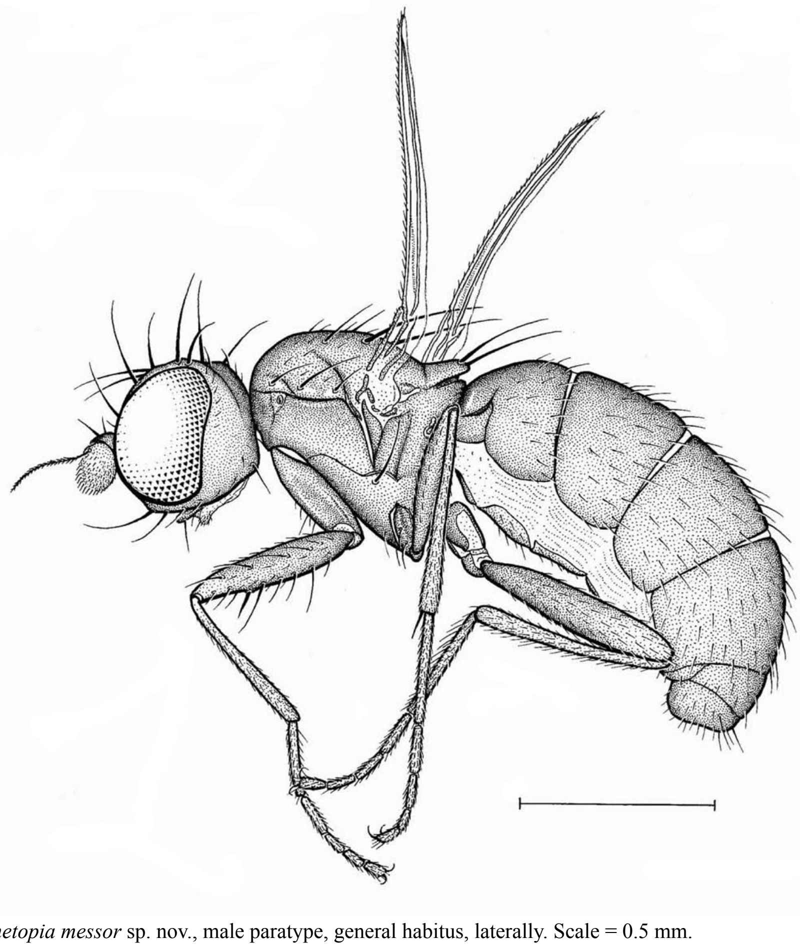
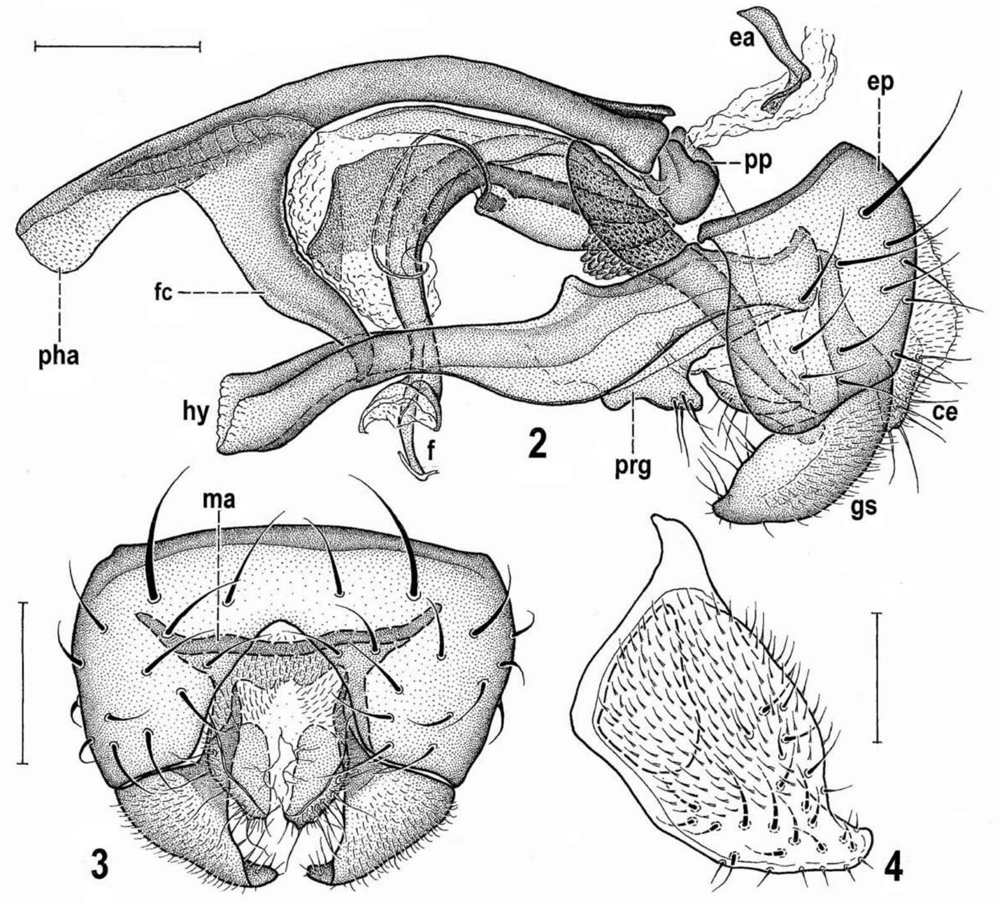


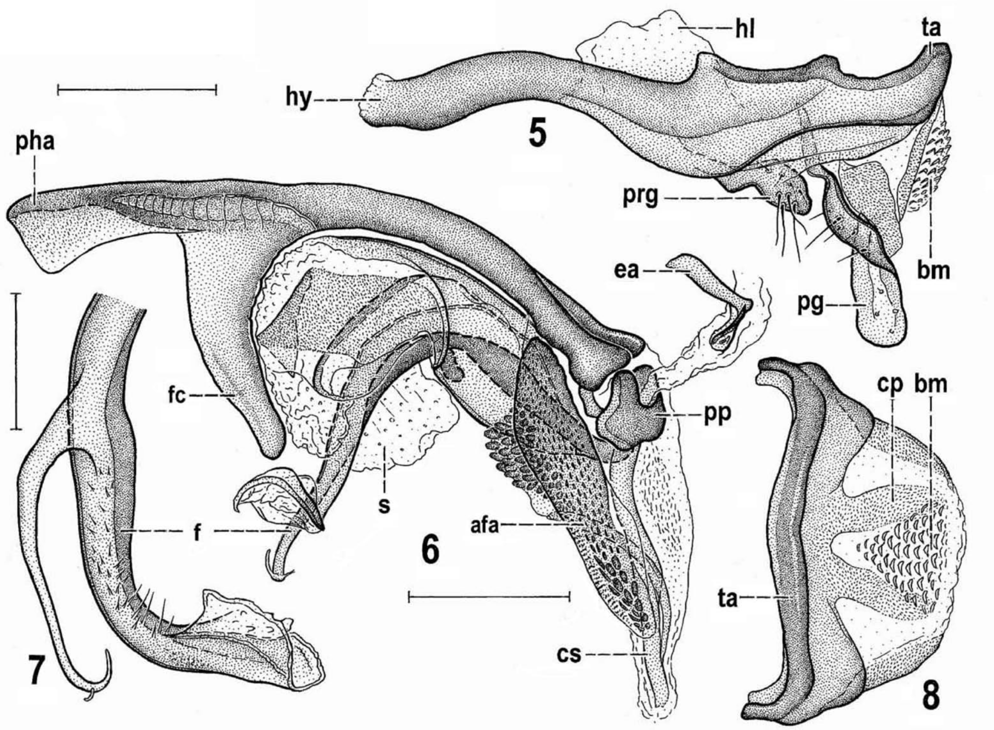
Fig. 1. *Mumetopia messor* sp. nov., male paratype, general habitus, laterally. Scale = 0.5 mm.



Figs. 2–4. *Mumetopia messor* sp. nov., male paratype. 2 – genitalia, laterally. 3 – external genitalia, caudally. 4 – left gonostylus, posteroventrally (widest extension). Scales: Fig. 4 = 0.05 mm, others = 0.1 mm. For abbreviations see text.

and weaker than posterior dc; ppl reduced to hairlike microseta; only 1 long (posterior) stpl macroseta; anterior stpl reduced to microseta; sternopleuron otherwise almost bare except for 1–2 setulae in ventralmost corner. Scutellum short, rounded triangular, with distinctly convex disc. Legs (Fig. 17) rather variable in colouration, usually ochreous yellow with brownish darkened coxae, proximal half (to two-thirds) of femora and distal parts of tarsi (or only terminal tarsomere), but sometimes (less mature specimens ?) lighter yellow with only pale ochreous-brown tinge visible on fore and/or hind femora. f_1 with ctenidial spine slightly to distinctly longer than maximum width of t_1 (Fig. 1) and inserted near (below) longest seta of posteroventral row; fore basitarsus with 2–3 longer and thicker setulae ventrobasally. t_2 with relatively short ventroapical seta. f_3 without specialised setae in posteroventral row, uniformly setulose; hind basitarsus with 2–3 thickened basal setulae in ventral row. Wing (Fig. 18) strongly reduced (reaching only to half or two-thirds of abdomen), narrowed and its shape resembling a scythe-blade. Wing membrane pale brownish ochreous, veins yellowish brown. C reaching beyond apex of R_{4+5}, with sparse but distinct spinulae in addition to usual setulae. Sc reduced, coalesced to basal part of R_1; R_1 distinct, robust, short as usual. R_{2+3} very shortened (hence Cs_3 unusually long) and weakened (faint), sometimes ending before reaching C. R_{4+5} entire, long, running parallel to C and meeting with it slightly before apex of wing. Cross-vein r-m strongly reduced, usually indistinct (confluent with M), thus M seemingly fused with R_{4+5}; no remnant of M behind point of this fusion. Basal medial, discal medial (dm) and posterior cubital (cup) cells as well as CuA_1 absent. A_1 short but very robust, not reaching wing margin despite anal lobe strongly reduced; alula absent. Wing measurements: length 0.87–1.03 mm, maximum width (near base of wing) 0.087–0.095 mm; wing vein indexes (Cs_3 : Cs_4; r-m\dm-cu : dm-cu) not measurable due to reductions or absence of veins. Haltere extremely reduced, visible (best in dorsal view) as a small ochreous tubercle.

