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Research article

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Exceptional diversity of Tischeriidae (Lepidoptera) from a single tropical forest site in Belize, Central America

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Abstract. We report on fourteen species and four genera of Tischeriidae recorded from Las Cuevas, a single tropical forest locality in Belize, Central America. This is the highest number of species of Tischeriidae recorded from a single locality worldwide, exceeding the species and generic diversity of the entire Tischeriidae fauna of Europe and accounting for about 9% of the documented global fauna for this family. We describe and name six new species: *Astrotischeria papilloma* Diškus & Stonis sp. nov., mining on *Lasianthaea fruticosa* (L.) K.M.Becker (Asteraceae); *A. scutifera* Diškus & Stonis sp. nov., mining on *Sida glabra* Mill. (Malvaceae); *A. basilobata* Remeikis & Stonis sp. nov., mining on *Lasianthaea fruticosa*; *Paratischeria robinsoni* Diškus & Stonis sp. nov., mining on *Otopappus verbesinoides* Benth. (Asteraceae); *P. tubifex* Diškus & Stonis sp. nov., mining on *Lasianthaea fruticosa*; and *P. belizensis* Remeikis & Stonis sp. nov. (host plant unknown). Additionally, we review eight previously described species from the same period of collecting at Las Cuevas in 1997–1998: *A. selvica* Diškus, Carvalho-Filho & Stonis, 2018, mining on *Sphagnetocola trilobata* (L.) Pruski and *Synedrella nodiflora* (L.) Gaertn. (Asteraceae); *A. casila* Diškus & Stonis, 2018, mining on *Montanoa atriplicifolia* (Pers.) Sch.Bip. (Asteraceae); *A. furcata* Diškus & Stonis, 2018 (host plant unknown); *Paratischeria neotropicana* (Diškus & Stonis, 2015), mining on *Sida* L. (Malvaceae), including *S. rhombifolia* L.; *Dishkeya gouaniae* (Stonis & Diškus, 2007), mining on *Gouania polygama* (Jacq.) Urb. (Rhamnaceae); *Coptotriche pulverea* (Walsingham, 1897), mining on *Terminalia amazonia* (J.F.Gmel.) Exell (Combretaceae); *C. forsteroniae* Stonis & Diškus, 2008, mining on *Forsteronia myriantha* Donn Sm. (Apocynaceae); and *C. singularis* Stonis & Diškus, 2008 (host plant unknown). All taxa, except for *C. singularis*, are illustrated with photographs of the adults and their genitalia. We also briefly discuss the discovery of some novel characters for *Astrotischeria* Pupulesis & Diškus, 2003 and *Paratischeria* Diškus & Stonis, 2017, Tischeriidae, and provide the first photographic documentation of *Coptotriche pulverea* and *C. forsteroniae*.

Keywords. Biodiversity, Belize, Las Cuevas Research Station, leaf miners, tropical forest.

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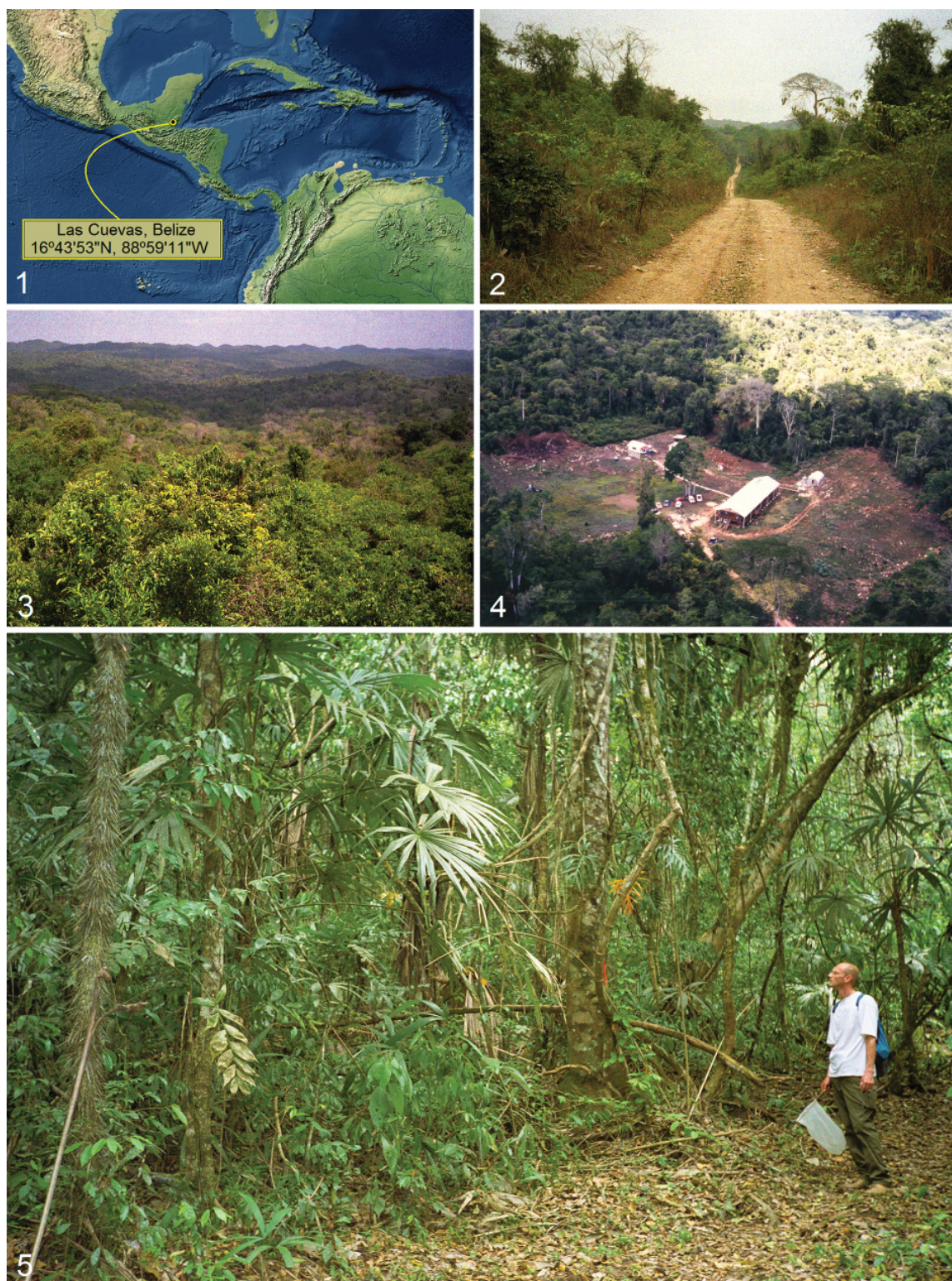
Introduction

Larvae of Tischeriidae (trumpet moths) are specialized miners of the green tissues of plants, producing mostly irregular, blotch-like, sometimes slender and sinuous or other leaf mines. The morphological and ecological characteristics of these primitive, monotrystian microlepidopterans are summarised by Braun (1972), Puplesis & Diškus (2003), Xu *et al.* (2017, 2018) and Stonis *et al.* (2017, 2018a, 2019a, 2019b). Species of Tischeriidae are represented in a wide variety of terrestrial ecosystems from the tropics to the temperate regions but, as a rule, the family is more abundant in subtropical and tropical regions, except for cooler habitats of the tropics at elevations above 3500–4000 m (Stonis *et al.* 2018a).

The tiny size of the adults, the concealed mining life-style of the larvae within leaves and the lack of qualified specialists on these insects go some way towards explaining why trumpet moths are still so little studied in many regions, including the Neotropics. For example, until recently not a single species of Tischeriidae was reported from Colombia (Stonis *et al.* 2015), which is regarded as one of the world's 'megadiverse' countries. Only during the last year have the first two species of Tischeriidae been described from this country (Stonis *et al.* 2019b). The study of the Tischeriidae fauna in the Neotropics began in the late nineteenth to early twentieth century with the descriptions of the first species (Walsingham 1897, 1914; Meyrick 1915). However, only during the last two decades has the study of Neotropical Tischeriidae become more purposeful and active through collecting in the field and the compilation of species inventories for Central and South America (Stonis *et al.* 2019a). It has been suggested that Tischeriidae might make up a significant portion of the Neotropical fauna of leaf-mining insects (Stonis *et al.* 2019a).

This paper reports on samples of material of leaf mines collected at Las Cuevas, Belize (Fig. 1) by Owen T. Lewis in 1997 and 1998 (Lewis *et al.* 2002). Mining larvae of tischeriids were very sparse during the dry season but more abundant during more humid periods of the year. Additional material was obtained at Las Cuevas in April 1998 by light trapping by Jonas R. Stonis (formerly R. Puplesis) and Simon R. Hill (Puplesis & Hill 1998; Puplesis & Robinson 2000).

Las Cuevas (16°43'53" N, 88°59'11" W) is a research station in the hilly Maya Mountains at an elevation of about 550 m, deep in the Chiquibul Forest Reserve (Figs 2–5). The Chiquibul Forest represents nearly 8% of Belize's terrestrial surface and is a part of the tri-national Maya Forest bioregion forming the largest remaining contiguous block of tropical forest north of the Amazon (Las Cuevas Research Station 2020). The Chiquibul tropical forest is classified as a Tropical and Subtropical Broadleaf Forest (World Wildlife Fund 2020b) or Submontane Broadleaf Moist Forest (Folkard-Tapp 2020: fig. 10) bordering with Submontane Broadleaf Wet Forest. It belongs to one of seven ecoregions of Belize, the Petén-Veracruz moist forest (World Atlas 2019; World Wildlife Fund 2020a). The Chiquibul Forest was subject to selective logging for timber during much of the 20th Century. The majority of the vegetation around Las Cuevas is recovering from selective logging during the past ca 40–50 years, although a few pockets of relatively undisturbed or primary forest remain. The Chiquibul receives between 1500 and 2000 mm of rain per year. Rainfall is seasonal, with a dry season typically from February to June (approximately) and sometimes a shorter dry period of two to three weeks in August (Puplesis & Robinson 2000). Hilltops, hillsides, and valley bottoms have markedly different forests both in terms of structure and species composition. At our main collecting sites (on hillsides and in valley bottoms) the forest has a greater proportion of evergreen species, e.g., *Manilkara zapota* (L.) P.Royen, *Calophyllum brasiliense*



Figs 1–5. Map and locality. **1.** Las Cuevas, Belize, Central America, 16°43'53" N, 88°59'11" W (Map base courtesy of T. Patterson, USA). **2–3.** Road to Las Cuevas Research Station, located in the heart of the Chiquibul Forest in the Maya Mountains of Belize. **4.** The site of Las Cuevas Research Station (formerly Las Cuevas Biological Station), shortly after its establishment by the Forest Department of Belize and the Natural History Museum, London in 1994 (courtesy of NHMUK). **5.** Habitat, moist tropical forest (at right, collector Simon R. Hill, 1998).

Cambess. and *Aspidosperma megalocarpon* Müll.Arg., although deciduous species such as *Swietenia macrophylla* King and *Terminalia amazonia* (J.F.Gmel.) Exell were still a significant component (Puplesis & Robinson 2000). Las Cuevas is an important centre for biological or ecological research, established jointly by the Forest Department of Belize and the Natural History Museum, London in 1994 and now co-managed by the Friends for Conservation and Development and the Government of Belize.

The collected material from Las Cuevas has yielded fourteen species of Tischeriidae. Externally all species collected at Las Cuevas look very similar (Figs 6–34). External characters are not sufficient for species identification; therefore, we do not use them in the diagnoses of the species.

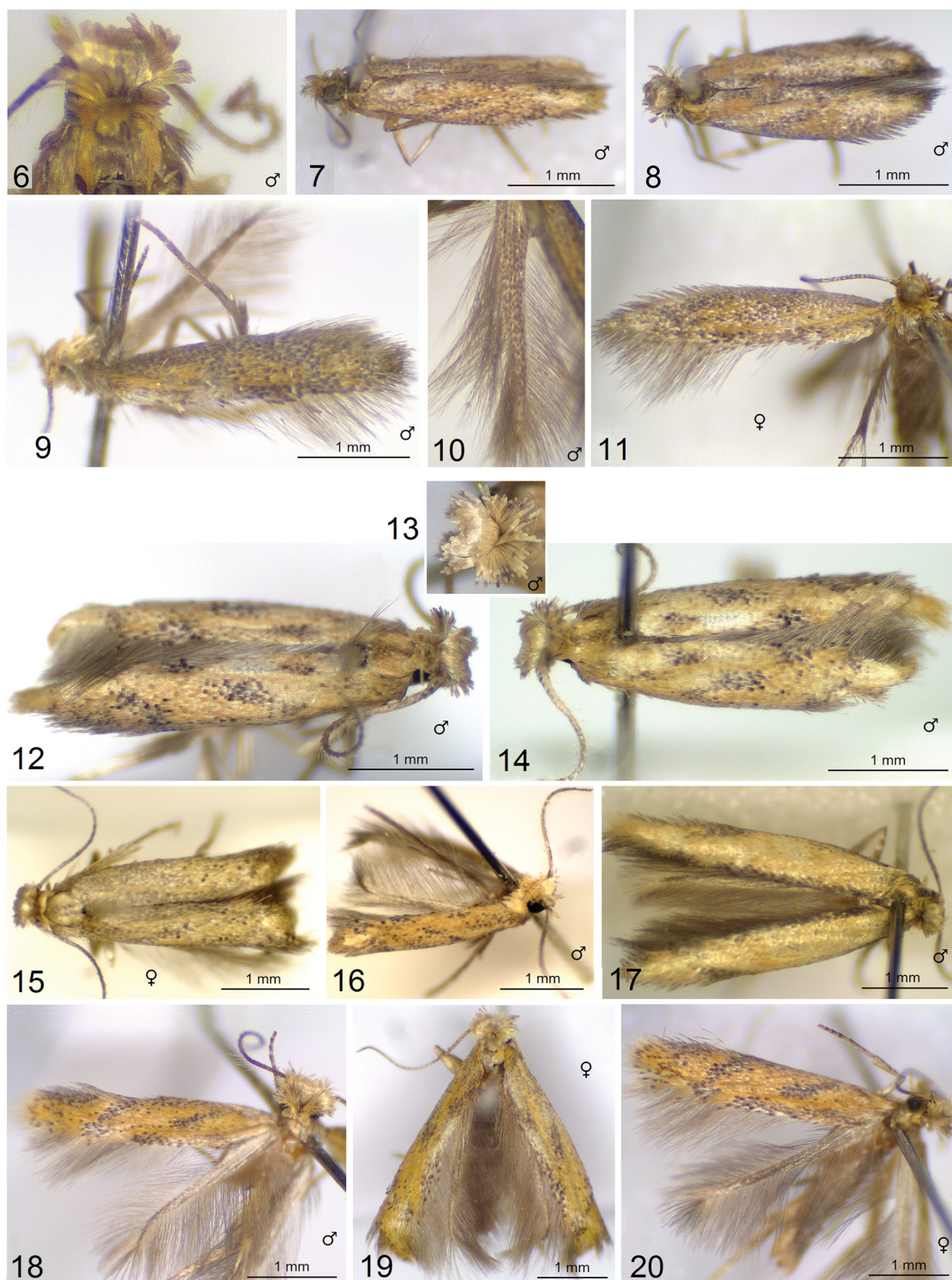
With one exception, *Coptotriche pulverea* (Walsingham, 1897), all species of Tischeriidae collected at Las Cuevas appear to be new to science. *Dishkeya gouaniae* (Stonis & Diškus, 2007) was described within a review of the genus *Tischeria* Zeller, 1839 (Stonis & Diškus 2007), and *Coptotriche forsteroniae* Stonis & Diškus, 2008 and *C. singularis* Stonis & Diškus, 2008 in the first review of *Coptotriche* Walsingham, 1890 in the Americas (Stonis & Diškus 2008). *Paratischeria neotropicana* (Diškus & Stonis, 2015) was described in a separate article indicating the broadest distribution of trumpet moths (Diškus & Stonis 2015). Three other species, *Astrotischeria selvica* Diškus, Carvalho-Filho & Stonis, 2018, *A. casila* Diškus & Stonis, 2018 and *A. furcata* Diškus & Stonis, 2018, were documented along with a recent review of three-lobed *Astrotischeria* Puplesis & Diškus, 2003 (Stonis *et al.* 2018a). In the current paper we describe and name the remaining six new species from the collecting at Las Cuevas: *Astrotischeria papilloma* Diškus & Stonis sp. nov., *A. scutifera* Diškus & Stonis sp. nov., *A. basilobata* Remeikis & Stonis sp. nov., *Paratischeria robinsoni* Diškus & Stonis sp. nov., *P. tubifex* Diškus & Stonis sp. nov. and *P. belizensis* Remeikis & Stonis sp. nov. We also provide the first photographic documentation of adults and male genitalia of the following species: *Tischeria gouaniae*, *Coptotriche pulverea* (Walsingham, 1897) and *C. forsteroniae*.

International concern over the biodiversity crisis has underscored the urgency to inventory global biotas and to provide taxonomic reviews of diverse groups of organisms, particularly in poorly-studied yet species-rich tropical areas (Puplesis & Robinson 2000). This account of taxa recorded from a single locality is intended to illustrate the high local diversity of Tischeriidae that can occur within the tropical forests of Central America. It will provide a foundation upon which we and others can build a more detailed account of the diversity of Central American and Neotropical Tischeriidae.

