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Genera of Tischeriidae (Lepidoptera): a review of the global fauna, with descriptions of new taxa

JONAS R. STONIS[1*], ARŪNAS DIŠKUS[2,6], ANDRIUS REMEIKIS[1,7],
SVETLANA ORLOVSKYTĖ[1,8], M. ALMA SOLIS[3,9], BRIGITA PAULAVIČIŪTĖ[4,10],
JIASHENG XU[5,11] & XIAOHUA DAI[5,12]

[1] *State Research Institute Nature Research Centre, Akademijos g. 2, 08412, Vilnius, Lithuania.*
[2] *Vytautas Magnus University, K. Donelaičio g. 58, 44248, Kaunas, Lithuania.*
[3] *Systematic Entomology Laboratory, ARS, US Department of Agriculture, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20013-7012, USA.*
[4] *Tadas Ivanauskas Zoological Museum, Laisvės al. 106, 44253, Kaunas, Lithuania.*
[5] *Leafminer Group, School of Life Sciences, Gannan Normal University, Jiangxi 341000, China.*
[6] *diskus.biotaxonomy@gmail.com; https://orcid.org/0000-0003-0106-5546*
[7] *remeikis.andrew@gmail.com; https://orcid.org/0000-0002-9310-1112*
[8] *s.orlovskyte@gmail.com; https://orcid.org/0000-0002-1643-7712*
[9] *alma.solis@usda.gov; https://orcid.org/0000-0001-6379-1004*
[10] *bpaulaviciute@yahoo.com; https://orcid.org/0000-0003-0955-3894*
[11] *xjstis@163.com; https://orcid.org/0000-0002-2252-8784*
[12] *ecoinformatics@gmail.com; https://orcid.org/0000-0002-2891-159X*
[*] *Corresponding author. stonis.biotaxonomy@gmail.com; https://orcid.org/0000-0002-8411-3162*

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Abstract

For the first time, genera of leaf mining Tischeriidae of the global fauna are reviewed and four new genera are described: *Coptotrichoides* Diškus & Stonis, **gen. nov.**, trophically associated with Sapindaceae from Central and South America; *Rytietia* Diškus, Xu & Dai, **gen. nov.**, trophically associated with Annonaceae from East and South East Asia; *Pafazaria* Diškus & Stonis, **gen. nov.**, trophically associated with Fabaceae and Malvaceae from East and South East Asia; and *Gnathitischeria* Diškus, **gen. nov**., trophically associated with Malvaceae and Asteraceae from Central America. In addition to the descriptions of new genera, all previously described genera (*Coptotriche* Walsingham, 1890; *Dishkeya* Stonis, 2020; *Tischeria* Zeller, 1839; *Manitischeria* Diškus & Stonis, 2021; *Neotischeria* Diškus & Stonis, 2021; *Paratischeria* Diškus & Stonis, 2017; and *Astrotischeria* Puplesis & Diškus, 2003) are characterized and a pictorial identification key for all 11 genera is provided. Morphological and biological characteristics of all genera are supplemented with some molecular data. We described 12 new species: South East Asian *Coptotriche sapaensis* Diškus & Stonis, **sp. nov.**; Central American *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.** and *Tischeria neokristenseni* Diškus & Stonis, **sp. nov.**; South East Asian *Rytietia uncinata* Diškus, Xu & Dai, **sp. nov.**, East Asian *R. chongyiensis* Xu & Dai, **sp. nov.**; South East Asian *Pafazaria capitata* Diškus & Stonis, **sp. nov.** and *P. faboidica* Diškus & Stonis, **sp. nov.**; Central American *Neotischeria antigua* Diškus & Remeikis, **sp. nov.** and *N. subantigua* Diškus & Remeikis, **sp. nov.**; South American *Astrotischeria incae* Diškus & Stonis, **sp. nov.**; and Central American *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.** and *G. arcana* Diškus & Stonis, **sp. nov.** The taxonomic rank of the East Asian subspecies *Tischeria decidua siorkionla* Kozlov, 1986 is elevated to species rank: *T. siorkionla* Kozlov (**stat. nov.**). The male genitalia of holotypes, paratypes, lectotypes or paralectotypes, or non-type specimens of some little-known species are examined for the first time. We provide the first morphological documentation for the following: *Tischeria ceanothi* lectotype and paralectotype; *T. immaculata* (**stat.**

restored) paratype; *Coptotrichoides deliquescens* (Meyrick) lectotype and paralectotype; lectotypes of *Coptotriche aenea* (Frey & Boll), *Astrotischeria plagifera* (Meyrick), *A. helianthi* (Frey & Boll), and *A. ephaptis* (Meyrick); *Coptotriche berberella* (De Prins) paratype; and the first photographic documentation of *Tischeria lvoskyi* Kozlov holotype. Some non-type specimens deposited at NHMUK, including a few previously neglected species, are also examined and documented, including the American *Astrotischeria solidagonifoliella* (Clemens) and *A. omissa* (Braun). Nine new combinations are provided: *Coptotrichoides deliquescens* (Meyrick, 1915), **comb. nov.**; *C. singularis* (Stonis & Diškus) **comb. nov.**; *C. suprafasciata* (Diškus & Stonis) **comb. nov.**, *C. serjaniphaga* (Remeikis & Stonis) **comb. nov.**; *C. braziliensis* (Diškus & Stonis) **comb. nov.**; *Pafazaria jingdongensis* (Xu & Dai), **comb. nov.**; *Neotischeria explosa* (Braun) **comb. nov.**; *N. pallidipennella* (Braun) **comb. nov.**; and *Astrotischeria heteroterae* (Frey & Boll) **comb. nov.** The synonymization of *Tischeria longeciliata* Frey & Boll, 1878 with *Astrotischeria helianthi* (Frey & Boll, 1878) is confirmed. One new species group, the *Tischeria ceanothi* group, is established. We also report a new distribution record of *T. dodonaea* Stainton from the Caucasus, Armenia. Three tables and 569 figures of adult external morphology, male and female genitalia, leaf mines, and cladograms based on molecular characters are provided.

Key words: *Coptotrichoides*, DNA barcodes, generic composition, *Gnathitischeria*, leaf mines, mtDNA CO1-5’, monophagous, nidus, *Pafazaria*, *Rytietia,* taxonomy, oligophagous, trumpet moths

Introduction

Tischeriidae, commonly known as trumpet moths (or trumpet leafminer moths), is a relatively small lepidopteran family of leaf miners currently comprised of 186 described species globally (Stonis *et al*. 2020b, 2021a, 2021c, 2021d, 2022a, 2022b; Dobrynina *et al*. 2022), including the 12 new species described here. Tischeriids are not well-known or common in museum holdings worldwide and are probably among the least studied lepidopteran groups of the tropical or subtropical regions worldwide (Stonis *et al*. 2020c, 2020b). In the wild, adults of Tischeriidae are easily recognizable by their characteristic body shape, common ochre-brown colour, and specific lifted resting pose (Figs 1, 2).

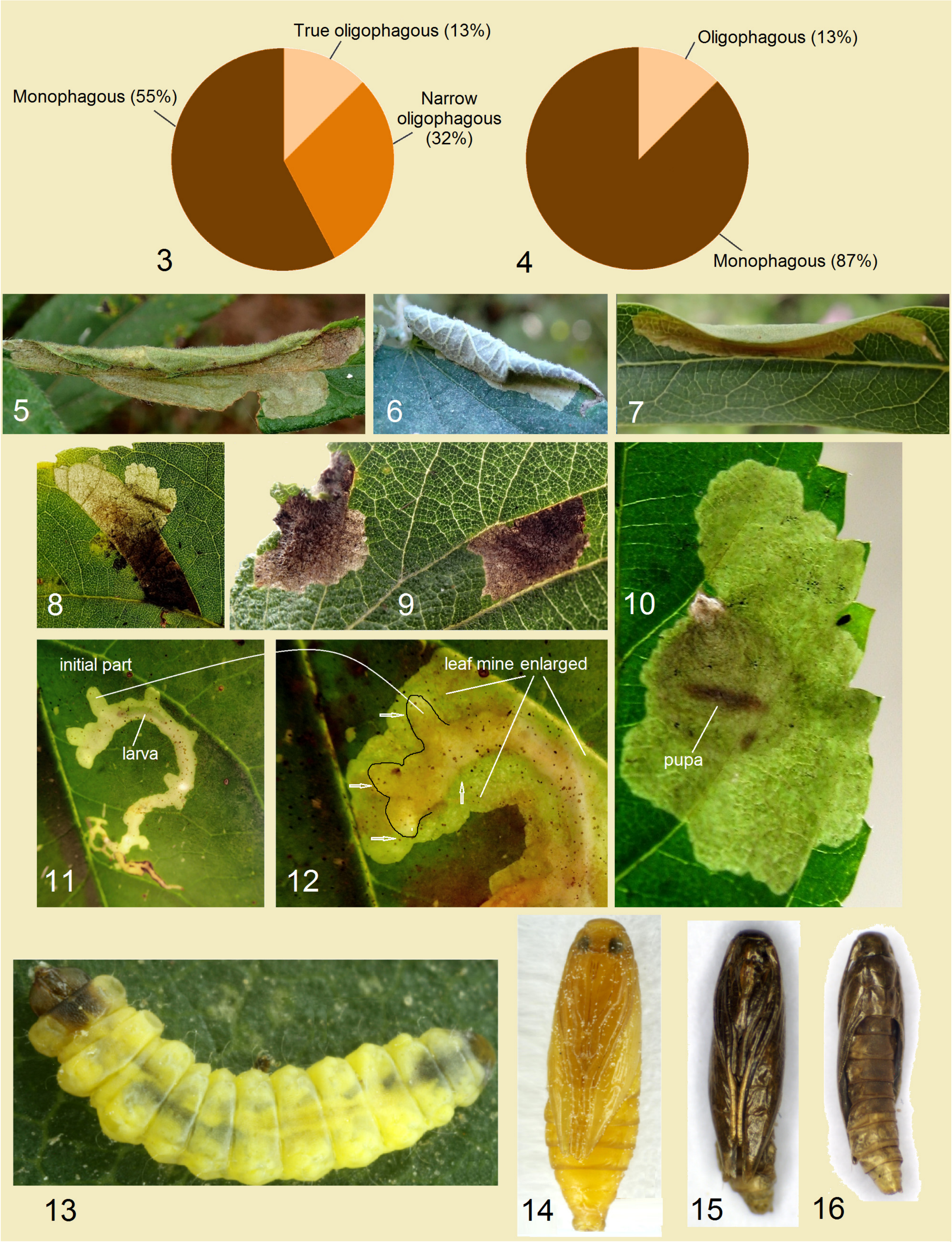
FIGURES 1, 2. Adults of tischeriid moths in their natural resting pose with the front lifted. 1, *Coptotriche marginea* (Haworth), Austria, Wien, Lobau; 2, *Tischeria ekebladella* (Bjerkander), Niederösterreich, Austria, SSE Bad Erlach (courtesy of our colleague Peter Buchner, Austria)

According to a review of the smallest Lepidoptera which included suggested terminology for size categories of small moths (see Stonis *et al*. 2021e), Tischeriidae are medium small to small in size, with a wingspan usually ranging from 6.5 to 7.3 mm. Only a few tischeriid species are very small, i.e., with a wingspan of 4.1 mm and some are significantly larger than the average with a wingspan of over 11 mm (Stonis *et al*. 2021e).

Tischeriidae larvae are leaf miners and feed on numerous wild and cultivated plants. Larvae of these moths are selective of their host plants, i.e., they are stenophagous which includes monophagy and oligophagy (Stonis *et al*. 2018a; Xu *et al*. 2021). But there is a lack of agreement regarding the terms "monophagous" and "oligophagous". Following long-existing terminology which was reviewed and schematically presented in Stonis *et al*. (2016c), "strictly monophagous" herbivores are those which feed on a single plant species, whereas, herbivores trophically associated with two or more plant species from the same genus are called "narrow oligophagous", and those trophically associated with various plant genera of the same plant family are recognized as "true oligophagous" or, in some particular cases of unrelated host-plant genera, "disjunct oligophagous" (Stonis *et al*. 2016c). Under this concept, oligophagous species comprise about 45% among the currently studied Tischeriidae worldwide, whereas monophagous species comprise about 55% (Fig. 3). However, the concept of the term "monophagous" sometimes is expanded to larvae which utilize a few closely related plant species within the same plant genus (e.g., Bernays & Chapman 1994; Schoonhoven *et al*. 2005). If interpreted this way, monophagous species among the trophically investigated Tischeriidae would comprise 87% in the world's fauna (Fig. 4). Nevertheless, these proportions will undoubtedly change upon future research since some currently known monophagous species are insufficiently investigated, i.e., monophagous species may be discovered to feed on more plants than currently known, so oligophagous species may be more common among Tischeriidae (Stonis *et al*. 2018a).

Plant families utilized by Tischeriidae are continuously updated, i.e., the list of host plants grows with research of the global fauna (Davis 1999; Puplesis & Diškus 2003; Xu *et al*. 2018; Stonis *et al*. 2020b, 2021d). Recently, based on studies in China and adjacent northern territories of Vietnam, two new host-plant families, Nyssaceae and Staphyleaceae, were added by Xu *et al*. (2021); one more novel host-plant family, Annonaceae, was added in this current publication (see below). Now Tischeriidae are known to be trophically associated with 22 plant families in 13 orders of flowering plants (rosids and asterids I core eudicot angiosperms): Magnoliales (Annonaceae); Malpighiales (Hypericaceae and Phyllanthaceae, including the host-plant genus *Bridelia* Willd. formerly placed in Euphorbiaceae); Fabales (Fabaceae); Rosales (Rhamnaceae, Rosaceae, Ulmaceae, and Urticaceae); Fagales (Betulaceae and Fagaceae); Myrtales (Combretaceae and Lythraceae); Crossosomatales (Staphyleaceae); Sapindales (Anacardiaceae and Sapindaceae); Malvales (Malvaceae, including the former Sterculiaceae and Tiliaceae); Cornales (Nyssaceae); Ericales (Ericaceae, Symplocaceae, and Theaceae); Gentianales (Apocynaceae); Asterales (Asteraceae).

The biology of Tischeriidae, especially of the immature stages (Figs 13–16, 25, 26), is insufficiently studied. A concise description of tischeriid larvae was first provided by Davis (1999), but the most exhaustive study of immature stages was recently provided by Alipanah *et al.* (2022) based on the Caucasian *Tischeria caucasica* Klasiński & Stonis, 2020 that was discovered to occur in Iran. Larvae of Tischeriidae mine inside the green, photosynthetic tissues of plant leaves during all instars and produce leaf mines (Figs 5–12, 17–24). The mines are usually irregular blotch-like or blotch-like with a trumpet-like start, but occasionally leaf mines are linear or have another shape. Sometimes, in certain genera of Tischeridae, larvae fold or roll the leaf margin before pupation (Figs 5–7). Frass does not remain in the mine, except for some species which leave a little frass in the initial part of the mine. Fresh leaf mines look transparent, but sometimes they are slightly stained with dark frass from inside; old mines sometimes become beige-brown (or white), and less transparent. Pupation occurs inside the leaf mine (Figs 10, 20, 22, 24), usually in a round (or irregularly shaped) silk-lined nidus (Figs 17–24). The nidus can be distinctive and visible or invisible through the epidermis of the leaf mine, especially if it is formed under the leaf vein or the leaf mine is stained with dark frass, or folded. The nidus serves both as a hiding place for a disturbed larva, and for pupation.



FIGURES 3–16. Biology of Tischeriidae. 3, predominance of monophagous species (after Xu *et al*. 2021); 4, same, following the concept of the term "monophagous" when feeders utilize a few closely related plant species within the same plant genus; 5, leaf mine, *Astrotischeria truncata* (after Stonis *et al*. 2019b); 6, same, *A. ochrimaculosa*; 7, same, *A. parvisacculata*; 8, same, *A. colombiana* (after Stonis *et al*. 2019c); 9, same, *A. trilobata* (after Stonis *et al*. 2018a); 10, same, *Neotischeria neotropicana* (after Diškus & Stonis 2015); 13, *Tischeria ulmella*, larva (after Xu *et al.* 2018); 14–16, same, pupa

Many species of Tischeriidae were described by Meyrick from tropical regions (Meyrick 1908, 1915a, 1915b, 1934, 1936) and by Braun from the USA (1915, 1923, 1925, 1927, 1972). Nearly 20 species, mostly subtropical species from South Africa, South America, Mediterranean, East Asia and other areas, were described by Puplesis & Diškus (2003). It is interesting to note that two new species were described by Bernard Landry from the Galapagos (Landry & Roque-Albelo 2004), a remote world-famous archipelago. Recently, most species were discovered from the continental Central and South America (Diškus & Puplesis 2003; Stonis & Diškus 2007, 2008; Diškus & Stonis 2015; Stonis *et al*. 2016a, 2017, 2018a, 2019b, 2019c, 2020a, 2020b, 2020c, 2021b, 2021c, 2022a, 2022b; Stonis & Solis 2020) and East and South East Asia (Diškus & Puplesis 2003; Stonis *et al*. 2014, 2021d; Kobayashi *et al.* 2016; Xu *et al*. 2017, 2018, 2021; Kim *et al.* 2022), tropical and subtropical Africa (Puplesis & Diškus 2003; Mey 2010; including Madagascar (Lees & Stonis 2007). Dobrynina *et al*. (2022) found that 37 researchers worldwide have contributed to the description of Tischeriidae species. Additionally, many Neotropical and Oriental species have been collected, dissected, and recognized as new by Arūnas Diškus, Charley Eiseman, Chris Snyers, Jiasheng Xu, Xiaohua Dai, and others not mentioned here because they are aware of unnamed taxa awaiting description or are in the process of preparation for description.

It was hypothesized that Tischeriidae are probably more speciose in Central America than anywhere else in the world (Puplesis & Diškus 2003) which was eventually supported by the discovery of 14 species from a single tropical forest site in Belize (Stonis *et al*. 2020a). To date, this is the highest number of Tischeriidae species recorded from a single locality worldwide, and to put this exceptional species diversity in perspective, the fauna from this single site in the tropical forest of Central America exceeds the entire European fauna (Stonis *et al*. 2019c, 2020a).

Phylogenetically, Tischeriidae is one of the most intriguing families that belongs to the oldest (Monotrysian) lineages of extant Lepidoptera (see Regier *et al*. 2015 for a phylogenetic discussion). As an important step for the comprehensive study of Tischeriidae worldwide, we review all Tischeriidae genera of the global fauna for the first time, describe four new genera and 12 new species based on morphological, biological, and some molecular studies. Despite the comprehensive nature of our study, the taxonomic placement of a few tischeriid species remains uncertain (see Discussion). Although there has been much recent activity in the description of new taxa (Dobrynina *et al*. 2022), there are still many species, presumably with novel morphological characters, and their biologies to be discovered from equatorial Africa, as well as other tropical and subtropical regions of South and South Eastern Asia, and South America. Phylogenies and classifications can sometimes significantly change when challenged by the addition of substantial numbers of species with unique and highly modified morphologies, and we expect that this will happen with the Tischeriidae upon future discoveries in tropical countries. The inventory of Earth's species, as well as mapping their distribution and uncovering their relationships, is very important, and are among the main tasks of biological systematics (Vane-Wright 1992, 1996; Wheeler *et al*. 2012a, 2012b).

We hope that the data provided in this illustrated monograph will contribute to general knowledge about these peculiar, tiny leaf miners, and stimulate further studies.

Material and methods

The descriptions of the new species and genera are based on material belonging to the collection of Museum für Naturkunde, Berlin, Germany (MfN), and Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark (ZMUC). Specimens were collected by various reseachers in Central and South America and South East Asia during 2012–2020. Some specimens are also deposited in the collection of the Leafminer Group, School of Life Sciences, Gannan Normal University, Jiangxi, China.

Collecting methods and techniques of adult rearing from mining larvae are described in detail in our previous publications (Stonis *et al*. 2018a; Diškus & Stonis 2022; and Stonis & Remeikis 2022).

Genitalia were dissected and permanently prepared on microscope slides following the method outlined in Stonis *et al*. (2022c). These slides were photographed and studied with a Leica DM2500 microscope and a Leica DFC420 digital camera. Adults were measured and studied using Lomo stereoscopic microscopes MBS-10 and photographed using a Leica S6D stereoscopic microscope with an attached Leica DFC290 digital camera, except for Figs 25, 26, 35 which were photographed using a Lomo MBS-10 stereoscopic microscope with a temporarily attached Samsung Galaxy S7 cellular telephone with a camera. Figures 13–16 were photographed using a Leica M-205C microscope with an attached Olympus DP-26 digital camera. SEM photography was performed with scanning electron microscopes FEI Quanta 250 (NRC, Vilnius) (Figs 28, 37–47) and Joel JSM-840 (ZMUC, Copenhagen) (Figs 52, 57).

Leaf-mine photographs were taken with various cameras having Macro or SuperMacro applications, including Canon Power Shot S-3 and Olympus TG-2 or Olympus DP-26 cameras. Some leaf mines have been photographed in the wild using smartphones (especially those with good photography capabilities, such as a Samsung Galaxy S with a Leica lens).

Host-plant classification follows Angiosperm Phylogeny Group (2016) and Cole *et al*. (2019).

The molecular analysis was performed at the Centre for Biodiversity Genomics (CBG), formerly the Biodiversity Institute of Ontario: DNA extraction, PCR amplification, and sequencing of 28 partial sequences of CO1 were successfully obtained following the standard protocols (Hajibabaei *et al.* 2005; Ivanova *et al.* 2006; deWaard *et al.* 2008; CCDB 2013; Hebert *et al.* 2013). The two pairs of primers used for PCR and sequencing were as follows: MLepF1 (5'-gctttcccacgaataaataata-3') and LepR1 (5'-taaacttctggatgtccaaaaaatca-3');

LepF1 (5'-attcaaccaatcataaagatattgg-3') and MLepR2 (5'-gttcawccwgtwccwgcyccattttc-3') (https://boldsystems.org/index.php/Public_Primer_PrimerSearch) (accessed 4 August 2023).

The remainder of the molecular data (20 sequences) was obtained by the authors at the Nature Research Centre (NRC, Vilnius). It began with the total genomic DNA extraction from 96% ethanol-preserved whole adult specimens or their legs, using the GeneJet Genomic DNA Purification Kit (Thermo Fisher Scientific Baltics, Vilnius, Lithuania) in accordance with the manufacturer's specifications. The partial sequence of the mtDNA CO1-5' gene was amplified with the primers T3Lep-f (5'-attaaccctcactaaagtcwachaatcataaaratattgg-3'; modified Lep-f1 (Hebert *et al.* 2003)) and T7Nancy-r (5'-aatacgactcactataggdaraattaraatrtaaacytcwg-3'; modified Nancy (Simon *et al*. 1994)). PCR mixture contained 12.5 μL of 2× DreamTaq PCR Master Mix (Thermo Fisher Scientific Baltics, Vilnius, Lithuania), 2.5 μL of 10 pmol of each primer, 1 μL of genomic DNA, and deionised water up to a volume of 25 μL. The conditions of PCR were as follows: initial denaturation at 95°C for 1 min; 45 cycles of denaturation at 94°C for 40 s, annealing at 45°C for 40 s, extention at 72°C for 1 min; a final extension at 72°C for 5 min. The success of PCRs was estimated by horizontal electrophoresis on 1.5% agarose gel (Thermo Fisher Scientific Baltics, Vilnius, Lithuania) stained with 10 000× GelRed (Biotium, Fremont, California, USA) and run with the GeneRuler Express DNA Ladder (Thermo Fisher Scientific Baltics, Vilnius, Lithuania). The excess of primers and dNTPs were removed using Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase enzymes (Thermo Fisher Scientific Baltics, Vilnius, Lithuania). The automatic sequencing was performed by the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California, USA) in Macrogen Inc. (Seoul, South Korea) with the universal T3 (5'-attaaccctcactaaag-3') and T7 (5'-aatacgactcactatag-3') primers.

The sequences were manually aligned using BioEdit v. 7.2.5 (Hall 1999). As a result, 48 (150–674 bp long) sequences belonging to 34 Tischeriidae species were successfully obtained for the first time (GenBank accession numbers are OQ413527–OQ413574) (Table 1). In addition, the analysis also included 51 previously published sequences of 31 Tischeriidae species (as well as the distantly related *Elachista alpinella* Zeller (Ditrysia: Elachistidae) and *Pseudopostega bogotensis* Vargas (Monotrysia: Opostegidae)) whose sequences were downloaded from the Barcode of Life Data System (BOLD) platform (Ratnasingham & Hebert 2007) (www.barcodinglife.org) or the NCBI GenBank database (www.ncbi.nlm.nih.gov/genbank). The final dataset includes the dataset of 608 bp long sequences.

The divergences within and between species were calculated using the best-fit Kimura 2-parameter distance model (Kimura 1980) and graphically displayed in the Neighbor-Joining (NJ) (10.000 bootstrap replications) or the Maximum Likelihood (ML) (1.000 bootstrap replications) trees by the MEGA v. 7 software (Kumar *et al.* 2016).

TABLE 1. The IDs of barcoded Tischeriidae specimens. Sample IDs are specimen identifiers in BOLD, where all details of collecting data are available. Asterisks (*) mark those GenBank accession IDs, whose sequences were used in Figs 62–64

Species	Sample ID	GenBank accession ID
Astrotischeria atlantica Diškus & Stonis	L2547	OQ413527
Astrotischeria bacchariphaga Diškus & Stonis	L2573	OQ413528
Astrotischeria bacchariphaga Diškus & Stonis	NEPTI020-17	OQ413529*
Astrotischeria chilei Puplesis & Diškus	NEPTI013-17	OQ413530

......*continued on the next page*

TABLE 1. (Continued)

Species	Sample ID	GenBank accession ID
Astrotischeria colombiana Stonis & Vargas	AC2543	OQ413531
Astrotischeria cornuata Diškus & Stonis	NEPTI021-17	OQ413532
Astrotischeria dondavisi Stonis & Diškus	AO2554	OQ413533
Astrotischeria dondavisi Stonis & Diškus	AO2555	OQ413534
Astrotischeria guatemalica Diškus & Stonis	NEPTI008-17	OQ413535
Astrotischeria guatemalica Diškus & Stonis	NEPTI009-17	OQ413536
Astrotischeria jociui Diškus & Stonis	L2579	OQ413537
Astrotischeria jociui Diškus & Stonis	NEPTI026-17	OQ413538
Astrotischeria ochrimaculosa Diškus, Stonis & Vargas	AO2542	OQ413539
Astrotischeria plagifera (Meyrick)	NEPTI066-17	OQ413540
Astrotischeria sanjosei Diškus & Stonis	F2557	OQ413541
Astrotischeria sanjosei Diškus & Stonis	F2558	OQ413542
Astrotischeria selvica Diškus, Carvalho-Filho & Stonis	NEPTI022-17	OQ413543
Astrotischeria trilobata Diškus & Stonis	NEPTI014-17	OQ413544
Astrotischeria trilobata Diškus & Stonis	NEPTI015-17	OQ413545
Astrotischeria truncata Diškus & Stonis	L2578	OQ413546
Astrotischeria yungasi Diškus & Stonis	L2569	OQ413547
Coptotriche asiana Diškus & Stonis	NEPTI019-17	OQ413548
Coptotriche inclinata Puplesis & Diškus	NEPTI016-17	OQ413549*
Coptotriche inclinata Puplesis & Diškus	NEPTI017-17	OQ413550
Coptotriche parvisacculata Diškus & Stonis	L2544	OQ413551
Gnathitischeria arcana Diškus & Stonis, **sp. nov.**	NEPTI023-17	OQ413552
Gnathitischeria arcana Diškus & Stonis, **sp. nov.**	L2574	OQ413553
Gnathitischeria atitlani Diškus & Stonis, **sp. nov.**	NEPTI001-17	OQ413554*
Gnathitischeria atitlani Diškus & Stonis, **sp. nov.**	NEPTI002-17	OQ413555
Manitischeria ptarmica (Meyrick)	L2777	OQ413556*
Neotischeria antigua Diškus & Remeikis, **sp. nov.**	NEPTI006-17	OQ413557
Neotischeria antigua Diškus & Remeikis, **sp. nov.**	NEPTI007-17	OQ413558
Neotischeria conexa Diškus & Stonis	NEPTI012-17	OQ413559
Neotischeria guarani (Diškus & Stonis)	L2545	OQ413560
Neotischeria longa Diškus & Stonis	NEPTI025-17	OQ413561
Neotischeria mesoamericana Diškus & Stonis	NEPTI004-17	OQ413562
Neotischeria mesoamericana Diškus & Stonis	NEPTI005-17	OQ413563
Pafazaria capitata Diškus & Stonis, **sp. nov.**	L3253	OQ413564*
Pafazaria faboidica Diškus & Stonis, **sp. nov.**	L3252	OQ413565
Paratischeria boehmerica Diškus & Stonis	L3255	OQ413566
Paratischeria boehmerica Diškus & Stonis	L3256	OQ413567
Paratischeria ferruginea Diškus & Stonis	NEPTI024-17	OQ413568
Paratischeria grossa Diškus & Stonis	L3254	OQ413569
Paratischeria hestias (Meyrick)	NEPTI064-17	OQ413570
Paratischeria hestias (Meyrick)	NEPTI065-17	OQ413571
Rytietia uncinata Diškus, Xu & Dai, **sp. nov.**	NEPTI018-17	OQ413572*
Tischeria neokristenseni Diškus & Stonis, **sp. nov.**	NEPTI010-17	OQ413573*
Tischeria neokristenseni Diškus & Stonis, **sp. nov.**	NEPTI011-17	OQ413574

Abbreviations of institutions

BRG*—Biosystematic Research Group, currently based at the State Research Institute Nature Research Centre, Vilnius, Lithuania;
GNU—Leafminer Group, School of Life Sciences, Gannan Normal University, Jiangxi, China;
LEU (formerly abbreviated as VPU)—Lithuanian University of Educational Sciences, Vilnius (now closed down, with scientific collections transferred to ZMUC or temporarily in the possession of the BRG and NRC*), Lithuania;
MfN*—Museum für Naturkunde, Berlin, formerly known as the Museum für Naturkunde der Humboldt Universität zu Berlin or Museum für Naturkunde—Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (in the past, variously abbreviated as LIEB, MFNB, MHB, MHUB, MNB, MNHU, MNHUB, NHMU, NKMB, ZMB, ZMHB, ZMHU, ZMHUB, ZMNB), Germany;
MPUJ—Laboratorio de Entomología, UNESIS, Departamento de Biología, Pontificia Universidad Javeriana, Bogotá (also known as MPUJ_ENT—Coleccion de Entomologia, Museo Javeriano de Historia Natural, Pontificia Universidad Javeriana, Bogotá), Colombia;
NHMUK (formerly abbreviated as BMNH)—The Natural History Museum, London, United Kingdom;
NMNH (formerly abbreviated as USNM)—National Museum of Natural History, Smithsonian Institution, Washington D.C., formerly known as U.S. National Museum of Natural History, USA;
NRC*—State Research Institute Nature Research Centre, Vilnius, Lithuania;
ZIN*—Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia;
ZMUC—Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark.

* Because of the current political situation and international sanctions, all published or unpublished materials collected by the BRG and earlier declared as belonging to ZIN have not been transferred to ZIN. The specimens are currently in the possession of the BRG and will be deposited in the MfN for safekeeping. Such re-deposition (time and list of deposited material) will be announced in future publication(s) by members of the BRG (Stonis, Remeikis, and Diškus).

Diagnostic characters of Tischeriidae

Adults possess various distinctive diagnostic characters (Figs 27–54) which were already extensively reviewed by Braun (1972), Davis (1999), Diškus & Puplesis (2003), and supplemented by Stonis *et al*. (2018a) and Stonis & Solis (2020). Briefly, the following characters are the most distinctive for recognizing the family Tischeriidae: very long, cilia-like sensilla trichodea on the male antenna (Figs 46, 47, 49, 52–54); greatly elongated third antennal segment (Figs 48, 49, 51); flattened adult head with a frontal tuft of slender lamellar scales overlapping the triangular, smoothly scaled frons; often extremely slender phallus in the male genitalia; rounded ovipositor lobes with dark, strongly thickened (stout but short) modified setae; and presence of prela in the female genitalia.

Head slightly (Fig. 50) or distinctly flattened dorso-ventrally (Figs 48, 51). Compoud eyes round or oval, large (Figs 39, 40, 44, 48–51), according to Davis (1999) interocular index is about 2.2. Ocelli absent. Externally, adult head with a frontal tuft (Figs 27, 28, 37–40) comprised of long, relatively wide, lamellar scales overlapping the triangular, smoothly scaled frons (Figs 37, 39, 40); sometimes frontal tuft comprising of both lamellar and piliform scales. Colour of frontal scales often resembling the colour of thorax and forewing and has little or no significance for species differentiation (Diškus & Puplesis 2003). Mouthparts weakly developed. Mandibles greatly reduced as small lobes, not functional. Haustellum (proboscis) relatively long (usually 3–3.5 times longer than length of labial palpi) (Figs 48, 50), with scales at base or in entire proximal part; distal half of the haustellum scaleless but with scutiform, sclerotized plates externally (Figs 41–43). Maxillary palpi short, one to three segments. Labial palpi (Figs 37, 41, 48) three-segmented, usually with the distal (third) segment elongated (Figs 48, 50). Antenna slightly or distinctly longer than 1/2 of the forewing, with a pecten, a slender tuft of long scales on the first segment (scape) and projecting over eye (Figs 38, 40, 44); scape only slightly enlarged, not forming an eye-cap as in the Nepticuloidea (Figs 48, 49). Flagellum of antenna piliform, covered with rows of slender scales on upper side and laterally (Fig. 45); underside (venter) of flagellum scaleless but with sensilla trichodea (singular: sensillum); upper side of female flagellum with short, usually inconspicous sensilla, venter of male antenna with very long sensilla trichodea which are about 2.7–3.5 times longer than the width of the antenna (Figs 46, 47, 49, 54); occasionally male sensilla trichodea slightly shorter or sometimes longer, 4–4.5 times exceeding width of the antenna. Antennal sensilla trichodea are recurved basally (Figs 52–54) although it is difficult to observe/document recurved sensilla because sensilla usually become lost in mounting procedure; we have observed recurved sensilla in species of key genera such as *Coptotriche*, *Tischeria*, and *Astrotischeria*; third segment of the antenna (i.e., the first flagellomere of flagellum) is greatly elongated (Figs 48, 49, 51); the ratio between third segment and the following (fourth) segment is 1:2.6–3.8 (i.e., third segment of antenna is 2.6–3.8 times longer than the fourth segment or distal segments. Collar (Figs 27, 28) usually distinctly paired (sometimes weakly paired), comprised of relatively wide lamellar scales or, occasionally slender, piliform-looking scales.

Metathorax with furcal apophysis joined to secondary arms of metafurcasternum (D. R. Davis, pers. comm.). Forewing lanceolate (Figs 29–31), often irregularly speckled with dark scales, especially abundant in apical half and along dorsal and costal margins; sometimes forewing with a small dark irregular dorsal spot (Figs 32, 33) or with bright, usually yellow-ochre antemedian and postmedian patches; distinctive pattern of forewing (including a fascia) developed only occasionally; forewing underside with small scaleless patches basally covered with microtrichia. Hindwing slender, only occasionally widened and with androconia in males; hindwing underside often with small, basal, scaleless patches.

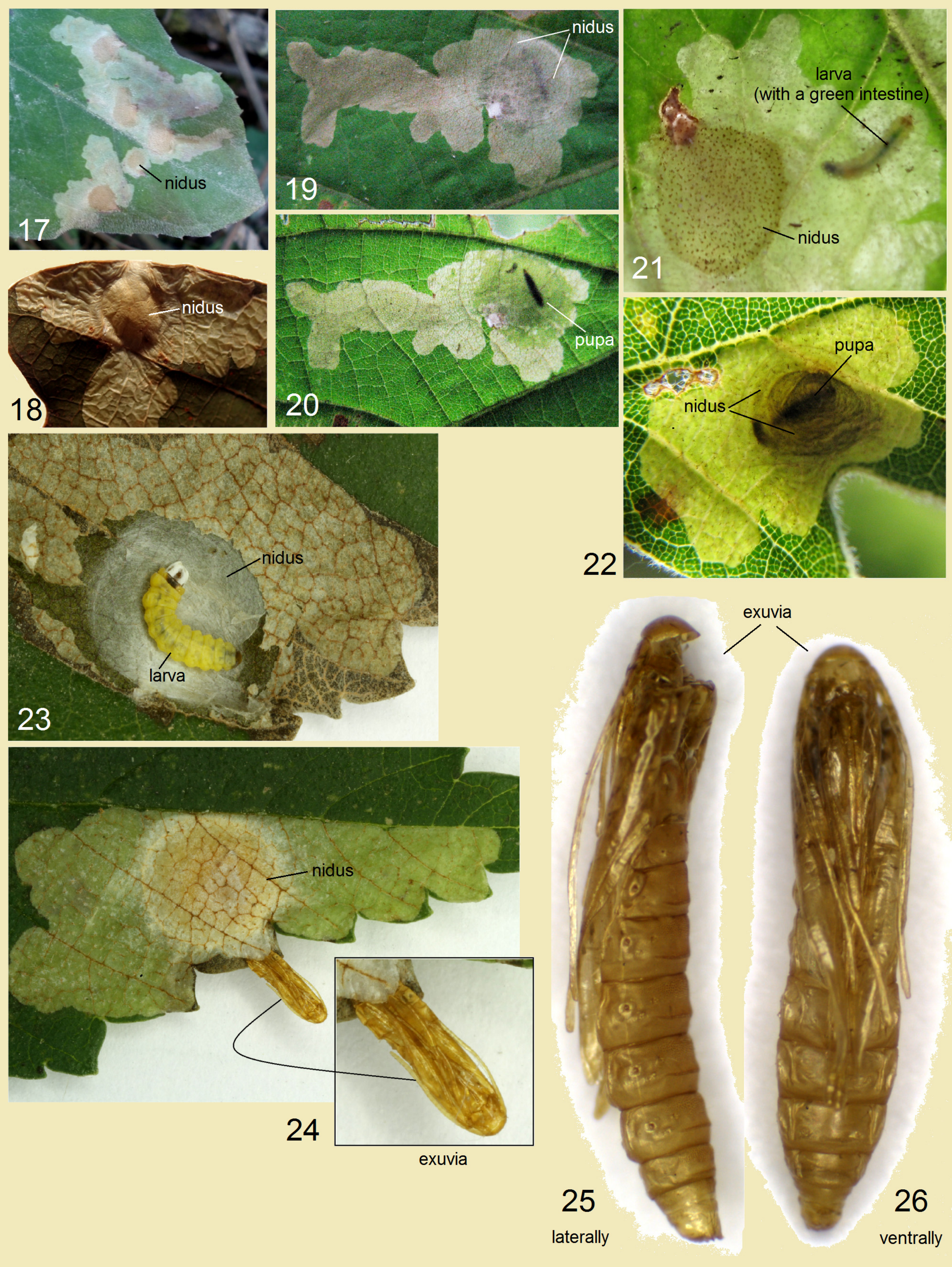
Wing venation is reduced (Figs 29–31), with medial and cubital veins of forewing usually unbranched and discal cell not closed (reduced); five radial veins terminate on costa. Hindwing with open discal cell and usually unbranched medial and cubital veins; male hindwing with a frenulum, a single, strong bristle sometimes followed by a few thickened setae; female with two closely set frenular setae or bristles (Davis, 1999).

Forelegs smooth, midlegs with a pair of sub-basal spurs on tibia; hind tibia with a pair of short, apical spurs, and a pair of longer or very long basal spurs with long spreading or appressed hairs (Diškus & Puplesis 2003).

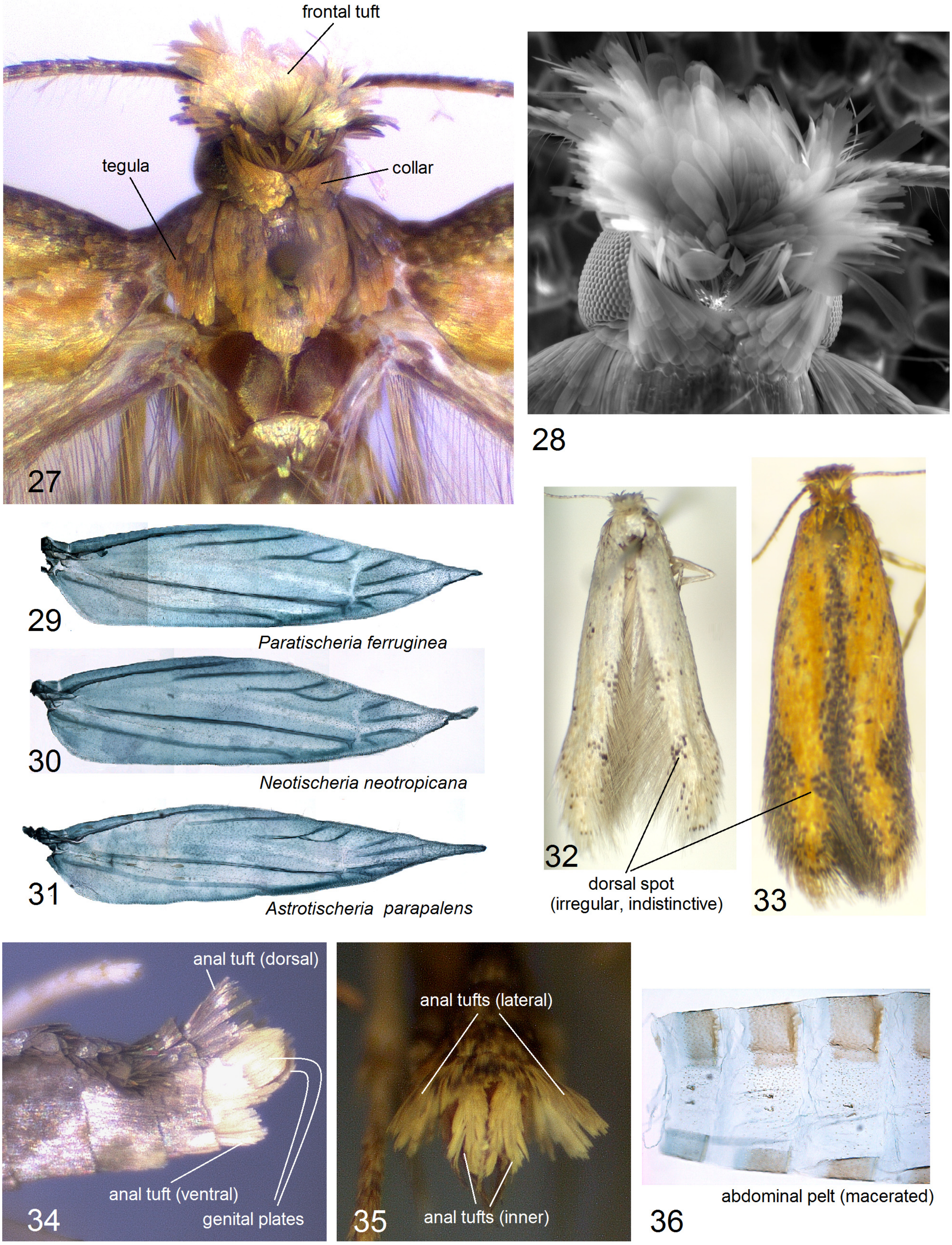
Male abdomen (Fig. 36) with anal tuft(s) of relatively long, very slender, occasionally piliform scales (Fig. 34); anal tufts are usually dorsal, long, and supplemented with ventral but short tufts; occasionally there are additional lateral and inner (median) tufts (Fig. 35).

In the male genitalia, capsule with membranous, usually paired and spined socii; gnathos absent; occasionally replaced by a pseudognathos formed either by thickened socii or formations (outgrows) of the diaphragm of the tegumen. Uncus large, usually with two long lateral or four lobes of different length. Transtilla with a transverse bar occurs only in a single genus, *Coptotriche*; all remaining genera of Tischeriidae do not possess a transtilla, except for a few species having a dorsal transverse joint of the valvae, i.e., a false transtilla. Phallus usually strongly narrowed, extremely slender, rod-like, bifurcated or with spines at its apex, only sometimes wide.

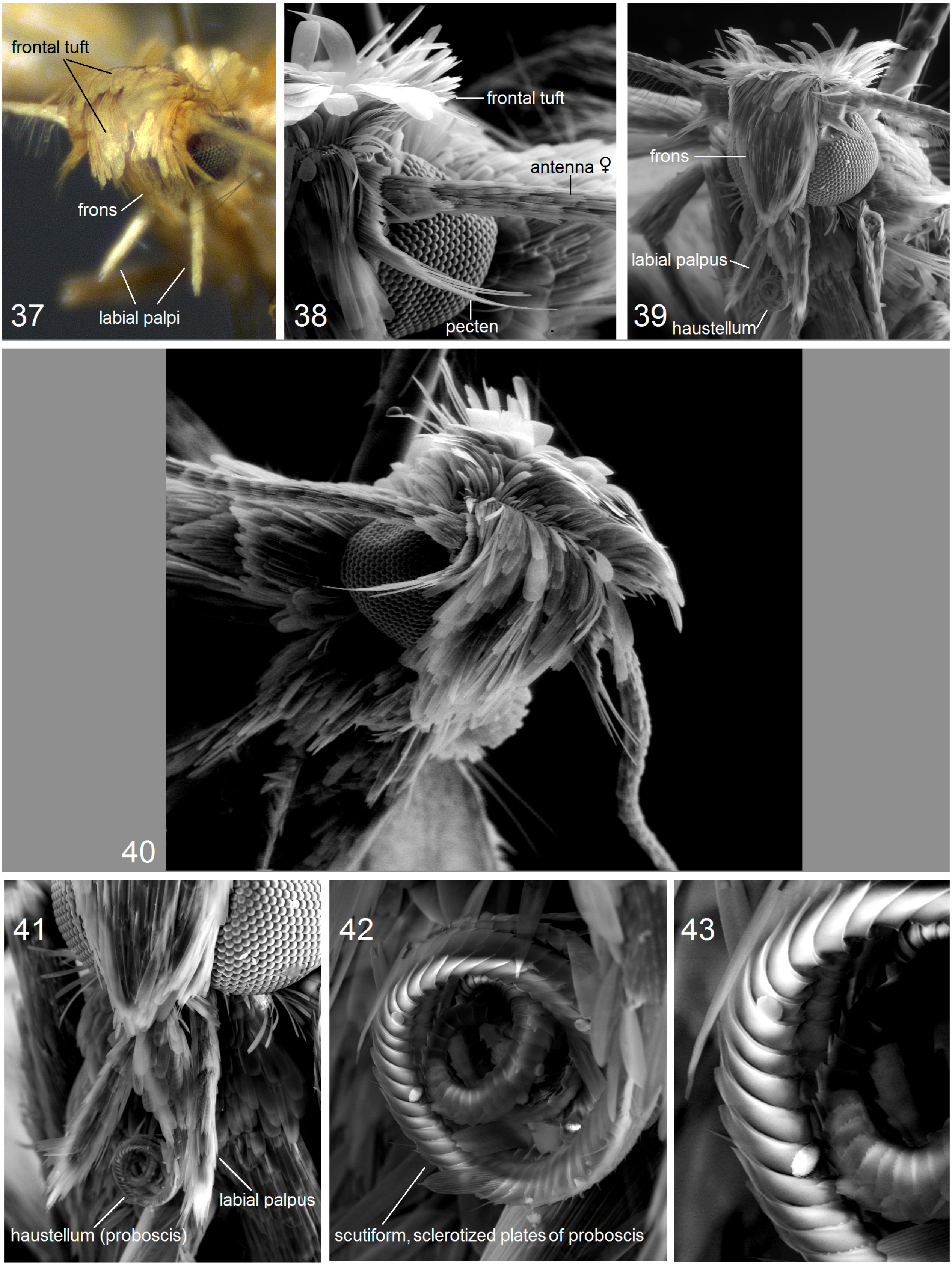
In the female genitalia (Figs 55–60), ovipositor non-extensible and usually non-piercing, except for a very few *Astrotischeria* species with a strongly modified ovipositor (see Stonis *et al.* 2020c), clothed with short, stout and dark modified setae (peg setae) (Figs 57, 59); occasionally peg setae slightly bifid distally; a few species were found without peg setae (e.g., the South American *Astrotischeria atlantica* Diškus & Stonis and *A. incae* Diškus & Stonis, **sp. nov.**, described in this publication). The second pair of ovipositor lobes, lateral and anterior to the main ovipositor lobes, usually significantly smaller, bearing very long slender setae; lateral lobes, lateral and anterior to the second ovipositor lobes, vary from short to long. Anterior and posterior apophyses long and stout, especially the posterior apophyses (Figs 58, 59). Remaining three (occasionally two) apophyses pairs represent slender rod-like or basally wide rod-like projections (possibly from modified 8th and 9th sternites) collectively referred to as the prela and the morphology was described by Braun (1972) (Figs 58, 59). Ventral anterior margin of 8th segment divided into relatively wide rod-like arms (transverse prela), the tip of each arm articulating with an anterior apophysis in a groove 1/2 way of its length; median and inner prela usually shorter, sometimes only the inner prela is long, but slender. Vestibulum usually without a distinctive, thickened plate, or antrum, however, the membrane between two inner prela sometimes can be thickened; a distinctive antrum is present in *Tischeria* Zeller*, Rytietia* **gen. nov.**, and *Manitischeria* Diškus & Stonis. Ductus bursae sometimes with tiny spines proximally, rarely with minute sclerotisations (pectinations) on the main body (Fig. 59). Ductus spermathecae often very narrow, with 2–18 (usually 4–10) coils (Fig. 60); only rarely ductus spermathecae without coils, only slightly sinuous.



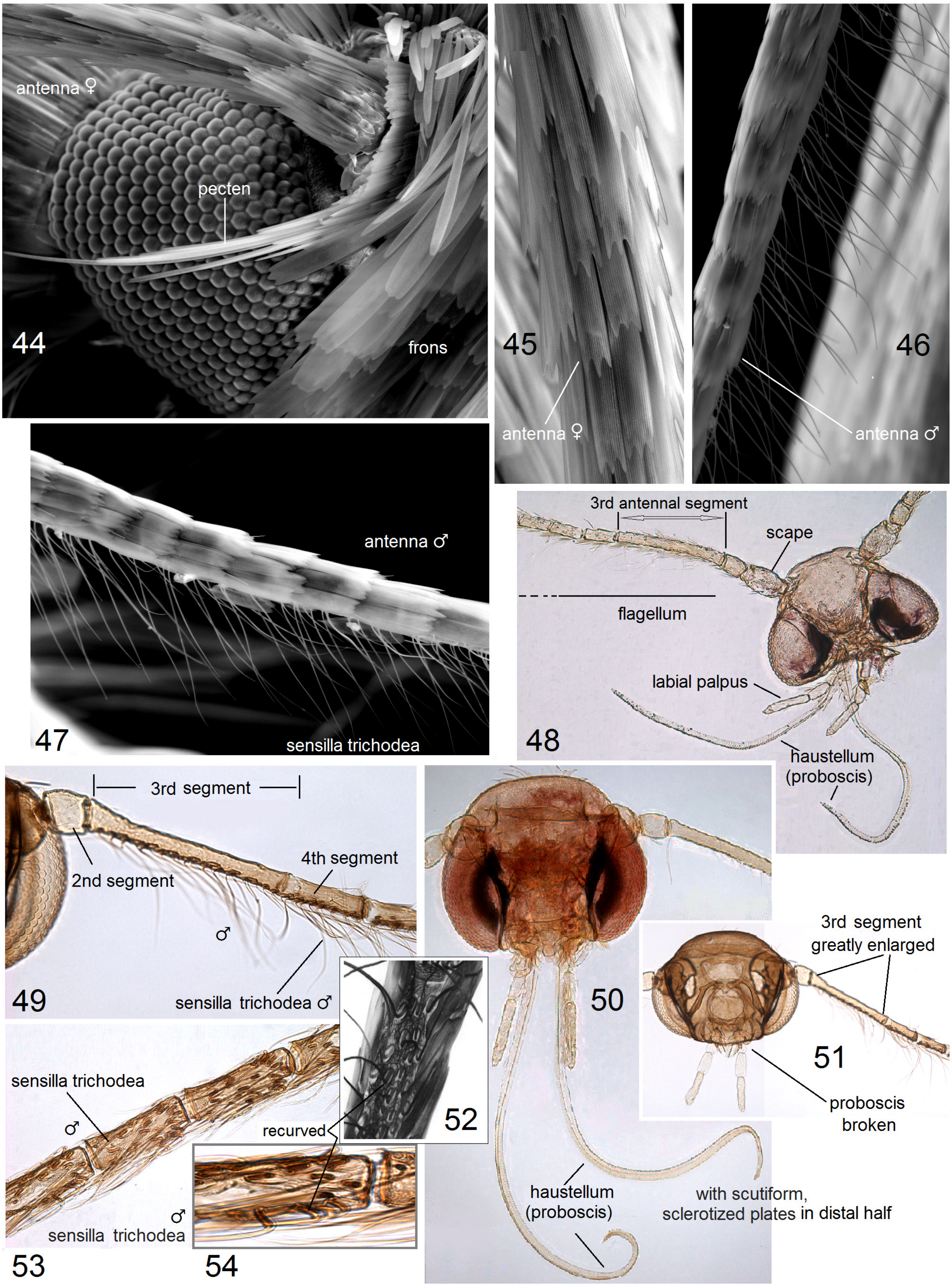
FIGURES 17–26. Leaf mines with a nidus and exuviae of Tischeriidae. 17, South American *Neotischeria conexa* (after Stonis *et al*. 2021c); 18, East Asian *Tischeria sichotensis* (after Stonis *et al*. 2014); 19, 20, South East Asian *Paratischeria hestias* (after Xu *et al*. 2017); 21, South American *Neotischeria conexa* (after Stonis *et al*. 2021c); 22, European *Tischeria decidua* (after Stonis *et al*. 2014); 23, 24, East Asian *T. ulmella* (after Xu *et al*. 2018); 25, 26, South American *Paratischeria ferruginea* (after Stonis *et al*. 2017)



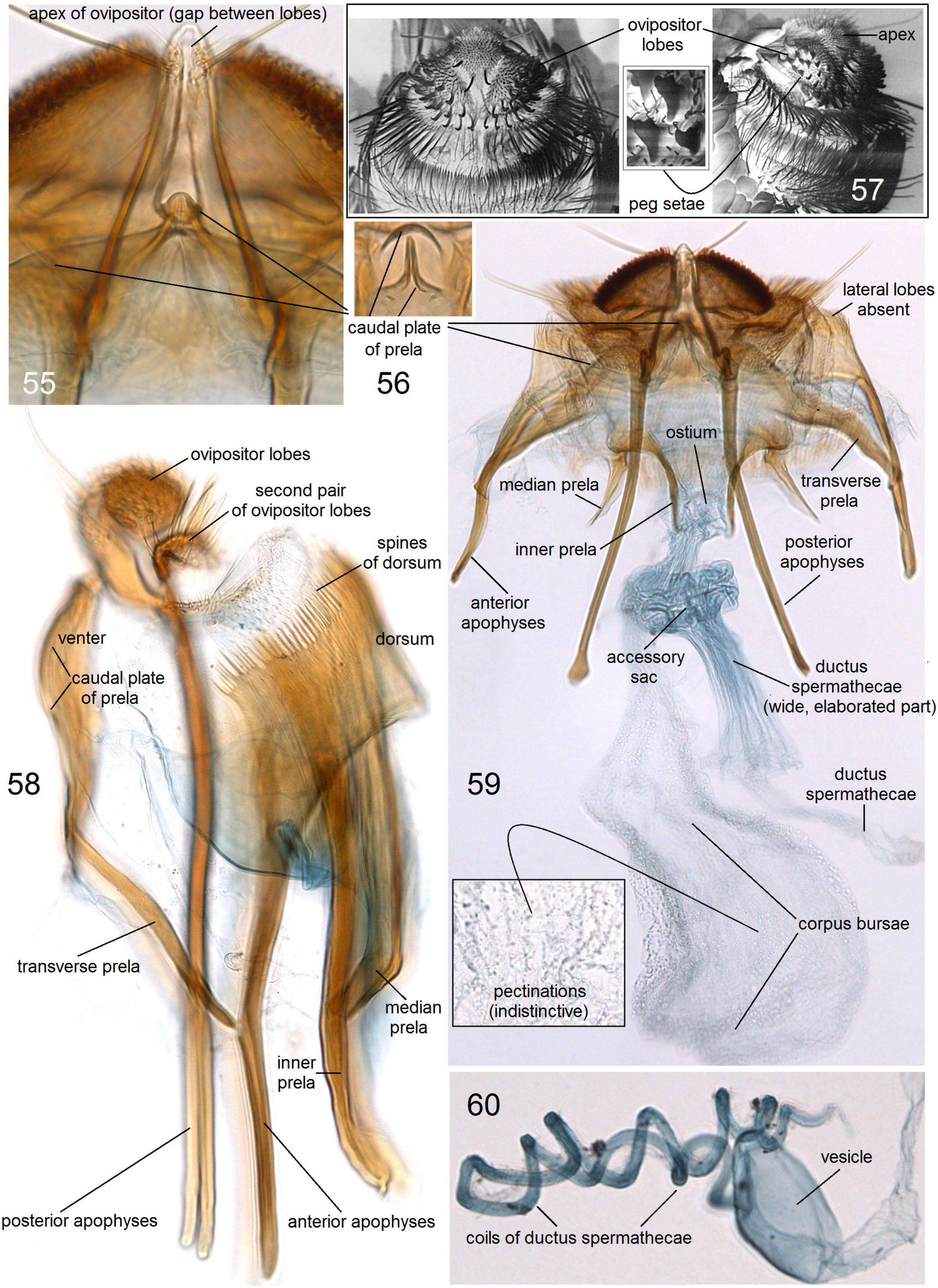
FIGURES 27–36. Details of Tischeriidae morphology. 27, 28, dorsal view of head, *Coptotriche marginea* (Haworth); 29–31, forewing venation (after Stonis *et al*. 2017); 32, habitus, *Astrotischeria heliopsisella* (Chambers) (after Stonis *et al*. 2020c); 33, same, *A. trilobata* Diškus & Stonis (after Stonis *et al*. 2018a); 34, abdomen with anal tufts, *Coptotriche marginea*; 35, same, *A. dondavisi* Stonis & Diškus (after Stonis *et al*. 2019b); 36, macerated abdominal pelt, *Paratischeria ferruginea* Diškus & Stonis (after Stonis *et al*. 2017)



FIGURES 37–43. Details of Tischeriidae head morphology. 37, Caucasian *Tischeria caucasica* Klasiński & Stonis (after Klasiński *et al*. 2020); 38, South East Asian *Rytietia uncinata* **sp. nov.**; 39, European *Coptotriche marginea* (Haworth); 40, *Rytietia uncinata*; 41–43, *Coptotriche marginea*



FIGURES 44–54. Details of Tischeriidae head morphology. 44, 45, South East Asian *Rytietia uncinata* **sp. nov.**; 46, 47, European *Coptotriche marginea* (Haworth); 48, Neotropical *Neotischeria neotropicana* (Diškus & Stonis) (after Stonis *et al*. 2017); 49, South American *Paratischeria ferruginea* Diškus & Stonis (after Stonis *et al*. 2017); 50, Central American *Neotischeria mesoamericana* Diškus & Stonis, slide no. AD874) (after Stonis *et al*. 2017); 51, *P. ferruginea* (after Stonis *et al*. 2017); 52, European *Tischeria ekebladella* (Bjerkander) (after Diškus & Puplesis 2003); 53, 54, *P. ferruginea* (after Stonis *et al*. 2017)



FIGURES 55–60. Details of Tischeriidae female genitalia. 55, South East Asian *Coptotriche asiana* Diškus & Stonis (after Xu *et al*. 2021); 56, South East Asian *Paratischeria boehmerica* Diškus & Stonis (after Stonis *et al*. 2021a); 57, European *Coptotriche angusticolella* (Duponchel) (after Diškus & Puplesis 2003); 58, Central American *Astrotischeria guatemalica* Diškus & Stonis (after Stonis *et al*. 2019b); 59, 60, *Coptotriche asiana* (after Xu *et al*. 2021)

Generic composition of Tischeriidae

Prior to 2003, all Tischeriidae species were combined into a single genus, *Tischeria* Zeller, 1839. In 2003, Puplesis & Diškus (2003) restored the genus *Coptotriche* Walsingham, 1890 to generic status and simultaneously the genus *Astrotischeria* Puplesis & Diškus, 2003 was erected for North and South American tischeriid species with striking apomorphies in the genitalia and larval feeding preference on Asteraceae and Malvaceae host plants. Recently four additional genera were described: *Paratischeria* Diškus & Stonis, 2017 (Stonis *et al*. 2017), *Dishkeya* Stonis, 2020 (Stonis & Solis 2020), *Manitischeria* Diškus & Stonis, 2021 (Stonis *et al*. 2021d), and *Neotischeria* Diškus & Stonis, 2021 (Stonis *et al*. 2021c). Thus prior to our study, seven taxa of generic rank had been discovered and described.

Tischeriidae are taxonomically diverse despite the fact that it represents a relatively small, monophyletic lepidopteran family and share many striking morphological and biological characteristics, including very similar, sometimes identical wing venation and external characters of adults. We discovered morphological diversity in the male and female genitalia, and biology (Tables 2, 3).

Morphological and biological studies, supplemented with some molecular research, have revealed a total of 11 taxa at the generic rank. All previously described genera, including the recently named *Dishkeya* Stonis (Stonis & Solis 2020) and *Manitischeria* Diškus & Stonis (Stonis *et al*. 2021d), were well-supported in this study. Four new genera appeared to be new and are described in this paper: *Coptotrichoides* Diškus & Stonis, **gen. nov.**; *Rytietia* Diškus, Xu & Dai, **gen. nov.**; *Pafazaria* Diškus & Stonis, **gen. nov.**; and *Gnathitischeria* Diškus, **gen. nov.**

Since all Tischeriidae taxa of generic rank are quite distinctive in the male genitalia, a diagnostic key of recognised Tischeriidae genera is provided on the basis of the male genitalia, supplemented with some characters of the female genitalia and larval feeding-preference data (Fig. 61).

According to the molecular analysis, all Tischeriidae genera appear to form separate, distinctive clades (Figs 62, 63). However, this analysis was only possible on randomly selected species because at least in a couple of genera (*Astrotischeria* and *Gnathitischeria*) the partial sequence of mtDNA CO1-5’ gene did not provide resolution (see Discussion). Among our numerously obtained molecular trees, the placement of genera and dichotomies slightly varied depending on a selected outgroup and species for analyses. Four genera (*Gnathitischeria* + *Astrotischeria*) + (*Neotischeria* + *Pafazaria*) (Fig. 63) or five (those mentioned previously + *Paratischeria*) (Fig. 62) were clustered together (see Discussion).

Manitischeria sometimes clustered with (*Pafazaria* + *Neotischeria*) + (*Gnathistischeria* + *Astrotischeria* + *Paratischeria*) (Fig. 62) or with *Paratischeria* + (*Pafazaria* + *Neotischeria*) + (*Gnathitischeria* + *Astrotischeria*) (Fig. 63). However, we hypothesize that the relationship of *Manitischeria* with *Tischeria* (Fig. 64), or with any other juxta-possessing genus (but not *Paratischeria*), is the most probable because of the strong support of the morphological data (e.g., the presence of a distinctive, highly-derived sclerite, i.e., a juxta).

Because of the presence of a transtilla, a unique character of the male genitalia among Tischeriidae, the basal position of *Coptotriche* (Figs 63, 64) was among the most interesting but a predictable outcome (see Discussion and clusters shown in Fig. 65).

In our analyses, one species, *Coptotriche serjaniphaga*, persistently had a position close to, but separate from *Coptotriche*. This motivated us to revise the taxonomic status of *C. serjaniphaga* and to re-check all morphologically and biologically similar species. Our findings suggested a new genus, *Coptotrichoides*, for all currently known Sapindaceae-feeding species with distinctive characters in the male genitalia described in this paper (Tables 2, 3; Figs 62–64).

The status and uniqueness of the recently described genus *Dishkeya* (Stonis & Solis 2020; Stonis *et al*. 2022a) was supported in this study (Figs 62–64); however, only on the basis of a single species, *D. bifurcata* (Braun) (Fig. 66). Usually *Dishkeya* and *Coptotrichoides* grouped together as sister taxa (Figs 62, 63). It is interesting to note that *Dishkeya* occasionally also clustered in some our analyses as a sister taxon to *Rytietia* (Fig. 66), a new genus described in this publication.