Abdomen large and broad compared to reduced thorax. Preabdominal terga completely dark brown, all large and broad, reaching onto lateral sides of abdomen, with well-developed setosity. T1 short (one-third of T2) and with anteromedial emargination; T1 and T2 together about as long as T3; T3–T5 subequal in length. Preabdominal sterna brown, small and narrow, becoming wider posteriorly (S5 widest); S1 reduced to a small dark, transverse and bare remnant; S2 slightly wider than long and with emarginate anterior margin; S3 and S4 longer than broad; S5 largest, as long as broad, with slight posterior emargination; S2–S5 finely setose. T6 bare, short, transverse and



Figs. 5–8. *Mumetopia messor* sp. nov., male paratype. 5 – hypandrial complex, laterally. 6 – aedeagal complex, laterally. 7 – filum of distiphallus, anteroventrally. 8 – transandrium, caudally. Scales: Fig. 7 = 0.05 mm, others = 0.1 mm. For abbreviations see text.

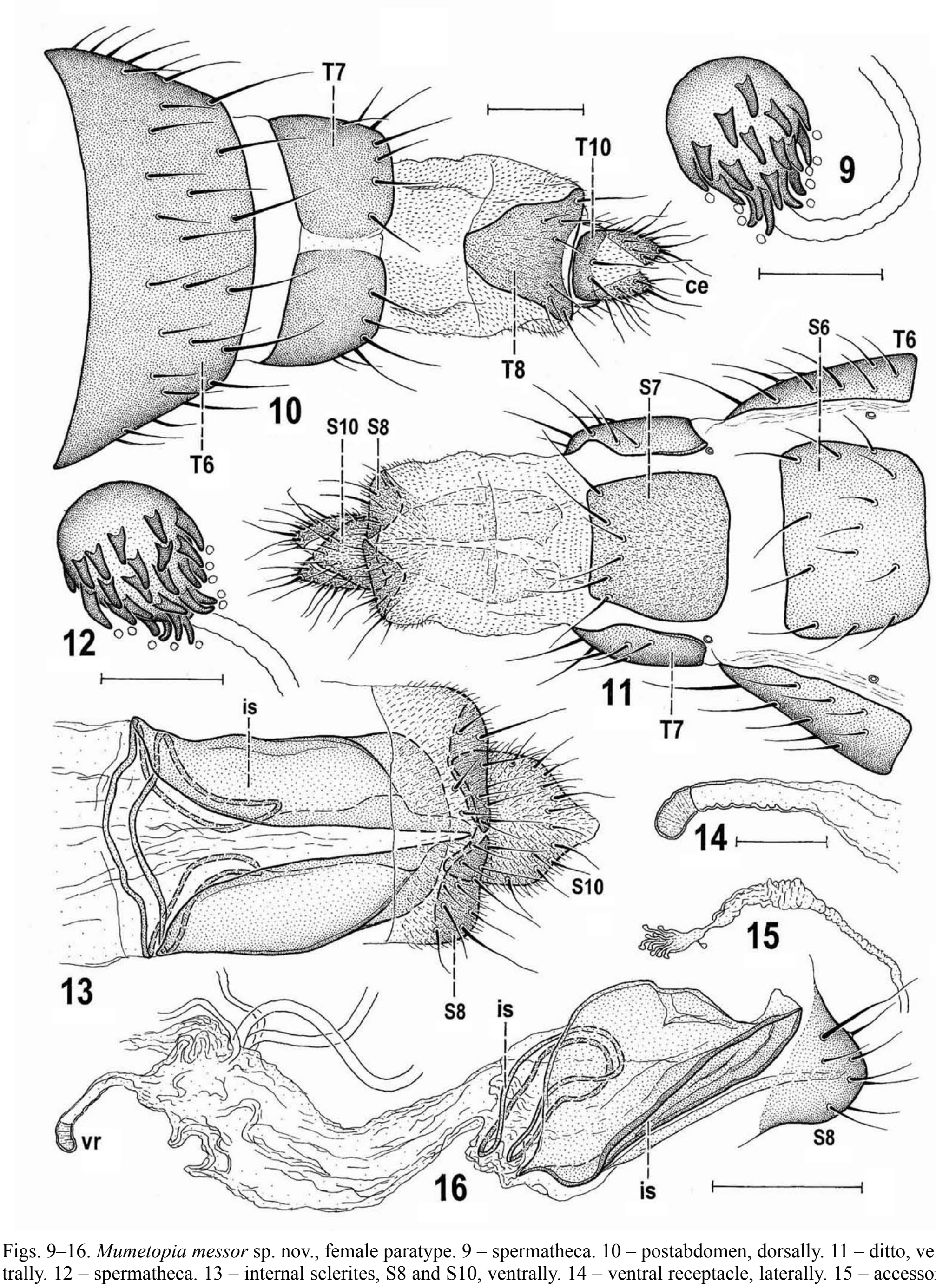
asymmetrical (3 times longer on right side), having medial third membranous and unpigmented; its lateral thirds brown and well sclerotized (left part markedly smaller than the right part). S6–S8 dark brown, partly (dorsally) coalesced; S6 very short and transverse with strongly sclerotized and blackish brown anterior marginal ledge; S7 longer but also anteriorly (more narrowly) dark-margined; S6 with 3–4 setae and S7 with 2 setae; S8 large but with sparse (7–8) setae.

Genitalia. Epandrium (Figs 2–3) small compared to internal genitalia, medium long but broad, markedly wider than high, with relatively sparse setae, 1 dorsolateral distinctly enlarged and thickened; dorsal margin of epandrium very slightly convex; anal fissure rather small, rounded subtriangular. Cercus rather small, turned around its longitudinal axis so that its largest sclerotized (lateral) side is faced internally (anteriorly) and posterior side is narrowed, shortly and finely setose. Medandrium (Fig. 3) with deep rectangular ventromedial incision and with strongly laterally prolonged dorsolateral corners. Gonostylus (Figs 2, 4) relatively low (short), bent internally and anteriorly, with shortly projecting and rounded anteroventral apex, micropubescence densely covering large part of outer side except for anterior and distal marginal areas; longer but fine setae situated at anterior margin of inner side. Internal genitalia relatively large. Hypandrium (Fig. 5) robust, sinuately bent in lateral view; internal hypandrial lobes distinct but largely membranous and pale-pigmented. Transandrium relatively broad (Fig. 8), with distinct (though weakly sclerotized) medial caudal process of forked shape; basal membrane armed with transverse spine-like tubercles which extend in membrane between arms of caudal fork. Pregonite (Fig. 5) forming short, posteroventrally projecting lobe having a ventral emargination and about 8 (half of them internal and shorter) setae. Postgonite (Fig. 5) relatively large, with darker proximal half provided with about 5 (one longer) setae inserted on its inner side and with paler, flat, almost hairless, broadly rounded distal half. Aedeagal complex (Fig. 6). Phallapodeme robust, with deeply forked proximal end, but simple apical part. Aedeagal part of folding apparatus (afa) strongly sclerotized and dark-pigmented (particularly in dorsal half), external side with fine dark tubercles, internal side with a dense group of blunt tuberculiform excrescences projecting anteriorly in its proximal third; connecting sclerite slender, long and bare, paler than afa. Phallophore short, compact, frame-shaped, with a small anterior sclerite connecting it with base of phallapodeme; basal part of distiphallus distinctly sclerotized. Saccus of distiphallus medium sized, dorsally and laterally with sclerotized plates, hence membranous part relatively small and provided with sparse, small to minute tubercles (Fig. 6). Filum of distiphallus rather compact, sclerotized, in distal third bifid, thus besides thicker main branch with a long, slender, apically curved hook-like projection having, in turn, a preapical minute finely bicuspidate process (? spine); main branch of filum spinose in distal third and with complex, dilated, partly membranous apex provided with several small processes and tubercles (Figs 6, 7). Ejacapodeme relatively large, with digitiform projection distally flattened and much larger than proximal part (Fig. 6).