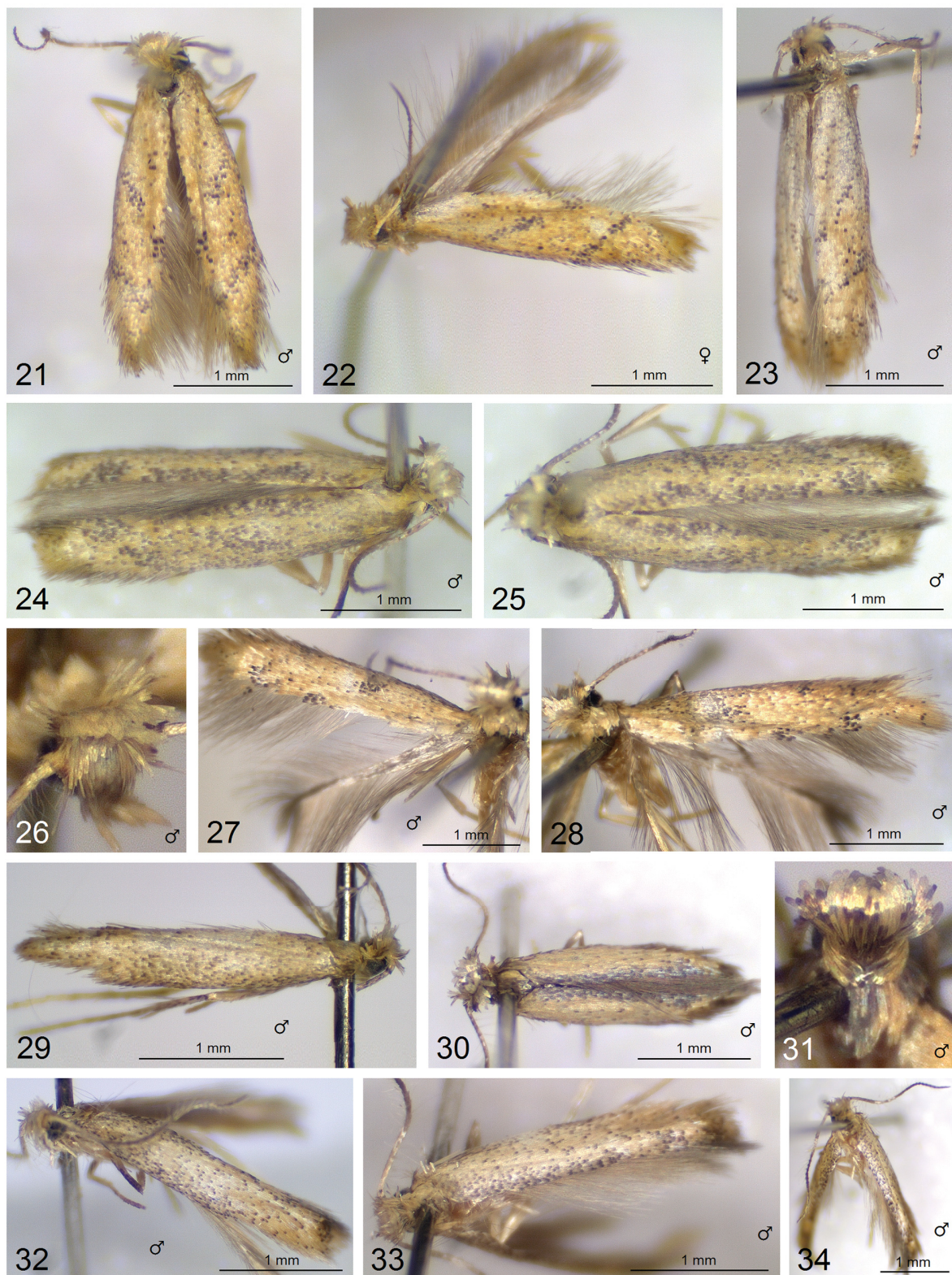
Material and methods

Leaf mines containing living larvae were sampled from tropical forest vegetation from September 1997 to September 1998. Sampling occurred in all months except December, January and May. The sampling regime for larval leaf miners was described by Lewis *et al.* (2002) and concentrated on vegetation growing along the margins of four-wheel drive vehicle tracks within 4 km of the field station. Mines were reared individually in airtight plastic containers, lined with absorbent paper. Alternative techniques for rearing adults from mining larvae were described in detail by Stonis *et al.* (2018a). Adult moths emerged from the mines typically within 20 days (maximum 35 days) of collection. Overall, 2053 living mines of Tischeriidae were collected, of which 654 died during rearing, 901 produced adult moths and 498 produced Hymenoptera parasitoids (35.6% parasitism across all Tischeriidae). Interactions between parasitoid species and leaf miner hosts were reported and analysed by Lewis *et al.* (2002), and a manipulative experiment on the host–parasitoid food web (also comprising non-tischeriid leaf miners) was reported in Morris *et al.* (2004). The text below associates, for the first time, the morphospecies names used in those ecological studies with species identifications and descriptions.

Adult moths were collected by attracting them to mercury-vapour light from a lamp suspended slightly above eye-level and 5–10 cm in front of a white screen (Puplesis & Robinson 2000), rather closer than is



Figs 6–20. Tischeriidae collected in Las Cuevas, Belize. **6.** *Astrotischeria papilloma* sp. nov., head, paratype (NHMUK 010289202). **7.** Same, holotype (010289201). **8.** Same, paratype (010289202). **9.** *A. scutifera* sp. nov., holotype (010289214). **10.** Same, paratype, hindwing (010289218). **11.** Same, paratype (010289221). **12.** *A. basilobata* sp. nov., holotype (010289226). **13.** Same, frontal tuft. **14.** Same, dorso-lateral view. **15.** *A. selvica*, paratype (010289241). **16.** *A. casila*, holotype (010289244). **17.** *A. furcata*, holotype (010289261). **18.** *Paratischeria robinsoni* sp. nov., holotype (010289262). **19.** Same, paratype (010289269). **20.** Same, paratype (010289270).



Figs 21–34. Tischeriidae collected in Las Cuevas, Belize. **21.** *Paratischeria tubifex* sp. nov., holotype (NHMUK 010289272). **22.** Same, paratype (010289282). **23.** Same, paratype (010289276). **24–25.** *P. belizensis* sp. nov., holotype (010289283). **26–28.** *P. neotropicana* (010289285). **29.** *Dishkeya gouaniae*, paratype (010289320). **30.** *Coptotriche pulverea* (010289324). **31.** Same (010289322). **32–34.** *C. forsteroniae*, paratype (010289330).

usual in the standard method for light collecting (described by Robinson *et al.* 1994) in which the lamp is about 0.5 m from the illuminated surface. A Honda EX 350 generator was used as a power source. Moths attracted to the screen were collected in small glass tubes.

Preparation of temporary and permanent micro-mounts of genital structures was undertaken following the standard method described by Stonis *et al.* (2014). After maceration of the abdomen in 10% KOH and subsequent cleaning, abdominal pelts and female genitalia were stained with Chlorazol Black (Direct Black 38/Azo Black), but male genitalia were left unstained. Both male and female genitalia were mounted in Euparal. The genitalia were fixed with the ventral part facing up; occasionally, some sclerites were disassembled from the capsule; the phallus was usually removed from the capsule; the pelt or loose sclerites of the genital armature (e.g., removed phallus) were fixed under a separate cover slip, always on the same slide. Sometimes we rolled and photographed genitalia in Euparal before finally closing the mount with a cover slip; this generated images of the genitalia in lateral view, especially useful with complex structures, viewed differently from the ventral side. In our study, the genital micro-mounts were examined using a Leica DM2500 microscope and a Leica DFC420 digital camera connected to the microscope and the computer; each photograph of a genitalia slide was supplied with the slide number and species name.

The descriptive terminology of morphological structures follows Puplesis & Diškus (2003), except for the term ‘aedeagus’, which is referred to here as ‘phallus’, and the term ‘cilia’, which is referred to here as ‘fringe’.

Repositories

Descriptions of the new species treated in this paper are based on material deposited in the collection of the Natural History Museum, London (NHMUK). Additionally, some specimens of *Astrotischeria papilloma* sp. nov. were available for our study from Honduras, and they are deposited at the collection of the Biosystematics Research Group (former Lithuanian University of Educational Sciences, formerly abbreviated as LEU or VPU), Vilnius, Lithuania (with subsequent transfer to the Zoological Institute of the Russian Academy of Sciences, ZIN, because of the LEU closure).

Results

Class Insecta Linnaeus, 1758
Order Lepidoptera Linnaeus, 1758
Family Tischeriidae Spuler, 1898
Genus *Astrotischeria* Puplesis & Diškus, 2003

Astrotischeria papilloma Diškus & Stonis sp. nov.

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Figs 6–8, 35–52

Tischeria sp. 7 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the unique, highly specific, finger-like dorsal lobe of the valva (Fig. 42), the bifurcated dorsal lobe of the uncus (Fig. 35) and the angular apex of the valva (Fig. 40) distinguish *Astrotischeria papilloma* sp. nov. from other congeneric species. In the female genitalia, the slender band of long chetae (Fig. 49) is hypothesized to be unique to this species. This character may not remain valid for species differentiation because females of many other species of *Astrotischeria* remain to be discovered. The host plant,

Lasianthaea fruticosa (L.) K.M.Becker (Asteraceae Bercht. & J.Presl), coincides with the host plant of another new species, *Paratischeria tubifex* sp. nov., described below.

Etymology

The species name is derived from the Latin ‘*papilla*’ with the prefix ‘*oma*’, i.e., the widely used medical term *papilloma* (an outward finger-like frond), in reference to the unique, finger-like dorsal lobe of the valva in the male genitalia.

Type material

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 3–16 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 010316182♂; NHMUK 010289201.

Paratypes

BELIZE • 9 ♂♂, 3 ♀♀; same locality as for holotype; 21 Sep.–4 Nov. 1997 and 13 Apr.–20 Jul. 1998; O.T. Lewis leg.; mining larva on *Lasianthaea fruticosa* (L.) K.M.Becker (Asteraceae); field card nos 18.008-13/4♂, 16.020-2/10♂, 29.046-1/10♂, 16.005-21/9♂, 16.013-21/9♂, 16.097-20/7♂, 16.014-2/10♂, 18.025-13/4♂, 84-20/7♂, 1364-4/11♀, 83-20/7♀, 16.098-20/7♀; genitalia slide nos 010316181♂, 010316183♂, 010316184♂, 010316185♂, 010316186♀; NHMUK 010289202 to 010289213.

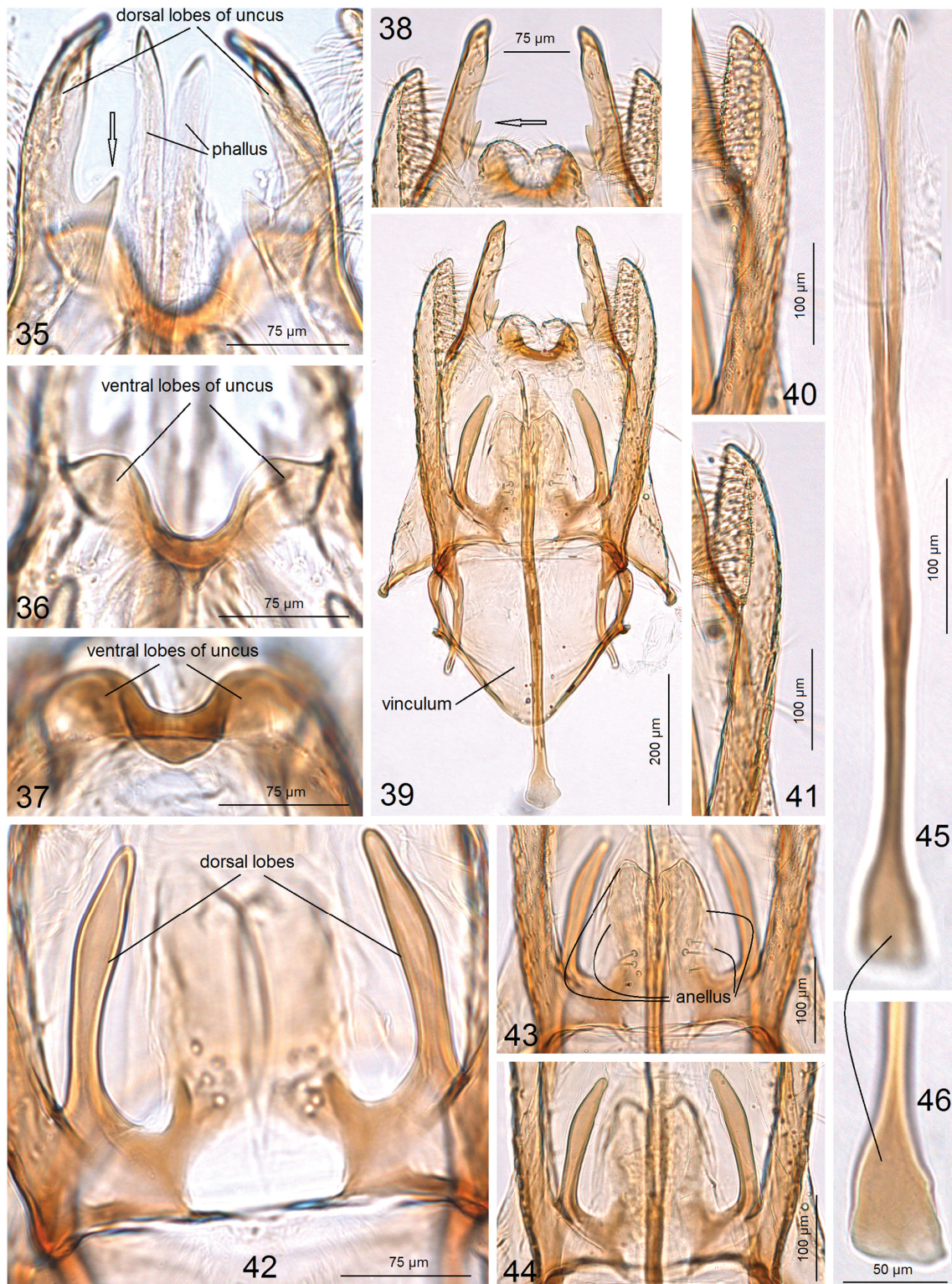
HONDURAS • 6 ♂♂, 3 ♀♀; Copán Department, Copán Archaeological Site Ruinas; 14°50'13" N, 89°08'37" W; alt. 620 m; 15 Feb. 2012; A. Diškus leg.; from feeding larvae (Asteraceae host plant, species unidentified); field card no. 5088; genitalia slide nos AD911♂, AD1007♂, AD1008♂, AD916♀; ZIN.

Description

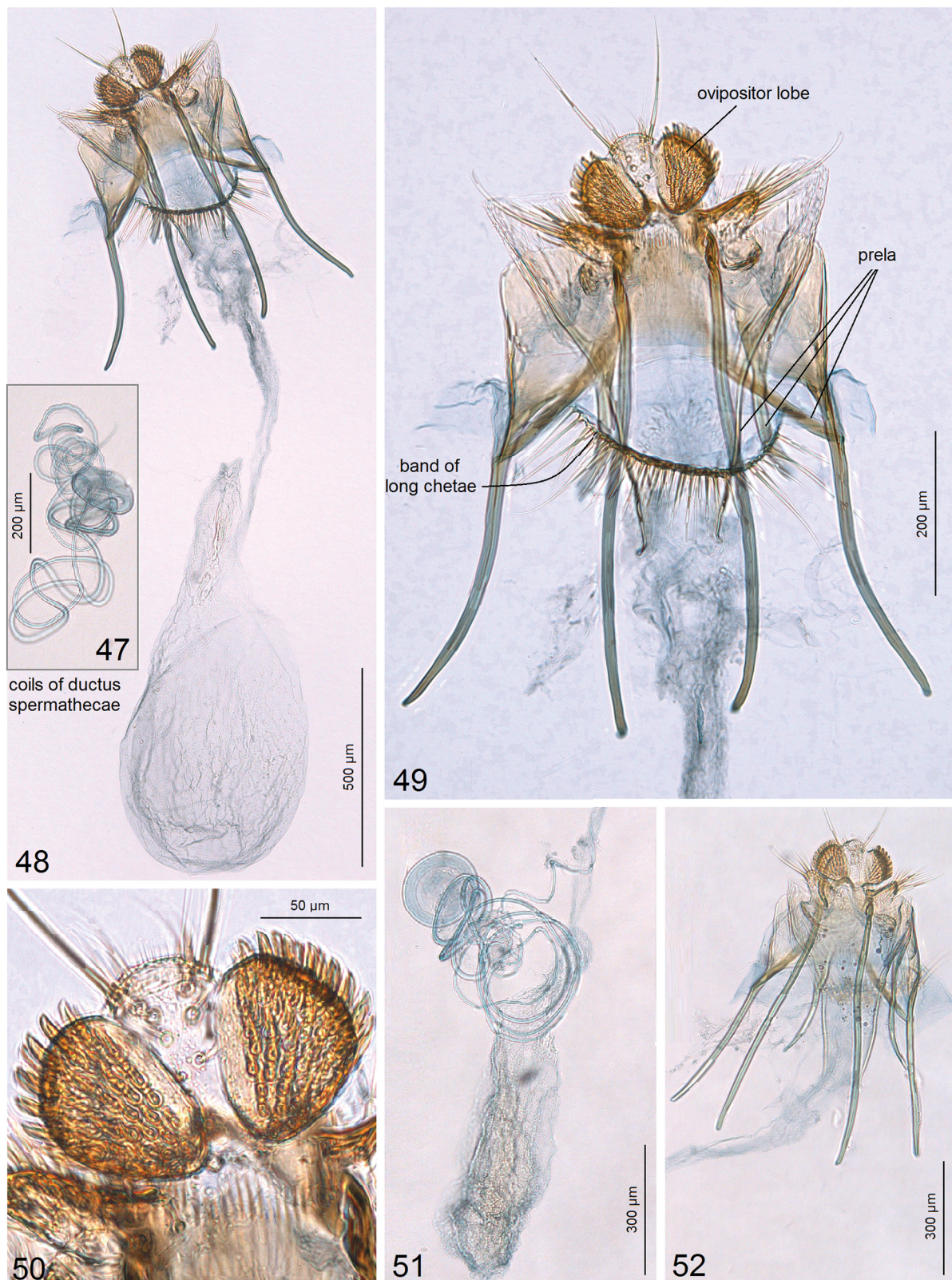
Male

EXTERNAL CHARACTERS (Figs 6–8). Forewing length 2.3–2.5 mm; wingspan 5.2–5.5 mm (n = 6). Head: palpus, pecten and frons cream; frontal tuft comprised of lamellar scales, from yellowish ochre or ochre cream to pale grey, often with pale grey, cream-tipped or cream, brown-tipped scales medially; collar comprised of lamellar, yellowish cream scales; antenna exceeding ½ of forewing; flagellum cream, brown-annulated to entirely grey-brown. Thorax glossy, pale grey-brown medially, yellowish cream to ochre laterally; tegula pale grey-brown. Forewing variable, usually silver glossy to cream, irregularly speckled with grey-brown and some ochre scales, sometimes with a wide band of bright ochre scales along fold; fringe ochre cream to golden ochre; fringe line often irregular, indistinctive, comprised of dark brown scales; forewing underside dark grey, without spots or androconia. Hindwing and fringe grey on upper side and underside, without androconia. Legs cream, glossy to grey or dark grey; forelegs and midlegs with blackish brown scales on upper side. Abdomen grey-brown with some purple iridescence on upper side and underside, but distally ochre cream on underside; genital plates pale grey to greyish cream; anal tufts large, grey.