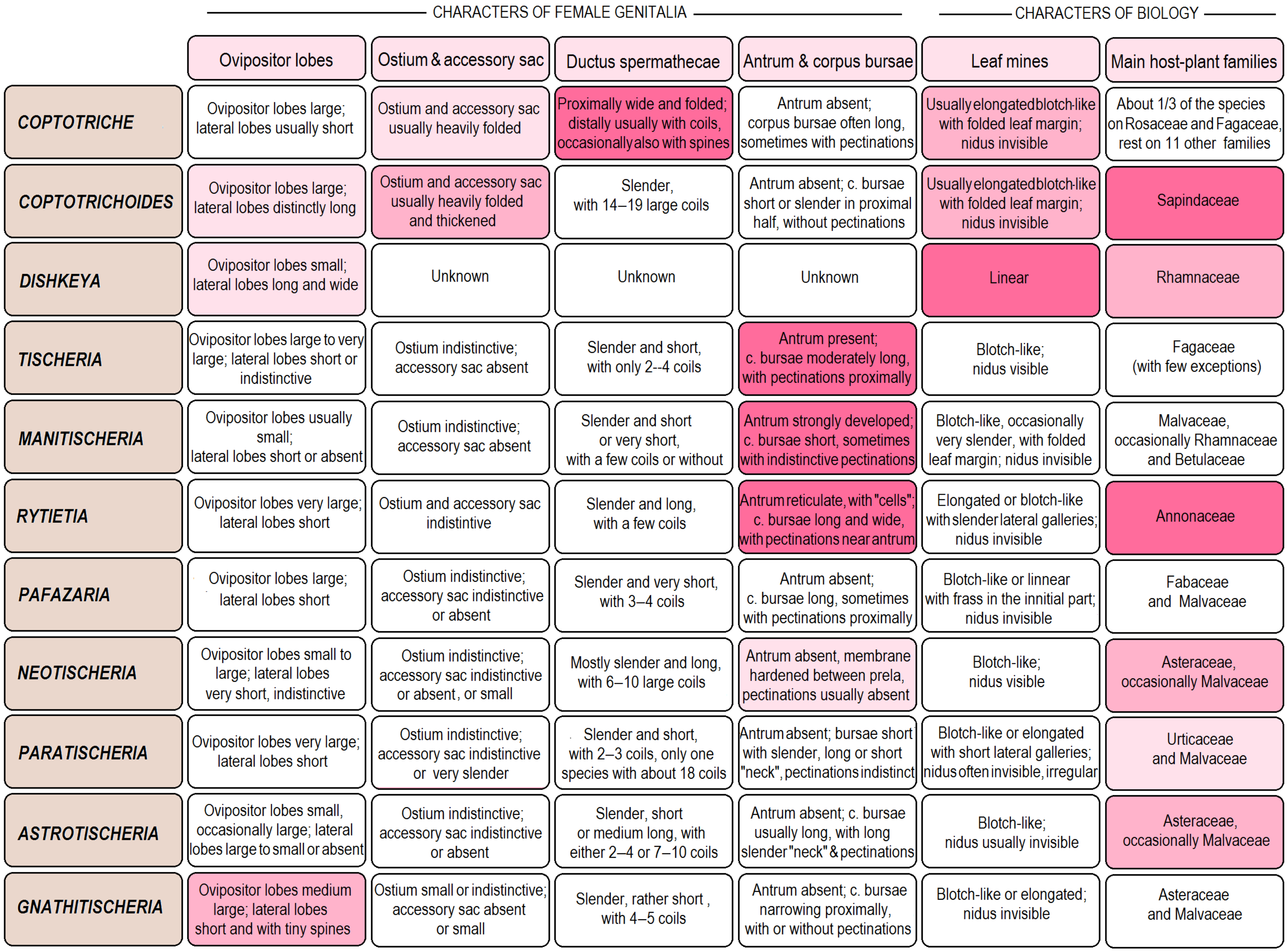
TABLE 2. Genera of Tischeriidae and their diagnostic characters of male genitalia

	CHARACTERS OF MALE GENITALIA					
	Uncus & socii	Tegumen & diaphragm	Valva	Transtilla	Anellus, juxta & vinculum	Phallus
COPTOTRICHE	Uncus with two large lobes; socii membranous, spinose	Tegumen short, diaphragm distinctly spinose	Wide apically	Present, with a distinctive transverse bar	Anellus membranous, spinose; vinculum short, sometimes with a process	Tulip-shaped with many large spines or rod-like with two apical lobes and a few spines
COPTOTRICHOIDES	Uncus with two long, rather slender lobes; socii membranous, spinose	Tegumen usually long; diaphragm only occasionally little spinose	Tapering towards apex, wide basally	Absent	Anellus absent; juxta absent; vinculum short, with a rather long to very long process	Rod-like, usually very long, with slender lateral lobes and median process apically
DISHKEYA	Uncus with long slender or wide lobes; socii modified, usually as a pseudognathos	Tegumen long; diaphragm without spines	Slender, often with small to large inner process or lobe	Absent	Anellus absent; juxta absent; vinculum long distally rounded or truncated	Very wide, with lateral processes and carinae
TISCHERIA	Uncus with two large lobes; socii membranous, spinose	Tegumen usually long; diaphragm only occasionally little spinose	Very slender in apical third, wide basally	Absent	Anellus absent; juxta present, well-developed	Wide to very wide, with long lateral processes
MANITISCHERIA	Uncus with two long, slender lobes; socii membranous, weakly spinose	Tegumen with a frame-like thickening, rather short; diaphragm without spines	With a lateral process ("arm") apically, wide basally	Absent	Anellus absent; juxta present, well-developed	Rod-like, with basal projections
RYTIETIA	Uncus with two large lobes; socii membranous, spinose	Tegumen rather short; diaphragm without spines	Very slender in apical third, wide basally	Absent	Anellus absent; juxta present, well-developed	Rod-like, with basal projections
PAFAZARIA	Uncus with two wide lobes; socii large, membranous, spinose	Tegumen rather short; diaphragm with a spinose lobe-like projection	Slender to wide basally, with inner lobe(s)	Absent	Anellus and juxta present; juxta with a "hood"; vinculum short	Rod-like, sometimes expanded apically
NEOTISCHERIA	Uncus usually with two, occasionally four lobes; socii membranous, spinose	Tegumen usually long; diaphragm without spines	Slender to wide basally, without dorsal lobe(s)	Absent	Anellus well-developed, laterally thickened; vinculum short to long	Rod-like, bifid apically, without lobes or spines
PARATISCHERIA	Uncus with two long lobes; socii membranous, spinose, moderately small	Tegumen rather long; with a unique dorsal plate; diaphragm without spines	Slender to wide basally, with a very long basal process	Absent	Anellus thickened laterally; vinculum often long, rounded or triangular	Rod-like, bifid apically, sometimes with apical lobes, expanded at the base
ASTROTISCHERIA	Uncus usually with four medially short lobes; socii membranous, spinose	Tegumen usually long; diaphragm without spines	Divided, with a slender ventral lobe and elaborated dorsal lobe(s)	Absent	Anellus often thickened laterally; vinculum long, triangular or rounded distally	Rod-like, bifid apically, with slender lobes or spines
GNATHITISCHERIA	Uncus with two elaborated lobes; socii very large, indistinctly spinose	Tegumen frame-like; pseudognathos present; diaphragm without spines	Divided, with a slender ventral lobe and elaborated dorsal lobe(s)	Absent	Anellus thickened only caudally or absent; vinculum long, rounded distally	Rod-like, with two wide lateral lobes apically

🟥 Most striking characters of a genus

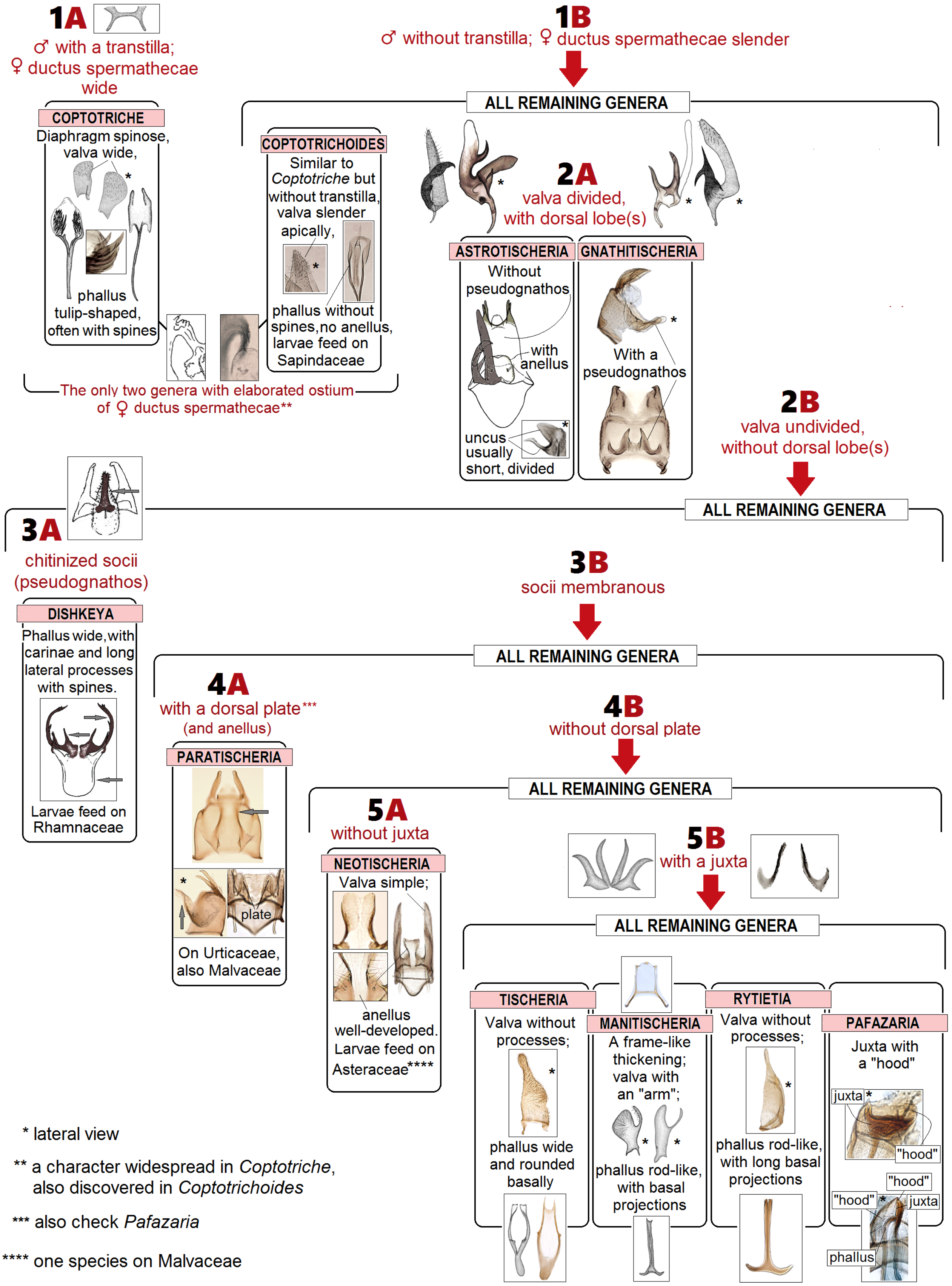
▨–□ Other important characters of the generic diagnostics

TABLE 3. Genera of Tischeriidae and their diagnostic characters of female genitalia and biology



	CHARACTERS OF FEMALE GENITALIA				CHARACTERS OF BIOLOGY	
	Ovipositor lobes	Ostium & accessory sac	Ductus spermathecae	Antrum & corpus bursae	Leaf mines	Main host-plant families
COPTOTRICHE	Ovipositor lobes large; lateral lobes usually short	Ostium and accessory sac usually heavily folded	Proximally wide and folded; distally usually with coils, occasionally also with spines	Antrum absent; corpus bursae often long, sometimes with pectinations	Usually elongated blotch-like with folded leaf margin; nidus invisible	About 1/3 of the species on Rosaceae and Fagaceae, rest on 11 other families
COPTOTRICHOIDES	Ovipositor lobes large; lateral lobes distinctly long	Ostium and accessory sac usually heavily folded and thickened	Slender, with 14–19 large coils	Antrum absent; c. bursae short or slender in proximal half, without pectinations	Usually elongated blotch-like with folded leaf margin; nidus invisible	Sapindaceae
DISHKEYA	Ovipositor lobes small; lateral lobes long and wide	Unknown	Unknown	Unknown	Linear	Rhamnaceae
TISCHERIA	Ovipositor lobes large to very large; lateral lobes short or indistinctive	Ostium indistinctive; accessory sac absent	Slender and short, with only 2--4 coils	Antrum present; c. bursae moderately long, with pectinations proximally	Blotch-like; nidus visible	Fagaceae (with few exceptions)
MANITISCHERIA	Ovipositor lobes usually small; lateral lobes short or absent	Ostium indistinctive; accessory sac absent	Slender and short or very short, with a few coils or without	Antrum strongly developed; c. bursae short, sometimes with indistinctive pectinations	Blotch-like, occasionally very slender, with folded leaf margin; nidus invisible	Malvaceae, occasionally Rhamnaceae and Betulaceae
RYTIETIA	Ovipositor lobes very large; lateral lobes short	Ostium and accessory sac indistintive	Slender and long, with a few coils	Antrum reticulate, with "cells"; c. bursae long and wide, with pectinations near antrum	Elongated or blotch-like with slender lateral galleries; nidus invisible	Annonaceae
PAFAZARIA	Ovipositor lobes large; lateral lobes short	Ostium indistinctive; accessory sac indistinctive or absent	Slender and very short, with 3–4 coils	Antrum absent; c. bursae long, sometimes with pectinations proximally	Blotch-like or linnear with frass in the initial part; nidus invisible	Fabaceae and Malvaceae
NEOTISCHERIA	Ovipositor lobes small to large; lateral lobes very short, indistinctive	Ostium indistinctive; accessory sac indistinctive or absent, or small	Mostly slender and long, with 6–10 large coils	Antrum absent, membrane hardened between prela, pectinations usually absent	Blotch-like; nidus visible	Asteraceae, occasionally Malvaceae
PARATISCHERIA	Ovipositor lobes very large; lateral lobes short	Ostium indistinctive; accessory sac indistinctive or very slender	Slender and short, with 2–3 coils, only one species with about 18 coils	Antrum absent; bursae short with slender, long or short "neck", pectinations indistinct	Blotch-like or elongated with short lateral galleries; nidus often invisible, irregular	Urticaceae and Malvaceae
ASTROTISCHERIA	Ovipositor lobes small, occasionally large; lateral lobes large to small or absent	Ostium indistinctive; accessory sac indistinctive or absent	Slender, short or medium long, with either 2–4 or 7–10 coils	Antrum absent; c. bursae usually long, with long slender "neck" & pectinations	Blotch-like; nidus usually invisible	Asteraceae, occasionally Malvaceae
GNATHITISCHERIA	Ovipositor lobes medium large; lateral lobes short and with tiny spines	Ostium small or indistinctive; accessory sac absent or small	Slender, rather short , with 4–5 coils	Antrum absent; c. bursae narrowing proximally, with or without pectinations	Blotch-like or elongated; nidus invisible	Asteraceae and Malvaceae

🟥 Most striking characters of a genus ▨—☐ Other important characters of the generic diagnostics



* lateral view

** a character widespread in *Coptotriche*, also discovered in *Coptotrichoides*

*** also check *Pafazaria*

**** one species on Malvaceae

FIGURE 61. Pictorial key to the genera of Tischeriidae

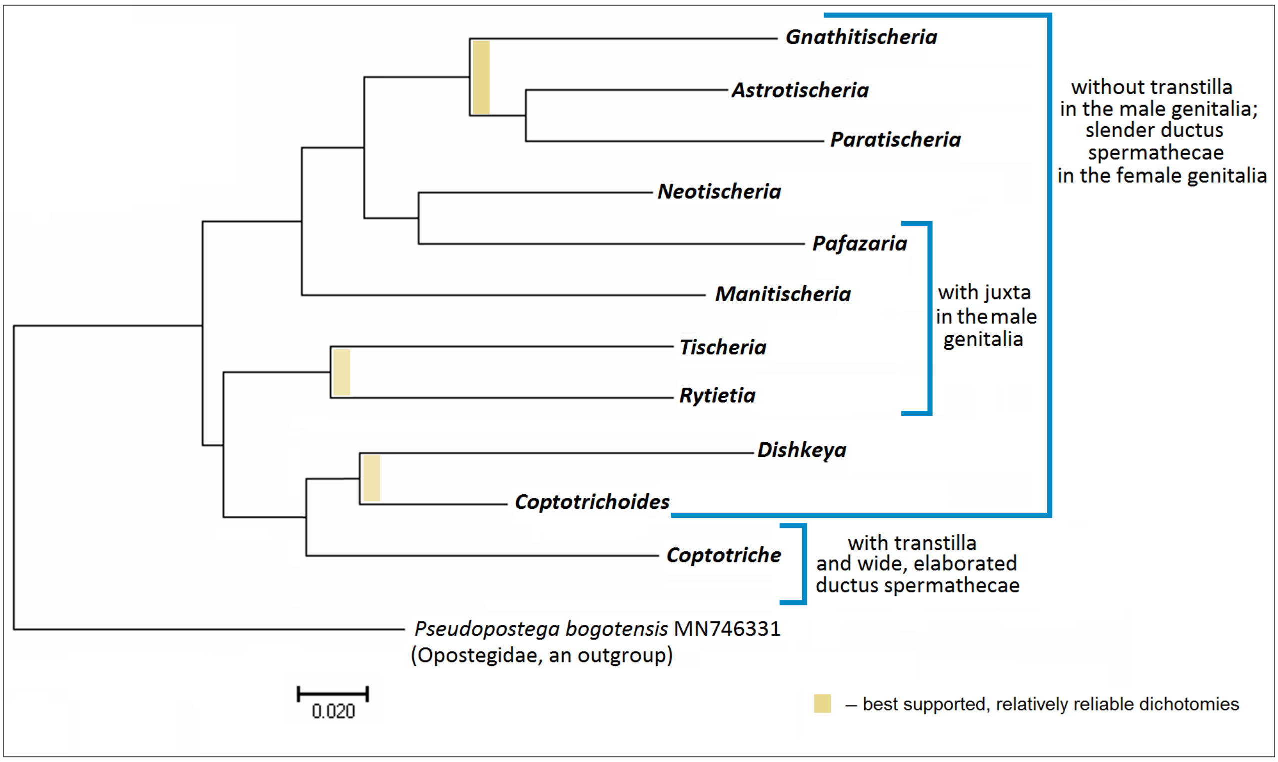
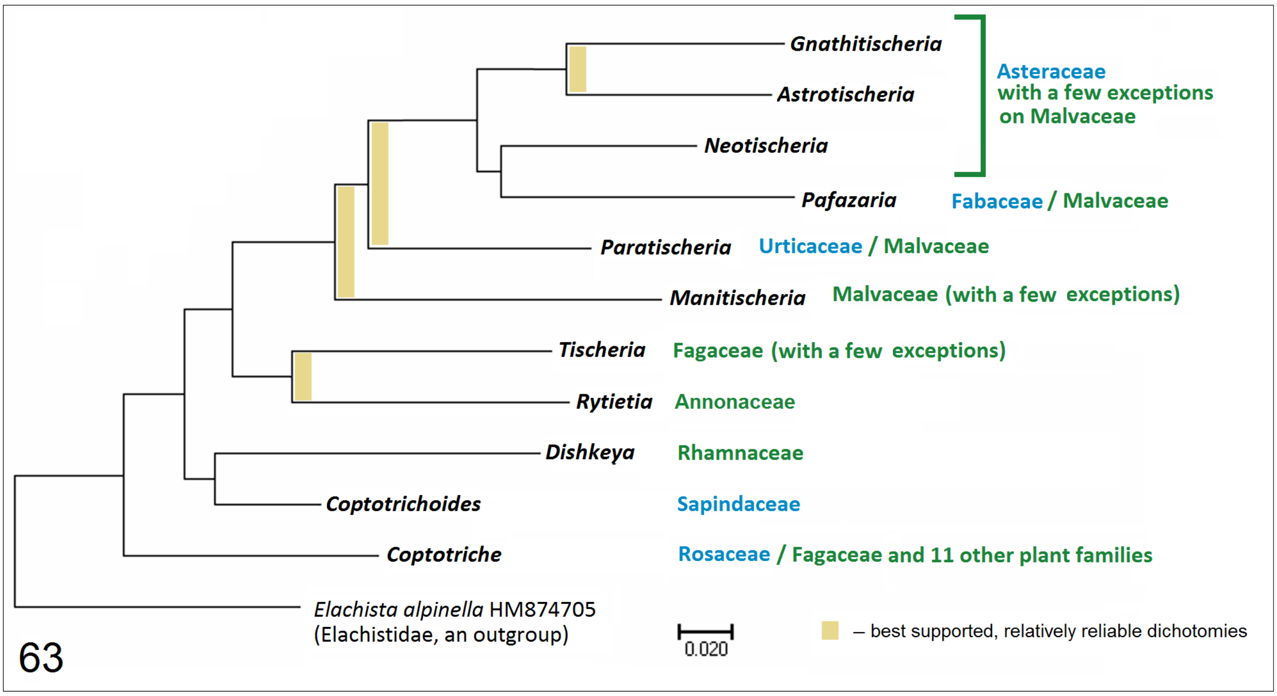
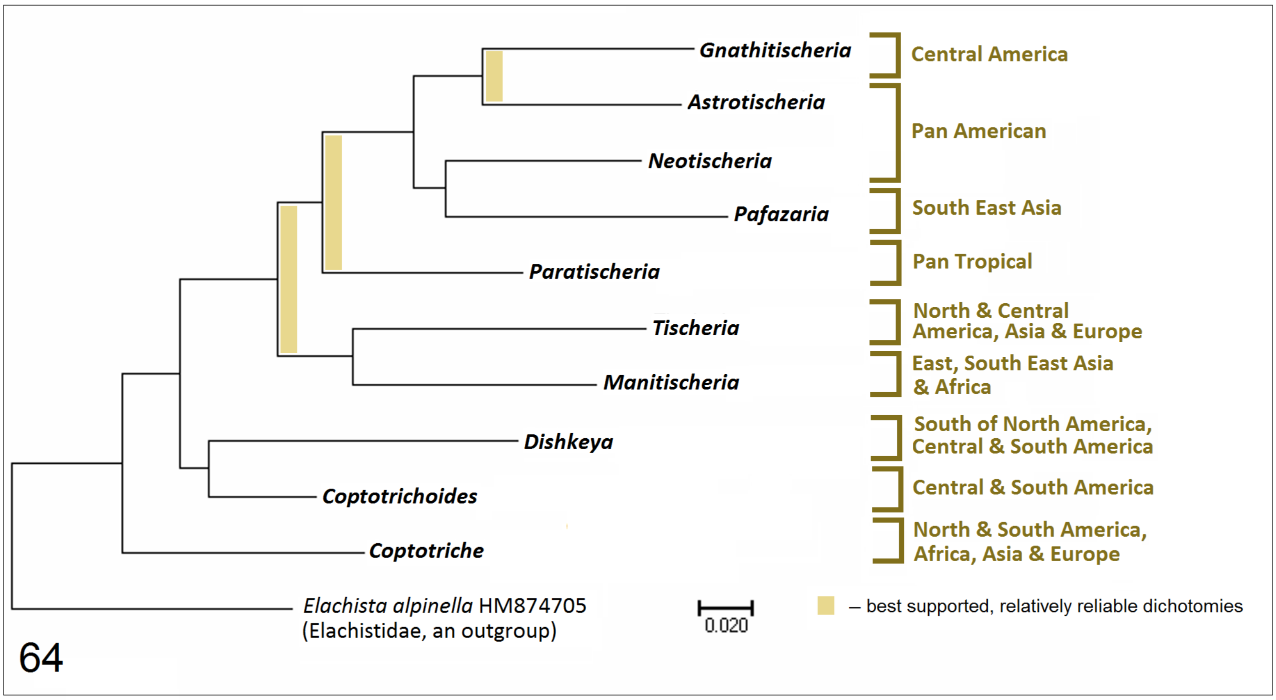


FIGURE 62. The Maximum Likelihood tree of 11 randomly selected sequences of species representing 11 genera of Tischeriidae (Table 1 + downloaded *Paratischeria ferruginea* HM244395, *Neotischeria neotropicana* HM244391, *Dishkeya bifurcata* LNAUT3265-15, *Coptotrichoides serjaniphaga* OK017167) based on the 608 bp long mtDNA CO1-5' sequences). The Kimura 2-parameter model (1.000 replicates) was used to calculate divergence. The best supported and resolved dichotomies are highlighted. The morphological differences of genitalia are shown to the right of the tree

Among Tischeriidae, there are only four genera (*Pafazaria*, *Manitischeria*, *Tischeria, Rytietia*) with a juxta in the male genitalia. In our best resolved trees, these four genera often clustered together as separate branches: *Tischeria* as a sister clade to *Rytietia*, and *Manitischeria* as a sister clade to *Pafazaria* (Fig. 67).

Species currently in *Manitischeria* (Stonis *et al.* 2021d) were previously treated as members of *Tischeria*. However, in our molecular trees, *Manitischeria* and *Tischeria* were always distinctly separate clades and strongly supported two genera. When *Rytietia* was omitted from the analysis, *Manitischeria* always grouped with *Tischeria* as a sister taxon (Fig. 64). This is expected since they are genera characterized by the presence of a juxta (but no anellus) in the male genitalia and a unique antrum in the female genitalia. From a functional point of view, the appearance of the juxta is an important evolutionary, morphological adaptation, and is strongly developed in both genera. The juxta is the most important morphological feature, not only in the diagnosis of genera, but also to differentiate species in these genera. However, in most of our other trees, *Manitischeria* did not cluster with *Tischeria*, but appeared in a dichotomy with (*Pafazaria* + *Neotischeria*) + (*Astrotischeria* + *Gnathitischeria*) (Fig. 63) and *Paratischeria* (Fig. 62), or appeared as the sister clade to *Pafazaria* (Fig. 67).





FIGURES 63, 64. The Maximum Likelihood trees of Tischeriidae based on the 608 bp long mtDNA CO1-5' sequences. The Kimura 2-parameter model (1.000 replicates) was used to calculate divergence. The best supported and resolved dichotomies are highlighted. 63, using the same (as in the Fig. 62) 11 randomly selected sequences of species representing 11 genera of Tischeriidae; the families of host plants are shown to the right of the tree; 64, same, but omitting *Rytietia uncinata* **sp. nov.**; the distribution of species is shown to the right of the tree

Neotischeria, in contrast to all other Tischeriidae genera, seems to be a taxon with a few, and not very distinctive diagnostic morphological or biological characters (apomorphies) (see Tables 2, 3; Fig. 61). Nevertheless, *Neotischeria* appears as a separate clade in our molecular trees. In our best resolved molecular cladograms, this recently described genus (Stonis *et al*. 2021c) usually clustered as the sister taxon to *Pafazaria* (Figs 62, 63), and with the omission of *Pafazaria* in analyses, it clusters with *Astrotischeria* (Fig. 77).

In this analysis, *Paratischeria* (*sensu stricto*, see the concept by Stonis *et al*. 2021c) sometimes grouped as the sister taxon to *Neotischeria* (Fig. 69) or *Astrotischeria* (Fig. 62). However, most often *Paratischeria* was the sister taxon to the clade *Pafazaria* + *Neotischeria* (Fig. 68), though this dichotomy was weakly supported. But *Paratischeria* also appears as the sister taxon to the cluster (*Neotischeria* + *Pafazaria*) + (*Astrotischeria* + *Gnathitischeria*) or in one dichotomy *Paratischeria* grouped with *Astrotischeria* (Figs 62–64). Within the genus *Paratischeria* (Figs 70–76), the species exhibited an unexpected dichotomous pattern, not always congruent with morphology or host-plant data (see Discussion).

The genus *Astrotischeria*, along with the newly erected *Gnathitischeria*, are probably among the most morphologically striking taxa of Tischeriidae because of the divided valva, possessing one or two dorsal lobes, and also the presence of a modified, elaborated uncus. In our molecular research both *Astrotischeria* and *Gnathitischeria* were recognised as two taxa at the generic rank (Figs 62, 63). However, when the available sequences were analysed all together, species in these two genera were unresolved and bootstrap support values were often very low in the majority of the dichotomies (see Figs 78, 79 and Discussion).

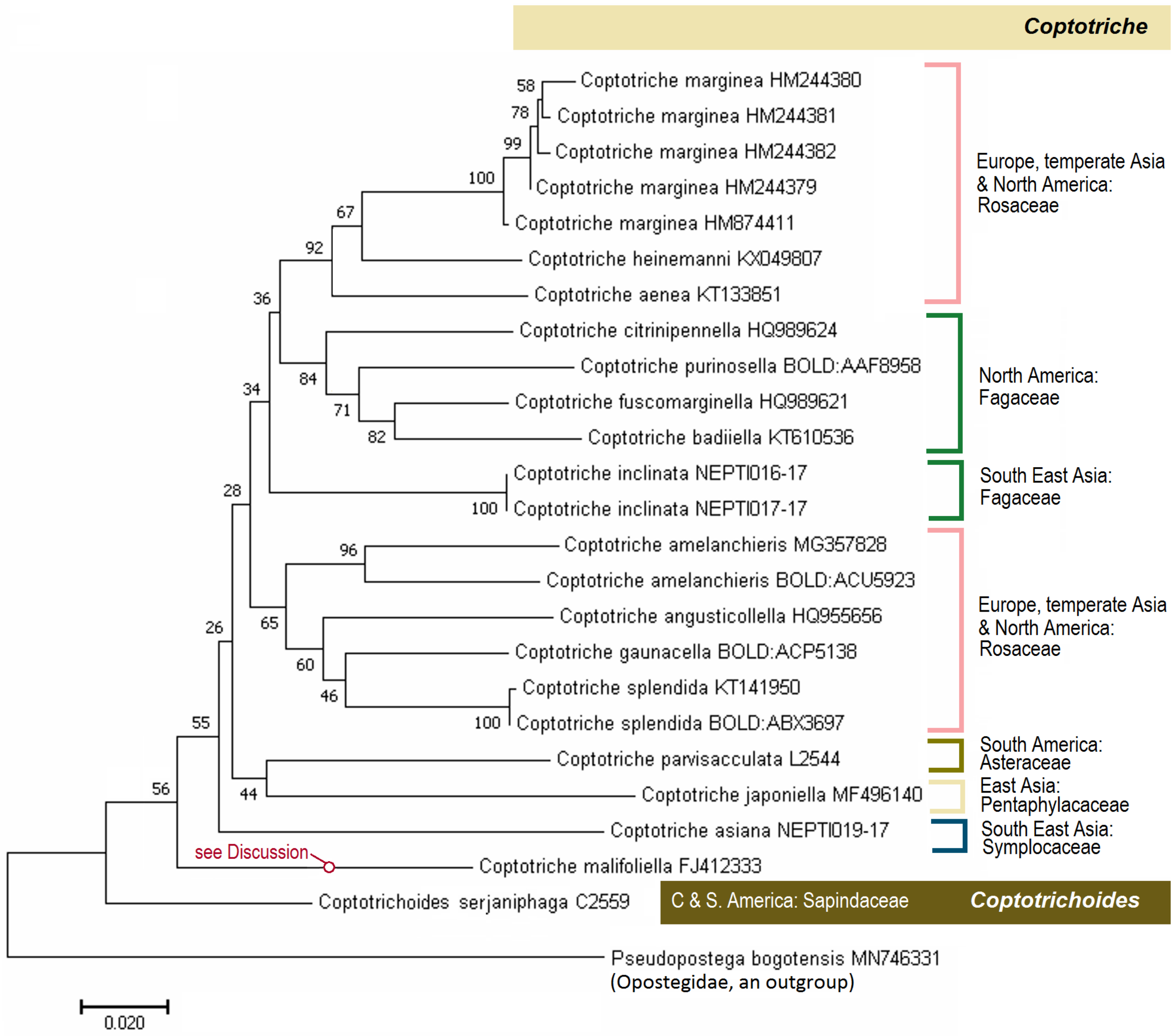
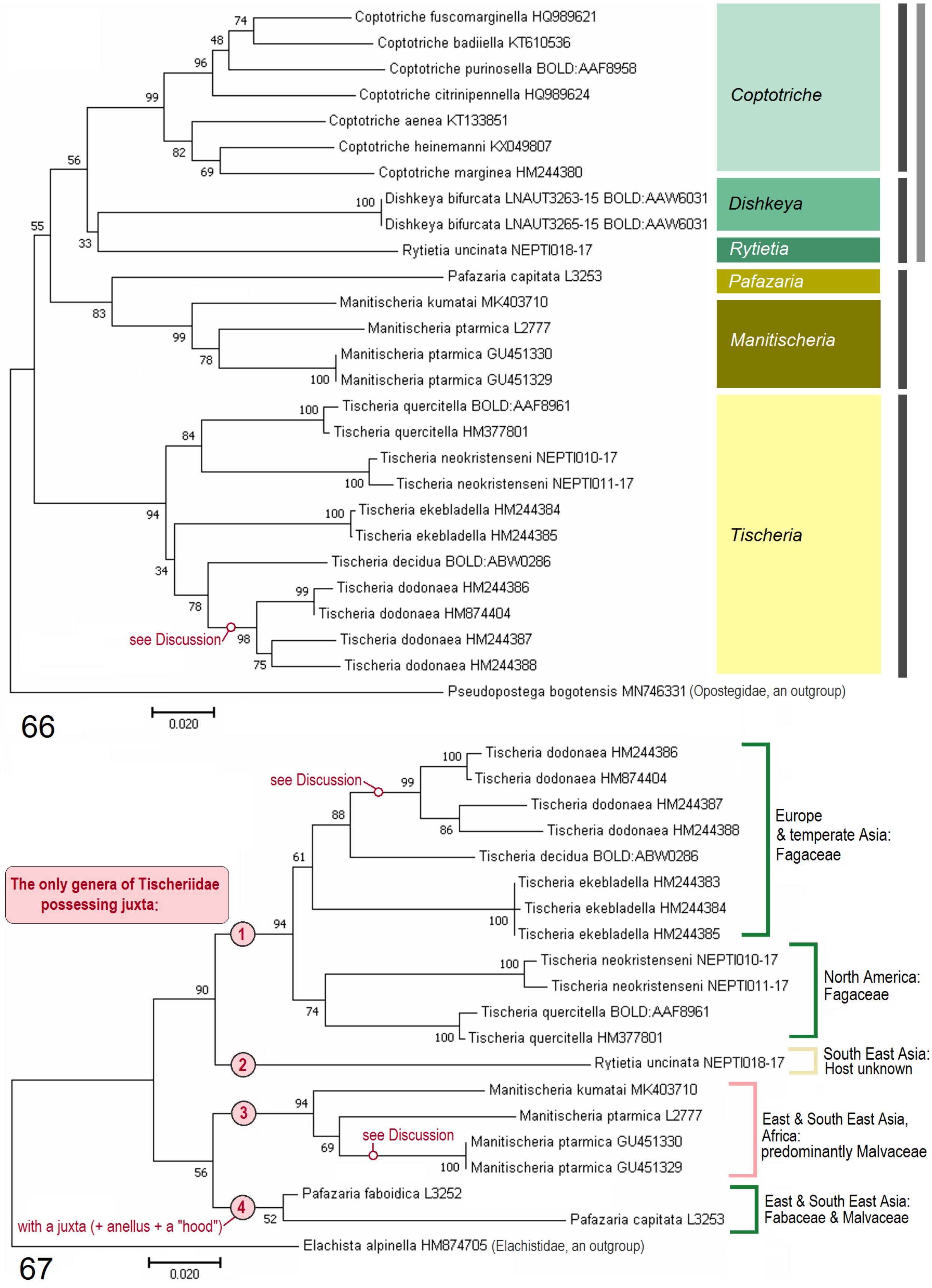
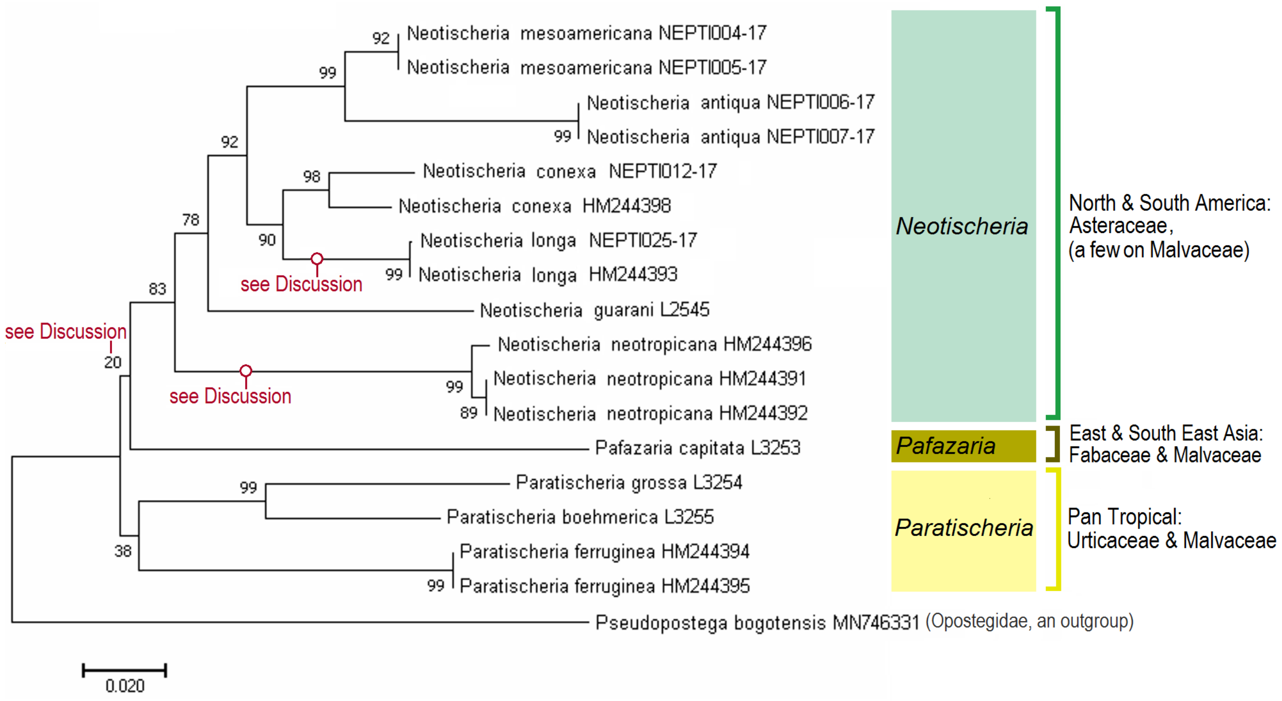


FIGURE 65. The Neighbor-Joining tree of the 608 bp long mtDNA CO1-5’ *Coptotriche* and *Coptotrichoides* **gen. nov.** sequences. The Kimura 2-parameter model was used to calculate divergence. The percentage of replicate trees, in which the associated taxa clustered together in the bootstrap test (10.000 replicates), are shown next to the branches. The families of host plants and species distribution are shown to the right of the tree. (Remark: this was also performed applying the Maximum Likelihood method and the results were identical)



FIGURES 66, 67. The Neighbor-Joining tree based of the 608 bp long mtDNA CO1-5' Tischeriidae sequences. The Kimura 2-parameter model was used to calculate the divergence. 66, using the sequences of *Coptotriche, Dishkeya*, *Rytietia* **gen. nov.**, *Pafazaria* **gen. nov.**, *Manitischeria*, and *Tischeria* species; 67, using sequences of genera with a juxta in the male genitalia (Remark: this was also performed applying Maximum Likelihood method and the results were similar)



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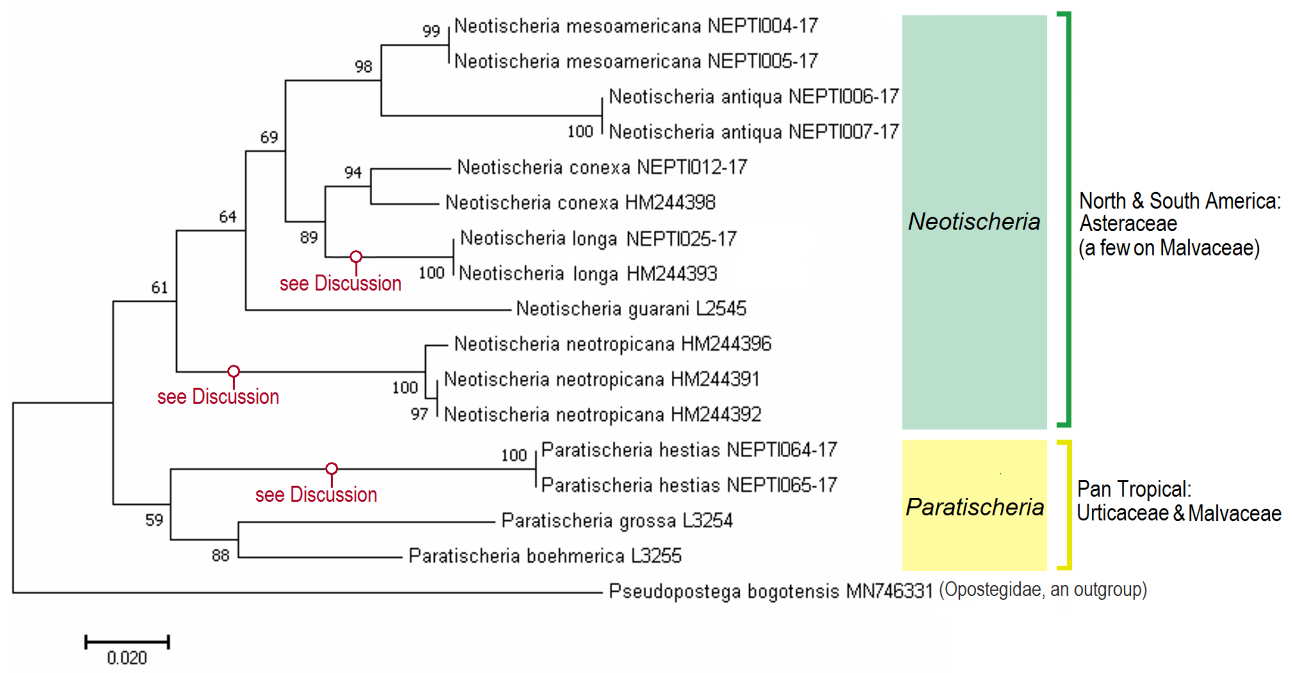

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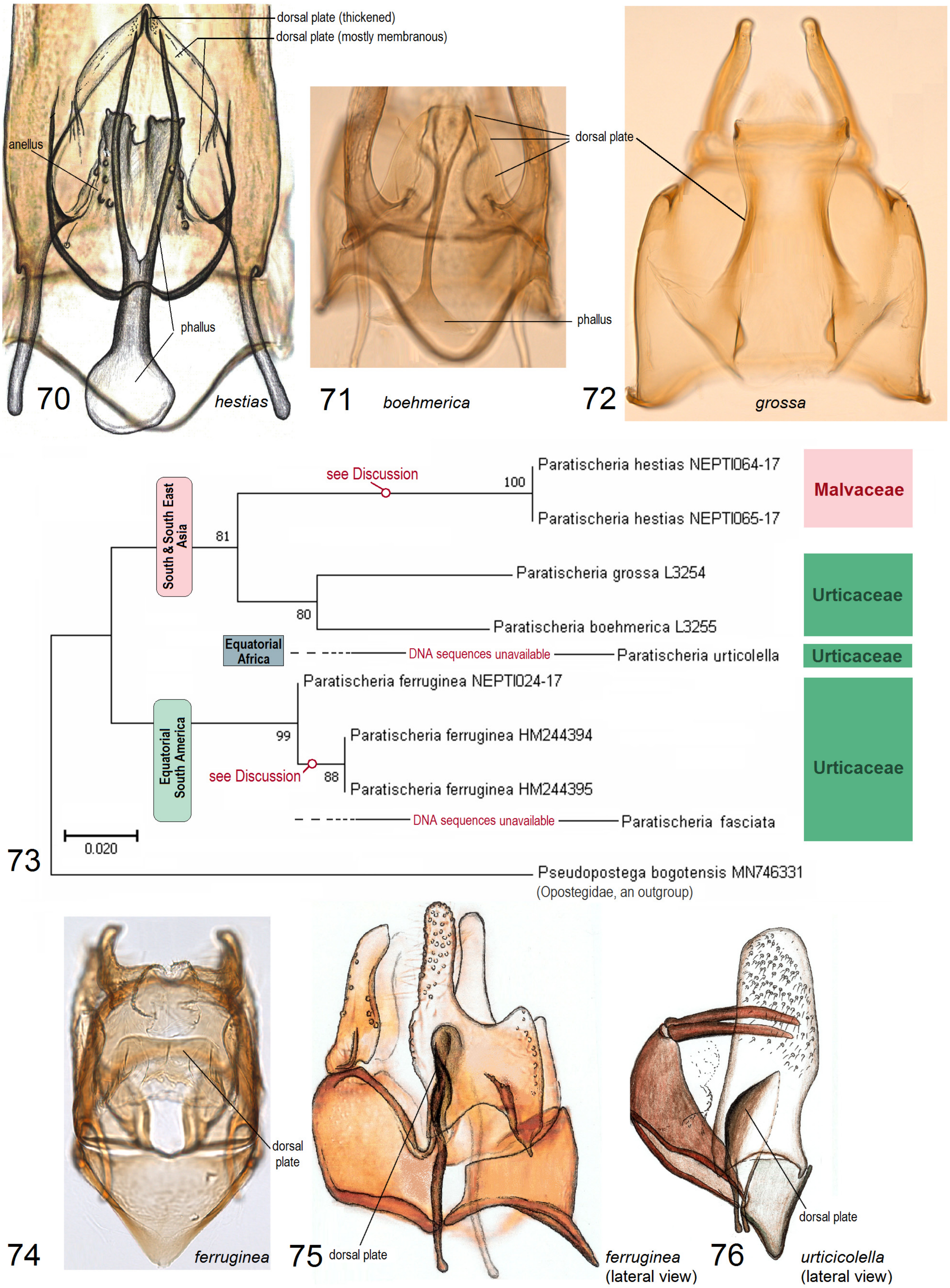
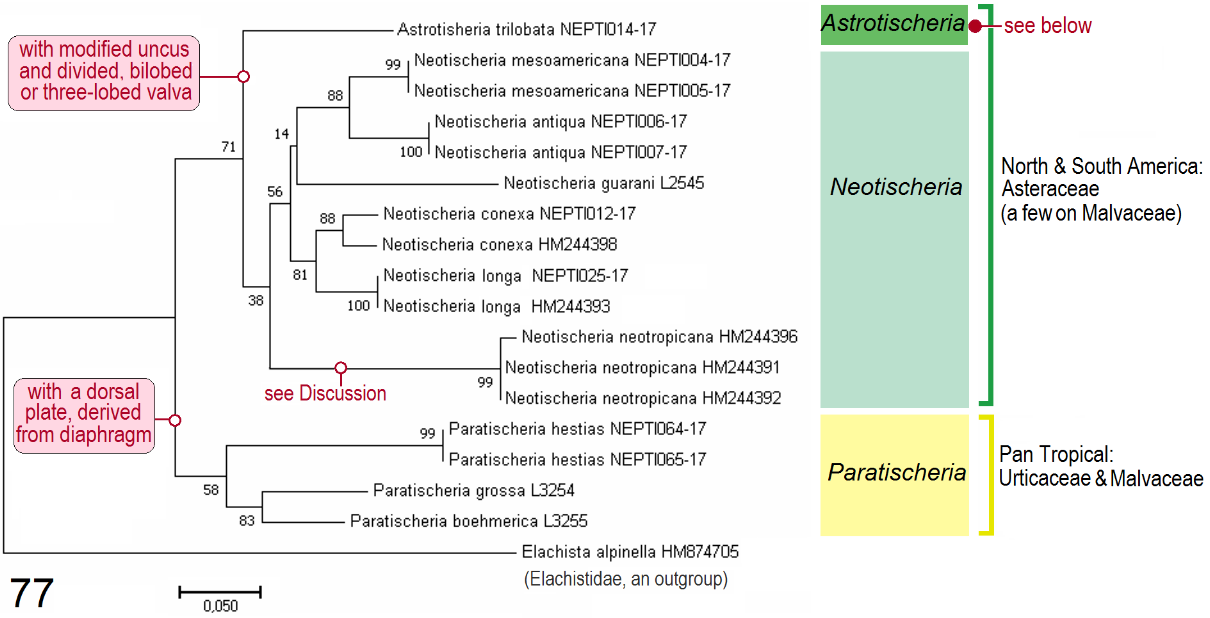
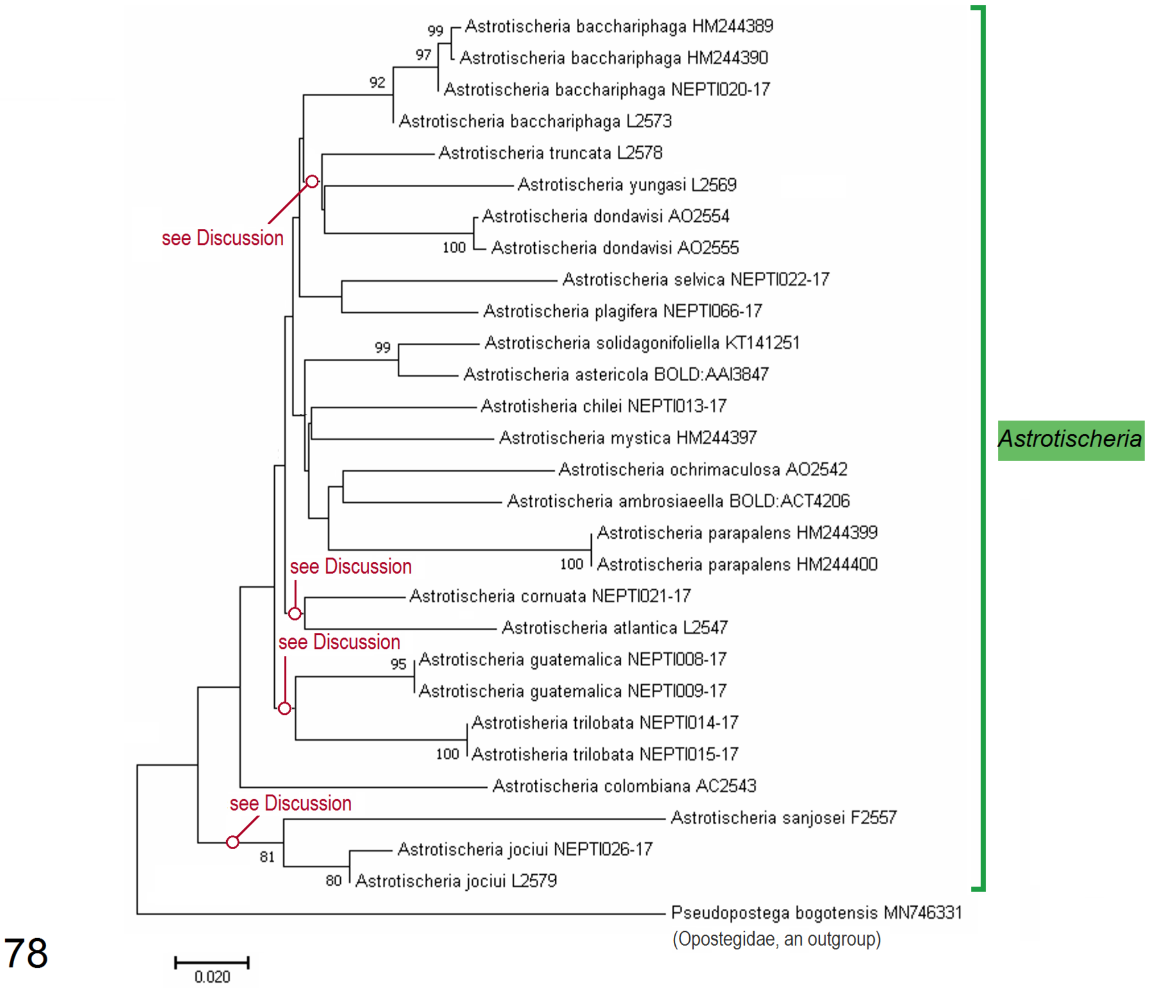
FIGURES 68, 69. The Neighbor-Joining trees based of the 608 bp long mtDNA CO1-5' Tischeriidae sequences. Divergence was calculated using the Kimura 2-parameter model. 68, using the sequences of *Neotischeria*, *Pafazaria* **gen. nov.**, and *Paratischeria*; 69, using the sequences of *Neotischeria* and *Paratischeria*



FIGURES 70–76. Species of *Paratischeria*. 70–72, fragments of the male genitalia of the South East Asian *P. hestias* (after Xu *et al.* 2017), *P. boehmerica*, and *P. grossa* (after Stonis *et al.* 2021a); 73, the Neighbor-Joining tree of the 608 bp long mtDNA CO1-5' of *Paratischeria* sequences; divergence was calculated using the Kimura 2-parameter model; the families of host plants are shown to the right of the tree; 74, 75, capsule of the South American *P. ferruginea*; 76, lateral view of capsule of the Central African *P. urticicolella* (after Stonis *et al.* 2017)





FIGURES 77, 78. The Maximum Likelihood trees of Tischeriidae based on the 608 bp long mtDNA CO1-5' sequences. Divergence was calculated using the Kimura 2-parameter model. 77, using the sequences of *Neotischeria* spp., *Paratischeria* spp., and *Astrotischeria trilobata*; the host-plant families and species distribution are shown to the right of the tree. 78, using the sequences of *Astrotischeria* species

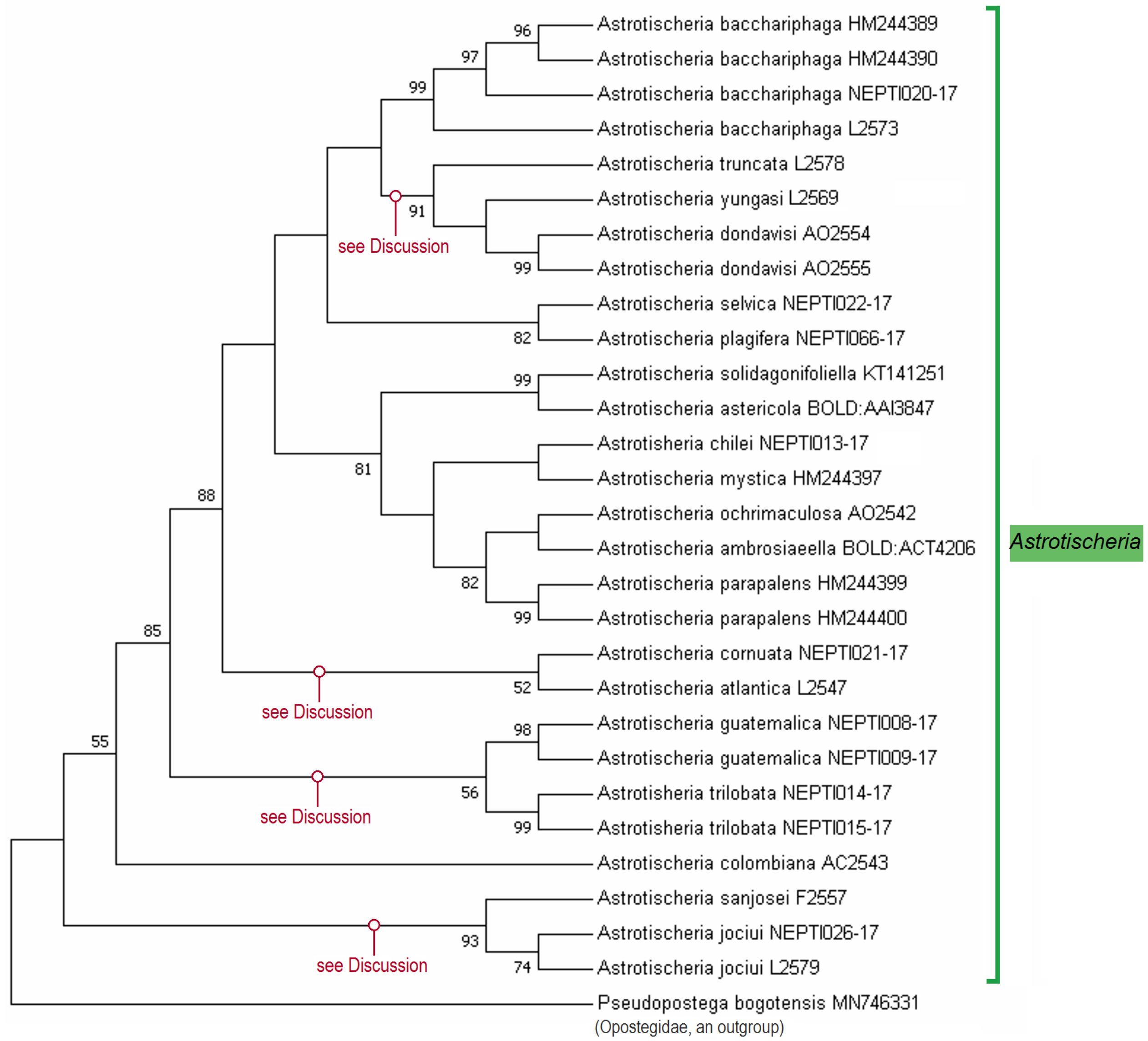


FIGURE 79. The Neighbor-Joining tree based of the 608 bp long mtDNA CO1-5' sequences of *Astrotischeria* species. Divergence was calculated using the Kimura 2-parameter model

Generic review of Tischeriidae with descriptions of new genera and species

Fam. Tischeriidae Spuler, 1898

1. Genus *Coptotriche* Walsingham, 1890

(Figs 80–142)

Coptotriche Walsingham, 1890: 322–323. Type species: *Tischeria complanoides* Frey & Boll, 1873: 220–221 (junior syn. of *T. zelleriella* Clemens, 1859).

Emmetia Leraut, 1993: 64–65. Type species: *Coptotriche marginea* (Haworth), 1828: 556.

Diagnosis. In the male genitalia, species of *Coptotriche* are characterized by presence of a transtilla (the only Tischeriidae genus with a transtilla), wide valva, spined anellus, and a spined diaphragm of the tegumen; phallus is either tulip-shaped with numerous small or large spines or with two large apical lobes bearing a few spines. In the female genitalia, the genus is usually characterized by a strongly developed, heavily folded accessory sac, and a proximally wide, usually elaborated (twisted) ductus spermathecae. Fully developed leaf mines of *Coptotriche* are characterized by the folded margin of the mined leaf (folded leaf mine), except for some East and South East Asian species; a round nidus inside the leaf mine is inconspicuous. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. External characters of adults, including wing venation are not informative and, therefore, insufficient for differentiation of *Coptotriche* because of their general uniformity or, in some cases, variability of these characters within the entire family.

Molecular data provided relatively strong support for distinctness of this genus (see Discussion). Depending on the selected outgroup, *Coptotriche* is either the sister taxon to *Coptotrichoides* + *Dishkeya* (Fig. 62) or the most distinct, basal genus, separate from the rest of the Tischeriidae genera (Figs 63, 64).

Adult (Figs 105–120). Head: frontal tuft overlapping the frons, comprised of long, slender lamellar scales; sometimes frontal tuft is comprised of two different types of scales: pale, slender lamellar scales and dark, piliform scales (Xu *et al*. 2021); occasionally frontal tuft is extremely long and comprised of slender lamellar scales, e.g., in *Coptotriche imperator* Puplesis & Diškus (Diškus & Puplesis 2003); collar distinctly paired, comprised of slender lamellar scales. Forewing often with a small dark tornal spot; forewing color varies from almost uniform, yellowish ochre or dark ochre with some grey-black scales to entirely dark brown; occasionally forewing with four large, pale, irregular spots. Hindwing usually slender, occasionally significantly wider in males of a few species; male androconial scales in only a few species.

Male genitalia (Figs 80–98). Uncus with two large (always long and basally wide) lateral lobes which look triangular in ventral view. Socii membranous, often large, usually weakly, occasionally distinctly paired, and always spinose, with numerous tiny spines. Tegumen short or very short, with a unique, distinctly spinose diaphragm; pseudognathos absent. In lateral view, valva usually very wide and rounded or truncated apically; basal process of the valva short; occasionally, e.g., *C. basipectinella* valva with a few distinctive pectens on basal half (Puplesis *et al*. 2004). Transtilla present, always with a distinctive, long, or sometimes short transverse bar; sublateral processes of the transtilla relatively short; occasionally, transverse bar of the valva with a large triangular posterior lobe. Anellus membranous, ring or conus-shaped, usually with numerous small spines; juxta absent. Vinculum usually short or very short, with a band-like or triangular ventral plate; sometimes ventral plate with a short or long anterior process medially. Phallus usually tulip-like, with numerous spines on a wide apical lobe or with two apical lobes possessing two or four large spines; in some two lobed-phalli spines are minute and numerous or absent.

Female genitalia (Figs 99–104). Ovipositor lobes usually large or very large and usually covered with relatively large, robust modified setae, peg-setae; the gap between ovipositor lobes varies from relatively broad to narrow; second pair of ovipositor lobes two–three times smaller or equal in size in comparison to main ovipositor lobes; second pair of ovipositor lobes sometimes with long wide setae instead usual piliform chetae. Lateral lobes usually short, rarely long, and wide, occasionally absent. Apophyses often stout (robust), large and heavily chitinized. Anterior apophyses significantly to slightly shorter than posterior apophyses. Prela usually with three pairs of projections; inner pair with a slightly to strongly widened base, sometimes rod-like. Caudal sclerite strongly developed, inverted U-shaped, rounded caudally. Antrum absent. Accessory sac usually folded, slender; ductus spermathecae usually very wide and variously folded, sometimes with distinctive spines (pectinations) in proximal half, slender, usually with 0.5–2 coils (sometimes with many small, occasionally large coils) in distal half; vesicle often small, irregularly-shaped, occasionally large, oval-shaped. Corpus bursae varies from long to very short, gradually narrowing towards caudal end or with a short slender "neck"; occasionally slender part (the "neck") is of the same length as the wider part; pectinations of corpus bursae absent, only occasionally cover whole corpus bursa.

Bionomics. The genus is characterized by the greatest host-plant diversity among Tischeriidae. However, more than a third of the currently known species have been reared from Rosaceae host plants, and almost a third from Fagaceae host plants; the remaining species are known to be feed on Combretaceae and Symplocaceae, also nine species feed on the following nine families (one species per family): Hypericaceae, Phyllanthaceae, Betulaceae, Staphyleaceae, Anacardiaceae, Nyssaceae, Ericaceae, Theaceae, and Apocynaceae. In total, 13 host-plant families are utilized by *Coptotriche*. Host-plant relationships of a third *Coptotriche* species are still unknown. Larvae mine leaves and produce irregular blotch-like (usually elongated) leaf mines; occasionally, initial part of the mine is gallery-like with a few short but slender lateral galleries. Frass is not deposited in leaf mines; occasionally very small amounts of scattered frass can be found in a leaf mine. Usually leaf mines are close to the leaf margin and the mining larva folds a margin of the mined leaf before pupation. The nidus is invisible through the epidermis, so dissection of the mine is necessary for study of the nidus.

Species diversity and geographical distribution. The total number of currently described *Coptotriche* species is 66. The majority are from the temperate regions: North America, Europe, and non-tropical Asia, including the Russian Far East and Japan. A substantial number of *Coptotriche* species have been described from South and South East Asia: *C. compta* (Meyrick) (Meyrick 1915b), *C. imperator* Puplesis & Diškus, *C. inclinata* Puplesis & Diškus, *C. thailandi* Puplesis & Diškus, *C. terminaliae* Puplesis & Diškus, *C. bifurcula* Puplesis & Diškus (Diškus & Puplesis 2003), *C. camptotheca* Xu & Dai (Figs 97, 104), *C. turpinia* Xu & Dai, *C. asiana* Diškus & Stonis (Fig. 113) (Xu *et al*. 2021); one new South East Asian species, *C. sapaensis* Diškus & Stonis, **sp. nov.**, is described in this publication (see below). Some species were recorded from South Africa: *C. zimbabwiensis* Puplesis & Diškus, *C. africana* Puplesis & Diškus (Fig. 83), *C. basipectinella* Puplesis & Diškus, *C. versicolor* Stonis, Diškus & Mey (Puplesis & Diškus 2003; Stonis *et al.* 2019a), and one odd species, *C. alavelona* Lees & Stonis, from Madagascar (Lees & Stonis 2007; Lees & Minet 2022). Recently, a few species of *Coptotriche* were also discovered to occur in Central America: *C. forsteroniae* Stonis & Diškus (Stonis & Diškus 2008), and *C. pulverea* (Walsingham) (Stonis *et al*. 2008), a species formerly known only from the Caribbean (Walsingham 1897). A couple species were also discovered from South America: *C. carmencita* Stonis & Diškus from Peru and *C. parvisacculata* Diškus & Stonis (Figs 85, 90, 98, 108) from Argentina (Stonis *et al.* 2019b).

Coptotriche sapaensis Diškus & Stonis, sp. nov.

urn:lsid:zoobank.org:act:B6B226A0-C331-4838-86C3-7319D49BDC61
(Figs 114–142)

Type material. Holotype: ♂, VIETNAM: Lao Cai Prov., 15 km NW Sapa, 22°20’58”N, 103°46’16”E, elevation 1920 m, feeding larva 20.ii.2015, ex pupa iii.2015, field card no. 5203, leg. A. Diškus, genitalia slide no. AD1111 (MfN). Paratypes: 1 ♂, 2 ♀ same label data as holotype, genitalia slide no. AD1109♀ (MfN); 1 ♂, same label data, genitalia slide no. AD1106♂ (GNU).

