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How high can trumpet moths occur: documentation of mountainous leaf-mining Tischeriidae, featuring a species from record-high elevations

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Abstract

This publication describes four new high-altitude species of Tischeriidae, all within the genus *Astrotischeria* Puplesis & Diškus: *A. peruanica* Diškus & Stonis, **sp. nov.**, *A. montivaga* Diškus & Stonis, **sp. nov.**, *A. viscacha* Diškus & Stonis, **sp. nov.**, and *A. andina* Diškus & Stonis, **sp. nov.** Notably, *A. andina* **sp. nov.**, is the highest-recorded Tischeriidae species, documented at an elevation of 3,600 meters, the highest altitude recorded for the family worldwide to date. The study also provides a summary of current species distribution data, indicating that species from altitudes up to 2,000 meters are predominant, with high-elevation species above 3,000 m comprising about 5% in the tropics and 2% globally. It is hypothesized that there is a high probability of discovering more high-elevation Tischeriidae within the genus *Astrotischeria*, particularly those feeding on *Baccharis* L. in the Andes, South America. Additionally, a new elevation record for the mountainous species *Astrotischeria parapallens* Diškus & Stonis is documented. The article is illustrated with 63 figures, including photographs of the adults, male and female genitalia, leaf mines and their habitats, a molecular topology, and graphics depicting trends in Tischeriidae occurrence across different elevations.

Key words: Andes, *Astrotischeria*, *Baccharis*, leaf mines, new species, taxonomy, trumpet leafminer moths, trumpet moths

Introduction

Trumpet moths or trumpet leafminer moths (Tischerioidea: Tischeriidae) remain insufficiently studied globally. It is a nearly cosmopolitan family found worldwide, with the exception of Australia and Antarctica. Numerous species inhabit diverse ecoregions and a wide range of habitats, with the highest diversity occurring in tropical and subtropical areas.

Tischeriidae larvae are leaf miners feeding inside plant leaf-tissues of both wild and cultivated plants, and producing irregular, usually blotch-like mines (although some are slender or branched). Pupation occurs within the leaf mine, often in a round, silken-lined nidus.

Trumpet moths belong to one of the oldest lineages of extant Lepidoptera (Regier *et al.* 2015) and are morphologically distinctive (Stonis *et al.* 2020b). They are small, with a wingspan of 5–10 mm and an enlarged 3rd antennal segment. Males have long antennal sensilla trichodea, exceeding the flagellum width by 4.5–10 times, with strongly recurved bases. In male genitalia, the phallus is slender and usually bifurcated or spined at the apex (Stonis *et al.* 2020b). Female genitalia feature ovipositor lobes covered with peg-like setae and three pairs of unique projections called prela. For detailed morphological and biological information, see Braun (1972), Puplesis & Diškus (2003), and Stonis *et al.* (2023).

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Currently, the family Tischeriidae comprises 192 species worldwide, including those described in our paper. This number is constantly rising; for instance, Dobrynina *et al*. (2022) reported 170 species just two years ago. The most comprehensive monograph on Tischeriidae (Stonis *et al*. 2023) recognizes eleven genera: *Coptotriche* Walsingham, 1890; *Coptotrichoides* Diškus & Stonis, 2023 (originally described in Stonis *et al*. 2023); *Dishkeya* Stonis, 2020 (originally described in Stonis & Solis 2020); *Tischeria* Zeller, 1839; *Manitischeria* Diškus & Stonis, 2021 (originally described in Stonis *et al*. 2021d); *Rytietia* Diškus, Xu & Dai, 2023 (originally described in Stonis *et al*. 2023); *Pafazaria* Diškus & Stonis, 2023 (originally described in Stonis *et al*. 2023); *Neotischeria* Diškus & Stonis, 2021 (originally described in Stonis *et al*. 2021c); *Paratischeria* Diškus & Stonis, 2017 (originally described in Stonis *et al*. 2017); *Gnathitischeria* Diškus, 2023 (originally described in Stonis *et al*. 2023); and *Astrotischeria* Puplesis & Diškus, 2003 (originally described in Diškus & Puplesis 2003).

Astrotischeria is the second-largest genus within Tischeriidae, primarily comprising species that feed on Asteraceae plants, with occasional instances of *Astrotischeria* found on Malvaceae hosts. Asteraceae-feeding Tischeriidae are exclusively known from the Americas, despite the rich presence of Asteraceae plants in other regions worldwide. The hypothesis of a dietary shift to Asteraceae and the extensive species diversification among Tischeriidae feeding on Asteraceae (Diškus & Puplesis 2003; Stonis *et al.* 2023) underscores the significant ecological niche occupied by these trumpet moths. Diagnostic characters of *Astrotischeria* are evident in both male and female genitalia. In the male genitalia, species are characterized by a unique, divided valva with variously developed dorsal lobe(s), typically a long tegumen and vinculum, a rod-like phallus that is bifid, and a modified, usually four-lobed uncus. In the female genitalia, the genus is distinguished by small ovipositor lobes (which can be fully reduced or strongly modified to be thickened and non-rounded), and usually a very long and slender proximal part of the corpus bursae (Stonis *et al.* 2023). Currently, the genus *Astrotischeria* includes about 50 named species, with numerous additional species collected but awaiting publication. The genus is restricted to the Western Hemisphere. Southernmost discoveries include Uruguay (Stonis *et al.* 2020b), Argentina (Bourquin 1962) and Chile (Diškus & Puplesis 2003; Stonis *et al.* 2016a). Notably, two *Astrotischeria* species were described from the Galapagos Islands (Landry & Roque-Albelo 2004). Despite efforts, no *Astrotischeria* species were found on Easter Island during a survey conducted by Arūnas Diškus.

Biodiversity inventories, including studies on Tischeriidae, enhance our understanding of nature and play a crucial role in unraveling the intricate mechanisms of global biota. They are essential for developing strategies to swiftly preserve biodiversity amidst ongoing crises and climate change.

The main goal of this publication is to document the new elevation record of the mountainous *Astrotischeria parapallens* Diškus & Stonis (occurring at an elevation of 3,320 m) and describe four new Tischeriidae species from mountainous areas, all belonging to *Astrotischeria*: *A. peruanica* Diškus & Stonis, **sp. nov.** (at elevation of 2,110 m), *A. montivaga* Diškus & Stonis, **sp. nov.** (at elevation of 3,320 m), *A. viscacha* Diškus & Stonis, **sp. nov.** (at elevation of 2,990 m), and *A. andina* Diškus & Stonis, **sp. nov.** The latter species represents a Tischeriidae taxon occurring at record-high elevations (3,600 m). Therefore, it is of interest to summarize the elevational ranges where the greatest species diversity is currently known.

Targeted searches for Tischeriidae at high elevations were a priority during this study. Arūnas Diškus, sometimes accompanied by a co-author or other research partners, regularly conducted fieldwork focusing on mountainous or high-altitude mountainous Tischeriidae.

We hope that this publication will stimulate further studies on mountainous Tischeriidae and contribute to a more comprehensive understanding of the diversity of these fascinating leaf-mining micromoths.

Material and methods

Material. The study material, consisting of thirteen tischeriid specimens, was made available through the Environmental Programme at the Andes Office of NGO DAR Peru. This was facilitated by training courses and fieldwork conducted under the project 'Rapid assessment of biodiversity plots of critical value in the provinces of Chanchamayo and Satipo, Peru', in collaboration with the Baltic-American Biotaxonomy Institute. Additionally, the material was collected under the Memorandum of Understanding between Peru and the European Union, involving Peruvian authorities responsible for forest conservation, protected areas, and wildlife. The collected specimens will be deposited in the collection of the Museum für Naturkunde (MfN) in Berlin, Germany.

Sampling methods. Detailed methods and techniques for collecting adults and rearing them from mining larvae are described in our previous publication (Stonis *et al*. 2018).

Specimen dissection and documentation. Methods and protocols for specimen dissection, species identification, and description followed monographs where these procedures were detailed (Puplesis & Diškus 2003; Stonis *et al.* 2022a). During dissection, male genital capsules were extracted following abdomen maceration in 10% potassium hydroxide, cleaned, and mounted with the ventral side facing up. In many cases, the phallus was dissected and mounted alongside the genital capsule. Abdominal pelts were consistently preserved in this study. Permanent preparations on microscope slides were photographed and examined using a Leica DM2500 microscope equipped with a Leica DFC420 digital camera. Adult specimens were measured and examined using a Lomo stereoscopic microscope MBS-10, with images captured using a Leica S6D stereoscopic microscope paired with a Leica DFC290 digital camera. During the examination, illumination of adult specimens was achieved using a ring light LED 60, directly attached to the stereo microscope lens. This light source offers adjustable illumination intensity and a color temperature range of 7000 to 11000 K, providing 8000 Lux illumination at a 100 mm distance.

Molecular analysis. The thorax, the head and three fragments of legs of the air-dried *Astrotischeria andina* **sp. nov.** specimen was used for the DNA extraction according to the protocol of the GeneJet Genomic DNA Purification Kit (Thermo Fisher Scientific Baltics). The attemption to study the partial sequence of the mitochondrial DNA cytochrome c oxidase subunit 1 (mtDNA CO1-5') that includes the standard barcode region of 650 base pairs (bp) (Hebert *et al.* 2003a) failed due to possible DNA degradation. Consequently, the shorter 133 bp long fragment of CO1-5' corresponding to the location of the universal mini-barcode (Meusnier *et al.* 2008) was amplified. The primers T3Lep-f (attaaccctcactaaagtchacwaaycayaaarayatygg; modified Lep-f1 (Hebert *et al.* 2004)) and T7PEM-r1 (aatacgactcactatagaraaaattatdayraadgcrtg; original) were used during the polymerase chain reaction (PCR) under the following conditions: initial denaturation at 95°C for five minutes; 45 cycles of denaturation at 94°C for one minute, annealing at 43°C for one minute, extension at 68°C for 1.5 minutes; final extension at 68°C for five minutes. The PCR mixture in a volume of 25 µL consisted of 12.5 µL of 2× DreamTaq PCR Master Mix (Thermo Fisher Scientific Baltics), 2 µL of 10 pmol/µL of each primer, 4.5 µL of deionised water, and 4 µL of genomic DNA. The purification of PCR product was performed with exonuclease I and FastAP thermosensitive alkaline phosphatase (Thermo Fisher Scientific Baltics) prior to the automatic Sanger sequencing with the ABI 3730xl 96-capillary DNA analyzer (Applied Biosystems) in BaseClear B.V. (Leiden, The Netherlands). The successfully obtained 133 bp long CO1-5' sequence was aligned by BioEdit v.7.2.5 (Hall 1999) and deposited in the NCBI GenBank database (Benson *et al.* 2013) under the accession number PQ064484. For comparison with *A. andina* **sp. nov.**, the CO1-5' sequences of related species and the outgroup were obtained from our earlier studies and deposited in the same database. Pairwise deletion was applied for the missing parts of the DNA sequences. MEGA v.7 (Kumar *et al.* 2016) was used to estimate the *p*-distances and to construct the Neighbor-Joining (NJ) tree applying the Tamura 3-parameter model (Tamura 1992) with gamma distribution (T92+G) and 10,000 bootstrap replicates.