MALE GENITALIA (Figs 35–46). Capsule about 750 µm long, 310–360 µm wide. Uncus with long, bifid dorsal lobes (Figs 35, 38), very short, rounded ventral lobes (Figs 36–37) and wide, thickened medial excavation. Valva about 470 µm long; ventral (main) lobe slender and straight, apically angular (Figs 40–41); dorsal lobe finger-like, distinctly connected with anellus (Figs 39, 42, 44); anellus with triangular lobes apically (Fig. 43); transtilla and juxta absent. Ventral lobe of vinculum large, triangular, distally rounded (Fig. 39). Phallus 580–650 µm long, apically divided (Fig. 45), basally widened (Fig. 46).



Figs 35–46. Male genitalia of *Astrotischeria papilloma* Diškus & Stonis sp. nov. (NHMUK). **35–36.** Dorsal and ventral lobes of uncus, paratype (genitalia slide no. 010316184). **37.** Ventral lobes of uncus, paratype (genitalia slide no. 010316185). **38.** Dorsal lobes of uncus, holotype (genitalia slide no. 010316182). **39.** General view, uncus, holotype (genitalia slide no. 010316182). **40–41.** Same, valva. **42.** Dorsal lobe of valva, paratype (genitalia slide no. 010316185). **43–44.** Anellus and dorsal lobe of valva, holotype (genitalia slide no. 010316182). **45–46.** Phallus, paratype (genitalia slide no. 010316185).



Figs 47–52. Female genitalia of *Astrotischeria papilloma* Diškus & Stonis sp. nov. **47–50.** General view and details, paratype from Belize (genitalia slide no. 010316186, NHMUK). **51.** Corpus bursae and coils of ductus spermathecae, paratype from Honduras (genitalia slide no. AD916, ZIN). **52.** Same, apophyses and ovipositor lobes.

Female

EXTERNAL CHARACTERS. Forewing length 2.3–2.9 mm; wingspan 5.0–6.2 mm (n = 3). Forewing predominantly ochre with small brown scales. Abdomen mostly ochre cream on underside, without anal tufts. Otherwise, similar to male.

FEMALE GENITALIA (Figs 47–52). Abdominal wall with a slender band of long chetae (Fig. 49); abdominal apex wide, with triangular lobes laterally. Genitalia (Fig. 48) about 2170 µm long. Ovipositor lobes large (Fig. 49), clothed with short, modified setae ('peg setae'); area between ovipositor lobes widely rounded (Fig. 50), with tiny papillae and two very long setae. Second pair of lobes lateral and anterior to ovipositor lobes, much smaller than ovipositor lobes, triangular and bearing long slender setae, without stout, modified 'peg setae'. Posterior and anterior apophyses almost equal in length (Figs 48, 52); prela comprised of three pairs of rod-like projections (Fig. 49). Corpus bursae long and narrow, distally oval-shaped (Fig. 48), with numerous, indistinctive pectinations. Accessory sac inconspicuous; ductus spermathecae very slender, with numerous large coils (Figs 47, 51).

Biology

Host plant: *Lasianthaea fruticosa* (L.) K.M.Becker (Asteraceae). Larvae were recorded mining leaves throughout the year (i.e., during all months of fieldwork), with 810 records in total. The leaf mine is a pale, translucent blotch on the upper leaf surface, located along the leaf margin. It causes the leaf margin to curl and roll upwards and inwards in a characteristic manner reminiscent of the mines of the European species *Coptotriche gauacella* (Duponchel, 1843). This species was listed as '*Tischeria* sp. 7' by Lewis *et al.* (2002), a morphospecies grouping which incorrectly grouped this species with *A. basilobata* sp. nov., which shares the host plant. Retrospectively, records of these two species can now be distinguished on the basis of characteristics of the leaf mine.

Flight period

Based on a single specimen collected at light, adults fly in April; based on rearing data, adults are likely to occur year-round. Adults eclose for up to 33 days after the collection of mines.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Astrotischeria scutifera Diškus & Stonis sp. nov.

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Figs 9–11, 53–69

Tischeria sp. 6 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the presence of a unique pseudotranstilla (Figs 61, 63–64), a shield-like lobe on the valva (Figs 57, 60), a bifid dorsal lobe of the uncus (Fig. 54) and the unique phallus (Fig. 59) distinguish *Astrotischeria scutifera* sp. nov. from other congeneric species. In the female genitalia, the strongly reduced ovipositor lobes make this species similar to the other Malvaceae-feeding species of *Astrotischeria* (which make up a minority of the genus); however, unlike *A. omissa* (Braun, 1927) or *A. heliopsisella* (Chambers, 1875), females of *A. scutifera* sp. nov. do not possess thickened tooth-like projections or curved hooks distally on the ovipositor.

Etymology

The species name is derived from the Latin ‘*scutum*’ (a ‘shield’) and ‘*fero*’ (‘to bear’, ‘to carry’) in reference to the valva possessing a shield-like lobe in the male genitalia.

Type material

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 22 Sep. 1997; O.T. Lewis leg.; mining larva on *Sida glabra* Mill. (Malvaceae); field card no. 115-22/9; genitalia slide no. 010316175♂; NHMUK 010289214.

Paratypes

BELIZE • 4 ♂♂, 7 ♀♀; same collection data as for holotype; 22 Sep.–21 Nov. 1997 and 3–14 Jul. 1998; O.T. Lewis leg.; field card nos 202-2/10♂, 4236-3/7♂, 205-23/9♂, 188-23/9♂, 113-22/9♀, 196-23/9♀, 233-24/9♀, 519-9/10♀, 29.002-1/10♀, 23.080-14/7♀, 31.009-21/11♀; genitalia slide nos 010316174♂, 010316176♂, 010316177♂, 010316178♀, 010316179♀, 010316180♀; NHMUK 010289215 to 010289225.

Description

Male

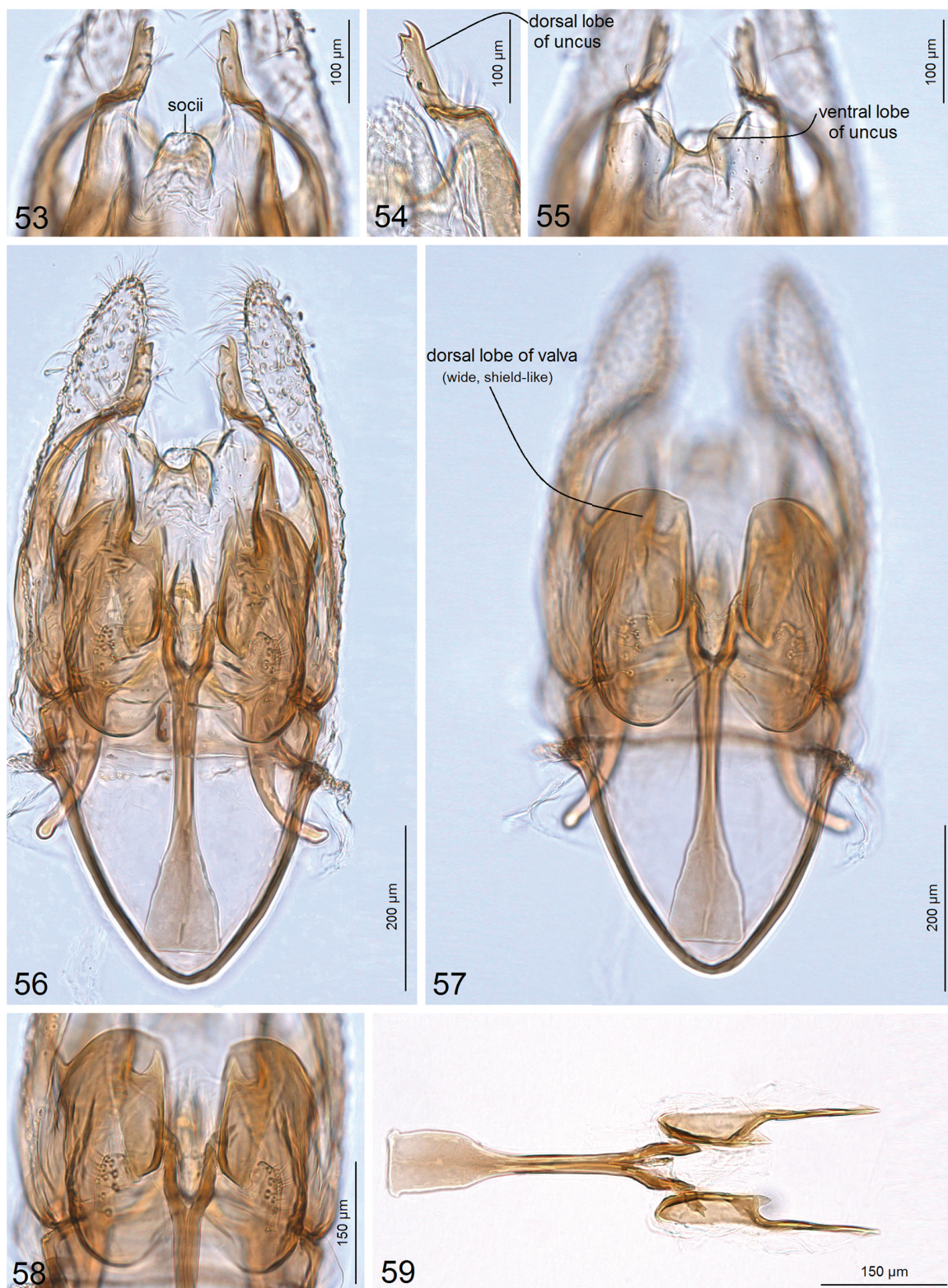
EXTERNAL CHARACTERS (Figs 9–10). Forewing length 2.5–3.0 mm; wingspan 5.4–6.5 mm (n = 5). Head: palpus cream, frons ochre cream; frontal tuft comprised of lamellar, golden cream scales; collar pale brown, comprised of lamellar, cream-tipped scales; antenna approximately ½ of forewing; flagellum pale grey. Thorax pale brownish grey, laterally sometimes ochre; tegula pale brownish grey. Forewing variable, densely speckled with dark grey scales and irregular, pale ochre to bright ochre spots or a band along fold; sometimes, instead a band or spots, ochre scales form only a line along fold; fringe grey; fringe line often irregular, indistinctive, comprised of a few dark brown scales; forewing underside with some purple iridescence, entirely covered with dark grey scales, without spots or androconia. Hindwing and fringe grey-brown on upper side and underside, without androconia. Legs glossy, with purple iridescence, pale grey or grey to yellowish cream. Abdomen dark brown on upper side and underside, with purple and blue iridescence on upper side; genital plates greyish cream to pale grey; anal tufts large, grey to yellowish grey.

MALE GENITALIA (Figs 53–64). Capsule 780–830 µm long, 340–445 µm wide. Uncus with long, bifid dorsal lobes (Figs 54, 63) and very short, rounded ventral lobes (Fig. 55); medial excavation of uncus shallow. Valva 500–620 µm long; basally with a shield-like lobe (Figs 57, 60) and a distinctive, basally wide, apically pointed dorsal lobe (Fig. 64). Anellus replaced with a unique structure which we name here a pseudotranstilla (Figs 61, 63–64). Ventral lobe of vinculum large, distally rounded (Figs 63–64) or almost triangular (Figs 56–57). Phallus 580 µm long, apically with two bifid lobes (Fig. 59), basally widened (Figs 56–57, 59).

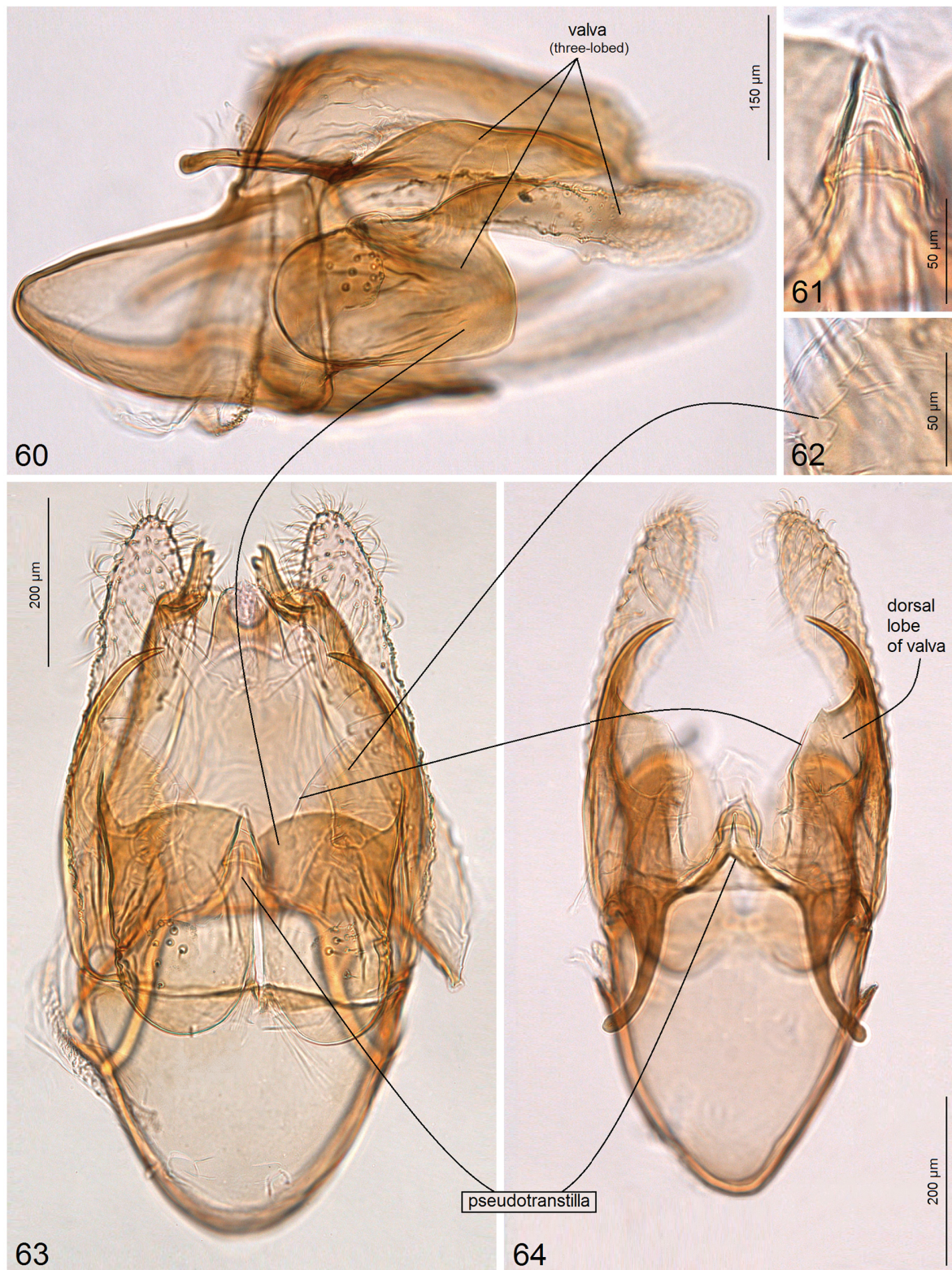
Female

EXTERNAL CHARACTERS (Fig. 11). Forewing length 3.0–3.1 mm; wingspan 6.6–6.8 mm (n = 3). Similar to male but ochre scales of forewing prevail and form large ochre spots. On underside, abdomen covered with ochre cream medially and distally, without anal tufts. Otherwise, similar to male.

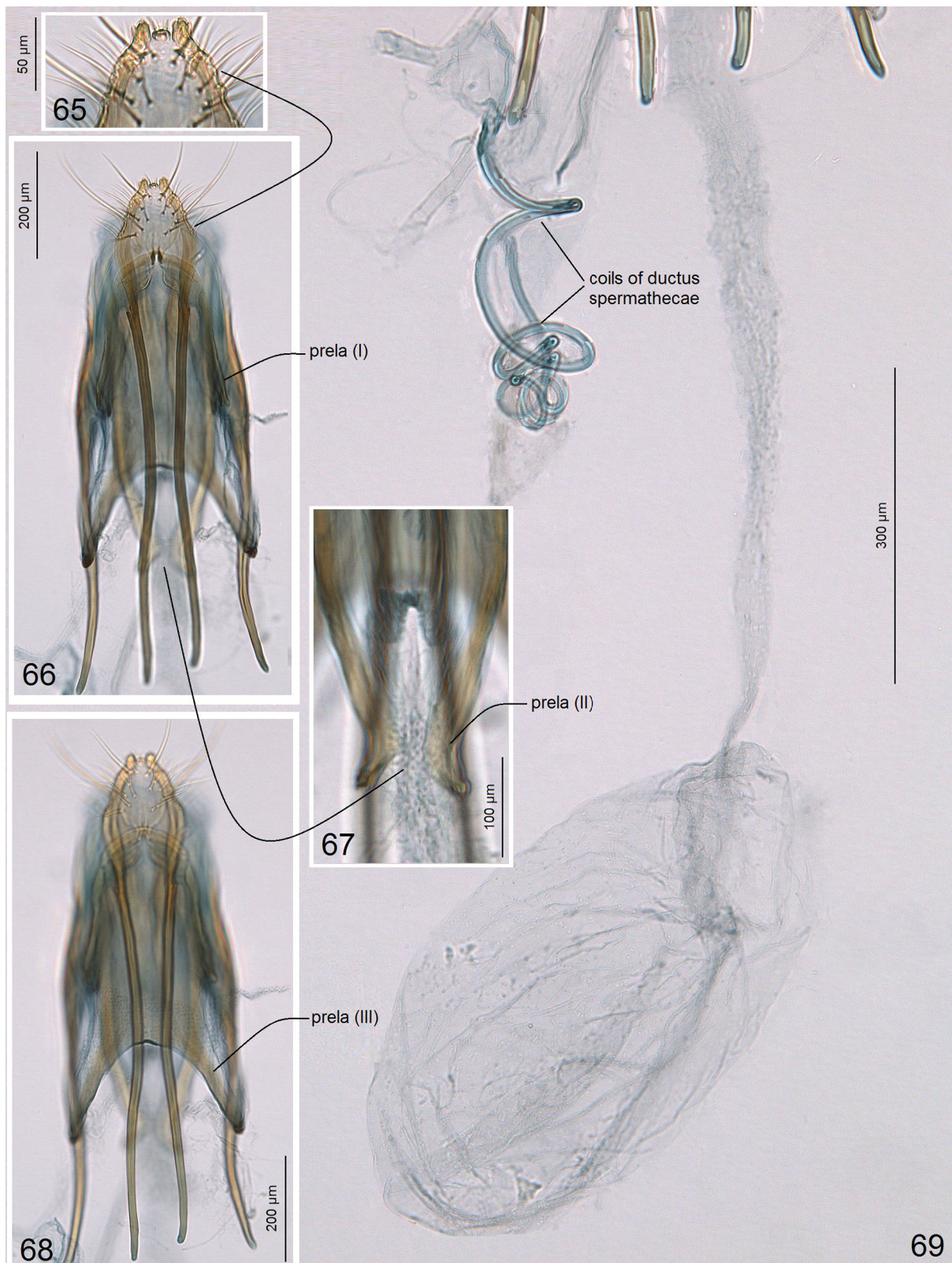
FEMALE GENITALIA (Figs 65–69). Abdominal apex slender, with two caudal papillae (Fig. 65). Genitalia 1570 µm long. Ovipositor lobes reduced (absent) (Fig. 66). Posterior and anterior apophyses almost equal in length (Figs 66, 68); prela comprised of three pairs of rod-like projections (Figs 66–68). Corpus bursae very long and narrow, distally oval-shaped (Fig. 69), pectinations indistinctive. Accessory sac inconspicuous; ductus spermathecae very slender, with numerous large coils (Fig. 69).