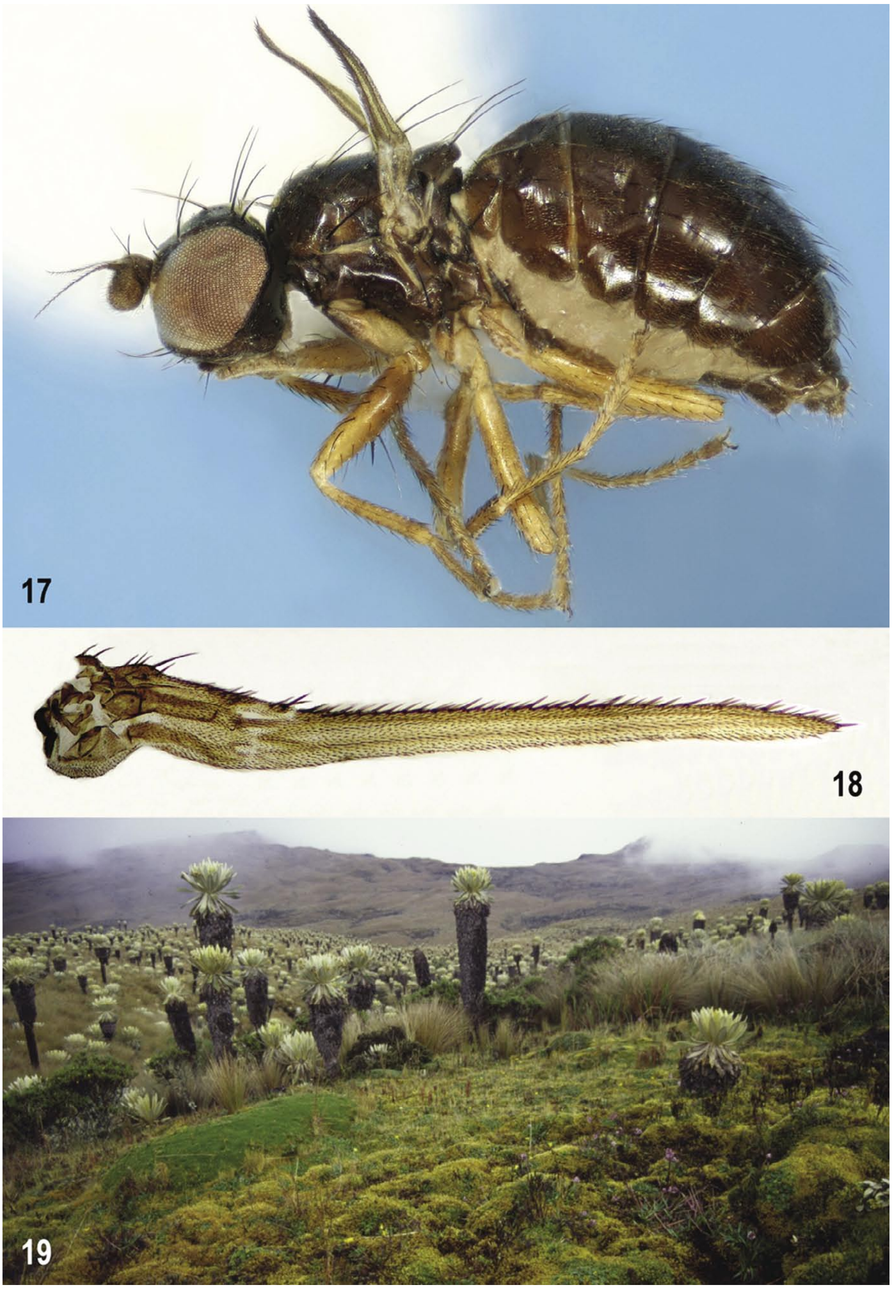
Female. Similar to male unless mentioned otherwise. Total body length 1.78–2.10 mm. Ctenidial spine on f_1 generally shorter than in male, as long as or slightly longer than maximum width of t_1; ventroapical seta on t_2 slightly longer. Wing measurements: length 0.80–1.12 mm, width 0.079–0.095 mm.

Abdomen (Fig. 17) markedly broader and, consequently, T1–T5 more transverse and shorter than in male, all uniformly brown to dark brown. T1+T2 distinctly narrower and slightly longer than T3 but T3–T5 subequal in length. S1 reduced to transverse, dark brown and bare strip. S2–S5 brown, less elongate than in male (S3–S4 as long as broad and S5 sometimes slightly wider than long), becoming wider posteriorly; S5 the widest but narrower (and darker) than S6. Setosity of preabdominal terga and sterna similar to that of male.

Postabdomen (Figs 10–11). T6 uniformly dark brown, transverse, tapered posteriorly and setose in posterior two-thirds (Fig. 10). S6 trapezoidal with rounded corners, wider posteriorly, brown,



Figs. 9–16. *Mumetopia messor* sp. nov., female paratype. 9 – spermatheca. 10 – postabdomen, dorsally. 11 – ditto, ventrally. 12 – spermatheca. 13 – internal sclerites, S8 and S10, ventrally. 14 – ventral receptacle, laterally. 15 – accessory gland. 16 – female genital chamber and S8 (micropubescence omitted), laterally. Scales: Figs 9, 12, 14 = 0.05 mm, others = 0.1 mm. For abbreviations see text.



Figs 17–19. *Mumetopia messor* sp. nov.: 17 – female paratype, habitus, laterally (body length 1.9 mm), photo by M. Deml; 18 – wing (length 1.1 mm), male paratype, photo by J. Roháček; 19 – habitat of *M. messor*, páramo ecosystem with *Espeletia* sp. (low yellow hummocks in foreground) and large bromeliads *Puya* sp. in Páramo El Angel, Ecuador (3400 m), photo by S. A. Marshall.

with rather sparse setae. T7 and S7 disparate. T7 dark brown, dorsomedially narrowly divided (or membranous – see Fig. 10) and with all setae arising along posterior margin. S7 large (Fig. 11), dark brown, with enlarged micropubescence and reduced setosity (with only 6 long setae at posterior margin). 7th spiracle situated at anteroventral corner of T7. T8 (Fig. 10) dark, anteriorly strongly narrowed (subtriangular), with posterior margin emarginate and posterolateral corners projecting, finely sparsely setose posteriorly. S8 (Fig. 11) short, medially unpigmented and posteromedially incised to divided, with posterior part bent dorsally, finely setose and micropubescent (see also Fig. 13). Internal structures of genital chamber (Figs 13, 16) distinct, elongate, formed by fusion of 2 pairs of flat sclerites and by 1 anterior, very slender, transversely compressed and dorsolaterally bent looped sclerite. Ventral receptacle (Figs 14, 16) weakly sclerotized, pale, rounded subcylindrical, very slightly bent and with finely ringed surface, set on membranous duct. Accessory gland small (Fig. 15), formed by a tuft of minute digitiform processes with globulate apices on subterminally slightly dilated duct. Spermathecae (1+1) shortly pyriform lacking duct cervix (Figs 9, 12), with dense robust dark spines on most of surface. T10 (Fig. 10) very short and transverse, dark-pigmented, with 2 long posteromedial setae and very fine micropubescence. S10 much larger than T10, roughly pentagonal with distinctly emarginate anterior margin, projecting and pale posteriomedial corner and micropubescent in posterior two-thirds (Fig. 13). Cerci small, short, with rich setae (apical and lateral setae subequal in length) and very short micropubescence (Figs 10–11).

Discussion. *M. messor* undoubtedly is closely allied to *M. taeniata* (for their differences see under that species) not only because of its similarly reduced wing and its venation but also owing to highly similar structures of the male genitalia and female postabdomen. Both these species differ from other (fully winged) related species, viz. *M. occipitalis* Melander, 1913 and allies, in having a shortly pubescent arista, a secondarily reduced supracervical microtomentose patch (very distinctive and silvery glittering in *M. occipitalis* and relatives), a well-developed (though short) anterior ors and in lacking thickened posteroventral setae in the distal third of the male hind femur.

Biology. This high-montane species (collected at 3400 m) was found to be associated with rotting endemic Andean plants of the genera *Espeletia* (Asteraceae) and *Puya* (Bromeliaceae) growing at high altitudes in the páramo ecosystem (Fig. 19); the type specimens were collected by means of pan traps placed among or sifted from litter under *Espeletia* sp. and also aspirated from under dead stems of *Puya* sp. in October–November.

Distribution. Ecuador.

***Mumetopia taeniata* sp. nov.**
(Figs 20–35)

Type material. Holotype male labelled: "COLOMBIA: Bogota, June 1986, N. L. H. Krauss" (USNM, genit. prep., head glued to rest of body being mounted on pinned card point). Paratypes: COLOMBIA: same data as for holotype, 7 females (USNM, 1 female SMOC, 3 females with genit. prep.).

Etymology. The species is named "taeniata" (= L. ribbon-shaped) owing to its extremely narrow, ribbon-shaped wing.