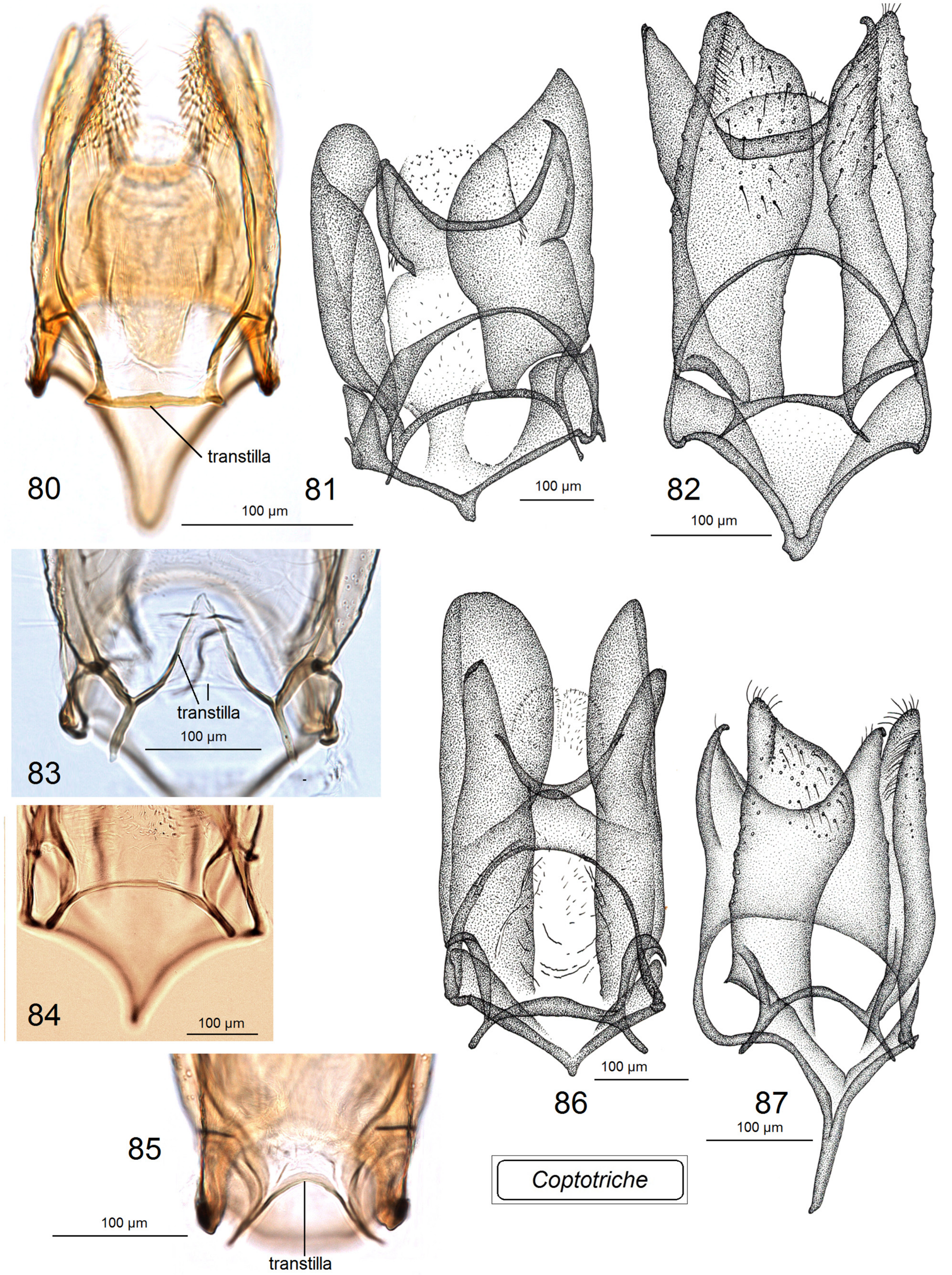
Diagnosis. Externally, this new species is similar to and can be confused with some other bright ochre-colored *Coptotriche* species with distinctive black markings on the forewing apex, including the South East Asian *C. asiana* Diškus & Stonis and *C. turpinia* Xu & Dai. In the male genitalia, this new species can be easily differentiated from all congeneric species by the phallus with curved lateral clusters of large spines and unique morphology of phallus apex (see Fig. 122). In the female genitalia, the new species is characterized by the combination of a distinctly globular, heavily folded accessory sac, stout prela, and inconspicuous pectinations of corpus bursae.

DNA barcode. Unavailable.

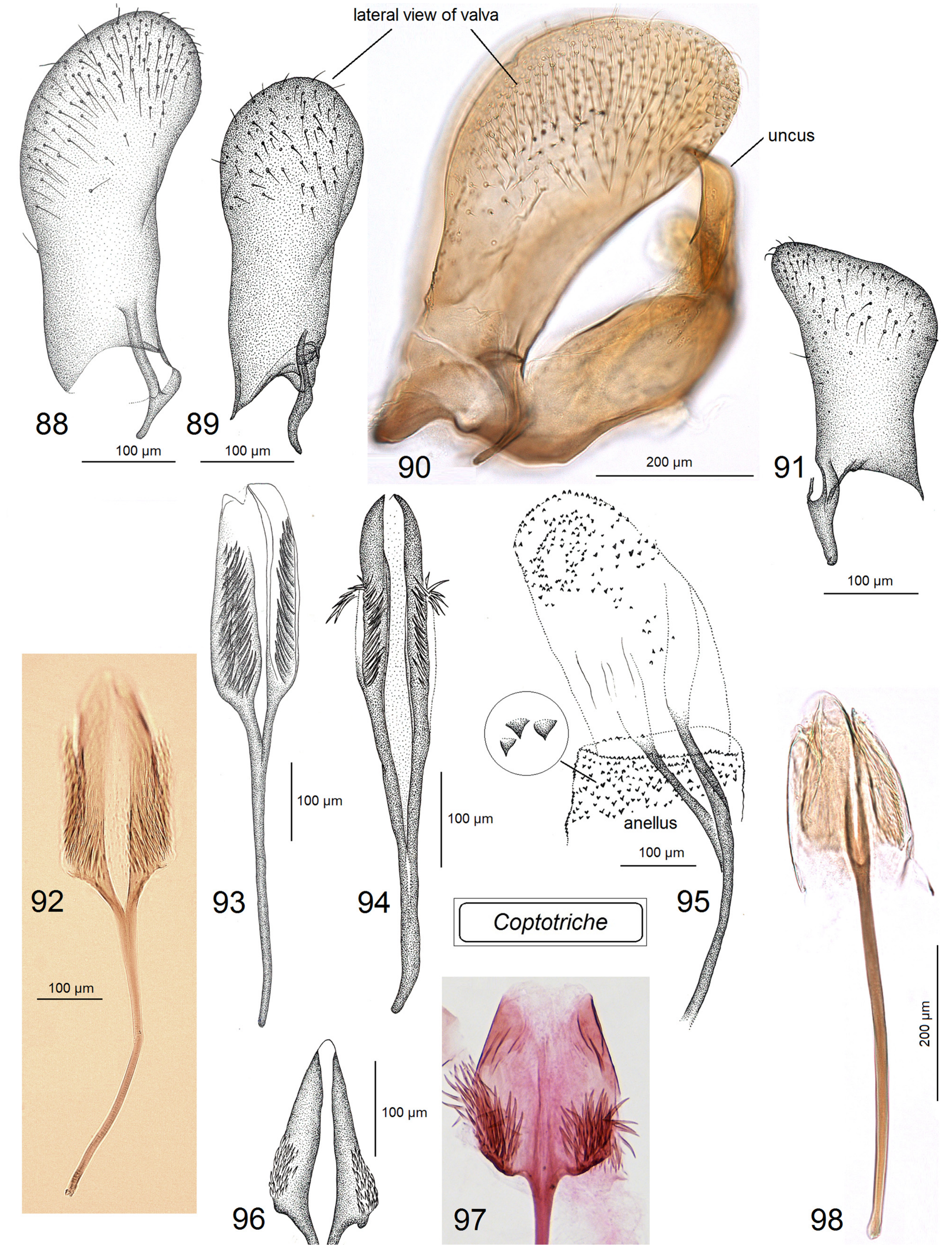
Description. *Male* (Figs 114–118). Forewing length 4.5 mm; wingspan 10 mm (n = 1). Head: frons, palpi and pecten glossy yellow cream; frontal tuft comprised of golden cream lamellar scales and dark brown, long, piliform-like scales (Figs 114, 115); collar ochreous yellow; antenna significantly longer than one half of the length of forewing; flagellum pale ochre-yellow; sensilla whitish cream, very fine, almost indistinctive. Thorax: bright ochreous yellow, with dark brown scales medially; tegula ochreous yellow. Forewing bright ochreous yellow, with some brown-black to black scales which scattered along costal margin and especially along dorsal margin and apex, and form a small irregular spot on tornus; fringe intense yellow-ochre, ochre-grey on tornus; fringe line absent; forewing underside with ochreous brown scales, except for the large, yellowish cream area below the fold. Hindwing dark brown-grey on upper side and underside; fringe ochre-brown. Legs ochre-yellow, densely covered with dark grey-brown scales on upper side. Abdomen dark brown with a very, strong golden gloss and some purple irridescence on upper side, pale brown, golden glossy on underside, yellow cream laterally; genital segments medium large, yellow cream; anal tuft dorsal, small, comprised of lamellar grey scales.

Female (Figs 119, 120). Forewing length 5.0–5.1 mm; wingspan 11.1–11.2 mm (n = 2). Similar to male, but without antennal sensilla, anal tuft yellowish cream; ovipositor not protruding. Otherwise, identical with male.

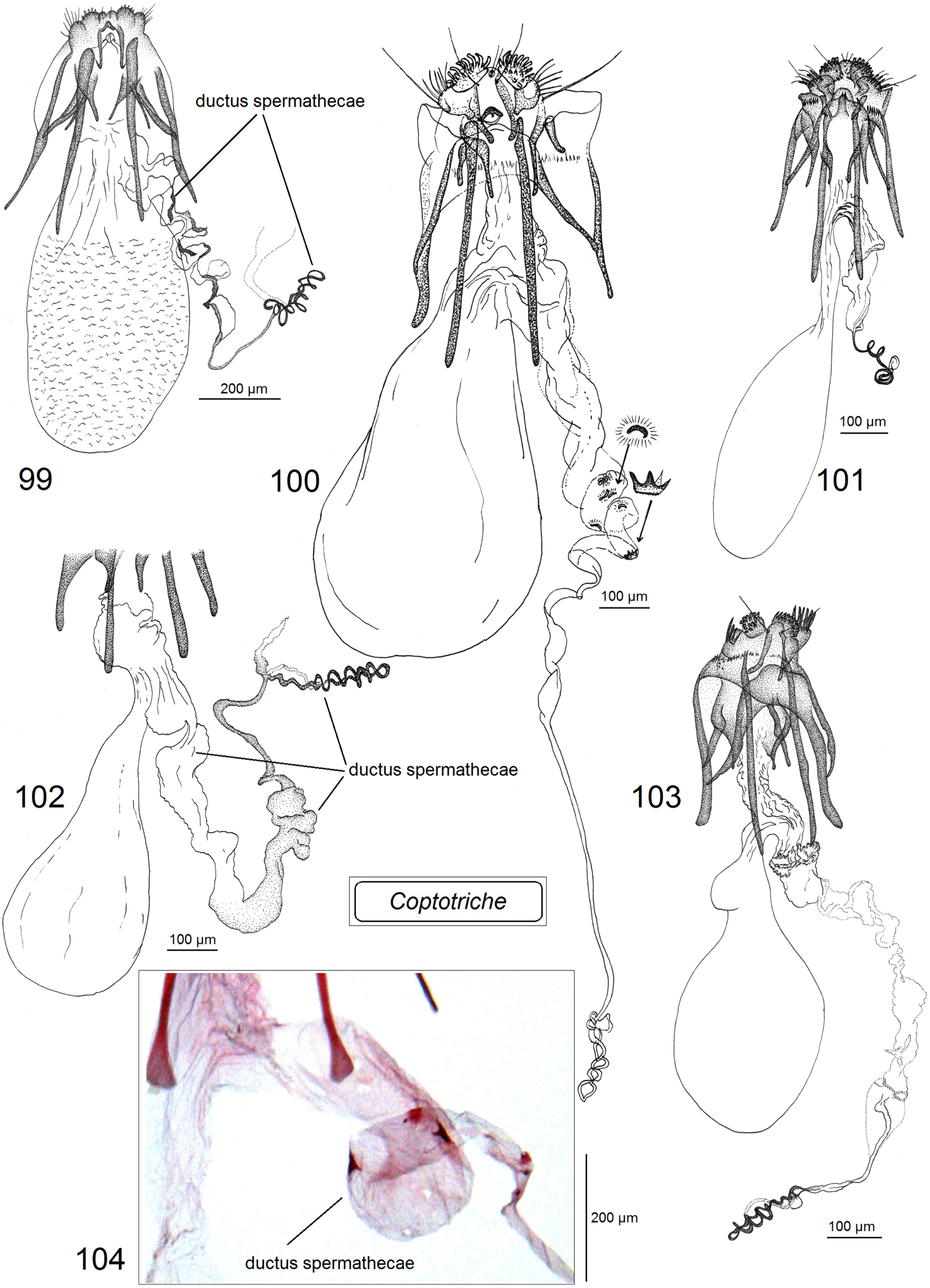
Male genitalia (Figs 121–130) with capsule about 730 µm long, 380–385 µm wide. Uncus comprised of two large, triangular lobes. Socii relatively large, weakly paired, membranous. Tegumen very, short medially, with long lateral arms. Diaphragm covered with numerous tiny spines. Valva ca. 700 µm long, wide in lateral view. Transtilla with a long transverse bar and short sublateral processes. Anellus mostly membranous, indistinctive. Vinculum short, triangular. Phallus about 770 µm long, apically tulip-shaped, with three distinctive rod-like thickenings and lateral clusters of large, outwardly curved spines.



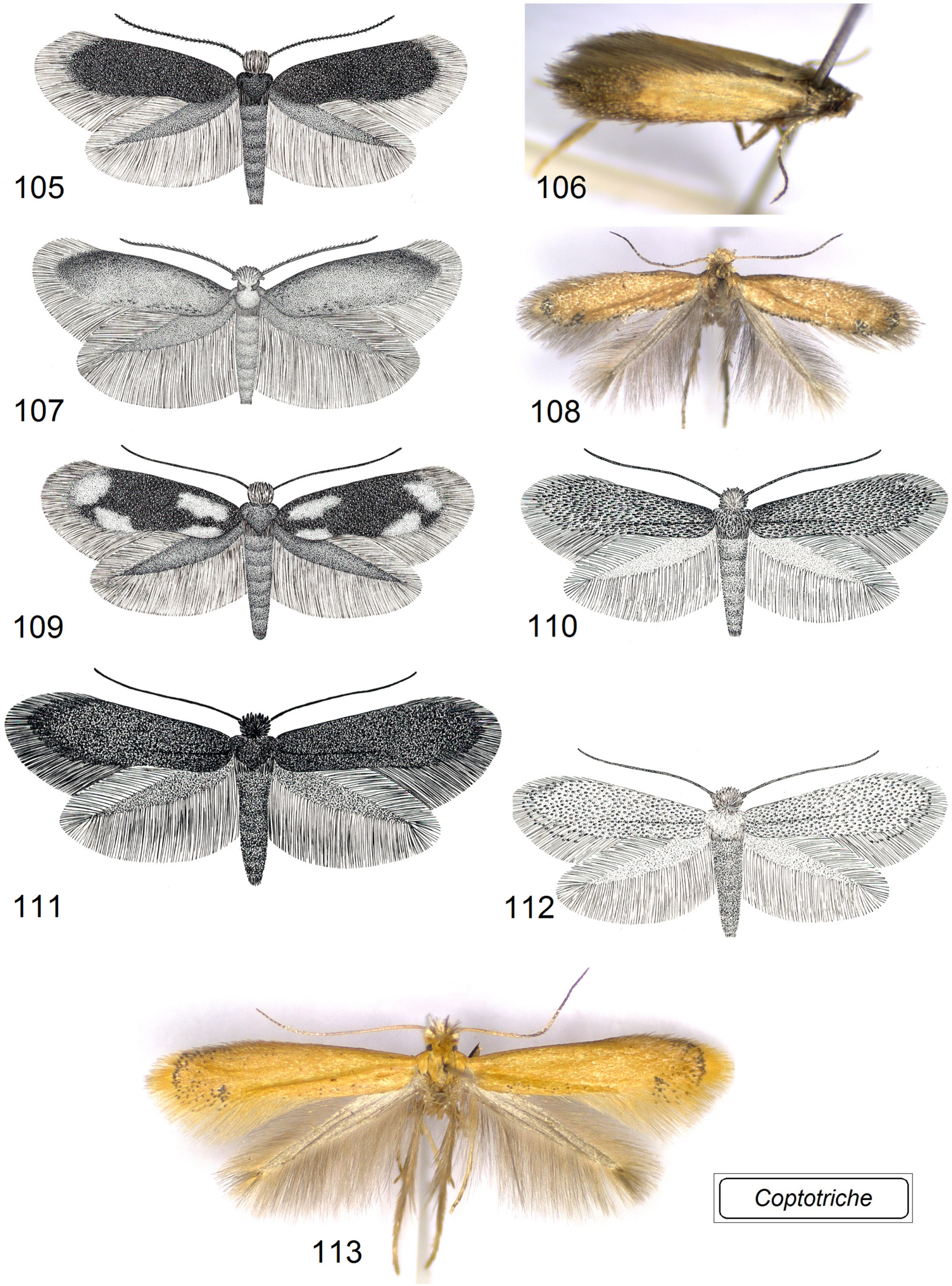
FIGURES 80–87. Male genital capsule of *Coptotriche*. 80, *C. minuta* Diškus & Stonis, Far Eastern Russia (Stonis *et al.* 2014); 81, *C. citripenipennella* (Clemens), USA, slide no. 28961 BMNH; 82, *C. gaunacella* (Duponchel), Turkmenistan, a genitalia mount in glycerin (MfN); 83, *C. africana* Puplesis & Diškus, South Africa (Stonis *et al.* 2019a); 84, *C. confusa* (Braun), USA (Stonis *et al.* 2020c); 85, *C. parvisacculata* Diškus & Stonis, Argentina (Stonis *et al.* 2019b); 86, *C. longiciliatella* (Rebel), Tenerife, Canary Is., slide no. Diškus088 ZMUC; 87, *C. paulula* Diškus, Tajikistan (after Diškus 1998)



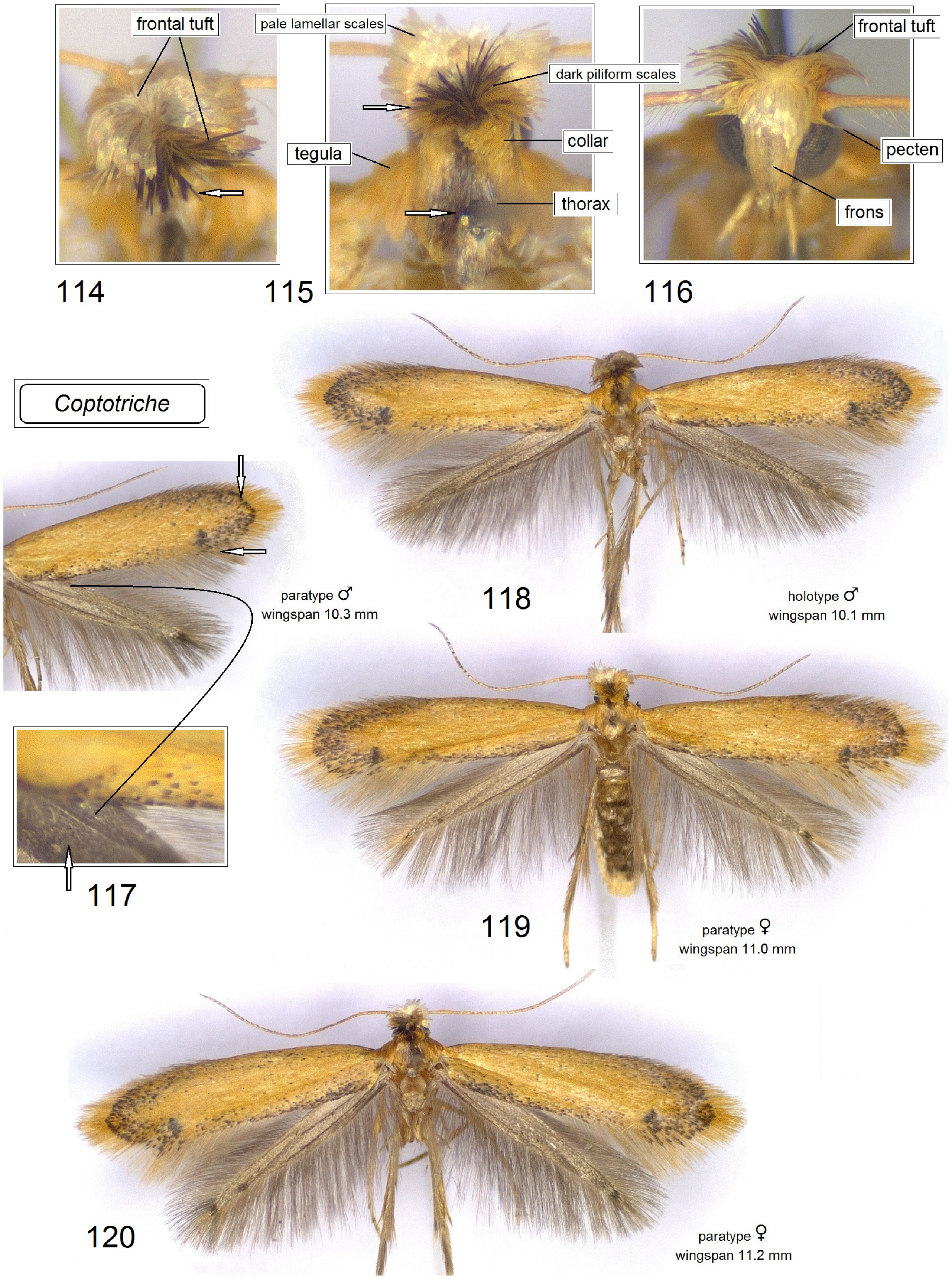
FIGURES 88–98. Valva and phallus of *Coptotriche*. 88, *C. berberella* (De Prins), Marocco, **first documentation of paratype** no. Diškus093 ZMUC; 89, *C. longiciliatella* (Rebel), Tenerife, Canary Is., slide no. Diškus133 ZMUC; 90, *C. parvisacculata* Diškus & Stonis, Argentina (Stonis *et al.* 2019b); 91, *C. paulula* Diškus, Tajikistan (Diškus 1998); 92, *C. confusa* (Braun), USA (Stonis *et al.* 2020c); 93, *C. berberella*, paratype no. Diškus089 ZMUC; 94, *C. longiciliatella*, slide no. Diškus088 ZMUC; 95, *C. citripenipennella* (Clemens), USA, slide no. 28961 NHMUK; 96, *C. paulula*; 97, *C. camptotheca* Xu & Dai, China (Xu *et al.* 2021); 98, *C. parvisacculata* (Stonis *et al.* 2019b)



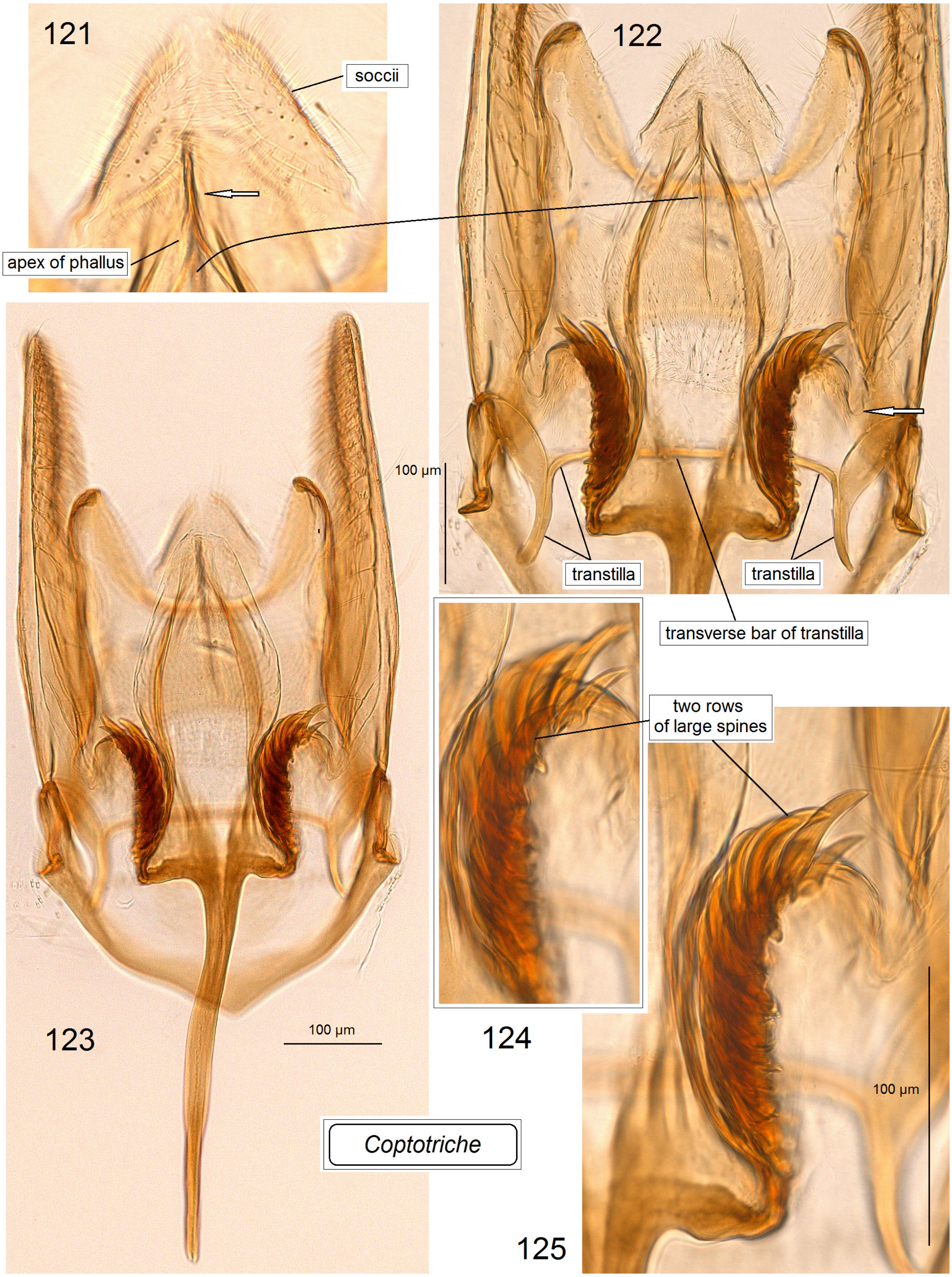
FIGURES 99–104. Female genitalia of *Coptotriche*. 99, *C. aenea* (Frey & Boll), USA, **first documentation of lectotype**, slide no. 28944 NHMUK; 100, *C. szoecsi* (Kasy), Austria, genitalia slide no. Diškus066 ZMUC; 101, *C. longiciliatella* (Rebel), Tenerife, Canary Is., slide no. Diškus068 ZMUC; 102, *C. angusticolella* (Duponchel), Slovakia, slide no. Diškus079 ZMUC; 103, *C. gaunacella* (Duponchel), Poland, slide no. Diškus129 ZMUC; 104, *C. camptotheca* Xu & Dai, China (Stonis *et al.* 2019b)



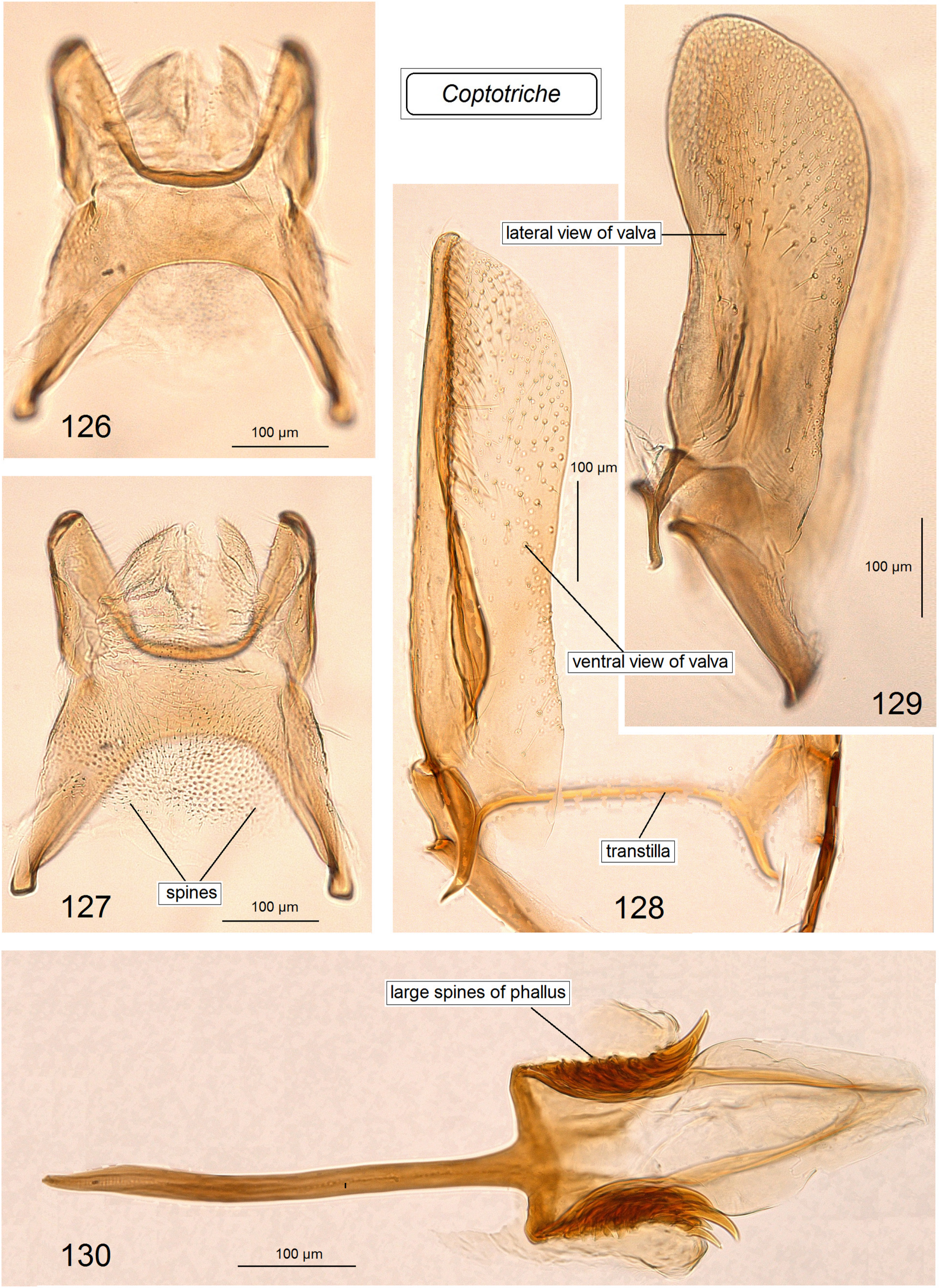
FIGURES 105–113. Adults of *Coptotriche*. 105, *C. longiciliatella* (Rebel), Tenerife, Canary Is.; 106, *C. minuta* Diškus & Stonis, Far Eastern Russia, holotype (Stonis *et al*. 2014); 107, *C. berberella* (De Prins), Marocco, paratype; 108, *C. parvisacculata* Diškus & Stonis, Argentina, holotype (Stonis *et al*. 2019b); 109, *C. longiciliatella*; 110, *C. gaunacella* (Duponchel), Turkmenistan; 111, *C. angusticolella* (Duponchel), Belgium; 112, *C. rosella* (Gerasimov), Uzbekistan; 113, *C. asiana* Diškus & Stonis, Vietnam, paratype (Xu *et al*. 2021)



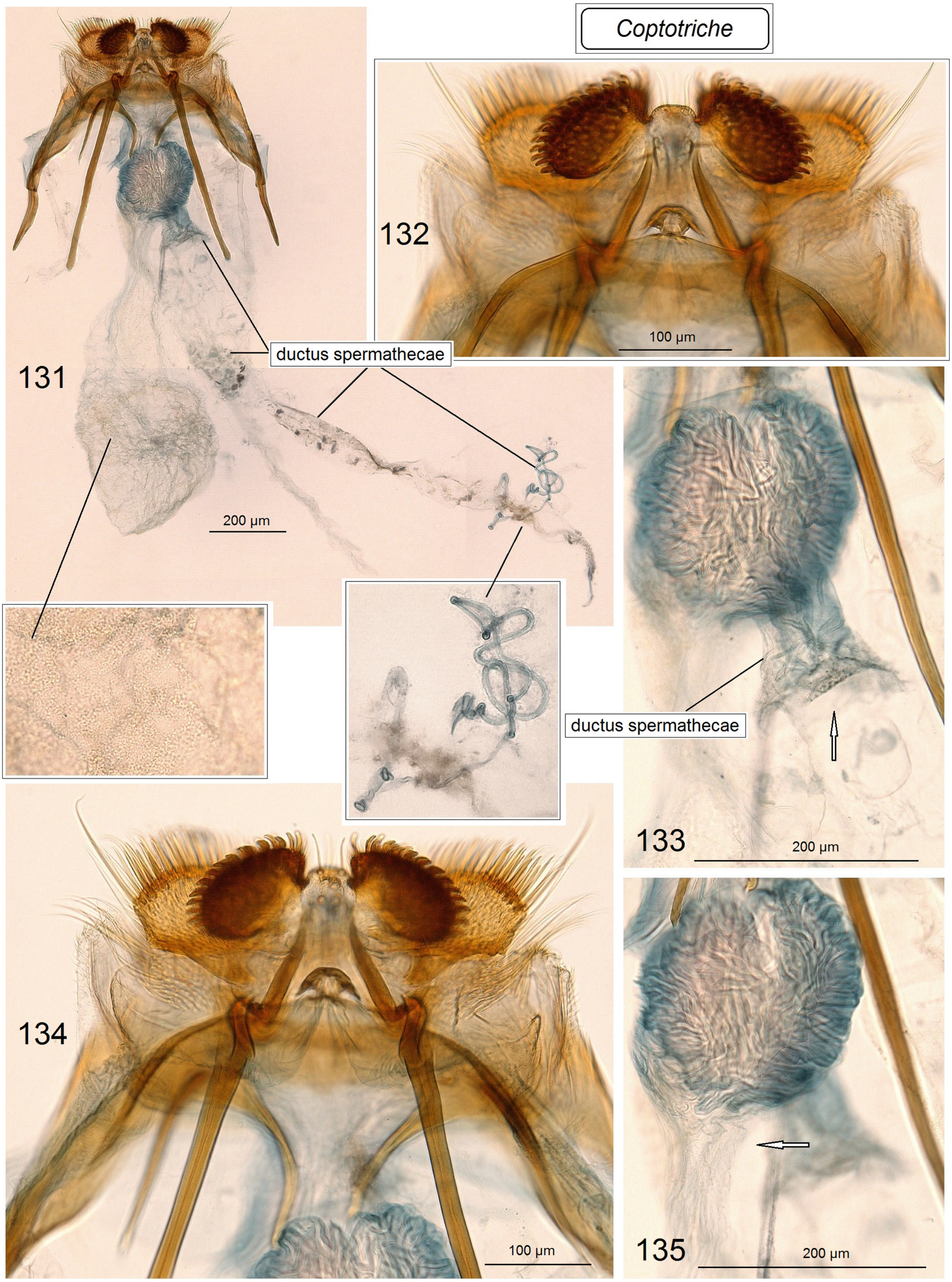
FIGURES 114–120. Adults of *Coptotriche sapaensis* Diškus & Stonis, **sp. nov.**, northern Vietnam. 114–116, head; 117–120 general view of holotype and paratypes (MfN)



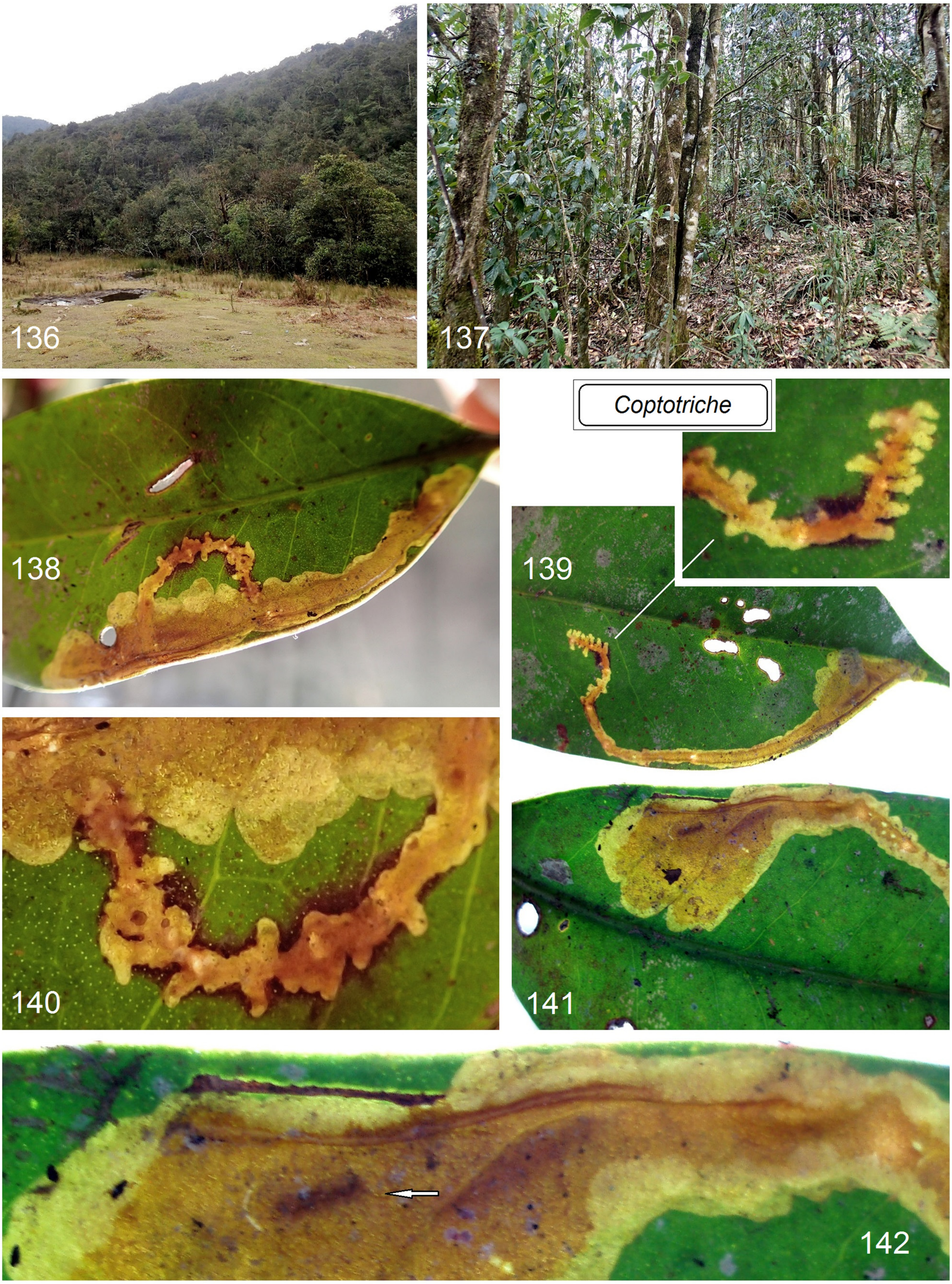
FIGURES 121–125. Male genitalia of *Coptotriche sapaensis* Diškus & Stonis, **sp. nov.**, northern Vietnam, holotype, genitalia slide no. AD1111 (MfN). 121, socii and apex of phallus; 122, uncus and apical part of phallus; 123, general view; 124, 125, spines of phallus



FIGURES 126–130. Male genitalia of *Coptotriche sapaensis* Diškus & Stonis, **sp. nov.**, northern Vietnam, paratype, genitalia slide no. AD1106 (MfN). 126, 127, socii, tegumen and spined diaphragm; 128, valva and transtilla, ventral view; 129, valva, lateral view; 130, phallus



FIGURES 131–135. Female genitalia of *Coptotriche sapaensis* Diškus & Stonis, **sp. nov.**, northern Vietnam, paratype, genitalia slide no. AD1109 (MfN). 131, general view; 132, ovipositor lobes; 133, rounded accessory sac and proximal part of ductus spermathecae; 134, ovipositor lobes; 135, accessory sac and "neck" (slender proximal part) of corpus bursae



FIGURES 136–142. Bionomics of *Coptotriche sapaensis* Diškus & Stonis, **sp. nov.** 136, 137, habitat, elevation 1920 m, 15 km NW of Sapa, 22°20’58”N, 103°46’16”E, Lao Cai Prov., northern Vietnam; 138–142, leaf mines on unidentified Symplocaceae plant

Female genitalia (Figs 131–135) about 1445 μm long. Ovipositor lobes relatively large, with dark peg-like setae; second pair of ovipositor lobes large, with numerous relatively short setae and one very long seta on each lobe. Posterior apophyses only slightly longer than anterior apophyses; prela comprised of three pairs of stout, rod-like projections; transverse prela unusually wide. Corpus bursae gradually widening towards basal part, with numerous inconspicuous pectinations. Accessory sac globular, heavily folded. Ductus spermathecae wide proximally, slender, tube-like distally, with about 8–9 medium large and small coils.

Bionomics (Figs 136–142). Host plant unidentified but is probably Symplocaceae (Fig. 138). Larvae mine leaves in February. Initially, the mine is slender with numerous lateral corridors; later, the mine widens to an elongated blotch-like mine (yellowish to pale brown, without frass). Adults occur in March. Otherwise, biology is unknown.

Distribution. This species is known from a single locality in northern Vietnam near the border with China: Lao Cai Province, 15 km NW Sapa, at the elevation of 1920 m (Figs 136, 137).

Etymology. The species is named after Sapa (Vietnam), the locality where it was found.

2. Genus *Coptotrichoides* Diškus & Stonis, gen. nov.

urn:lsid:zoobank.org:act:DB703D5A-F968-4D5F-907A-97444CA4F223

(Figs 143–182)

Type species: *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.** (described below).

Diagnosis. Externally, species of this new genus can be confused with other speckled Tischeriidae, including *Coptotriche.* The forewing of *Coptotrichoides* is usually irregularly speckled with dark scales, ocassionally with bright yellow-ochre patches. In the male genitalia, *Coptotrichoides* species resemble those of *Coptotriche,* however, *Coptotrichoides* is characterized by absence of the transtilla and anellus, an apically taperred valva, a slender uncus, a longer tegumen, a rod-like phallus with two slender lateral lobes and a median process apically, and unspined or scantly spined diaphragm of the tegumen. In the female genitalia, in contrast to *Coptotriche,* the new genus is characterized by a slender ductus spermathecae and a heavily folded and thickened accessory sac.

In contrast to the majority of other Tischeriidae, except *Coptotriche*, fully developed leaf mines of *Coptotrichoides* are sometimes characterized by a folded margin of the mined leaf (i.e., a folded leaf mine); a round nidus inside the leaf mine is inconspicuous.

See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. Although based on only one sequence, *Coptotrichoides* is always close to, but distinctly separate, from *Coptotriche*, and appears as a sister taxon to *Dishkeya* (Figs 62–64).

Adult. Head: frontal tuft overlapping the frons, comprised of long, relatively wide lamellar scales; pecten distinctly long; collar weakly paired or unpaired, comprised of very slender (almost piliform) lamellar scales. Forewing often irregularly speckled with dark scales especially abundant in apical half; sometimes forewing with two bright yellow-ochre antemedian and postemdian patches. Hindwing slender, androconia unknown.

Male genitalia (Figs 148–152). Uncus with two long, slender (except basal part) lateral lobes. Socii medium large to distinctly large, membranous, weakly paired or unpaired, with numerous tiny spines. Tegumen moderately long, without spines on the diaphragm; only one species, *C. singularis*, is known with a little spinose diaphragm; pseudognathos absent. In lateral and ventral view, valva tapering towands apex, basally wide; occasionally, valva with a small, pointed, inwardly directed apical process; basal process of the valva short. Transtilla always absent. Anellus absent or indistinctive; juxta absent. Vinculum always short or very short, with a medium long or extremely long (*C. braziliensis*) anterior process medially. Phallus long or very long, rod-like, with two slender lateral lobes and a distinctive median process apically; large or small lateral spines absent; occasionally there are tiny spines in the median area of the phallus apex.

Female genitalia (Fig. 147). Ovipositor lobes large; the gap between ovipositor lobes relatively slender; second pair of ovipositor lobes by 1/3 smaller in comparison to main ovipositor lobes. Lateral lobes distinctly long and proximally wide. Anterior and posterior apophyses usually similar in their length or anterior slightly shorter than posterior apophyses (or opposite). Prela usually with three pairs of rod-like projections; inner pair moderately or significantly long. Caudal sclerite strongly thickened distally, inverted V-shaped, pointed caudally. Antrum absent.

Accessory sac slender, strongly folded and thickened; ductus spermathecae without a wide and folded proximal part but slender, usually with 14–19 large coils; vesicle indistinctive, irregularly-shaped, small. Corpus bursae short or with slender "neck"; usually slender part ("neck") is of the same length as the wider part; pectinations of corpus bursae absent or indistinctive.

Bionomics. The genus is trophically associated with Sapindaceae host plants: *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.**, feed on *Serjania* Mill. (or *Paullinia* L.); *C. singularis* (Stonis & Diškus, 2008) **comb. nov.** on *Cardiospermum grandiflorum* Sw. (Stonis *et al*. 2020a), *C. suprafasciata* (Diškus & Stonis, 2020) **comb. nov.** on *Allophylus edulis* (A.St.-Hil., A.Juss. & Cambess.) Hieron. ex Niederl. (Fig. 143) (Stonis *et al*. 2020b); and *C. serjaniphaga* (Remeikis & Stonis, 2021) **comb. nov.** on *Serjania* Mill., possibly *S. squarrosa* Radlk. (Figs 144, 145) (Stonis *et al*. 2021b). Unfortunately, the host plants of the South American *C. deliquescens* (Meyrick, 1915a) **comb. nov.** and *C. braziliensis* (Diškus & Stonis, 2020) **comb. nov.** remain unknown. The leaf mines on *Serjania* Mill., possibly *S. grandis* Seem., documented from Peru by Stonis *et al*. (2021b) are expected to be a new *Coptotrichoides* species (Fig. 146).

Larvae mine leaves and produce irregular or elongated blotch-like leaf mines; often initial part of the mine is slender, trumpet-like. Frass absent in leaf mines. Usually leaf mines are close to the leaf margin and the mining larva folds a margin of the mined leaf before pupation. Nidus is invisible through the epidermis, so dissection of the mine is necessary to study the nidus.

Species diversity and geographical distribution. The genus is currently known only from Central America (Belize) and South America (Guyana, Peru, Brazil, and tropical northern Argentina). The genus is comprised of six species: the Central American *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.**, the type species described below; *C. singularis* (Stonis & Diškus, 2008) **comb. nov.** (Figs 148, 150–152), described from Belize (Stonis & Diškus 2008; Stonis *et al*. 2020a); *C. deliquescens* (Meyrick, 1915) **comb. nov**., a species described from Guyana (Meyrick 1915a), now trasferred to *Coptrichiodes* and illustrated for the first time here (Figs 178–182); *C. suprafasciata* (Diškus & Stonis, 2020) **comb. nov.** (Figs 143, 147), a species recently discovered in tropical northern Argentina near Iguazú (Stonis *et al*. 2020b); *C. braziliensis* (Diškus & Stonis, 2020) **comb. nov**. (Fig. 149), a species described from southern Brazil (Stonis *et al*. 2020b); and *C. serjaniphaga* (Remeikis & Stonis, 2021) **comb. nov.** (Figs 144, 145), an Andean Peruvian species recently incorrectly described in the genus *Coptotriche* (Stonis *et al*. 2021b).

Etymology. The genus is named after the genus it most resembles, *Coptotriche*, but with a different ending.

Coptotrichoides sapindoidum Diškus & Stonis, sp. nov.

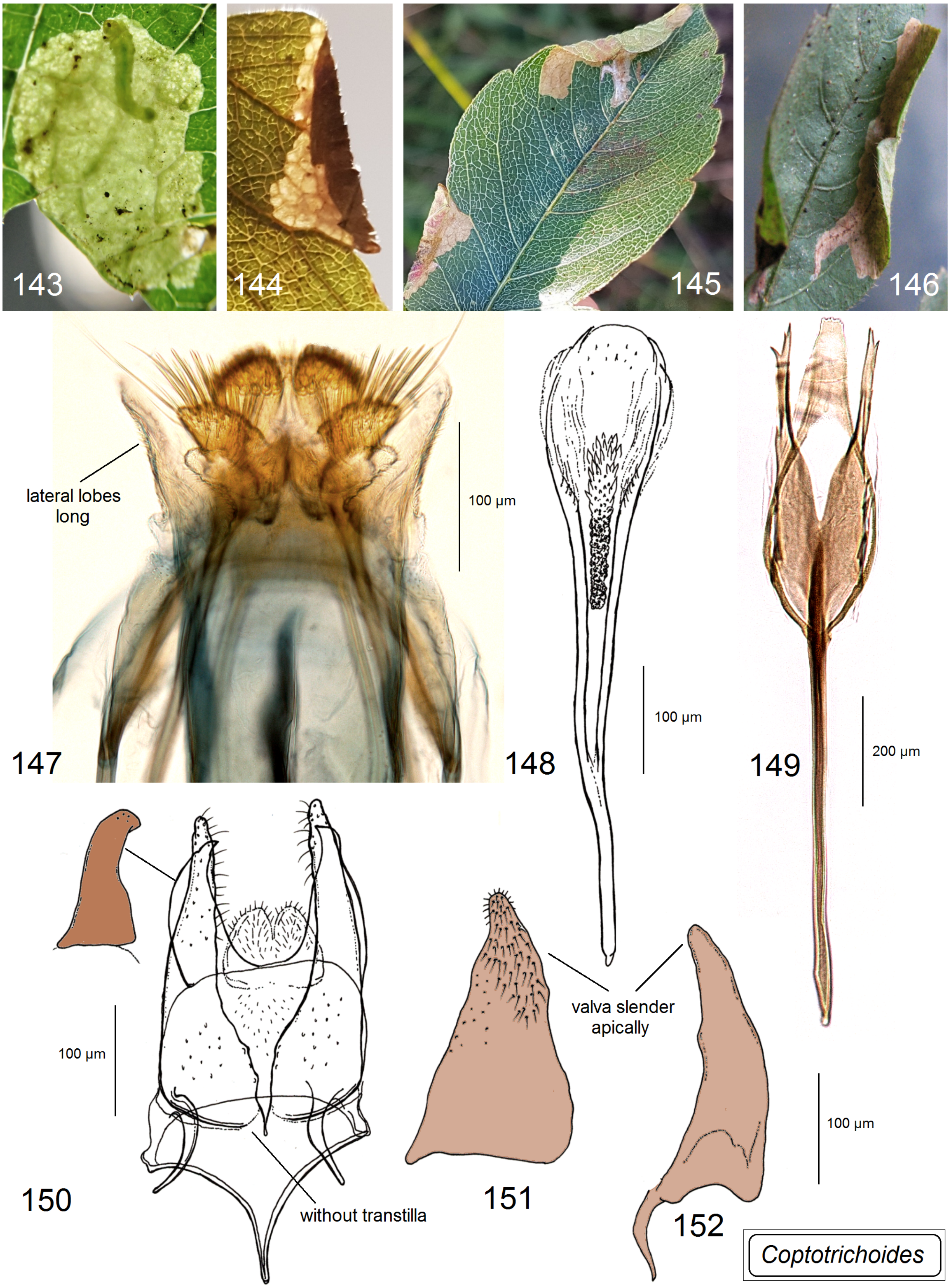
urn:lsid:zoobank.org:act:81F631EB-4B9E-4D88-BA6B-DFE0B997D11E

(Figs 153–177)

Type material. Holotype: ♂, HONDURAS: Copán Department, Copán, 14°50'13"N, 89°08'37"W, elevation 620 m, mining larva on Sapindaceae 15.ii.2012, ex pupa iii. 2012, field card no. 5089, leg. A. Diškus, genitalia slide no. AD537 (MfN). Paratypes: 1 ♂, 1 ♀, same label data as holotype, genitalia slides nos AD528♂, AD1091♀ (MfM); 4 ♂, 1 ♀, same label data, genitalia from adult in pupal skin, without pinned adults preserved, slide nos AD529♂, AD538♂, AD551♂ (MfN).

Diagnosis. Externally, this new species can be confused with other sparsely speckled Tischeriidae species. In the male genitalia, the unique shape of the phallus as well as the combination of very slender uncus and the long anterior process of vinculum make *C. sapindoidum* **sp. nov.** immediately recognizable. In the female genitalia, is also distinctive because of the combination of large coils of ductus spemathecae, greatly folded and thickened accessory sac, and long lateral lobes of ovipositor.

DNA barcode. Unavailable.



FIGURES 143–152. *Coptotrichoides* **gen. nov.** 143, leaf mine, *C. suprafasciata* (Diškus & Stonis) **comb. nov.** on *Allophylus edulis* (Stonis *et al*. 2020b); 144, 145, same, *C. serjaniphaga* (Remeikis & Stonis) **comb. nov.** on *Serjania* (Stonis *et al.* 2021b); 146, leaf mine of a possibly undescribed *Coptotrichoides* species on *Serjania* from Peru (Stonis *et al.* 2021b); 147, female genitalia, ovipositor lobes, *C. suprafasciata* (Diškus & Stonis) (Stonis *et al*. 2020b); 148, phallus, *C. singularis* (Stonis & Diškus) **comb. nov**. (Stonis & Diškus 2008); 149, phallus, *C. braziliensis* (Diškus & Stonis) **comb. nov.** (Stonis *et al*. 2020b); 150–152, valvae, *C. singularis* (Stonis & Diškus 2008)

153

holotype ♂
wingspan 5.5 mm

Coptotrichoides

154

paratype ♀
wingspan 6.1 mm

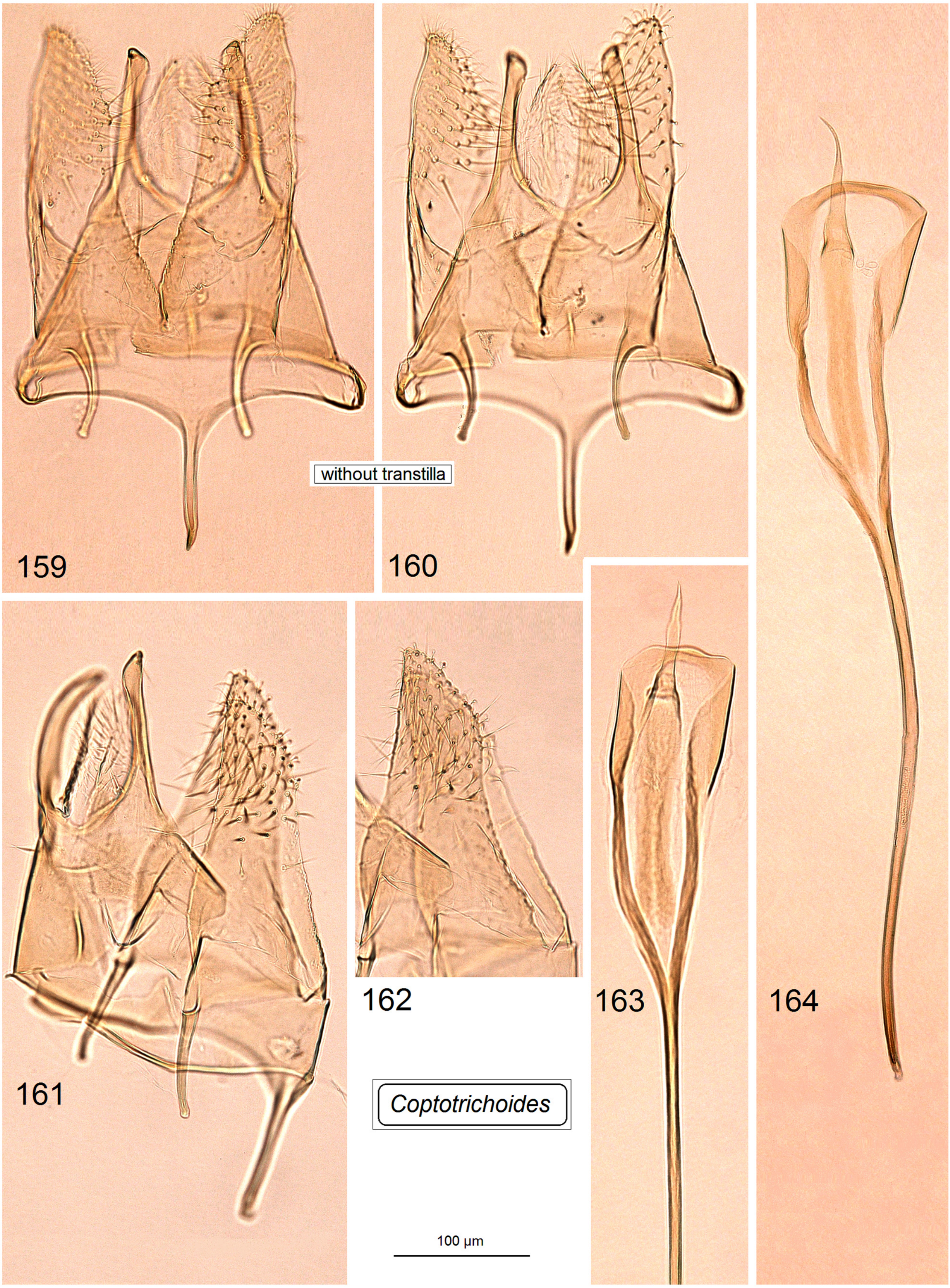
155

156

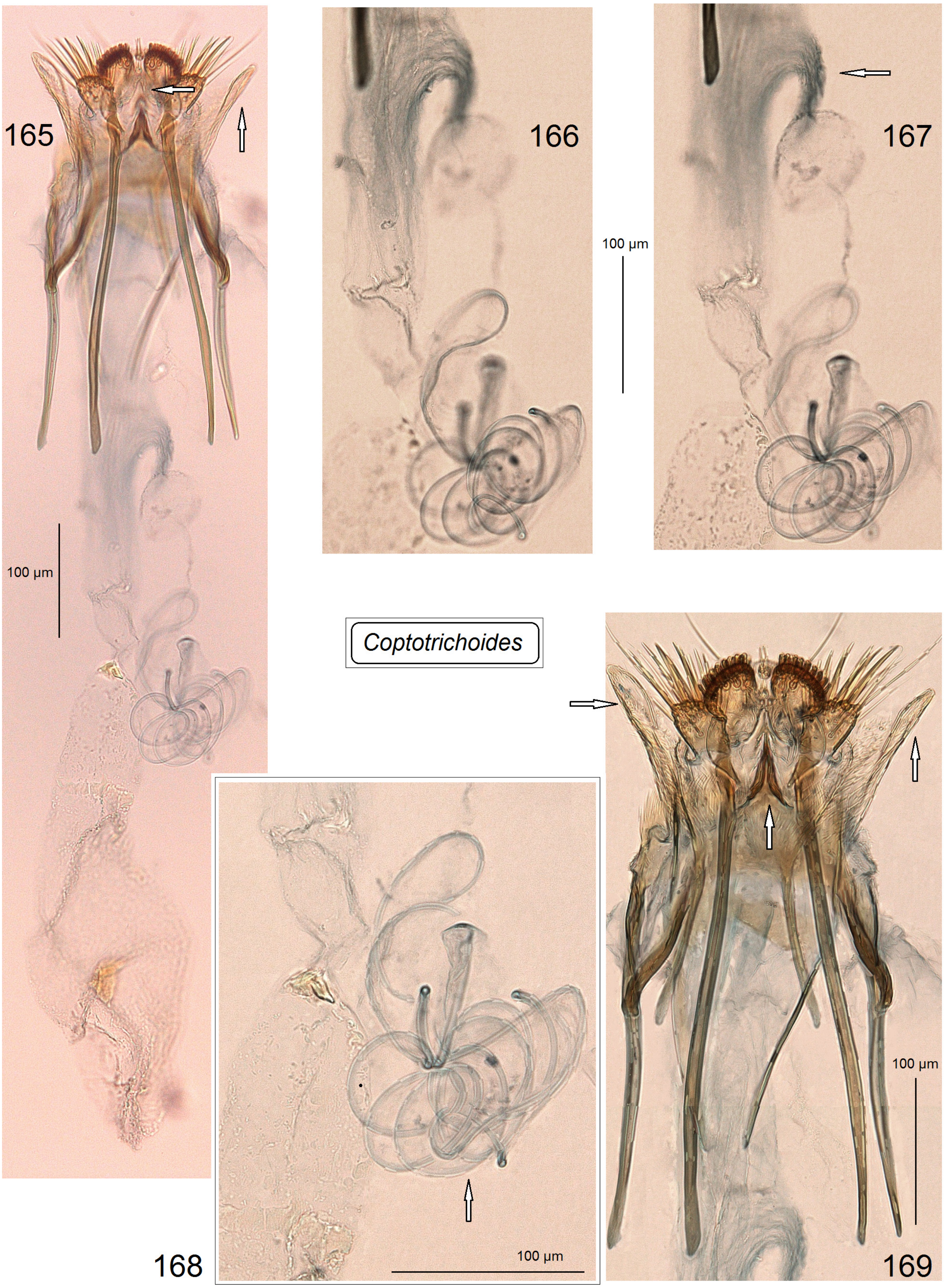
157

158

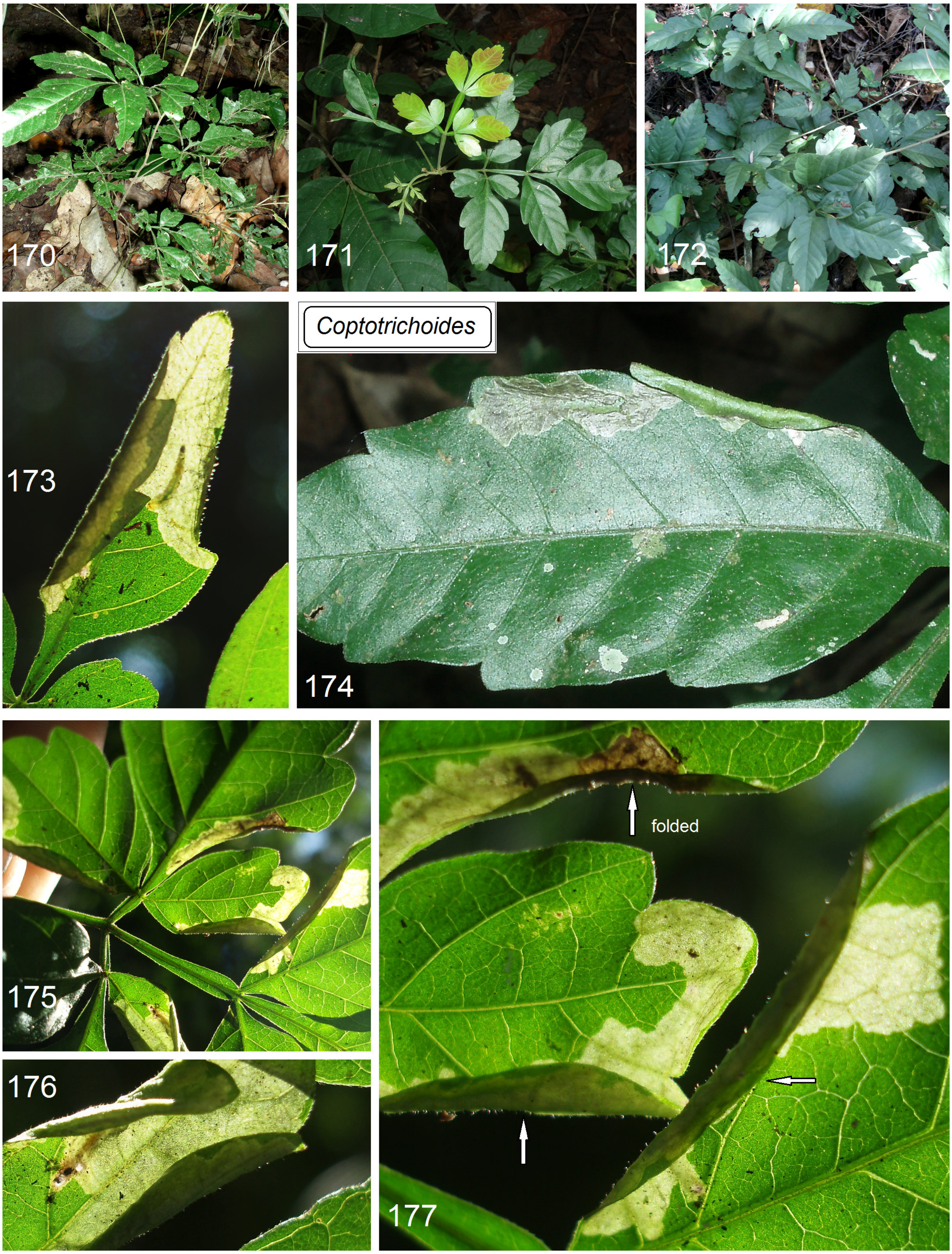
FIGURES 153–158. Adults of *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.**, Honduras. 153, general view without abdomen, male holotype; 154, same, female paratype; 155, details of head, male holotype; 156–158, same, female paratype (MfN)



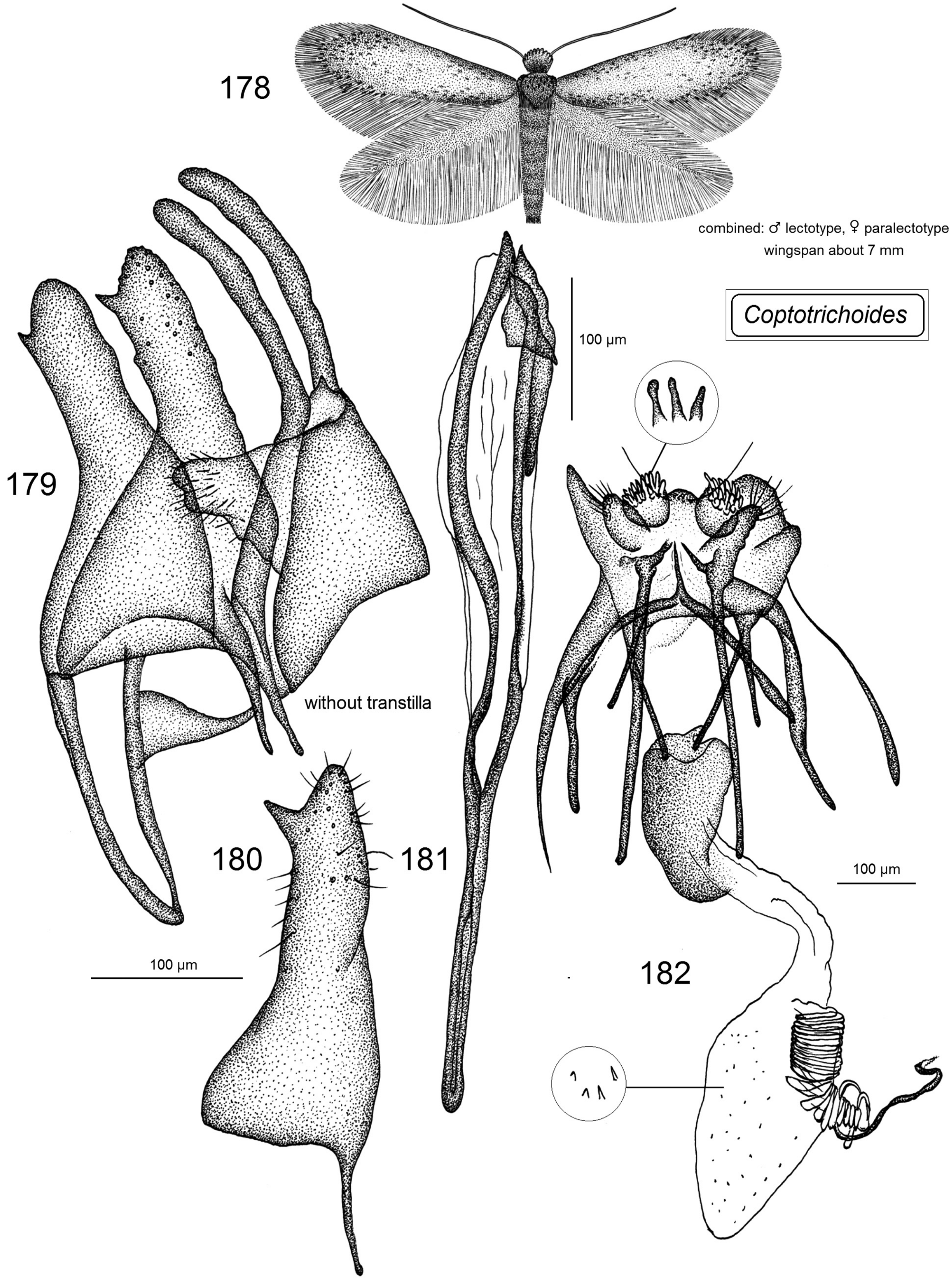
FIGURES 159–164. Male genitalia of *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.**, Honduras. 159, 160, capsule with phallus removed, holotype, genitalia slide no. AD537, ventral view; 161, same, paratype, genitalia slide no. AD528, lateral view; 162, same, valva; 163, phallus, paratype, genitalia slide no. AD528; 164, same, holotype, genitalia slide no. AD537 (MfN)



FIGURES 165–169. Female genitalia of *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.**, Honduras, paratype, genitalia slide no. AD1091 (MfN). 165, general view; 166, 167, ductus spermathecae; 168, coils of ductus spermathecae; 169, ovipositor lobes and apophyses



FIGURES 170–177. Bionomics of *Coptotrichoides sapindoidum* Diškus & Stonis, **sp. nov.**, Honduras. 170–172, unidentified host plant (probably *Serjania* Mill., but also possibly *Paullinia* L.), Copán, elevation 620 m; 173–177, leaf mines



FIGURES 178–182. First documentation of the lectotype and paralectotype of *Coptotrichoides deliquescens* (Meyrick, 1915), **comb. nov.**, Guyana (NHMUK). 178, general view of adult (combined of lectotype and paralectotype); 179, male genitalia, capsule with phallus removed, lateral view, lectotype [**designated here**], genitalia slide no. 28675BMNH; 180, same, valva; 181, same, phallus, ventral view; 182, female genitalia, paralectotype, genitalia slide no. 28676BMNH

Description. *Male* (Figs 153, 155). Forewing length 2.5–2.8 mm; wingspan 5.5–6.1 mm (n = 2). Head: frons glossy golden cream; pecten yellowish cream with some dark brown scales; frontal tuft yellowish cream, golden glossy; collar comprised of slender lamellar scales, pale ochreous yellow, golden glossy; antenna approximately about one half the length of forewing; flagellum ochreous yellow, glossy, with some pale brown scales on upper side. Tegula and thorax pale ochreous yellow, glossy. Forewing with blue and purple iridescence, pale ochreous yellow, sparsely speckled with black-brown scales; fringe pale ochreous yellow, with an indistintive fringe line comprised of brown-black scales; forewing underside brown. Hindwing pale grey to cream or slivery shiny, depending on the angle of view; on underside, hindwing pale brown, without androconia; fringe ochreous cream. Legs ochreous cream, glossy, speckled with grey-brown scales on upper side. Abdomen densely speckled with brown scales on upper side, ochreous yellow with some dark brown scales on underside; genital plates ochreous yellow; anal tufts indistinctive (or rubbed).