Figs 53–59. Male genitalia of *Astrotischeria scutifera* Diškus & Stonis sp. nov. (NHMUK). **53.** Socii, holotype (genitalia slide no. 010316175). **54.** Dorsal lobe of uncus, paratype (genitalia slide no. 010316177). **55.** Ventral lobes of uncus, holotype (genitalia slide no. 010316175). **56.** General view, holotype (genitalia slide no. 010316175). **57–58.** Same, shield-like lobe of valva. **59.** Phallus, paratype (genitalia slide no. 010316177).



Figs 60–64. Male genitalia of *Astrotischeria scutifera* Diškus & Stonis sp. nov. (NHMUK). **60.** Lateral view of capsule, with phallus removed, paratype (genitalia slide no. 010316177). **61.** Median element of modified anellus (pseudotranstilla), paratype (genitalia slide no. 010316176). **62.** Same, dentate margin of dorsal lobe of valva. **63.** Same, ventral view of capsule, with phallus removed. **64.** Pseudotranstilla and dorsal lobe of valva, paratype (genitalia slide no. 010316177).



Figs 65–69. Female genitalia of *Astrotischeria scutifera* Diškus & Stonis, sp. nov., paratype (genitalia slide no. 010316179, NHMUK). **65.** Papillae of ovipositor. **66–68.** Details of prela and apophyses. **69.** Corpus bursae and coils of ductus spermathecae.

Biology

Host plant: *Sida glabra* Mill. (Malvaceae Juss.). Larvae mine leaves in September to November. The leaf mine is a white, opaque blotch; as the larva matures it causes the leaf to distort or curl. This species was listed as '*Tischeria* sp. 6' by Lewis *et al.* (2002). Of 353 mines successfully reared, 189 produced parasitoids (53.5% parasitism).

Flight period

Based on reared specimens, adults occur throughout the year.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Astrotischeria basilobata Remeikis & Stonis sp. nov.

urn:lsid:zoobank.org:act:CEC5D64C-2122-4B6B-AB16-9A6220CD8430

Figs 12–14, 70–82

Tischeria sp. 7 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the new species mostly resembles *Astrotischeria selvica* Diškus, Carvalco-Filco & Stonis, 2018 and *A. maya* Diškus & Stonis, 2018; however, the absence of a distinctive second dorsal lobe on the valva distinguishes *A. basilobata* sp. nov. from these species.

Etymology

The species name is derived from the Latin '*basis*' (a 'base') and '*lobatus*' ('lobed') in reference to the basally thickened, lobe-like structure of the anellus in the male genitalia.

Type material

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 6 Jun. 1998; O.T. Lewis leg.; mining larva on *Lasianthaea fruticosa* (L.) K.M.Becker (Asteraceae); field card no. 3303-6/6; genitalia slide no. 010316194♂; NHMUK 010289226.

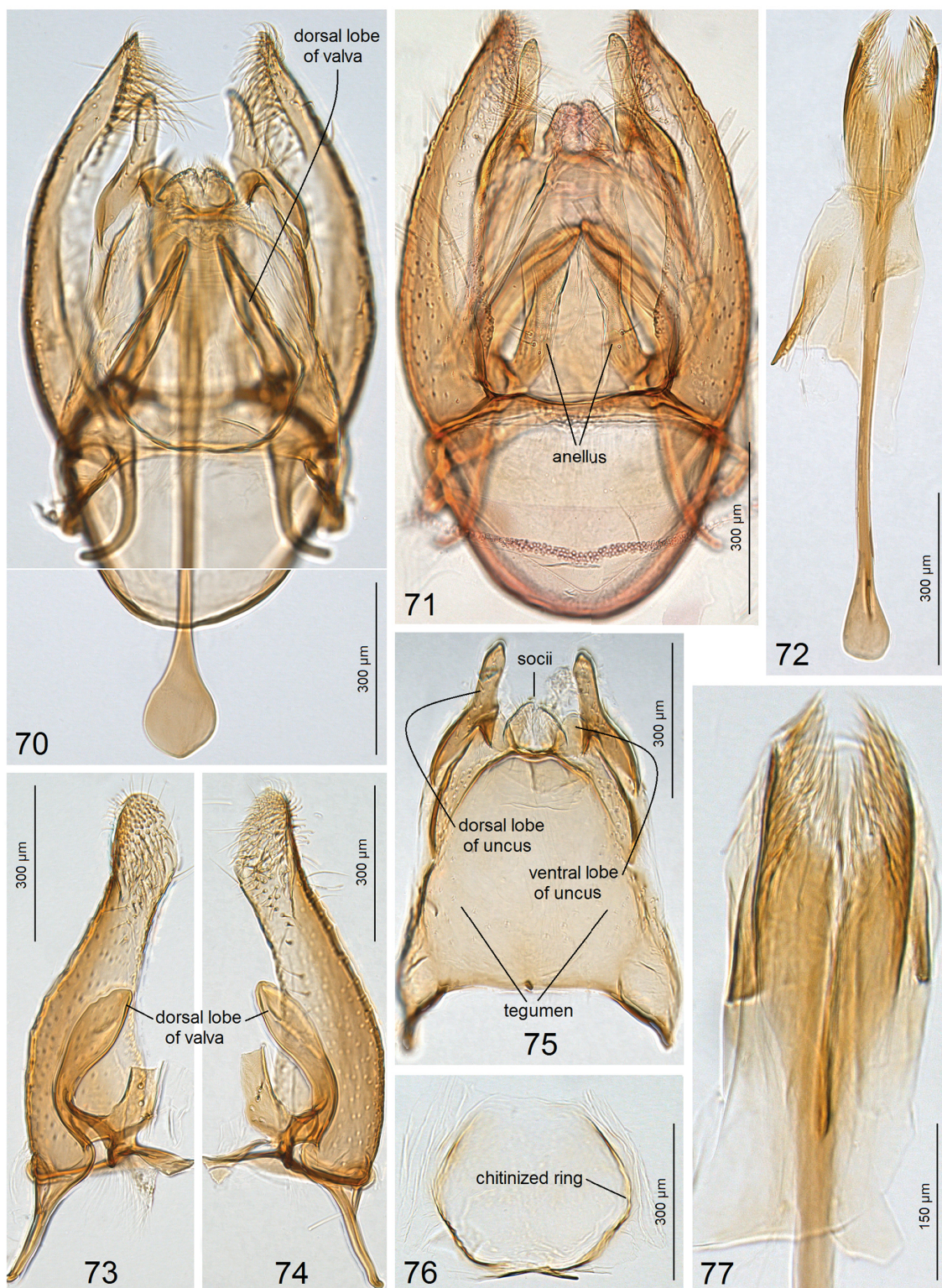
Paratypes

BELIZE • 7 ♂♂; same locality and host-plant data as for holotype; 17 Sep.–14 Oct. 1997 and 3 Apr.–30 Jun. 1998; O.T. Lewis leg.; field card nos 710-14/10♂, 38-17/9♂, 3537-10/6♂, 4422-30/6♂, 34.019-3/4♂, 289-25/9♂, 3536-10/6♂; genitalia slide nos 010316195♂, 010316196♂, 010316197♂, 010316198♂, 010316224♂; NHMUK 010289227 to 010289233.

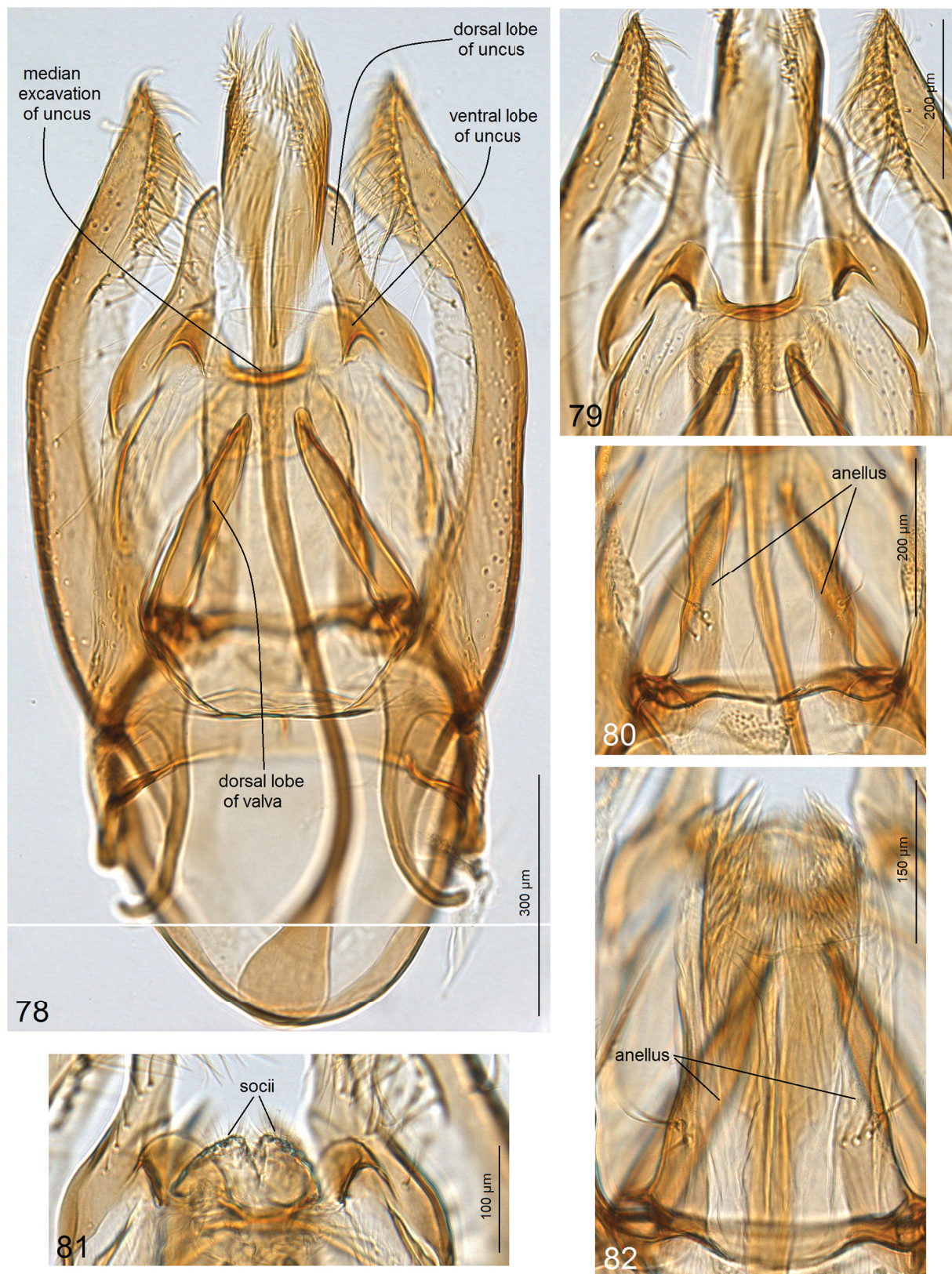
Description

Male

EXTERNAL CHARACTERS (Figs 12–14). Forewing length 2.6–3.1 mm; wingspan 5.5–6.6 mm (n = 7). Head: palpus yellowish cream, frons yellow ochre, smoothly scaled; frontal tuft and collar comprised of golden yellow or yellow-ochre to pale grey, slender, lamellar scales; antenna exceeding ½ of forewing; flagellum yellow cream, annulated with pale brown scales. Thorax ochre-yellow, medially covered with pale brown, cream-tipped scales; tegula covered with a mixture of ochre-yellow and pale brown



Figs 70–77. Male genitalia of *Astrotischeria basilobata* Remeikis & Stonis sp. nov. (NHMUK). **70.** Capsule, with phallus inside, holotype (genitalia slide no. 010316194). **71.** Capsule, with phallus removed, paratype (genitalia slide no. 010316198). **72.** Phallus, paratype (genitalia slide no. 010316196). **73–74.** Main element and dorsal lobe of valva, with anellus broken, paratype (genitalia slide no. 010316197). **75.** Same, uncus and tegumen. **76.** Same, chitinized ring of anellus. **77.** Same, apex of phallus.



Figs 78–82. Male genitalia of *Astrotischeria basilobata* Remeikis & Stonis sp. nov. (NHMUK). **78.** Capsule, with phallus inside, paratype (genitalia slide no. 010316195). **79.** Same, ventral lobe of uncus. **80.** Same, anellus. **81.** Socii, holotype (genitalia slide no. 010316194). **82.** Same, anellus.

scales or entirely covered with pale brown, cream-tipped scales. Forewing ochre-yellow with irregular markings of dark brown or black-brown scales; fringe pale brown, ochre-yellow apically; fringe line indistinctive or absent; forewing underside grey-brown to pale grey-brown, without spots or androconia. Hindwing pale brown; fringe brownish cream to pale brown with reddish tint, without androconia. Legs ochre cream, densely speckled or entirely covered with pale grey-brown scales on upper side. Abdomen dark brown to brown with some purple and green iridescence on upper side, yellowish ochre, annulated with dark brown scales on underside; genital plates yellowish cream; dorsal anal tuft large, comprised of ochre cream piliform scales.

MALE GENITALIA (Figs 70–82). Capsule 995–1170 μm long, 600–615 μm wide. Uncus with long, undivided dorsal lobes (Figs 75, 78), very short, rounded ventral lobes (Figs 75, 78) and wide medial excavation (Fig. 78). Valva 615–770 μm long, with a large dorsal lobe (Figs 70, 78); second dorsal lobes undeveloped, but anellus laterally thickened and, when broken, some development of second dorsal lobes can be observed (Figs 73–74). Anellus (Figs 71, 82) with four papillae laterally (Figs 80, 82); transtilla absent. Ventral lobe of vinculum large, distally widely rounded (Figs 70–71, 78). Phallus (Fig. 72) 1130–1140 μm long, apically bifid, with two clusters of long, slender spines (Figs 77), basally widened (Figs 70, 72, 78).

Female

Unknown.

Biology

Host plant: *Lasianthaea fruticosa* (L.) K.M.Becker (Asteraceae). Larvae mine leaves year-round. The leaf mine is a translucent blotch, not usually at the leaf margin, but the biology of this species is otherwise unknown. This species was listed as '*Tischeria* sp. 7' by Lewis *et al.* (2002), a morphospecies name which incorrectly grouped this species with *A. papilloma* sp. nov., which shares the larval host plant. Retrospectively, records of these two species can now be distinguished based on the appearance of the leaf mines.

Flight period

Based on reared specimens, adults occur throughout the year.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Astrotischeria selvica Diškus, Carvalho-Filho & Stonis, 2018
Figs 15, 83–84

Astrotischeria selvica Diškus, Carvalho-Filho & Stonis in Stonis *et al.*, 2018a: 36–37, figs 93–126.

Tischeria sp. 1 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, *Astrotischeria selvica* resembles the Central American *A. basilobata* sp. nov. and particularly *A. maya* Diškus & Stonis, 2018. From the latter *A. selvica* differs by the horn-like, apically pointed dorsal lobe of the valva and the distinctly wide gap between the median lobes of the uncus; from *A. basilobata*

sp. nov. *A. selvica* differs by the presence of two distinctive dorsal lobes on the valva (in *A. basilobata* sp. nov. only one dorsal lobe is distinctive). The fact that *A. selvica* feeds on *Synedrella* Gaertn., *Sphagneticola* O.Hoffm. and *Tilesia* G.Mey. also makes this species rather unique; however, host-plant data may not be valid for species differentiation because the biology of many other species of *Astrotischeria* is still incompletely known or, in some cases, totally unstudied.

Material examined

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 4 Nov. 1997; O.T. Lewis leg.; mining larva on *Sphagneticola trilobata* (L.) Pruski (Asteraceae); field card no. 1406-4/11; genitalia slide no. 010316213♂ (former no. AD920); NHMUK 010289234.

Paratypes

BELIZE • 2 ♂♂; 7 ♀♀; same locality and host-plant data as for holotype; 1 Oct. 1997 and 10 Jun.–14 Aug. 1998; O.T. Lewis leg.; field card nos 358, 359, 1403 to 1405, 4273, 3524, 5380, 3804; genitalia slide nos 010316214♂ (former no. AD298), 010316215♂ (former no. AD919); 010316217♀ (former no. AD921); NHMUK 010289235 to 010289243.

Description

This species was described and illustrated by Stonis *et al.* (2018a: 36–37, figs 93–126).

Biology

Host plants, all members of Asteraceae: *Sphagneticola trilobata* (L.) Pruski and *Synedrella nodiflora* (L.) Gaertn. in Central America, *Tilesia baccata* (L.) Pruski along with the main host plant *Synedrella nodiflora* in Brazil. Leaf mines were illustrated by Stonis *et al.* (2018a: figs 122–126). This species was listed as '*Tischeria* sp. 1' by Lewis *et al.* (2002) who found that, at Las Cuevas, the rate of parasitism was 24% (6 out of 25 mines reared successfully were parasitized).