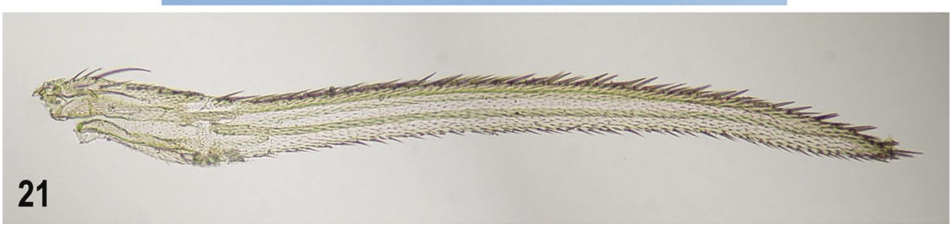
Description. Closely resembling *M. messor* but differing as follows. **Male**. Smaller, total body length 1.63 mm; brown to dark brown, more densely greyish microtomentose and less shiny, all extremities yellow to orange (Fig. 20). Head similar to that of *M. messor* but frons with grey microtomentose stripes between frontal triangle and orbits, the latter darker and more shiny. Frontal triangle large, reaching anterior margin of frons, sparsely microtomentose and (including ocellar triangle) relatively shiny; bare spots on both sides of ocellar triangle smaller than in *M. messor*; lunule hardly visible. Face distinctly lighter, dirty yellow (only ventrally brownish darkened) and distinctly silvery white microtomentose. Parafacialia, gena and postgena as in *M. messor*, but parafacialia narrowly brown-margined. Mouthparts (including palpus) pale brown, proboscis ochreous to yellow. Cephalic chaetotaxy: pvt very minute, often reduced to microseta and hardly visible, convergent; vte, vti, oc and posterior ors strong but, in contrast to *M. messor*, vti very long, longest of cephalic setae; vte and posterior ors slightly to distinctly shorter than vti; oc subequal to or slightly shorter than posterior ors; 2 ors, both situated in anterior two-fifths of frons, but only posterior ors long and strong; anterior ors weak and shortened, about one-fourth length of posterior ors; orbital microsetula absent or very minute; also medial microsetula in front of anterior frontal margin rarely visible; vi shorter and weaker than posterior ors but still rather long; subvibrissa, peristomals and postoculars as in *M. messor*. Eye with more sparse pilosity and broader than that of *M. messor*; its longest diameter about 1.25 times as long as shortest; gena lower, its smallest height 0.09 times as long as shortest eye diameter. Palpus more slender, with similar setosity to that in *M. messor*. Antenna yellow to orange; 1st flagellomere usually darker around base of arista and cilia on its apex slightly longer than those of arista. Arista about 2.1 times as long as antenna, having longer cilia than that of *M. messor*.

Thorax resembling in shape and colour that of *M. messor* but humeral and notopleural areas concolourous with mesonotum, dark brown. Mesonotum more densely dark grey microtomentose and less shining. Thoracic chaetotaxy similar to that in *M. messor* but macrosetae (anterior npl and both dc in particular) yet longer and number of ac microsetae strongly reduced, represented by only 1–2 (often incomplete) pairs in front of level of anterior dc or completely absent. Besides 1 long (posterior) stpl macroseta there are 1–2 stpl microsetae in front of it. Scutellum short, rounded triangular, with slightly convex disc. Legs distinctly lighter than in *M. messor*, entirely pale to brightly yellow (Fig. 20), at most with terminal tarsal segments darker (ochreous). f_1 with ctenidial spine slightly longer than maximum width of t_1 but inserted somewhat farther (more distally) from longest posteroventral seta than in *M. messor*; fore basitarsus, t_2, f_3 and hind basitarsus with similar chaetotaxy to that in *M. messor*. Wing (cf. Fig. 21) similarly reduced to that in *M. messor* but usually longer compared to body length, strongly narrowed, almost ribbon-shaped. Wing membrane yellowish white to dirty white, thicker veins (C, R_1) yellowish, thinner veins (R_{2+3}, R_{4+5}) yellowish white. C ending beyond apex of R_{4+5}, and having sparse spinulae among usual setosity. R_1 distinct, very short. R_{2+3} weakened, running close to C and meeting with it in distal third to fourth of wing. R_{4+5} long but thinner than that in *M. messor*, running parallel to C and ending at it slightly before apex of wing. Cross-vein r-m confluent with reduced M as in *M. messor*; basal medial, dm, and cup cells and CuA_1 absent. A_1 yet shorter than in *M. messor*; alula absent. Wing measurements: length 1.04 mm, maximum width (near base of wing) 0.071 mm; wing vein indexes not measurable. Haltere extremely reduced, visible (best in dorsal view) as a small ochreous tubercle.

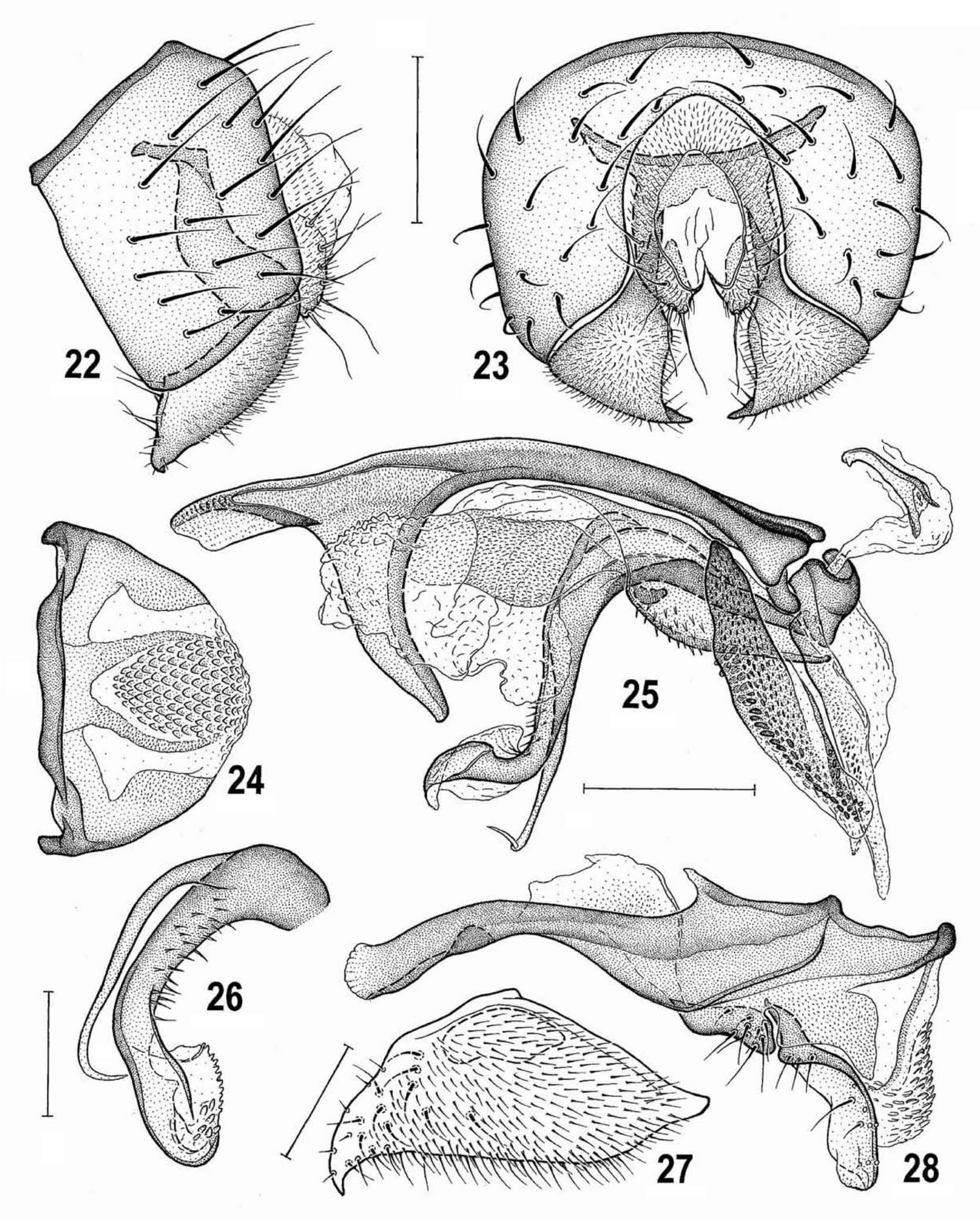
Abdomen. Preabdominal terga similar to that in *M. messor* including setosity. T1+T2 slightly shorter than T3; T3–T5 subequal in length. Preabdominal sterna small, brown and becoming wider posteriorly as in *M. messor* but somewhat wider; S1 and S2 undescribed (not visible in dissected holotype; but see below under female); S3 and S4 about as long as broad; S5 largest, distinctly wider than long, slightly posteriorly emarginate. T6 with bipartite pigmentation as that of *M. messor* but its left sclerotized part smaller and narrower. S6–S8 as in *M. messor* but S6 with only 1 (relatively long) seta and S7 with 2 setae, one markedly longer than other.

Genitalia. Epandrium (Figs 22–23) similar to that of *M. messor* but with more setae none of which is distinctly enlarged, dorsal margin of epandrium more convex and anal fissure suboval. Cercus yet smaller than that of *M. messor* but with the same type orientation. Medandrium (Fig.