Female (Figs 154, 156–158). Forewing length 2.8–2.9 mm; wingspan 6.0–6.1 mm (n = 2). Otherwise, similar to male.

Male genitalia (Figs 159–164) with capsule 385–415 µm long, about 255 µm wide. Uncus comprised of two very slender and long lobes. Socii large, weakly paired, densely covered with minute spines. Tegumen moderately short, without spines. Valva about 245 µm long, almost gradually tapering towards apex; basal processes slender, relatively long. Anellus indistinctive. Vinculum very short, with a very slender and long anterior process. Phallus 690–700 µm long, very slender but wide apically; apex thickened laterally and with a prominent, pointed, median process.

Female genitalia (Figs 165–169) ca. 3410 µm long. Ovipositor lobes relatively large, rounded, densely covered with peg-like setae; second pair of ovipositor lobes almost of the same size as the main lobes but with numerous long setae; lateral lobes distinctly long (Fig. 169). Anterior and posterior apophyses equal in length; prela comprised of three pairs of unique, rod-like projections; inner prela very slender and long. Corpus bursae long; pectination indistinctive or absent. Ductus spermathecae with about 13–15 very large coils.

Bionomics (Figs 170–177). Host plant is *Serjania* Mill. (or *Paullinia* L.), Sapindaceae (Figs 170–172). Larvae mine leaves in February. The blotch-like mine is irregular, but usually elongated, whitish and transparent, without frass. Usually leaf mines are close to the leaf margin and the mining larva folds a margin of the mined leaf before pupation. The nidus is invisible through the epidermis, so dissection of the mine is necessary to see the nidus. Adults occur in March.

Distribution. This species is known from a single locality in Honduras, Copán Department, Copán, at the elevation of 620 m.

Etymology. The species is named after the tropical host-plant subfamily Sapindoideae, in reference to its feeding on *Serjania* Mill. (or *Paullinia* L.), Sapindoideae, Sapindaceae.

3. Genus *Dishkeya* Stonis, 2020

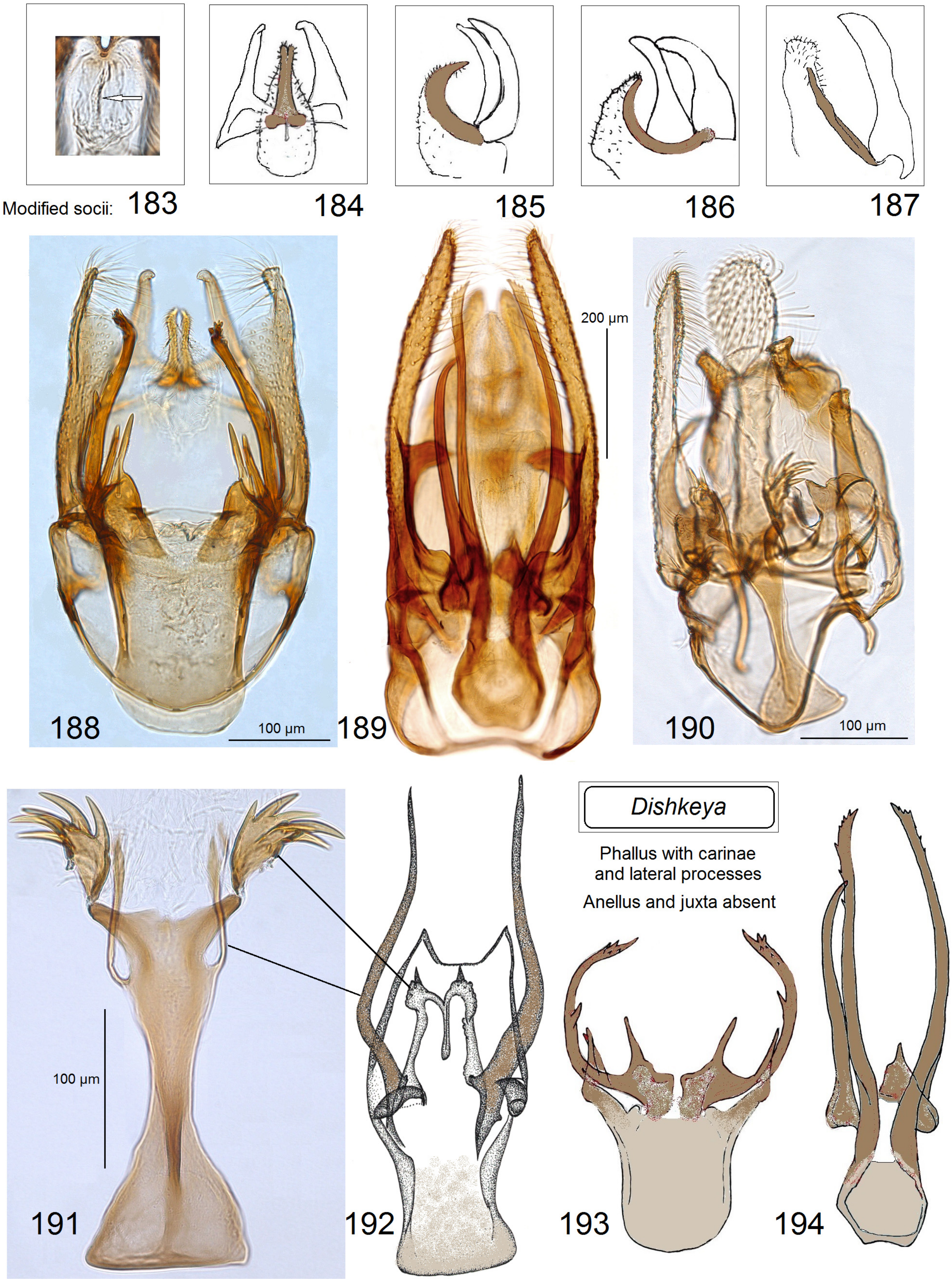
(Figs 183–194)

Dishkeya Stonis, 2020: 125–127. Type species: *Dishkeya gouaniae* (Stonis & Diškus, 2007: 1286–1291).

Diagnosis. In the male genitalia, species of *Dishkeya* are characterized by the modified socii usually forming a pseudognathos, a wide phallus with lateral processes and variously developed carinae, and absence of a juxta or anellus. In the female genitalia, the genus is characterized by the small ovipositor lobes and large lateral lobes. In contrast to majority of Tischeriidae, leaf mines of *Dishkeya* are linear on Rhamnaceae host plants. For major diagnostic characters of *Dishkeya* and their occurrence in other genera of Tischeriidae see Tabs 2, 3.

Molecular notes. According to the molecular analysis, *Dishkeya* is a separate clade, and always branches with *Coptotrichoides*; together these two genera are often close to the *Coptotriche* genus (Figs 62, 64).

Adult. Head: frontal tuft overlapping the frons, comprised of long, slender lamellar and piliform scales; collar comprised of slender lamellar scales. Forewing without a distinct pattern, yellowish ochre to pale grey, irregularly speckled with some darker scales (Stonis & Solis 2020). Hindwing slender, without androconia.



FIGURES 183–194. Male genitalia of *Dishkeya* Stonis (after Stonis & Solis 2020; Stonis *et al*. 2022a). 183, modified socii, *D. ursipedella* Diškus, Mey & Stonis, ventral view; 184, same, *D. gouaniae* (Diškus & Stonis), ventral view; 185, same, lateral view; 186, same, *D. bifurcata* (Braun), lateral view; 187, same, *D. gothica* Diškus & Stonis, lateral view; 188, male genitalia, *D. gouaniae*, slide no. 010316202 (NHMUK); 189, same, *D. gothica*, slide no. AD1010 (ZMUC); 190, *D. ursipedella*, slide no. AD1119 (MfN); 191, phallus, *D. ursipedella*; 192, same, *D. bifurcata*; 193, same, *D. gouaniae*; 194, same, *D. gothica*

Male genitalia (Figs 183–194). Uncus with two long, very slender or wide lateral lobes. Socii spinose, modified, usually thickened medially and forming a pseudognathos (Figs 183–187). Tegumen long, without lateral frame-like thickening; diaphragm without spines. Valva slender to medium wide, usually with inner process or larger inner lobe; basal process of valva very short, except for *D. ursipedella* Diškus, Mey & Stonis (Stonis *et al*. 2022a) which is characterized by very long basal processess. Transtilla or anellus absent. Vinculum long, widely rounded or truncated distally. Phallus wide to very wide, occasionally constricted medially, with strongly developed lateral processes (sometimes also possessing spines) and variously developed, usually asymmetrical apical carinae (Figs 191–194); the recently described Colombian *D. ursipedella* (Stonis *et al*. 2022a) posseses particularly developed, five-claw carinae (Figs 190, 191).

Female genitalia. Ovipositor lobes small; the gap between ovipositor lobes relatively wide; second pair of ovipositor lobes almost equal in size to the main ovipositor lobes or divided. Lateral lobes very large, wide proximally. Anterior apophyses slightly shorter than posterior apophyses. Prela with three pairs of rod-like projections; caudal sclerite strongly developed, inverted V-shaped, with a large pointed lobe caudally. Antrum absent. Otherwise, female genitalia are unknown.

Bionomics. The genus is trophically associated with Rhamnaceae and known leaf mines are linear. However, there remains a need to discover and study the biology of additional species in this genus.

Species diversity and geographical distribution. Currently the genus is comprised of four species. It is predicted that this genus might have an almost continuous distribution along the West coast of the Americas (Stonis & Solis 2020); recently one new species was described from the Colombian Andes (Stonis *et al.* 2022a).

4. Genus *Tischeria* Zeller, 1839

(Figs 195–264)

Tischeria Zeller, 1839: 219. Type species: *Tinea complanella* Hübner, 1817: pl. 64, fig. 428, junior syn. of *Tischeria T. ekebladella* (Bjerkander, 1795).

Philodoxa Gistel, 1848: xi. Type species: *Tinea complanella* Hübner, 1817: pl. 64, fig. 428, junior syn. of *Tischeria ekebladella* (Bjerkander, 1795).

Evexia Gistel, 1850: 486. Type species: *Tinea complanella* Hübner, 1817: pl. 64, fig. 428, junior syn. of *Tischeria ekebladella* (Bjerkander, 1795).

Diagnosis. External characters of the adults and wing venation characters are not informative and, therefore, insufficient for the differentiation of *Tischeria* because of their general uniformity. However, the majority of the species have a bright ochreous yellow forewing speckled with darker scales apically or, occasionally, also with a small black tornal spot. In the male genitalia, species of *Tischeria* are characterized by the presence of a juxta and medium wide to very wide phallus with usually long lateral processes, but without carinae. In the female genitalia, the genus is characterized by the presence of antrum and a slender, short ductus spermathecae with only 2–4 coils. Leaf mines of *Tischeria* are mostly on Fagaceae host plants, blotch-like, with a distinctive round nidus inside the leaf. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. Molecular data provided relatively strong support for the distinctness of this genus. In all cases *Tischeria* appears as a sister taxon to *Rytietia* **gen. nov.** (described below) (Figs 62, 63, 67).

Adult. Head: frontal tuft overlapping the frons, comprised of long, slender or relatively wide lamellar scales; pecten distinctive; collar distinctly paired, comprised of relatively wide lamellar scales. Forewing usually bright ochreous yellow speckled with darker scales in apically half, occasionally also with a small black tornal spot. Hindwing slender, without androconia.

Male genitalia (Figs 195–208). Uncus with two long and basally wide lateral lobes which look triangular in ventral view. Socii membranous, often usually distinctly paired (occasionally unpaired), with numerous tiny spines. Tegumen large to medium large, usually without spines on the diaphragm, occasionally diaphragm little spinose; pseudognathos absent. Valva simple-shaped, slightly sinuous in lateral view, wide basally, gradually tapering towards apex; basal process of valva short. Transtilla and anellus absent. Juxta present, well-developed, comprised of either one or two pairs of horn-like processes, well demarcated from the phallus. Vinculum large to small; ventral plate usually triangular, with a short anterior process or rounded distally. Phallus usually wide to moderately wide, occasionally slender, with well-developed lateral processes, without spines or carinae.

Female genitalia (Figs 209–213). Ovipositor lobes usually large or very large; the gap between ovipositor lobes wide; second pair of ovipositor lobes twice smaller in comparison to main ovipositor lobes. Lateral lobes usually short and wide, occasionally indistinctive. Anterior apophyses usually distinctly shorter than posterior apophyses. Prela with three pairs of rod-like projections; these projections sometimes slightly or strongly widened basally. Caudal sclerite strongly developed, inverted V-shaped, with slender and pointed projection caudally. Antrum present, variously developed. Accessory sac absent; ductus spermathecae short, slender, with 2–4 coils; vesicle usually large, rounded. Corpus bursae long to medium long, usually gradually narrowing towards caudal end, with short spines proximally.

Bionomics. Generally, the species of the genus are associated with Fagaceae (mainly known from *Quercu*s L.). However, one species has been recorded from an Ulmaceae host plant in China (Xu *et al*. 2018), three other species of uncertain taxonomic position (placement) have been reared from Rhamnaceae host plants in the USA (Braun 1972) (see Discussion), and one species has been recorded from Lythraceae in Indonesia (Meyrick 1936). Larvae mine leaves and produce blotch-like leaf mines with no frass deposited; a nidus is distinctly visible throughout the mine.

Species diversity and geographical distribution. The genus is widespread in Europe, temperate Asia, and North America. Species were believed to occur in South Africa (Puplesis & Diškus 2003; Puplesis *et al*. 2004) until recently when these African species were transferred to another genus, *Manitischeria* (Stonis *et al*. 2019a). In Central America only two *Tischeria* species, including *T. elongata* Walsingham (Walsingham 1914; Stonis & Diškus 2007) and *T. neokristenseni* Diškus & Stonis, **sp. nov.**, were recognized. The genus is not yet known to occur in South America (notably from Colombia where *Quercus*, a potential host plant, occurs).

In total, it consists of twenty described species worldwide. This number includes the recently described Caucasian-Iranian *T. caucasica* Klasínski & Stonis (Klasínski *et al.* 2020; Alipanah *et al.* 2022), Central American *T. neokristenseni* Diškus & Stonis **sp. nov.** (described below), the hitherto little known Mexican *T. elongata* Walsingham (see our documentation of the holotype; Figs 214–217), North American *T. quercitella* Clemens (see documentation of a specimen deposited at NHMUK; Figs 218–223), Japanese *T. quercifolia* Kuroko (see our new documentation of the male genitalia of the species; Figs 224–229), the East Asian *T. lvoskyi* Kozlov (see the first photographic documentation of the holotype; Figs 230–236), and East Asian *T. siorkionla* Kozlov. The latter was described as an allopatric East Asian subspecies of the European *T. decidua* Wocke, 1876 (Kozlov 1986) and subsequently treated as a subspecies (Kozlov 1997; Stonis *et al*. 2014). In the current publication, we elevate the taxonomic rank of *siorkionla* to species for the following reasons: 1) *T. siorkionla* Kozlov, 1986 (**stat. nov.**) differs from the European *T. decidua* Wocke, at least in some morphological characters of the male genitalia (Figs 200, 201, 205–208); 2) there is a significant, well-known gap between East Asia and Europe in the distribution range of *Quercus* (e.g., Menitsky 2005); 3) to avoid usage of subspecies category.

Here, we also report a new distribution record of *T. dodonaea* Stainton, 1858 from the Caucasus, Armenia, feeding on the Caucasian oak (=Persian oak) *Quercus macranthera* Fisch. & C.A.Mey. ex Hohen.: 1 ♂, 1 ♀, ARMENIA, Aragatsotn Province, southern slope of the Mount Aragats, Antarut, 40°21’50”N, 44°16’25”E, the Caucasian oak forest, 1780 m, 2.viii.2022, leg. J.R. Stonis, genitalia slide no. AD1125♂ (MfN); 1 ♀, ARMENIA, Yerevan, Jrvezh Forest Park, 21.viii.2022, 40°11’06”N, 44°37’11”E, 1514 m, at light, leg. J.R. Stonis (MfN).

Currently, the genus includes six species with a doubtful placement. The taxonomic position at least of three North American species previously attributed to *Tischeria* need an in-depth revision (see Discussion).

Tischeria neokristenseni **Diškus & Stonis, sp. nov.**

urn:lsid:zoobank.org:act:105B1D1F-7081-419B-B39C-E9B3E7CF9129
(Figs 237–264)

Type material. Holotype: ♂, GUATEMALA: El Quiché Department, Santa Cruz del Quiché, 15°1’22”N, 91°10’17”W, elevation 2020 m, mining larva on *Quercus* sp. (Fagaceae) 20.ii.2012, ex pupa iii.2012, field card no. 5101, leg. A. Diškus, genitalia slide no. AD1077 (MfN). Paratypes: 5 ♂, 2 ♀ same label data as holotype, genitalia slide nos AD521♂, AD1076♀ (MfN); 8 ♂, 8 ♀, Antigua Guatemala, San Juan del Obispo, 14°31’7”N, 90°43’50”W, elevation 1680 m, mining larvae on *Quercus* sp. (Fagaceae) 25.ii.2012, ex pupa iii.2012, field card no. 5111, leg. A. Diškus, genitalia slide no. AD927♂ (from adult in pupal skin) (MfN).

Diagnosis. Externally, this new species can be confused with some other similar *Tischeria* species, however, the new species is characterized by a slightly darker (than usual) coloration of the forewing. In the male genitalia, the unique shape of the juxta (see Figs 245, 248) distinguishes *T. neokristenseni* **sp. nov.** from all known congeneric species. In the female genitalia, the combination of a unique, well-developed, elaborated antrum, long stout anterior apophyses, and a large, round vesicle of the ductus spermathecae can differentiate this species from all congeneric species.

DNA barcode. We barcoded two paratypes; sequences are available in the GenBank database under accession numbers OQ413573 and OQ413574.

Description. *Male* (Figs 237–239, 241, 242). Forewing length 2.8–3.9 mm; wingspan 6.2–8.6 mm (n = 12). Head: palpi yellowish cream; frons ochreous yellow; frontal tuft and distinctly paired collar comprised of lamellar scales, yellow-ochre distally, dark brown basally; antenna slightly or distinctly longer than one half the length of forewing; flagellum ochre-yellow, distinctly annulated with blackish brown scales. Tegula, thorax, and forewing yellow ochre to bright yellow-ochre; some brown-black or black scales with small amount of purple iridescence scattered along costal margin and at apex of forewing to form a distinctive tornal spot; fringe blackish grey, ochreous only apically, without fringe line; forewing underside brown-black, without androconia. Hindwing black-grey on upper side and underside, without androconia; fringe grey to dark grey-brown. Legs yellow-ochre, densely speckled with black-brown scales on upper side. Abdomen dark grey, with some golden gloss and purple iridescence on upper side, pale ochre, sometimes with some brown-grey scales on underside; genital plates large, yellow-ochre; anal tufts distinctive, relatively long, lateral, dark grey.

Female (Figs 240, 243). Forewing length 3.5–4.2 mm; wingspan 7.6–9.3 mm (n = 9). Similar to male, only sometimes larger and more brightly coloured, without long antennal sensilla; ovipositor not protruding. Otherwise, identical with male.

Male genitalia (Figs 244–249) with capsule 800–885 µm long, 395–405 µm wide. Uncus comprised of two large lobes. Socii large, paired, membranous. Valva 390–415 µm long. Transtilla and anellus absent. Juxta complex (see Figs 245, 248). Vinculum with a triangular ventral plate extended into a relatively slender anterior process. Phallus 785–800 µm long, bifid; lateral processes lobe-like apically.

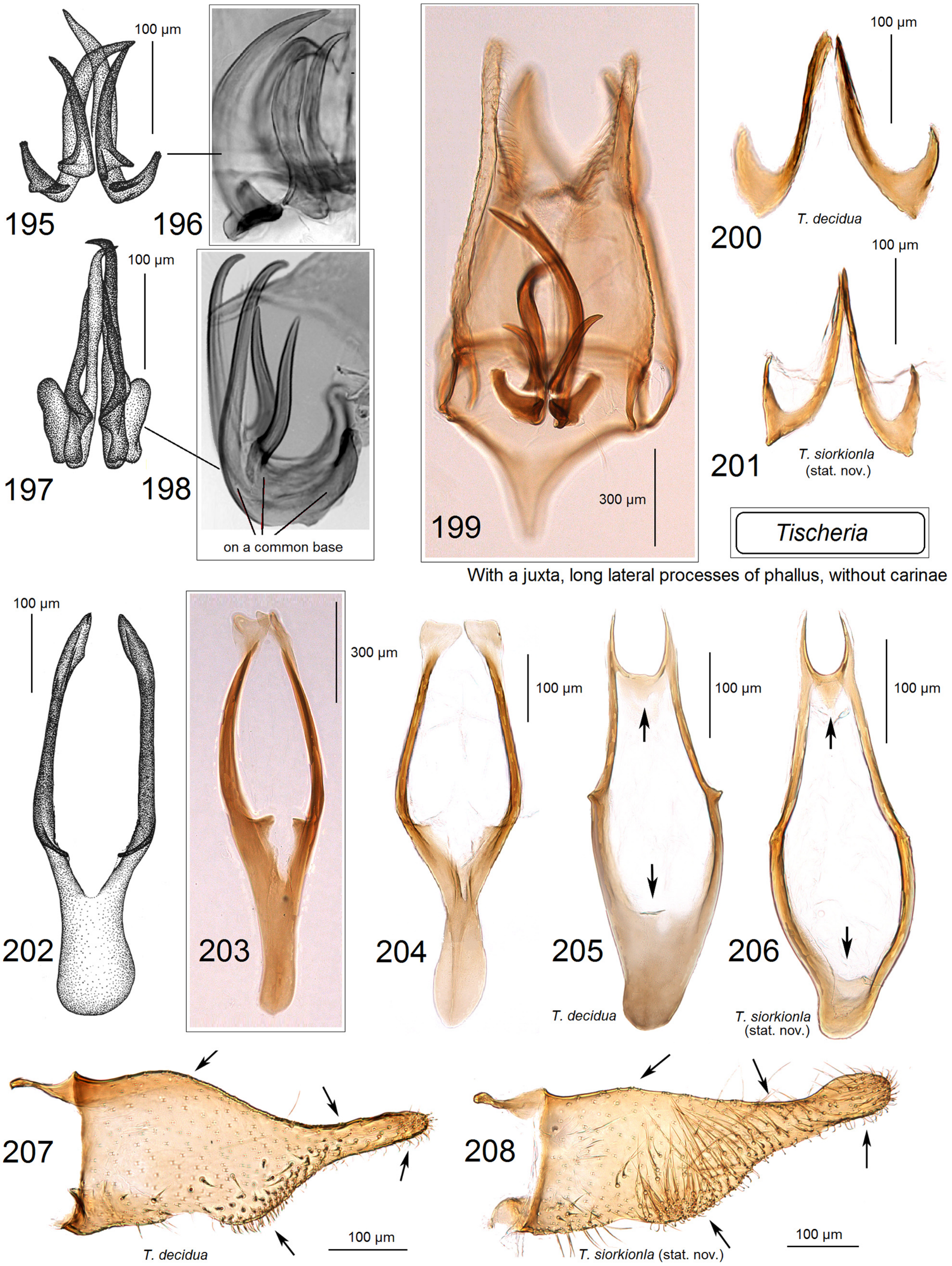
Female genitalia (Figs 250–257) ca. 1640 µm long. Ovipositor lobes large, rounded, densely covered with relatively long peg-like setae; second pair of ovipositor lobes twice as small, with numerous wide setae. Posterior apophyses significantly longer than anterior apophyses; prela with only two pairs of clearly visible rod-like projections. Antrum well-developed, elaborated (see Figs 253, 257). Corpus bursae medium long, with a slender and folded proximal part and oval-shaped main body with indistinctive pectinations. Ductus spermathecae very slender, sinuous, with 2–2.5 medium large coils and large, round, plate-like vesicle.

Bionomics (Figs 258–264). Host plant is *Ouercus* L. (section Lobatae, Fagaceae) (Figs 258–260). Larvae mine leaves in February. Leaf mines are blotch-like, transparent, with a distinctive round nidus inside, without frass. Adults occur in March.

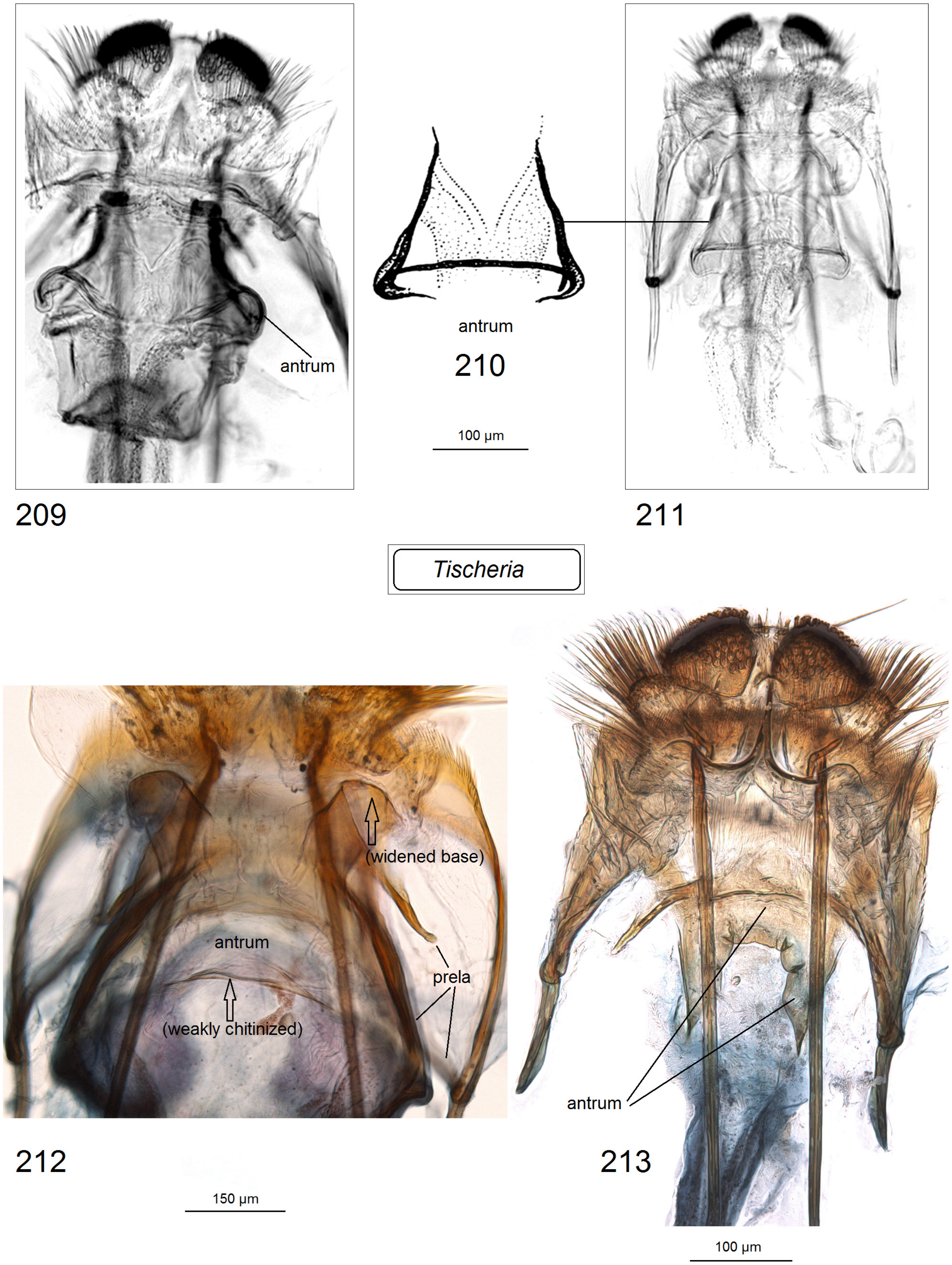
Distribution. This species is known from two localities in Guatemala (Santa Cruz del Quiché and Antigua) at an elevation of 1680–2020 m.

Etymology. By combining the prefix "neo" (meaning new and derived from the Neotropics) and the surname of our late colleague, this species is named in honour of Professor DSc. Niels Peder Kristensen (1943–2014), one of the greatest Lepidoptera morphologist and taxonomist of all time, an inspiring teacher, and outstanding supervisor, editor-in-chief of two Lepidoptera volumes of "Handbook of Zoology", former director of Zoologisk Museum of Københavns Universitet, and honorary member of academic societies (see Simonsen *et al*. 2015 for honors and awards).

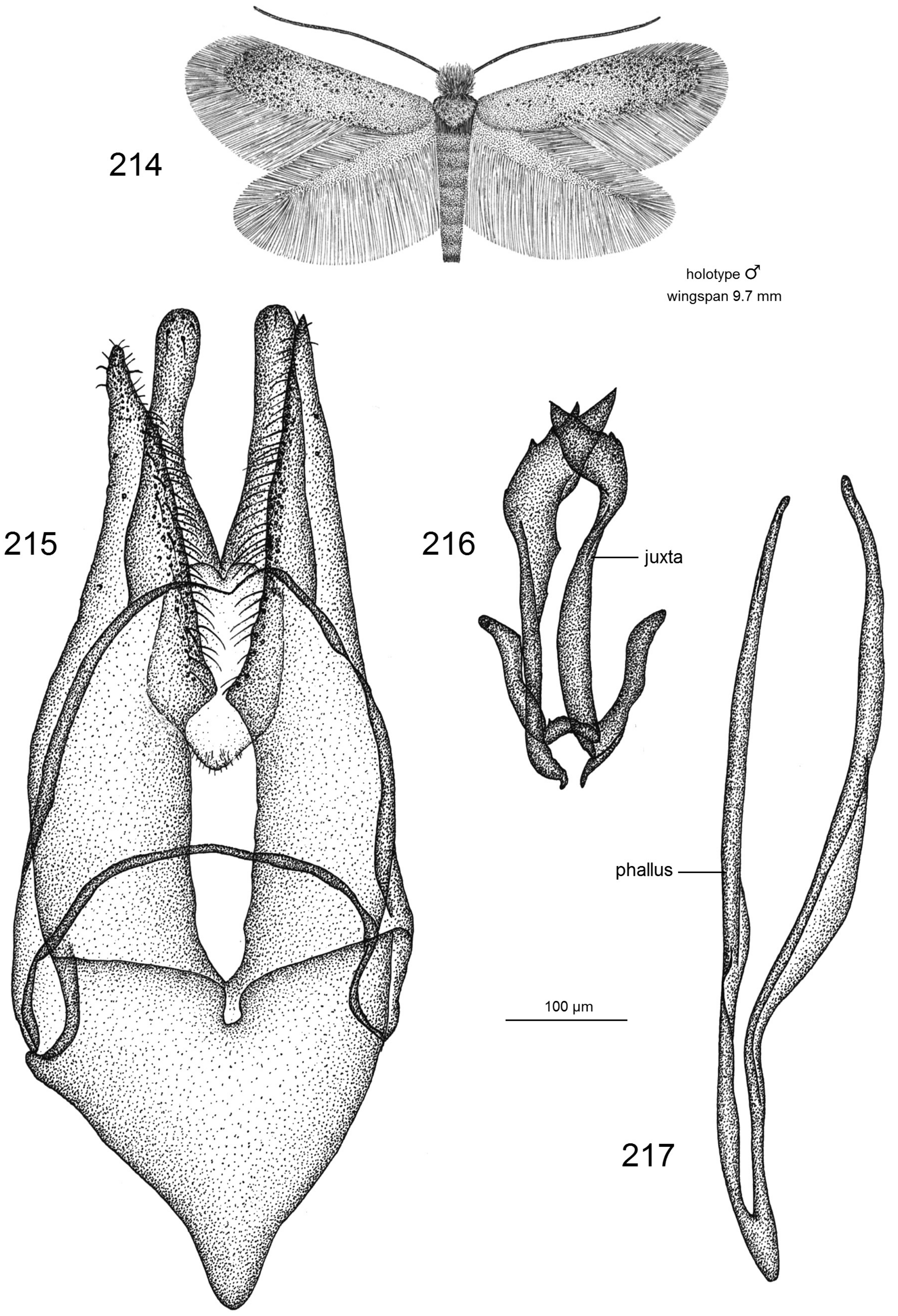
The authors of the new Tischeriidae species description, Arūnas Diškus and Jonas R. Stonis, are deeply indebted to our late colleague Niels Peder Kristensen for his generous support and enthusiastic motivation for our studies of the Neotropical Nepticuloidea and global Tischerioidea. This is the second species we have named in honour of Niels Peder Kristensen, the first one was *Stigmella kristenseni* Diškus & Stonis (Stonis *et al.* 2016b).



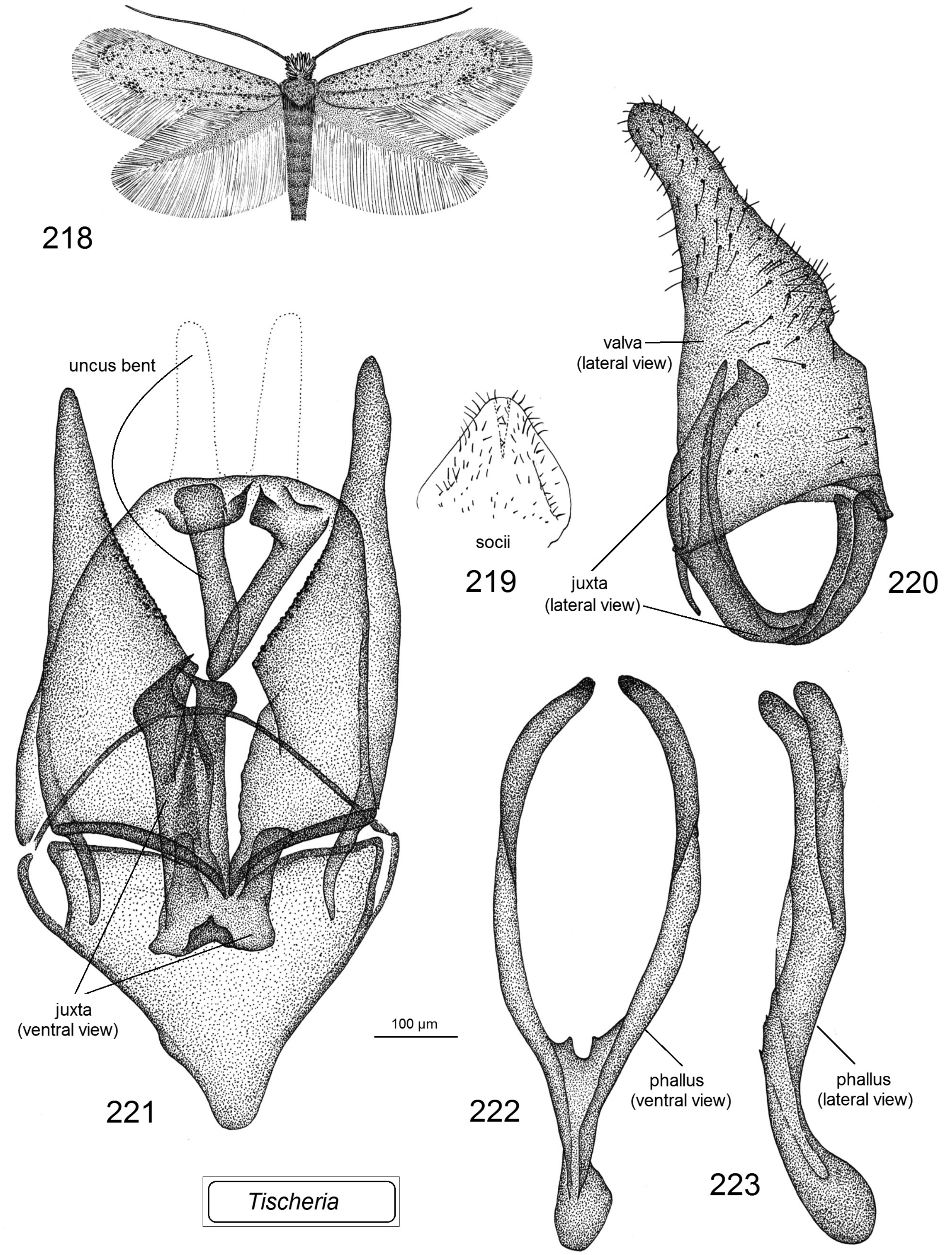
FIGURES 195–208. Male genitalia of *Tischeria.* 195, juxta of *T. ekebladella* (Bjerkander); 196, same, lateral view; 197, *T. ekebladoides* Puplesis & Diškus; 198, same, lateral view; 199, *T. caucasica* Klasínski & Stonis; 200, juxta of *T. decidua* Wocke, Crimea; 201, same, *T. siorkionla* Kozlov, 1986, slide no. AD589 (ZIN); 202, phallus, *T. ekebladoides*; 203, same, *T. caucasica*; 204, same, *T. ekebladella*; 205, same, *T. decidua*; 206, same, *T. siorkionla*; 207, valva, lateral view, *T. decidua*, slide no. AD590; 208, same, *T. siorkionla* slide no. AD589 (195–198, after Diškus & Puplesis 2003; 199, 203, Klasínski *et al.* 2020; 200, 201, 205–208 Stonis *et al.* 2014)



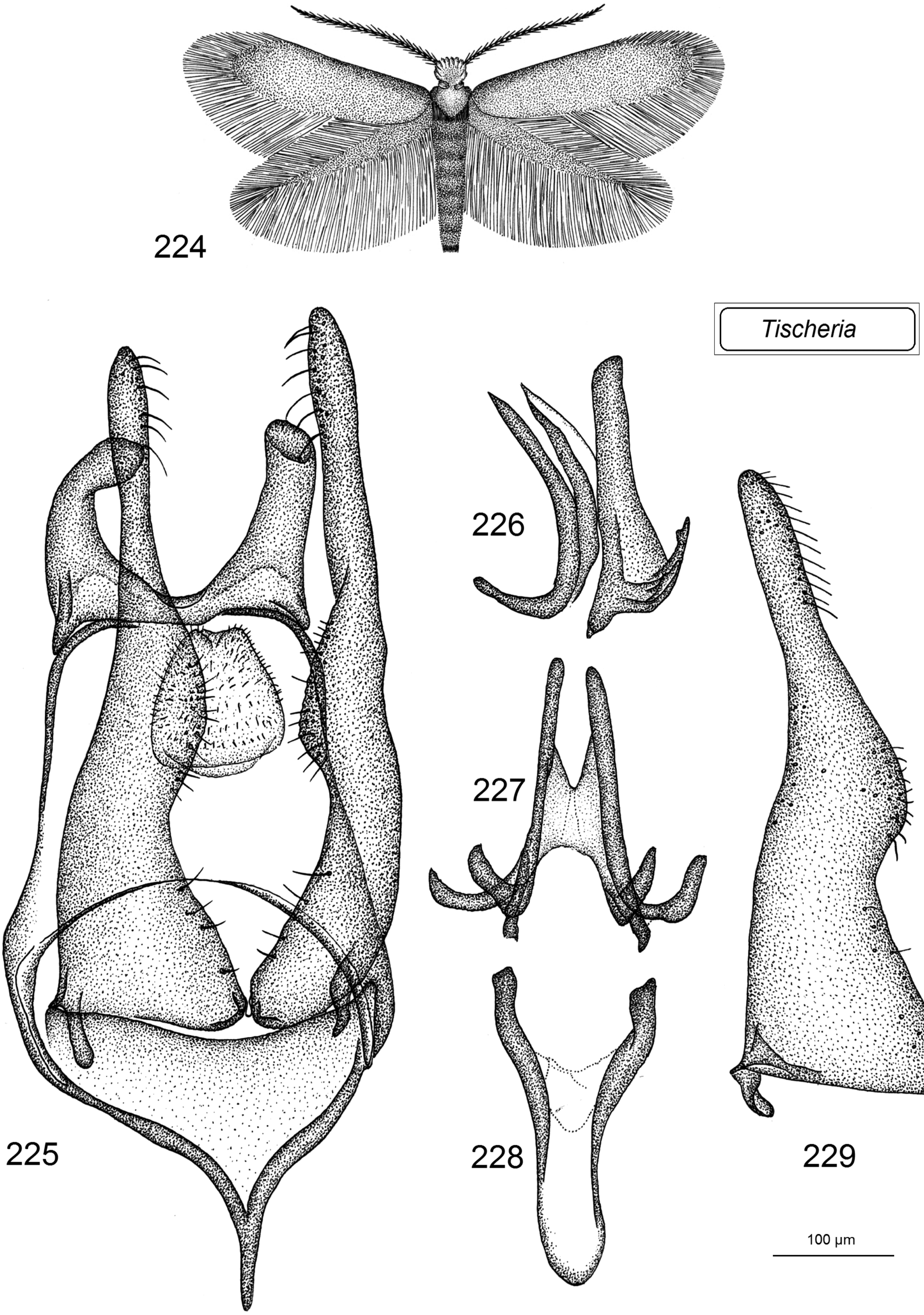
FIGURES 209–213. Details of antrum in the female genitalia of *Tischeria.* 209, *T. ekebladoides* Puplesis & Diškus, Tunisia, paratype, slide no. Diškus074 ZMUC (after Diškus & Puplesis 2003); 210, 211, *T. ekebladella* (Bjerkander), Poland, slide no. Diškus073 ZMUC (after Diškus & Puplesis 2003); 212, *T. caucasica* Klasínski & Stonis, Georgia, paratype, slide no. RA1082 MfN (after Klasínski *et al*. 2020); 213, *T. sichotensis* Ermolaev, Far Eastern Russia, slide no. AD587 MfN (after Stonis *et al.* 2014)



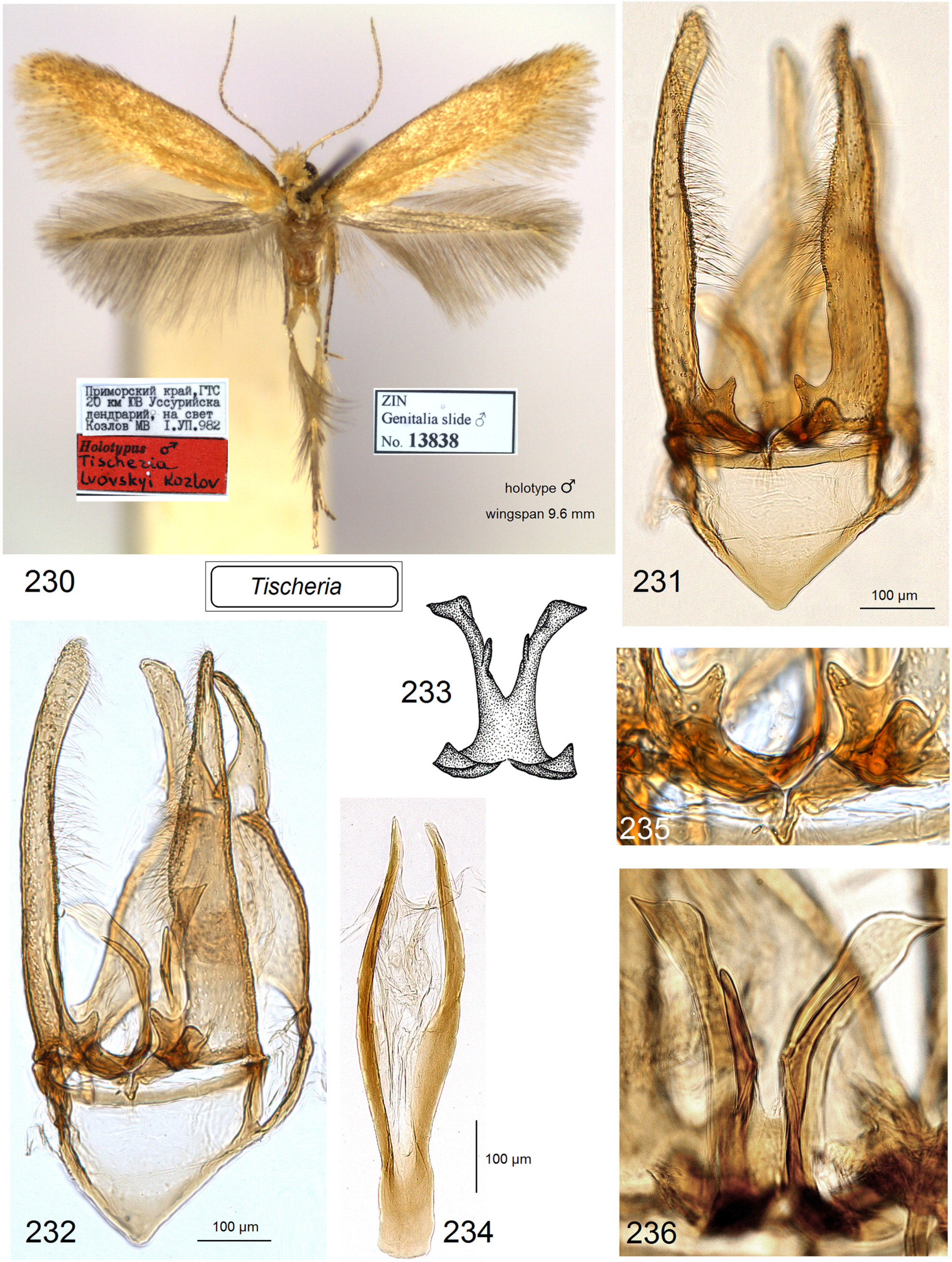
FIGURES 214–217. Re-study and re-documentation of holotype of *Tischeria elongata* Walsingham, Mexico, holotype (NHMUK). 214, male adult; 215, male genitalia, slide no. 15283 BMNH, capsule with phallus removed; 216, same, juxta; 217, same, phallus



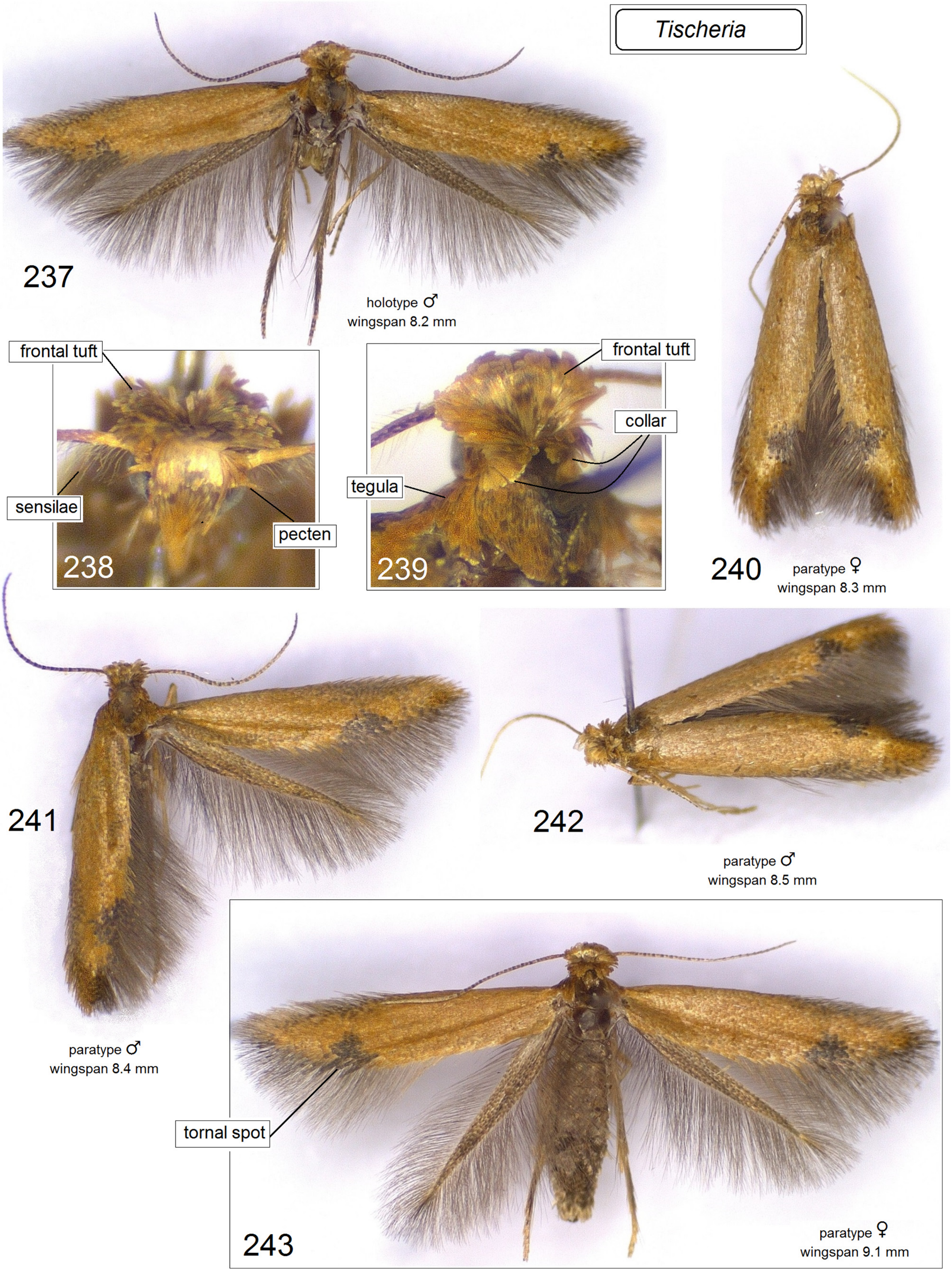
FIGURES 218–223. Documentation of *Tischeria quercitella* Clemens, USA, Kirkwood, St. Louis, 18.vii.1883 (NHMUK). 218, male adult; 219, male genitalia, slide no. 28955 BMNH, socii; 220, same, valva; 221, same, capsule with phallus removed; 222, same, ventral view of phallus; 223, same, lateral view of phallus



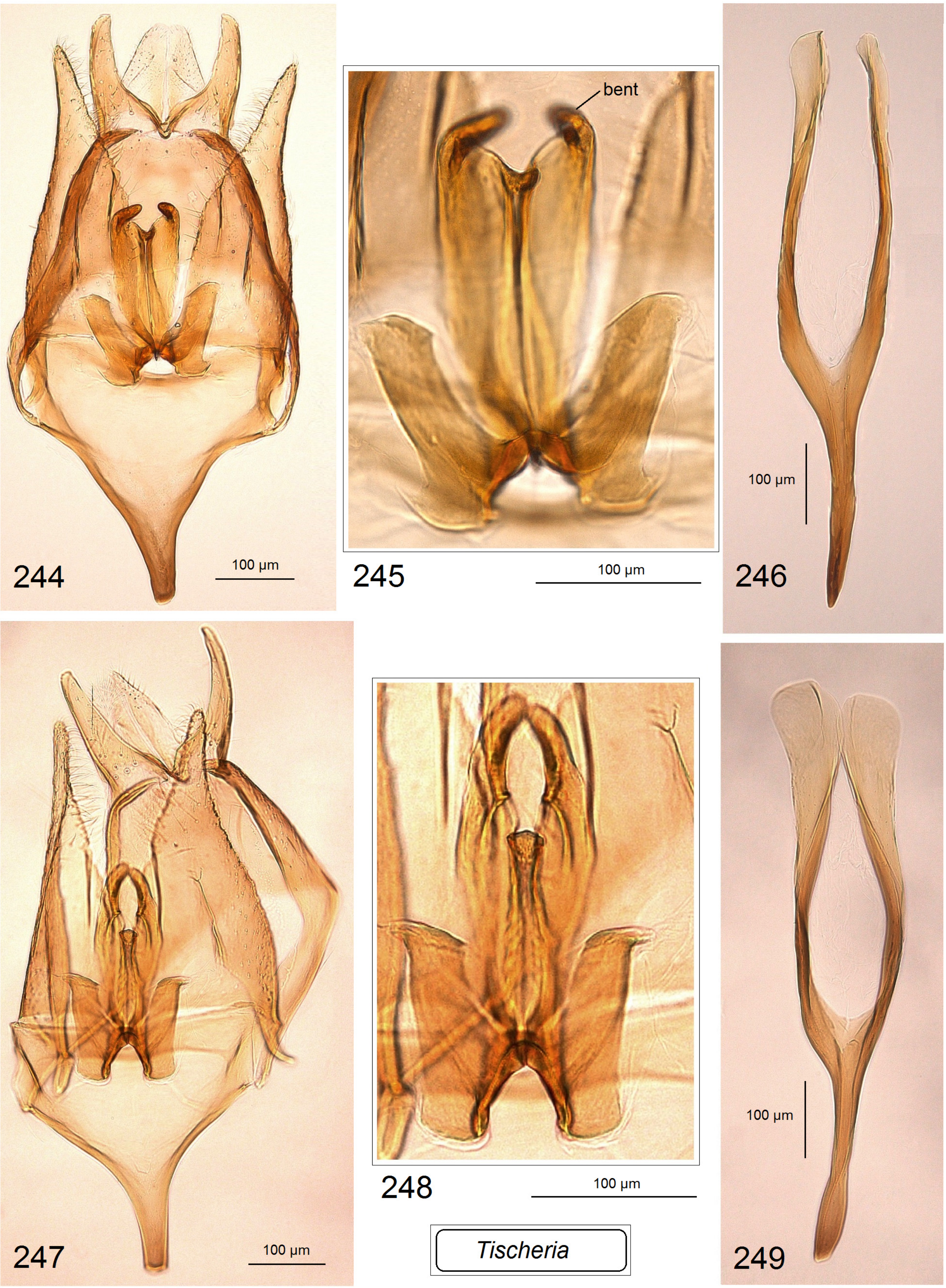
FIGURES 224–229. *Tischeria quercifolia* Kuroko, Japan, Honsyu, Nagana-ken, Hukusima, 4.v.1976, T. Kumata (ZMUC). 224, male adult; 225, male genitalia, slide no. Diškus087 ZMUC, capsule with phallus removed; 226, same, lateral view of juxta; 227, same, ventral view of juxta; 228, phallus; 229, lateral view of valva



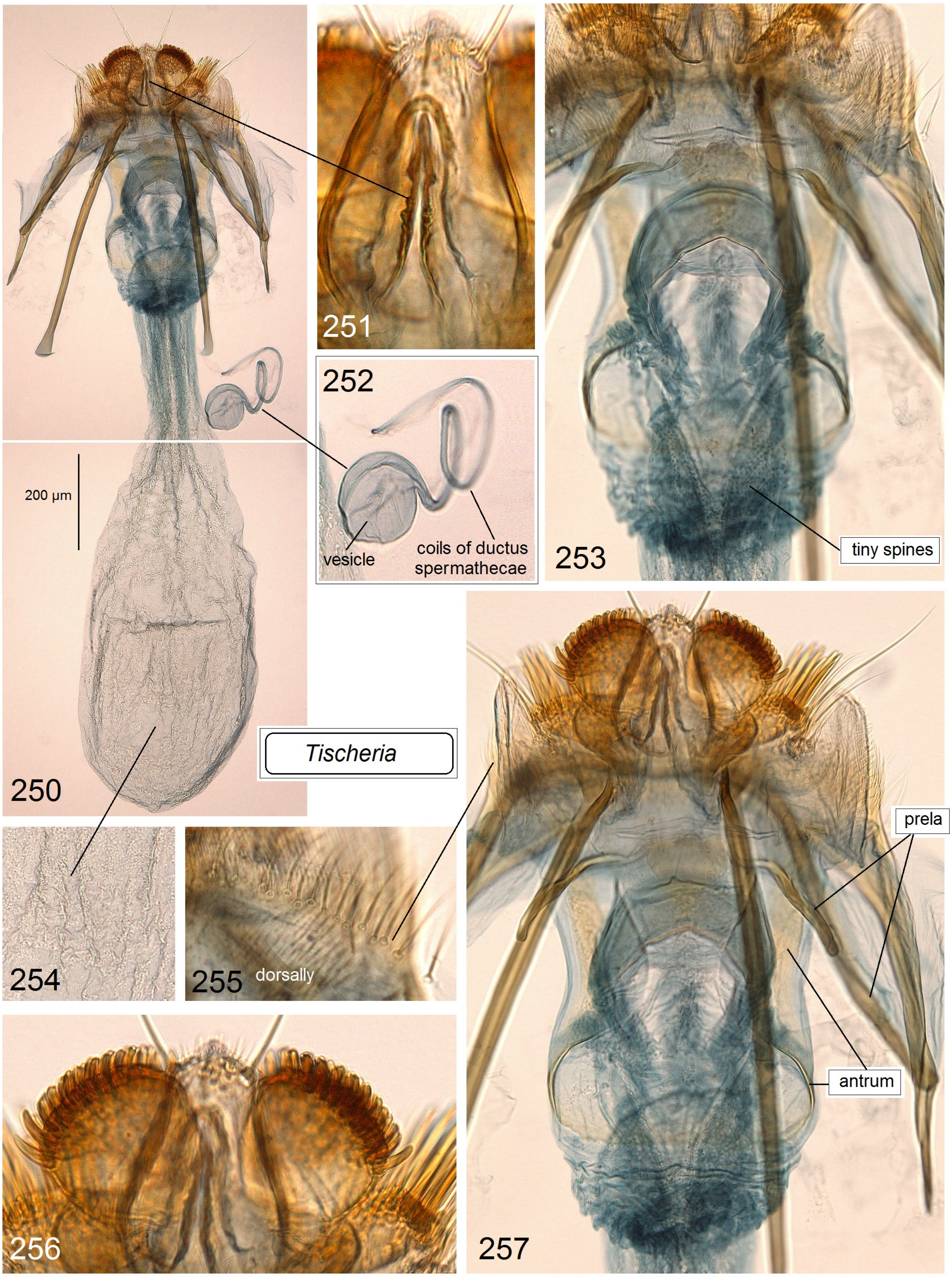
FIGURES 230–236. First photographic documentation of *Tischeria lvovskyi* Kozlov, Far Eastern Russia. 230, male holotype; 231, 232, male genitalia, holotype, slide no. 13838 (ZIN), capsule with phallus removed; 233, juxta in glycerol of a non-type specimen collected at the type locality by R. Puplesis, 4.vii.1982 (ZIN); 234, holotype, slide no. 13838 (ZIN), phallus; 235, same, basal processes of valvae; 236, same, juxta



FIGURES 237–243. Adults of *Tischeria neokristenseni* Diškus & Stonis, **sp. nov.**, Guatemala. 237, male, holotype without abdomen, general view; 238, male head, paratype, frontal view; 239, same, dorsal view; 240, paratype, female; 241, 242, paratypes, males; 243, paratype, female (MfN)



FIGURES 244–249. Male genitalia of *Tischeria neokristenseni* Diškus & Stonis, **sp. nov.**, Guatemala. 244, capsule with phallus removed, holotype, genitalia slide no. AD1077; 245, same, juxta; 246, same, phallus; 247, capsule with phallus removed, paratype, genitalia slide no. AD521; 248, same, juxta; 249, same, phallus; (MfN)



FIGURES 250–257. Female genitalia of *Tischeria neokristenseni* Diškus & Stonis, **sp. nov.**, Guatemala, paratype, genitalia slide no. AD1076 (MfN). 250, general view; 251–257, details of genitalia

FIGURES 258–264. Bionomics of *Tischeria neokristenseni* Diškus & Stonis, **sp. nov.** 258–260, habitat and host plant, *Quercus* sp. (section Lobatae), montane mixed forest at elevation 2020 m, Santa Cruz del Quiché, El Quiché Department, Guatemala; 261–264, leaf mines

5. Genus *Manitischeria* Diškus & Stonis, 2021
(Figs 265–274)

Manitischeria Diškus & Stonis, 2021: 253–256. Type species: *Manitischeria ptarmica* (Meyrick, 1908: 399).

Diagnosis. In the male genitalia, species of *Manitischeria* are characterized by the unique valva with a lateral "arm" (process), frame-like thickening of tegumen, presence of juxta, and a slender, rod-like phallus with basal projections laterally. In the female genitalia, the genus is characterized by a strongly developed antrum and short lateral lobes of ovipositor. Leaf mines of *Manitischeria* are blotch-like, occasionally very slender; in contrast to many other Tischeriidae, except for *Coptotriche* and *Coptotrichoides*, fully developed leaf mines of *Manitischeria* are characterized by the folded or rolled-up margin of the mined leaf; a round nidus inside the leaf mine is inconspicuous. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. External characters of the adults are not informative and, therefore, insufficient for the differentiation of *Manitischeria* from other genera. Molecular data provided the relatively strong support for the distinctness of this genus. *Manitischeria* reliably separated from the cluster composed of *Astrotischeria*, *Gnathitischeria*, *Neotischeria, Pafazaria*, and *Paratischeria* genera (Figs 62, 63) or appeared to be a sister clade with *Pafazaria* (Fig. 67).