Flight period

Adults are known from February, April, June–July, and October–November; based on reared specimens from Las Cuevas, adults are likely to occur year-round in Belize.

Distribution

Currently known from Central America (Belize and Guatemala), the Caribbean (U.S. Virgin Islands) and equatorial Brazil (State of Pará) (Stonis *et al.* 2018a).

Astrotischeria casila Diškus & Stonis, 2018

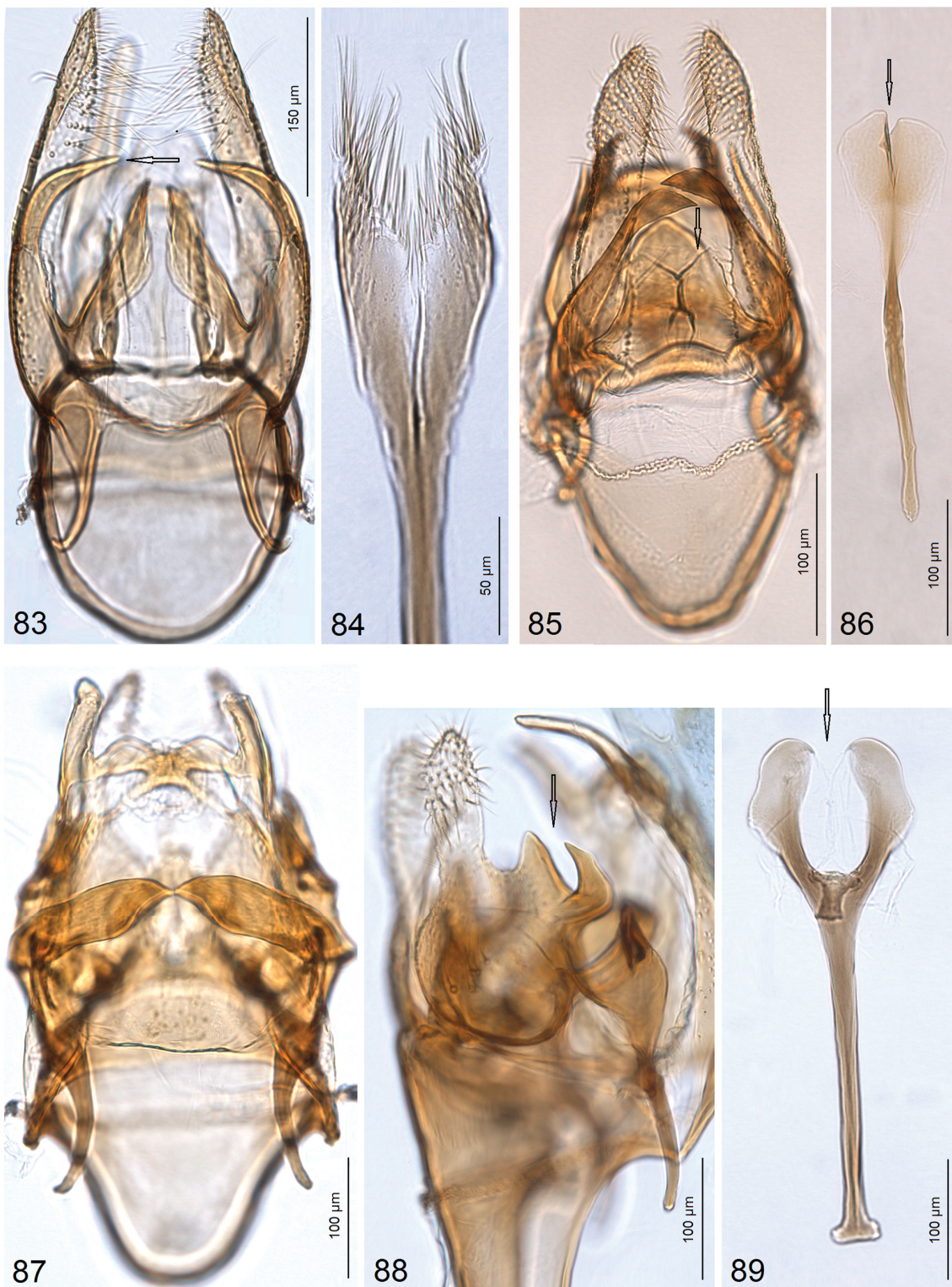
Figs 16, 85–86

Astrotischeria casila Diškus & Stonis in Stonis *et al.*, 2018a: 37, 43, figs 127–159.

Tischeria sp. 9 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the combination of a unique, helmet-like anellus, a large dorsal lobe on the uncus and weakly divided apical lobes of the phallus in the male genitalia distinguishes *A. casila* from all other congeneric species.



Figs 83–89. Male genitalia of *Astrotischeria* spp. (NHMUK). **83.** *A. selvica* Diškus, Carvalho-Filho & Stonis, 2018, capsule with phallus removed, holotype (genitalia slide no. AD920). **84.** Same, phallus, paratype (genitalia slide no. AD919). **85.** *A. casila* Diškus & Stonis, 2018, capsule with phallus removed, holotype (genitalia slide no. AD939). **86.** Same, phallus. **87.** *A. furcata* Diškus & Stonis, 2018, capsule with phallus removed, holotype (genitalia slide no. AD925). **88.** Same, lateral view of capsule. **89.** Same, phallus.

Material examined

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 29 Jun. 1998; O.T. Lewis leg.; mining larvae on *Montanoa atriplicifolia* (Pers.) Sch.Bip. (Asteraceae); field card no. 3954-29/6; genitalia slide no. 010316219♂ (former no. AD939); NHMUK 010289244.

Paratypes

BELIZE • 9 ♂♂, 6 ♀♀; same locality and host-plant data as for holotype; 2 Apr. 1998 and 13 Jun.–12 Jul. 1998; O.T. Lewis leg.; field card nos 2850, 3676 to 3679, 3944, 3953, 4202, 4247, 2.096, 3.030, 23.029, 27.046, 30.026; genitalia slide nos 010316220♂ (former no. AD849), 010316221♂ (former no. AD295), 010316223♀ (former no. AD940); NHMUK 010289245 to 010289253 and NHMUK 010289255 to 010289260 • 1 ♂; Cayo District, San Ignacio, secondary forest; 17°09'15" N, 89°04'04" W; alt. 85 m; 17–18 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 010316222♂ (former no. AD934); NHMUK 010289254.

Description

The species was described and illustrated by Stonis *et al.* (2018a: 37, 43, figs 127–159).

Biology

Host plant: *Montanoa atriplicifolia* (Pers.) Sch.Bip. (Asteraceae). The leaf mine is a blotch which forms a translucent window in the leaf. This species was listed as '*Tischeria* sp. 9' by Lewis *et al.* (2002). Of 213 mines reared successfully, 59 (27.7%) produced parasitoids.

Flight period

Based on reared specimens from Las Cuevas, adults occur during April and June–October.

Distribution

Currently known only from the Cayo District of Belize (Las Cuevas and San Ignacio).

Astrotischeria furcata Diškus & Stonis, 2018
Figs 17, 87–89

Astrotischeria furcata Diškus & Stonis in Stonis *et al.*, 2018a: 49, figs 176–189.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the combination of a wide uncus, uniquely shaped dorsal lobes on the valva and the widely divided apex of the phallus distinguishes *A. furcata* from all other congeneric species.

Material examined

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 3–16 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 010316212♂ (former no. AD925); NHMUK 010289261.

Description

This species was described and illustrated by Stonis *et al.* (2018a: 49, figs 176–189).

Biology

Host plant: unknown.

Flight period

Based on a single specimen collected at light, adults occur in April.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Genus *Paratischeria* Diškus & Stonis, 2017

Paratischeria robinsoni Diškus & Stonis sp. nov.

urn:lsid:zoobank.org:act:655A3435-7DF0-408C-B0F0-A7A86C381B93

Figs 18–20, 90–106

Tischeria sp. 5 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the unique four-lobed uncus (Fig. 97) and the presence of pectens on the valva (Fig. 96) distinguish *Paratischeria robinsoni* sp. nov. from other congeneric species. In the female genitalia, the combination of a specific shape of prela (Fig. 101), large ovipositor lobes, densely covered with peg setae (Fig. 103), and a dentate thickening on the tergum (Figs 104–105) is hypothesized to be unique to this species. The Asteraceae host plant, *Otopappus verbesinoides* Benth., make this species unique in the Neotropical fauna.

Etymology

This species is named after the late Dr Gaden Sutherland Robinson (1949–2009), former curator and leading research scientist at the Natural History Museum, London, our former colleague and friend, and one of the greatest professionals on systematics and biodiversity. The first author is indebted to Gaden S. Robinson for his principal role in facilitating R. Puplesis' fieldwork at Las Cuevas (1998).

Type material

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 4 Jul. 1998; O.T. Lewis leg.; mining larva on *Otopappus verbesinoides* Benth. (Asteraceae); field card no. 30.035-4/7; genitalia slide no. 010316187♂; NHMUK 010289262.

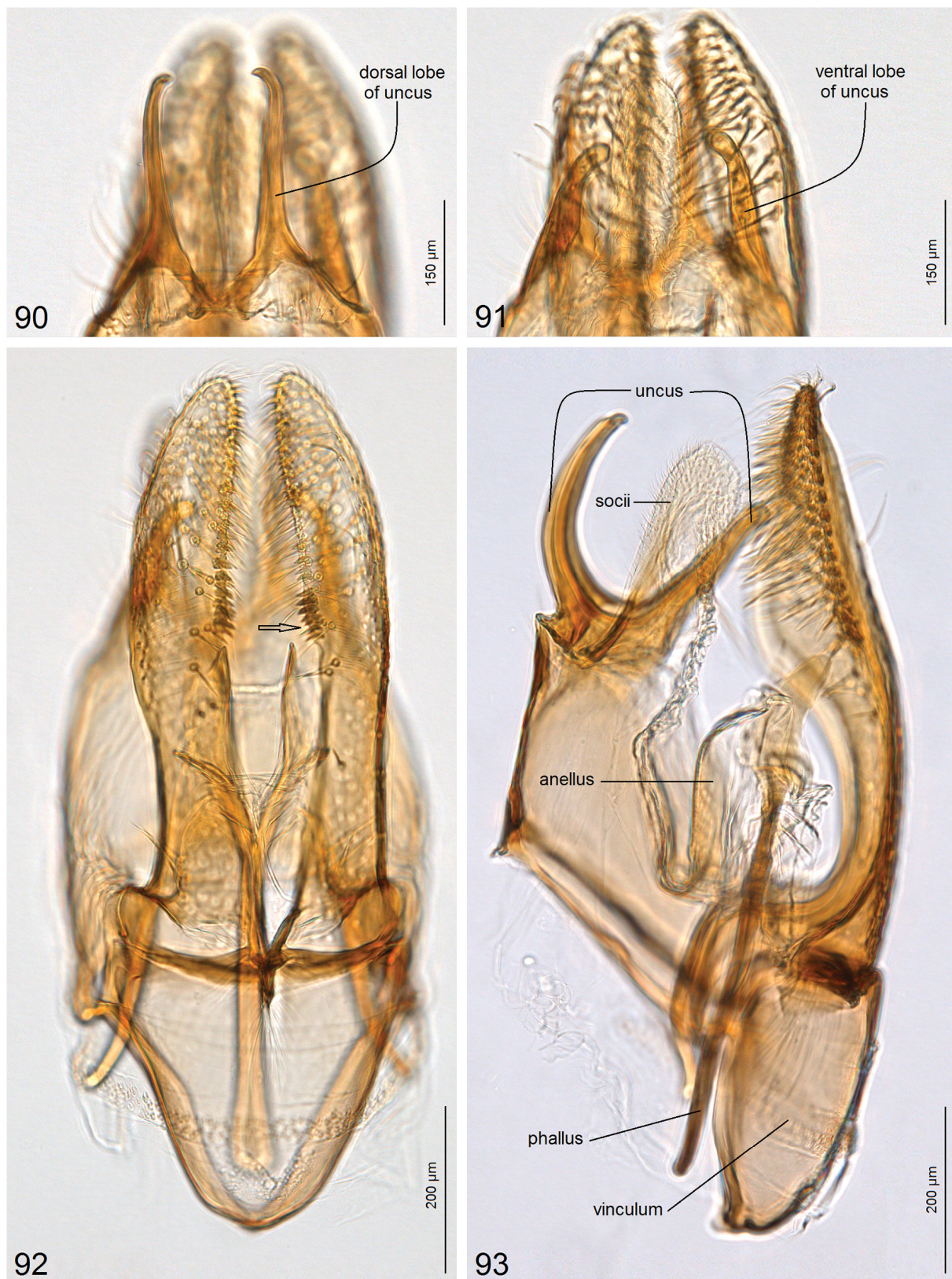
Paratypes

BELIZE • 3 ♂♂, 6 ♀♀; same collection data as for holotype; 5 Nov. 1997 and 11 Feb.–14 Jul. 1998; field card nos 23.048-14/7♂, 3.032-14/6♂, 25.054-7/3♂, 1540-5/11♀, 25.058-11/2♀, 25.057-11/2♀, 30.036-4/7♀, 25.056-11/2♀, 1541-5/11♀; genitalia slide nos 010316188♂, 010316190♂, 010316191♂, 010316189♀, 010316192♀; NHMUK 010289263 to 010289271.

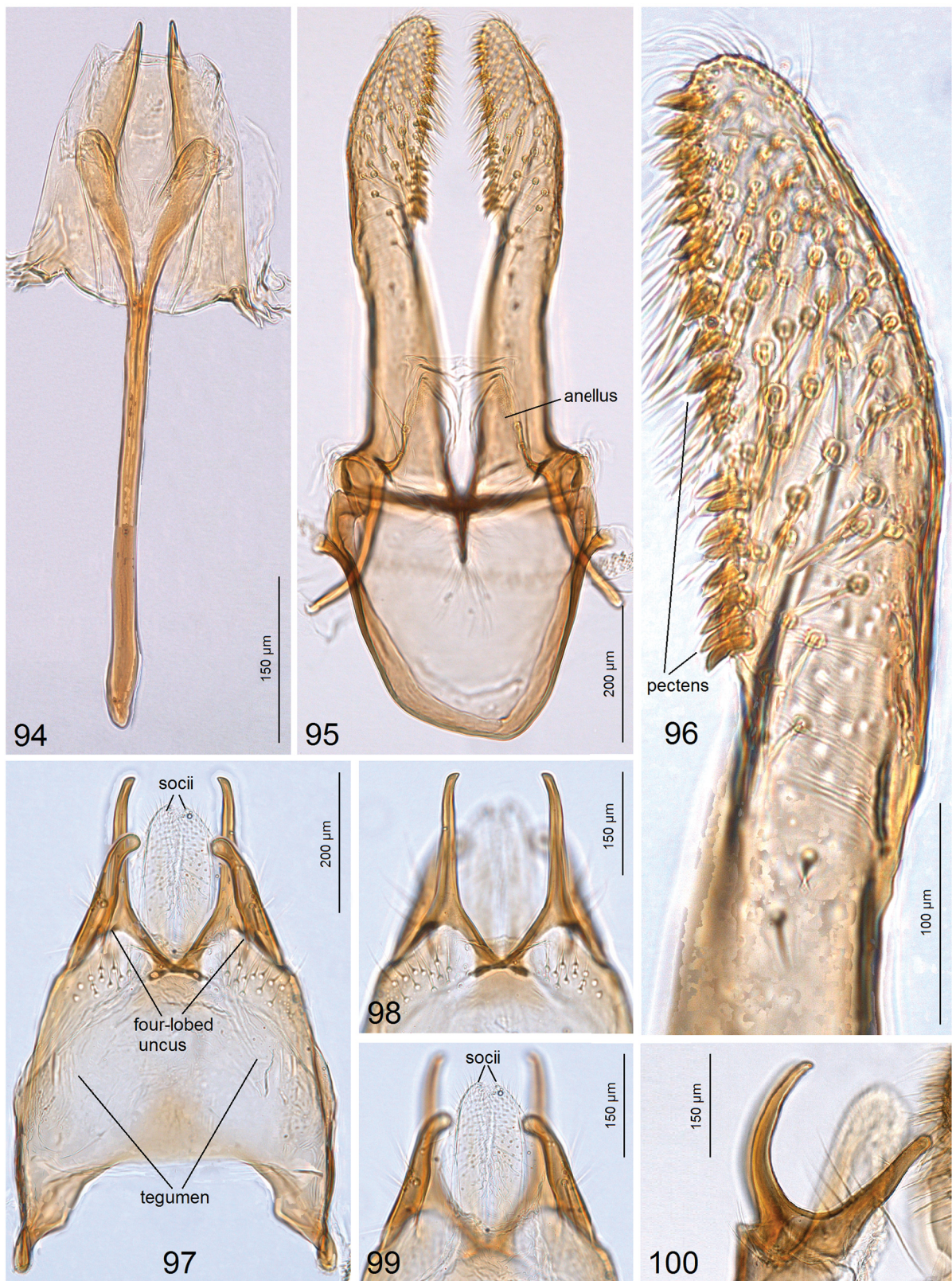
Description

Male

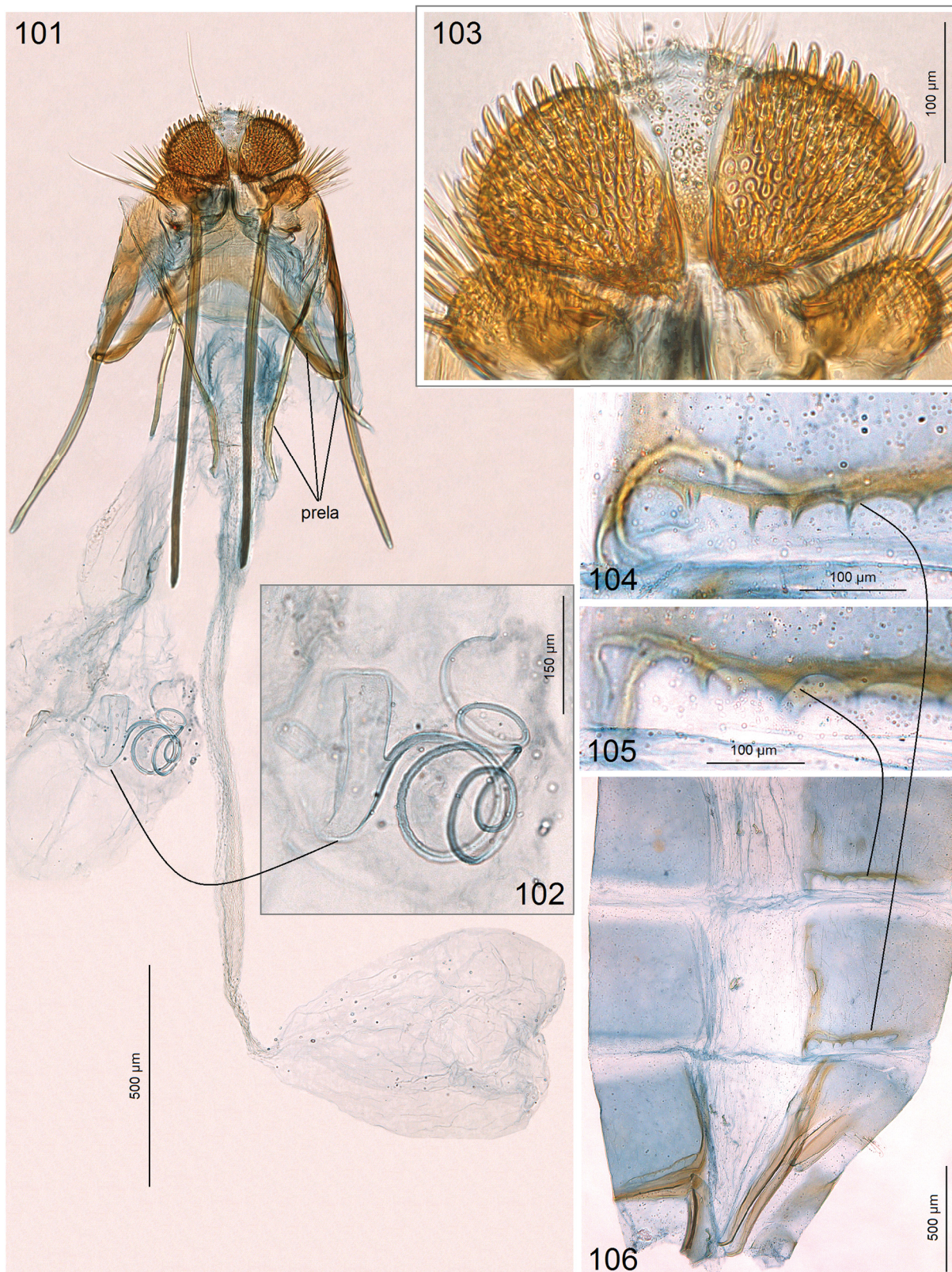
EXTERNAL CHARACTERS (Fig. 18). Forewing length 2.6–3.0 mm; wingspan 5.5–6.3 mm (n = 4). Head: palpus, pecten and frons ochre cream; frontal tuft and collar comprised of ochre cream and some brown-