23) with deep ventromedial incision being medially deepened and with projecting dorsolateral corners. Gonostylus (Figs 22, 27) shorter in lateral view than that of *M. messor*, bent internally and with curved and sharply pointed anteroventral apex (Figs 23, 27); its micropubescence somewhat denser and setae on inner side shorter. Internal genitalia closely resembling those of *M. messor*. Hypandrium (Fig. 28) more slender and more strongly bent anteriorly. Transandrium dorsally straighter (Fig. 24), with arms of forked caudal process markedly longer and more slender; basal membrane with denser (and more) flattened spine-like tubercles covering also most of membrane



Figs. 20–21. *Mumetopia taeniata* sp. nov.: 20 – female paratype, habitus, laterally (body length 1.6 mm), photo by M. Deml. 21 – wing (length 1.05 mm), female paratype, photo by J. Roháček.



Figs. 22–28. *Mumetopia taeniata* sp. nov., male holotype. 22 – external genitalia, laterally. 23 – ditto, caudally. 24 – transandrium, caudally. 25 – aedeagal complex, laterally. 26 – filum of distiphallus, anteroventrally. 27 – left gonostylus, ventrolaterally (widest extension). 28 – hypandrial complex, laterally. Scales: Figs. 26, 27 = 0.05 mm, others = 0.1 mm.

between arms of caudal fork. Pregonite (Fig. 28) similar to that in *M. messor* but less projecting, attached to hypandrium and with about 9 (4 of them on inner side shorter) setae. Postgonite (Fig. 28) resembling that of *M. messor* in structure and setosity but its darker proximal part smaller and with only 3 subequal setae on inner side and its distal part larger, curved, and provided with 2 (1 long) setae in addition to minute sensilae. Aedeagal complex (Fig. 25). Phallapodeme robust, more slender apical part. Aedeagal part of folding apparatus sclerotized and dark as in *M. messor*, but its external side with bigger dark tubercles and internal side with less projecting group of blunt tuberculiform excrescences; connecting sclerite finely granulose. Phallophore short but more projecting ventrally and sclerite connecting it with base of phallapodeme larger; basal part of distiphallus sclerotized as in *M. messor* but its ventral sclerite armed with small spines (Fig. 25). Saccus of distiphallus not larger but lateral sclerotized plates longer and membranous part dorsoapically with more distinct tubercles (Fig. 25). Filum of distiphallus more robust than that of *M. messor* although of highly similar bifid construction; its main branch thicker, spinulose and with dilated apex differently armed (with a series of tubercles) and more sclerotized than that of *M. messor*; its slender branch bare, less and simply hooked, without additional process (Figs 25, 26). Ejacapodeme also different from that of *M. messor*, with short, wider proximal part and long projection distally bent (Fig. 25).

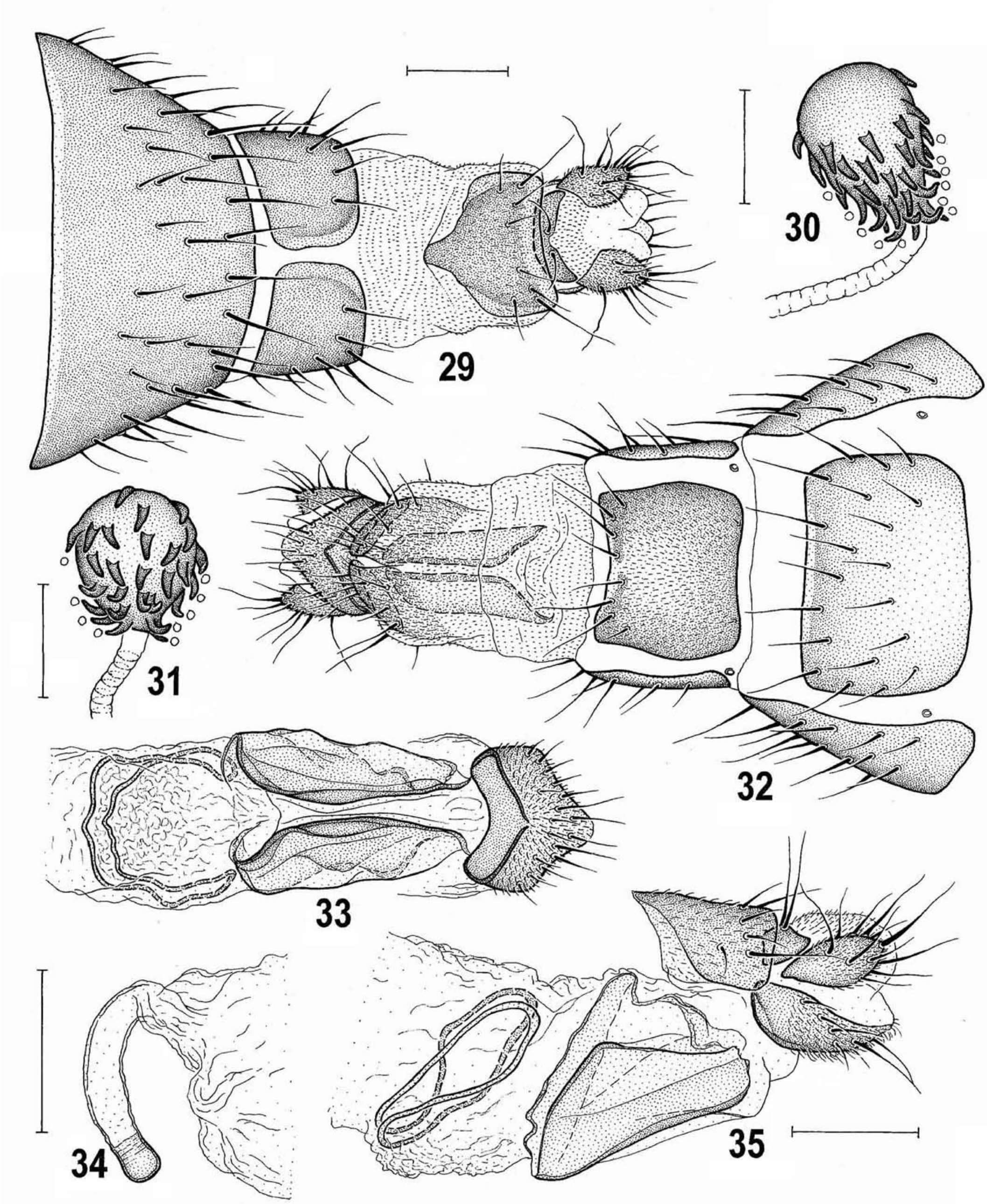
Female. Similar to male unless mentioned otherwise. Total body length 1.47–1.94 mm. Antenna often darker, orange and 1st flagellomere more darkened anterodorsally than in male. Wing measurements: length 1.01–1.30 mm, width 0.079–0.103 mm.

Abdomen. T1–T5 as in *M. messor*. S1 modified to transverse, dark brown, bent (posteriorly convex) strip. S2 as long as broad, wider and distinctly emarginate anteriorly, tapered posteriorly. S3–S4 slightly longer than broad; S5 somewhat wider than long but distinctly narrower (not darker) than S6.

Postabdomen (Figs 29, 32). T6 dark brown except narrow anterior margin, less transverse, longer and more setose (Fig. 29) than in *M. messor*. S6 transversely suboblong, brown (darker posteriorly), wider and with more setae than in *M. messor*. T7 narrower, more distinctly dorsomedially divided (Fig. 29) and with setae also laterally. S7 (Fig. 32), darker brown than S6, wider and with more (8) setae at posterior, slightly emarginate, margin. T8 dark, anteriorly strongly narrowed to form a projecting anteromedial corner and posterior marginal stripe paler pigmented, with longer setae in posterolateral corners than in *M. messor*. S8 short, medially divided, with posterior part dark and bent dorsally, longer setose than that of *M. messor*. Internal structures of genital chamber (Figs 33, 35) resembling those of *M. messor* but posterior fused sclerites smaller, paler, narrower in dorsal view and looped sclerite (very slender) positioned more anteriorly and bent on lateral sides of genital chamber. Ventral receptacle (Fig. 34) also similar but shorter, with semispherical apex and only proximally ringed. Accessory gland as in *M. messor*. Spermathecae (Figs 30–31) slightly more elongately pyriform, without cervix and with more and smaller dark spines on surface than those of *M. messor*. T10 (Fig. 29) yet shorter than in *M. messor*, with 2 long erect posteromedial setae and very fine micropubescence. S10 similar in shape to that of *M. messor* but anterior bare part separated from posterior micropubescent part by blackish lines (see Fig. 33). Cerci (Figs 29, 32) more robust, widely separated each from other and with yet shorter micropubescence than those of *M. messor*.

Discussion. *M. taeniata* superficially closely resembles *M. messor* but differs from the latter in many details of external body characters as well as genitalic features (see in the above description). Both species can be easily distinguished as follows:

– Larger; antenna with scape and pedicel dark brown and 1st flagellomere pale brown; humeral callus (postpronotum) and notopleuron lighter than mesonotum, pale brownish to ochreous; vti as long as vte and posterior ors; legs somewhat



Figs. 29–35. *Mumetopia taeniata* sp. nov., female paratype. 29 – postabdomen, dorsally. 30, 31 – spermathecae. 32 – postabdomen, ventrally. 33 – internal sclerites and S10, ventrally. 34 – ventral receptacle, laterally. 35 – internal sclerites with apex of abdomen (T8, T10, S10 and cercus), laterally. Scales: Figs 30, 31, 34 = 0.05 mm, others = 0.1 mm. For abbreviations see text.

bicolourous, dark yellow with pale brownish coxae and ochreous-brown darkened proximal half of (at least fore and hind) femora (Fig. 17); wing membrane and veins darker, brownish ochreous (Fig. 18). Epandrium with 1 enlarged (dorsolateral) seta; gonostylus longer in lateral view (Fig. 2) and its anteroventral apex rounded (Fig. 4). Female T6 more transverse (Fig. 10) and S6 narrower, with sparse setae (Fig. 11); S7 narrower and with only 6 setae (Fig. 11); S10 simple, without dark lines (Fig. 13); female cerci more elongate and close to each other (Fig. 10). .... *M. messor* sp. nov.