Abbreviation for Institutions. BRG—Biosystematics Research Group, currently based at the State Research Institute Nature Research Centre (NRC), Vilnius, Lithuania; MfN—Museum für Naturkunde, formerly known as the Museum für Naturkunde der Humboldt Universität zu Berlin or Museum für Naturkunde / Leibniz-Institut für Evolutions und Biodiversitätsforschung, Berlin, Germany.

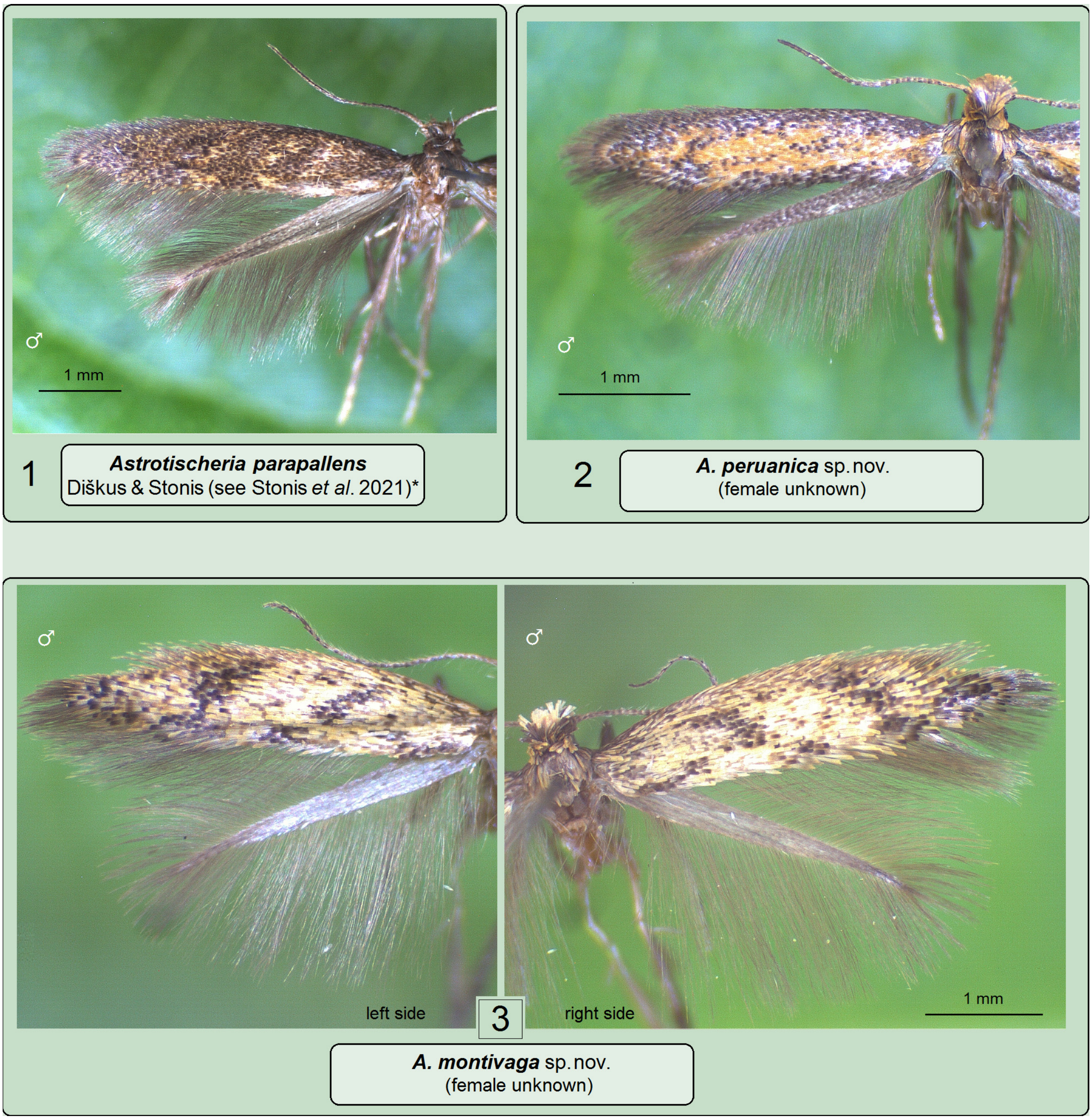
Taxonomic account: description of four new mountainous *Astrotischeria* species, with a new elevation record of *A. parapallens* Diškus & Stonis

Astrotischeria parapallens Diškus & Stonis, 2021: photographic documentation and a new elevation record

http://zoobank.org/NomenclaturalActs/3ae6711c-34c4-404d-befd-f29c9c048b02

(Figs 1, 11–15, 47)

Material examined. 1 ♂, PERU, Huamanga Province, 37 km NE of Ayacucho, Quinua, 13°2'50"S, 74°8'8"W, elevation ca. 3,320 m, mining larvae on *Baccharis* sp., 28.x.2008, ex pupa xi.2008, field card no. 4955, leg. A. Diškus, genitalia slide no. AD1140 (MfN).



FIGURES 1–3. Adults of mountainous *Astrotischeria* species. 1, *A. parapallens* Diškus & Stonis, 3,320 m, non-type specimen, a new elevation record; 2, *A. peruanica* Diškus & Stonis, **sp. nov.**, holotype, 2,110 m; 3, *A. montivaga* Diškus & Stonis, **sp. nov.**, paratype, 3,320 m (MfN).

Diagnosis. Externally, this species can be confused with other densely speckled *Astrotischeria* species. In the male genitalia, *A. parapallens* is distinguished by a slender and straight valva, a relatively short and distally wide-lobed phallus, an anteriorly thickened vinculum, and distally wide, dentate dorsal lobes.

Description. The species was described by Stonis *et al.* (2021b). The newly examined specimen from an altitude of 3,320 m, with a forewing length of 4.5 mm and a wingspan of 9.8 mm (n = 1) (Fig. 1), is larger than previously known specimens (3.9–4.0 mm in forewing length, 8.4–8.6 mm in wingspan). In the male genitalia (Figs 11–15), the capsule of the examined new specimen is 580 µm long and 280 µm wide; the phallus (Fig. 14) is 390 µm long. For a full description, see Stonis *et al.* (2021b).

Bionomics. The host plant is *Baccharis* L., possibly *B. latifolia* (Ruiz & Pav.) Pers., Asteraceae. Larvae mine leaves in late October. The blotch mine is irregular, elongated, usually pale brownish, with little or no frass (Stonis *et al*. 2021b). Adults occur in November.

Distribution. Previously, this species was known from a single locality in Peru (Muyurina, 9 km East of Ayacucho), at an elevation of about 2,500 m (Stonis *et al.* 2021b). Now, this species has been recorded in Quinua, 37 km NE of Ayacucho, Huamanga Province of Peru, at an elevation of 3,320 m (a new elevation record) (Fig. 47).

Astrotischeria peruanica Diškus & Stonis, sp. nov.

http://zoobank.org/NomenclaturalActs/312A8B5E-186B-4A62-BC1A-FBD89EEE8D91

(Figs 2, 16–23, 48–50)

Type material. Holotype: 1 ♂, PERU, Urubamba Province, near Machu Picchu, 13°9'44"S, 72°32'25"W, elevation ca. 2,110 m, from feeding larva on Asteraceae, 19.x.2008, ex pupa xi.2008, field card no. 4942, leg. A. Diškus, genitalia slide no. AD1180 (MfN). Paratype 1 ♂, same label data as holotype, genitalia slide no. AD1172♂ (MfN).

Diagnosis. Externally, this species resembles other *Astrotischeria* species with ochre-colored spots. In the male genitalia, it is distinguished by a slender, straight valva; a slender, deeply divided phallus distally; a basally greatly extended uncus; and slender, slightly curved dorsal lobes, characters that differentiate it from all other species within the genus.

Male (Fig. 2). Forewing length 3.0–3.5 mm; wingspan 6.7–7.7 mm (n = 2). Head: frons ochre; palpi ochreous cream; pecten very slender, brownish, distally ochre; frontal tuft glossy grey to brown, ochreous distally; collar distinctive, ochre, pale brown distally; antenna slightly longer than half the length of forewing; flagellum glossy brown on upper side, ochre on underside. Thorax grey-brown medially, ochre laterally; tegula dark grey-brown. Forewing dark grey-brown, with large elongated ochre patches medially; fringe grey-brown; fringe line indistinct; forewing underside dark brown, without spots or androconia. Hindwing and its fringe grey-brown to dark grey-brown, without androconia. Legs grey-brown.

Male genitalia (Figs 16–23). Capsule 480–540 µm long, 230–240 µm wide. Uncus comprised of two long lobes strongly widened and thickened basally, partially divided into two lobes: long lateral and short rounded medial (Figs 18, 19, 21, 22). Socii large, slender, membranous, covered with tiny spines. Valva divided: ventral lobe (main body) very narrow and straight (Fig. 16); dorsal lobe inwardly slightly sinuous, slender (Figs 17, 20). Transtilla absent. Anellus slightly thickened laterally with about three chetae on each side (Figs 17, 20). Phallus (Figs 17, 23) 255–340 µm long, slender, apically deeply divided (Fig. 23).

Female. Unknown.

Bionomics (Figs 48–50). Host plant is unidentified, possibly *Baccharis trinervis* Pers., Asteraceae (Fig. 48). Larvae mine leaves in October, producing irregular or rounded blotch mines (Figs 49, 50). Adults occur in November. Otherwise, the biology is unknown.

Distribution. This species is currently known from a single locality in Peru, Urubamba Province, near Machu Picchu, at an elevation of 2,110 m.

Etymology. The new species is named after Peru, the country of its occurrence.