Figs 90–93. Male genitalia of *Paratischeria robinsoni* Diškus & Stonis sp. nov., holotype (genitalia slide no. 010316187, NHMUK). **90.** Uncus, dorsal lobes. **91.** Uncus, ventral lobes. **92.** Capsule with phallus inside, ventral view. **93.** Capsule with phallus inside, lateral view.



Figs 94–100. Male genitalia of *Paratischeria robinsoni* Diškus & Stonis sp. nov., paratype (genitalia slide no. 010316191, NHMUK). **94.** Phallus. **95.** Capsule, with uncus, tegumen and phallus removed. **96.** Apical part of valva. **97.** Uncus, socii and tegumen. **98.** Uncus, dorsal lobes. **99.** Uncus, ventral lobes and socii. **100.** Uncus, ventral lobes and socii, lateral view.



Figs 101–106. Female genitalia of *Paratischeria robinsoni* Diškus & Stonis sp. nov., paratype (genitalia slide no. 010316192, NHMUK). **101.** General view. **102.** Coils of ductus spemathecae. **103.** Ovipositor lobes. **104–106.** Dentate thickenings on tergum.

grey slender lamellar scales; antenna exceeding $\frac{1}{2}$ of forewing; flagellum yellowish ochre, irregularly annulated with grey-black scales. Thorax yellowish ochre with some grey-brown scales; tegula covered either with grey-brown or mixture of yellow-ochre and grey-brown scales. Forewing yellow-ochre with irregular markings of brown-black scales; fringe yellowish brown, apically yellow-ochre; fringe line absent or indistinctive; forewing underside grey-brown, without spots or androconia. Hindwing grey-brown on upper side and underside, without androconia, fringe pale grey-brown. Legs: foreleg and midleg dark grey-brown; hindleg ochre-cream with grey and brown scales and some purple iridescence. Abdomen grey-brown with some purple iridescence on upper side, brownish or yellow-ochre with some grey-brown scales on underside; genital plates pale grey to greyish cream; anal tufts grey.

MALE GENITALIA (Figs 90–100). Capsule 980–990 μm long, 435–490 μm wide. Uncus with four long, slender lobes: two dorsal and two ventral (Figs 90–91, 93, 97–100). Valva about 695 μm long, apically with thickened, tooth-like pectens (Fig. 96); anellus membranous (Figs 93, 95); transtilla and juxta absent. Ventral lobe of vinculum large, distally truncated or rounded (Figs 92–93). Phallus 540–640 μm long, apically divided, with lateral lobes (Fig. 94).

Female

EXTERNAL CHARACTERS (Figs 19–20). Forewing length 3.0–3.9 mm; wingspan 6.5–8.1 mm ($n = 6$). Abdomen without anal tufts. Otherwise, similar to male.

FEMALE GENITALIA (Figs 101–106). Total length about 2990 μm . Ovipositor lobes very large (Fig. 103), densely covered with modified setae ('peg setae'); area between ovipositor lobes widely rounded, with tiny papillae and two very long setae. Second pair of lobes, lateral and anterior to ovipositor lobes, much smaller than ovipositor lobes, elongated and bearing long slender setae, without stout 'peg setae'. Posterior and anterior apophyses almost equal in length (Fig. 101); prela comprised of three pairs of rod-like projections (Fig. 101). Proximally, corpus bursae very slender, with numerous fine spines, distally oval-shaped, without pectinations. Ductus spermathecae very slender, with 5–6 large coils (Fig. 102). Abdominal wall with slender, dentate thickenings on tergum (Figs 104–106).

Biology

Host plant: *Otopappus verbesinoides* Benth. (Asteraceae). Larvae mine leaves in February–March and June–November. The leaf mine is a transparent, window-like blotch. This species was listed as '*Tischeria* sp. 5' by Lewis *et al.* (2002). Of 40 mines reared successfully, 9 (22.5%) produced parasitoids.

Flight period

Based on rearing data, adults are likely to occur throughout much of the year.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Paratischeria tubifex Diškus & Stonis sp. nov.

urn:lsid:zoobank.org:act:91DCD98C-A844-431A-A844-D3849FF1DE9B

Figs 21–23, 107–123

Tischeria sp. 4 – Lewis *et al.* 2002: 872.

Diagnosis

External characters and characters of the female genitalia are of little or no use in the identification of this species. However, in the male genitalia, the very unusual, wide valva (Fig. 108), apically covered

with modified, spine-like setae (Fig. 110), the unusually large tube-like socii (Figs 113–114), and the large, deeply divided uncus (Fig. 114) instantly distinguish *Paratischeria tubifex* sp. nov. from other Tischeriidae. The host plant, *Lasianthaea fruticosa* (Asteraceae), coincides with the host plant of another new species, *Astrotischeria papilloma* sp. nov., described above.

Etymology

The species name is derived from the Latin ‘*tubus*’ (‘tube’) and ‘*fex*’, i.e., from the Latin ‘*facere*’ (‘to make’) in reference to the unusually large, tube-like socii in the male genitalia.

Type material

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 6 Apr. 1998; O.T. Lewis leg.; mining larva on *Lasianthaea fruticosa* (L.) K.M.Becker (Asteraceae); field card no. 3009-6/4; genitalia slide no. 010316168♂; NHMUK 010289272.

Paratypes

BELIZE • 6 ♂♂, 3 ♀♀; same collection data as for holotype; 11 Feb.–24 Apr. 1998; O.T. Lewis leg.; field card nos 3013-6/4♂, 25.053-11/2♂, 3014-6/4♂, 3016-6/4♂, 17.073-4/3♂, 17.079-4/3♂, 3010-6/4♀, 3007-24/4♀, 3015-6/4♀; genitalia slide nos 010316169♂, 010316170♂, 010316171♂, 010316173♀; NHMUK 10289273, 10289274, 10289276 to 010289282 • 1 ♂; same locality as for holotype; 3–16 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 010316172♂; NHMUK 010289275.

Description

Male

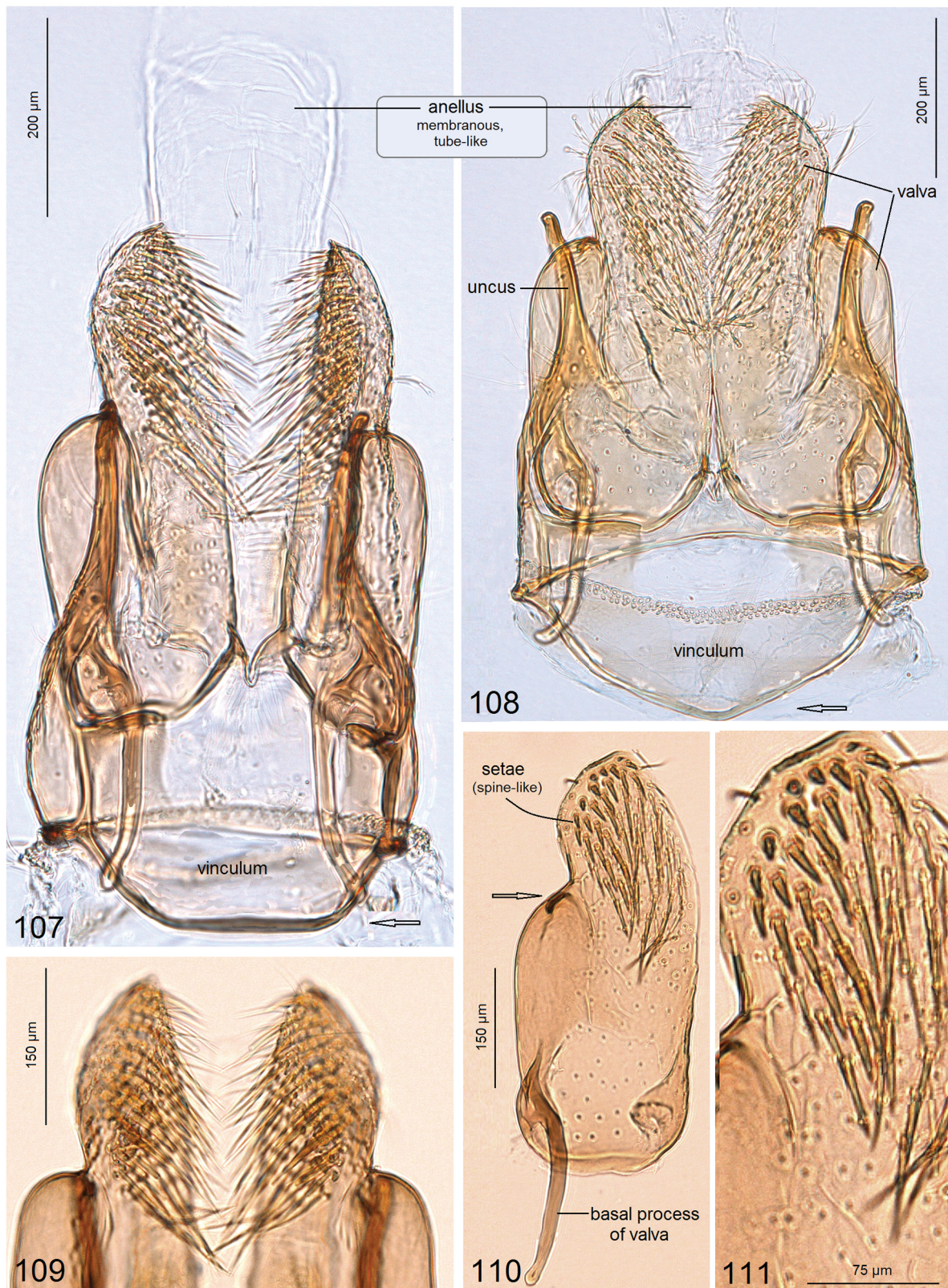
EXTERNAL CHARACTERS (Figs 21, 23). Forewing length 2.4–2.7 mm; wingspan 5.4–5.8 mm (n = 8). Head: palpus, pecten and frons golden cream; frontal tuft and collar yellowish cream, comprised of slender lamellar scales; antenna length ½ of forewing; flagellum golden cream, with a few irregularly scattered brown scales on upper side. Thorax yellowish cream, glossy; tegula covered with yellowish cream and pale brown-grey scales. Forewing yellowish ochre with irregular makings of grey-brown scales; fringe yellowish cream; fringe line usually distinctive, formed by blackish brown scales; forewing underside densely covered with grey scales, without spots or androconia. Hindwing grey to yellowish grey on upper side and underside, without androconia, fringe pale grey to ochre-grey or ochre cream. Legs glossy, yellowish cream, densely covered with blackish brown scales on foreleg and midleg upper side. Abdomen glossy, with some purple iridescence; pale grey, silvery glossy on upper side, yellowish cream, annulated with pale grey-brown scales on underside; genital plates cream; anal tufts large, cream.

MALE GENITALIA (Figs 107–117). Capsule 450–610 µm long, 390–520 µm wide. Uncus large, deeply divided, with two lateral lobes (Figs 112, 114). Socii unusually large, tube-like (Figs 112–114). Valva (Fig. 108) about 445–530 µm long, basally very wide, with a tiny process (Figs 110, 112), apically with thickened setae (Figs 110–111); anellus membranous, indistinctive; transtilla and juxta absent. Ventral lobe of vinculum short, distally truncated or rounded (Figs 107, 112, 114). Phallus 2520 µm long, apically with three pointed lobes (Figs 115–117).

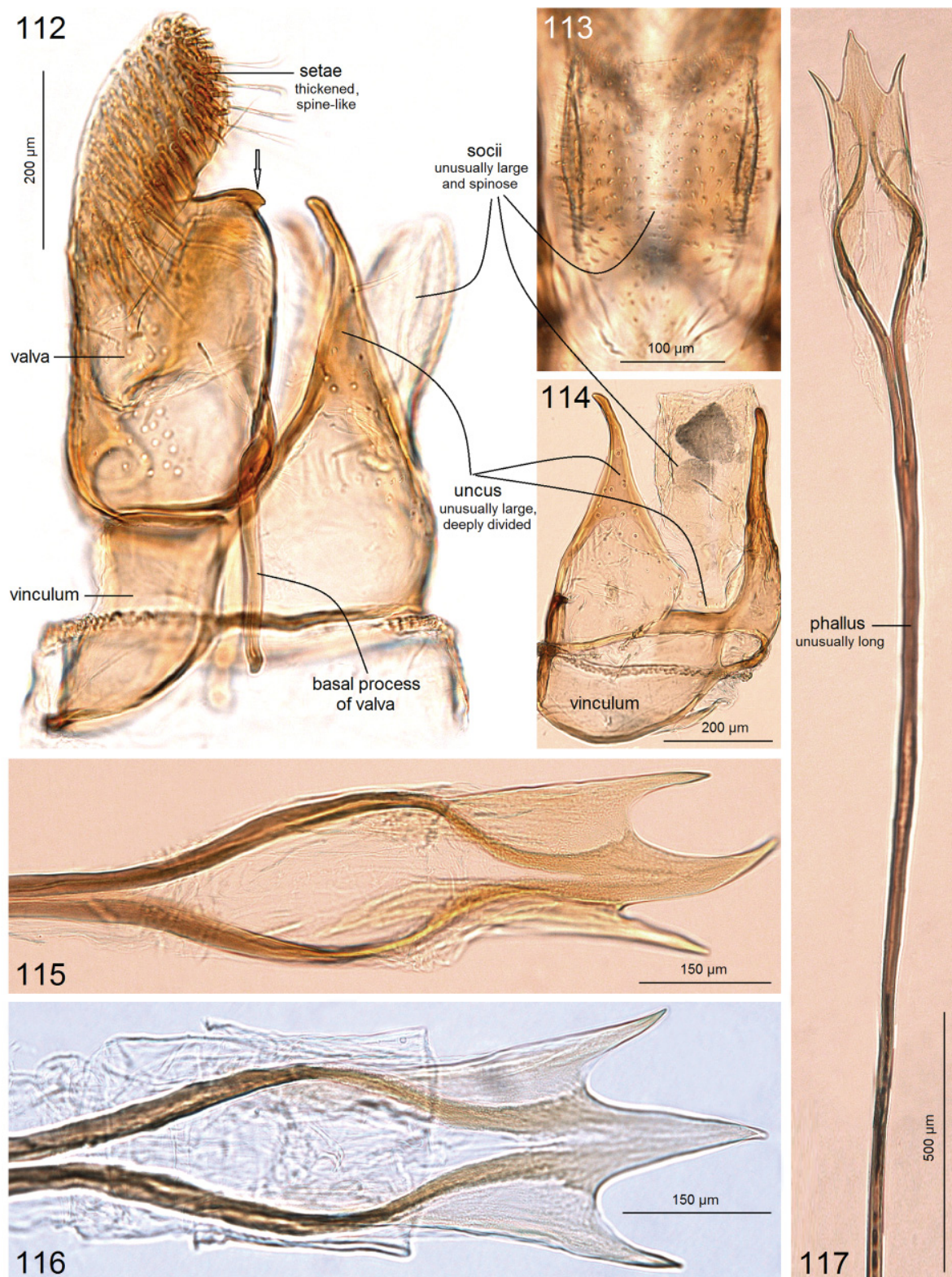
Female

EXTERNAL CHARACTERS (Fig. 22). Abdomen without anal tufts. Otherwise, similar to male.