– Smaller; antenna orange to yellow; vti distinctly longer than vte or posterior ors; humeral callus dark brown, concolourous with mesonotum; vti longer than vte and posterior ors; legs uniformly yellow including coxae (Fig. 20); wing membrane and veins paler, dirty whitish to yellowish white (Fig. 21). Epandrium without enlarged seta; gonostylus shorter in lateral view (Fig. 22) and its anteroventral apex sharply pointed (Fig. 27). Female T6 narrower, longer (Fig. 29) and S6 wider, with more setae (Fig. 32); S7 wider, with 8 setae (Fig. 32); S10 with dark lines separating bare and micropubescent parts (Fig. 33); female cerci robust and widely separated (Fig. 29). .... *M. taeniata* sp. nov.

Biology. Unknown. Type specimens were found in (vicinity of) Bogota, i.e. at high altitudes (more than 2500 m), in June.
Distribution. Colombia.

PHYLOGENY

Morphological analysis

From more than 80 morphological characters currently used to characterize genera of Anthomyzidae (see e.g. Roháček 2006, 2007) only 27, mostly from the male genital and female postabdominal structures, have been selected, because others either appear only in plesiomorphic states within the group of genera under study, or commonly occur as homoplasies in various and distantly related clades of Anthomyzidae. The list below shows the character states derived from our original morphological investigations and from the literature reviewed for the present study with comments about their reliability, significance, modifications and occurrence in the group under study as well as the family Anthomyzidae as a whole. Distribution of character states in the genera investigated is shown in Table 1 (data matrix of character states used for the cladistic analysis).

List of characters of the *Chamaebosca* group of genera

The character states are indicated as follows:
0 – the presumed plesiomorphic condition; 1, 2 – apomorphic conditions.

01 microtomentose supracervical patch: 0 – absent; 1 – double; 2 – united to single spot

The solid silvery microtomentose supracervical patch is well developed in *Mumetopia* s. str. and the closely related Genus *B* and Genus *M* but is secondarily reduced in both species described above, *M. messor* sp. nov. and *M. taeniata* sp. nov., probably because it has lost its function in visual communication in the terricolous habitat. This may also be true for the *Chamaebosca* species (but the patch may have been overlooked in the holotype of *Ch. microptera* as it had been originally preserved in ethanol and was re-mounted in glycerine, see Roháček 1998). The double supracervical microtomentose patch is, however, not so unique a feature; besides occurring in *Stiphrosoma* a similar condition is known in some species of the distantly related genus *Anthomyza* Fallén, 1810 (including the *A. socculata* group), *Ischnomyia* and some other undescribed Neotropical taxa.

02 prs and sa setae: 0 – small to minute; 1 – enlarged

The strikingly enlarged thoracic setae, prs and sa in particular, are considered a strong synapomorphy of the Genus *B*. In all other allied genera, the prs and sa are reduced to microsetae (and other thoracic macrosetae are markedly shorter) which is regarded a groundplan character of the group under study.

03 costal spines and setae on Cs_1: 0 – small; 1 – enlarged

The costal spines and setae on Cs_1 are developed in all genera under study. However, in the Genus *B* they are unusually enlarged (and thickened), a condition unknown in all other described Anthomyzidae.

04 postgonite: 0 – slender and simple; 1 – widened distally and with different proximal and distal parts

The modified postgonite, with broadened distal part and different (protruding or twisted) proximal part, is considered a distinct synapomorphy of genera most closely allied to *Mumetopia* s. str.

05 postgonite: 0 – with single seta; 1 – with several setae (also proximally)

The postgonite with more setae, mainly on its proximal part, is probably a unique character within the known taxa of Anthomyzidae; consequently this character is considered strongly apomorphic.

06 medandrium: 0 – ventrally shallowly emarginate; 1 – ventrally deeply incised

The deeply ventrally incised medandrium undoubtedly is an apomorphic feature delimiting the clade comprised of *Chamaebosca*, *Mumetopia* s.str., Genus *B* and Genus *M*. A seemingly similar condition can be found in several species of the unrelated genera *Amygdalops* Lamb, 1914, *Paranthomyza* Czerny, 1902, *Anthomyza* and also in the allied *Stiphrosoma* but in these cases this incision is more shallow, seems to be of a different type(s) and is interpreted to have evolved independently.

07 medandrium: 0 – with dorsolateral corners simple, short; 1 – with dorsolateral corners prolonged

In some species of the *Mumetopia nigrimana* group the dorsolateral corners of the medandrium are somewhat projecting (similar cases can also be found in a few unrelated genera of Anthomyzidae). However, this condition is not considered to be homologous with the markedly prolonged corners of Genus *M*, Genus *B* and *Mumetopia* s. str. and is thus coded as plesiomorphic.

08 aedeagal part of folding apparatus: 0 – dorsally membranous; 1 – dorsally sclerotized

The aedegal part of the folding apparatus (afa) may be partly sclerotized narrowly along its anterodorsal margin in the *Mumetopia nigrimana* group (found in 3 species) but this condition is not homologous with the (apomorphic) complete dorsal sclerotization and darkening of the structure (e.g. in the Genus *M*, Genus *B* and *Mumetopia* s. str.). The (homologous) dorsal sclerotization of afa in *Cercagnota* (see Roháček 2006: Fig. 437) probably evolved independently (in parallel) because there is no other synapomorphy linking this genus with the *Mumetopia* s.str. clade.

09 filum of distiphallus: 0 – simple or with short robust preapical process; 1 – with slender curved projection in distal third; 2 – bifid in distal third (projection almost as long as main branch of filum)

The most plesiomorphic condition of the filum was found in some (3) species of the *Mumetopia nigrimana* group where it is formed by two dark ribbon-shaped sclerites. Within the same group the filum may further be modified by reduction (and desclerotization) of one of these sclerites and dilatation of the other, or by fusion of both of them. The same conditions also occur in *Stiphrosoma* species. In addition, there is a tendency to split the apex of the filum preapically or to form a preapical robust process, as found in a few species of *Stiphrosoma* (cf. Roháček 1996 and Roháček & Barber 2005) or in *Chamaebosca microptera* (cf. Roháček 1998). However, all these conditions are considered plesiomorphic with respect to the very slender, long and more proximal projection being considered synapomorphic for the Genus *M*, Genus *B* and *Mumetopia* s. str.

10 filum of distiphallus: 0 – bare; 1 – spinulose

The spinulose filum has only be found in *Mumetopia* s. str. species (it may be a unique feature within the Anthomyzidae) and is, therefore, considered a strong synapomorphy of this group.

11 saccus of distiphallus: 0 – with flat tubercles, at most with sparse microspinulae; 1 – spinose or densely setulose

The armature of the saccus varies greatly within the Anthomyzidae so that the spinose or setulose surface of the membrane of the saccus (considered apomorphic within the group analyzed) is known also in a number of unrelated genera. The character apparently evolved several times in the various clades of the family, so it should be regarded as a rather weak synapomorphy of the *Stiphrosoma* + *M*. *nigrimana* group. Moreover, the saccus in *Cercagnota* is provided with short spines, although these are flat and weakly sclerotized.

12 male cercus: 0 – simple in shape; 1 – enlarged and projecting anteriorly

The peculiarly anteriorly expanded male cercus of *Cercagnota* (see Roháček 2006: Fig. 435) is a distinctive apomorphic feature of this genus. Within Anthomyzidae, an enlarged cercus is otherwise known only in species of the Afrotropical genus *Margdalops* (see Roháček & Barraclough 2003).

13 male cercus: 0 – in normal position; 1 – turned around its longitudinal axis

The unusually turned male cercus is a distinctive synapomorphy linking *Mumetopia* s. str. and Genus *B*.

14 caudal process of transandrium: 0 – absent; 1 – present and forked

The forked and/or double caudal process of the transandrium, considered a synapomorphy of the group under study (including *Cercagnota*), may be short and inconspicuous in some species of the *Mumetopia nigrimana* group and is completely lost in *Stiphrosoma* and *Chamaebosca*. These conditions are interpreted to be secondary reductions of this structure (reversal of the character).

15 gonostylus: 0 – disparate; 1 – fused to epandrium

Fusion of the gonostylus (besides medandrium) to the epandrium is a distinctive autapomorphy of *Chamaebosca*. Otherwise this character state is not known in the Anthomyzidae as a whole.