Astrotischeria montivaga Diškus & Stonis, sp. nov.

http://zoobank.org/NomenclaturalActs/59EE4B18-6259-4D57-9AC3-29D2E5E4E540

(Figs 3, 24–28)

Type material. Holotype: 1 ♂, PERU, Huamanga Province, 37 km NE of Ayacucho, Quinua, 13°2'50"S, 74°8'8"W, elevation ca. 3,320 m, mining larvae possibly on *Baccharis* sp., 28.x.2008, ex pupa xi.2008, field card no. 4955, leg. A. Diškus, genitalia slide no. AD1185 (MfN). Paratypes 2 ♂, same label data as holotype, genitalia slide no. AD746♂ (MfN).

Diagnosis. Externally, this species is characterized by a yellow-ochre forewing with irregular dark brown patches. In the male genitalia, the combination of a very slender and straight valva, a phallus with two wide and double-folded apical lobes, a basally greatly extended uncus, and wide, distally distinctly pointed dorsal lobes distinguishes the new species from all other species of the genus.

Male (Fig. 3). Forewing length ranges from 3.7 to 3.9 mm; wingspan from 8.1 to 8.4 mm (n = 3). Head: frons pale ochre to yellow-ochre; palpi yellowish cream; frontal tuft dark grey proximally, transitioning to yellowish cream distally; collar yellowish cream; antenna distinctly longer than half the length of forewing; flagellum glossy dark grey or annulated with dark grey. Thorax pale yellowish with some grey scales; tegula predominantly grey with some yellowish scales. Forewing yellow-ochre to pale yellowish with irregular blackish brown to dark brown patches; fringe pale grey to grey; fringe line indistinctive or absent; forewing underside grey, without spots or androconia. Hindwing and its fringe pale greyish cream to grey (depending on the angle of view), grey on underside, without androconia. Legs glossy grey.

Male genitalia (Figs 24–28). Capsule measures 575–580 µm in length, 255–500 µm in width. Uncus comprised of two long lobes strongly widened basally, partially divided into two lobes: a long lateral lobe and a short rounded medial lobe (Figs 24, 25). Socii relatively small, membranous, covered with tiny spines. Valva divided: ventral lobe (main body) very narrow and straight (Fig. 24); dorsal lobe inwardly curved, wide, and distinctly pointed distally (Figs 24, 25). Transtilla absent. Anellus only slightly thickened laterally with about three chetae on each side (Fig. 24). Phallus (Figs 27, 28) measures 535–540 µm in length, slender in basal half, broadly divided into two double-folded lobes in apical half.

Female. Unknown.

Bionomics. Host plant is unknown, possibly *Baccharis* L., Asteraceae. Larvae mine leaves in October, producing irregular blotch-like mines. Adults occur in November. Otherwise, the biology is unknown.

Distribution. This species is currently known from a single locality in Quinua, 37 km NE of Ayacucho, Huamanga Province of Peru, at an elevation of 3,320 m (Fig. 47).

Etymology. The species name derived from the Latin *montivagus* (mountain-wandering or living in the mountains), in reference to the mountainous distribution of this new species.

Astrotischeria viscacha Diškus & Stonis, sp. nov.

http://zoobank.org/NomenclaturalActs/2293E13D-4DBB-4492-95E3-DFE7FD203817
(Figs 4–6, 29–33, 43, 44, 51, 52)

Type material. Holotype: 1 ♂, PERU, Calca Province, Písac, 13°25'17"S, 71°50'36"W, elevation ca. 2,990 m, mining larvae on *Baccharis salicifolia*, 22.x.2008, ex pupa xi.2008, field card no. 4949, leg. A. Diškus, genitalia slide no. AD1177♂ (MfN). Paratypes 2 ♀, same label data as holotype, genitalia slide no. AD1176♀ (MfN).

Diagnosis. This species exhibits strong sexual dimorphism; males are characterized by irrorated forewings, while females display distinctive cream and dark brown oblique patches on the forewings. In the male genitalia, the combination of a chunky, wide uncus and a slender phallus with unique, T-shaped lateral lobes distinguishes the new species from all other species within the genus.

Male (Fig. 4). Forewing length 4.8 mm; wingspan 10.3 mm (n = 1). Head: frons glossy grey cream; palpi cream; frontal tuft and collar glossy grey cream; antenna slightly longer than half the length of forewing; flagellum pale brown to dark brown. Thorax and tegulae glossy grey cream. Forewing glossy grey cream, densely irrorated with ochre and numerous dark brown scales, some ochre-tipped; fringe pale ochreous brown; fringe line indistinctive or absent; forewing underside pale brown, without spots or androconia. Hindwing and its fringe pale grey to pale ochreous brown (angle-dependent), without androconia. Legs pale grey-brown.

Male genitalia (Figs 29–33). Capsule 550 µm long, 250 µm wide. Uncus relatively short and chunky, with wide lateral lobes and short, wide inner lobes (Figs 29, 30). Socii relatively large, membranous, covered with tiny spines. Valva divided: ventral lobe (main body) very slender and slightly sinuous (Fig. 31); dorsal lobe inwardly curved, strongly chitinized, distinctly pointed distally (Fig. 31). Transtilla absent. Anellus weakly chitinized, indistinctive. Phallus (Figs 32, 33) 420 µm long, slender, deeply divided apically, with T-shaped lobes distally (Fig. 32).

Female (Figs 5, 6). Forewing length 4.3–4.5 mm; wingspan 9.3–9.7 mm (n = 2). Head: frons ochreous cream; palpi cream; frontal tuft and collar yellow ochre but pale grey-brown distally and laterally; antenna slightly longer than half the length of forewing; flagellum pale, sparsely annulated with brown scales. Thorax and tegulae yellow-ochre. Forewing with oblique yellow-ochre and dark brown patches; fringe pale ochre; fringe line indistinctive or absent; forewing underside pale ochreous brown, without spots or androconia. Hindwing and its fringe grey cream, without androconia. Legs pale grey-brown.

Female genitalia (Figs 43, 44) 840 µm long. Ovipositor lobes large, flattened, clothed with short, modified setae ('peg setae'); area between ovipositor lobes relatively narrow, with tiny indistinctive papillae and some short setae. Second pair of lobes, lateral and anterior to the ovipositor lobes, three to four times smaller than ovipositor lobes, but bearing setae. Anterior apophyses distinctly shorter than posterior apophyses; prela comprised of two pairs of unique projections (Fig. 44). Corpus bursae with a very long and slender "neck"; the main part small and oval-shaped, without distinctive pectinations or signum. Accessory sac absent. Ductus spermathecae short and very slender, with about 4–5 medium-large or small coils and an indistinctive vesicle.

Bionomics. Host plant is *Baccharis salicifolia* (Ruiz & Pav.) Pers., Asteraceae (Figs 51, 52). Larvae mine leaves in October; adults occur in November. Otherwise, the biology is unknown.

Distribution. This species is currently known from a single locality in Peru (Pisac, Calca Province), at the elevation of 2,990 m.

Etymology. The species name is derived from the name of the viscacha, rodents of the family Chinchillidae living in the Andes. It refers to the specific chunky uncus found in the male genitalia of the new species, which reminds one of the ears of the viscacha.

Astrotischeria andina Diškus & Stonis, sp. nov.

http://zoobank.org/NomenclaturalActs/9A4D6DD9-71FF-419C-96B3-309945CC1507

(Figs 7–10, 34–42, 45, 46, 53–59)

Type material. Holotype: 1 ♂, PERU, Cusco Province, Cusco (Saqsaywaman), 13°30'31"S, 71°58'45"W, elevation ca. 3,595 m, from feeding larva on *Baccharis buxifolia*, 24.x.2008, ex pupa xi.2008, field card no. 4952, leg. A. Diškus, genitalia slide no. AD1160 (MfN). Paratypes 2 ♂, 1 ♀, same label data as holotype, genitalia slides nos AD748♂, AD1179♀ (MfN).

Diagnosis. Externally, this species is characterized by striking sexual dimorphism; the males are distinguished by a densely irrorated forewing, while the females exhibit an entirely yellowish cream forewing. In the male genitalia, the combination of an uncus with slender lateral lobes and pronounced rounded median lobes, sinuous, dentate dorsal valval lobes, and a phallus that is widely bilobed distinguishes the new species from all other species of the genus.

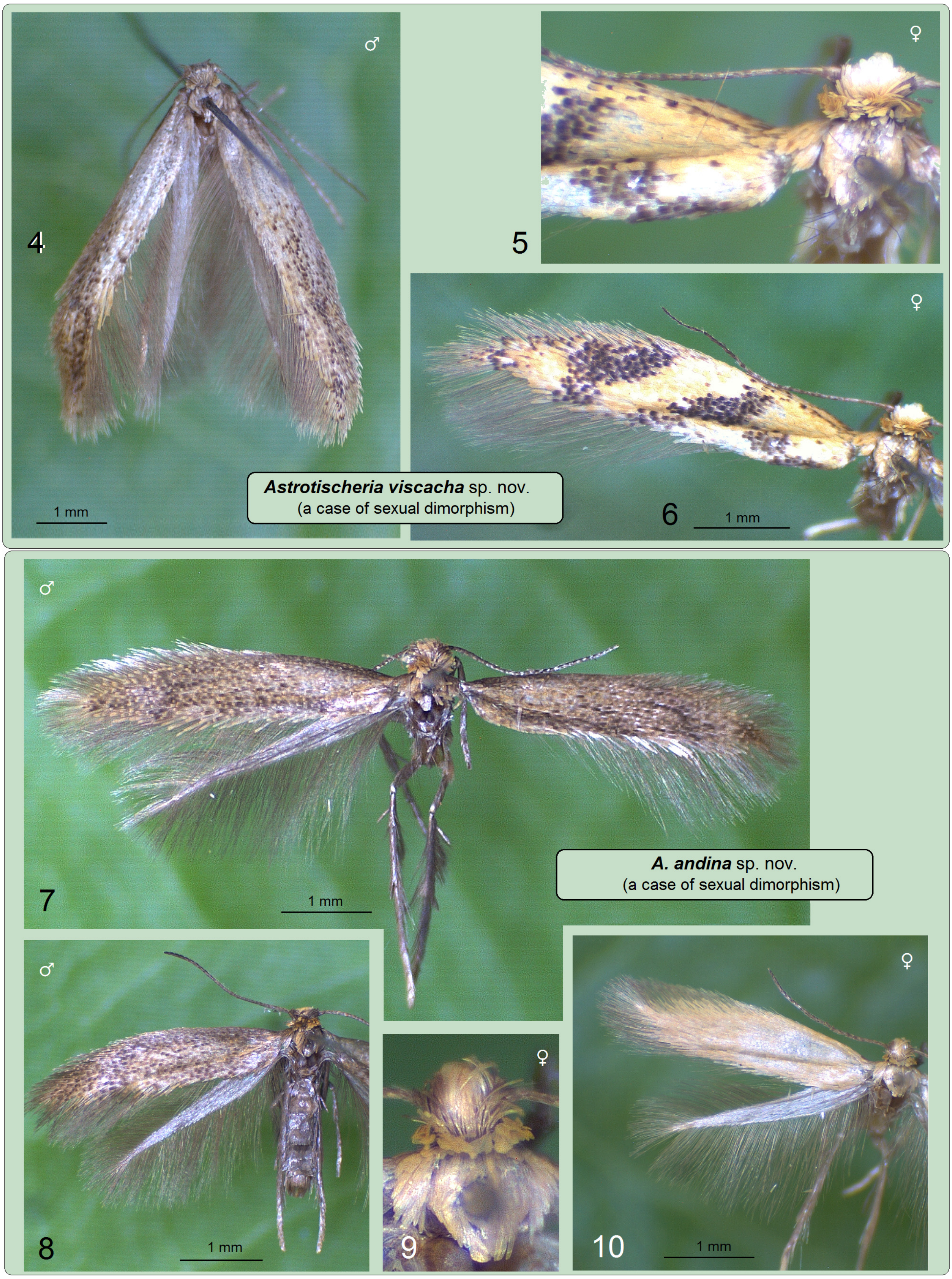
Male (Figs 7, 8). Forewing length 3.5–4.0 mm; wingspan 7.7–8.7 mm (n = 2). Head: frons and palpi ochre cream; frontal tuft ochreous brown to yellowish ochre laterally, dark ochreous brown distally; collar pale ochreous brown to ochre; antenna slightly longer than half the length of forewing; flagellum glossy dark brown on the upper side, blackish brown on the underside. Thorax pale ochreous brown to ochre. Tegula grey-brown. Forewing pale brownish grey densely irrorated with dark brown ochre-tipped scales; fringe pale brownish grey to grey; fringe line absent; forewing underside grey-brown, without spots or androconia. Hindwing and its fringe pale brownish to grey, without androconia. Legs glossy grey; forelegs and midlegs densely covered with dark brown or dark grey scales on the upper side. Abdomen glossy grey on the upper side and underside.