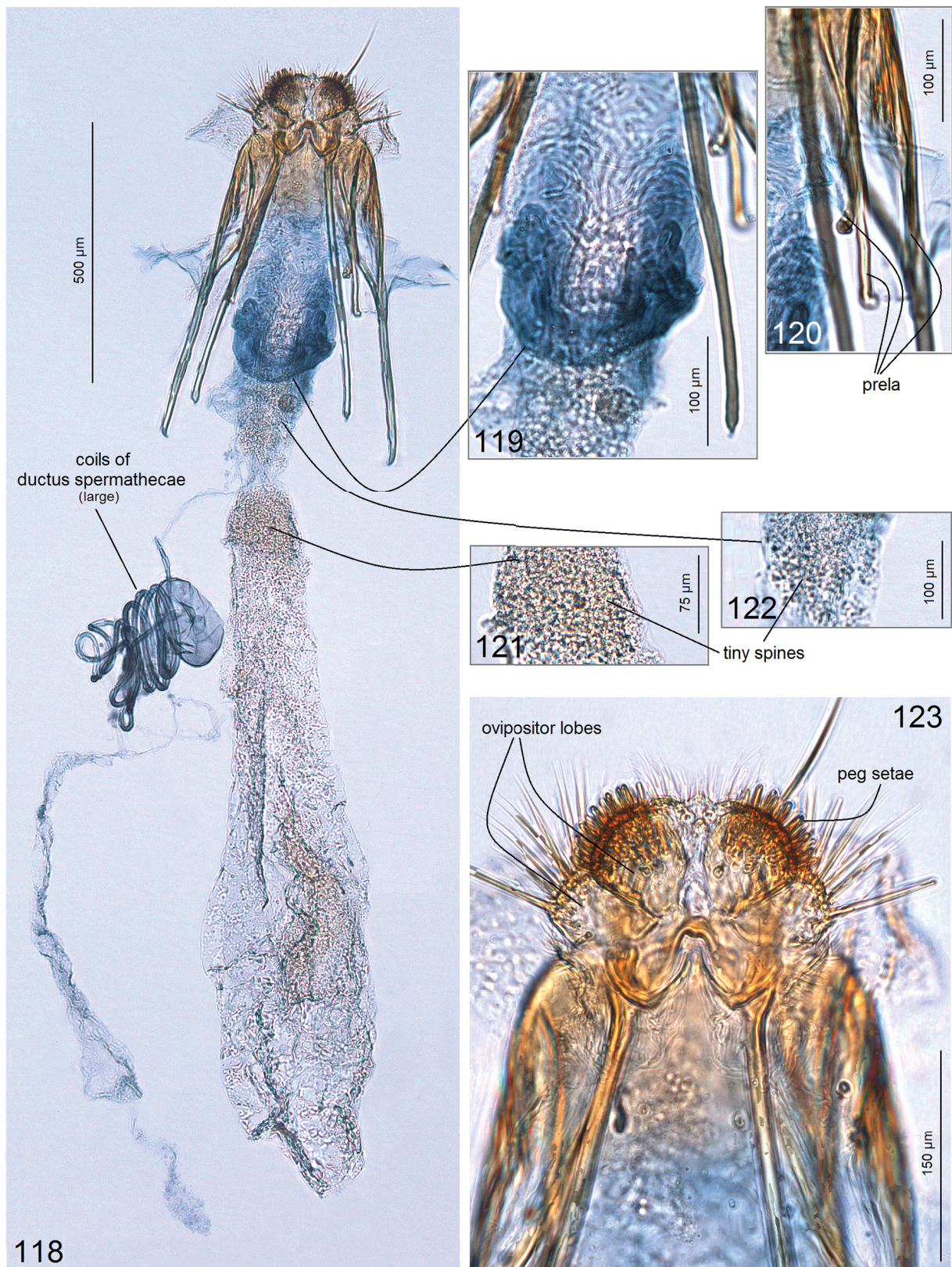
FEMALE GENITALIA (Figs 118–123). Total length about 2140 µm. Ovipositor lobes large (Fig. 123), with modified setae (‘peg setae’); area between ovipositor lobes widely rounded, with tiny papillae and two very long setae. Second pair of lobes, lateral and anterior to ovipositor lobes, much smaller than ovipositor lobes, oval, bearing long slender setae, without stout ‘peg setae’. Anterior apophyses slightly longer than posterior apophyses (Fig. 118); prela comprised of three pairs of rod-like projections



Figs 107–111. Male genitalia of *Paratischeria tubifex* Diškus & Stonis sp. nov. (NHMUK). **107.** Capsule, with phallus removed, holotype (genitalia slide no. 010316168). **108.** Capsule with phallus removed, paratype (genitalia slide no. 010316171). **109.** Apical parts of valvae, paratype (genitalia slide no. 010316172). **110–111.** Valva, paratype (genitalia slide no. 010316169).



Figs 112–117. Male genitalia of *Paratischeria tubifex* Diškus & Stonis sp. nov. (NHMUK). **112.** Lateral view of capsule with phallus removed, paratype (genitalia slide no. 010316170). **113.** Socii, paratype (genitalia slide no. 010316172). **114.** Uncus, socii and vinculum, ventro-lateral view, paratype (genitalia slide no. 010316169). **115.** Same, apex of phallus. **116.** Apex of phallus, paratype (genitalia slide no. 010316170). **117.** Phallus, general view, holotype (genitalia slide no. 010316168).



Figs 118–123. Female genitalia of *Paratischeria tubifex* Diškus & Stonis sp. nov., paratype (genitalia slide no. 010316173, NHMUK). **118.** General view. **119–122.** Details. **123.** Ovipositor lobes.

(Fig. 120). Proximal, slender part of corpus bursae with numerous spines (Figs 121–122), gradually expanding into slightly wider, distal part; pectination of latter indistinctive. Ductus spermathecae very slender, with about 6–8 large coils (Fig. 118).

Biology

Host plant: *Lasianthaea fruticosa* (L.) K.M.Becker (Asteraceae). Larvae mine leaves in February–April. The leaf mine is a blotch (unstudied and undocumented). This species was listed as ‘*Tischeria* sp. 4’ by Lewis *et al.* (2002). Of 29 mines reared successfully, none were parasitised.

Flight period

Based on a single specimen collected at light, adults fly in April; based on rearing data, adults occur in February–September.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Paratischeria belizensis Remeikis & Stonis sp. nov.

urn:lsid:zoobank.org:act:1182B62C-7E7E-4EA8-866C-BCF6578F9F34

Figs 24–25, 124–127

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the phallus being fused with the anellus, with two apical, pointed lobes (Figs 124, 127), and the elaborated uncus (Fig. 125) distinguish *Paratischeria belizensis* sp. nov. from other congeneric species.

Etymology

This species is named after Belize where it occurs.

Type material

Holotype

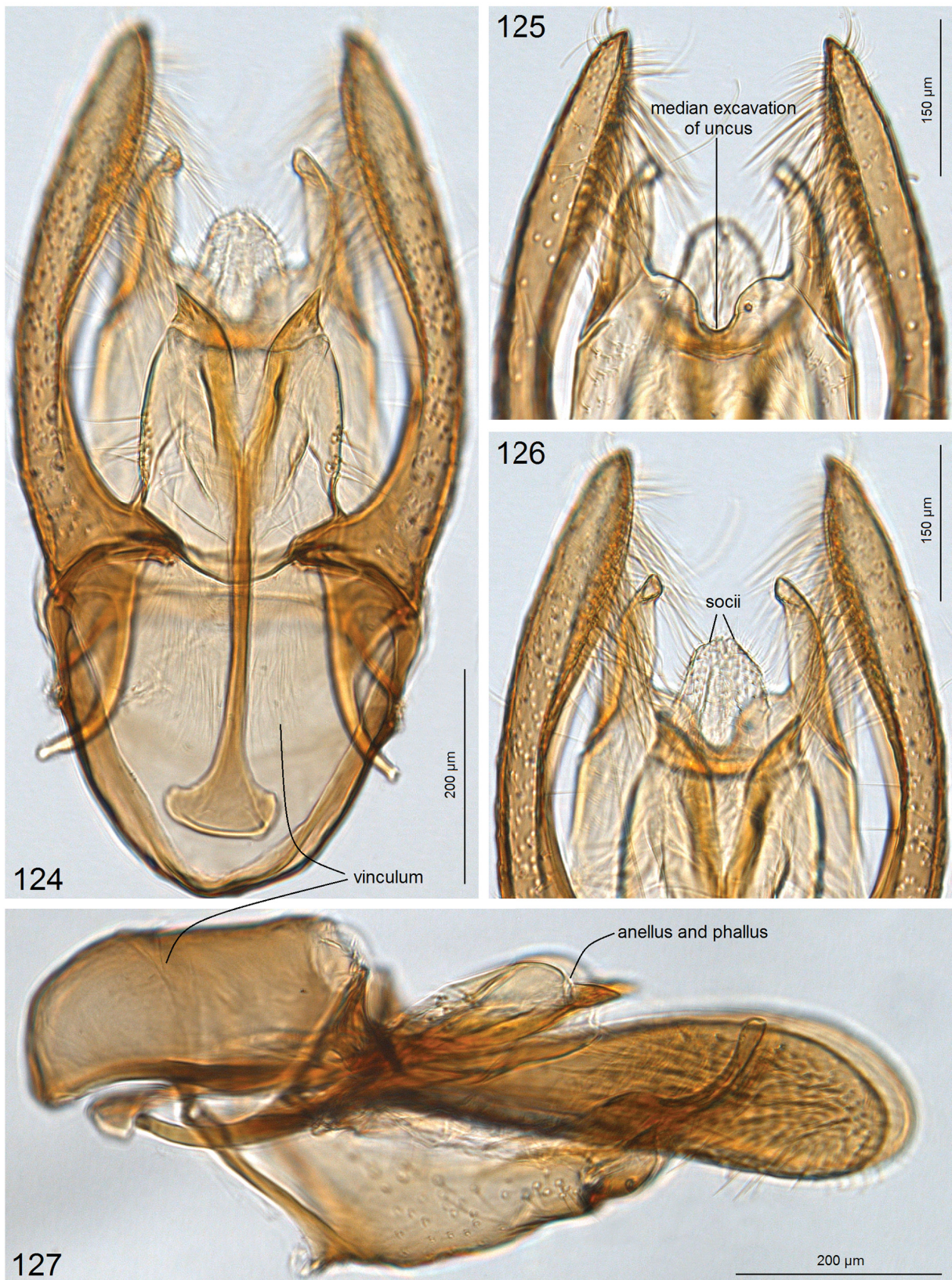
BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 3–16 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 010316193♂; NHMUK 010289283.

Description

Male

EXTERNAL CHARACTERS (Figs 24–25). Forewing length 2.8 mm; wingspan 6.1 mm (n = 1). Head: palpus, pecten and frons golden cream, glossy; frontal tuft golden cream with some pale grey scales; antenna slightly exceeding ½ of forewing; flagellum pale grey, glossy. Thorax ochre-yellow, with some pale grey scales medially; tegula pale grey, with a few ochre-yellow scales. Forewing ochre-yellow, irregularly speckled with grey-brown scales; fringe grey, apically ochre-yellow; fringe indistinctive; forewing underside grey-brown. Hindwing and fringe pale brown. Legs ochre-yellow, covered with grey-brown scales on upper side (particularly abundant on forelegs). Abdomen unknown (unstudied before dissection).

MALE GENITALIA (Figs 124–127). Capsule about 710 µm long, 430 µm wide. Uncus with long but slender lateral lobes (Figs 125–126) and oval excavation (Fig. 125). Valva about 520 µm long, without additional



Figs 124–127. Male genitalia of *Paratischeria belizensis* Remeikis & Stonis sp. nov., holotype (genitalia slide no. 010316193, NHMUK). **124.** Capsule, with phallus inside. **125.** Median excavation of uncus. **126.** Socii. **127.** Lateral view of capsule with phallus inside.

lobes, inwardly curved (Fig. 124); anellus fused with phallus (Figs 124, 127); transtilla and juxta absent. Ventral lobe of vinculum large, distally rounded (Figs 124, 127). Phallus about 515 µm long.

Female

Unknown.

Biology

Host plant and biology unknown.

Flight period

Based on a single specimen collected at light, adults fly in April.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Paratischeria neotropicana (Diškus & Stonis, 2015)

Figs 26–28, 128–129

Astrotischeria neotropicana Diškus & Stonis, 2015: 457–465, figs 9–27.

Diagnosis

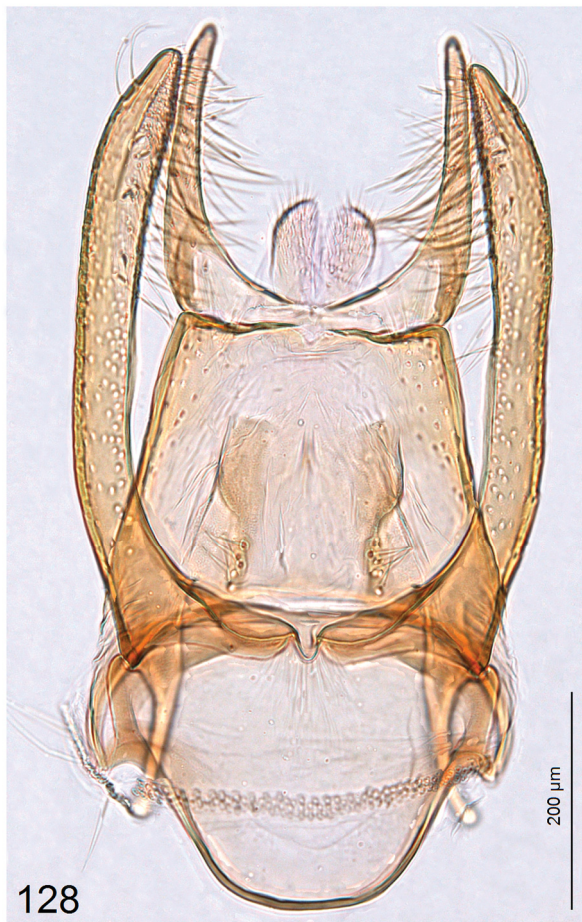
External characters are not sufficient for the identification of this species. In the male genitalia, the combination of a slender valva, a long, simple uncus, a unique, distally bilobed anellus (Fig. 128) and an apically deeply divided phallus (Fig. 129) distinguish *Paratischeria neotropicana* from other congeneric species. The host plant genus, *Sida* L. (Malvaceae), coincides with the host plant of only two other species, *Astrotischeria scutifera* sp. nov., described above, and the Nearctic *A. omissa* (Braun, 1927); however, *A. scutifera* sp. nov. and *A. omissa* belong to the genus *Astrotischeria* and are characterized by a very different genitalic morphology.

Material examined

BELIZE • 18 ♂♂, 15 ♀♀; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 17 Sep.–17 Nov. 1997 and 6 Feb.–13 Jun. 1998; O.T. Lewis leg.; mining larvae on *Sida* sp.; field card nos 31-17/9♂, 2131-19/2♂, 1274-3/11♂, 2077-19/2♂, 1311-4/11♂, 1270-3/11♂, 2210-24/2♂, 1897-8/2♂, 2211-24/2♂, 1280-3/11♂, 319-25/9♂, 3683-13/6♂, 1302-4/11♂, 320-25/9♂, 681-13/10♂, 1309-17/11♂, 2078-19/2♂, 1787-6/2♂, 1312-4/11♀, 1277-27/10♀, 1282-3/11♀, 1276-27/10♀, 346-25/9♀, 1275-3/11♀, 1279-3/11♀, 342-25/9♀, 1271-3/11♀, 2848-2/4♀, 2185-24/2♀, 1785-6/2♀, 2209-24/2♀, 1300-4/11♀, 1313-4/11♀; genitalia slide nos 010316205♂, 010316206♂, 010316207♂, 010316208♂, 010316209♂, 010316210♂, 010316211♀; NHMUK 010289284 to 010289316.

Description

This species was described and illustrated by Diškus & Stonis (2015: 457–465, figs 9–27). Here, on the basis of the studied material, we provide the first photographic documentation of the male genitalia of this species from Las Cuevas (Figs 128–129).



Figs 128–131. Male genitalia of Tischeriidae from Las Cuevas, Belize (NHMUK). **128.** *Paratischeria neotropicana* (Diškus & Stonis, 2015), capsule with phallus removed (genitalia slide no. 010316205). **129.** Same, phallus. **130–131.** *Dishkeya gouaniae* (Diškus & Stonis, 2007), paratype (genitalia slide no. 010316202).

Biology

Host plants: various species of *Sida* L. (Malvaceae), including *S. rhombifolia* L. At Las Cuevas, larvae mine throughout the year. The leaf mine was illustrated by Diškus & Stonis (2015: figs 9–11). Of 117 living mines collected and reared successfully, 37 (31.6%) were parasitised.

Flight period

Based on the rearing data from Belize, adults are likely to occur throughout the year.

Distribution

Paratischeria neotropicana is the tischeriid species with the broadest distribution range yet documented in the Neotropics, having been recorded from various localities in Belize, Mexico, Guatemala, Ecuador, Peru and Bolivia (Stonis & Solis 2020).

Genus *Dishkeya* Stonis & Solis, 2020

Dishkeya gouaniae (Stonis & Diškus, 2007)

Figs 29, 130–131

Tischeria gouaniae Stonis & Diškus, 2007: 1287–1291, figs 2, 3a–c, 4a–b.

Tischeria sp. 12 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, *Dishkeya gouaniae* resembles the Nearctic *D. bifurcata* (Braun, 1915); however, *D. gouaniae* is distinguishable from the latter by its widely rounded vinculum, spiny juxta and slender apical processes of the phallus. The host plant, *Gouania polygama* (Jacq.) Urb. (Rhamnaceae Juss.), makes *D. gouaniae* exceptional among all other Tischeriidae (the related *D. bifurcata* feeds on *Ceanothus*, another genus of Rhamnaceae).

Material examined

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 19 Mar. 1998; O.T. Lewis leg.; mining larvae on *Gouania polygama* (Jacq.) Urb. (Rhamnaceae); field card no. 2529; genitalia slide no. 31442♂; NHMUK 010289317.

Paratypes

BELIZE • 3 ♂♂; same collection data as for holotype; 25 Sep. 1997 and 6 Apr.–3 Jul. 1998; field card nos 2966, 4213, 321; genitalia slide nos 31443♂, 010316202♂; NHMUK 010289318 to 010289320.

Description

This species was described and illustrated by Stonis & Diškus (2007: 1287–1291, figs 2, 3a–c, 4a–b).

Biology

Host plant: *Gouania polygama* (Jacq.) Urb. (Rhamnaceae). Larvae mine leaves in March–July and September. The leaf mine has a linear or corridor shape (not preserved by the collector with the reared specimens, and therefore not studied in detail). This species was listed as '*Tischeria* sp. 12' by Lewis *et al.* (2002). Of 25 living mines reared successfully, 14 (56%) were parasitised.

Flight period

Based on reared specimens, adults occur during March–September.