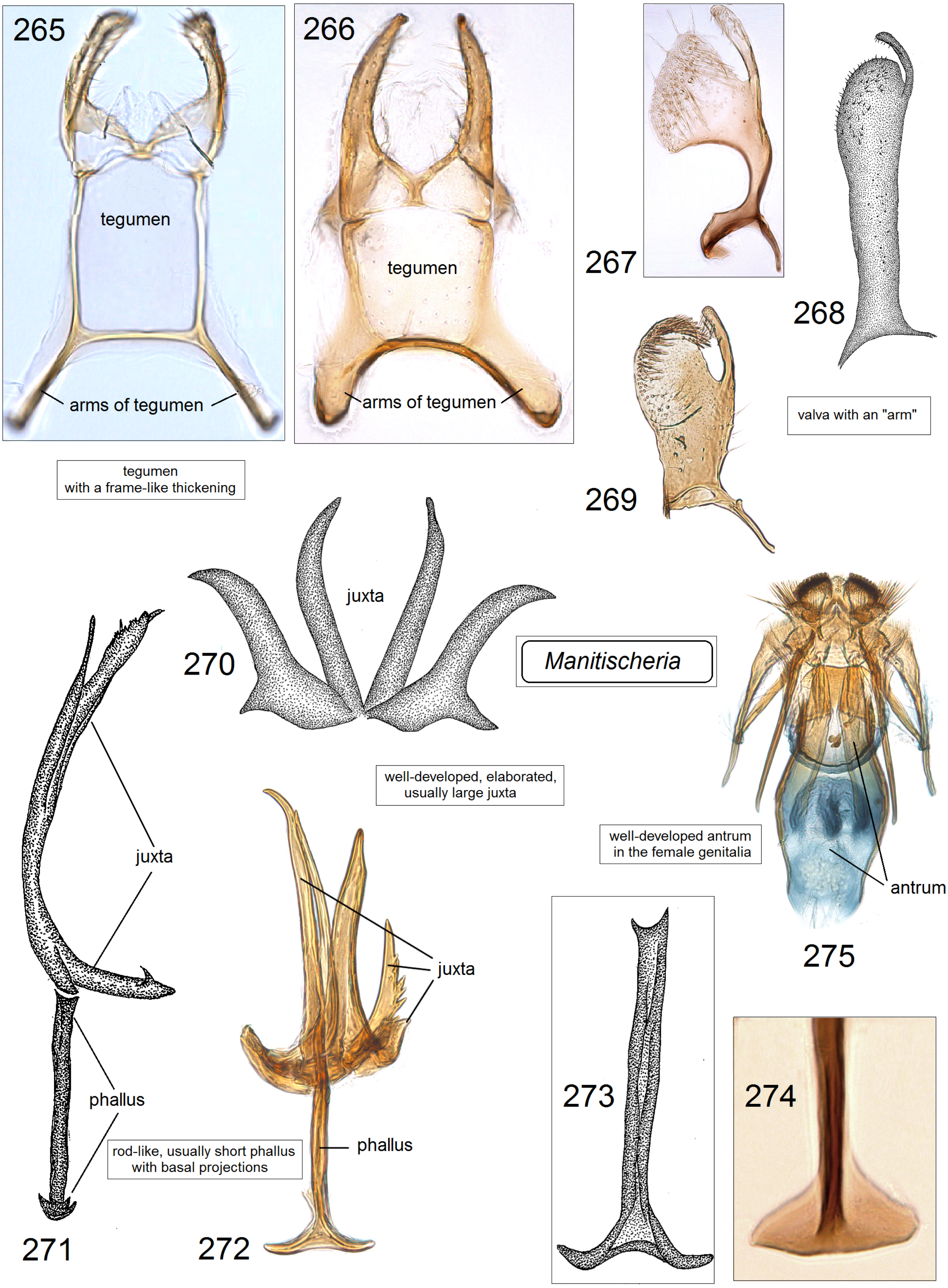
Adult. Head: frontal tuft overlapping the frons, comprised of long, slender to relatively wide lamellar scales; pecten sometimes small; collar paired, comprised of slender to relatively wide lamellar scales. Forewing without a distinctive pattern, irregularly speckled, sometimes with an irregular tornal spot or more irregular spots, occasionally dark. Hindwing slender, without androconia.

Male genitalia. Uncus with two long and slender lateral lobes. Socii membranous, slightly or distinctly paired, weakly, indistinctly spinose. Tegumen short, with a distinctive frame-like thickening, occasionally also with anterior projections; diaphragm without spines; pseudognathos absent. Valva with an "arm" (slender lateral process) apically, wide basally, usually gradually tapering towards apex; basal process of the valva varies: usually long to very long, occasionally short. Transtilla and anellus absent. Juxta present, well-developed, usually comprised of large horn-like processes, weakly demarcated (or not demarcated) from the phallus; sometimes juxta much longer and wider than phallus. Vinculum medium large, occasionally small; ventral plate triangular, pointed, truncated or rounded distally. Phallus relatively short, rod-like, with strongly developed lateral projections basally, occasionally rounded, plate-like basally.

Female genitalia. Ovipositor lobes usually small, occasionally medium; the gap between ovipositor lobes medium wide; second pair of ovipositor lobes twice as small in comparison to main ovipositor lobes. Lateral lobes usually short and wide, occasionally indistinctive. Apophyses usually equal in length, occasionally anterior apophyses slightly or distinctly shorter than posteriorapophyses. Prela with three pairs of rod-like projections or two pairs of rod-like projections and one pair with widened, plate-like proximal part. Caudal sclerite present, sometimes weakly developed, inverted V-shaped, occasionally with a slender and pointed projection caudally. Antrum present, variously developed (see Stonis *et al*. 2021d). Accessory sac absent; ductus spermathecae short to very short, slender, with a few or without coils; vesicle small to medium large, rounded or irregular in shape. Corpus bursae medium long to long, usually gradually narrowing toward caudal end, sometimes with short spines proximally, occasionally with some indistinctive pectination in the main body of corpus bursae.

Bionomics. The majority of the species of *Manitischeria* are associated with Malvaceae host plants, and occasionally with Rhamnaceae and Betulaceae. Larvae mine leaves and produce blotch-like leaf mines with no frass deposited; occasionally being very slender and long, the leaf mine looks like a gallery. Some species with fully developed leaf mines are characterized by a folded or rolled up margin of the mined leaf; a round nidus inside the leaf mine is inconspicuous.

Species diversity and geographical distribution. The genus was recently reviewed, and many species illustrated (see Stonis *et al*. 2021d). Currently, the genus is comprised of 18 species and is only known from the Eastern Hemisphere: East, South East and South West Asia, and equatorial and southern Africa.



FIGURES 265–275. Genitalia of *Manitischeria.* 265, *M. armata*, South Africa, paratype; 266, *M. sparmanniae*, South Africa, paratype; 267, *M. ptarmica*, Laos; 268, *M. antilope*, Namibia, holotype; 269, *M. unca*, Far Eastern Russia, paratype; 270, *M. tyrocnistis*, India, lectotype; 271, *M. martinkrugeri*, South Africa, holotype, lateral view; 272, *M. unca*, Far Eastern Russia, holotype; 273, *M. tyrocnistis*, India, lectotype; 274, *M. baryshnikovae*, Laos, holotype; 275, *M. unca*, Far Eastern Russia, paratype (after Stonis *et al.* 2021d)

6. Genus *Rytietia* Diškus, Xu & Dai, gen. nov.

urn:lsid:zoobank.org:act:EABA4920-58D4-477A-A2F6-5B9A00EB1134
(Figs 276–305)

Type species: *Rytietia uncinata* Diškus, Xu & Dai, **sp. nov.** (described below).

Diagnosis. Externally, adults with a distinctive forewing pattern with two colour zones, and a distinctive fringe line (Figs 276, 277).

In the male genitalia, *Rytietia* mostly resembles *Tischeria* and *Manitischeria.* From the latter, *Rytietia* is distinguishable by the simple valva without a lateral "arm" (process), and absence of a distinctive frame-like thickening of tegumen. From *Tischeria* the new genus is distinguishable by the long basal process of valva and a slender, rod-like phallus with basal projections laterally. In the female genitalia, *Rytietia* is characterized by the unique reticulate antrum, as well as elaborate caudal plate and wide processes of transverse prela. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Leaf mines are elongated with a few short, but slender, lateral galleries or wide, blotch-like. Larvae feed on Annonaceae host plants (see Remarks below).

Notes. Molecular data provides good support for the distinctness of this genus; it always clusters separately from *Tischeria*, however usually as the sister taxon to *Tischeria* (Figs 62, 63, 67).

Adult. Head: frontal tuft overlapping the frons, comprised of long, slender lamellar scales; pecten large, distinctive; collar distinctly paired, comprised of relatively wide lamellar scales. Forewing pattern with a distinctive pattern (Figs 276, 277, 283). Hindwing slender or moderately wide, without androconia.

Male genitalia. Uncus with two large lateral lobes (long and wide basally). Socii membranous, distinctly paired and spinose. Tegumen short, without a distinctive frame-like thickening; diaphragm without spines; pseudognathos absent. Valva simple, wide basally, gradually tapering toward apex; basal process of the valva long. Transtilla and anellus absent. Juxta present, well-developed, wide, comprised of plate-like processes, bifolded distally, weakly demarcated from the phallus. Vinculum long to short, trapezioid but rounded distally. Phallus relatively short, rod-like, with weakly or extremely strongly developed basal projections laterally.

Female genitalia. Ovipositor lobes very large; the gap between ovipositor lobes narrow; second pair of ovipositor lobes three times smaller in comparison to main ovipositor lobes; lateral lobes short. Apophyses robust, heavily thickened; anterior apophyses distinctly shorter than posterior apophyses. Prela with three pairs of rod-like projections: transverse prela long and unusually wide, median prela very slender and long, inner prela slender and long, distally fused with reticulate antrum; caudal sclerite elaborated, well connected with transverse prela, caudally inverted V-shaped, pointed, strongly chitinized. Antrum short but wide, in *R. uncinata* Diškus, Xu & Dai, **sp. nov.** distinctly reticulate. Accessory sac small, indistinct; ostium discernable; in *R. uncinata* **sp. nov.**, ductus spermathecae slender except for relatively wide proximal part, with a few coils and a very small, irregular vesicle. Corpus bursae long and wide, with short spines proximally, near antrum; the main body of corpus bursae without pectinations.

Bionomics. Host plant family is possibly Annonaceae (the genus *Fissistigma*; see Remarks below on *R. uncinata* **sp. nov.**, and *R. chongyiensis* **sp. nov.** Larvae mine leaves and produce slender, elongated, or wide blotch-like leaf mines, sometimes with a few short but slender lateral galleries, and with no or scant frass deposited; the nidus is invisible through the epidermis, so dissection of the mine is necessary to study the nidus.

Species diversity and geographical distribution. The genus is known only from East—South East Asia: northern Vietnam and southern China, and comprises two species.

Etymology. The genus name is derived from the Lithuanian word *rytietiška* (adjective for "of the eastern nature, origin") with an arbitrarily modified ending, in reference to the region where the genus occurs.

Rytietia uncinata Diškus, Xu & Dai, sp. nov.

urn:lsid:zoobank.org:act:6E9527F6-581B-4849-8840-74260093D6B3
(Figs 276–280, 284, 285, 287–290, 294, 296–302.)

Type material. Holotype: ♂, VIETNAM: Lao Cai Province, Sapa, 22°21'44"N, 103°46'47"E, elevation 1850 m, feeding larva on *Fissistigma chloroneurum* (Hand.-Mazz.) Tsiang (see Remarks), 20.ii.2015, ex pupa iv.2015, field card no. 5202, leg. A. Diškus, genitalia slide no. AD1011 (MfN). Paratypes: 9 ♂, 4 ♀, same label data as holotype, genitalia slides nos AD896♂ (from adult in pupal skin), AD1012♀ (MfN); 1♂, 1♀, same label data data (GNU).

Diagnosis. Externally, this new species is characterized by a distinct forewing pattern with a dark apical area; it makes *R. uncinata* **sp. nov.** immediately recognizable among all other Tischeriidae, except for the externally sometimes indistinguishable *R. chongyiensis* Xu & Dai, **sp. nov.** (described below). In the male genitalia, the combination of a one-lobed valva and extremely long basal projections of the phallus distinguish *R. uncinata* from all known Tischeriidae species. This species is also distinctive because of the elaborated juxta with two large apical lobes, each bearing a well-thickened but short spine. For differentiation of the male genitalia of *R. uncinata* from those of the related *R. chongyiensis*, see diagnosis of *R. chongyiensis*. In the female genitalia, *R. uncinata* is characterized by the extremely large ovipositor lobes and unique, distinctly reticulate antrum (in *R. chongyiensis*, antrum is non-reticulate or indistincly reticulate).

R. uncinata and *R. chongyiensis* also differ in their geographical distribution, different host plants, and shape of the leaf mines (see diagnosis of *R. chongyiensis*).

DNA barcode. We barcoded one specimen of the type series, but not the holotype; the sequence is available in the GenBank database under accession number OQ413572.

Description. *Male* (Figs 276, 278–280). Forewing length 3.9–4.1 mm; wingspan 8.4–9.0 mm (n = 10). Head: palpi and frons yellow ochre; pecten long, yellow-ochre; frontal tuft grey, golden shiny, yellow distally; collar yellow-ochre, comprised of lamellar scales; antenna slightly or distinctly longer than one half the length of forewing; flagellum grey, golden glossy or irregularly annulated with dark grey scales; basal part of flagellum usually golden cream. Tegula, thorax, and forewing intense yellow-ochre; apical area of forewing densely covered with dark grey-brown or black-brown scales; fringe blackish grey, pale grey to ochre cream on tornus; fringe line distinctive, comprised of black scales; forewing underside dark grey-brown, except for black special scales along costal margin on forewing base; no androconia. Hindwing dark brown-grey to black-grey on upper side and underside; fringe grey to ochreous grey. Legs yellow-ochre, covered with dark grey-brown scales on upper side. Abdomen grey-brown with some purple iridescence on upper side, yellow-ochre on underside; genital plates large, yellow-ochre; anal tufts long, mostly dorsal, pale grey to ochreous-yellow or golden cream.

Female (Fig. 277). Forewing length 3.8–4.3 mm; wingspan 8.5–9.4 mm (n = 5). Similar to male, but frontal tuft dark grey-brown, golden yellow distally; collar sometimes grey-brown proximally; tegula and thorax speckled with grey-brown scales; basal half of forewing sometimes sparsely speckled with small dark scales. Otherwise, identical with male.

Male genitalia (Figs 284, 285, 287–290) with capsule 790–805 µm long, 420–470 µm wide. Uncus comprised of two large lobes. Socii medium small, paired, membranous. Valva ca. 550 µm long, without a lateral "arm" or dorsal lobe. Anellus absent. Juxta large, 180–190 µm long, 120–150 µm wide, elaborated, with two large apical lobes, each bearing a well-thickened but very short spine. Vinculum large, rounded distally. Phallus 275–285 µm long, rod-like, with extremely long lateral projections basally.

Female genitalia (Figs 294, 296, 297) ca. 1860 µm long. Ovipositor lobes unusually large, rounded, densely covered with peg-like setae; second pair of ovipositor lobes three times smaller, with numerous long setae. Posterior apophyses much longer than anterior apophyses, widened at tips; prela comprised of three pairs of rod-like projections; transverse processes of prela unusually wide. Antrum unique, angular and reticulate. Corpus bursae relatively long, oval-shaped, without distinctive pectination. Ductus spermathecae short, with about three small and one large coils, and small, elongated vesicle.

Bionomics (Figs 298–302). Host plant is *Fissistigma chloroneurum* (Hand.-Mazz.) Tsiang (see Remarks) (Fig. 299). Larvae mine leaves in February. Leaf mine is irregular but elongated, slender, often with lateral corridors, and with no frass. A nidus is inconspicuous. Adults occur in April. Otherwise, biology is unknown.

Distribution. This species is known from a single locality in northern Vietnam, near the border with China (Lao Cai Province: Sapa, Fig. 298), at the elevation about 1850 m.

Etymology. The species name is derived from Latin *unicatus* (hooked), in reference to the elaborated juxta with well-thickened spines in the male genitalia.

Remarks. The host plant, *Fissistigma chloroneurum* (Hand.-Mazz.) Tsiang, was identified solely on the basis of photographs taken in the field; no herbarium samples were preserved. *F. chloroneurum* is known to be a liana. However, according to the collector, the host was a tree. Therefore, the first two authors of this monograph are not fully certain about the accuracy of the host plant identification. If the host plant is identified correctly, then *Fissistigma*-feeding *R. uncinata* and *R. chongyiensis* Xu & Dai, **sp. nov.** (described below) provide a new host plant family, Annonaceae, for global Tischeriidae.

Rytietia chongyiensis Xu & Dai, sp. nov.

urn:lsid:zoobank.org:act:D5F198EB-00C5-4FF0-887D-F71C0F3FDF50
Figs 281–283, 286, 291–293, 295, 303–305.

Type material. Holotype: ♂, CHINA, Yangling, Chongyi County, Ganzhou City, Jiangxi Province, 25.649318 N, 114.316492 E, elevation 395 m, feeding larvae on *Fissistigma oldhamii* (Hemsl.) Merr. (Annonaceae) (see Remarks), adults emerged 7.v.2018, leg. Jiasheng Xu, genitalia slide no. LIU0094♂ (GNU). Paratypes: 1 ♂, 1 ♀, same label data as holotype, genitalia slide nos LIU0098♂, LIU0097♀ (GNU); 2 ♂, CHINA, Qiyunshan, Chongyi County, Ganzhou City, Jiangxi Province., elevation 576 m, feeding larvae on *Fissistigma oldhamii* (Hemsl.) Merr. (Annonaceae), adults emerged 17–19.iv.2019, leg. Jiasheng Xu (GNU).

Diagnosis. Externally, this new species is very similar to *R. uncinata* Diškus, Xu & Dai, **sp. nov.** (described above), but often with a less distinctive dark apical fascia and females of *R. chongyiensis* tend to be slightly larger; sometimes, especially in worn specimens, these two related species are indistinguishable externally. In the male genitalia, the weakly developed basal projections of the phallus, proximally less thickened ventral plate of the vinculum, longer apical spines and widely separated apical lobes of the juxta, and medially less thickened uncus distinguish *R. chongyiensis* from *R. uncinata*. In the female genitalia, *R. chongyiensis* differs from *R. uncinata* by the antrum which is distinctly reticulate in *R. uncinata* but non-reticulate (or indistinctly reticulate) in *R. chongyiensis*.

These two species also differ in their geographical distribution, host plants, and leaf mines: *R. chongyiensis* feeds on *Fissistigma oldhamii* in China and produces predominantly very large, wide blotch-like leaf mines, while the Vietnamese *R. uncinata* feeds on another species of *Fissistigma* (see Remarks above on *R. uncinata*) and produces predominantly slender leaf mines.

DNA barcode. Unknown.

Description. *Male* (Figs 281, 282). Forewing length about 4 mm; wingspan about 8.9 mm (n = 1). Head: palpi and frons yellow ochre; pecten long, yellow ochre; frontal tuft greyisch cream, golden glossy; collar yellowish ochre, comprised of lamellar scales; antenna distinctly longer than one half the length of forewing; flagellum golden ochre in distal 2/3 annulated with dark grey scales. Tegula, thorax, and forewing bright ochre; apical area of forewing densely covered with black-brown scales; fringe dark grey, pale grey on tornus; fringe line comprised of brown-black scales; forewing underside dark grey-brown, except for black special scales along costal margin on forewing base; no androconia. Hindwing blackish grey on upper side and underside; fringe dark grey. Legs ochre-yellow, darkened with blackish grey scales on upper side. Abdomen dark grey-brown on upper side, yellowish ochre on underside; genital plates yellowish grey; anal tufts long, mostly dorsal, grey.

Female (Fig. 283). Forewing length about 5.1 mm; wingspan about 11.2 mm (n = 1). Externally, similar to male.

Male genitalia (Figs 286, 291–293). Uncus comprised of two large lobes; in contrast to *R. uncinata*, these lobes moderately chitinized medially (Fig. 286). Socii medium large, paired, membranous. Valva without a lateral "arm" or dorsal lobe. Anellus absent. Juxta large, with two large, well-separated apical lobes (Figs 291, 293), each bearing a well-thickened, long spine (Figs 291–293). Vinculum medium small, widely rounded distally and weakly chitinized proximally. Phallus rod-like, with weakly developed basal projections laterally (Figs 291, 293).

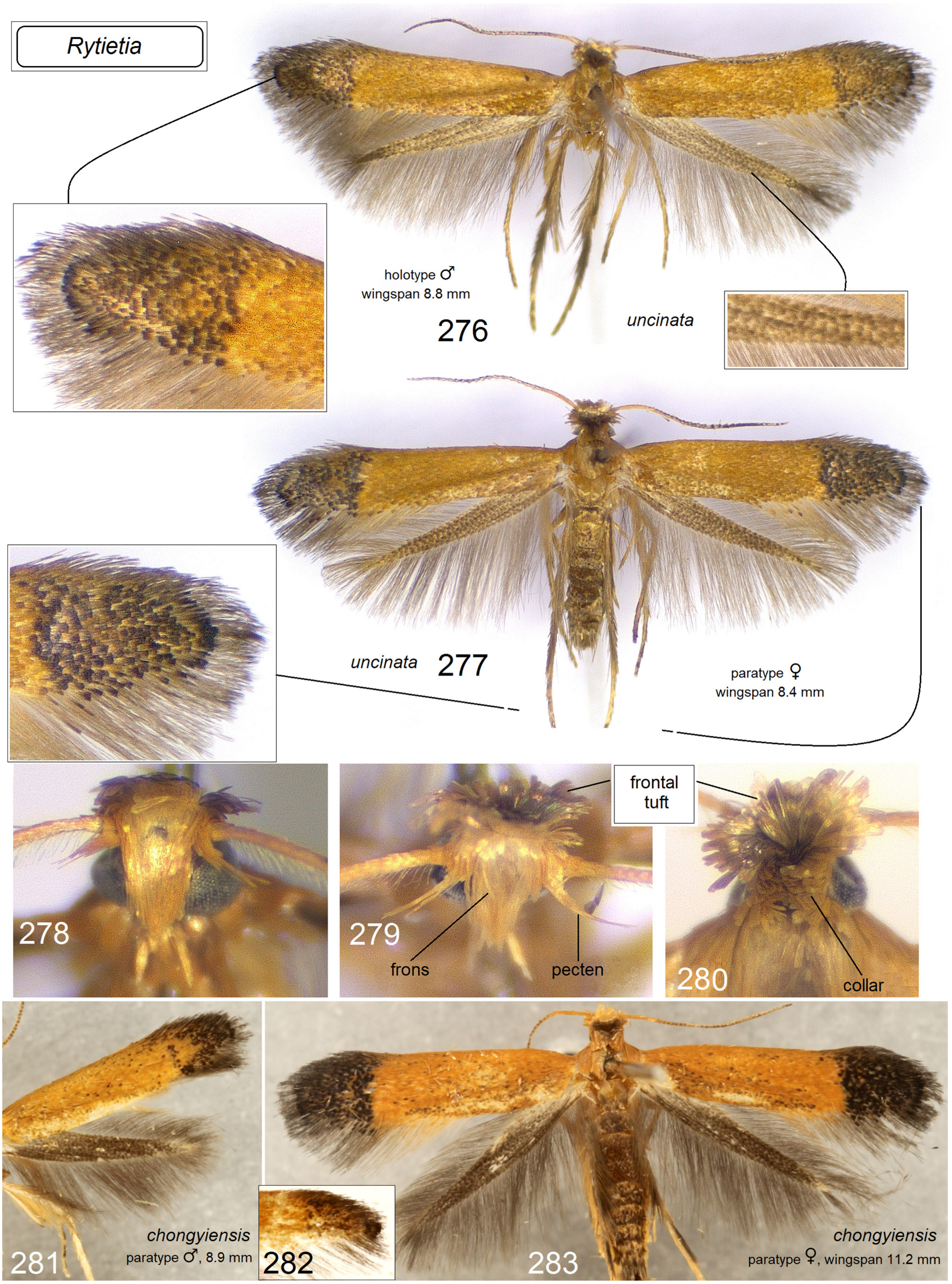
Female genitalia (Fig. 295). Ovipositor lobes very large, rounded, densely covered with peg-like setae; second pair of ovipositor lobes three-four times smaller, with numerous long setae. Posterior apophyses much longer than anterior apophyses, widened at tips; prela comprised of three pairs of rod-like projections; transverse processes of prela unusually wide. Antrum non-reticulate or indistinctly reticulate. Corpus bursae relatively long, oval-shaped, without distinctive pectination. Ductus spermathecae short, weakly chitinized.

Bionomics (Figs 303–305). Host plant is *Fissistigma oldhamii* (Hemsl.) Merr. (Annonaceae) (Fig. 304) (also see Remarks). Larvae mine leaves in March. Leaf mine is large, irregular, blotch-like, with no or very little frass. A nidus is inconspicuous. Adults occur in April and May. Otherwise, biology is unknown.

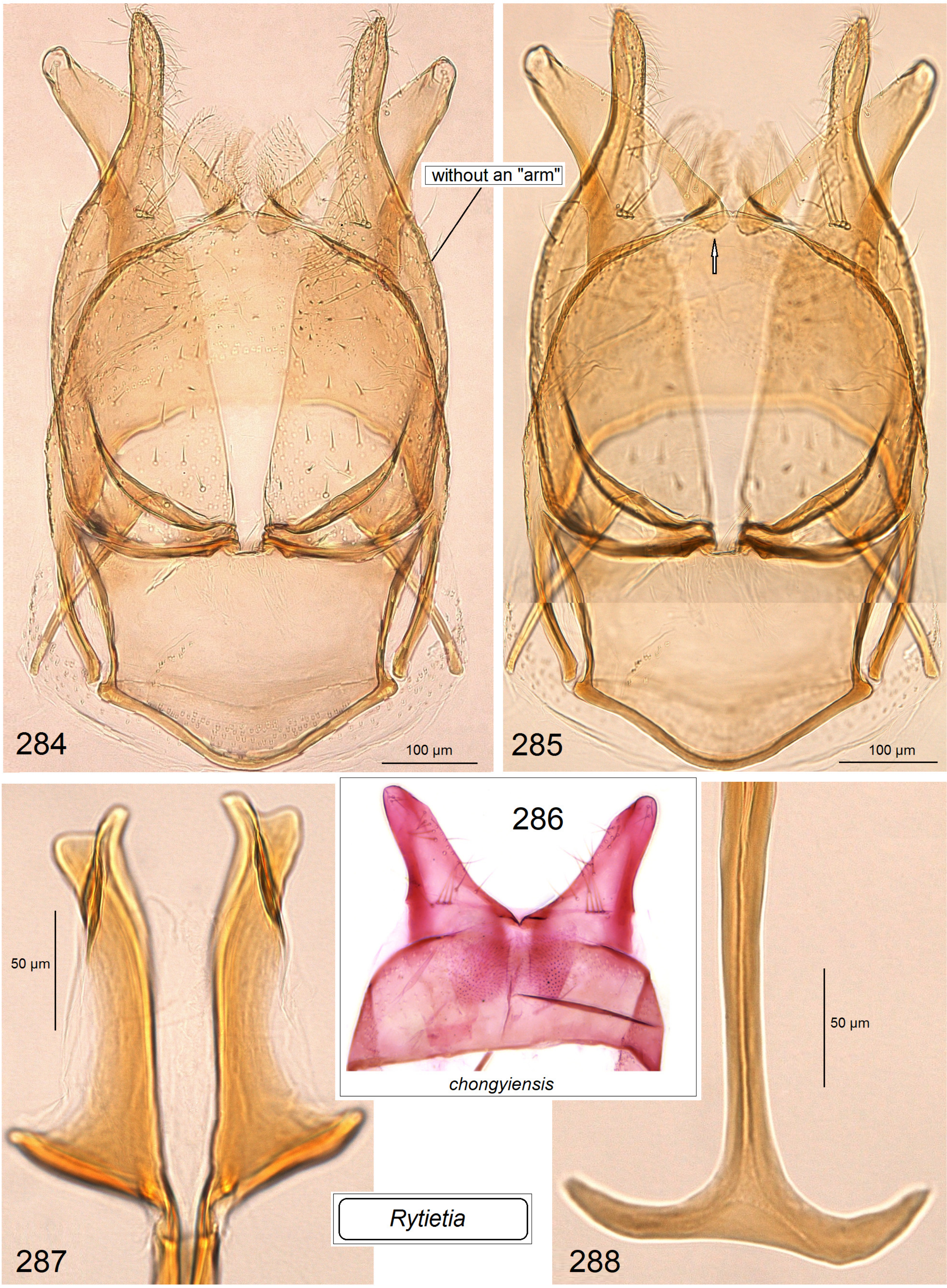
Distribution. This species is known from two localities in southern China at elevation of about 400–600 m.

Etymology. The species is named after Chongyi County, China, where it was discovered.

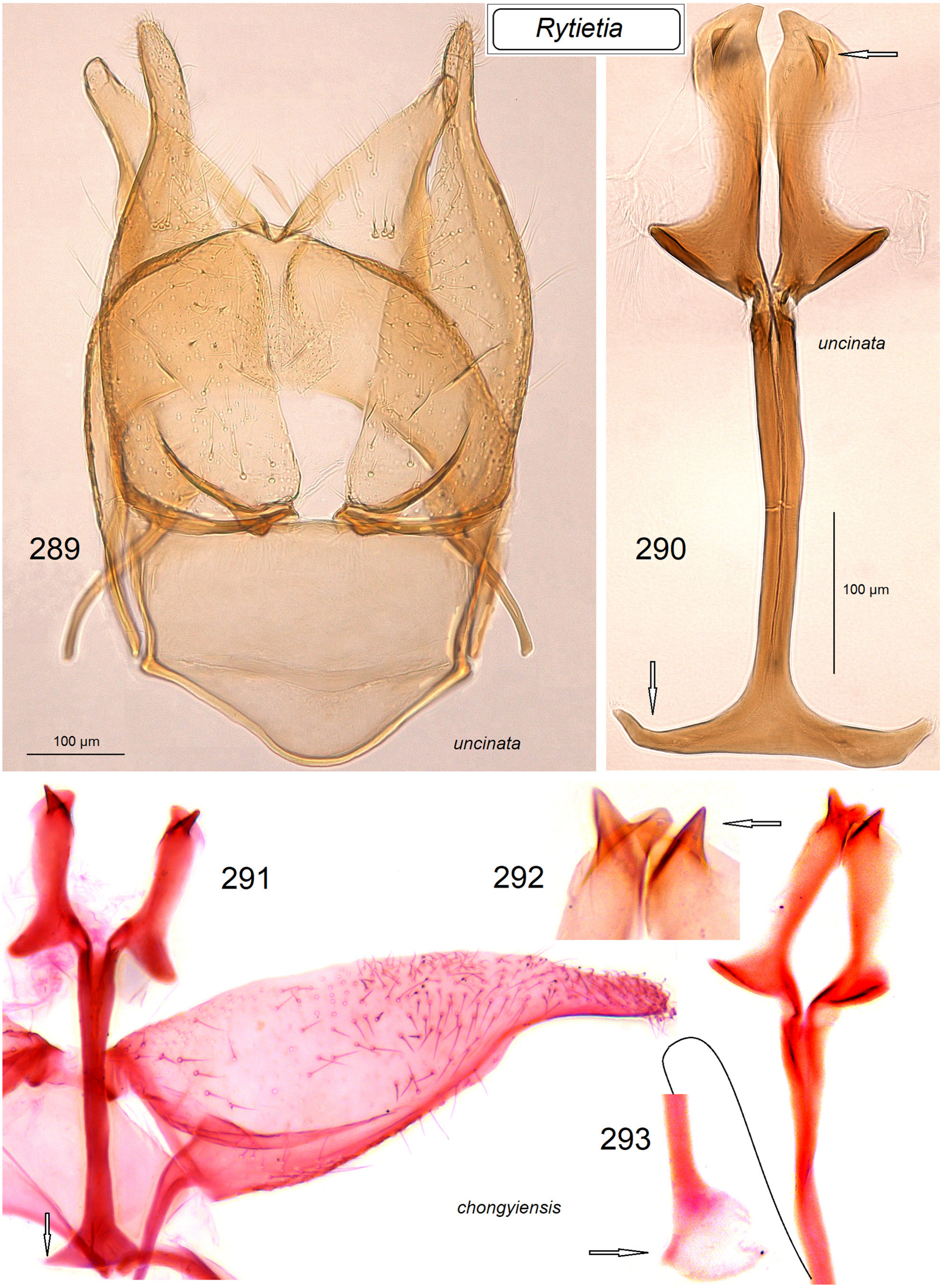
Remarks. The host plant identification is the sole responsibility of the Chinese co-authors. If identification of the host plants of the *Fissistigma*-feeding species *R. uncinata* and *R. chongyiensis* are correct, Annonaceae proves to be a new host plant family for global Tischeriidae.



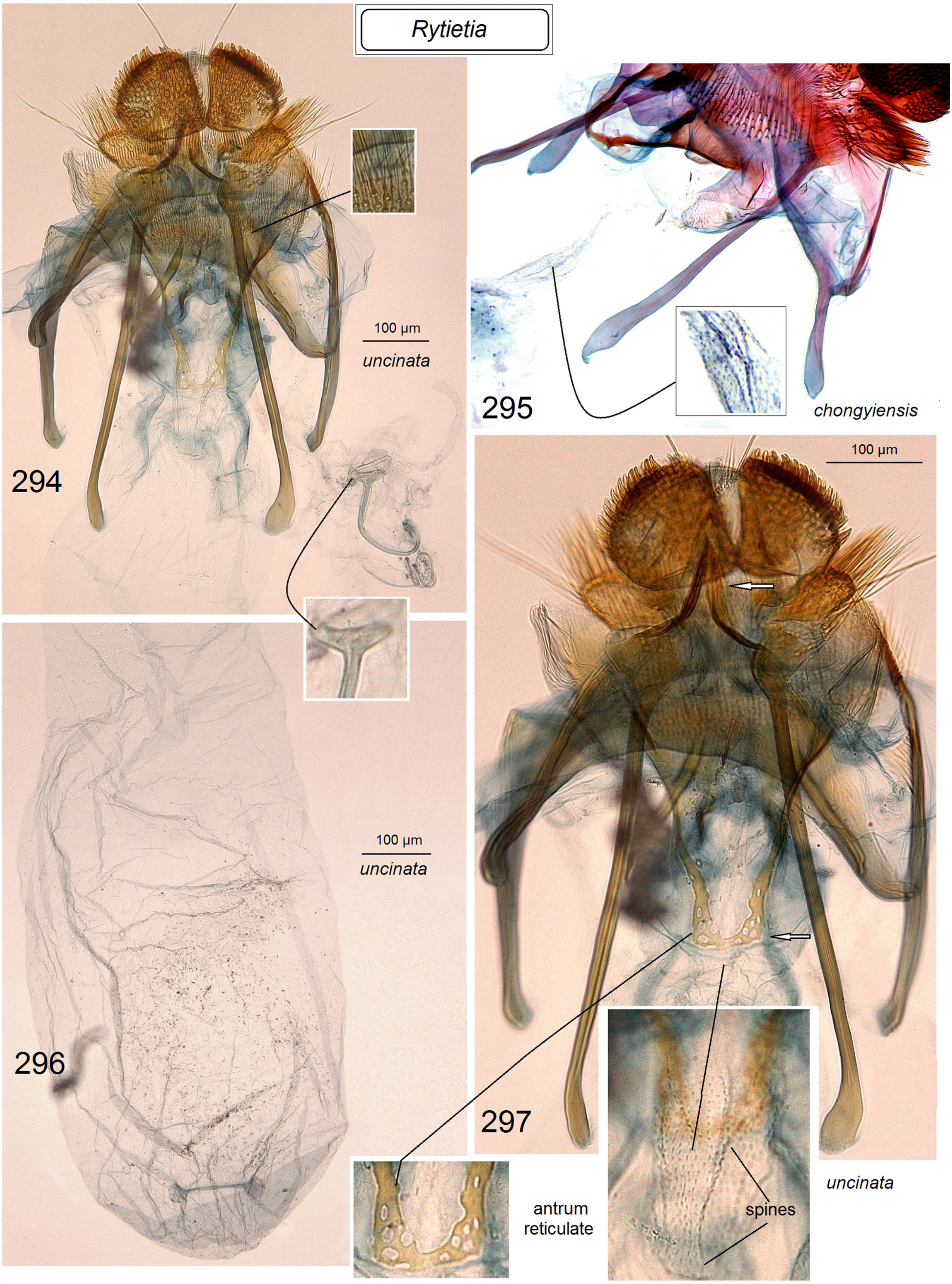
FIGURES 276–283. Adults of *Rytietia* spp. 276, *R. uncinata* Diškus, Xu & Dai, **sp. nov.**, general view without abdomen, male holotype; 277, same, with abdomen, female paratype; 278–280, same, details of head, male paratypes (MfN); 281, *R. chongyiensis* Xu & Dai, **sp. nov.**, right side, male paratype; 282, same, apex of forewing, male paratype; 283, same, general view, female paratype (GNU)



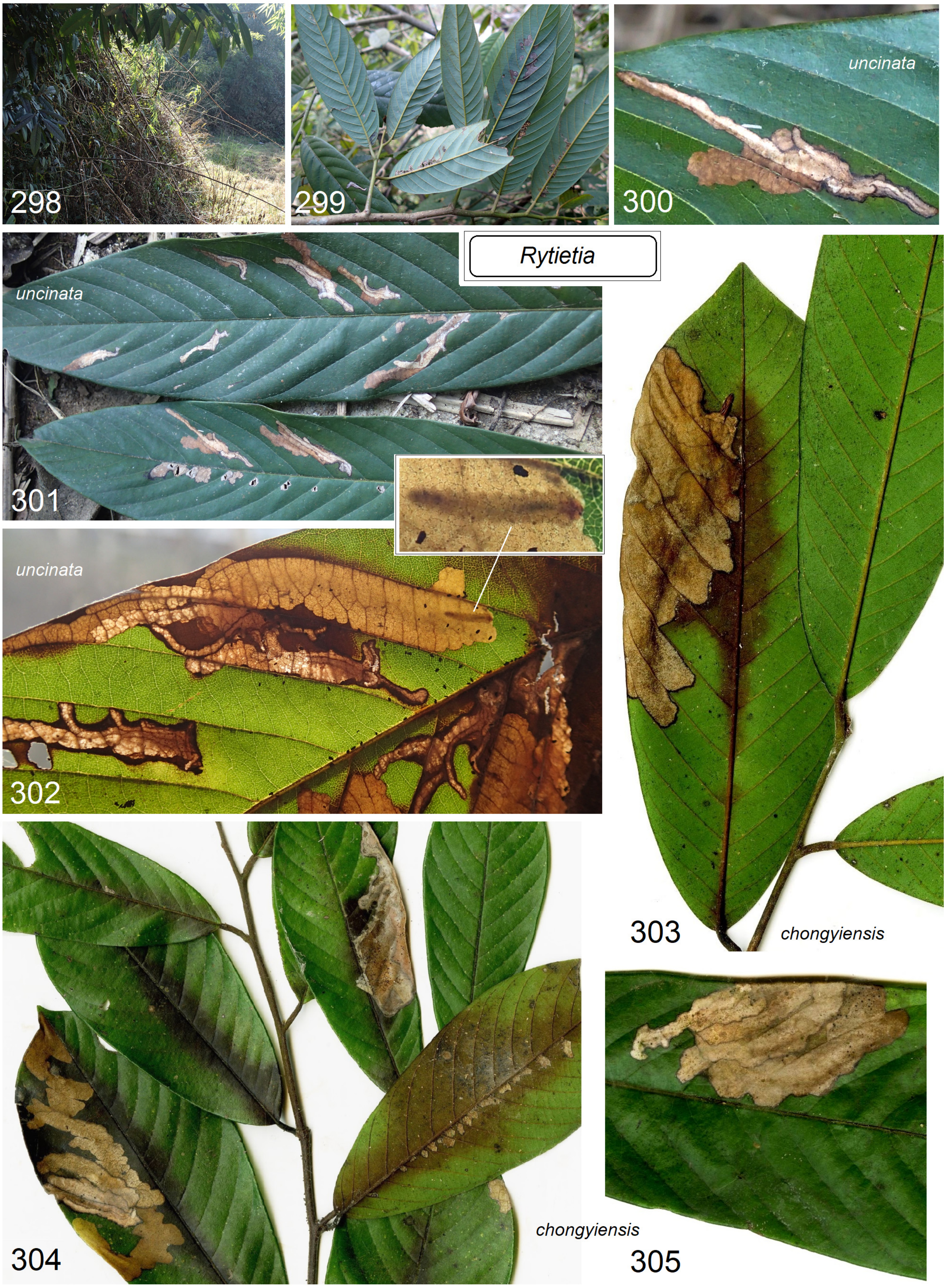
FIGURES 284–288. Male genitalia of *Rytietia* spp. 284, 285, *R. uncinata* Diškus, Xu & Dai, **sp. nov.**, northern Vietnam, holotype, genitalia slide no. AD1011, capsule with phallus and juxta removed (MfN); 286, *R. chongyiensis* Xu & Dai, **sp. nov.**, China, holotype, genitalia slide no. LIU0094, uncus and tegumen (GNU); 287, *R. uncinata*, holotype, genitalia slide no. AD1011, juxta; 288, same, phallus (MfN)



FIGURES 289–293. Male genitalia of *Rytietia* spp. 289, *R. uncinata* Diškus, Xu & Dai, **sp. nov.**, northern Vietnam, paratype, genitalia slide no. AD896, capsule with phallus and juxta removed (a fresh mount in glycerol, not covered with a cover slip); 290, same, phallus and juxta (MfN); 291, *R. chongyiensis* Xu & Dai, **sp. nov.**, China, holotype, genitalia slide no. LIU0094, juxta, phallus and valva; 292, 293, same, paratype, genitalia slide no. LIU0099, juxta and phallus (GNU)



FIGURES 294–297. Details of female genitalia of *Rytietia* spp. 294, 296, 297, *R. uncinata* Diškus, Xu & Dai, **sp. nov.**, northern Vietnam, paratype, genitalia slide no. AD1012 (MfN); 295, *R. chongyiensis* Xu & Dai, **sp. nov.**, China, paratype, genitalia slide no. LIU0097, apophyses (GNU)



FIGURES 298–305. Bionomics of *Rytietia* spp. 298, *R. uncinata* Diškus, Xu & Dai, **sp. nov.**, northern Vietnam, Lao Cai Province, Sapa, at the elevation about 1850 m, habitat; 299, same, host plant (see Remarks); 300–302, same, leaf mines; 303–305, *R. chongyiensis* Xu & Dai, **sp. nov.**, China, leaf mines

7. Genus *Pafazaria* Diškus & Stonis, gen. nov.

urn:lsid:zoobank.org:act:AB0293A9-622E-41F7-954C-11F24524F027
(Figs 306–364)

Type species: *Pafazaria capitata* Diškus & Stonis, **sp. nov.** (described below)

Diagnosis. In the male genitalia, species of *Pafazaria* are characterized by the presence of both an anellus and juxta (the only Tischeriidae genus with both structures together); uniquely there is a "hood" over the juxta that does not occur elsewhere. In the female genitalia, the genus is characterized by absence of an antrum which is characteristic of genera possessing a juxta in the male genitalia. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. Based on molecular data, *Pafazaria* appears to be a distinct genus, and quite close to *Neotischeria* (Figs 62–64, 68). On the other hand, if the analysis includes only genera possessing a juxta, then *Pafazaria* aligns as a sister taxon with *Manitischeria* (Fig. 67).

Adult. Head: frontal tuft overlapping the frons, comprised of long but slender lamellar scales, collar paired to unpaired, comprised of very slender but lamellar (not piliform) scales. Forewing brownish grey to ochreous brown, without a distinctive pattern but apically darker. Hindwing slender, without androconia.

Male genitalia. Uncus with two wide lateral lobes. Socii membranous, large, distinctly paired, spinose, with numerous tiny spines. Tegumen short or medium short, without additional thickenings; diaphragm with a large spinose lobe-like projection; pseudognathos absent. Valva varies from slender to basally wide with inner lobe(s); basal process of the valva usually absent; occasionally, long. Transtilla absent. Anellus membranous to slightly thickened laterally, without chetae or spines. Juxta present, variously developed, with a unique "hood" caudally. Vinculum short, with triangular or truncated ventral plate. Phallus slender, rod-like, apically slender or with lateral lobe-like projections.

Female genitalia. Ovipositor lobes large; second pair of ovipositor lobes three times smaller or equal in size in comparison to main ovipositor lobes; sometimes each lobe of the second pair of ovipositor lobes divided into two smaller lobes. Lateral lobes short or small. Anterior apophyses significantly to slightly shorter than posterior apophyses. Prela usually with three pairs of rod-like projections; in contrast to many other Tischeriidae, transverse prela relatively slender and projections of the inner prela connected to each other distally. Caudal sclerite of prela strongly developed, inverted U- or V-shaped, with a pointed and well-chitinized projection caudally. Antrum absent (probably replaced by a distal joint between projections of the inner prela). Accessory sac indistinctive or absent; ductus spermathecae slender and very short, with 3–4 coils and large, oval-shaped vesicle. Corpus bursae long, gradually narrowing towards caudal end or with a long and slender "neck" covered with tiny spines; pectinations in main body of corpus bursae absent.

Bionomics. The genus is trophically associated with Fabaceae and Malvaceae host plants. Larvae mine leaves and produce either irregular or rounded blotch-like leaf mines, or linear (gallery-like) leaf mines; frass absent in blotch-like leaf mines but deposited in initial part of the linear leaf mines. A nidus is invisible.

Species diversity and geographical distribution. Currently, the genus is known only from East—South East Asia: China (Yunnan) and Laos. In total, three species. One species from Yunnan, China was originally described in the genus *Paratischeria* (Xu *et al*. 2017); here, this species is transferred to a new genus: *Pafazaria jingdongensis* (Xu & Dai, 2017), **comb. nov.**

Etymology. The genus name is derived from the Lao *pafa* (east) and arbitrarily combined with the Slavian *zaria* or *zoria* (dawn) referring to the region of distribution.

Pafazaria capitata Diškus & Stonis, sp. nov.
urn:lsid:zoobank.org:act:780CEFC1-71FD-45E0-8DE7-C320F97812EA
(Figs 306–311, 314–340)

Type material. Holotype: ♂, LAOS: Luang Prabang Prov., Nong Khiaw, 20°33'07"N, 102°36'21"E, elevation 1070 m, mining larva on *Helicteres* sp. (Malvaceae), 10.ii.2020, ex pupa iii. 2020, field card no. 5322, leg. A. Diškus & M. Jocius, genitalia slide no. AD1040 (MfN). Paratypes: 2 ♀, same label data as holotype, genitalia slide no. AD1058♀ (MfN).

Diagnosis. In the male genitalia, this new species can be easily differentiated from other congeneric species by the unique shape of the juxta (see Figs 314, 315, 317–319). In the female genitalia, the new species is characterized by the thickened membrane between the inner prela.

DNA barcode. We barcoded one specimen of the type series, but not the holotype; the sequence is available in the GenBank database under the accession number OQ413564.

Description. *Male* (Figs 306–309). Forewing length 3.3 mm; wingspan 7.1 mm (n = 1). Head: palpi greyish cream; frons pale grey, glossy, with some purple irridence; frontal tuft dark grey, glossy, with some purple iridescence, comprised of relatively wide lamellar scales; collar grey; antenna distinctly longer than one half the length of forewing; flagellum grey, annulated with dark grey scales; sensilla cream, relatively short. Tegula, thorax and forewing dark ochre-brown, densely speckled with blackish brown or brown-black scales with purple iridescence; these dark scales are distinctly cream-tipped in apical half of the forewing; tornal spot developed but almost indistinctive; fringe dark grey, without fringe line; forewing underside black-brown, without andronia or spots, except for a row of black special scales along costa basally. Hindwing black-brown on upper side and underside, without androconia or spots, except for small cream scaleless area basally; fringe brown-grey. Legs brownish black, with some purple iridescence on upper side, brownish cream on underside. Abdomen metallic glossy, dark grey with some purple iridescence on upper side, grey on underside; genital plates large, grey; anal tufts short, grey.

Female (Figs 310, 311). Forewing length 2.5–2.8 mm; wingspan 6.1–6.6 mm (n = 2). Similar to male.

Male genitalia (Figs 314–326) with capsule about 350 µm long, 225 µm wide. Uncus comprised of two large lobes. Socii medium large, weakly paired, membranous. Valva about 275 µm long, with an additional, inner lobe dorsally (see Fig. 326). Anellus present, membranous, without setae or spines (see Figs 316, 325). Juxta elaborated, large (Figs 314, 317–319), covered with a "hood" (see Fig. 318). Vinculum short, triangular. Phallus about 280 µm long, bifid only at apex (see Fig. 324).

Female genitalia (Figs 327–331) about 1380 µm long. Ovipositor lobes large, rounded, with peg-like setae; second pair of ovipositor lobes three times smaller; lateral lobes indistinctive. Anterior and posterior apophyses almost equal in length; prela comprised of three pairs of unique, rod-like projections; inner prela unusually long; the area between processes of inner prela is thickened. Corpus bursae long, with a slender proximal part and very small, oval-shaped main body without distinctive pectination. Ductus spermathecae short, with about 3 large coils.

Bionomics (Figs 332–340). Host plant is *Helicteres viscida* Blume (Malvaceae, former Sterculiaceae) (Fig. 332). Larvae mine leaves in February. Leaf mine is linear, with parallel or lateral corridors (Figs 333–340); frass fills most of the width of the initial part of the gallery. Adults occur in March.

Distribution. This species is known from a single locality in Laos (Luang Prabang Province: Nong Khiaw) at elevation 1070 m.

Etymology. The species name is derived from Latin *capitatus* (headed), in reference to the unusual, head-like juxta with horns in the male genitalia.

Pafazaria faboidica Diškus & Stonis, sp. nov.
urn:lsid:zoobank.org:act:CA02E7BE-8BCA-4BDC-8058-4A2CB1CE0274
(Figs 312, 313, 341, 350, 353–364)

Type material. Holotype: ♂, LAOS: Luang Prabang Prov., Nong Khiaw, 20°32'48"N, 102°38'21"E, elevation 410 m, mining larva on *Dalbergia* sp. (Fabaceae) 12.ii.2020, ex pupa iii. 2020, field card no. 5330, leg. A. Diškus & M.

Jocius, genitalia slide no. AD1060 (MfN). Paratypes: 1 ♂, same label data as holotype, genitalia slide no. AD1096♂ (MfN); 1 ♂, same label data as holotype (GNU); 1 ♂, 3 ♀, Vientiane Prov., Vang Vieng, 18°55’56”N, 102°26’14”E, elevation 230 m, mining larvae on *Dalbergia* sp. (Fabaceae), 2.ii.2020, field card no. 5306, leg. A. Diškus & M. Jocius, genitalia slide nos AD1038♂ (from adult in pupal skin), AD1061♀ (MfN).

Diagnosis. Externally, this new species can be confused with some dark speckled species, including the most externally similar *P. capitata* Diškus & Stonis, **sp. nov.** (described above); however, *P. faboidica* **sp. nov.** is smaller and paler. From the related *P. jingdongensis* (Xu & Dai) (**comb. nov.**), the new species differs in the grey frontal tuft (ochre in *P. jingdongensis*) and smaller overall size. In the male genitalia, the combination of a unique anellus, elaborated membranous structures around the phallus (Figs 348–350), and a rounded base of the phallus makes *P. faboidica* easily recognizable. Note that in the related *P. jingdongensis*, the anellus has rounded lateral arcs (Figs 351, 352) and the phallus possesses slender lateral extensions. The characters of the female genitalia are of limited use for species differentiation. However, the new species is characterized by the coalescent distal tips of inner prela (Fig. 354), relatively slender processes of transverse prela (wide in *P. jingdongensis*), a well-developed caudal plate, and slightly smaller ovipositor lobes but with a large gap between these lobes.

So far, *P. faboidica* and the related *P. jingdongensis* are the only *Dalbergia*-feeding Tischeriidae species. However, *P. faboidica* occurs in the lowland tropical habitats of Laos, while *P. jingdongensis* is known from the mountains of Yunnan (Jingdong Yi Autonomous County, China).

DNA barcode. We barcoded one specimen, but not the holotype; the sequence is available in the GenBank database under the accession number OQ413565.

Description. *Male* (Fig. 313). Forewing length 2.5–2.8 mm; wingspan 5.4–6.1 mm (n = 3). Head: frons and palpi glossy, greyish cream to ochreous cream; frontal tuft comprised of pale grey, cream-tipped scales; collar grey; antenna only slightly longer than one half the length of forewing; flagellum pale grey, annulated with grey scales. Tegula and thorax glossy, dark ochre-grey with some purple iridescence. Forewing with purple iridescence, densely covered with dark ochre-brown scales, and speckled with blackish brown scales along the costal margin and apically; fringe grey, without a fringe line; forewing underside dark grey-brown, without spots or androconia. Hindwing grey-brown on upper side and underside, without androconia; fringe ochre-grey. Legs dark brown-grey or black-grey on upper side, golden cream on underside. Abdomen glossy dark grey with some purple iridescence on upper side, glossy greyish cream on underside; genital plates ochreous cream; anal tufts coalescent, comprised of relatively long but slender lamellar scales, almost inconspicuous.

Female (Fig. 312). Forewing length 2.4–2.8 mm; wingspan 5.1–6.1 mm (n = 3). Forewing with stronger purple iridescence, densely speckled with brown-grey or dark brown, ochre-tipped scales. Otherwise, similar or identical with male.

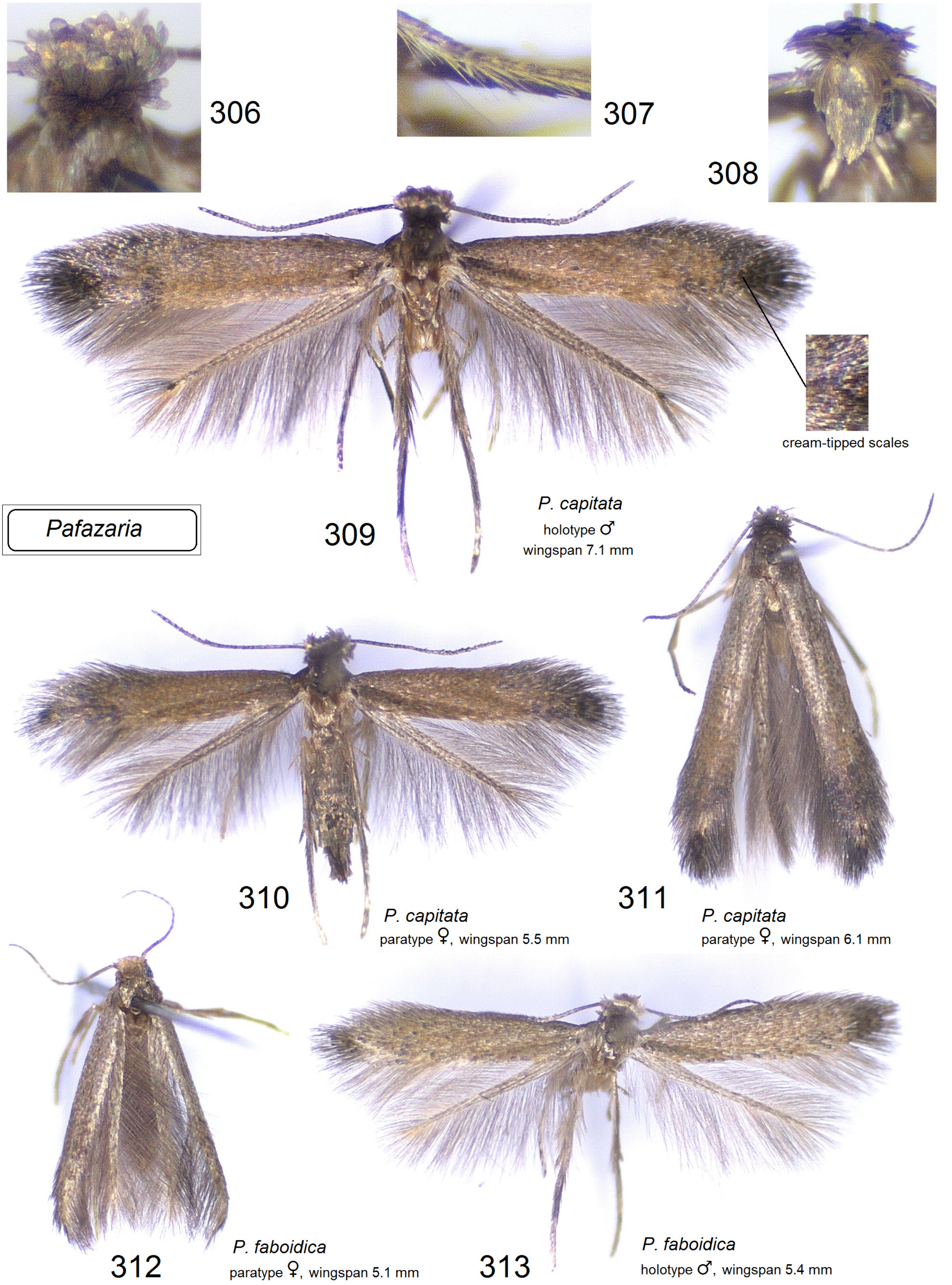
Male genitalia (Figs 341–350) with capsule about 320 µm long, 210 µm wide. Uncus comprised of two larger, distally wide lobes (Figs 343, 344). Socii relatively small, weakly paired, membranous. Valva slender, ca. 250 µm long. Anellus mostly membranous, slender, folded laterally. Vinculum very short, widely rounded distally. Phallus about 345 µm long, apically truncate, with lateral projections, covered by a “hood” (Fig. 349).

Female genitalia (Figs 353–356) about 1245 µm long. Ovipositor lobes medium large, rounded, with weakly thickened peg-like setae; second pair of ovipositor lobes large, divided, with numerous long setae; lateral lobes very short. Posterior apophyses significantly longer than anterior apophyses; prela comprised of three pairs of rod-like projections; processes of inner prela with coalescent distal tips. Corpus bursae long, gradually widening towards base. Ductus spermathecae with 6–8 large and small coils.

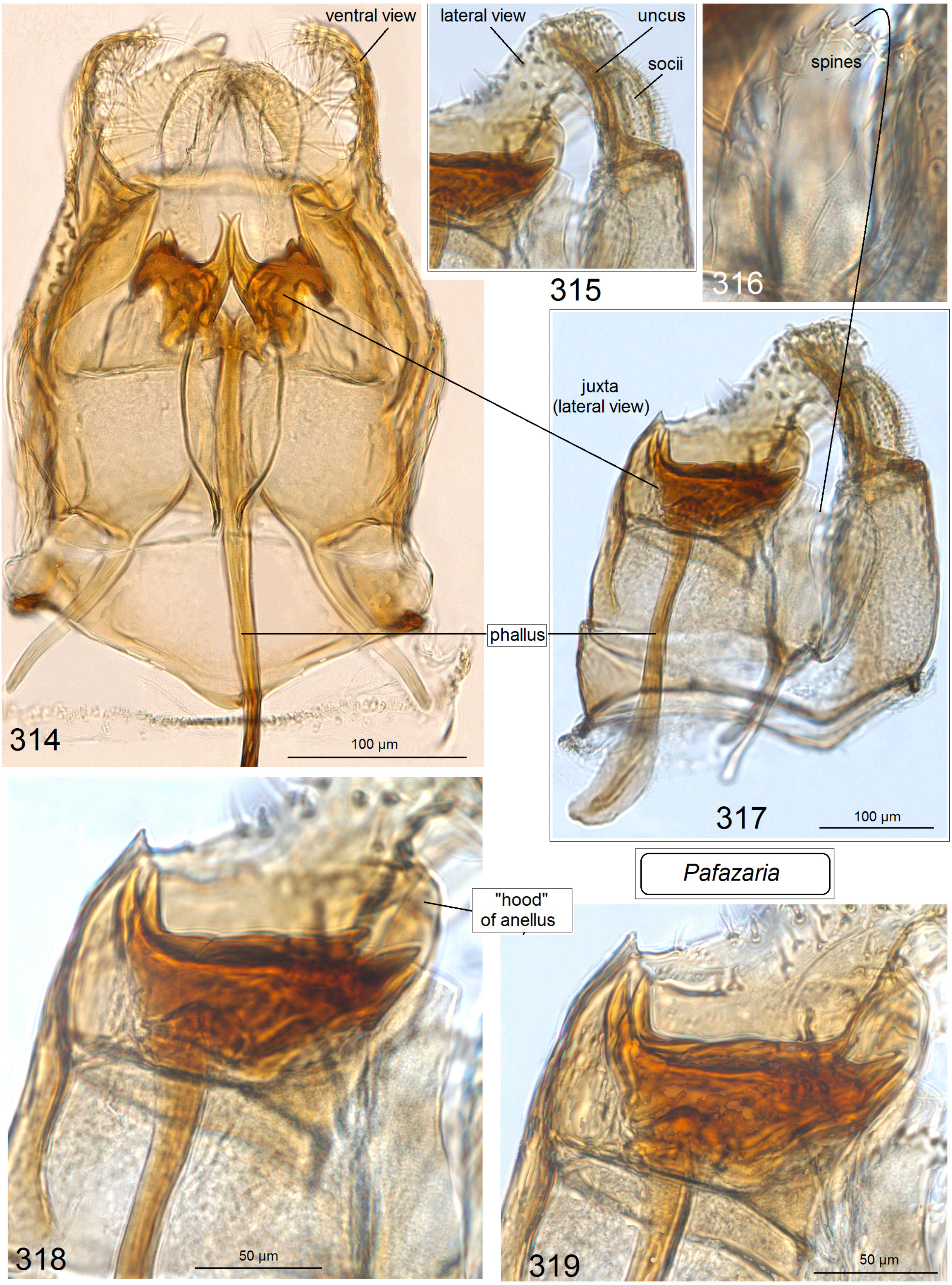
Bionomics (Figs 357–364). Host plant is *Dalbergia* sp., Fabaceae (Fig. 358). Larvae mine leaves in February. The blotch-like mine is irregular or round, without frass. Adults occur in March. Otherwise, biology is unknown.

Distribution. This species is known from two lowland tropical localities in Laos, Luang Prabang and Vientiane provinces, at elevation of 280–410 m.

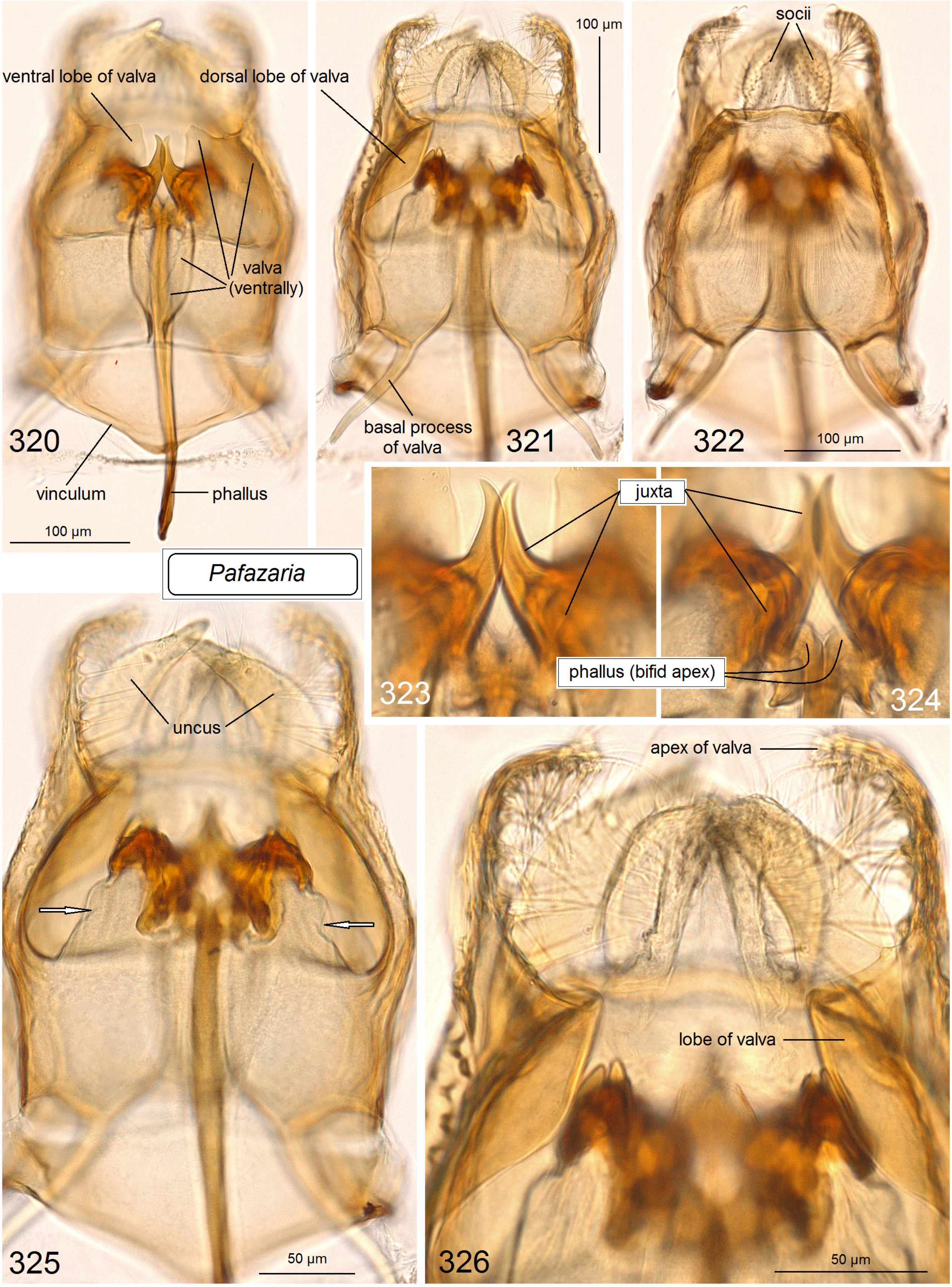
Etymology. The species is named after the host-plant subfamily Faboideae Rudd (=Papilionoideae DC.), Fabaceae.