Male genitalia (Figs 34–42). Capsule 540–595 µm long, 280 µm wide. Uncus with long, slender lateral lobes (Figs 36, 37, 41) and short but rounded median lobes; the gap between the median rounded lobes is distinctly wide and thickened (Fig. 38). Socii relatively small, membranous, covered with tiny spines. Valva divided: ventral lobe (main body) very slender and slightly sinuous (Fig. 41); dorsal lobe slightly sinuous, inwardly curved, strongly chitinized, distinctly pointed distally, dentate on the inner side (Fig. 40). Transtilla absent. Anellus weakly chitinized, indistinctive. Phallus (Figs 34, 35) 410–500 µm long, slender, divided apically, with two wide apical lobes.

Female (Figs 9, 10). Forewing length 3.2 mm; wingspan 7.1 mm (n = 1). Head: frons, palpi, and collar yellowish cream; frontal tuft yellowish cream, but grey-brown laterally; antenna slightly longer than half the length of forewing; flagellum glossy grey. Thorax, tegula, and forewing yellowish cream; forewing underside pale brownish-grey, without spots or androconia. Hindwing and its fringe cream, without androconia. Legs brownish cream.

Female genitalia (Figs 45, 46) 1650 µm long. Ovipositor lobes large, distinctly flattened, clothed with short, modified setae ('peg setae'); area between ovipositor lobes medium wide, with tiny indistinctive papillae and some short setae. Second pair of lobes, lateral and anterior to the ovipositor lobes, three to four times smaller than ovipositor lobes, but bearing setae. Anterior and posterior apophyses almost equal in length; prela comprised of three pairs of unique projections (Fig. 46). Corpus bursae with a very long and slender "neck" (Fig. 45); the main part small and oval-shaped, without distinctive pectinations or signum. Accessory sac absent. Ductus spermathecae short and very slender, with about 3 large coils and weakly chitinized, plate-like vesicle.

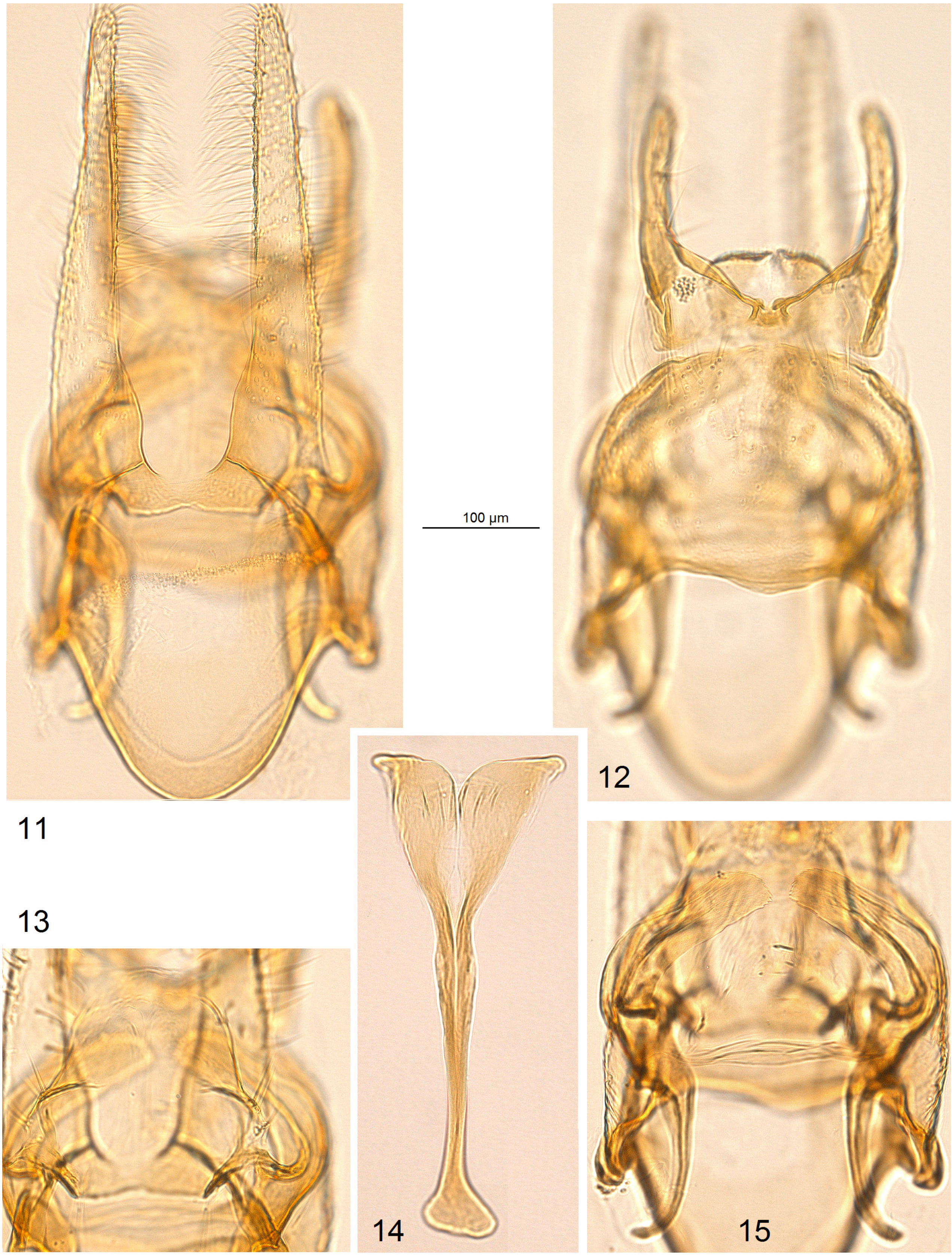
Bionomics (Figs 53–59). The host plant is *Baccharis buxifolia* (Lam.) Pers. (=*Baccharis peruviana* Cuatrec.), Asteraceae (identified by Liliana Katinas) (Figs 55–57). Larvae mine leaves in October. The leaf mine is blotch-like, pale brownish-yellow to brown (Figs 58, 59). Adults occur in November. Otherwise, the biology is unknown.