Distribution

Currently known only from a single locality in Belize (Las Cuevas), at an elevation of about 550 m.

Genus *Coptotriche* Walsingham, 1890

Coptotriche pulverea (Walsingham, 1897)

Figs 30–31, 132–134

Tischeria pulverea Walsingham, 1897: 145.

Coptotriche pulverea – Stonis *et al.* 2008: 165–166, figs 1, 2a–b, 3a–e.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, *Coptotriche pulverea* resembles *C. forsteroniae* Stonis & Diškus, 2008; however, *Coptotriche pulverea* is distinguishable from the latter and all other *Coptotriche* by the extremely short, rod-like vinculum and the gradually narrowed, tulip-shaped apex of the phallus (in *C. forsteroniae* the apex of the phallus is rhomboid). The host plant, *Terminalia amazonia* (J.F.Gmel.) Exell (Combretaceae R.Br.) makes *C. pulverea* unique among all other Tischeriidae (the morphologically similar *C. forsteroniae* feeds on *Forsteronia myriantha* Donn.Sm., Apocynaceae Juss.).

Material examined

BELIZE • 1 ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 3–16 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 010316204♂; NHMUK 010289321 • 1 ♂; Cayo District, San Ignacio, secondary forest; 17°09'15" N, 89°04'04" W; alt. 85 m; 17–18 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; NHMUK 010289323 • 1 ♀; same collection data as for preceding; NHMUK 010289324 • 1 ♂; same locality as for preceding; 13 Mar. 1998; O.T. Lewis leg.; mining larvae on *Terminalia amazonia* (J.F.Gmel.) Exell (Combretaceae); field card no. 6.040-13/3; genitalia slide nos 010316203♂; NHMUK 010289322.

Description

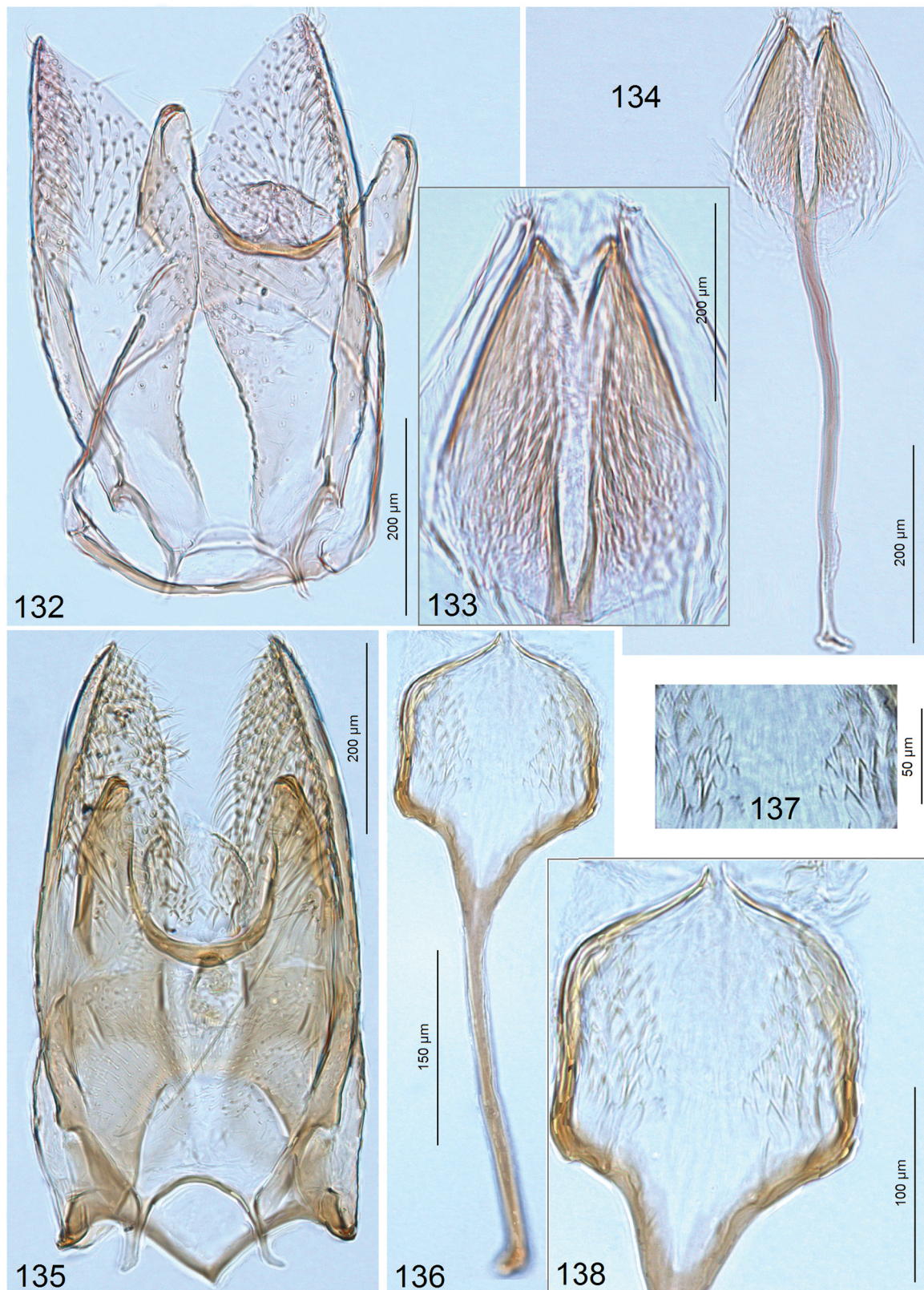
This species was redescribed and illustrated by Stonis *et al.* (2008: 165, 166, figs 1, 2a–b, 3a–e). Here, on the basis of the material from Belize, we provide the first photographic documentation of the male genitalia of the species (Figs 132–134).

Biology

Host plant: *Terminalia amazonia* (J.F.Gmel.) Exell (Combretaceae). Larvae mine leaves in March. The leaf mine starts as a corridor, broadening into a blotch as the larva develops. The leaf mine sample was not preserved by the collector with the reared specimen and is therefore not documented in detail.

Flight period

Based on specimens collected at light, adults occur in April. Based on reared specimens in Belize and the Caribbean (lectotype), adults also occur in March.



Figs 132–138. Male genitalia of Tischeriidae from Las Cuevas, Belize (NHMUK). **132.** *Coptotriche pulverea* (Walsingham, 1897), capsule with phallus removed (genitalia slide no. 010316203). **133–134.** Same, phallus. **135.** *C. forsteroniae* Stonis & Diškus, 2008, capsule with phallus removed, paratype (genitalia slide no. 010316201). **136–138.** Same, phallus.

Distribution

This species was described from the Caribbean (Virgin Is., USA) (Walsingham 1897) and was recently recorded from Belize (Stonis *et al.* 2008).

Coptotriche forsteroniae Stonis & Diškus, 2008

Figs 32–34, 135–142

Coptotriche forsteroniae Stonis & Diškus, 2008: 104–105, fig. 5a–c.

Tischeria sp. 8 – Lewis *et al.* 2002: 872.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, *Coptotriche forsteroniae* resembles *C. pulvereana* (Walsingham, 1897); however, *C. forsteroniae* is distinguishable from the latter and all other species of *Coptotriche* by the rhomboid apex of the phallus (Fig. 138). The host plant, *Forsteronia myriantha* Donn.Sm. (Apocynaceae), makes *C. forsteroniae* unique among all other Tischeriidae (the morphologically similar *C. pulvereana* feeds on *Terminalia amazonia* (J.F.Gmel.) Exell (Combretaceae)).

Material examined

Holotype

BELIZE • ♂; Cayo District, San Ignacio, secondary forest; 17°09'15" N, 89°04'04" W; alt. 85 m; 17–18 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 31446; NHMUK 010289325.

Paratypes

BELIZE • 4 ♂♂; same collection data as for holotype; genitalia slide no. 31445♂; NHMUK 010289326 to 010289329 • 6 ♂♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 3–16 Apr. 1998; R. Puplesis and S.R. Hill leg.; at light; genitalia slide no. 010316200♂; NHMUK 010289330 to 010289335 • 4 ♂♂; same locality as for preceding; 24 Mar. 1998; O.T. Lewis leg.; mining larvae on *Forsteronia myriantha* Donn.Sm. (Apocynaceae); genitalia slide nos 010316199♂, 010316201♂; NHMUK 010289336 to 010289339.

Description

The species was described and illustrated by Stonis & Diškus (2008: 104–105, fig. 5a–c). Here, on the basis of the studied material, we are the first to provide photographic documentation of the male genitalia of the species (Figs 135–142).

Biology

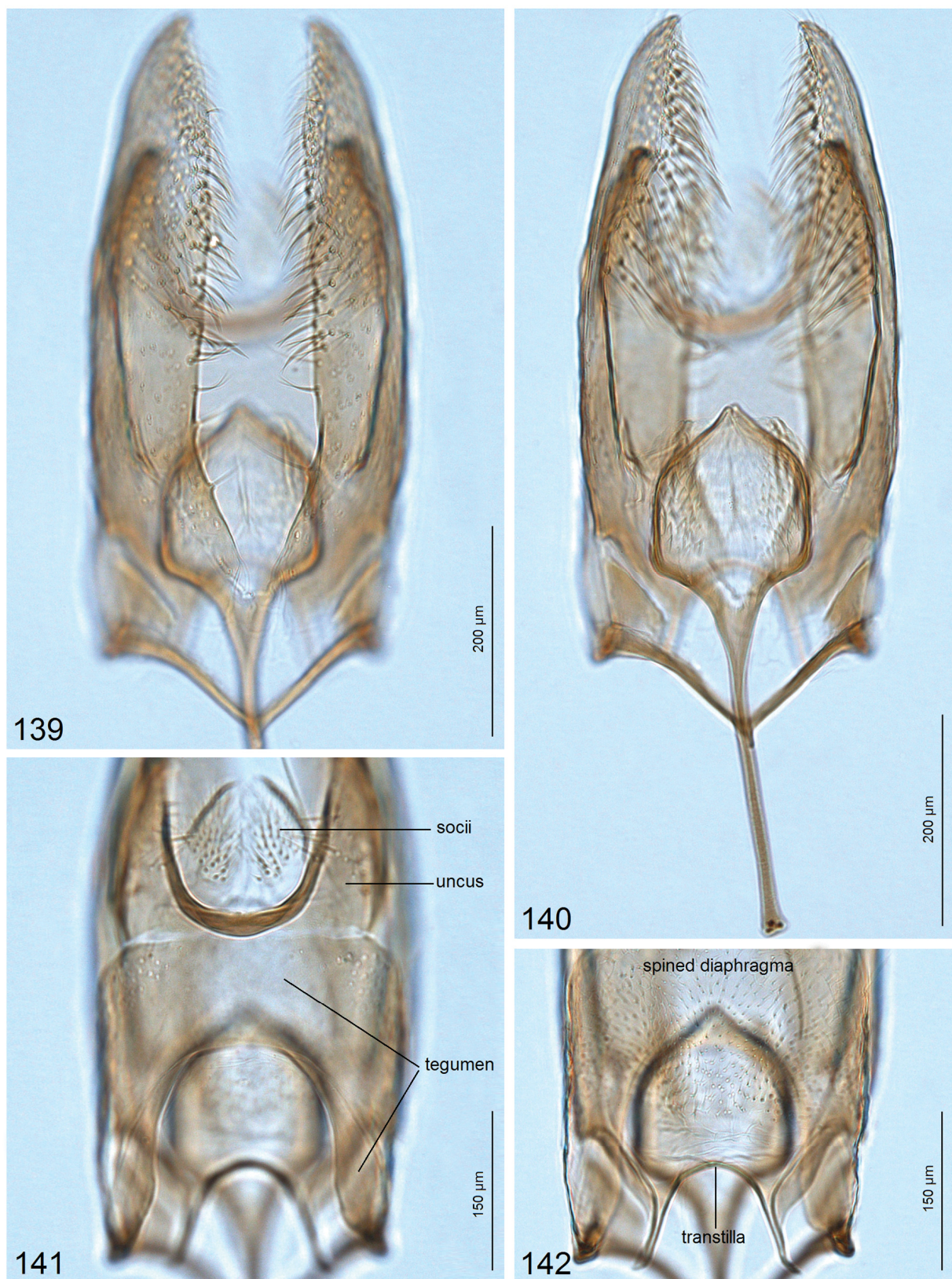
Host plant: *Forsteronia myriantha* Donn.Sm. (Apocynaceae). Larvae mine leaves in March and probably at other times of the year. The leaf mine has a blotch shape (not preserved with the reared specimens by the collector and therefore not studied in detail and undocumented). This species was listed as '*Tischeria* sp. 8' by Lewis *et al.* (2002). Of 6 living mines reared successfully, none were parasitised.

Flight period

Based on specimens collected at light, adults occur in April. Based on reared specimens, adults also occur in March.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.



Figs 139–142. Male genitalia of *Coptotriche forsteroniae* Stonis & Diškus, 2008, paratype (genitalia slide no. 010316200, NHMUK). **139–140.** General view. **141.** Socii, uncus and tegumen. **142.** Transtilla.

Coptotriche singularis Stonis & Diškus, 2008

Coptotriche singularis Stonis & Diškus, 2008: 104, figs 2, 3a–e.

Diagnosis

External characters are not sufficient for the identification of this species. In the male genitalia, the apically narrowing valva, absence of transtilla and highly specific, apically gradually widening phallus distinguish *Coptotriche singularis* from other congeneric species.

Material examined

Holotype

BELIZE • ♂; Cayo District, Chiquibul Forest Reserve, Las Cuevas; 16°43'53" N, 88°59'11" W; alt. 550 m; 17 Sep. 1997; O.T. Lewis leg.; mining larva on *Cardiospermum grandiflorum* Sw. (Sapindaceae); field card no. 39-17/9; genitalia slide no. 31444♂; NHMUK 010289340.

Description

The species was described and illustrated by Stonis & Diškus (2008: 104, figs 2 (male adult), 3a–e (male genitalia)).

Biology

The larvae are leaf miners, creating a blotch-type mine, and the host plant is recorded as *Cardiospermum grandiflorum* Sw. (Sapindaceae). Only a single mine was reared successfully.

Flight period

Based on the single reared specimen, adults also occur in September or early October.

Distribution

So far this species is known from a single locality in Belize, Chiquibul Forest Reserve, Las Cuevas, at an elevation of about 550 m.

Discussion

One of the most unexpected results of our study of the Belize material collected in Las Cuevas was the discovery of a diverse fauna of Tischeriidae, a total of fourteen species including representatives of four of five currently known genera of the family. This represents the highest number of species ever recorded from a single locality worldwide. In total, the documented global fauna of Tischeriidae now comprises 148 described species, including all these species reported from Las Cuevas. Twelve species are known from Europe, the most investigated region with respect to Tischeriidae: eight species of *Coptotriche* and four species of *Tischeria* (Karsholt & van Nieukerken 2013). Forty-six species are known from the Nearctic and 49 from the Neotropics, including 21 from Central America. The identified fauna of Las Cuevas, a single locality in the Central American tropical forest, exceeds the European fauna and represents almost one third of the Tischeriidae fauna of the Neotropics (for the updated Neotropical data see Stonis *et al.* 2020), about 67% of the fauna currently described from Central America and 9% of the documented global fauna. Considering the insufficient sampling in most of Central America, it is possible that the diversity observed at Las Cuevas is just the tip of the iceberg and that the tropical forests of Central America are more widely characterized by high richness and taxonomic diversity of Tischeriidae.

It should also be noted that the Tischeriidae documented from Las Cuevas exhibit a remarkable range of morphological structures. This is probably due to the historical and ecological biogeography of the Neotropical region, which is currently dominated by warmer conditions in comparison to the Holarctic region, and also to the particularities of the members of the host tribes of Asteraceae that predominate, and probably originated in the Neotropics (Stonis *et al.* 2018b).

Despite their very close external resemblance (see Figs 6–34), internally, in the male genitalia, the species from Las Cuevas seem morphologically very distinct and apparently more isolated from each other than is typical of Nearctic or Palaearctic species. Species differences in the European fauna are generally slight, and problems of identification of similar species may be compounded by intraspecific variation. The fauna of Tischeriidae from Las Cuevas comprises clearly differentiated and disjunct species, with hypothesized old origin. Our study revealed novel morphological characters previously unknown for the family, including: a specialized uncus with a bifid dorsal lobe in *Astrotischeria papilloma* sp. nov. and *A. scutifera* sp. nov.; a pectinifer on the valva of *Paratischeria robinsoni* sp. nov. and spine-like setae on the valva of *P. tubifex* sp. nov.; very large socii in *P. robinsoni* sp. nov.; and extremely long phallus and enormously enlarged socii in *P. tubifex* sp. nov. We hypothesize that these features may represent derived characters and our documentation of the genital morphology of the species from Las Cuevas contributes to a better understanding of the morphology of Tischeriidae and their possible evolutionary trends.

Acknowledgements

We would like to thank our Belize and NHMUK scientific partners, including those who helped organize or participated in our fieldwork in 1997–1998. We are indebted to the late Dr Gaden S. Robinson, former curator at NHMUK, for his vital role in organizing fieldwork by R. Puplesis at Las Cuevas. We thank the Godman Exploration Fund (Hon. Secretary Judith Marshall) for support, Dr Alex Monro and Dr Pat Haynes (NHMUK) for pre-fieldwork advice, and the staff of the Las Cuevas Research Station, particularly the late Nicodemus (Chapal) Bol and Chris Minty, for various help during the course of the fieldwork. We are hugely indebted to our colleague Caroline Whitefoord (NHMUK and the Royal Botanic Gardens, Kew, London) for her friendly companionship and the invaluable identifications of the host plants of Tischeriidae, and to Prof. Jane Memmott, Prof. Charles Godfray and Dr Chris Lyal for their support and advice to O.T. Lewis. We also thank the owners of Pook's Hill Nature Reserve, Belize, Vicky and Ray Snaddon, for their hospitality and interest in the project. We thank Prof. Jack Schuster (Universidad del Valle de Guatemala, Guatemala City, Guatemala) and the Consejo Nacional de Areas Protegidas (CONAP) Guatemala, C.A. for the Licencia de Collecta o Aprovechamiento de Vida Silvestre (No. 12900) during our collecting in neighbouring Guatemala or Honduras. We are also grateful to anonymous reviewers for their useful remarks and suggestions. This research was partially funded by a grant (S-MIP-19-30, 'DiagnoStics') from the Research Council of Lithuania.

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