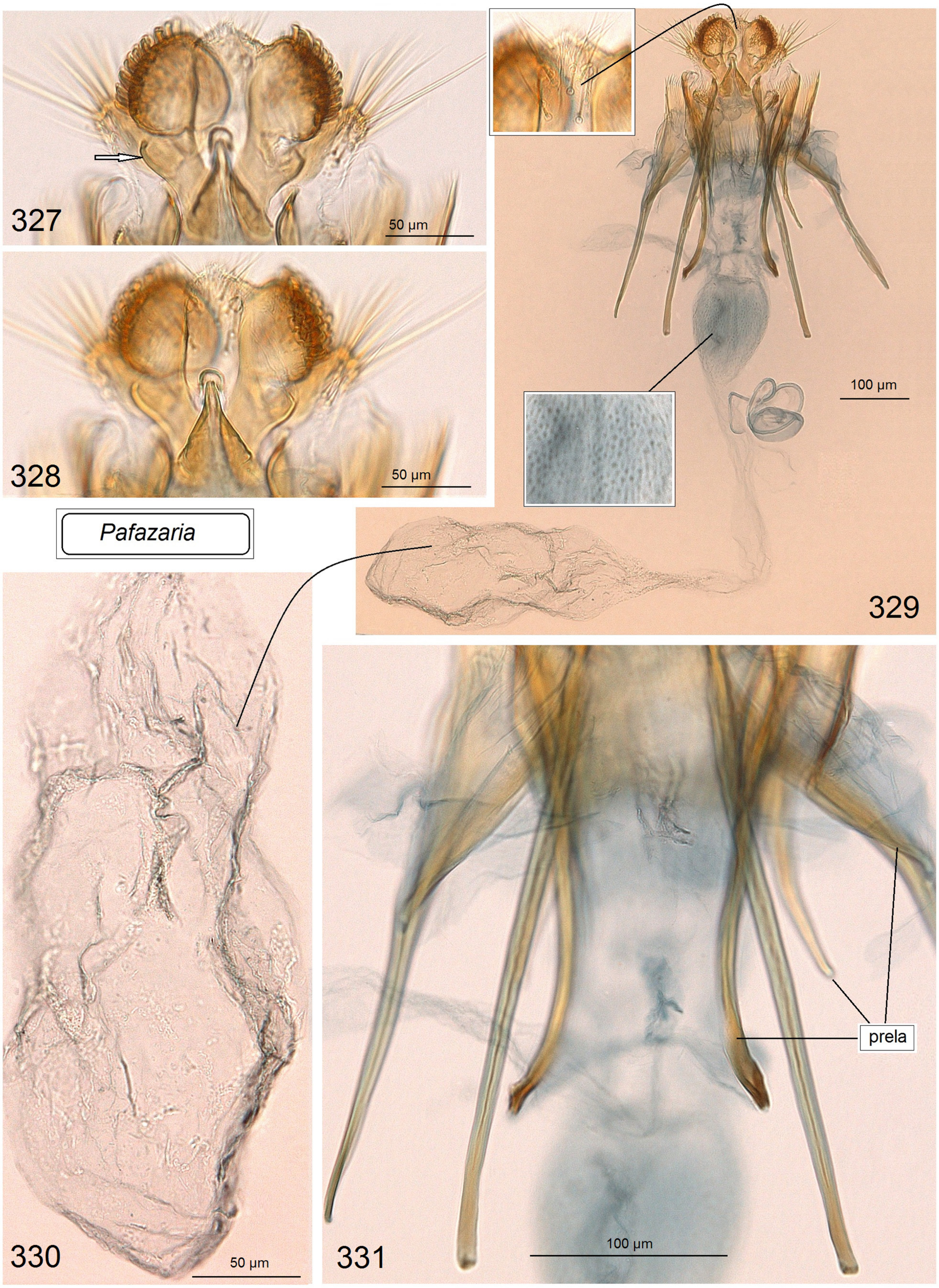
FIGURES 306–313. Adults of new *Pafazaria* species. 306, *P. capitata* Diškus & Stonis, **sp. nov.**, Laos, frontal tuft, dorsal view; 307, same, fragment of antenna; 308, same, head, frontal view; 309, same, general view without abdomen, male holotype; 310, same, with abdomen, female paratype; 311, same, another female paratype (MfN); 312, *P. faboidica* Diškus & Stonis, **sp. nov.**, female paratype; 313, same, male holotype, without abdomen (MfN)



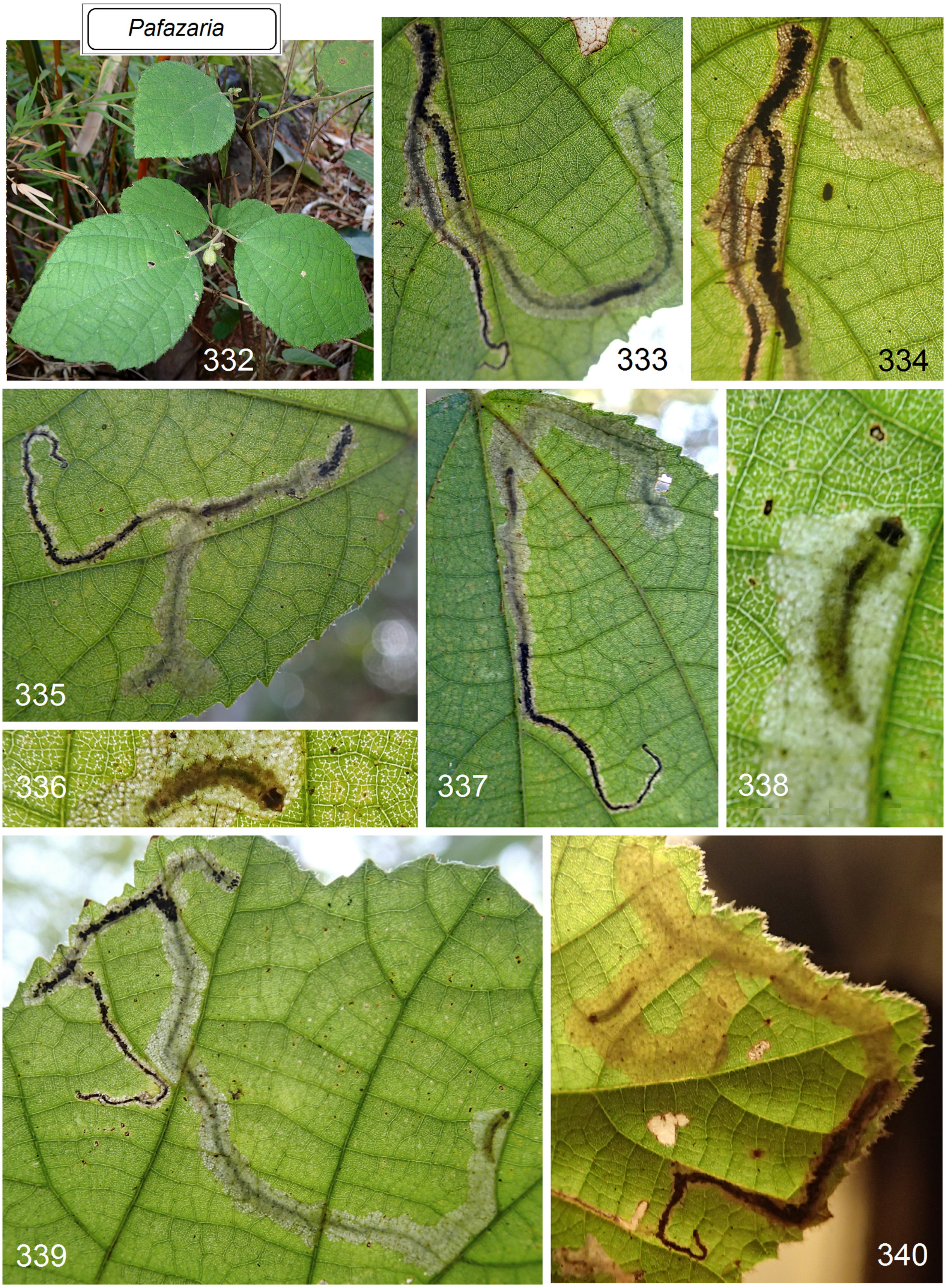
FIGURES 314–319. Male genitalia of *Pafazaria capitata* Diškus & Stonis, **sp. nov.**, Laos, holotype, genitalia slide no. AD1040 (MfN). 314, capsule, ventral view; 315–317, details of capsule, lateral view; 318, 319, juxta, lateral view



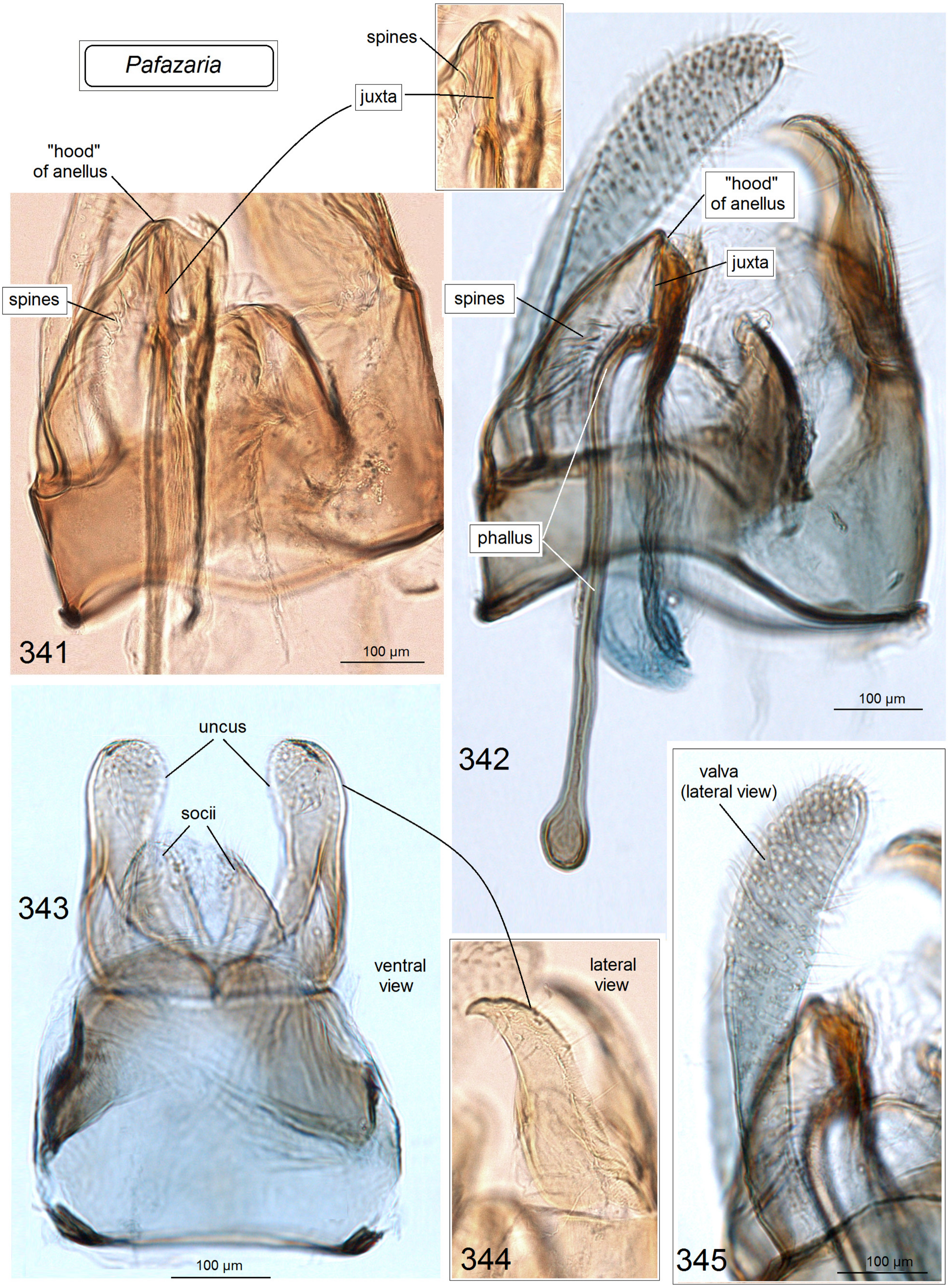
FIGURES 320–326. Male genitalia of *Pafazaria capitata* Diškus & Stonis, **sp. nov.**, Laos, holotype, genitalia slide no. AD1040 (MfN). 320–322, capsule with phallus and juxta inside; 323, 324, spines of juxta; 325, capsule, focused on uncus; 326, same, focused on valval lobe



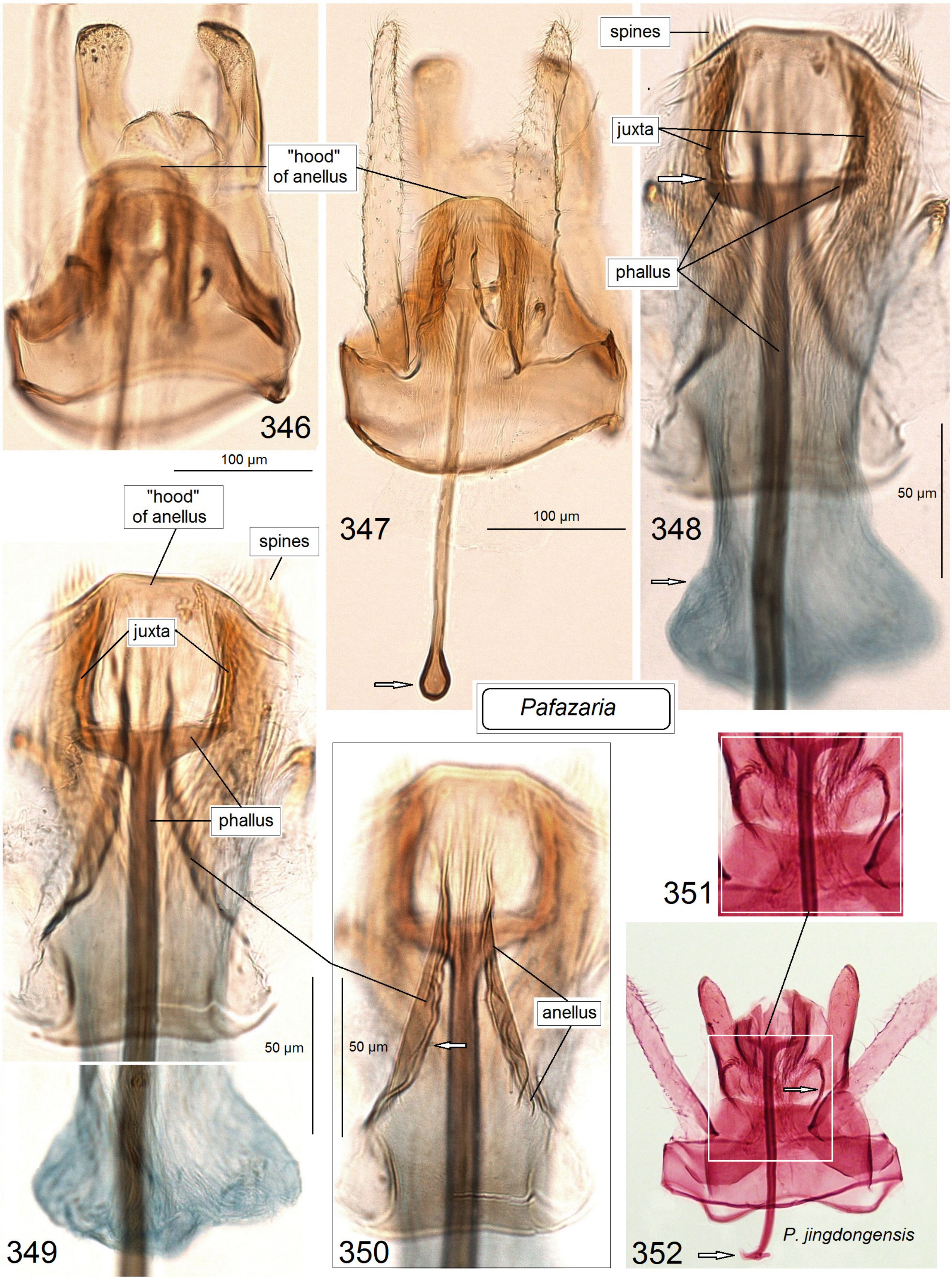
FIGURES 327–331. Details of female genitalia of *Pafazaria capitata* Diškus & Stonis, **sp. nov.**, Laos, paratype, genitalia slide no. AD1058 (MfN). 327, 328, ovipositor; 329, general view of genitalia; 330, corpus bursae; 331, prela



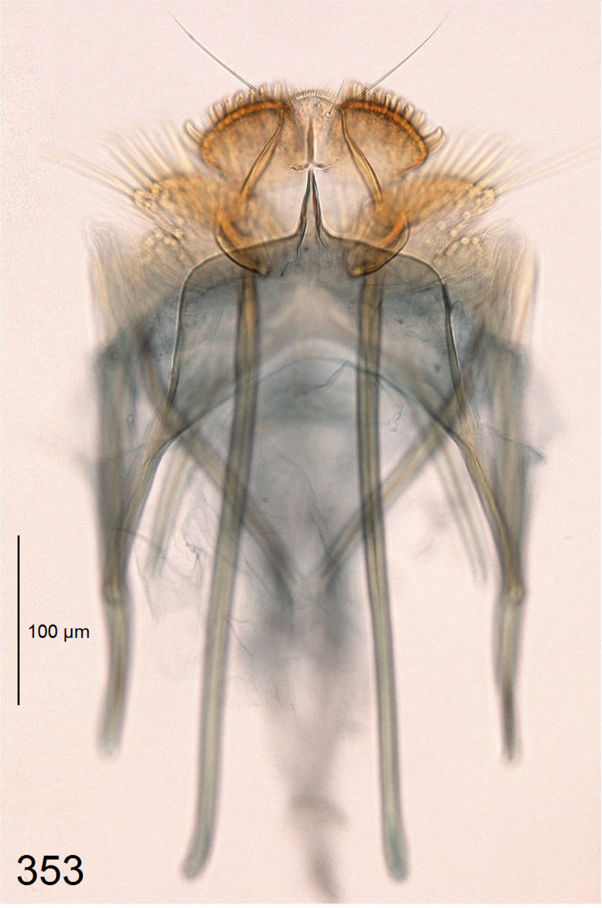
FIGURES 332–340. Bionomics of *Pafazaria capitata* Diškus & Stonis, **sp. nov.**, Laos. 332, host plant, *Helicteres viscida* Blume (Malvaceae, former Sterculiaceae); 333–340, leaf mines



FIGURES 341–345. Male genitalia of *Pafazaria faboidica* Diškus & Stonis, **sp. nov.**, Laos, holotype, genitalia slide no. AD1060 (MfN). 341, fragment of capsule with juxta and phallus inside, ventral view; 342, capsule with juxta and phallus inside, ventral view; 343, capsule with valvae, juxta and phallus removed, ventral view; 344, lateral view of uncus; 345, lateral view of valva



FIGURES 346–352. Male genitalia of *Pafazaria* spp. 346–350, details of *P. faboidica* Diškus & Stonis, **sp. nov.**, Laos, holotype, genitalia slide no. AD1060 (MfN); 351, 352, details of *P. jingdongensis* (Xu & Dai, 2017) **comb. nov.**, China, holotype, genitalia slide no. BH16008 (GNU) (after Xu *et al*. 2017)



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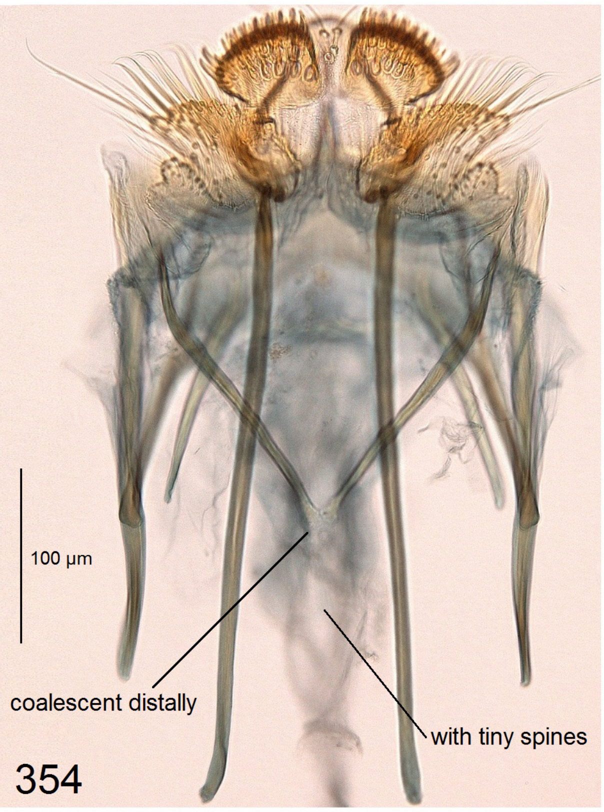

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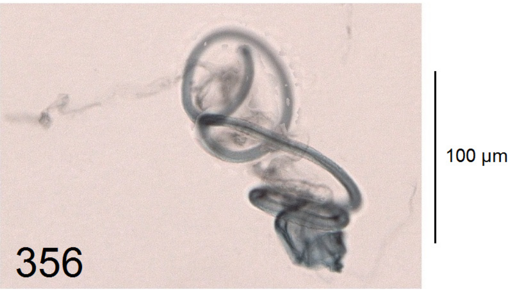
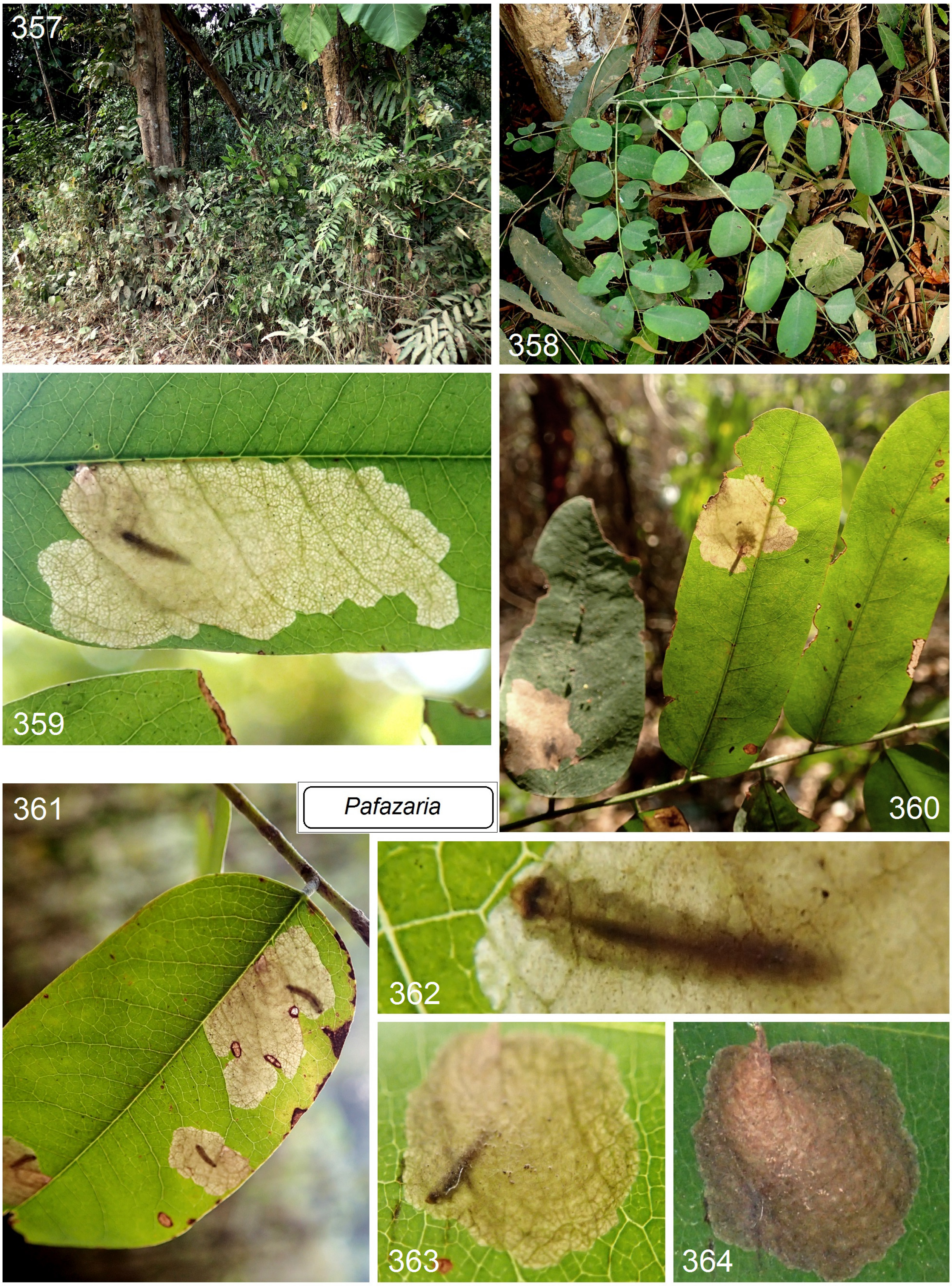
Pafazaria



356

FIGURES 353–356. Female genitalia of *P. faboidica* Diškus & Stonis, **sp. nov.**, Laos, paratype, genitalia slide no. AD1061 (MfN). 353, 354, ovipositor and apophyses; 355, corpus bursae; 356, coils of ductus spermathecae



FIGURES 357–364. Bionomics of *P. faboidica* Diškus & Stonis, **sp. nov.**, Laos. 357, lowland tropical habitat, elevation of 230 m, Vientiane Prov., Vang Vieng, 18°55’56”N, 102°26’14”E; 358, host plant, *Dalbergia* sp. (Faboideae, Fabaceae); 359–364, leaf mines

8. Genus *Neotischeria* Diškus & Stonis, 2021

(Figs 365–410)

Neotischeria Diškus & Stonis, 2021: 149. Type species: *Neotischeria neotropicana* (Diškus & Stonis, 2015: 457–465).

Diagnosis. In the male genitalia, species of *Neotischeria* are characterized by a simple, slender valva without dorsal lobe(s), a strongly developed, laterally thickened, caudally bilobed anellus usually possessing three pairs of lateral chetae, and a slender, distally bifurcated phallus. In the female genitalia, the genus is characterized by the hardened membrane between the inner prela and often large 6–10 coils of ductus spermathecae. Leaf mines of *Neotischeria* are irregular blotch-like on Asteraceae (occasionally Malvaceae) host plants and, unlike the most similar *Astrotischeria*, with a distinctive rounded nidus. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. External characters of the adults and wing venation characters are not informative and, therefore, insufficient for differentiation of *Neotischeria* because of their general uniformity or, in some cases, variability of these characters within the entire family. Molecular analysis showed *Neotischeria* as a separate clade from other genera. In the case where all genera are included in the analysis, *Neotischeria* forms a monophyletic group with *Pafazaria* (Figs 62–64); with the omission of *Pafazaria*, it clusters with *Astrotischeria* (Fig. 77).

Adult. Head: frontal tuft overlapping the frons, comprised of long, slender lamellar scales; pecten distinctive; collar distinctly paired, comprised of slender lamellar scales. Forewing usually without a distinctive pattern, speckled with darker scales, sometimes with irregular spots that are especially distinctive (large and bright) in females. Hindwing slender, androconia absent.

Male genitalia. Unlike the similar *Astrotischeria*, uncus always with long lobes; however, lobes usually widened basally or uncus with additional pair of very short rounded inner lobes; occasionally there are two pairs of long lobes. Socii membranous, large to very large, usually distinctly paired (occasionally unpaired), and always distinctly spinose. Tegumen long (except for a single species, *A. tubifex*, with a very short tegumen); diaphragm without spines; pseudognathos absent. Unlike the similar *Astrotischeria*, valva usually simple and slender, always without dorsal lobe(s); basal process of the valva long, occasiobally medium long. Transtilla and juxta absent. Anellus membranous, well developed, caudally bilobed, laterally usually thickened and with three (occasionally four) pairs of lateral chetae. Vinculum usually short or medium short, sometimes long, with rounded or widely rounded ventral plate (occasionally ventral plate of vinculum angular). Phallus slender, rod-like, apically divided, without spines or wide lobe-like projections.

Female genitalia. Ovipositor lobes small to large; the gap between ovipositor lobes wide; second pair of ovipositor lobes usually two, sometimes three times smaller in comparison to main ovipositor lobes. Unlike the similar *Astrotischeria*, lateral lobes very short, usually indistinctive, occasionally, in *N. neotropicana*, distinctive but short. Apophyses long or very long; anterior apophyses often equal in length with posterior apophyses, or slightly shorter, or longer. Prela with three pairs of relatively long rod-like projections; inner pair is the longest; membrane between inner prela is thickened. Caudal sclerite weakly developed, inverted U-shaped, pointed caudally; sometimes caudal sclerite invisible. Antrum absent. Accessory sac usually indistinctive or absent, occasionally relatively larger, rounded but weakly folded, membranous; ductus spermathecae slender, with usually 10 (sometimes 6–9) large coils; vesicle large, rounded. Corpus bursae long, gradually narrowing towards caudal end or with a very long and slender "neck"; pectinations of main body of corpus bursae absent but occasionally there are weakly chitinized, indistinctive tiny spines on slender "neck" of the bursa.

Bionomics. The genus is trophically associated with Asteraceae host plants (although a single species is known to feed on Malvaceae). Leaf mines of *Neotischeria* are irregular blotch-like, without frass, and, unlike the similar *Astrotischeria*, with a distinctive rounded nidus.

Species diversity and geographical distribution. The genus is widespread in the Americas (predominantly Central American and South American; only a couple of species occur in the southern states of the USA), but is not known to occur outside the Western Hemisphere. Recently, a few new *Neotischeria* species were described: the South American (Andean) *N. conexa* Diškus & Stonis, *N. ochripennata* Diškus & Remeikis, *N. longa* Diškus & Stonis, and Central American *N. poseidonia* Diškus & Stonis (Stonis *et al*. 2021c). In the same publication, several earlier described species were transferred to *Neotischeria* from other genera: the South American *N. capnota* (Meyrick), *N. guarani* (Diškus & Stonis), Central American *N. robinsoni* (Diškus & Stonis), *N. tubifex* (Diškus & Stonis), *N.*

belizensis (Remeikis & Stonis), *N. mesoamericana* (Diškus & Stonis), and *N. neotropicana* (Diškus & Stonis); the latter species is known to have the largest distribution area from Mexico to Bolivia (Stonis *et al.* 2020b).

The following two species described by Braun (1923, 1972) from the USA, and previously attributed to *Astrotischeria* by Puplesis & Diškus (2003), are transferred here to *Neotischeria: N. explosa* (Braun, 1923) (**comb. nov.**) from California and *N. pallidipennella* (Braun, 1972) (**comb. nov.**) from Arizona.

Therefore, together with two Central American species described here (*N. antigua* Diškus & Remeikis, **sp. nov.** and *N. subantigua* Diškus & Remeikis, **sp. nov.**, see below), the genus *Neotischeria* is now comprised of 15 species, the majority of which are from Central America.

Neotischeria antigua Diškus & Remeikis, sp. nov.

urn:lsid:zoobank.org:act:375B7E51-4D1A-41A0-9FE9-81C47047792B
(Figs 372–376, 384–396)

Type material. Holotype: ♂, GUATEMALA: Antigua Guatemala, San Juan del Obispo, 14°31’7”N, 90°43’50”W, elevation 1680 m, feeding larva 25.ii.2012, ex pupa iii. 2012, field card no. 5116, leg. A. Diškus, genitalia slide no. AD1110 (MfN). Paratypes: 13 ♂, 13 ♀, same label data as holotype, genitalia slides nos AD869♂, AD1075♂, AD1073♀, AD1074♀ (MfN).

Diagnosis. Externally, this new species can be confused with *N. subantigua* **sp. nov.** (described below), but the latter is larger and, in contrast to *N. antigua* **sp. nov.**, does not possesses a bright oblique median stripe of the forewing. The male genitalia differ from those of the similar *N. subantigua* in having a unique phallus with numerous, weakly chitinized slender apical spines. The female genitalia of *N. antigua* differ in the significantly smaller ovipositor lobes and more elaborate caudal plate of prela (compare Figs 391, 392 and 403, 407).

DNA barcode. We barcoded two specimens of the type series, but not the holotype; the sequences are available in the GenBank database under the accession numbers OQ413557 and OQ413558.

Description. *Male* (Figs 372, 374, 376). Forewing length 3.0–3.5 mm; wingspan 6.6–7.7 mm (n = 9). Head: palpi ochre cream; frons pale yellow-ochre; frontal tuft pale yellowish ochre with some pale brown scales; collar yellow-ochre; antenna distinctly longer than one half the length of forewing; flagellum pale grey, 3rd enlarged segment yellow-ochre. Tegula predominantly pale ochre-brown, ochreous cream distally; thorax covered with pale yellowish ochre and pale brown scales. Forewing densely irrorated with ochre, ochre-brown, and blackish brown scales, and with an indistinctive oblique subbasal stripe and a large, cream, postmedian stripe; the latter with sparsely irrorated black scales medially; fringe pale yellow ochre apically, pale grey on tornus; fringe line comprised of small black scales; forewing underside pale dark grey-brown, without spots or androconia, except for blackish brown special scales along costal margin at the forewing base. Hindwing pale grey to grey on upper side and underside, without androconia; fringe pale grey. Legs pale ochreous cream, densely covered with dark grey-brown scales on upper side. Abdomen glossy pale ochreous grey on upper side, yellow-ochre densely irrorated with dark brown scales on underside; genital plates predominantly yellow-ochre with some pale grey scales; anal tufts long, ochreous cream.

Female (Figs 373, 375). Forewing length 3.2–3.4 mm; wingspan 7.0–7.3 mm (n = 2). Similar to male, but pale median stripe of the forewing usually wider and more distinctive.

Male genitalia (Fig. 384) with capsule 440–450 μm long, 255 μm wide. Uncus comprised of two relatively short, elongated lateral lobes and two very short, rounded median lobes (Figs 384, 385). Socii medium large, weakly paired, membranous. Valva 335–380 μm long, simply-shaped, without a dorsal lobe but with strong chetae in apical half. Anellus mostly membranous, strongly thickened laterally. Vinculum very small, widely triangular or rounded distally. Phallus ca. 310 μm long, apically bifid, with numerous, weakly chitinized slender apical spines.

Female genitalia (Figs 390–396) 1380–1690 μm long. Ovipositor lobes small, rounded, relatively sparsely covered with weakly chitinized peg-like setae; second pair of ovipositor lobes slightly smaller with numerous long setae. Anterior and posterior apophyses almost equal in length; prela comprised of three pairs of slender rod-like projections; inner prela relatively very long; caudal plate elaborated and comprised of two elements. Corpus bursae with a very long and extremely slender proximal part, and a small oval-shaped main body without distinctive pectination. Ductus spermathecae short, sinuous, with 5–6 large coils, and a indistinctive vesicle.

Bionomics. Host plant is unknown (an unidentified species of Asteraceae). Larvae mine leaves in February. The leaf mine is blotch-like, irregularly shaped, without frass. Adults occur in March. Otherwise, biology is unknown.

Distribution. This species is known from a single locality in Guatemala, Antigua Guatemala, San Juan del Obispo, at elevation of 1680 m.

Etymology. The species is named after Antigua Guatemala, the locality where it was found.

Neotischeria subantigua Diškus & Remeikis, sp. nov.

urn:lsid:zoobank.org:act:FD9584D1-3F00-4DCF-9C87-8760117DFD94
(Figs 377–383, 397–410)

Type material. Holotype: ♂, GUATEMALA: Sololá Department, Panajachel, 14°45'6"N, 91°9'43"W, elevation 1660 m, feeding larva 22.ii.2012, ex pupa iii. 2012, field card no. 5105, leg. A. Diškus. genitalia slide no. AD1087 (MfN). Paratypes: 9 ♂, 8 ♀ same label data as holotype, genitalia slides nos AD872♂, AD1092♂, AD1118♂, AD1112♀ (MfN).

Diagnosis. Externally and in the genitalia, *N. subantigua* **sp. nov.** can be confused with *N. antigua* **sp. nov.** (described above); for characters to easily differentiate these two similar, and closely related, species see the Diagnosis of *N. antigua.*

DNA barcode. Unavailable.

Description. *Male* (Figs 377–380, 383). Forewing length 4.0–4.5 mm; wingspan 8.6–9.6 mm (n = 7). Head: palpi and frons cream to ochreous cream; frontal tuft yellowish cream with some brown-tipped scales; collar yellow-ochre; antenna slightly or distinctly longer than one half the length of forewing; flagellum yellowish cream indistinctly annulated with pale grey scales; 3rd enlarged segment ochreous cream. Tegula ochreous cream, densely irrorated with dark brown scales; thorax ochreous cream; sensila relatively short, almost indistinctive. Forewing densely irrorated with ochre, ochre-brown, and blackish brown scales, and with two short, oblique but indistinctive antemedian and subbasal stripes; fringe pale yellow ochre apically, pale ochreous grey on tornus; fringe line comprised of small brown-black scales; forewing underside pale greyish brown, without spots or androconia, except for dark grey-brown special scales along costal margin at the forewing base. Hindwing greyish cream to pale grey on upper side and underside, without androconia; fringe greyish pale ochre. Legs yellow cream, irrorated with pale grey-brown scales on upper side. Abdomen glossy pale ochreous grey on upper side, pale ochreous yellow densely irrorated with grey-brown scales on underside; genital plates large, pale ochreous yellow to yellowish cream; anal tufts long, yellowish cream.

Female (Figs 381, 382). Similar to male. Forewing length 3.8–4.4 mm; wingspan 8.2–9.5 mm (n = 5).

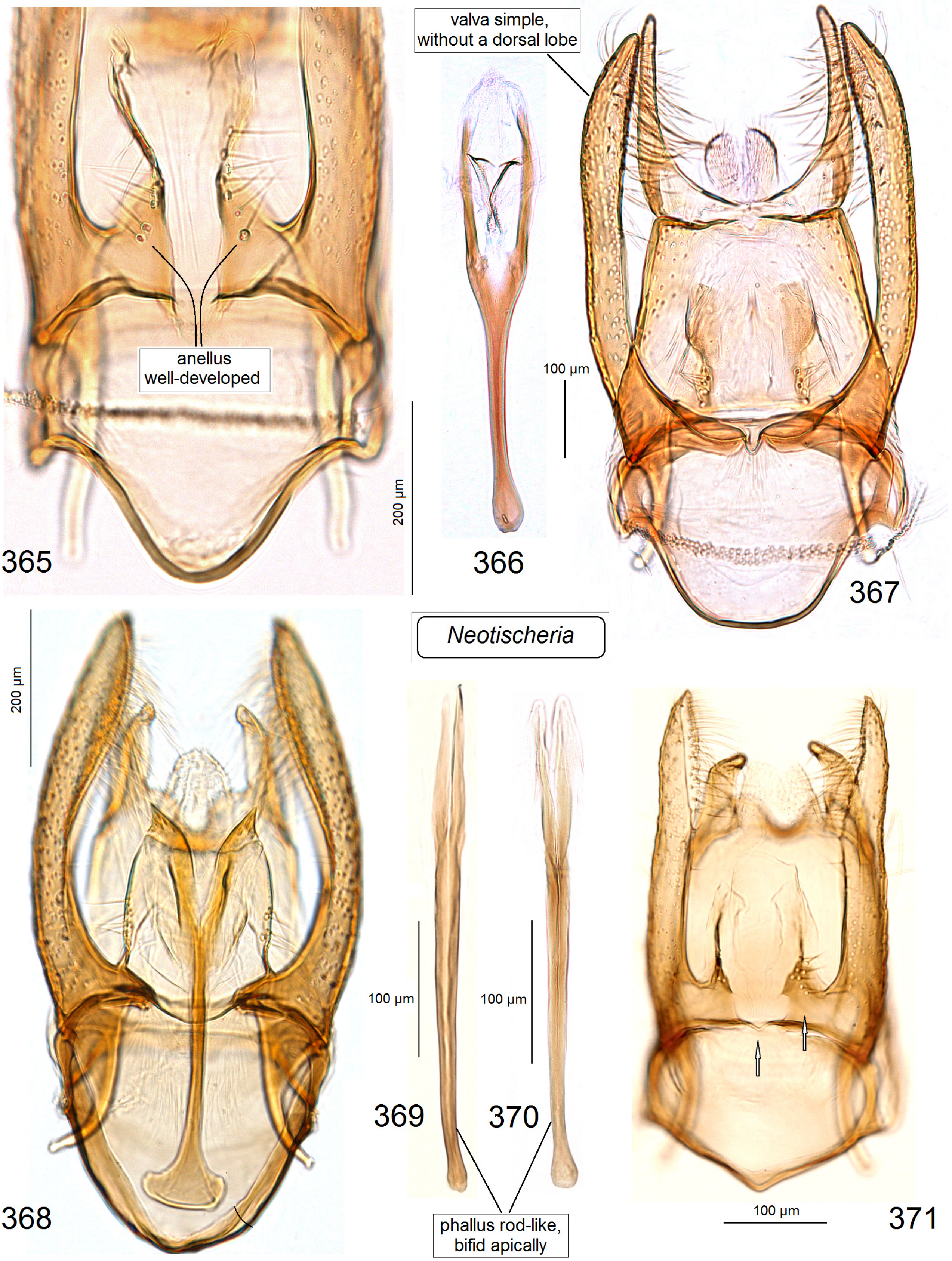
Male genitalia (Figs 397–402) with capsule 530–550 µm long, 345 µm wide. Uncus comprised of two relatively short, elongated lateral lobes and two very short, rounded median lobes (Fig. 399). Socii medium small, weakly paired, membranous. Valva 350–390 µm long, simply-shaped, without a dorsal lobe but with strong chetae in apical half. Anellus mostly membranous, strongly thickened laterally. Vinculum small, widely rounded distally. Phallus 370–385 µm long, apically bifid, with two pairs of very slender, long and pointed apical spines.

Female genitalia (Figs 403–410) ca. 1900 µm long. Ovipositor lobes large, rounded, densely covered with medium-chitinized peg-like setae; second pair of ovipositor lobes twice smaller, with numerous long setae. Anterior and posterior apophyses almost equal in length; prela comprised of three pairs of slender rod-like projections; inner prela very long, transverse prela unusually short; caudal plate comprised of a single element. Corpus bursae with a very long and extremely slender proximal part possessing some spines (Fig. 404), and small oval-shaped main body without distinctive pectination. Ductus spermathecae relatively short, sinuous, with 6–7 very large coils and an indistinctive vesicle.

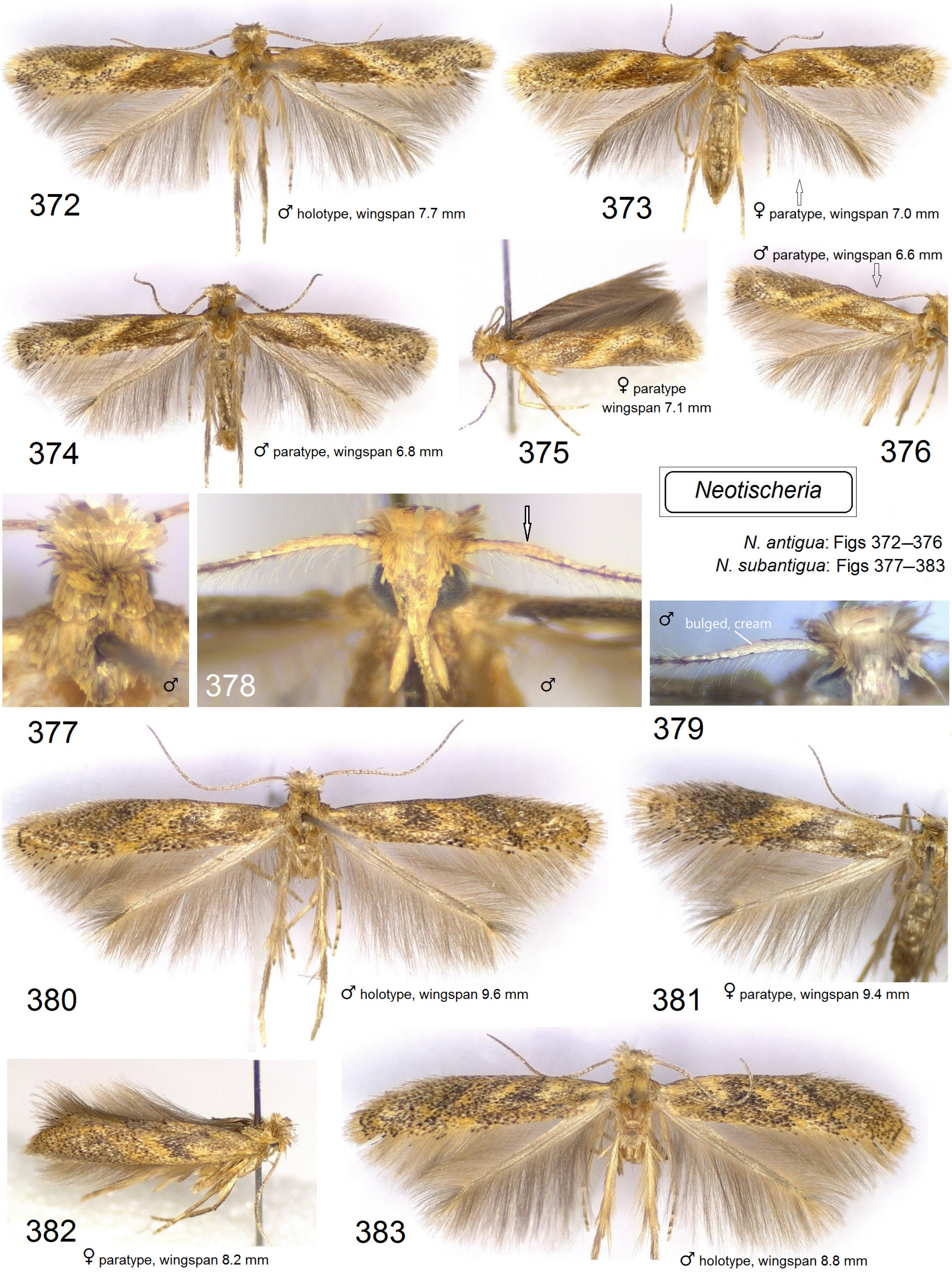
Bionomics. Host plant is unknown (an unidentified species of Asteraceae). Larvae mine leaves in February. The leaf mine is blotch-like, irregularly shaped, without frass. Adults occur in March. Otherwise, biology is unknown.

Distribution. This species is known from a single locality in Guatemala, Sololá Department, Panajachel, at elevation of 1660 m.

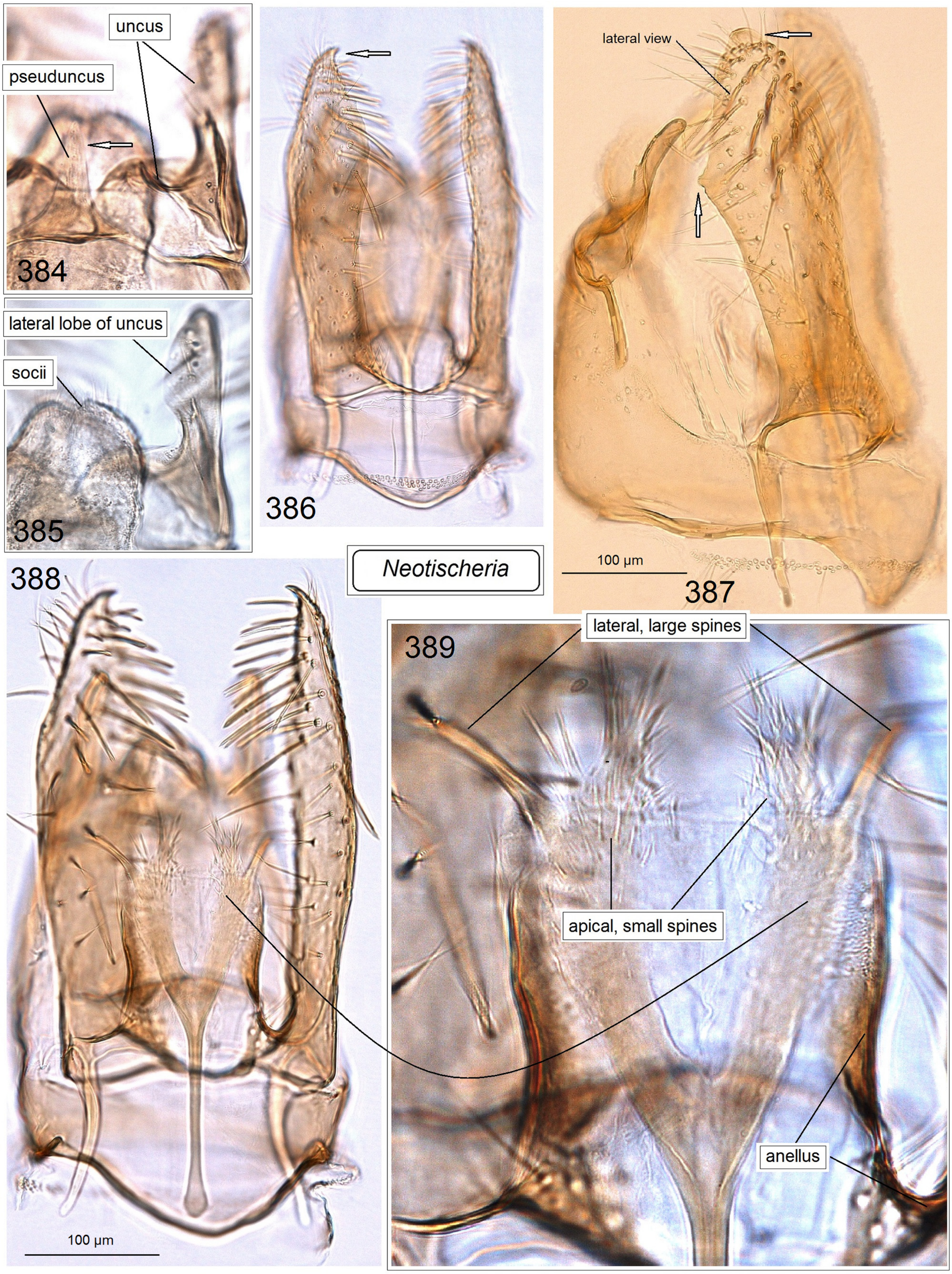
Etymology. *N. subantigua* is named after *N. antigua* Diškus & Remeikis, **sp. nov.**, a similar, and probably closely related species.



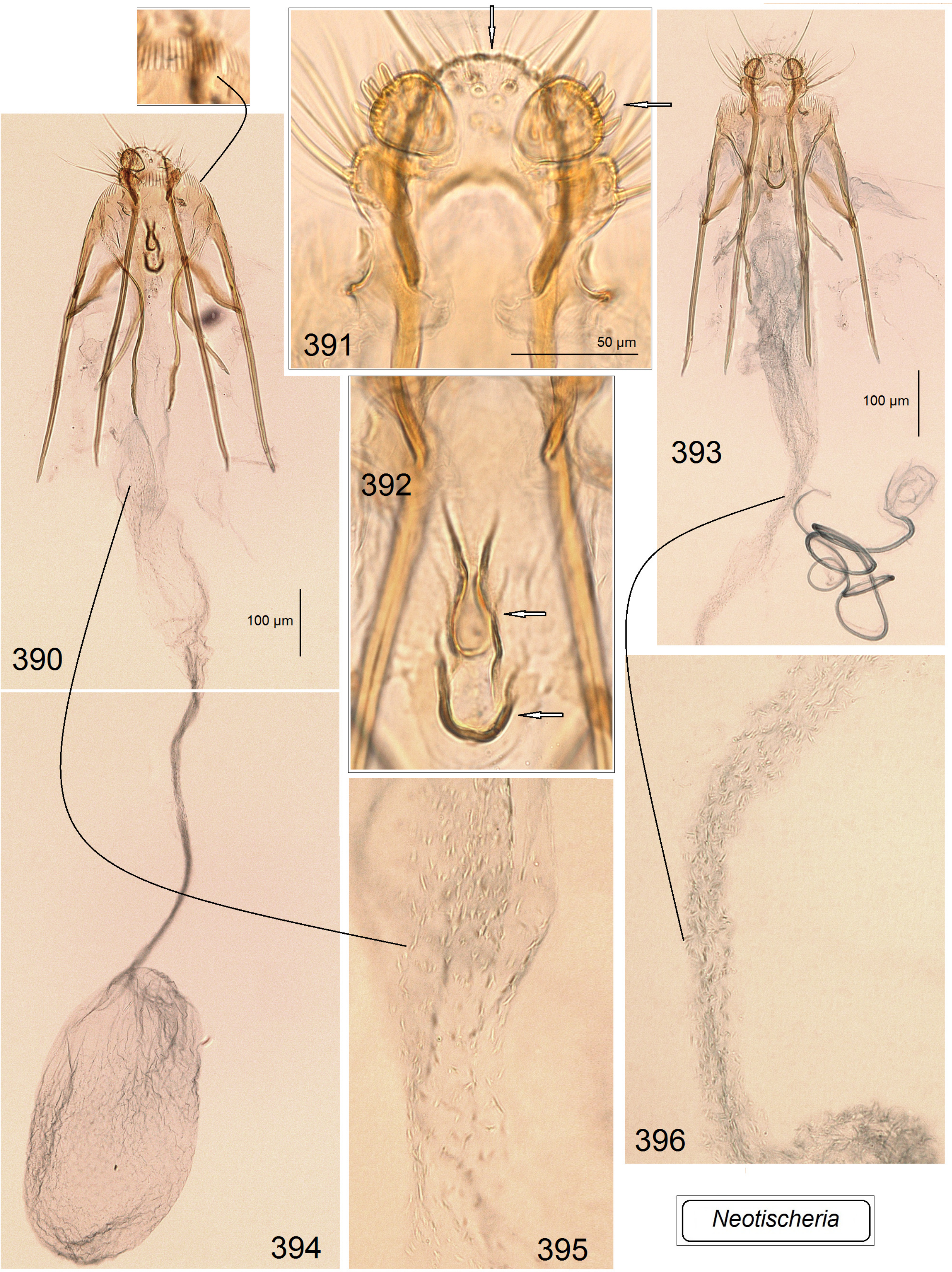
FIGURES 365–371. Details of male genitalia of *Neotischeria* spp. 365, *N. guarani* (Diškus & Stonis), holotype, genitalia slide AD988 (MfN) (after Stonis *et al.* 2020b); 366, 367, *N. neotropicana* (Diškus & Stonis), genitalia slide 010316205 (NHMUK); 368, *N. belizensis* (Remeikis & Stonis), holotype, genitalia slide 010316193 (NHMUK) (after Stonis *et al.* 2020a); 369–371, *N. conexa* Diškus & Stonis, holotype and paratype (after Stonis *et al.* 2021c)



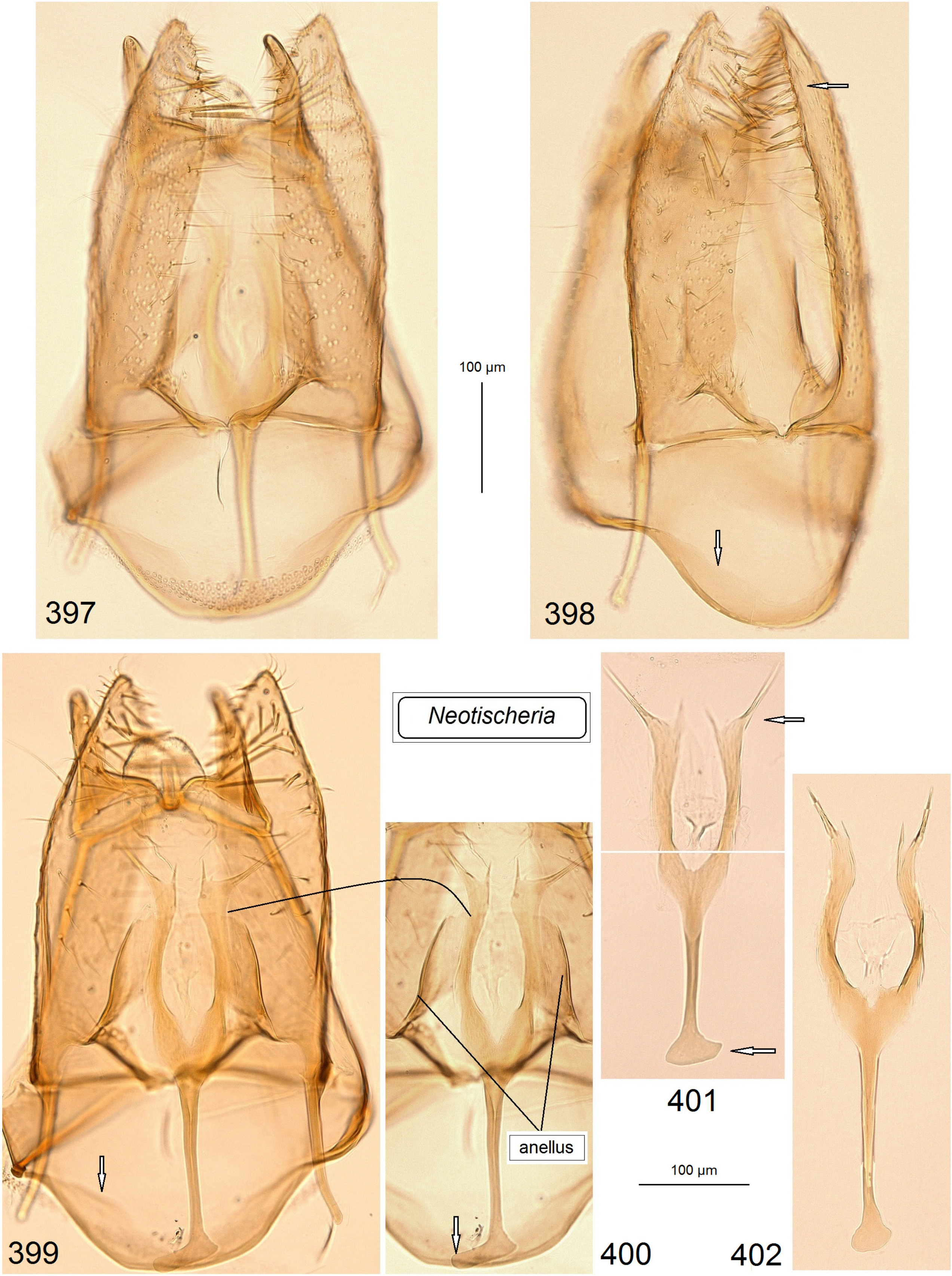
FIGURES 372–383. Adults of new *Neotischeria* species. 372–376, *N. antigua* Diškus & Remeikis, **sp. nov.** (MfN); 377–383, *N. subantigua* Diškus & Remeikis, **sp. nov.** (MfN)



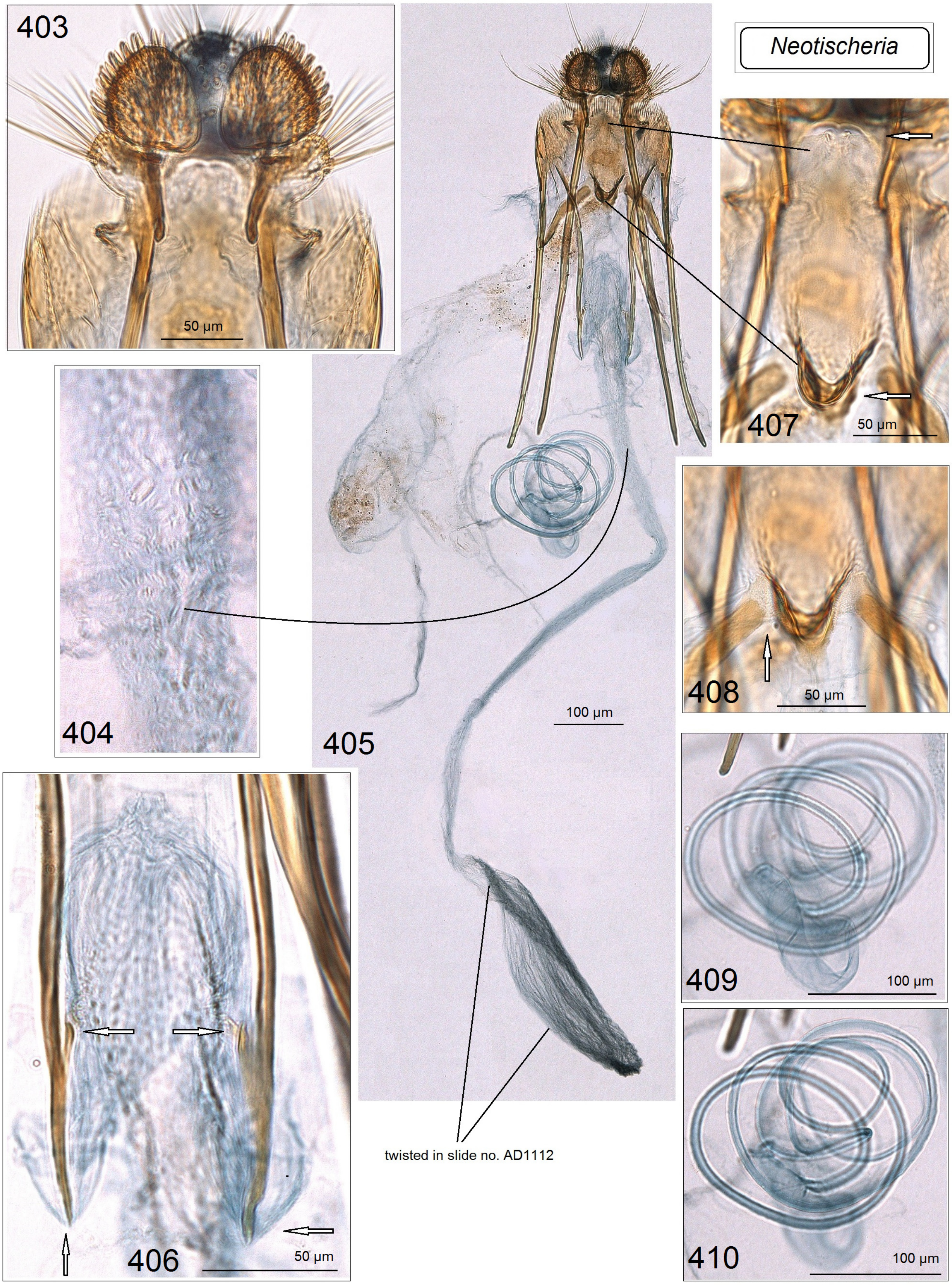
FIGURES 384–389. Male genitalia of *Neotischeria antigua* Diškus & Remeikis, **sp. nov.** 384–386, details of holotype, genitalia slide AD1110, ventral view; 387, paratype, genitalia slide no. AD1075, lateral view; 388, 389, general view of capsule, focused on phallus, holotype, genitalia slide AD1110, ventral view; (MfN)



FIGURES 390–396. Female genitalia of *Neotischeria antigua* Diškus & Remeikis, **sp. nov.** 390, 392, 394, 395, general view and details, paratype, genitalia slide no. AD1073; 391, 393, 396, another paratype, genitalia slide no. AD1074 (MfN)



FIGURES 397–402. Male genitalia of *Neotischeria subantigua* Diškus & Remeikis, **sp. nov.** 397, holotype, genitalia slide AD1087, ventral view; 398, paratype, genitalia slide AD1092, lateral view, with phallus removed; 399, 400, ventral view of capsule, focused on phallus, holotype, genitalia slide AD1087; 401, phallus, paratype, genitalia slide AD8742; 402, same, another paratype, genitalia slide AD1092 (MfN)



FIGURES 403–410. Female genitalia of *Neotischeria subantigua* Diškus & Remeikis, **sp. nov.**, paratype, genitalia slide no. AD1112 (MfN). 403, ovipositor lobes; 404, spines on "neck" of corpus bursae; 405, general view; 406–410, details

9. Genus *Paratischeria* Diškus & Stonis, 2017

(Figs 411–416)

Paratischeria Diškus & Stonis, 2017: 4. Type species: *Paratischeria ferruginea* Diškus & Stonis, 2017: 8–19.

Diagnosis. In the male genitalia, species of *Paratischeria* are characterized by the presence of a dorsal plate (sclerite) and anellus, as well as a very long basal process of the valva; phallus is usually expanded (with lateral projections) basally. In the female genitalia, the genus is characterized by large ovipositor lobes, small, indistinctive lateral lobes, and a longitudinally folded membrane between inner prela. Leaf mines of *Paratischeria* are irregular blotch-like, sometimes with short, relatively wide lateral galleries. Larvae feed on Urticaceae host plants but one South-South East Asian species, *P. hestias* (Meyrick), is recorded feeding on *Helicteres* spp., Malvaceae; a nidus is usually not round but elongated or irregular, often indistinctive.

External characters of the adults and wing venation characters are not informative and, therefore, insufficient for the differentiation of *Neotischeria* because of their general uniformity or, in some cases, variability of these characters within the entire family; however, at least some species are characterized by a bright ochre spot or ochre fascia for the forewing.