16 gonostylus: 0 – micropubescent on outer side; 1 – bare on outer side

Reduction of micropubescence of the gonostylus can be found in several unrelated genera of Anthomyzidae, e.g. in *Anagnota* Becker, 1902, *Santhomyza* Roháček, 1984 or *Typhamyza* Roháček, 1992, but within the group investigated it is an apomorphic feature, known only in *Chamaebosca*.

17 female T7: 0 – simple dorsally; 1 – dorsomedially divided or membranous

The dorsomedially divided or membranous female T7 is a synapomorphic character for all groups analyzed (except *Cercagnota*) despite the fact that in a few species of the *Mumetopia nigrimana* group, one of Genus *B* and in three species of *Mumetopia* s. str. T7 is dorsomedially (secondarily) partly or completely coalesced. The apomorphic state of this character is presupposed to occur also in the genus *Chamaebosca* where the female is unknown because its linking with *Mumetopia* s. str., Genus *B* and Genus *M* is supported by synapomorphy 06.

18 female S7: 0 – present (at least as remnants); 1 – unrecognizable, completely integrated into tergosternum T7+S7

The female S7 is completely fused with T7 (thus forming a tergosternal ring T7+S7 without any trace of a boundary between these sclerites) not only in *Cercagnota* but also in the wingless Afrotropical *Apterosepsis* and may be considered evidence of their relationship. However, the ring-shaped tergosternum is known to have evolved in Anthomyzidae several times, e.g. in unrelated genera *Anthomyza*, *Epischnomyia* Roháček, 2006, *Barbarista* Roháček, 1993, *Zealantha* Roháček, 2007 so that it cannot be considered a strong synapomorphy.

19 female S7: 0 – large and disparate; 1 – reduced to a remnant coalesced with T7

The female S7 reduced to a posteromedial remnant coalesced with a dilated T7 is considered a good synapomorphy of the *Stiphrosoma* + *Mumetopia nigrimana* group clade. An ostensibly similar reduction of S7 may be found in some species of unrelated *Anthomyza*, *Amnonthomyza* Roháček, 1993, *Receptrixa* Roháček, 2006 but in these cases the feature differs in detail and surely evolved independently.

20 female T8: 0 – broadest anteriorly; 1 – anteriorly tapered

The anteriorly strongly tapered (thus roughly triangular) female T8 is considered a strong synapomorphy of all genera under study except for *Cercagnota*. Consequently, it is presumed to occur also in the unknown females of *Chamaebosca*.

21 female S8: 0 – larger and undivided; 1 – shorter and deeply posteromedially incised or medially divided

The posteromedially incised or medially divided S8 is considered an apomorphic feature despite similar conditions of S8 found in several other genera of Anthomyzidae which, however, usually differ in detail and have probably evolved in parallel (see e.g. in *Amygdalops* Lamb, 1914 where S8 is posteromedially protruding – Roháček 2004). Because the apomorphic state of this character was found in all groups under study except for *Cercagnota* it is predicted also to occur in (unknown) females of *Chamaebosca*.

22 posterior internal sclerites of female genital chamber: 0 – submembranous; 1 – well sclerotized

The strong sclerotization of the internal sclerites of the female genital chamber is known in several clades within Anthomyzidae. Moreover, these structures also may be secondarily reduced or desclerotized. Despite this it is considered to be an apomorphic (although weak) feature within the group of genera under study.

23 posterior internal sclerites: 0 – short; 1 – long

The prolongation of the internal sclerites of the female genital chamber is a synapomorphic feature of the Genus *B* and *Mumetopia* s. str.

24 annular internal sclerite of female genital chamber: 0 – pale-pigmented; 1 – dark-pigmented

The dark and well-sclerotized annular sclerite is a distinctive synapomorphy of the *Mumetopia nigrimana* group.

25 spermathecae: 0 – spherical; 1 – pyriform

26 spermathecae: 0 – with plain surface; 1 – with robust surface spines

The pyriform spermathecae with strong surface spines are considered to be distinct synapomorphies of all genera under study (including *Chamaebosca* where female is unknown) except for

Cercagnota. However, it is to be noted that a very similar shape and armature of the spermathecae is known in several Oriental species of the distantly related genus *Amygdalops* Lamb, 1914 but in this case these structures differ in detail and, consequently, obviously evolved in parallel (see Roháček 2008).

27 ventral receptacle: 0 – short, subcylindrical, somewhat sclerotized; 1 – reduced, membranous, hyaline

The type of ventral receptacle (short, subcylindrical) occuring in most of the groups under study is surely plesiomorphic with respect to the reduced and desclerotized state found in *Cercagnota* but may be considered a groundplan character of the group under study; the same receptacle was also found in *Apterosepsis* (cf. Roháček 1998). The seemingly similar condition of the ventral receptacle known in other (mutually unrelated) genera of Anthomyzidae, e.g. *Anagnota*, *Paranthomyza*, *Typhamyza*, probably evolved independently.

Remark. In spite of the fact that the females of *Chamaebosca* are unknown, some characters of the female postabdomen can be predicted to occur in this genus with a high degree of probability because this genus is linked to the same clade as Genus *M*, Genus *B* and *Mumetopia* s. str. on the basis of male genitalic features. Thus characters 17, 20, 21, 25 and 26 are included in the analysis in their apomorphic states, and characters 18, 19 and 27 in plesiomorphic states as presupposed to occur in female *Chamaebosca*.

Notes on other characters

There are further (probably apomorphic) characters which can characterize the whole group (including also *Cercagnota* and, possibly, *Apterosepsis*).

(1) Tendency for reduction of anterior ors. This phenomenon occurs within most of the groups analysed, although sometimes in only some species of the respective genera. The anterior ors is very strongly reduced (to microseta or entirely absent) in *Apterosepsis*, *Cercagnota*, all but one species of the *M*. *nigrimana* group and the *Mumetopia* s. str. species (except brachypterous ones) but also in one species of *Stiphrosoma* (*S. fissum* Roháček, 1996). It is distinctly shortened (but thicker) in most species of Genus *M*, *Mumetopia messor* and *M*. *taeniata* and in several species of *Stiphrosoma*; only in Genus *B* (two species), *Chamaebosca* (1 species), 1 species of *M*. *nigrimana* group and most species of *Stiphrosoma* is a relatively long anterior ors retained. Because the reduction of the anterior ors also occurs (independently) in some unrelated genera of Anthomyzidae (e.g. in *Anagnota*, *Paranthomyza*) and due to its very frequent reversal, this character has not been used in the cladistic analysis here.

(2) Tendency for reduction of wings and/or wing venation. Within the family Anthomyzidae the species with reduced (or even absent) wings are only known in the group of genera under study (see also Introduction). The only species of *Apterosepsis* is wingless and that of *Cercagnota* has normal wings but reduced venation; in *Stiphrosoma* there are 3 wing-polymorphic species with brachypterous, intermediate and macropterous (often with reduced venation) forms, see Roháček & Barber (2005); in *Chamaebosca* both its known species are strongly brachypterous (Roháček 1998); in Genus *M* one unnamed species was found to have somewhat shortened wings and in *Mumetopia* s. str. two strikingly steno- and brachypterous are described above. Consequently, short-winged forms or species with reduced venation are absent only in the *M*. *nigrimana* group and in Genus *B*. It may be expected that further species with shortened to vestigial wings belonging to these genera will be discovered when the terricolous fly fauna is better studied, in tropical and high-montane areas in particular.

(3) There seems to be a general tendency for the prolongation of the cilia of the arista in the clade investigated. In *Cercagnota* and the *Mumetopia nigrimana* group the arista is pectinate, in *Stiphrosoma* it varies from long-ciliate to pectinate and in Genus *M* and *Mumetopia* s. str. from short- to long-ciliate. Only in species of *Chamaebosca* and Genus *B* is the arista invariably short-ciliate. On the other hand, the long-ciliate or pectinate arista also occurs in other genera of Anthomyzidae (*Anagnota*, *Amygdalops*, *Amnonthomyza*, *Barbarista*, as well as other undescribed Neotropical taxa) so it is clear that this condition evolved in the family several times.

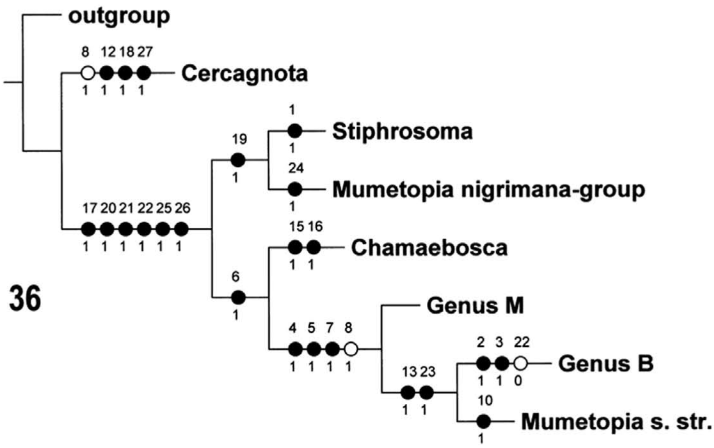
Phylogenetic analysis

The phylogenetic hypothesis resulted from the cladistic analysis of the character matrix given in Table 1. A single most parsimonious tree was obtained, with length of 34 steps, consistency index = 0.85, retention index = 0.82. Different character optimizations on this most parsimonious topology are shown in Figs 36–38.