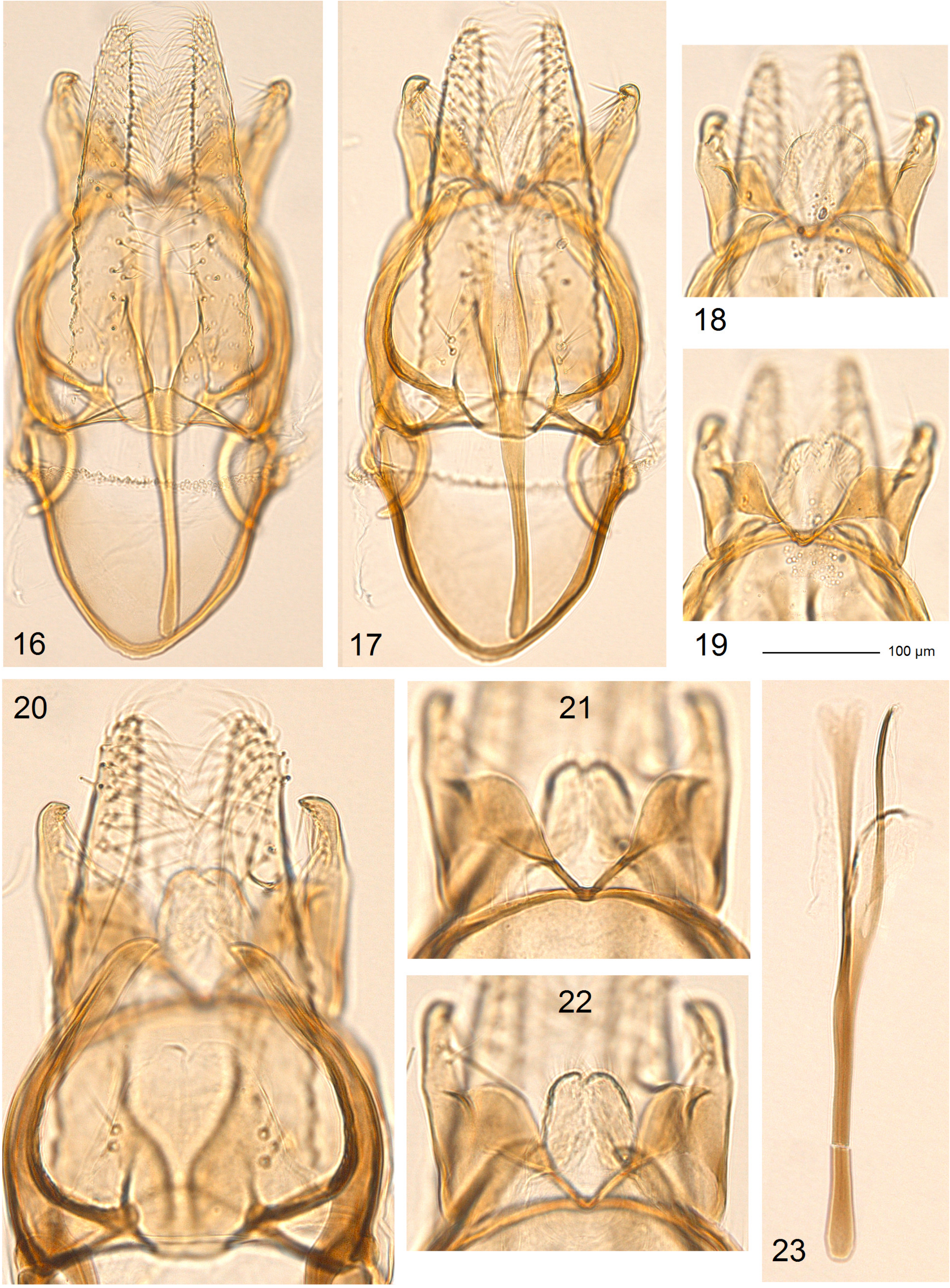
FIGURES 4–10. Adults of mountainous *Astrotischeria* species. 4, *A. viscacha* Diškus & Stonis, **sp. nov.**, 2,990 m, male holotype; 5, 6, same, female paratype; 7, *A. andina* Diškus & Stonis, **sp. nov.**, male holotype, 3,595–3,600 m; 8, same, male paratype; 9, 10, same, female paratype (MfN).

Distribution. This species is currently known from a single locality in Peru (Saqsaywaman, Cusco, at elevations of 3,595–3,600 m) (Figs 53, 54).

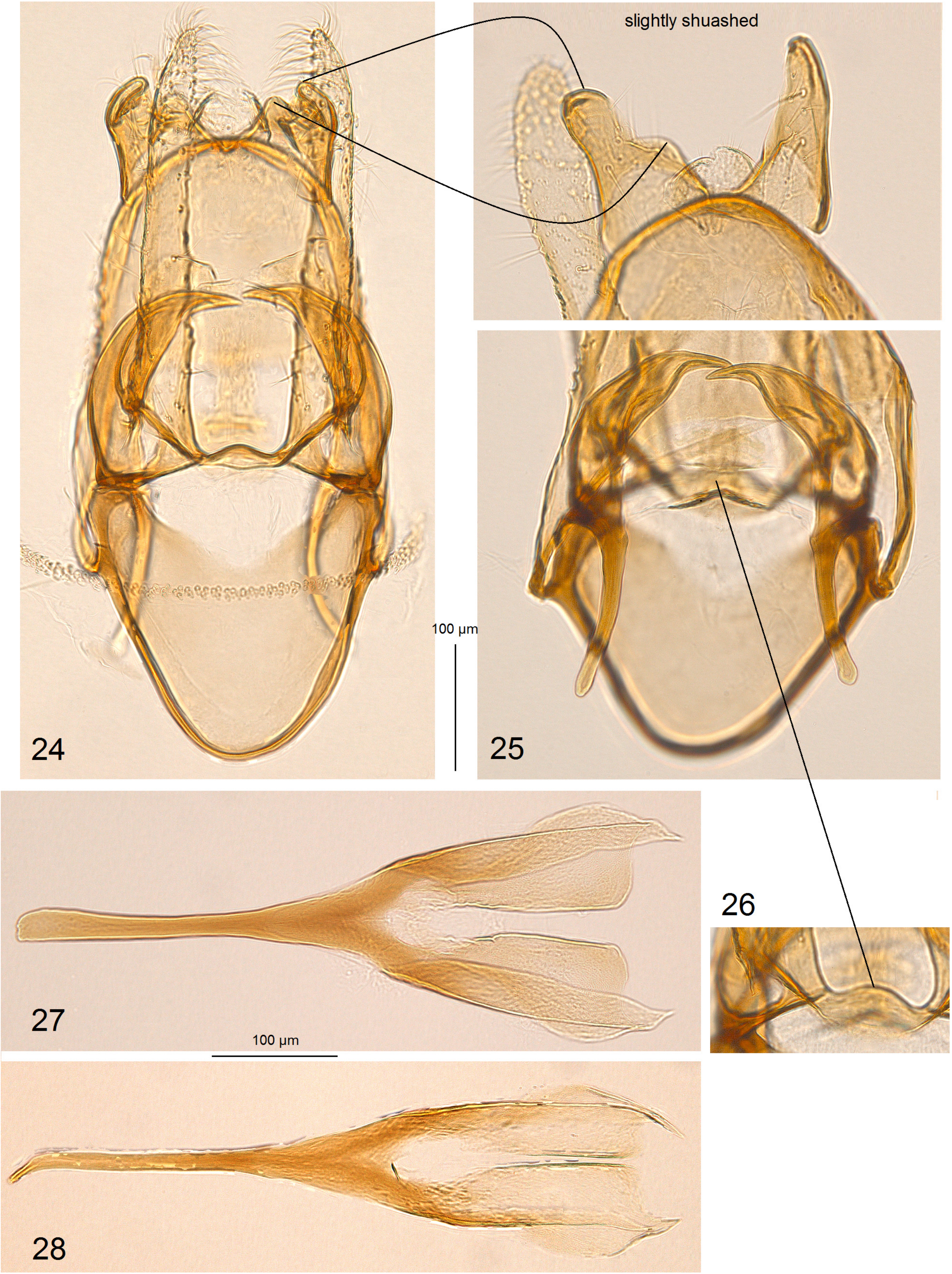
Etymology. The species is named after the Andes, the mountain ridge where it occurs.



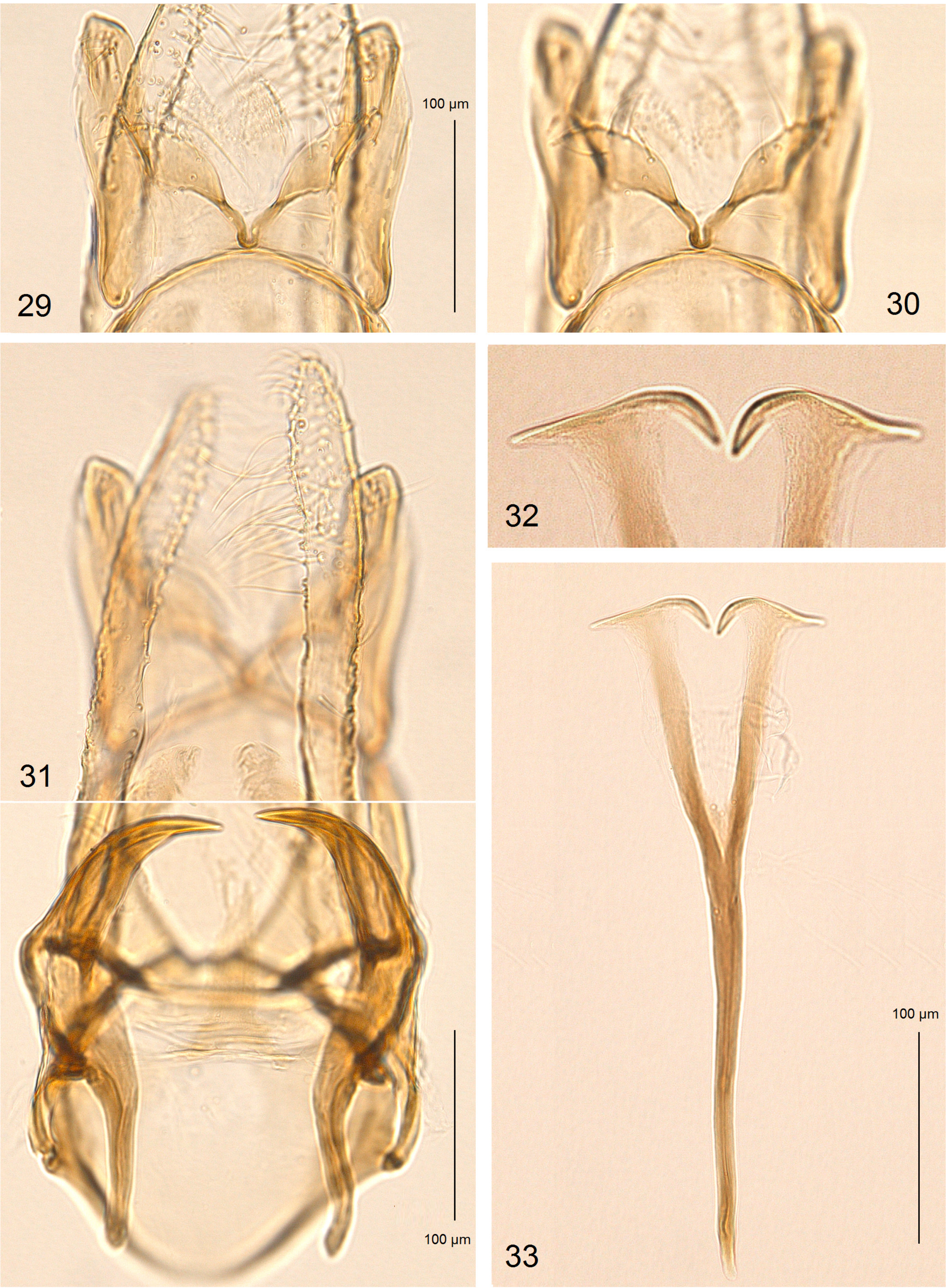
FIGURES 11–15. Male genitalia of *Astrotischeria parapallens* Diškus & Stonis, 3,320 m (a new elevation record), non-type specimen, genitalia slide no. AD1140 (MfN). 11, genitalia capsule with phallus removed, focused on the ventral view; 12, same, focused on the dorsal view; 13, anellus; 14, phallus; 15, basal processes of valvae.