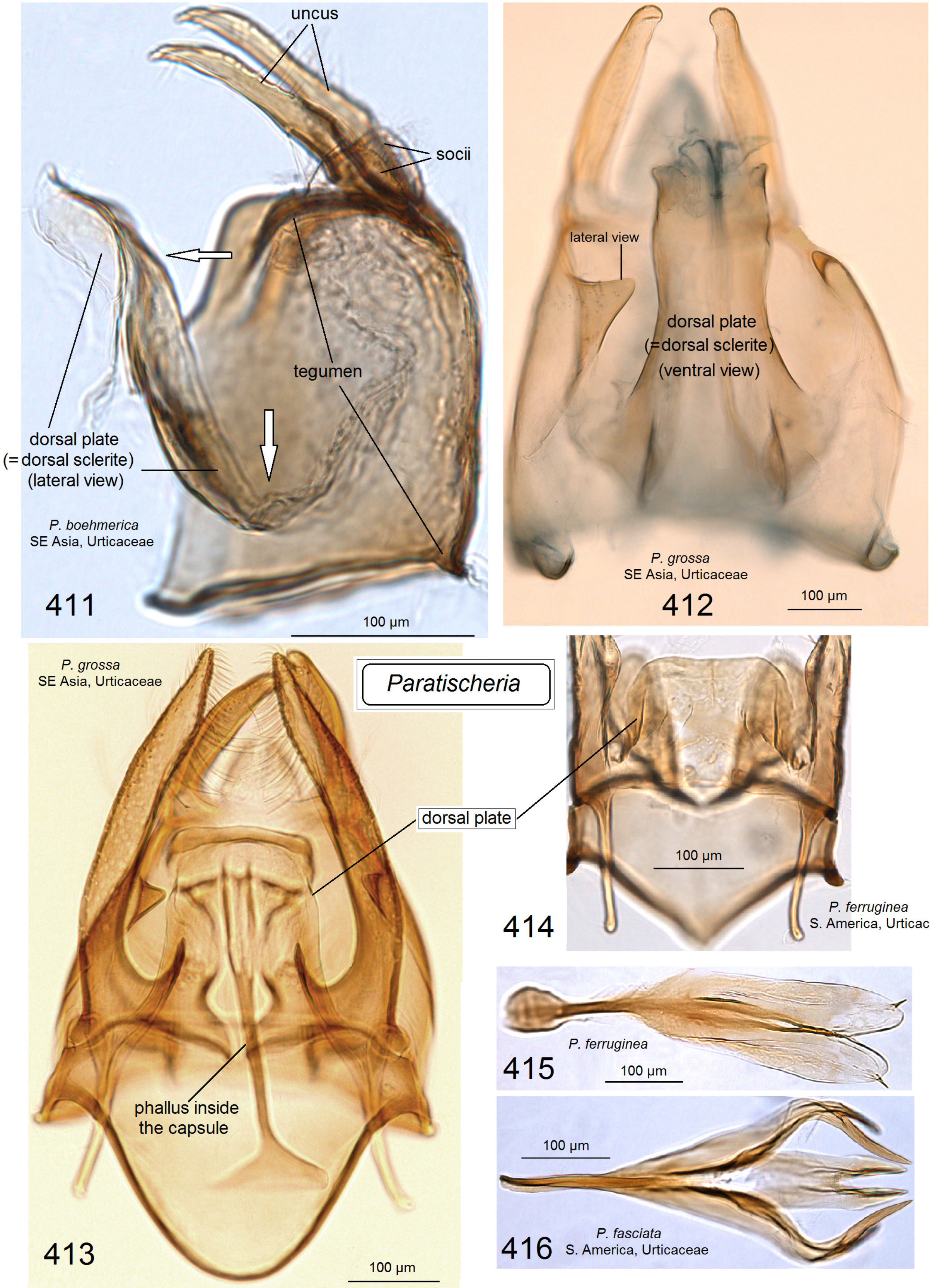
Notes. In our cladograms, *Paratischeria* appeared as a separate clade. Depending on the outgroup, it is either the sister taxon to the large cluster of (*Pafazaria* + *Neotischeria*) + (*Astrotischeria* + *Gnathitischeria*) (Figs 63, 64), or *Paratischeria* is the sister taxon to *Astrotischeria* (Fig. 62). Both cases do not conflict with the morphological data.

Adult. Head: frontal tuft overlapping the frons, comprised of long, slender lamellar scales; pecten distinctive; collar distinctly paired, comprised of slender lamellar scales. Forewing varies from unicolourous to sparsely speckled with dark scales apically and along costal and dorsal margins; South American species are known possessing a distinctive bright ochre spot or bright ochre fascia. Hindwing slender, androconia absent.

Male genitalia. Uncus always with two very long, usually slender, sometimes wide lateral lobes. Socii membranous, medium small, distinctly spinose, clearly paired (sometimes well-separated), only occasionally, in *P. hestias*, weakly paired. Tegumen long or moderately long, without a frame-like thickening, however, at least a couple of Asian species with thickened projections in corners laterally; diaphragm without spines; pseudognathos absent; dorsally to valvae, there is a distinctive but variously developed dorsal lobe (previously named the dorsal sclerite) (Stonis *et al*. 2017, 2021a). Valva slender to moderately wide, sometimes with a basal lobe; basal process of valva unusually very long. Transtilla and juxta absent. Anellus membranous, caudally slightly angular, bilobed, laterally with a few lateral chetae. Vinculum usually long or medium long, with a widely rounded triangular (occasionally band-like) ventral plate. Phallus slender, rod-like, basally usually expanded (with lateral projections at the base), apically divided, with two-four spines or without, rarely apically complex, additionally with four slender lateral lobes.

Female genitalia. Ovipositor lobes large to very large; the gap between ovipositor lobes wide; second pair of ovipositor lobes usually two–three times smaller in comparison to main ovipositor lobes; lateral lobes short, indistinctive. Anterior apophyses often almost equal in length with posterior apophyses, or slightly shorter, or longer. Prela with three pairs of relatively long rod-like projections; membrane between inner prela longitudinally folded; caudal sclerite with a distinctive slender and pointed caudal spine, otherwise, indistinctive, weakly thickened. Antrum absent. Accessory sac either absent or small and slender; ductus spermathecae short and slender, with usually 2–3 small coils; there are at least two exceptions known: a short ductus spermathecae with 10–12 large coils and a long ductus spermathecae with about 18 large coils; vesicle usually plate-like, irregularly rounded. Corpus bursae long, gradually narrowing towards caudal end or usually with a slender, short to very long “neck”; pectinations of main body of corpus bursae absent, but occasionally there are indistinctive tiny spines on slender “neck” of the corpus bursae.

Bionomics. The genus is trophically associated with Urticaceae and Malvaceae host plants. Leaf mines of *Paratischeria* are irregular blotch-like, sometimes elongated and with short, but relatively wide, lateral galleries; frass absent or very little sparsely deposited; a nidus is usually not rounded but elongated or indistinctive, invisible (larvae usually hiding under larger veins in the leaf mine).



FIGURES 411–416. Details of male genitalia of *Paratischeria* spp. 411, *P. boehmerica* Diškus & Stonis, uncus, tegumen and dorsal plate, lateral view, holotype, slide no. AD1055 (MfN); 412, *P. grossa* Diškus & Stonis, uncus, tegumen, and dorsal plate, ventral view, paratype, slide no. AD1037 (MfN); 413, same, capsule, holotype, slide no. AD1066 (MfN) (after Stonis *et al.* 2021a); 414, *P. ferruginea* Diškus & Stonis, dorsal plate and vinculum, paratype, slide no. AD842 (ZMUC); 415, same, phallus, slide no. AD867 (ZMUC); 416, *P. fasciata* Diškus & Stonis, phallus, holotype, slide no. AD868 (ZMUC) (after Stonis *et al.* 2017)

Species diversity and geographical distribution. The genus occurs in the tropical biome of South America (from Ecuador to Bolivia), equatorial Africa, and South and South East Asia (India, Laos and Vietnam). Currently, the genus is comprised of six species: South American *P. fasciata* Diškus & Stonis, *P. ferruginea* Diškus & Stonis, the equatorial African *P. urticicolella* (Ghesquière) (Stonis *et al*. 2017), South Asian *P. hestias* (Meyrick) (Xu *et al*. 2017), and South East Asian *P. boehmerica* Diškus & Stonis, *P. grossa* Diškus & Stonis (Stonis *et al*. 2021a).

According to the currently available data, *P. hestias* has the broadest distribution; this species was originally described from India (Meyrick 1915b), was recently found in northern Vietnam (Xu *et al*. 2017), and here we provide new data from Laos: 1 ♂, 2 ♀, LAOS: Luang Prabang Prov., Nong Khiaw, 20°38’33”N, 102°40’30”E, elevation 480 m, mining larva on *Helicteres* sp., 11.ii.2020, field card no. 5325, leg. A. Diškus, genitalia slide nos AD1116♂, AD1114♀ (MfN); 1 ♂, same label data, genitalia slide no. AD1101♂ (from adult in pupal skin, no pinned specimen preserved) (GNU).

10. Genus *Astrotischeria* Puplesis & Diškus, 2003

(Figs 417–481)

Astrotischeria Puplesis & Diškus, 2003: 109–111. Type species: *Astrotischeria karsholti* Puplesis & Diškus, 2003: 111–112.

Diagnosis. In the male genitalia, species of *Astrotischeria* are characterized by a unique, divided valva possessing variously developed dorsal lobe (or lobes), usually a long tegumen and vinculum, a rod-like, apically bifid phallus, and often a short, modified, four-lobed uncus (sometimes the lateral lobes are significantly longer and elongated in comparison to median lobes, the median lobes very short and rounded). In the female genitalia, the genus is characterized by small ovipositor lobes (occasionally they are fully reduced or strongly modified: thickened and not rounded), a weakly developed caudal plate of prela, and usually a very long and slender proximal part of the corpus bursae. Leaf mines of *Astrotischeria* are irregular blotch-like on Asteraceae (occasionally Malvaceae) host plants; before pupation fully grown larvae of a few species roll up the margin of the mined leaf; a nidus is usually invisible, indistinctive. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. External characters of the adults and wing venation characters are not informative and insufficient for the diagnosis of *Astrotischeria* because of their general uniformity or, in some cases, variability of these characters. Cases of sexual dimorphism are known among some *Astrotischeria* species (Stonis *et al.* 2019b, 2020b). According to the results of molecular analysis, *Astrotischeria* appeared as a distinct genus and a sister taxon either with *Gnathitischeria* (Figs 63, 64) or *Paratischeria* (Fig. 62). This is not in conflict with the morphology data.

Adult. Head: frontal tuft overlapping the frons, comprised of long lamellar scales; pecten distinctive; collar distinctly paired, comprised of slender lamellar scales. Forewing irregularly sparsely speckled or with darker scales at the apex and along costal and dorsal margin, or with a few irregular spots (the latter are wider and brighter in females). Hindwing slender, androconia absent.

Male genitalia. Uncus modified, with four lobes: two short or medium long lateral and two short, usually rounded median lobes; only sometimes uncus with a single pair of short or slightly longer lobes. Socii membranous, large, usually distinctly paired and always distinctly spinose. Tegumen usually long; diaphragm without spines; pseudognathos absent. Unlike other Tischeriidae (including the resembling *Neotischeria* but excluding *Gnathitischeria* gen. nov., described below), valva divided, with simple and slender ventral lobe and distinct, often pointed dorsal lobe(s); basal process of the valva varies from medium short to medium long; occasionally basal process is long. Transtilla and juxta absent. Anellus membranous, laterally often thickened and with about three pairs of lateral chetae or numerous tiny spines; occasionally anellus indistinctive, weakly developed. Vinculum usually long, occasionally medium short or short, with a triangular or widely rounded ventral plate. Phallus slender, rod-like, apically divided, occasionally with slender apical lobes or slender spines.

Female genitalia. Ovipositor lobes small, occasionally large; the gap between ovipositor lobes wide; second pair of ovipositor lobes usually two times smaller in comparison to main ovipositor lobes; lateral lobes small to large. Occasionally ovipositor lobes are fully reduced or modified: thickened and not rounded. One species, *A. ochrimaculosa* Diškus, Stonis & Vargas, possesses an additional, unique round structure, a telpek (see Stonis *et al.* 2019c). Anterior apophyses often equal in length with posterior apophyses, or the latter slightly shorter, or, occasionally, longer. Prela with three pairs of relatively long mainly rod-like projections; sometimes median and inner prela with wide, lobe-like basal parts; inner prela usually long, membrane between these prela is sometimes folded or even thickened. Caudal sclerite weakly developed, usually indistinctive, occasionally with a short, weakly chitinized caudal spine-like projection. Antrum absent. Accessory sac usually indistinctive or absent; ductus spermathecae slender, often with 2–4, sometimes 7–10 coils; vesicle usually small, irregularly shaped or ring-shaped. Corpus bursae often with a very long and slender "neck"; pectinations of main body of corpus bursae absent but often there are tiny spines or papilla-like pectinations on slender "neck" of the corpus bursae.

Bionomics. The genus is trophically associated with Asteraceae host plants, however, about five species are known to feed on Malvaceae. Leaf mines of *Astrotischeria* are irregular, blotch-like, usually without frass, occasionally with a little frass or a stained epidermis; fully grown larvae of a few species roll up margin of the mined leaf; a nidus is often indistinctive, invisible.

Species diversity and geographical distribution. Currently, *Astrotischeria* is the second largest Tischeriidae genus, comprising predominantly Asteraceae-feeding species. Many of the known species were primarily described as *Tischeria* (see Braun 1972), but many species were transferred after erecting the genus *Astrotischeria* (Diškus & Stonis, 2003). However, after the description of another predominantly Asteraceae-feeding genus, *Neotischeria*, the following few species without a dorsal lobe on the valva in the male genitalia were also subsequently transferred from *Astrotischeria* to *Neotischeria*: *N. neotropicana* (Diškus & Stonis, 2015), *N. capnota* (Meyrick, 1915a) (Stonis *et al.* 2021c), and two species previously attributed to *Astrotischeria* by Puplesis & Diškus (2003) are here transferred to *Neotischeria*: *N. explosa* (Braun, 1923) **comb. nov.**; *N. pallidipennella* (Braun, 1972) **comb. nov.**

Recently, one *Astrotischeria* species was previously incorrectly transferred to *Paratischeria* (Xu *et al*. 2017), and is here transferred back to *Astrotischeria*: *A. heteroterae* (Frey & Boll, 1878) **comb. nov.**

Some lectotypes, paralectotypes, or non-type specimens of five previously little known *Astrotischeria* species deposited at NHMUK were dissected for the first time and illustrated in the current publication (Figs 426–452): *A. plagifera* (Meyrick) (Figs 431–435); *A. helianthi* (Frey & Boll) (Figs 436–438); *A. ephaptis* (Meyrick) (Figs 440–443); *A. solidagonifoliella* (Clemens) (Figs 444–4446); and *A. omissa* (Braun) (Figs 451, 452).

Here, based on our studies of some material deposited at NHMUK, we confirm the previous synonymization of *Tischeria longeciliata* Frey & Boll, 1878: 259 with *Astrotischeria helianthi* (Frey & Boll, 1878) (synonymized by Stonis *et al.* 2018a). There were three scientific and practical reasons for this taxonomic act: (i) the male lectotype deposited at NHMUK ("Dalas, *T. longeciliata*, Frey & Boll, *Helianthus*, Frey collection / Walsingham collection 1910-427") was not dissected, genitalia are unknown because its abdomen is lost; (ii) externally, there is no possible way to distinguish or differentiate the slightly darker lectotype of *longeciliata* from the slightly paler lectotype of *Astrotischeria helianthi*; (iii) both lectotypes were reared from the same host plant, *Helianthus.*

Currently, the genus *Astrotischeria* is comprised of 45 named species, however, many other species have already been collected but await publication, including new taxa from the USA (Charley Eiseman, *pers. comm.*), as well as from Central and South American countries.

The geographical distribution of the genus is limited to the Nearctic and Neotropical regions, including the Caribbean, and is not known outside the Western Hemisphere. The following two species are recorded as far north as Canada: *A. occidentalis* (Braun), and *A. astericola* (Braun) (Braun 1972; Pohl *et al*. 2018). The most southern discoveries of the genus were from Uruguay (*A. atlantica* Diškus & Stonis, see Stonis *et al*. 2020b), Argentina, and Chile: *A. koehleri* (Bourquin, see Bourquin 1962), *A. pallens* Puplesis & Diškus, *A. chilei* Puplesis & Diškus (see Diškus & Puplesis 2003; Stonis *et al*. 2016a). It is important to note that two *Scalesia*-feeding *Astrotischeria* species, *A. scalesiaella* Landry and *A. alcedoensis* Landry, were described in 2004 from the remote Galapagos Islands (Landry & Roque-Albelo 2004). A search for *Astrotischeria* species was conducted on Easter Island by Arūnas Diškus, but a species of this genus was not detected.

Astrotischeria incae Diškus & Stonis, sp. nov.

urn:lsid:zoobank.org:act:4C61DB8E-7E6D-4019-BE53-0CC90FA3E2DC
(Figs 453–481)

Type material. Holotype: ♂, PERU: Urubamba Prov., near Machu Picchu, 13°9'58"S, 72°32'26"W, elevation 2370 m, feeding larvae 20.x.2008, field card no. 4947, leg. A. Diškus [in collaboration with Quechua counterparts], genitalia slide no. AD1115 (MfN). Paratypes: 1 ♂, 1 ♀, same label data as holotype, genitalia slide nos AD1107♂, AD1108♀ (MfN).

Diagnosis. Externally, this new species can be confused with other sparsely speckled *Astrotischeria* species. However, the new species is characterized by the unique feature of females: they possess unusually long antennal sensilla unlike other Tischeriidae. In the male genitalia, *A. incae* **sp. nov.** resembles the Andean *A. colombiana* Stonis & Vargas, *A. recta* Diškus, Mey & Stonis, and particularly *A. bachariphaga* Diškus & Stonis. However, the combination of an inwardly strongly bent dorsal lobe of valva (Fig. 466), shape of uncus (Fig. 462), a triangular vinculum, and a phallus with two simple apical lobes distinguishes *A. incae* from all known congeneric species. The female genitalia of *A. incae* are without peg-like setae (distinctly atypical for Tischeriidae) and, also unlike other Tischeriidae, with weakly divided, almost coalescent ovipositor lobes. The new species is also characterized by unique lobe-like projections of prela (Fig. 474), and numerous tiny spines on membrane between inner prela (Figs 473, 475).

DNA barcode. Unavailable.

Description. *Male* (Figs 453–458). Forewing length 3.3–3.6 mm; wingspan 7.1–8.0 mm (n = 2). Head: palpi greyish cream to pale brown-grey; frons very glossy, pale brown-grey; pecten small, very slender, predominantly pale grey; frontal tuft comprised of long grey-brown, cream-tipped lamellar scales, therefore, the frontal tuft pale grey-brown proximally, brownish cream distally; collar short, weakly paired, comprised of dark grey-brown, cream tipped lamellar scales; antenna slightly longer than one half the length of forewing; flagellum grey-brown; sensilla relatively short, very fine, almost indistinctive, whitish cream. Tegula dark grey-brown, with some cream-tipped scales distally; thorax grey-brown. Forewing yellow-ochre, densely irrorated with dark brown scales along the margins and on apex, with a tornal spot of dark brown scales (note that most of dark brown scales of forewing are cream-tipped); fringe grey-brown, without a fringe line; forewing underside grey-brown to dark grey-brown, without spots or androconia, except for small cream, irregular, scaleless spot basally. Hindwing grey-brown to dark grey-brown on upper side and underside, without androconia, but with very small scaleless basal spot; fringe pale ochreous brown to grey-brown. Legs densely covered with grey-brown scales, ochreous cream distally. Abdomen grey, golden glossy on upper side and underside; genital plates small, grey-cream, almost inconspicuous; anal tufts grey, relatively short.

Female (Fig. 459). Forewing length 3.9 mm; wingspan 8.6 mm (n = 1). Similar to male, but thorax and forewing tend to be paler, i.e., less speckled with dark brown scales. Palpi and frons grey-brown. Sensilla of antenna very fine, as for female, atypically long, i.e., of similar length as those in males.

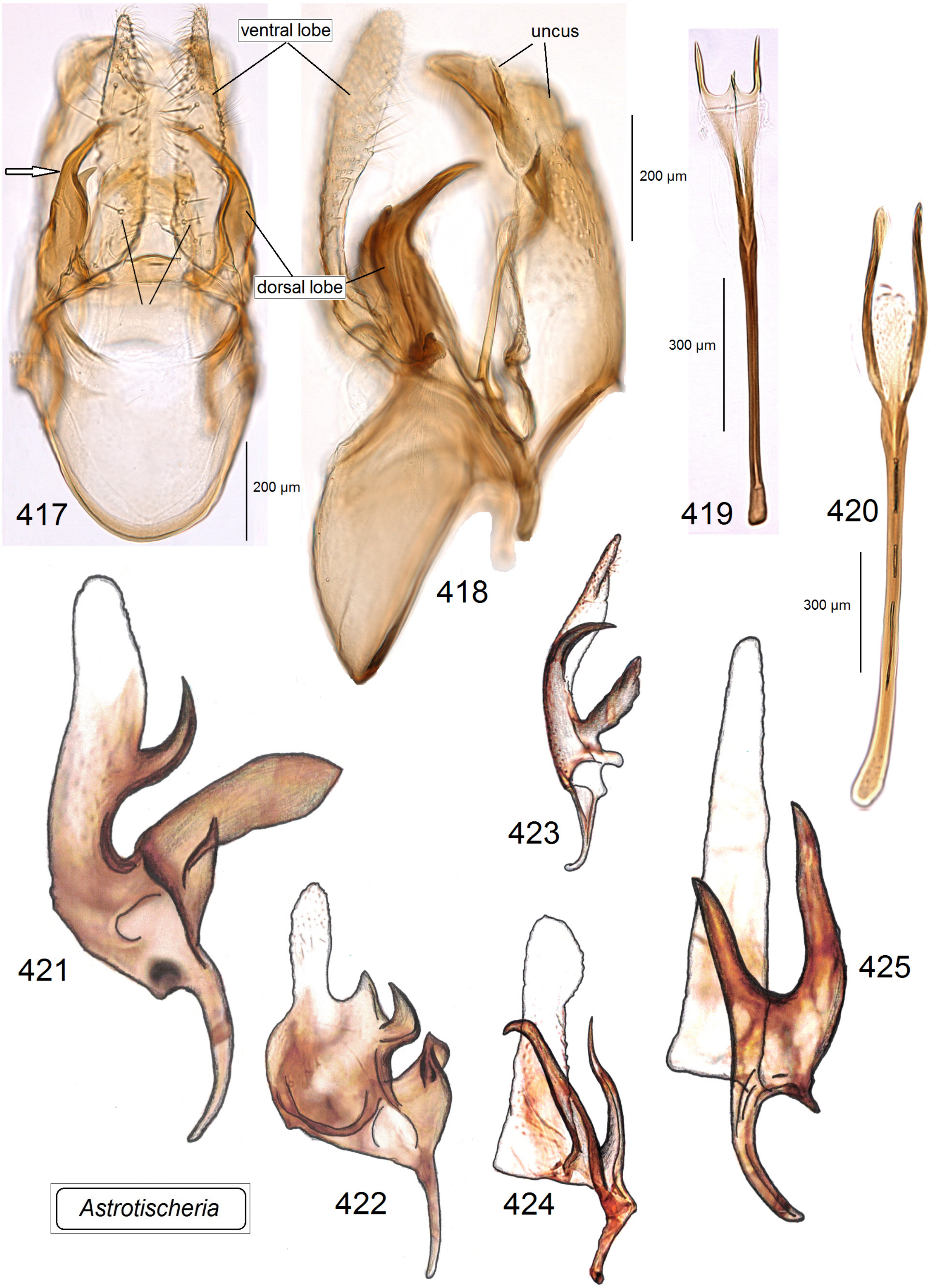
Male genitalia (Figs 460–467) with capsule 425–500 µm long, 230–240 µm wide. Uncus comprised of two relative short, elongated, lateral lobes (Fig. 462) and two very short, rounded, median lobes (Fig. 463). Socii relatively small, membranous, indistinctive. Valva ca. 335 µm long; ventral lobe (main body of valva) slender; dorsal lobe strongly thickened, strongly bent inwardly (Figs 461, 466), basally, with hardened folds (Fig. 465). Anellus mostly membranous, thickened only laterally. Vinculum triangular. Phallus ca. 340–410 µm long, rod-like, divided in two simple elongated lobes in apical half (Fig. 467).

Female genitalia (Figs 468–475) about 1710 µm long. Ovipositor lobes uniqually modified, very large, weakly individualized (almost undivided, coalescent), with numerous very slender setae but, in contrast to the general plan of the family Tischeriidae, without peg-like setae (Fig. 470); second pair of ovipositor lobes twice or three times smaller, with numerous relatively long setae. Posterior apophyses slightly shorter than anterior apophyses; prela comprised of three pairs of unique, rod-like projections, with lobe-like projections proximally (Fig. 474); inner prela long; membrane between the processes of inner prela with numerous tiny, weakly chitinized spines (Figs 473, 475). Corpus bursae with very long and extremely slender proximal part and small, oval-shaped main body without pectination (Fig. 472). Ductus spermathecae short, sinuous, with 3.5 relatively small but distinctive coils (Fig. 471) and large, irregularly shaped vesicle.

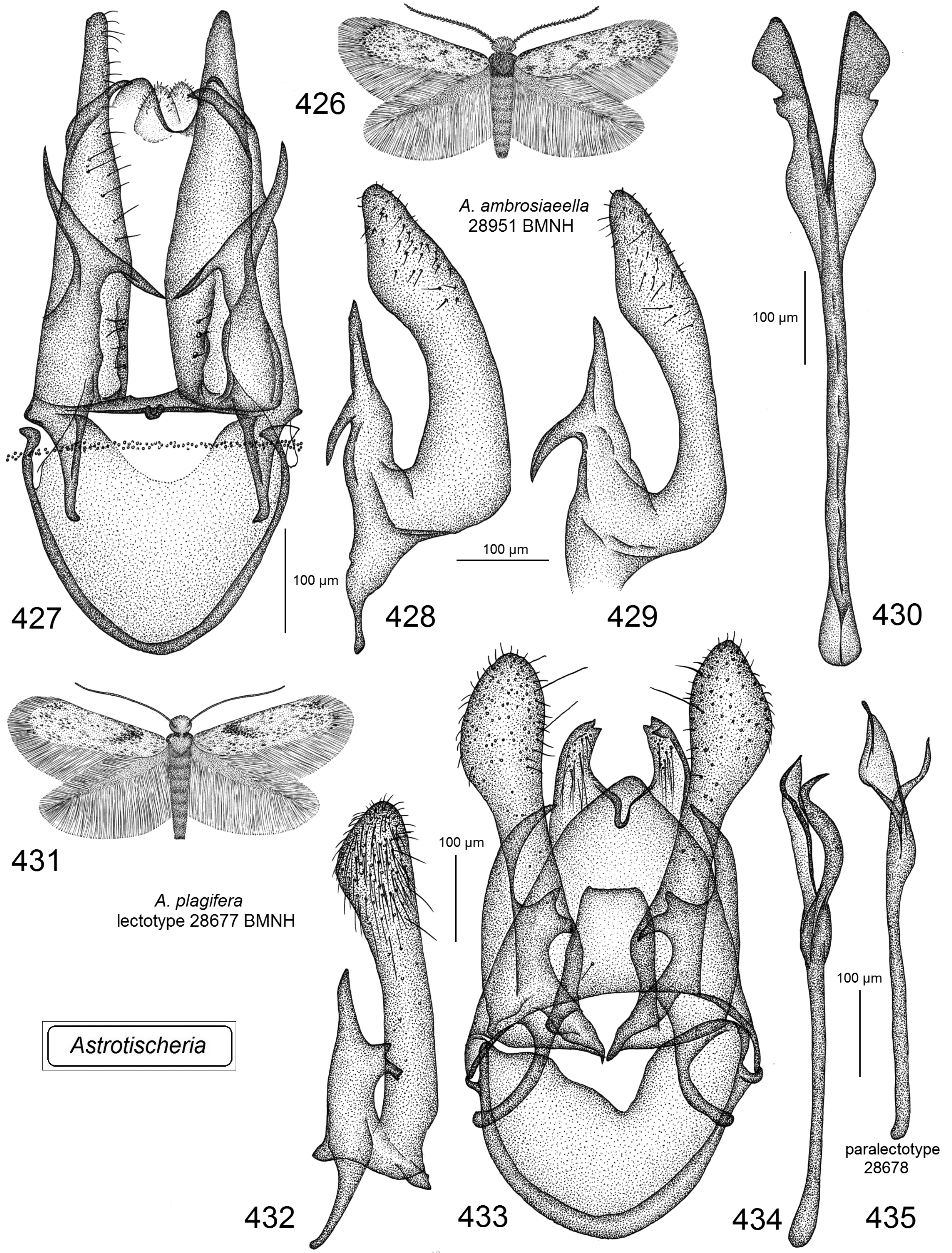
Bionomics (Figs 476–481). Host plant is unknown (unidentified Asteraceae plant) (Fig. 477). Larvae mine leaves in October. The initial part of the leaf mines is linear (gallery-like), almost completely filled with frass; later the leaf mine develops into an irregular blotch-like mine without frass or with very little frass. A nidus is invisible; the larva hides under a stained epidermis. Adults occur in late October—November. Otherwise, biology is unknown.

Distribution. This species is known from a single locality in Peru, Urubamba Province (near Machu Picchu), at an elevation of 2370 m.

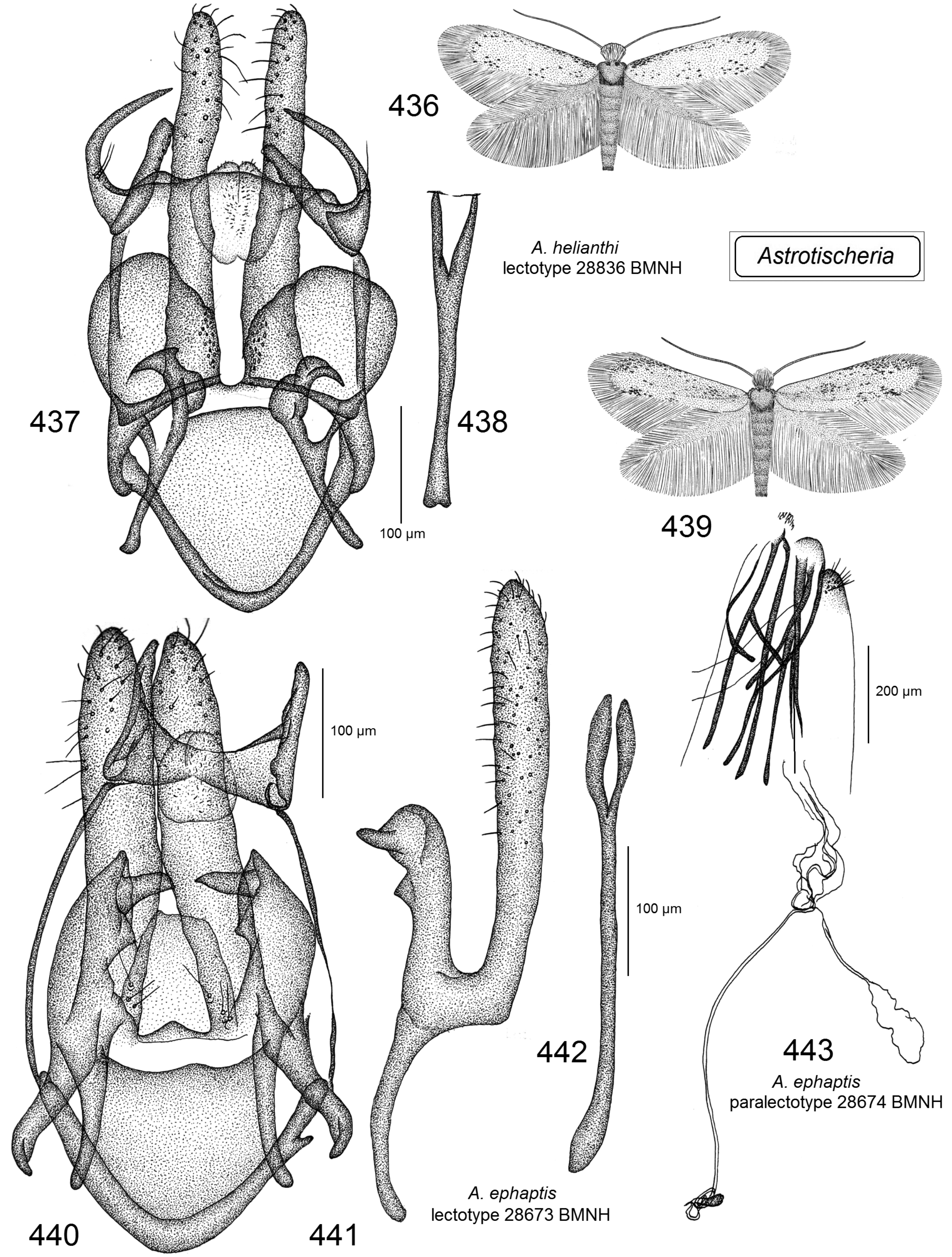
Etymology. This species is named after the Inca, ancient Empire of South America, referring to the locality where the species was collected by us and our Quechua counterpart in a river valley near Machu Picchu.



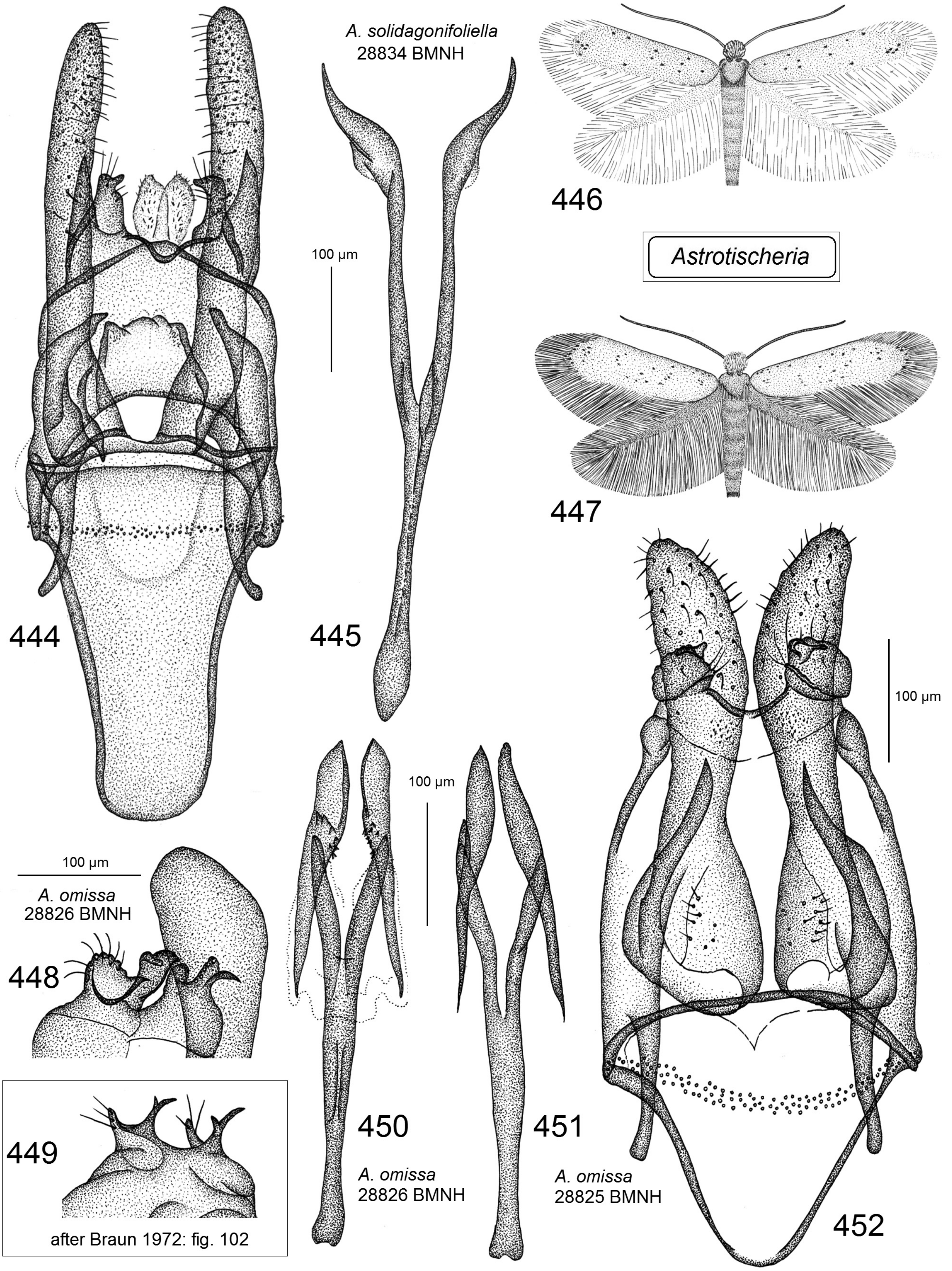
FIGURES 417–425. Male genitalia of *Astrotischeria*. 417, *A. guatemalica* Diškus & Stonis, capsule with phallus removed, holotype; 418, same, paratype; 419, same, phallus, holotype (Stonis *et al.* 2019b); 420, same, *A. truncata* Diškus & Stonis, paratype; 421, lateral view of valva, *A. furcata* Stonis & Diškus; 422, same, different angle of view; 423, same, *A. selvica* Diškus, Carvalho-Filho & Stonis; 424, same, *A. casila* Diškus & Stonis; 425, same, *A. amazonica* Diškus & Stonis (after Stonis *et al.* 2018a)



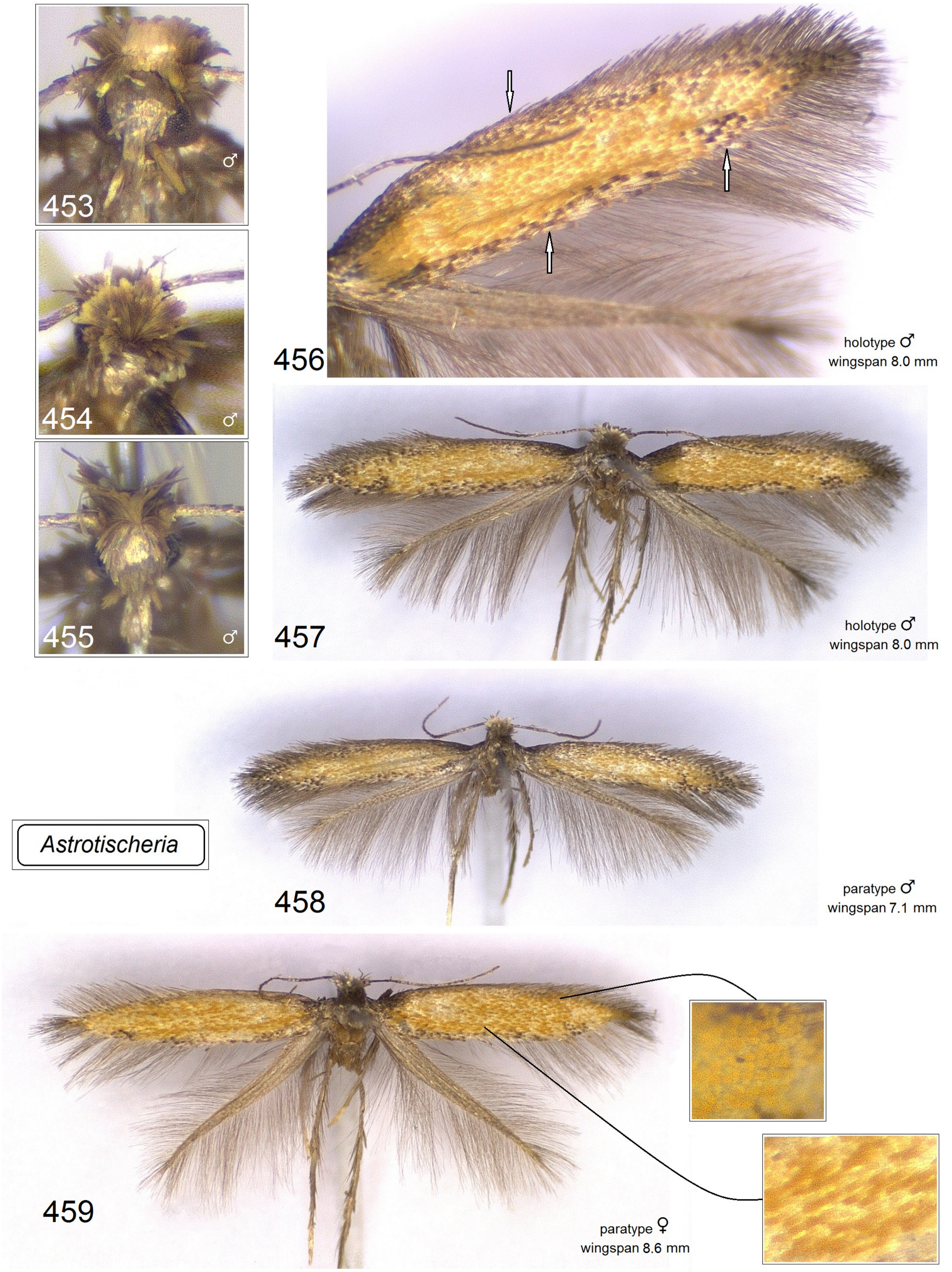
FIGURES 426–435. *Astrotischeria* spp. 426–430, *A. ambrosiaeella* (Chambers), USA, Kirkwood, St. Louis, on *Ambrosia trifida*, 13.ix.1886, Walsingham collection, genitalia slide no. 28951 BMNH (NHMUK); 431–434, **first documentation of lectotype** of *A. plagifera* (Meyrick), Huigra, Ecuador, vi.1914, genitalia slide no. 28677 BMNH (NHMUK); 435, same, paralectotype, genitalia slide no. 28678 BMNH (NHMUK)



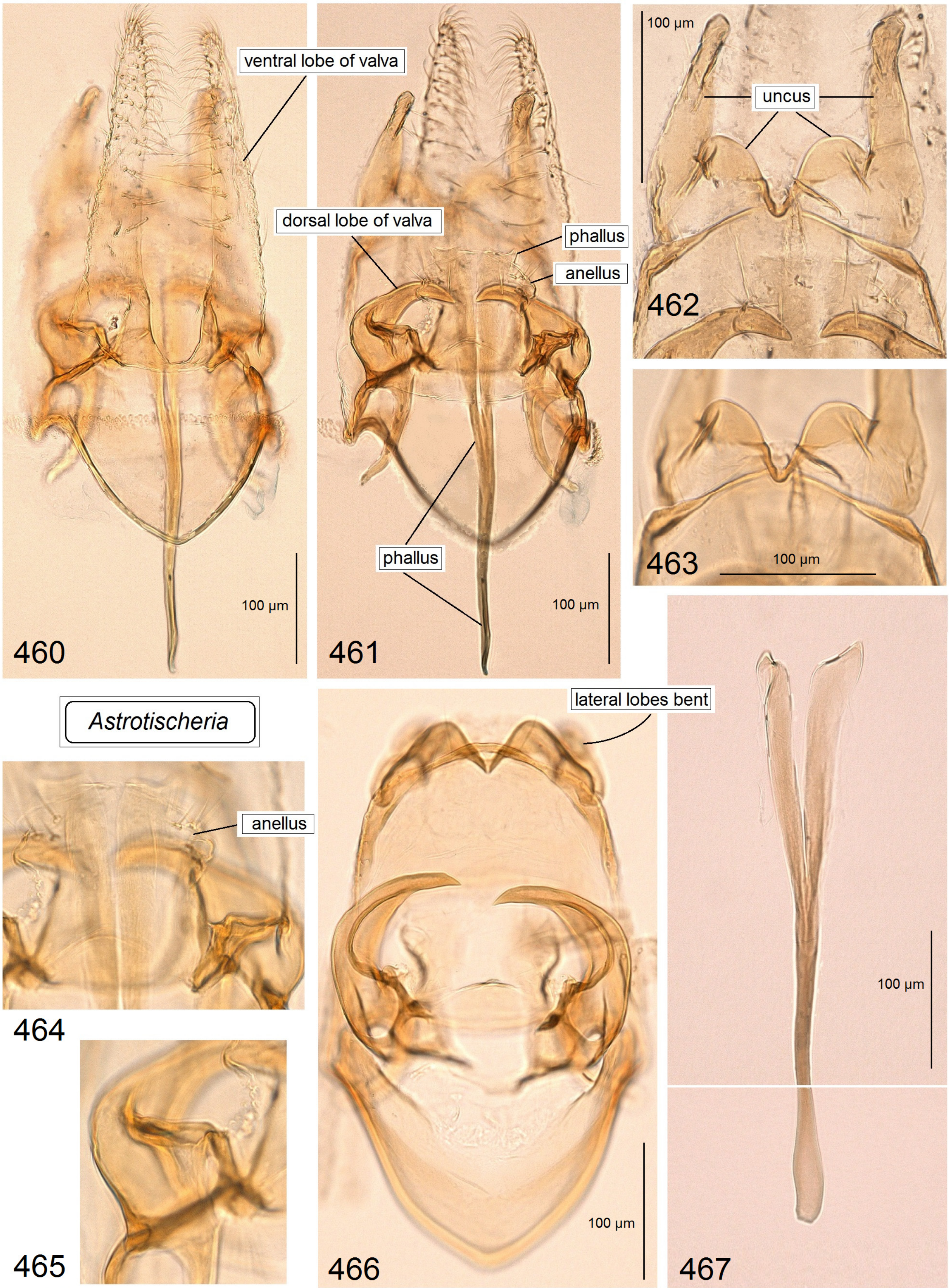
FIGURES 436–443. Documentation of lectotypes of *Astrotischeria* spp. 436–438, **first documentation of lectotype** of *A. helianthi* (Frey & Boll), USA, Dalas, on *Helianthus maximilianus*, Walsingham collection (ex Frey collection), genitalia slide no. 28836 BMNH (NHMUK); 439–442, **first documentation of lectotype** of *A. ephaptis* (Meyrick), Peru, vii.1914, genitalia slide no. 28677 BMNH (NHMUK); 443, same, paralectotype, genitalia slide no. 28674 BMNH (NHMUK)



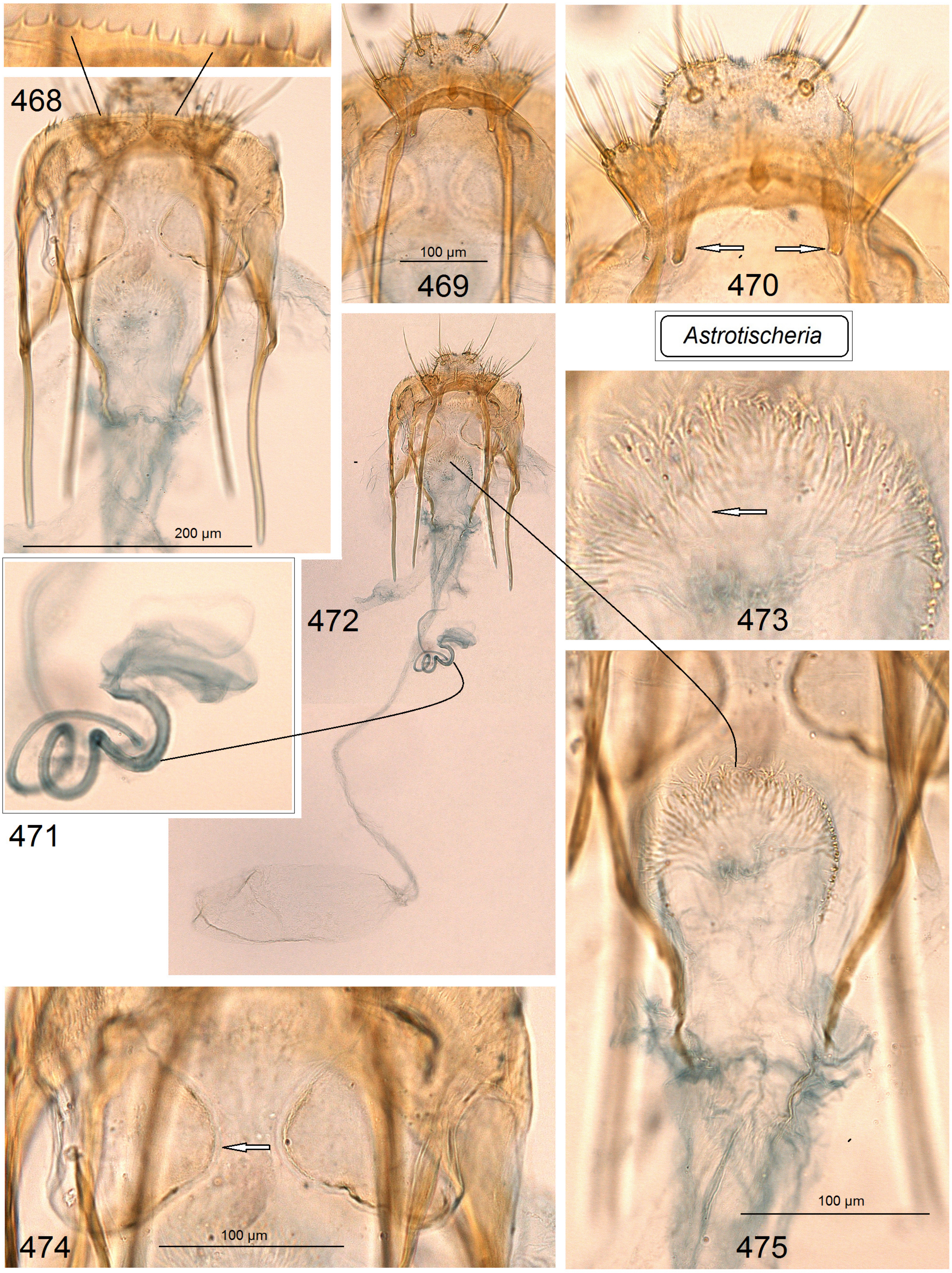
FIGURES 444–452. *Astrotischeria* spp. 444–446, *A. solidagonifoliella* (Clemens), USA, Texas, Walsingham collection ("Boll from Ragonot"), **first documentation of specimen** deposited at NHMUK, slide no. 28834 BMNH (NHMUK); 447, 448, 450, *A. omissa* (Braun), USA, California, Oroville, vii.1933, Meyrick collection, genitalia slide no. 28826 BMNH (NHMUK); 449, same, a fragment from drawing by Braun 1972: fig. 102; 451, 452, *A. omissa* (Braun), USA, California, Oroville, vii.1933, Meyrick collection, **first documentation of specimen** deposited at NHMUK, slide no. 28825 BMNH (NHMUK)



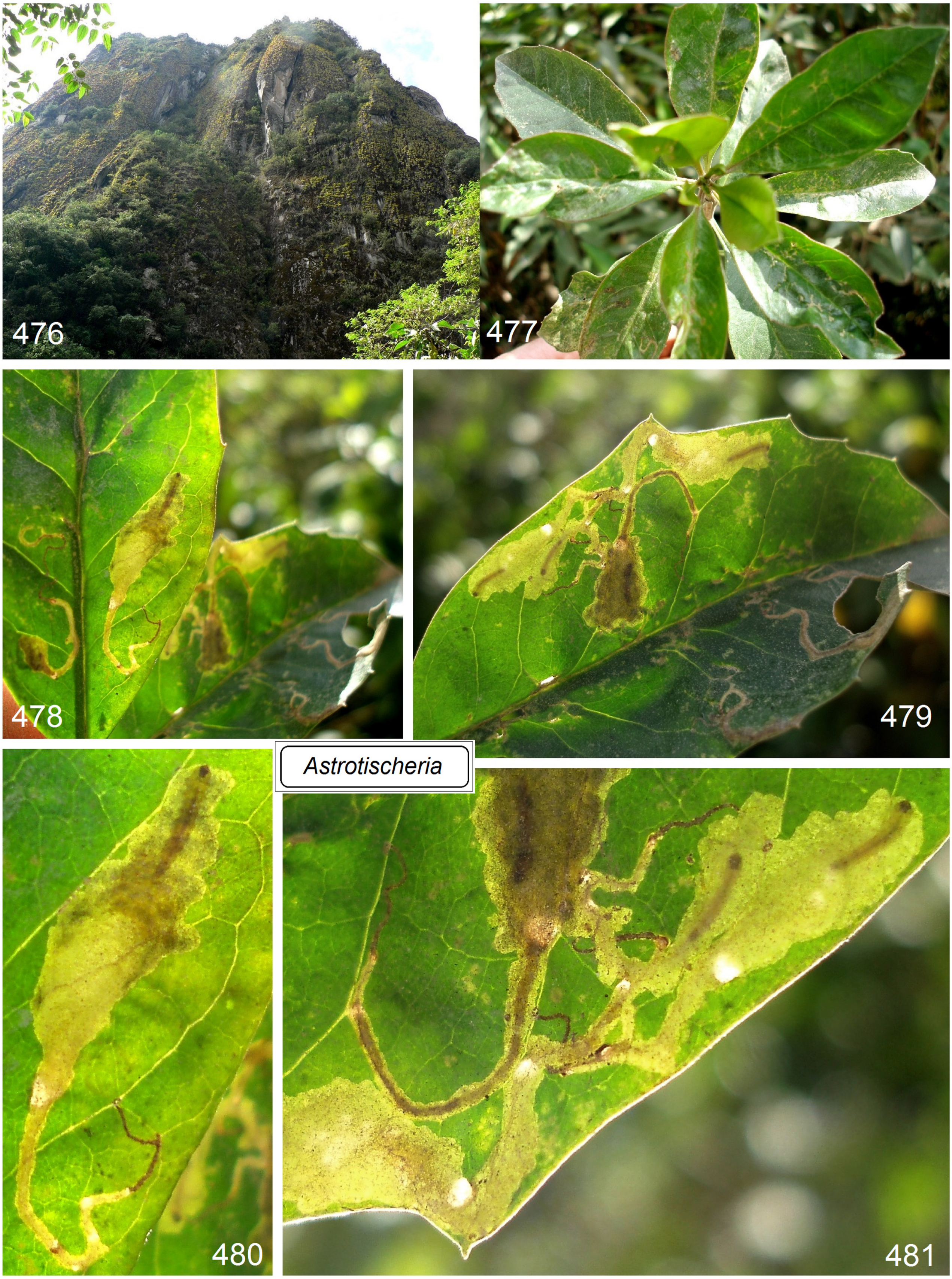
FIGURES 453–459. Adults of *Astrotischeria incae* Diškus & Stonis, **sp. nov.**, Peru. 453, head, male, holotype; 454, 455, same, paratype; 456, holotype, details of forewing pattern; 457, same, general view, with abdomen broken; 458, same, male paratype; 459, same, female paratype (MfN)



FIGURES 460–467. Male genitalia of *Astrotischeria incae* Diškus & Stonis, **sp. nov.** 460, 461, general view of capsule with phallus inside, holotype, genitalia slide no. AD1115 (MfN); 462, 463, same, details of uncus; 464, 465, same, anellus and basal part of dorsal lobe; 466, capsule, with phallus removed, paratype, genitalia slide no. AD1107 (MfN); 467, same, phallus



FIGURES 468–475. Female genitalia of *Astrotischeria incae* Diškus & Stonis, **sp. nov.**, paratype, genitalia slide no. AD1108 (MfN). 468, apophyses; 469, 470, ovipositor and lobes; 471, ductus spermathecae; 472, general view; 473, 475, tiny spines on membrane between inner prela; 474, lobe-like parts of prela



FIGURES 476–481. Bionomics of *Astrotischeria incae* Diškus & Stonis, **sp. nov.** 476, habitat, elevation of 2370 m, near Machu Picchu, Urubamba Province, Peru; 477, unidentified Asteraceae host plant; 478–481 leaf mines

11. Genus *Gnathitischeria* Diškus gen. nov.

urn:lsid:zoobank.org:act:67617B46-AA1E-4BF0-9CB6-2316094988EC

(Figs 482–561)

Type species: *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.** (described below).

Diagnosis. Externally, *Gnatitischeria* species are characterized by a pale (grey cream or ochreous cream) apical spot on the forewing (Figs 485, 489); females of the type species *G. atitlani* **sp. nov.** possess a distally cream antenna (Figs 487, 488). In the male genitalia, species of *Gnathitischeria* are easily recognizable by presence of a unique pseudognathos, a modified uncus, a frame-like thickening of tegumen, and a divided valva with a dorsal lobe (process). In the female genitalia, the genus is characterized by small, but spinose, lateral lobes of the ovipositor and a weakly developed caudal plate of the prela. Leaf mines of *Gnathitischeria* are irregular blotch-like or elongated with a triangular initial part, on Asteraceae and Malvaceae host plants; a nidus is indistinctive. See Tabs 2, 3 for occurrence of these diagnostic characters in other genera of Tischeriidae.

Notes. In our molecular trees, *Gnathitischeria* appeared as a separate clade at the generic rank. It clusters either with (*Astrotischeria* + *Paratischeria*) (Fig. 62), or only with *Astrotischeria* (Figs 63, 64).

Adult. Head: frontal tuft overlapping the frons, comprised of long relatively wide lamellar scales; pecten relatively short and slender; collar indistinctly paired or coalescent, comprised of relatively slender lamellar scales. Female of *G. atitlani* with distinctly cream antenna distally. Male forewing with elongated but irregular spots; female forewing with significantly brighter, ochre-yellow elongated spots; forewing apex with a fringe line and pale spot (grey cream in male and female of *G. arcana*, and ochre cream in female of *G. atitlani*). Hindwing slender, androconia absent.

Male genitalia. Uncus modified, comprised of two wide lobes with variously developed lateral thickenings. Socii membranous, unusually large, almost unpaired and indistinctly spinose. Tegumen greatly modified: moderately short however, unlike other Tischeriidae (excluding *Manitischeria*), tegumen with a frame-like thickening and well-developed, large pseudognathos; diaphragm without spines. Valva divided, with ventral and dorsal lobes; basal process of the valva long. Transtilla and juxta absent. Anellus membranous, thickened only caudally or absent. Vinculum long, ventral plate widely rounded distally. Phallus slender, rod-like, apically with wide lateral lobes, without spines.

Female genitalia. Ovipositor lobes large to medium large; the gap between ovipositor lobes large to very large; second pair of ovipositor lobes usually two times smaller in comparison to main ovipositor lobes; lateral lobes small and with tiny spines. Anterior apophyses either slightly longer or shorter than posterior apophyses. Prela with three pairs of long or very long rod-like projections; transverse prela unusually wide but indistictive proximally; membrane between inner prela is not thickened. Caudal sclerite weakly developed, indistinctive. Antrum absent. Accessory sac absent or small; ductus spermathecae slender, with 4–5 coils; vesicle relatively large, irregularly shaped. Corpus bursae long, gradually narrowing caudally; pectinations only proximally or absent.

Bionomics. The genus is trophically associated with Asteraceae and Malvaceae host plants. Leaf mines of *Gnathitischeria* are either irregular blotch-like or irregular elongated with a triangular initial part, without frass; a nidus is indistinctive, a disturbed larva hides under a large vein of the leaf.

Species diversity and geographical distribution. Currently, the genus is comprised of only two species, both known from Central America (Guatemala).

Etymology. The genus name is combined from the ancient Greek *gnathos* (in this case, a structure of the male genitalia) and *Tischeria* (a name of the type genus of Tischeriidae) referring to the presence of the unique pseudognathos in the male genitalia.

Gnathitischeria atitlani **Diškus & Stonis, sp. nov.**

urn:lsid:zoobank.org:act:9560FC51-EB06-4141-909F-40B3BBA5FE2D
(Figs 486–534)

Type material. Holotype: ♂, GUATEMALA: Sololá Department, San Marcos La Laguna, 14°43'19"N, 91°15'30"W, elevation 1580 m, mining larva on *Hibiscus* sp. (Malvaceae), 21.ii.2012, field card no. 5104, leg. A. Diškus, genitalia slide no. AD1095 (MfN). Paratypes: 17 ♂, 23 ♀, same label data as holotype, genitalia slide nos AD845♂, AD1071♂, AD1097♂, AD1113♂, AD846♀, AD1039♀ (MfN).

Diagnosis. Externally, this new species can be confused with *Gnathitischeria arcana* Diškus & Stonis, **sp. nov.** (described below), but the later is smaller and with less distinctive pale patches of the forewing; also female antenna of *G. atitlani* **sp. nov**. is cream distally. In the male genitalia, the unique shape of pseudognathos (see Figs 505, 514) and long, slender dorsal lobes (processes) of the valva instantly distinguish *G. atitlani* from the congeneric *G. arcana*. In the female genitalia, *G. atitlani* is characterized by small ovipositor lobes, very long apophyses, and unique prela (Figs 520, 523). This species is also distinctive because no other species of Tischeriidae is known to feed on *Hibiscus* L. Malvaceae.

DNA barcode. We barcoded two specimens of the type series, but not the holotype; the sequences are available in the GenBank database under the accession numbers OQ413554 and OQ413555.

Description. *Male* (Figs 490, 492, 493). Forewing length 3.3–4.0 mm; wingspan 7.3–8.5 mm (n = 16). Head: palpi and frons pale ochre-yellow to ochre cream; pecten and frontal tuft glossy grey; collar yellow-ochre; antenna distinctly longer than one half the length of forewing; flagellum dark grey or brown-grey, pale ochre at base. Tegula glossy dark grey; thorax and forewing glossy grey-brown to black-brown (sometimes with some purple iridescence), and with distinctive ochre-yellow spots; fringe dark grey, without fringe line; forewing underside dark grey-brown, without androconia or spots, except for a small scaleless basal spot. Hindwing dark grey-brown on upper side and underside, without androconia; fringe dark grey. Legs glossy grey to dark grey-brown. Abdomen dark grey-brown with some golden gloss on upper side, glossy pale grey to dark grey-brown, occasionally with some purple iridescence on underside; genital plates grey cream to grey; anal tufts indistinctive, small.

Female (Figs 486–489, 491). Forewing length 3.3–4.0 mm; wingspan 7.2–8.5 mm (n = 22). Similar to male, but antenna cream distally; thorax and abdomen underside with many ochre-yellow scales; forewing apex with an ochre cream spot (Fig. 489); fringe line present though indistinctive. Otherwise, identical with male.

Male genitalia (Figs 494–518) with capsule 470–500 µm long, 250–260 µm wide. Uncus comprised of two medium long, wide, almot triangular, stongly laterally thickened lobes (Fig. 506). Tegumen relatively short, with a larger, bolobed pseudognathos (see Remarks). Socii medium large, weakly paired, membranous. Valva ca. 320 µm long; dorsal lobe wide; ventral lobe of valva process-like. Anellus absent. Vinculum triangular, rounded distally. Phallus ca. 300–350 µm long, in apical half with two wide and long lobes (Fig. 516).

Female genitalia (Figs 519–523) ca. 1135 µm long. Ovipositor lobes small, rounded, sparsely covered with peg-like setae; second pair of ovipositor lobes twice smaller; lateral lobes short but wide, spinose. Anterior and posterior apophyses very long; posterior apophyses slightly shorter than anterior apophyses; prela comprised of three pairs of unique, rod-like projections: processes of median and inner prella very long, transverse prela weakly chitinized (Fig. 523). Corpus bursae very short and slender. Ductus spermathecae sinuous, with about five indistinctive coils (one large and four small) and irregularly-shaped, relatively large vesicle.

Bionomics (Figs 524–534). Host plant is *Hibiscus* sp. (Malvaceae) (Figs 524, 525). Larvae mine leaves in February. The blotch-like mine is irregular, but often starts as trumpet-like, without frass. Adults occur in March.

Distribution. This species is known from a single locality in Guatemala, Sololá Department, San Marcos La Laguna, at the elevation of 1580 m.

Etymology. The species is named after the lake Atitlán (*Lago de Atitlán*, Guatemala), in reference to its occurrence in the area around that lake.

Remarks. We found significant difference in shape of pseudognathos: paratype AD845 (Fig. 513) differs from the holotype (Fig. 510) and other paratypes (Fig. 505) in slender-looking lobes. However, no other morphological differences in the genitalia and external adult morphology were found. Therefore, we finally concluded that the difference in the shape of the pseuduncus (the slender-looking lobes in paratype AD845, Fig. 513) was caused by the position of these lobes in our slide mount.

Gnathitischeria arcana Diškus & Stonis, sp. nov.

urn:lsid:zoobank.org:act:DD981BA1-B22E-4C7D-BF34-8A9D4ABDB51C
(Figs 482–485, 535–561)

Type material. Holotype: ♂, GUATEMALA: Petén Department, Tikal, 17°13'22"N, 89°37'24"W, elevation 315 m, mining larva on *Acmella repens* (Walter) Pers. (Asteraceae), 6.ii.2012, field card no. 5074, leg. A. Diškus, genitalia slide no. AD1099 (MfN). Paratypes: 1 ♂, 1 ♀, same label data as holotype (MfN); 5 ♂, 3 ♀, Petén Department, El Remate, Biotopo Cerro Cahuí, 16°59'51"N, 89°42'13"W, elevation 120 m, mining larva on *Acmella repens* (Walter) Pers. (Asteraceae), 7.ii.2012, field card no. 5075, leg. A. Diškus, genitalia slide nos AD847♂, AD1072♂, AD936♀ (MfN).

Diagnosis. Externally, this new species can be confused with *G. atitlani* **sp. nov**. (described above), but the latter is larger and with much more distinctive pale patches on the forewing. In the male genitalia, the unique shape of a modified uncus (Fig. 536), a pseudognathos (Fig. 537) and large, greatly elaborated dorsal lobes of the valva (Fig. 542) instantly distinguish *G. arcana* from the congeneric *G. atitlani*. In the female genitalia, *G. aracana* differs from *G. atitlani* by larger ovipositor lobes, slightly shorter apophyses and a longer corpus bursae. This new species is also distinctive because it feeds on *Acmella repens*, Asteraceae.