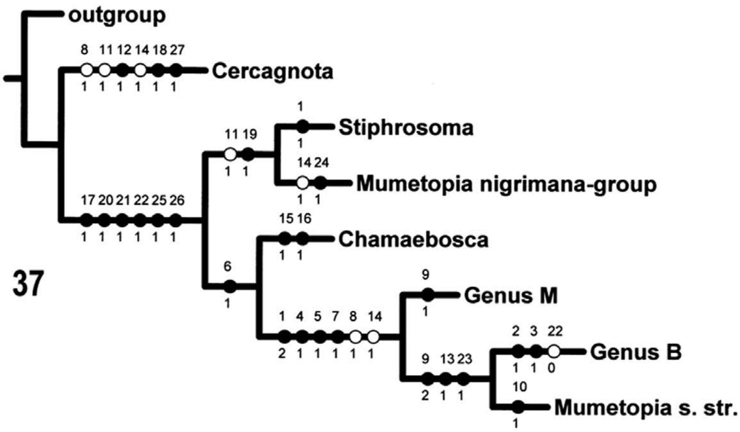
The monophyly of the entire group under study is relatively poorly supported by apomorphic states of characters No. 11 (reversed in the *Chamaebosca* + Genus M + Genus B + *Mumetopia* s. str. clade) and No. 14 (reversed in each of *Stiphrosoma* and *Chamaebosca*, see Fig. 38). Because of a number of plesiomorphies, the genus *Cercagnota* proved to be closest to the hypothetical outgroup and forms the most basal clade and a sister-group to all other analysed genera which are grouped on a well-supported branch. This cluster of undoubtedly closely allied genera, termed the *Chamaebosca* group of genera, is characterized by a number of distinct synapomorphies, particularly in the female postabdominal structures (No. 17, 20, 21, 25, 26, see Figs 36–38). It is comprised of two clades, one with the *Stiphrosoma* + *Mumetopia nigrimana* group pair, the other with all remaining genera including *Mumetopia* s. str. (= the *M. occipitalis* group). This is a very important finding demonstrating that the current concept of the genus *Mumetopia* is not monophyletic but polyphyletic. Thus, the *M. nigrimana* group proved to be most closely allied to *Stiphrosoma* (supported by synapomorphy No. 19; also the spinose and/or setulose distiphallus (No. 11) may be a synapomorphy of this clade despite a similar condition occurring in *Cercagnota*, see Fig. 37) and not to *Mumetopia* s. str. which should certainly be reflected in the re-classification of the *M. nigrimana* group as a separate genus of Anthomyzidae in the near future.

The genus *Stiphrosoma* is characterized by a distinctive bipartite microtomentose supracervical patch (No. 1, considered apomorphic with respect to the state occurring in the *Mumetopia nigrimana* group) but differs from the *M. nigrimana* group by mainly plesiomorphic features (not only No. 14 and 24 but also by the well-developed anterior ors and more microtomentose body). The *M. nigrimana* group is defined by the autapomorphy No. 24 (dark-pigmented annular internal sclerite) and also by the more or less developed caudal process of the transandrium (No. 14, cf. Fig. 37), but the group is characterized also by additional characters, such as the usually strongly reduced (to absent) anterior ors (well developed only in species #1), the densely haired to pectinate arista or the reduced microtomentum of the body.

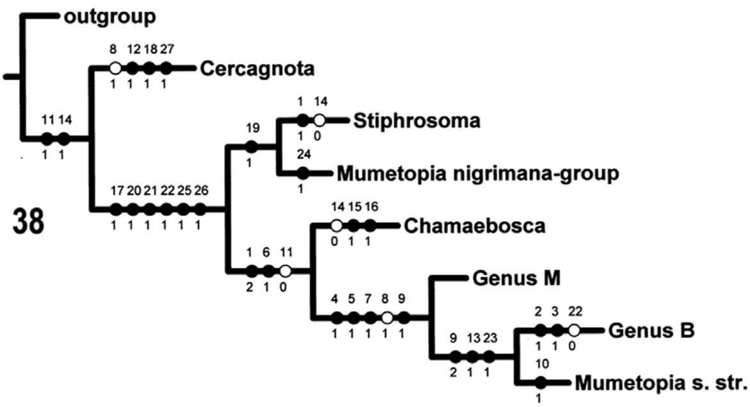
The other main clade grouped together the genera *Chamaebosca*, *Mumetopia* s. str. and two unnamed taxa referred to as Genus *M* and Genus *B* by Barber & Roháček (in prep.). It is supported by only one distinct synapomorphy (No. 6, the ventrally deeply incised medandrium, Figs 36–38). Figure 38 (characters and states optimized with accelerated transformation) indicates that this branch may be supported further by the single microtomentose supracervical patch (character No. 1) but its presence is unknown (and is probably absent) in *Chamaebosca* as mentioned above; consequently, this character state is to be interpreted as a synapomorphy of only *Mumetopia* s. str., Genus *B* and Genus *M* (see below). However, the lack of additional synapomorphies of the above main clade may be caused by the absence of knowledge of characters of the female internal genitalia



36



37



38

Figs. 36–38. The most parsimonious tree (34 steps, CI = 0.85, RI = 0.82) resulting from cladistic analysis. 36 – ambiguous optimization disallowed. 37 – DELTRAN optimization. 38 – ACCTRAN optimization. Full circles = non-homoplasious character states; empty circles = homoplasious character states.

in *Chamaebosca*. This poorly known genus is cladistically delimited by two distinct apomorphies, viz. No. 16 (gonostylus fused to epandrium) and No. 17 (gonostylus lacking micropubescence) and represents a sister-group to the remaining three genera (*Mumetopia* s. str., Genus *B* and Genus *M*) which, in turn, represent a strongly supported clade (synapomorphies No. 1, 4, 5, 7–9, all from the male genitalia) and are, consequently, very closely related (Figs 36–38).

There is no distinct apomorphic character delimiting Genus *M* (see Figs 36, 38) because character No. 9 (slender projection of filum of distiphallus) occurs in this genus in the apomorphic state 1 (see Fig. 37) and may be, therefore, plesiomorphic relative to state 2 which characterizes the *Mumetopia* s. str. + Genus *B* pair. The clade holding the latter pair of taxa is well supported by further characters No. 13 and 23 (Figs 36–38). It is to be stressed, that the male genitalic and female postabdominal structures are surprisingly similar in *Mumetopia* s. str. and Genus *B* despite the markedly different outer appearance of the species belonging to these groups (large, strongly bristled and pale coloured in Genus *B* and small, with reduced setosity and dark coloured in *Mumetopia* s. str.). Genus *B* can be delimited by two apomorphic (non-genitalic) features, viz. No. 2 and 3, while *Mumetopia* s. str. (particularly when the two species described above are included) by only one but a strong synapomorphy, the spinulose filum of the distiphallus (No. 10); *Mumetopia* s. str. also differs from Genus *B* by the apomorphic state of character No. 22 which occurs in most groups of the *Chamaebosca* group of genera (but unknown in *Chamaebosca*) and, hence, the plesiomorphic state in Genus *B* could be the result of a subsequent reversal (Figs 36–38).

The phylogenetic relationships of the last three groups as revealed here may be reflected in their future classification in two different ways. (1) Because of the strikingly similar construction of their male and female terminalia, they may be united under a single genus *Mumetopia* which would be well characterized by strong synapomorphic features (No. 1, 4, 5, 7, 8, 9). (2) Considering the morphological diversity of their external (non-genitalic) characters, they may be regarded as separate genera. The latter alternative, however, will need further investigation and a search for additional apomorphies to support better the validity of their classification on the generic level, particularly as regards Genus *M*.

BIOGEOGRAPHY

The *Chamaebosca* group of genera (= all groups under study excluding the southern Palaearctic genus *Cercagnota*) seems to originate in the New World, most probably the Neotropical Region. All genera (including unnamed taxa) of the *Chamaebosca* group of genera have their representatives in the Neotropical Region; moreover species of the genus *Chamaebosca*, Genus *M* and Genus *B* are known only from this region. The species-rich *Mumetopia nigrimana* group (more than 20 species) and *Mumetopia* s. str. are also predominantly Neotropical taxa because only one species of each penetrates to the Nearctic Region, viz. *M. nigrimana* to its southernmost areas (Florida) and the widespread *M. occipitalis* to more northerly parts of North America (up to Canada: Ontario). On the other hand, the genus *Stiphrosoma* plausibly originally evolved as a Nearctic clade (see Roháček & Barber 2005) which subsequently colonized northern areas of the Neotropical Region (viz. the *Stiphrosoma lucipetum*-group living in mangrove swamps of Central America) and penetrated, probably several times, into the Palaearctic Region (two species have Holarctic distribution, two are restricted to the E. Palaearctic and two to the W. Palaearctic, see Roháček 2006).

The genus *Cercagnota* probably is not of Palaearctic origin because it has no distinct (sister--group) relative in this area. It cannot be excluded that it was derived from an Afrotropical clade including the poorly known genus *Apterosepsis* Richards, 1962. Studies of the rich but largely unknown Afrotropical fauna of Anthomyzidae may reveal additional taxa related to *Cercagnota* and, subsequently, also to the *Chamaebosca* group of genera which would further elucidate the origin and biogeography of this group of genera.

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