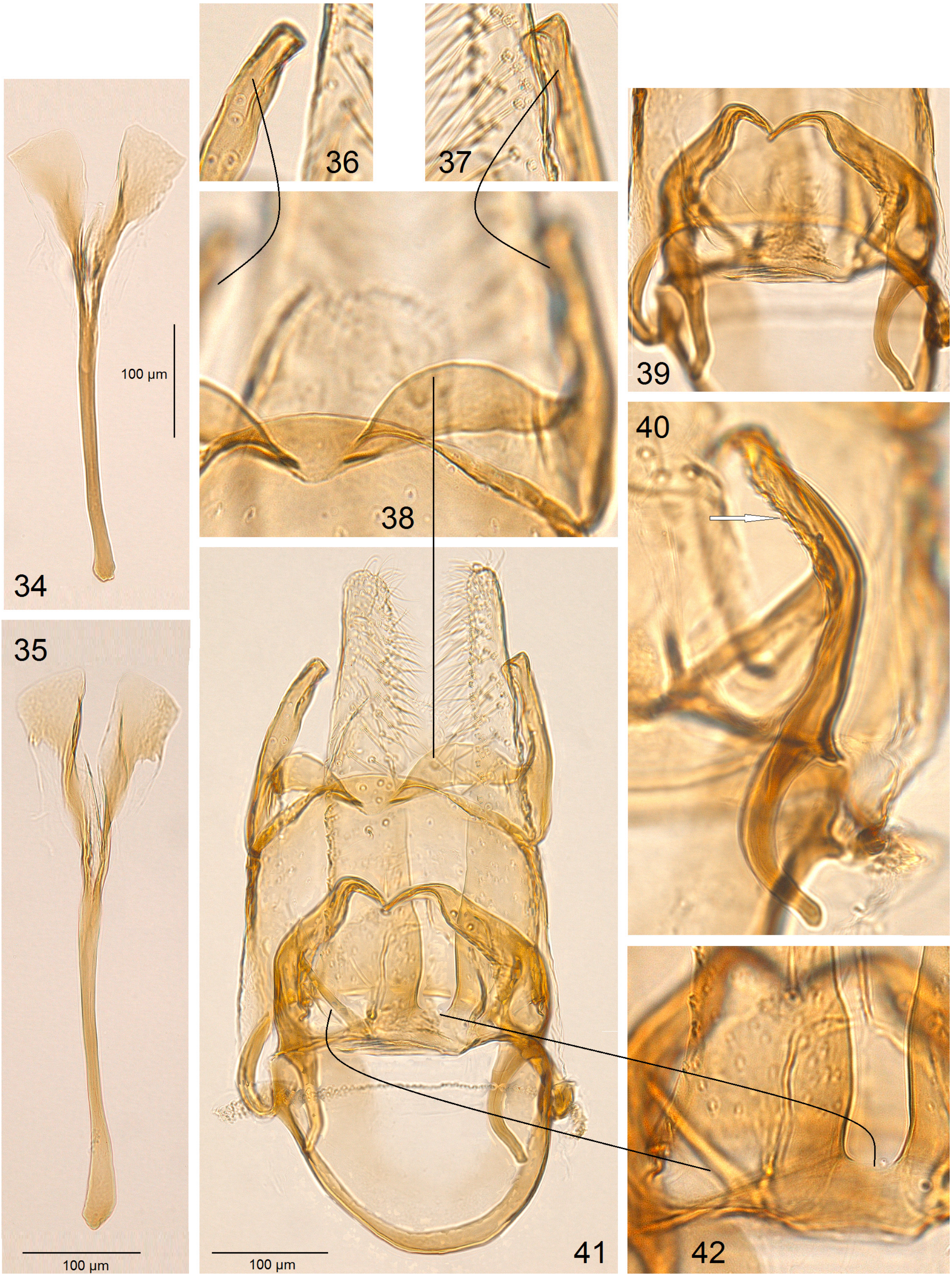
FIGURES 16–23. Male genitalia of *Astrotischeria peruanica* Diškus & Stonis, **sp. nov.**, 2,110 m. 16–19, holotype, genitalia slide no. AD1180 (MfN); 20–23, paratype, with phallus (23) removed, genitalia slide no. AD1172 (MfN).



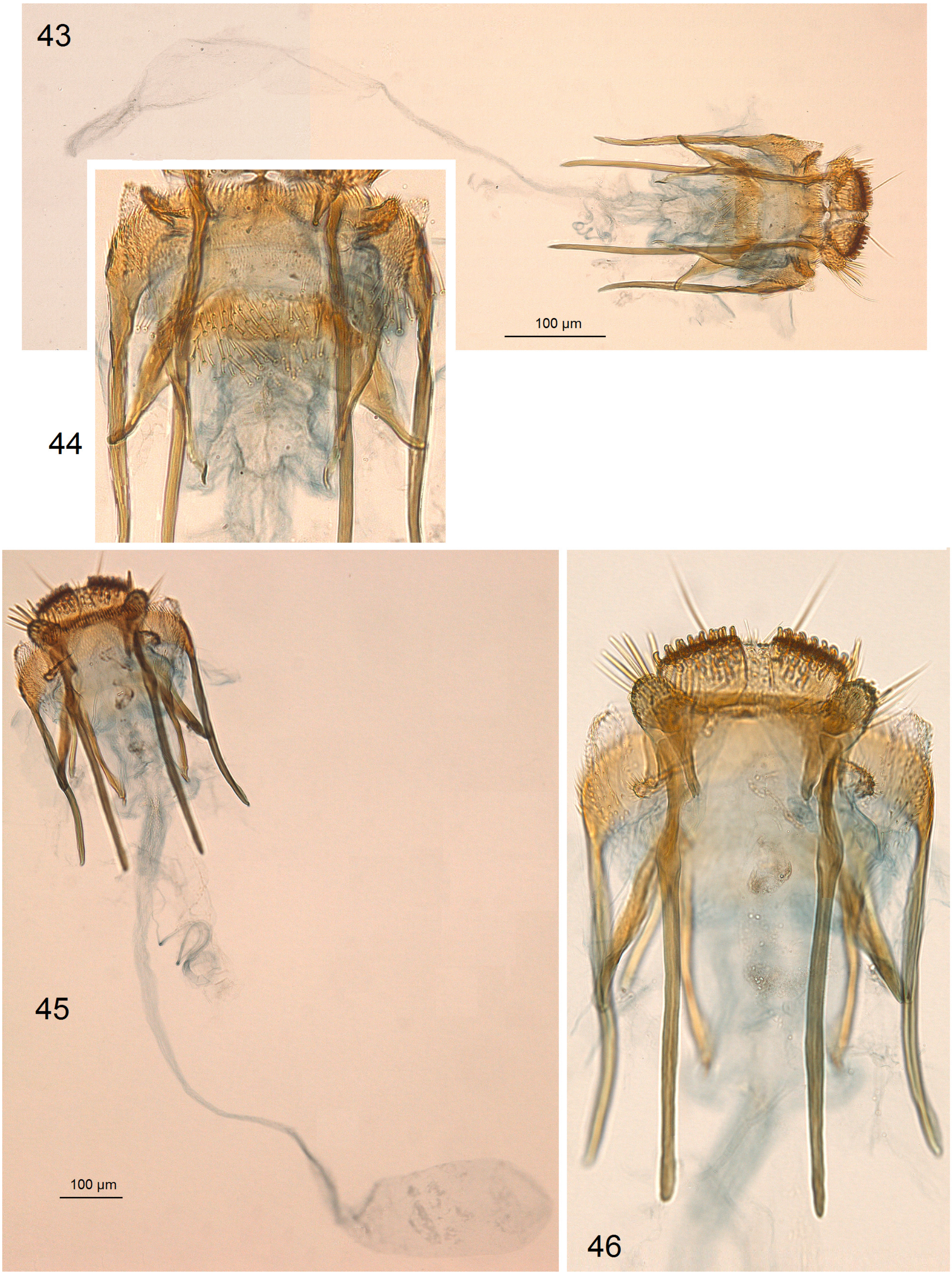
FIGURES 24–28. Male genitalia of *Astrotischeria montivaga* Diškus & Stonis, **sp. nov.**, 3,320 m. 24, genitalia capsule with phallus removed, holotype, slide no. AD1185 (MfN); 25, 26, same, paratype, genitalia slide no. AD746 (MfN); 27, same, phallus; 28, same, holotype, genitalia slide no. AD1185 (MfN).



FIGURES 29–33. Male genitalia of *Astrotischeria viscacha* Diškus & Stonis, **sp. nov.**, 2,990 m, holotype, genitalia slide no. AD1177 (MfN). 29, 30, uncus, 31, genitalia capsule with phallus removed, focused on valvae; 32, 33, phallus.



FIGURES 34–42. Male genitalia of *Astrotischeria andina* Diškus & Stonis, **sp. nov.**, 3,595–3,600 m. 34, phallus, paratype, genitalia slide no. AD748 (MfN). 35, same, holotype, genitalia slide no. AD1160 (MfN); 36–39, details of genitalia capsule, holotype, genitalia slide no. AD1160 (MfN); 40, dentate dorsal lobe of valva, paratype, genitalia slide no. AD748 (MfN); 41, 42, general view of genitalia capsule with phallus removed, holotype, genitalia slide no. AD1160 (MfN).



FIGURES 43–46. Female genitalia of mountainous *Astrotischeria* species. 43, 44, *A. viscacha* Diškus & Stonis, **sp. nov.**, 2,990 m, paratype, genitalia slide no. AD1176 (MfN); 45, 46, *A. andina* Diškus & Stonis, **sp. nov.**, 3,595–3,600 m, paratype, genitalia slide no. AD1179 (MfN).

FIGURES 47–52. Bionomics of mountainous *Astrotischeria* species. 47, habitat of *A. parapallens* Diškus & Stonis and *A. montivaga* Diškus & Stonis, **sp. nov.**, Ayacucho, Huamanga Province, Peru, 3,320 m; 48, unidentified host plant of *A. peruanica* Diškus & Stonis, **sp. nov.**, possibly *Baccharis trinervis* Pers., Asteraceae, 2,110 m; 49, 50, leaf mines with feeding larvae of *Astrotischeria peruanica* Diškus & Stonis, **sp. nov.**; 51, 52, *Baccharis salicifolia* (Ruiz & Pav.) Pers., Asteraceae, a host plant of *Astrotischeria viscacha* Diškus & Stonis, **sp. nov.,** Pisac, Calca Province, Peru at an elevation of 2,990 m.

FIGURES 53–59. Bionomics of *Astrotischeria andina* Diškus & Stonis, **sp. nov.** 53, 54, habitat, Saqsaywaman, Cusco, Peru, 3,595–3,600 m; 55–57, host plant *Baccharis buxifolia* (Lam.) Pers., Asteraceae; 58, 59, leaf mines.

Molecular considerations of *Astrotischeria andina* sp. nov. occurring at the record-high elevations

The 650 bp fragment of mtDNA CO1 is highly functional in species identification for various animal groups (Hebert *et al.* 2003a). However, it is difficult to obtain this sequence from air-dried museum specimens because of DNA degradation. For such cases, a universal DNA mini-barcode can be used (Hajibabaei *et al.* 2006; Meusnier *et al.* 2008).

In this study, we successfully sequenced the 133 bp long DNA mini-barcode of *Astrotischeria andina* Diškus & Stonis, **sp. nov.**, a species occurring at record-high elevations. This sequence was included in our molecular analyses using the NJ method with an Opostegidae outgroup. Unfortunately, none of them yielded a fully resolved tree: the best outcomes still had doubtful dichotomies and low bootstrap support values. The challenge of obtaining fully resolved molecular trees of *Astrotischeria* was briefly discussed in the monograph "Genera of Tischeriidae: a review of the global fauna" (Stonis *et al*. 2023). In this publication, it was hypothesized that the partial sequences of the mtDNA CO1 are not useful for discrimination of *Astrotischeria* species, what is common in cases where the rate of evolution is extremely high.

Nevertheless, our study showed that each species involved in the analyses is distinct, including *A. andina* **sp. nov.** According to Hebert *et al.* (2003b), 2% of evolutionary divergence of the mtDNA CO1 sequences is a threshold for 98% of animal species, while the distinction of analysed *Astrotischeria* species ranged from 5.26 ± 2.3% (between *A. andina* **sp. nov.** and *A. atlantica* Diškus & Stonis) to 17.69±4.07% (between *A. jociui* Diskus & Stonis and *A. colombiana* Stonis & Vargas).

In half of our molecular trees, *A. andina* **sp. nov.**, as a separate clade, clustered with *A. yungasi* Diškus & Stonis; however, this was never reliable, with very low bootstrap support values. In the other half of our analyses, *A. andina* **sp. nov.**, as a separate clade, clustered with *A. atlantica* (Fig. 60), and sometimes with sufficient bootstrap support values. While the cluster *A. andina* **sp. nov.** + *A. yungasi* is not supported by morphological data or biology (host plants are from Asteraceae but very different), the cluster *A. andina* **sp. nov.** + *A. atlantica* can be substantiated by certain similarities in the male genitalia. Moreover, both species feed on the same plant genus, *Baccharis* L.: *A. andina* **sp. nov.** on *B. buxifolia*, and *A. atlantica* on *B. spicata*.

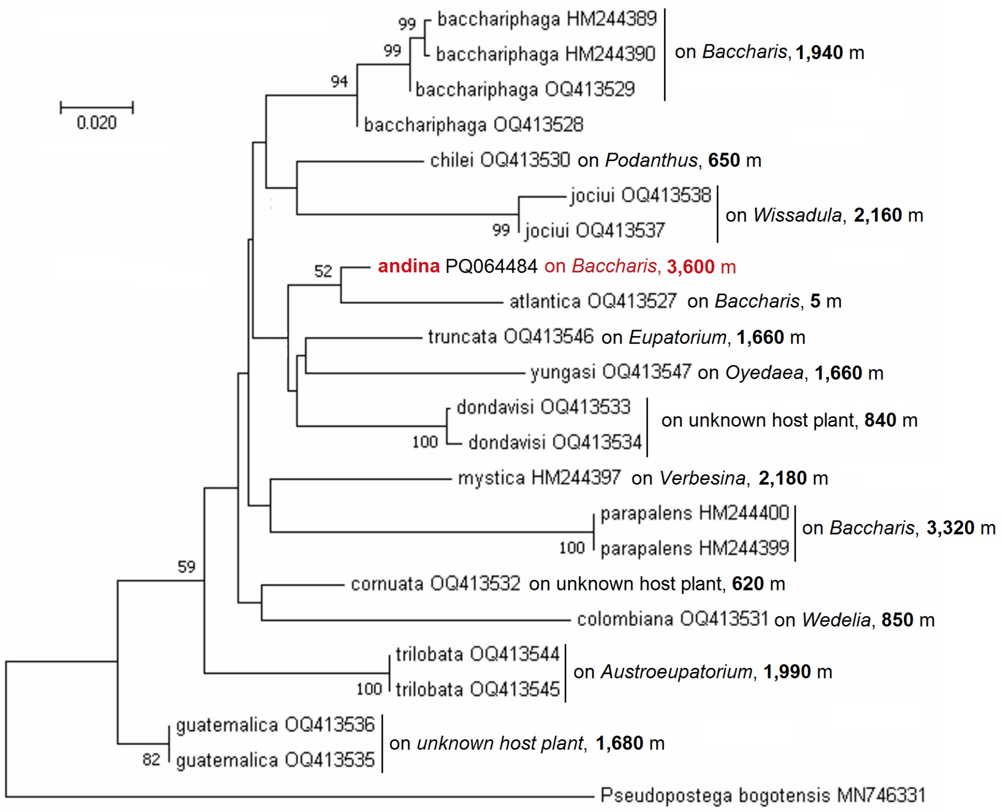
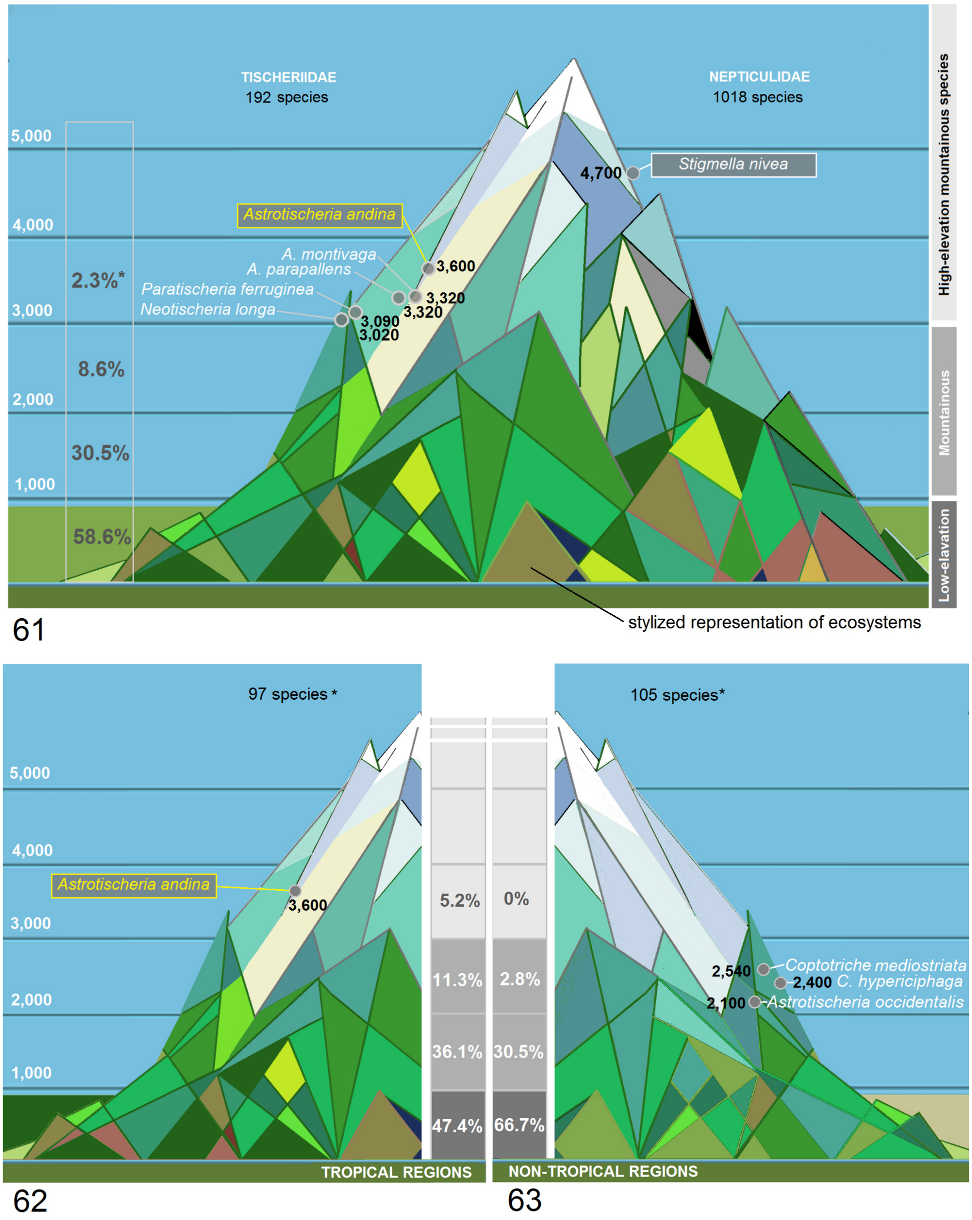


FIGURE 60. The Neighbor-Joining tree of the 133–639 bp long mtDNA CO1-5' sequences of *Astrotischeria andina* sp. nov. and related species. The divergence was calculated using the T92+G model and 10,000 replicates. Bootstrap values below 50 are not shown. *Pseudopostega bogotensis* Vargas was included as an outgroup.

Neither of our molecular trees have proven that species from high altitudes are closely related (i.e., represent a certain phylogenetic trend of high-elevation species). Moreover, *A. andina* **sp. nov.** and *A. atlantica*, two species forming one phylogenetic cluster, represent two opposite extremes: the first occurring at record-high altitudes in the Peruvian Andes, while the latter is known from an altitude around 5 m on the Atlantic coast of Argentina.

The most common altitudes for Tischeriidae to occur

With data on all currently known Tischeriidae species (192), we attempted to estimate the elevations where the most species are currently known to occur, thereby identifying the altitudes where Tischeriidae prevail.



FIGURES 61–63. Tischeriidae occurrence across different elevations. 61, based on the current data of the global fauna (192 species), with the record-high altitudes for Tischeriidae compared with the record-high altitude reported for Nepticulidae; 62, Tischeriidae in the tropical regions (97 species) showing *Astrotischeria andina* **sp. nov.** as a species discovered at record-high altitudes; 63, Tischeriidae in non-tropical regions (105 species) showing the species discovered at record-high altitudes in non-tropical regions. *Note that the distribution of some species overlaps across different altitudes, and some species have been discovered in both tropical (Fig. 62) and non-tropical regions (Fig. 63). The total current number of Tischeriidae species is still 192 (not 97+105). Note that this illustrative representation of the diversity of ecosystems, conveyed by J. R. Stonis, is presented in a stylized and idealized manner, without relying on precise depiction of the actual components.

The study showed that more than half of currently known species (58.6%) are associated with elevations lower than 1,000 m. Many species (30.5%) are known from the elevation range between 1,000 and 2,000 m, and about 8.6% from the elevation range between 2,000 and 3,000 m (Fig. 61; note that the diversity of ecosystems, conveyed by J. R. Stonis, is presented in a stylized and idealized manner, without relying on precise depiction of the actual components). The truly high-elevation species occurring above 3,000 m count for about 2.3%. These include *Neotischeria longa* Diškus & Stonis (at 3,020 m), *Paratischeria ferruginea* (Diškus & Stonis) (at 3,090 m), *Astrotischeria parapalens* Diškus & Stonis (at 3,320 m), *A. montivaga* Diškus & Stonis, **sp. nov.** (at 3,320 m), and *A. andina* Diškus & Stonis, **sp. nov.** (at 3,595–3,600 m). All these species occur in the Andes, South America. The latter species occupies record-high altitudes among Tischeriidae worldwide.

Naturally, the mountainous species are most common in tropical regions due to favorable living conditions at higher altitudes compared to harsher non-tropical areas. By tropical regions, we primarily refer to the areas within the tropical zone surrounding the Equator, defined in latitude by the Tropic of Cancer in the Northern Hemisphere and the Tropic of Capricorn in the Southern Hemisphere, consequently excluding the countries of southern Africa. As an exception, we included some lush areas of the lower western Himalaya but excluded the southernmost parts of China and the very north of Vietnam, which lack a tropical climate.

Among the species occurring in non-tropical areas, the mountainous species living above the elevation of 1,000 m count only for 33% (Fig. 63), while those in tropical regions count for about 53% (including the high-elevation mountainous species) (Fig. 62). Moreover, there are no Tischeriidae species known to occur above 3,000 m in non-tropical areas, and only a few known to occur above 2,000 m (Fig. 63). These include the North American *Astrotischeria occidentalis* (Braun) at the elevation of 2,100 m, *Coptotriche mediostriata* (Braun) at the elevation of 2,540 m, and the Himalayan *C. hypericiphaga* Puplesis & Diškus at the elevation of 2,400 m.

Discussion

Globally, trumpet moths (Tischeriidae) have a wide geographical distribution, ranging from North America and Europe to South America, South Africa, Madagascar, and Southeast Asia. These moths are found in various habitats at different elevations. Earlier studies noted that they are particularly common in the lowland or low-elevation tropical forests of Central America (Puplesis & Diškus 2003) and likely Southeast Asia (Stonis *et al*. 2021a, 2023). Recently, an exceptionally diverse fauna of Tischeriidae was reported from Belize, where fourteen species, including representatives of five genera, were collected at a single site at an elevation of about 550 m (Stonis *et al.* 2020a). This site not only holds the highest number of Tischeriidae species ever recorded from a single locality worldwide but also exceeds the total known European fauna.

The current study revealed Tischeriidae as a family particularly common in tropical regions, with a predominance of species occurring in low-elevation (lowland) areas globally. Mountainous species constitute approximately 41% of the total, but only about 2% are found at high altitudes worldwide (Fig. 61), and about 5% in tropical regions (Fig. 62). In non-tropical areas, high-elevation species belong to the genera *Coptotriche* and *Astrotischeria*. These species are associated with host plants from the Fagaceae, Hypericaceae, and Asteraceae families and have been recorded at elevations around 2,100–2,540 m (Fig. 63). In tropical regions, high-altitude species belong to the genera *Astrotischeria*, *Paratischeria*, and *Neotischeria*. These species are associated with host plants from the Urticaceae and Asteraceae families and have been reported at elevations between 3,000–3,600 m. This is notably lower compared to *Stigmella nivea* Remeikis & Stonis, a species of the Nepticulidae family recorded at a record-high elevation (Fig. 61). *Astrotischeria andina* **sp. nov.**, the species with the highest elevation reported in the current paper, is trophically associated with *Baccharis buxifolia* (Lam.) Pers. (= *Baccharis peruviana* Cuatrec.) (Asteraceae). This host plant is found in Colombia, Ecuador, and Peru. According to Beltrán (2016), it is widespread in Peru on the slopes of the Andes, at elevations between 3,000 and 4,000 m. This suggests that the high-elevation *Astrotischeria andina* **sp. nov.**, feeding on the widely distributed *Baccharis buxifolia*, might also be present in adjacent Ecuador and even Colombia.

All currently known high-elevation records of Tischeriidae are significantly lower than the treeline. The treeline, which marks the edge above which trees cannot tolerate the environmental conditions and thus cannot grow, is defined slightly differently by various authors. Generally, it ranges from about 3,000–3,300 m to about 4,300–4,500 m in the Himalayas (Chhetri *et al*. 2017; Shing *et al*. 2023) and from 3,800 m to 4,810 m in the Andes (Young & León 2007; He *et al*. 2016). This offers great potential for further discovery of high-altitude Tischeriidae, as trumpet moths are primarily associated with dendraceous plants. It is also worth mentioning that mountain treelines are rising globally in response to climate change (Climate Connections 2024).

In general, the genus *Astrotischeria* within the family Tischeriidae appears to be a "key genus" for high-altitude trumpet moth fauna, while the family Asteraceae is a "key family" for high-altitude leaf-mining species in the Andes.

The distribution of Asteraceae (Compositae) in the high Andes extends from northern Colombia and Ecuador to Chile and Argentina, encompassing Mount Aconcagua (6,960 m), the highest peak outside of the Himalayas. Asteraceae plants are found at elevations up to 5,000 m or higher. Some species of *Werneria* Kunth and *Perezia* Lag. reach 5,000 m (Calvo *et al*. 2020; Katinas 2012), while *Senecio gamolepis* Cabrera reaches 5,370 m (Körner 1999; Luteyn 1999; Tupayachi Herrera 2019) or 5,600 m (Beltrán 2008). This plant family in the high Andes represent a rich diversity of species, some of which are endemic to specific regions. Many Asteraceae species are exceptionally well-adapted to the severe conditions of high-altitude environments, exhibiting traits such as rosette and low growth forms, sclerophyllous and thickened leaves, and protective structures to withstand strong UV radiation, cold temperatures, and high winds. In the páramo ecosystems of the high Andes, Asteraceae species play critical roles, including contributing to soil stabilization and overall ecosystem functioning in these fragile environments (Luteyn 1999).

As regards Tischeriidae, *Baccharis* L. seems to be one of the most utilized host-plant genera of Asteraceae plants, especially for the trumpet moths belonging to *Astrotischeria*. Among the eight species belonging to this genus and occurring above 2,000 m, five species (63%) are already known to be leaf miners of *Baccharis*. It should be noted that *Baccharis* is a surprisingly large genus of the tribe Astereae, with 300 to more than 500 species (Nesom 1990; Giuliano 2001; Gonzáles *et al.* 2019) widely distributed in America, but with major diversity throughout the Andes. Solely in Peru, the genus contains about 77 species (Brako & Zarucchi 1993; Ulloa Ulloa *et al*. 2004), many of them being endemic to Peru with some species reaching 4,600 m (Gonzáles *et al*. 2019). Therefore, it can be hypothesized that more high-elevation Tischeriidae species can be found in the genus *Astrotischeria* and feeding on *Baccharis*. It is interesting to note that previous observations also indicate that high-elevation Tischeriidae species in Colombia are *Baccharis* feeders (A. Diškus, personal observation/unpublished).

High altitudes present unique challenges for insects, compelling them to develop various adaptations to thrive in these extreme conditions. In such environments, where temperatures fluctuate drastically and physical parameters like solar radiation and oxygen levels are specific, insects have likely evolved remarkable physiological and behavioral strategies.

A recent monograph on high-altitude Nepticulidae (Stonis *et al*. 2016b) documented *Stigmella nivea* Remeikis & Stonis, a species occurring at record-high altitudes worldwide (4,700 m). This work described a previously unknown fauna of pygmy moths from the Andean páramo and puna and provided some data on host-plant relationships of these high-elevation Nepticulidae. However, it did not delve into the specific adaptations of these tiny moths.

Recently, the first high-altitude record of a micro moth, *Bucculatrix mirnae* Vargas and Moreira (Bucculatricidae), was documented in the Andes of northern Chile (Vargas & Mundaca 2016). Several important ecological aspects of high-altitude insects were discussed by Mani (1968), and other studies have provided data on the diversity of Lepidoptera in high-altitude areas, such as Sanyal *et al*. (2013) and Zarikian *et al*. (2019). These latter studies attempted to link Lepidoptera species diversity with altitudinal parameters. Zarikian *et al.* (2019) recorded a significant relationship between elevation and species richness and abundance, following a typical hump-shaped curve. However, their findings revealed that diversity and evenness indices did not follow this pattern, but rather exhibited a semi-constant relationship with elevation. This was attributed to the presence of several species that are typically found only at the highest altitudes. According to Nève & Després *et al.* (2020), temperature is a major factor influencing the timing of activity and behavior in butterflies and might be a key driver of diversification along elevation gradients. This hypothesis suggests that local adaptation occurs along the elevation gradient, with high-elevation butterflies able to remain active at lower ambient temperatures compared to those from lower elevations. Furthermore, Sømme *et al*. (1996) provided important insights into the adaptations of insects at high altitudes through their study of carabid beetles in Chimborazo, Ecuador.

Despite their specialized ecological roles, moths inhabiting high altitudes, including Tischeriidae, remain insufficiently studied. This gap highlights the need for further research to understand their adaptations and ecological significance. Such studies could provide insights into broader ecological patterns and aid in conservation efforts for these fragile ecosystems.

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Although the host plants discussed in this paper were identified by Prof. Dr. Liliana Katinas, a co-author of this publication, J. R. Stonis also expresses his appreciation for earlier discussions on the indentification of various Tischeriidae host plants with Dr. Nixon Cumbicus Torres (Universidad Técnica Particular de Loja, Ecuador), Alexandre K. Monro (Royal Botanic Gardens, London, U.K.), and Dr. José Luis Fernández-Alonso (Universidad de Salamanca, Spain).

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