DNA barcode. We barcoded two specimens of the type series, but not the holotype; the sequences are available in the GenBank database under the accession numbers OQ413552 and OQ413553.

Description. *Male* (Figs 483–485). Forewing length 2.5–2.8. mm; wingspan 5.6–6.3 mm (n = 5). Head: palpi and frons cream; colour of frontal and collar unknown (rubbed); antenna slightly longer than one half the length of forewing; flagellum grey to grey cream. Tegula grey; thorax ochre-yellow; forewing brown-grey, with irregular ochre-yellow spots; fringe grey, grey cream apically, without fringe line; forewing underside dark grey-brown, without androconia or spots, except for a small scaleless basal spot. Hindwing dark grey-brown on upper side and underside, without androconia; fringe grey. Legs glossy cream, covered with dark grey scales on upper side. Abdomen grey-brown on upper side, grey-brown with ochre-yellow scales on underside; genital plates pale ochre; anal tufts moderately long, dark grey or brown-grey.

Female (Fig. 482). Forewing length 2.5–2.9 mm; wingspan 5.6–6.4 mm (n = 2). Similar to male but pale marking of the forewing is brighter and larger.

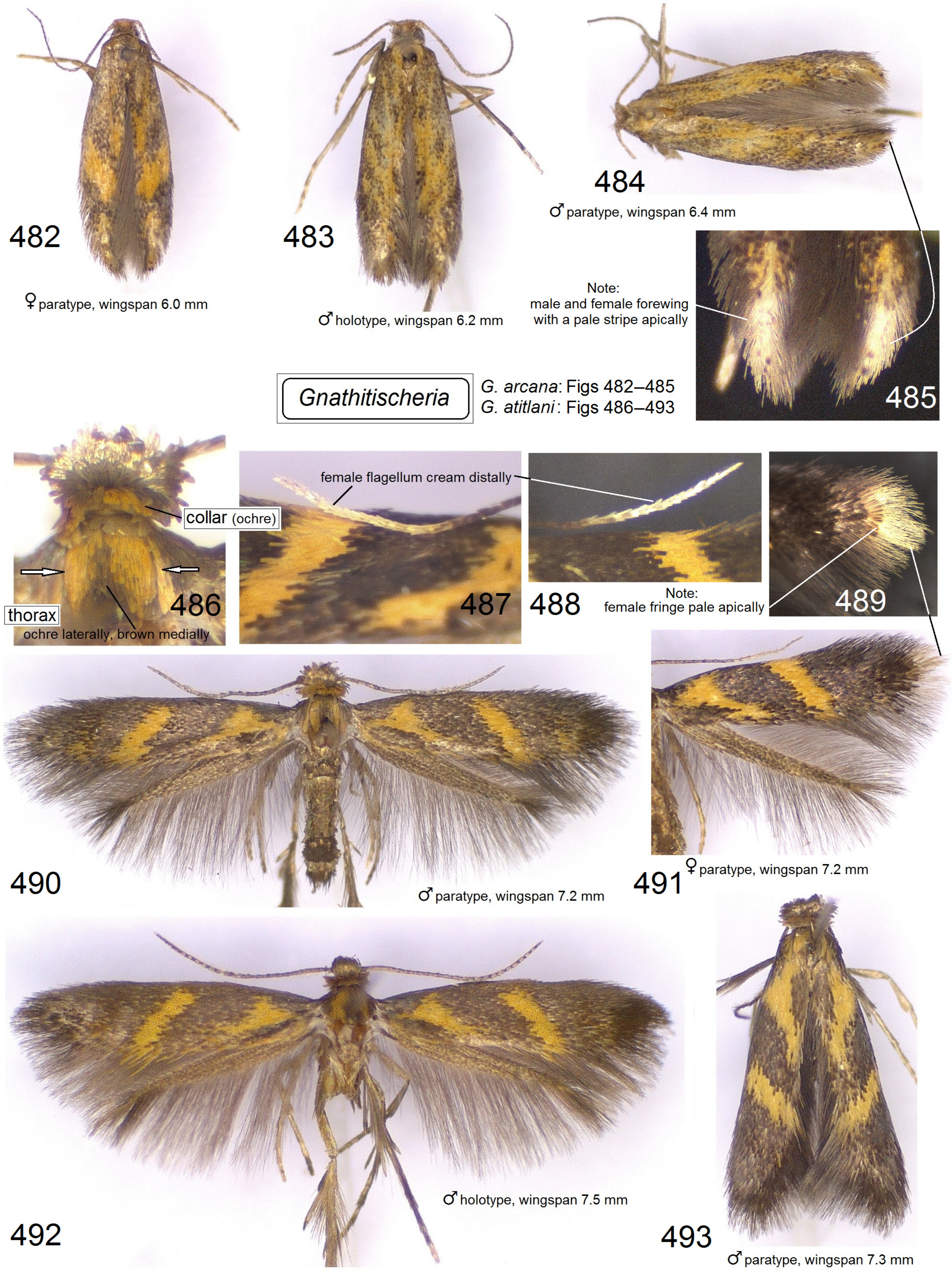
Male genitalia (Figs 535–549) with capsule 385–400 μm long, 245–285 μm wide. Uncus comprised of two medium long, wide, modified, strongly medially and distally thickened lobes (Fig. 536). Tegumen relatively short, with a large pseudognathos possessing two large, pointed lateral lobes. Socii medium large, weakly paired, membranous. Valva ca. 360–370 μm long; dorsal lobe slender and long; ventral lobe of valva greatly elaboarated, large, thickened, with sinous inner margin. Anellus present, thickened caudally (Fig. 539). Vinculum almost triangular but widely rounded distally. Phallus ca. 210 μm long, bifid apically, with wide but very weakly chitinized lateral lobes (Fig. 541).

Female genitalia (Figs 550–554) ca. 1350 μm long. Ovipositor lobes relatively large, rounded, sparsely covered with peg-like setae; second pair of ovipositor lobes almost three times smaller; lateral lobes short, indistinctive, possibly spinose. Posterior apophyses only slightly longer than anterior apophyses; prela comprised of three pairs of rod-like projections; median and inner processes almost equal in length; transverse prela weakly chitinized. Corpus bursae moderately long, very slender proximall third, round distally. Ductus spermathecae sinuous, with about four medium large and large coils and irregularly-shaped, indistinctive vesicle.

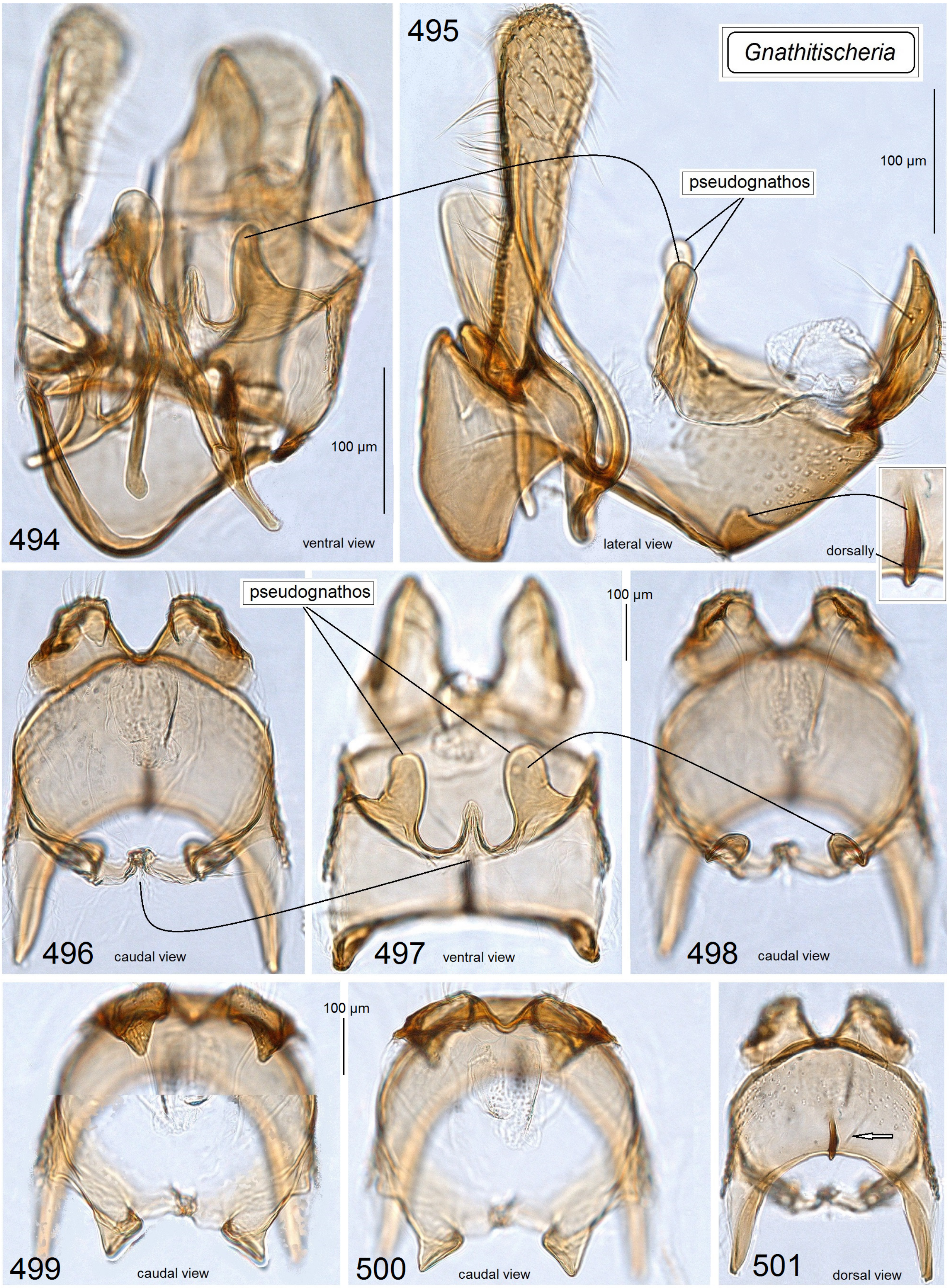
Bionomics (Figs 555–561). Host plant is *Acmella repens* (Walter) Pers. (Asteraceae) (Fig. 555). Larvae mine leaves in February. The blotch-like mine is irregular, without frass. Adults occur in March.

Distribution. This species is known from two lowland tropical forest localities in the Petén Department of Guatemala: Tikal at an elevation of 315 m and El Remate at an elevation of 120 m.

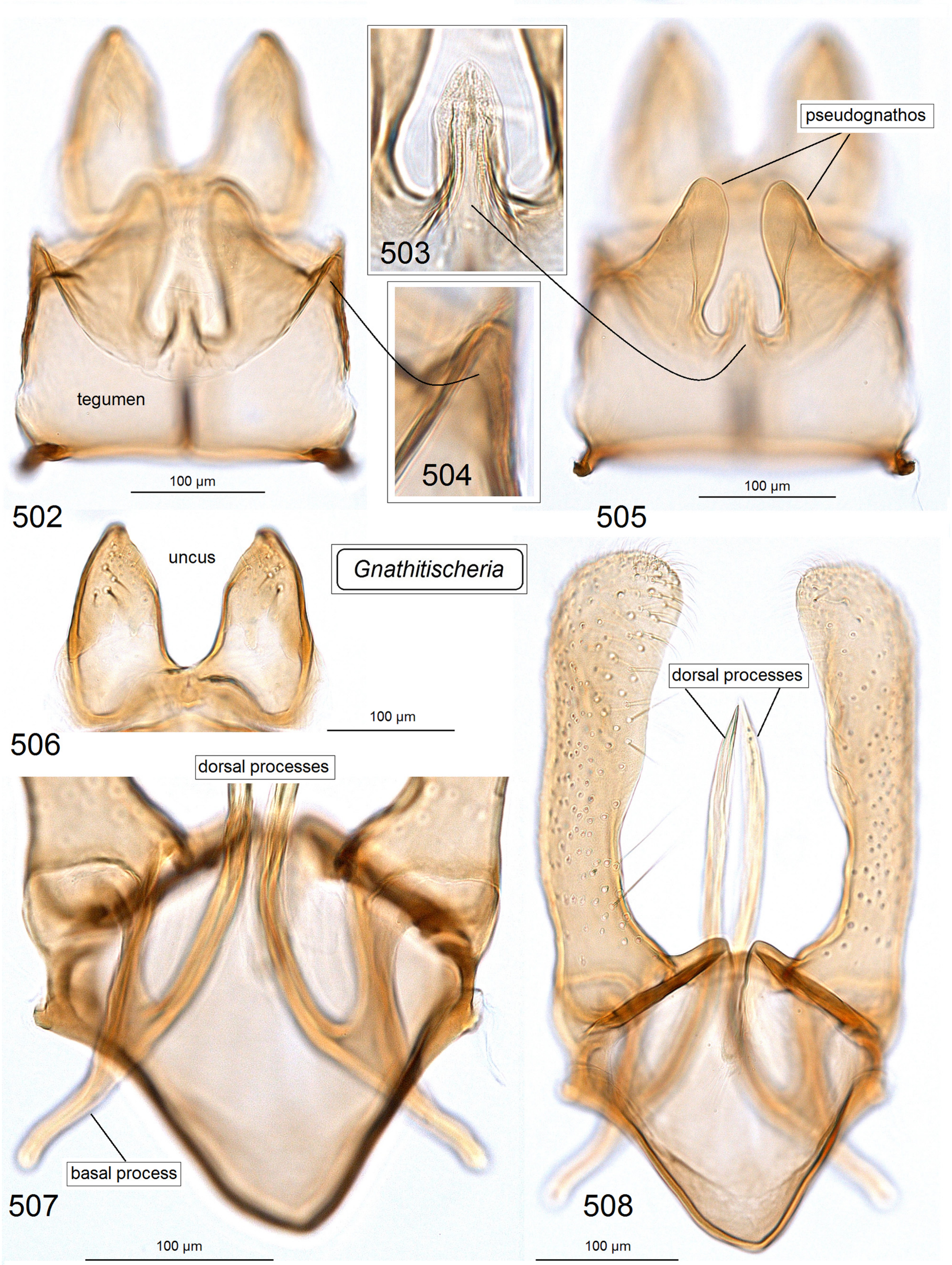
Etymology. The species name is derived from Latin *arcanus* (mysterious), in reference to the unusual shape of dorsal lobe of the valva in the male genitalia.



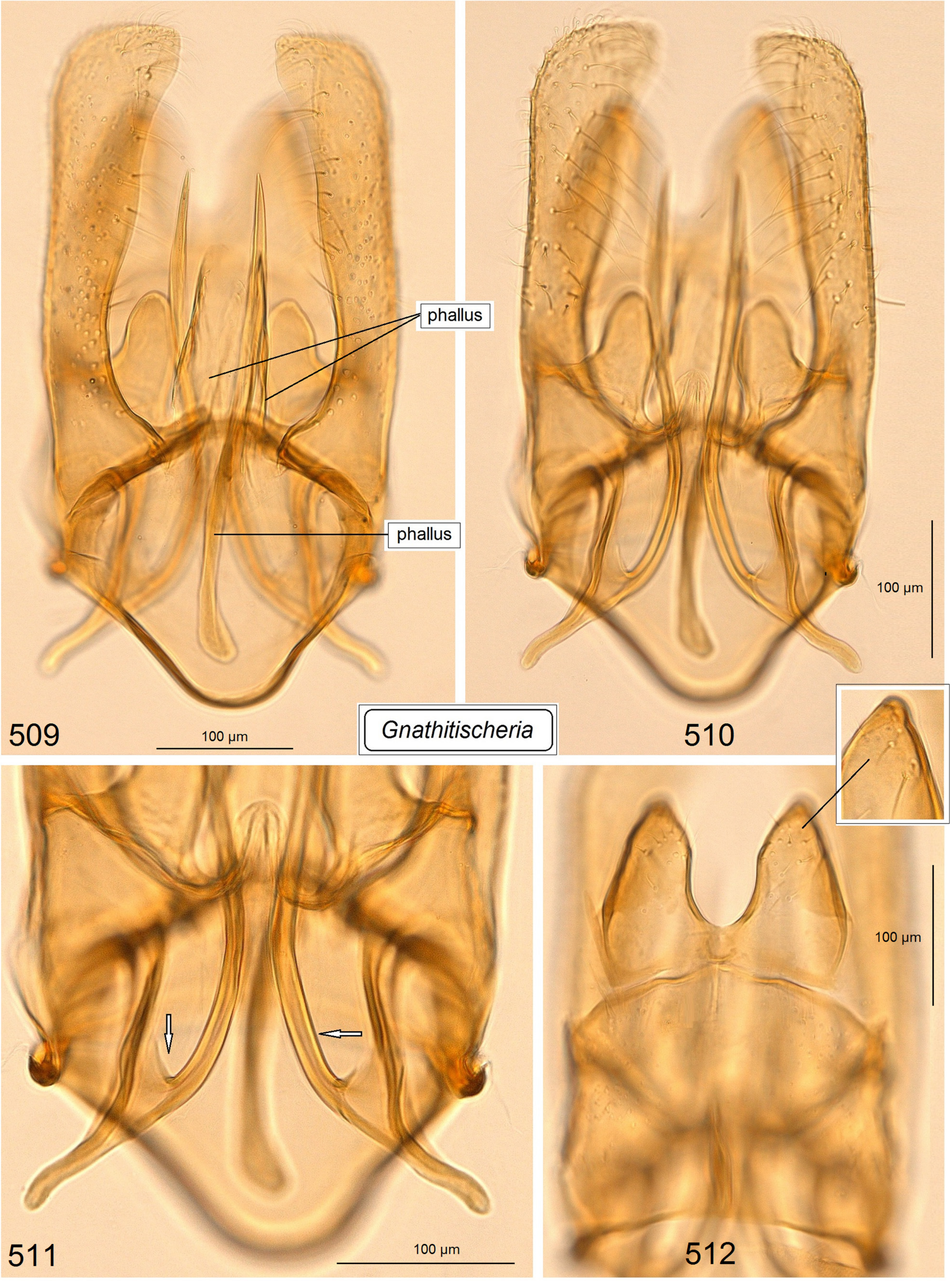
FIGURES 482–493. Adults of *Gnathitischeria* spp., Guatemala, Central America. 482–485, *G. arcana* Diškus & Stonis, **sp. nov.** (MfN); 486–493, *G. atitlani* Diškus & Stonis, **sp. nov.** (MfN)



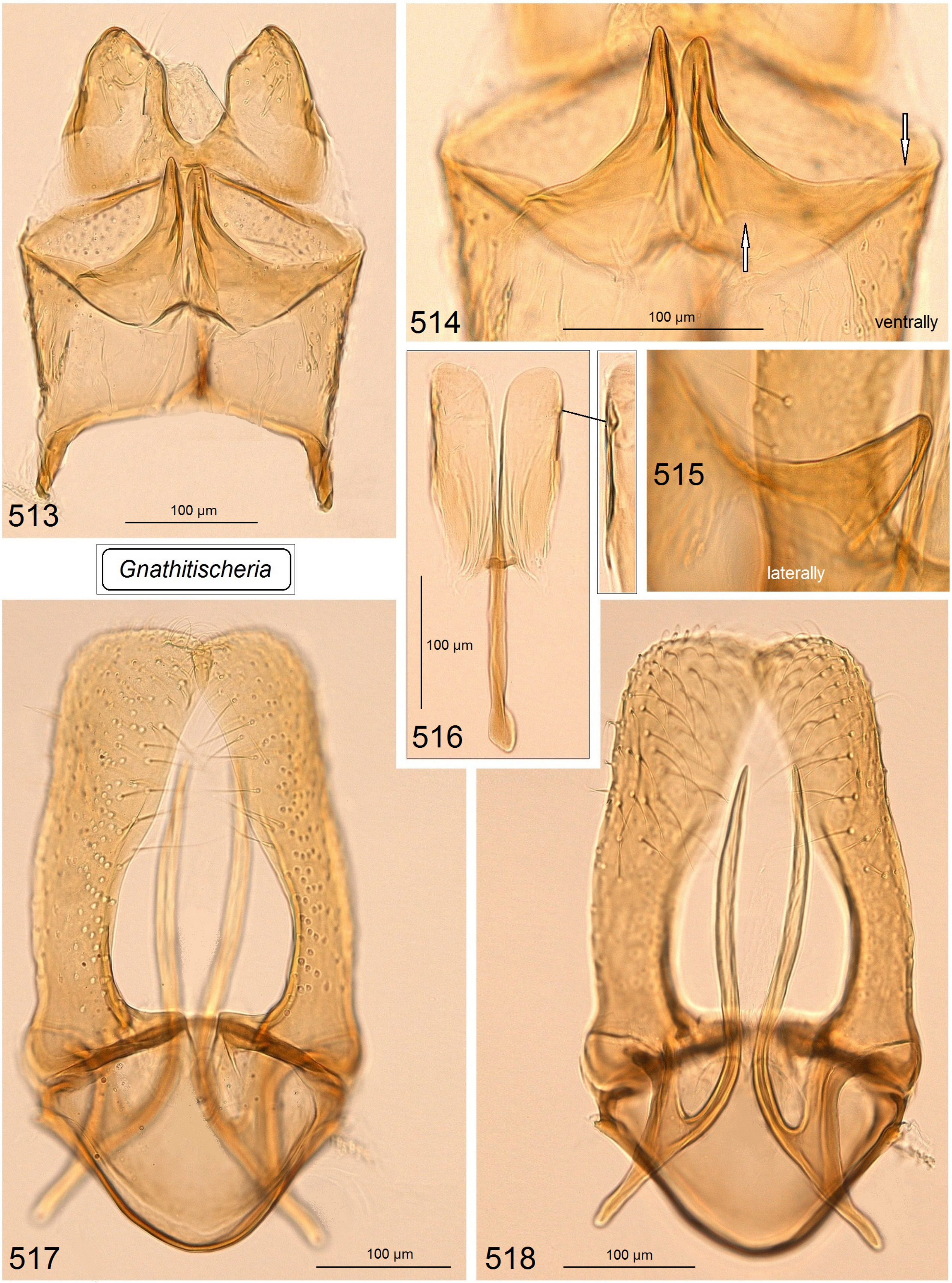
FIGURES 494–501. Male genitalia of *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.**, paratype, genitalia slide AD1097 (MfN). 494, 495, ventral and lateral view of capsule with phallus inside; 496–501, uncus, tegumen and pseudognathos at different angle of view



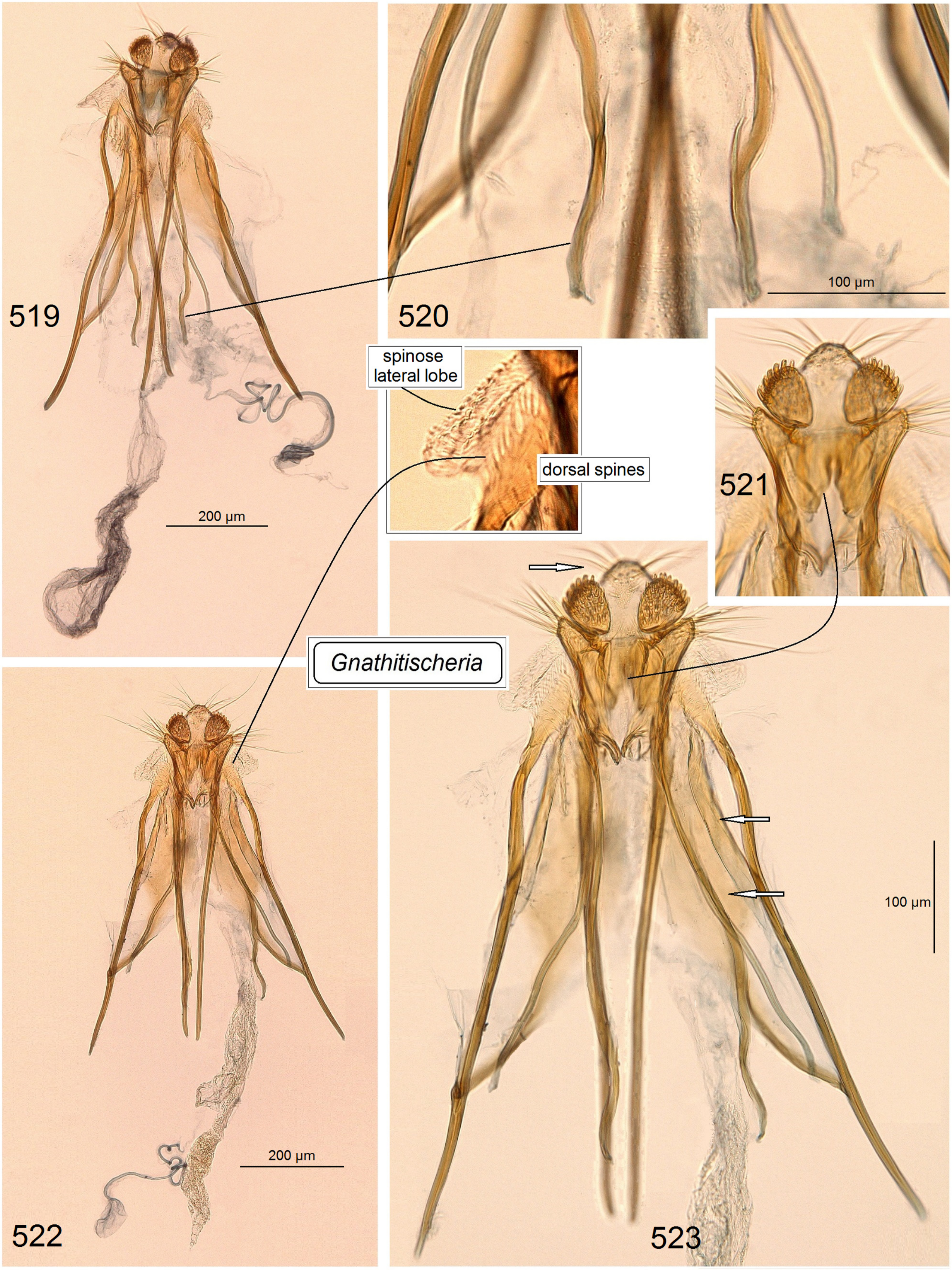
FIGURES 502–508. Details of male genitalia capsule of *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.**, paratype, genitalia slide AD1113 (MfN). 502–506, uncus, tegumen and pseudognathos; 507, 508, vinculum and valvae with dorsal processes



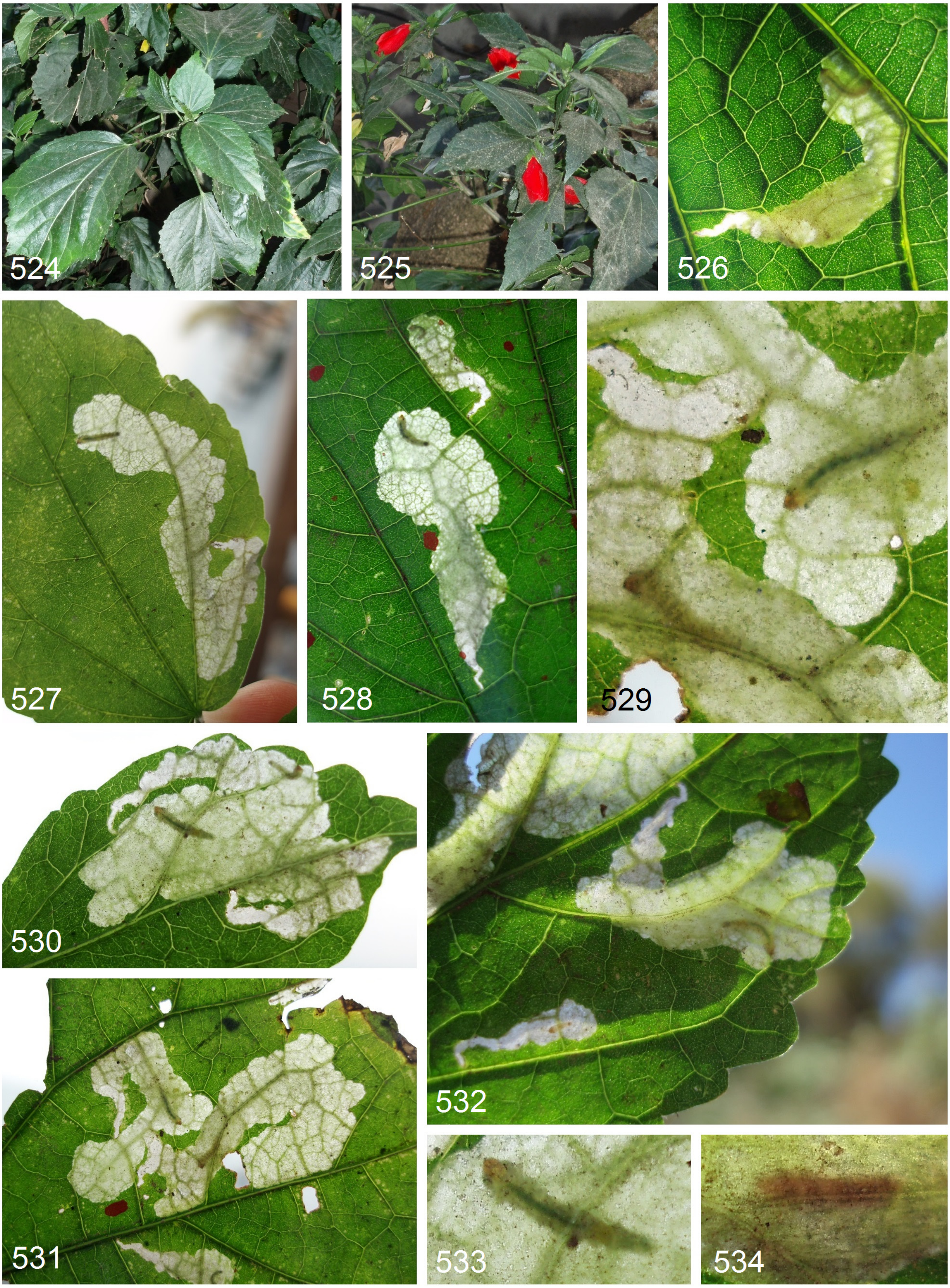
FIGURES 509–512. Male genitalia of *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.**, holotype, genitalia slide AD1071 (MfN)



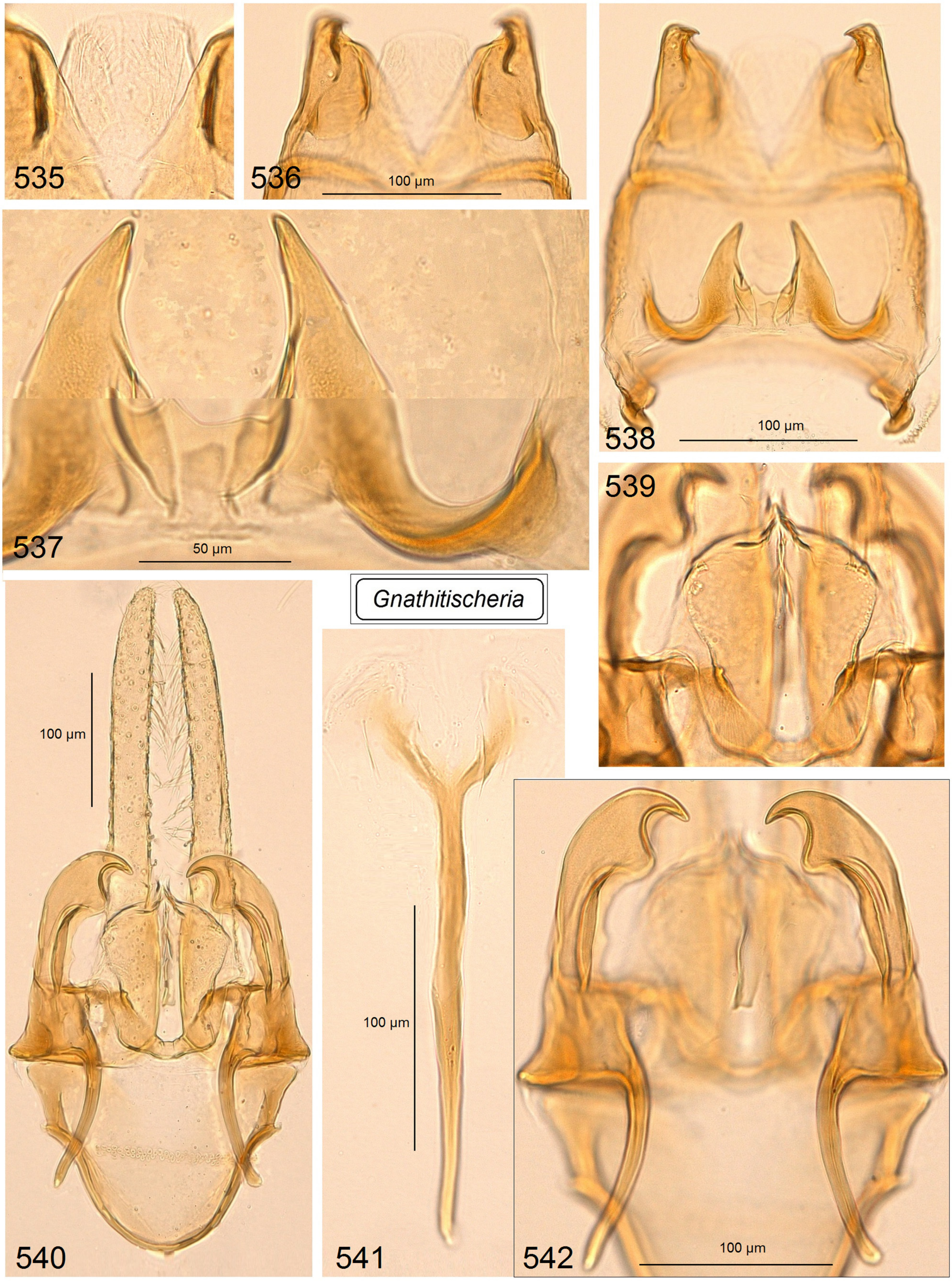
FIGURES 513–518. Details of male genitalia capsule of *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.** 513, 514, 516–518, paratype, genitalia slide AD845; 515, paratype, genitalia slide no. AD1071 (MfN)



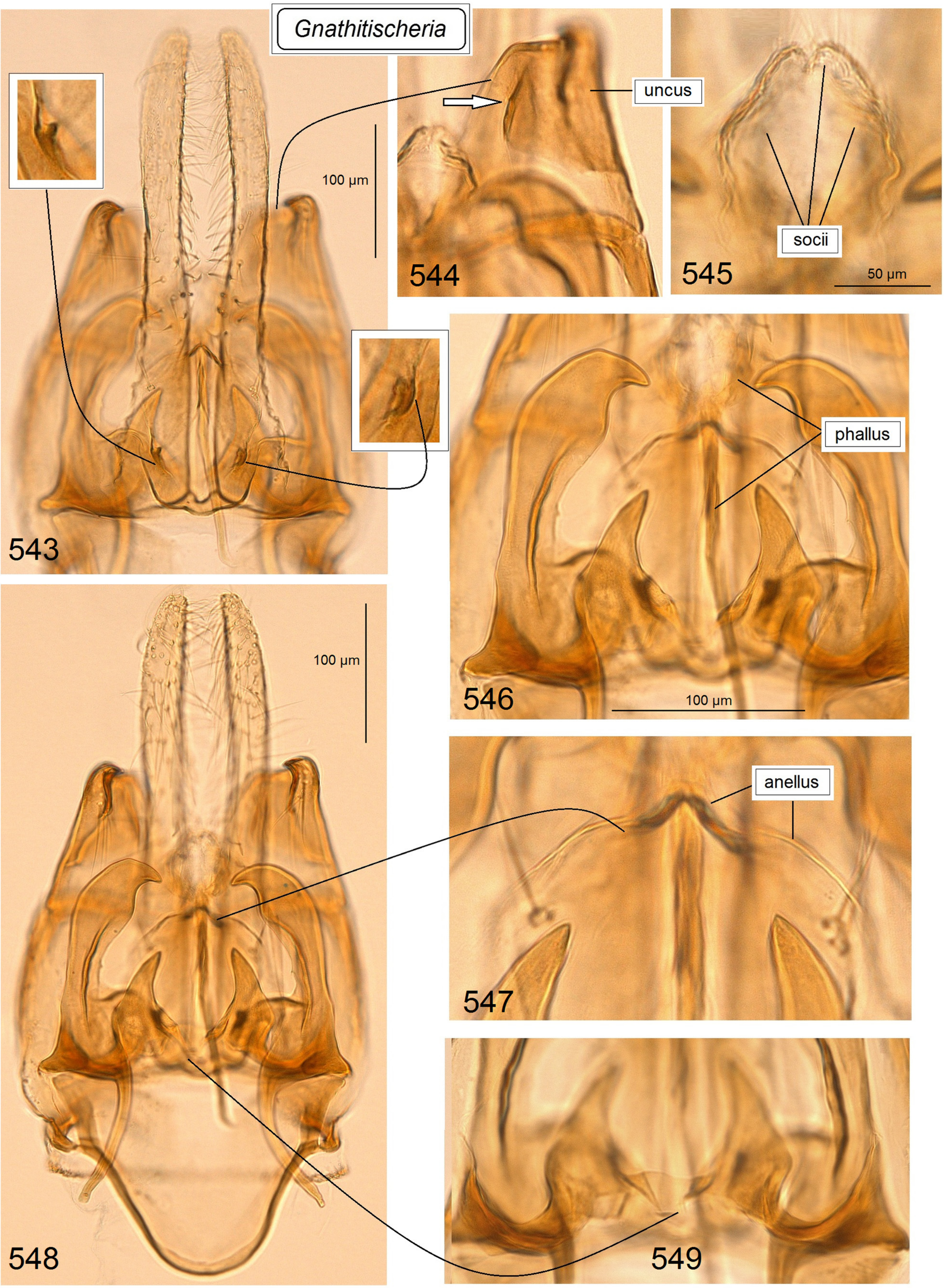
FIGURES 519–523. Female genitalia of *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.** 519, 520, paratype, genitalia slide no. AD846 (MfN); 521–523, another paratype, genitalia slide no. AD1039 (MfN)



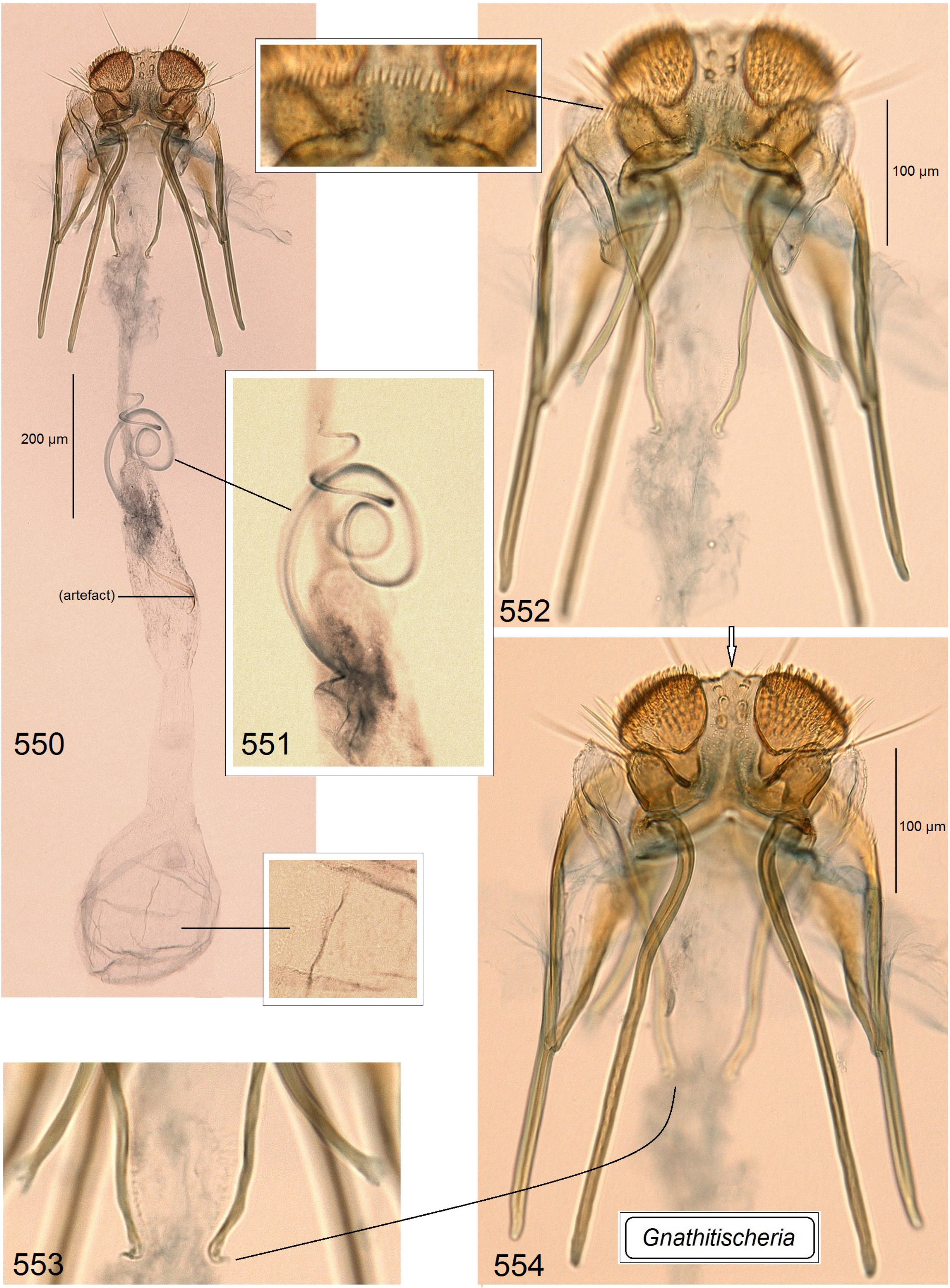
FIGURES 524–534. Bionomics of *Gnathitischeria atitlani* Diškus & Stonis, **sp. nov.**, Guatemala: Sololá Department, San Marcos La Laguna. 524, 525, host plant, *Hibiscus* sp., Malvaceae; 526–532, leaf mines; 533, feeding larva; 534, shadow of pupa visible under epidermis



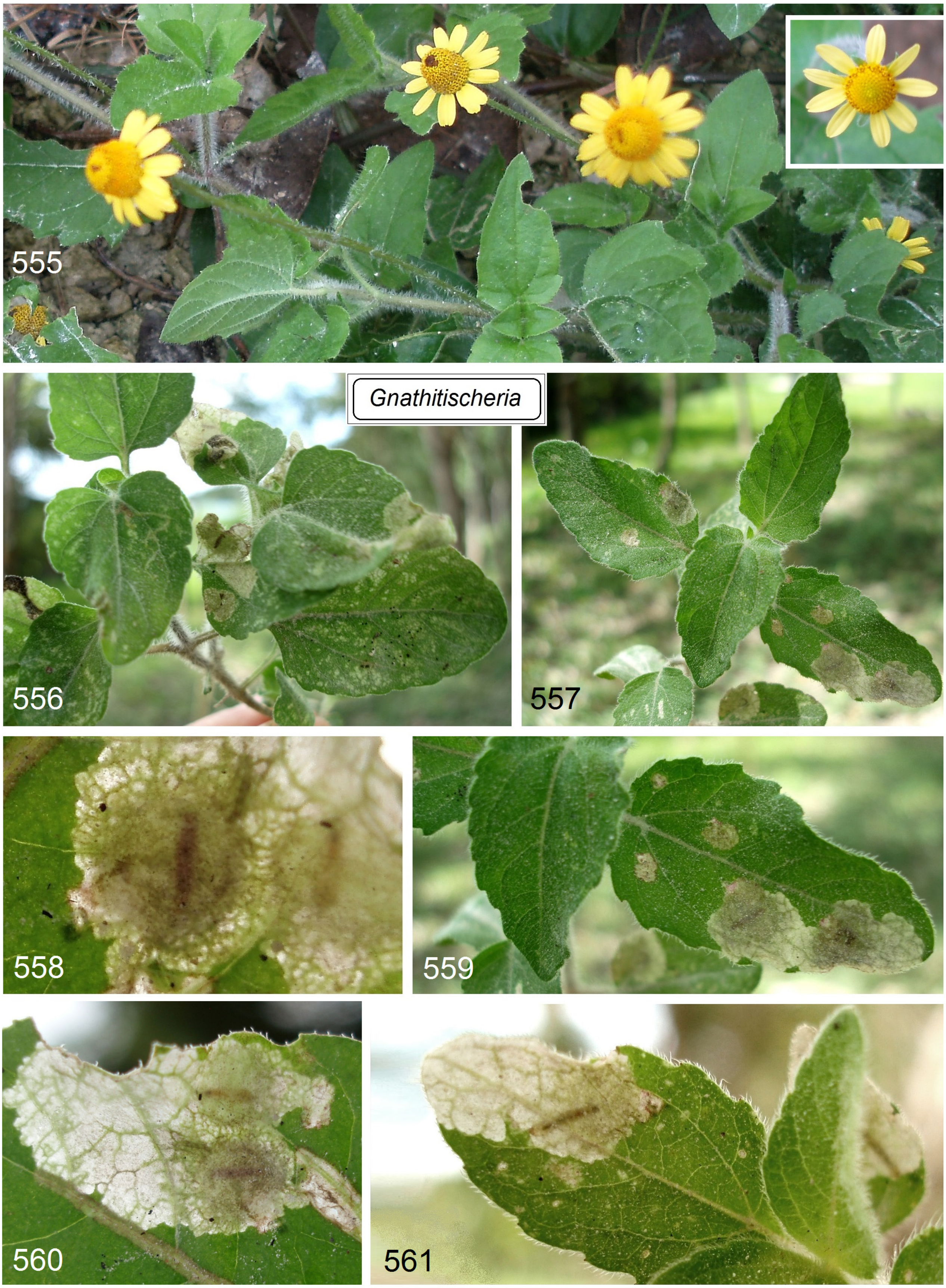
FIGURES 535–542. Male genitalia of *Gnathitischeria arcana* Diškus & Stonis, **sp. nov.**, paratype, genitalia slide AD847 (MfN). 535, membranous socii; 536, uncus; 537, 538, pseudognathos; 539, anellus; 540, general view of capsule with phallus removed; 541, phallus; 542, dorsal lobes (processes) of valva



FIGURES 543–549. Male genitalia of *Gnathitischeria arcana* Diškus & Stonis, **sp. nov.**, holotype, genitalia slide AD1099 (MfN). 543, ventral lobes of valva; 544, details of lateral lobe of uncus; 545, socii; 546, phallus and pseudognathos; 547, caudal part of anellus; 548, general view of capsule with phallus inside; 549, basal part of pseudognathos



FIGURES 550–554. Female genitalia of *Gnathitischeria arcana* Diškus & Stonis, **sp. nov.**, paratype, genitalia slide no. AD936 (MfN). 550, general view; 551, coils of ductus spermathecae; 552–554, ovipositor and apophyses



FIGURES 555–561. Bionomics of *Gnathitischeria arcana* Diškus & Stonis, **sp. nov.**, Guatemala: Petén Department. 555, host plant, *Acmella repens* (Walter) Pers. (Asteraceae); 556–561, leaf mines

Discussion

Our results show that morphological characters supplemented with biological and molecular data support the current, extended generic concept of Tischeriidae. Additionally, by describing four new genera and 12 new species we have increased the total number of global Tischeriidae to 186 named species and 11 genera.

The molecular research was performed using fragments of the mitochondrial DNA CO1 gene, the standard barcode region for the animal kingdom (Hebert *et al*. 2003). Because partial sequences of the CO1 gene are not always sufficient for a robust phylogenetic reconstruction, our multiple attempts to provide a well resolved Tischeriidae phylogeny using new barcodes with the previously known barcodes available from the public databases have been unsucessful. Therefore, in order to include all genera in one cladogram (Figs 62–64), we used randomly selected sequences of species and used two different outgroups, either *Pseudopostega bogotensis* Vargas (Fig. 62) or *Elachista alpinella* Stainton (Figs 63, 64).

Despite the clustering of *Gnathitischeria* + *Astrotischeria* + *Neotischeria* + *Pafazaria,* and sometimes *Paratischeria* (Figs 63, 64), based on our molecular analysis, this hypothetised relationship is doubtful because morphologically *Pafazaria*, *Manitischeria*, *Tischeria*, and *Rytietia* (but **not** *Neotischeria* or *Gnathitischeria* and *Astrotischeria*) possess a distinctive, conserved juxta in the male genitalia (Fig. 62). Due to this incongruity, in some analyses (like that figured in Fig. 66), *Pafazaria* also clustered with *Manitischeria*, but not *Neotischeria* or *Gnathitischeria* and *Astrotischeria*. Despite the morphological similarity of *Manitischeria* with other juxta-possessing genera, in our molecular trees, the placement of *Manitischeria* was unexpectedly inconsistent.

With a total number of 65 currently described species, *Coptotriche* is the largest genus of the Tischeriidae. Although the majority of the species occur in the temperate regions of North America, Europe, and Asia, some species were recently discovered in Central and South America, South Africa, Madagascar, and tropical South and South East Asia. This genus is trophically associated with 13 plant families and in that way exhibits the greatest diversity of trophic relationships among Tischeriidae.

Coptotriche had a basal position in our trees (Figs 63, 64). Based on morphology, this is the only genus with a transtilla and wide valvae in the male genitalia, and a proximally wide, elaborate (ribboned) ductus spermathecae in the female genitalia.

Among *Coptotriche* species, the analysis produced clusters according to host-plant family and geographical region (Fig. 65), but despite this fine clustering, one species, *C. malifoliella*, always clustered separately, taking a basal position on the tree (e.g., Fig. 65). The reason of this is unknown, but it may be due to the limited length of the sequence. Additionally, in many of our analyses, the Asian Pentaphylaceae-feeding *C. japoniella* clustered with the South American Asteraceae-feeding *C. parvisacculata* and the Asian Symplocaceae-feeding *C. asiana*, and usually this cluster appeared at the very base of the *Coptotriche* tree (Fig. 65). The latter, *C. asiana*, represents a separate, but not yet designated species group distributed in East and South East Asia and characterized by different morphology (Xu *et al*. 2021). But bootstrap support values of some basal dichotomies within *Coptotriche* are too low to support the results. Nevertheless, the three clusters or dichotomies of *C. marginea*–*C. aenea, C. citrinipenella*–*C. badiiella*, and *C. inclinata* shown in Fig. 65 probably represent good, monophyletic species groups, while the molecularly well-supported cluster of *C. amelanchieris*–*C. spendida* seems doubtful, not supported by morphology or biology. Recently, an interesting phylogeny of East Asian *Coptotriche* was provided by Kim *et al*. (2022).

Coptotrichoides serjaniphaga (Remeikis & Stonis), originally described in *Coptotriche* (Stonis *et al.* 2021b), always fell outside *Coptotriche* in our analyses. Unfortunately, *C. serjaniphaga* is only known from a single, but reared specimen from *Serjania* Mill. (Sapindaceae) with a missing abdomen. It was originally described without genital features, and based only on external characters, biology, and a unique DNA sequence. Even prior to this study, taxonomic placement of *C. serjaniphaga* was unclear. But now this and five other species that were found to be associated with Sapindaceae and possess similar morphology have been transferred to the new genus *Coptotrichoides*. Two South American species, *C. deliquescens* (Meyrick) and *C. braziliensis* (Diškus & Stonis), have unknown host plants, but it is expected that their host plants will belong to the tropical subfamily Sapindoideae (Sapindaceae). Sapindoideae species are very diverse, common in various habitats, and native to tropical America (Buerki *et al*. 2009, 2021). Finally, the lectotype and paralectotype of the hitherto little-known species *C. deliquescens* (Meyrick, 1915), **comb. nov.** (described from Guyana and deposited at the NHMUK) were designated, dissected, studied, and documented in this study for the first time (Figs 178–182).

In the best resolved trees, *Dishkeya* and *Coptotrichoides* almost always grouped together as sister taxa (Figs 62–64), although morphologically they look very different from each other. This persisted after replacing the Opostegidae outgroup with Elachistidae (Figs 63, 64). However, after removing *Coptotrichoides* from the analysis, *Dishkeya* appeared to be closest to *Rytietia* (Fig. 66), but **not** to *Tischeria* from where the species in this genus originated (see Stonis & Solis 2020). *Dishkeya*, a recently erected genus (Stonis & Solis 2020), is currently distributed along the West coast of the Americas and comprises four highly distinctive species, including a recently described taxon from the Colombian Andes, *D. ursipedella* Diškus, Mey & Stonis (Stonis *et al.* 2022a).

Tischeria is not only the oldest generic name, but also a distinctive, compact taxon characterized by the presence of a juxta, and medium wide to very wide phallus with usually long lateral processes but no carinae in the male genitalia, and the presence of an antrum in the female genitalia. It was interesting to note that European-Asian *Tischeria* and North American *Tischeria* were represented by two distinctly separate "geographical" (allopatric) clades, **not** following their morphological similarity. Additionally, we observed that the molecular difference in sequences within *Tischeria dodonaea* (Figs 66, 67) is great; however, there is still not enough evidence to split the rather morphologically uniform *T. dodonaea* and recognise two separate species solely on the basis of molecular differences.

The position of the juxta-possessing *Manitischeria* was slightly different in our various analyses (e.g., compare our best resolved Fig. 67 with 62 and 66). However, the greatest variability of position in our analyses was observed in *Pafazaria*, a new genus described in this study. *Pafazaria* often clustered with *Manitischeria* (Fig. 67), but also this genus was observed to cluster with *Neotischeria* (Figs 62, 63). The major morphological diagnostic difference between the juxta-possesing *Pafazaria* and juxta-possessing *Manitischeria*, *Rytietia*, and *Tischeria*, is the presence of an additional anellus and a "hood" in the male genitalia of *Pafazaria* (these structures are absent in *Manitischeria, Rytietia*, and *Tischeria*). These morphological features, along with molecular data, begs the questions whether the juxta-possessing complex of genera is monophyletic or whether the juxta in *Pafazaria* evolved independently.

Within *Manitischeria* genus, *M. ptarmica* characterized by molecular variability (Fig. 67). However, our morphological re-examination of specimens from various regions showed no clear morphological differences either in the male genitalia, female genitalia, or biological characteristics. Examination of the type material from India (deposited at NHMUK), newly collected material from Laos (deposited at MfN), and comparison with well-documented specimens of *M. ptarmica* from the Arab Emirates by van Nieukerken (2010) has not revealed any significant morphological characters indicating different species.

Previously, two species of *Neotischeria*, *N. conexa* Diškus & Stonis and *N. longa* Diškus & Stonis (Fig. 68), provisionally (before their description in Stonis *et al*. 2021c) were treated as a single species. They share host plants, similar biology, and an overlapping geographical distribution area. However, based on their genetic distances in this study and some differences previously discovered in the male morphology and biology (Stonis *et al*. 2021c), we now treat them as two closely related, but separate species.

A new, informal species group for *Neotischeria neotropicana* and closely related species was created recently (Stonis *et al*. 2021c). *N. neotropicana* always had a special position within the genus because of its unique morphological characters (and, subsequently, differences from the majority of *Neotischeria* species). The uniqueness of the *N. neotropicana* group was supported in all of molecular trees and it appeared as a long separate branch within *Neotischeria* trees (Figs 68, 69).

The species in the genus *Paratischeria* clustered into two groups depending on the included species. In some cases, species clustered based on their different host-plant families: *P. hestias* on Malvaceae, *P. grossa* and *P. boehmerica* on Urticaceae (Fig. 69). In other cases, species clustered according to their geographical regions (Fig. 68). It should be noted that *P. hestias* is the only known Malvaceae-feeding species in *Paratischeria* and possess the most different male genitalia morphology among the studied species of *Paratischeria* (Fig. 70). Nevertheless, in the *Paratischeria* tree (Fig. 73), Malvaceae-feeding *P. hestias* clustered together with the Urticaceae-feeding *P. grossa* and *P. boehmerica*. The two major clusters were based on their geography (i.e., allopatric), and did not reflect their host-plant preferences or male genitalia morphology.

Unfortunately, in our various mitochondrial CO1 analyses, we never managed to get a fully resolved tree of all *Astrotischeria* and *Gnathitischeria* species. Even the most striking species with a three-lobed valva from the *A. trilobata* group clustered randomly with various morphologically dissimilar species. The best outcome was obtained with solely included *Astrotischeria* species (Figs 78, 79), yet still with doubtful dichotomies and low bootstrap support values in many cases. It seems that the CO1 gene is not useful in discrimination in *Astrotischeria* (as well as the related genus *Gnathitischeria*). Unlike the majority of other Tischeriidae, *Astrotisheria* species are diverse Asteraceae feeders. It could be an extraordinary adaptation to chemically very distant or different host plants (see discussion below) occurring only in the Americas. It may be possible that NJ and ML methods simply do not work in *Astrotischeria*, as it is common in the cases where the rate of evolution is extremely high (see Mailund *et al.* 2006).

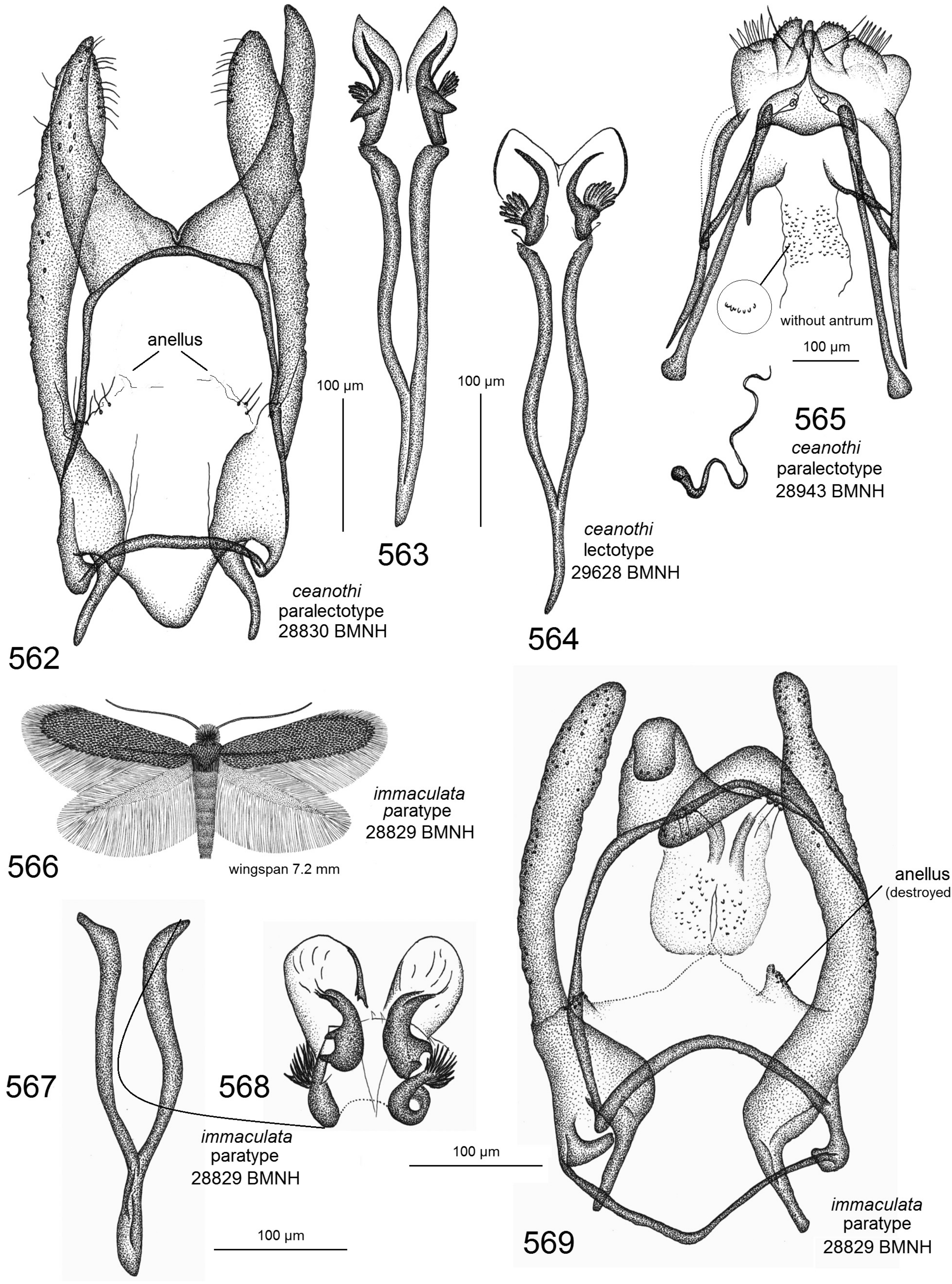
Nevertheless, in all our attempts to analyse *Astrotischeria*, some clusters persistently appeared. *Astrotischeria truncata* + *A. jungasi* + *A. dondavisi* always clustered together, *A. cornuata* always clustered with *A. atlantica*, and *A. guatemalica* clustered with *A. trilobata.* If we accept the latter, then the *trilobata* species group (Stonis *et al*. 2018a) may not be monophyletic (although it is still useful for their diagnostics). Two other clusters in all our trees were *A. jociui*+*A. sanjosei* and *A. ochrimaculosa*+*A. ambrosiaeella* (Figs 78, 79) which cannot be supported by morphological data or any other character-based reason. Finally, all analysed *A. bachariphaga* specimens appeared to be unexpectedly diverse (each specimen is characterized by different mitotype), although no morphological, biological, or geographical characters were found to explain this diversity.

We have only touched the surface of tischeriid biology with respect to their host plants. Although a few Tischeriidae genera are currently associated only with a single host-plant family (*Coptotricoides* with Sapindaceae, *Dishkeya* with Rhamnaceae, *Rytietia* with Annonaceae), host plants from one plant family appear commonly among Tischeriidae genera. We found that six tischeriid genera (of 11) include at least some Malvaceae-feeding species. Within the genus *Manitischeria*, Malvaceae miners clearly prevail and make about 80% of the currently investigated species. The genera *Helicteres* L. and *Sida* L. of the Malvaceae are the most common host plants.

A hypothetized trophic shift to Asteraceae and a very successful species radiation of tischeriid feeding on Asteraceae highlights a huge ecological niche for the Tischeriidae. Asteraceae is the largest vascular plant family, and its extant members are widespread in all continents, except Antarctica. It is well-represented in many terrestrial ecosystems (Funk *et al*. 2005; Mandel *et al*. 2017) and is more abundant in temperate areas or in higher (cooler) elevations of the tropics (Bohm & Stuessy 2001). Asteraceae-feeding Tischeriidae are known only from the Americas (see Fig. 63), although obviously Asteraceae occurs in other regions in the world. Along with Tischeriidae, other lepidopteran leaf miners are Asteraceae feeders in the Americas, e.g., Bucculatricidae (Vargas & Moreira 2012), and particularly Nepticulidae (Remeikis *et al*. 2016; Stonis *et al*. 2018b). The latter family is famous for its superdiverse Asteraceae-feeding fauna in South America (Stonis *et al*. 2018a) and New Zealand (Donner & Wilkinson 1989). According to Katinas *et al*. (2007) and Panero & Crozier (2016), the Central and South American Asteraceae flora is characterized by the greatest richness (highest number of Asteraceae genera and species): approximately 8040 Asteraceae species belonging to 580 genera are known from tropical America (Prunski & Sancho 2004). It is interesting to note that some Asteraceae tribes, such as Heliantheae or Eupatorieae, are the most preferred by *Astrotischeria* species (Stonis *et al*. 2018a); these tribes are largely found in the Neotropics and represented by native species (Prunski & Sancho 2004).

It is unknown why Tischeriidae or Nepticulidae have been successful on Asteraceae in the Americas, but it could be tied to the origin and diversity of Asteraceae in South America. Earliest plant fossils confidently assigned to Asteraceae suggest a South American-Antarctica origin: fossils have been discovered from the Middle Eocene (ca. 47 Mya) of Patagonia in Argentina (Barreda *et al*. 2010, 2012) and from the Late Cretaceous (76–66 Mya) of Antarctica (Barreda *et al.* 2015). Fossil pollen has been found in Antarctica (Barreda *et al*. 2015) suggesting that it inhabited this area in the past. Some members may have then migrated to Africa where the family underwent several radiations in parallel with South American radiations, and eventually colonized all continents (Katinas *et al.* 2013). By postulating that Asteraceae, a family of great species richness and diversity, may turn out to be host to an even greater proportion of Tischeriidae in the Americas, we expect many more *Neotischeria, Gnathitischeria*, and particularly *Astrotischeria* species to be discovered in this fascinating Asteraceae-feeding fauna.

During this study, we discovered atypical morphological characters for some newly described Tischeriidae. For instance, *Astrotischeria incae* Diškus & Stonis, **sp. nov.** was characterized by a unique feature in females: unlike other Tischeriidae, they possess rather long, distinctly visible antennal sensilla, similar to those of males. The female genitalia of *A. incae* are also unique among this lepidopteran family: ovipositor lobes are very large, almost undivided or coalescent with numerous very slender setae but, in contrast to the general plan of the family Tischeriidae, without peg-like setae.



FIGURES 562–569. First examination of the type-series specimens deposited at NHMUK of two species of the *T. ceanothi* group with an uncertain taxonomic position. 562, *Tischeria ceanothi* Walsingham, capsule of the male genitalia, paralectotype, USA, California, from *Ceanothus oliganthus* Nutt. (=*C. divaricatus*), 14.vi–4.vii.1871, slide no. 28830; 563, same, phallus; 564, same, lectotype, slide no. 29628; 565, same, details of the female genitalia, paralectotype, USA, California, from *Ceanothus oliganthus* Nutt. (=*C. divaricatus*), slide no. 28943; 566–569, *T. immaculata* Braun, paratype, slide no. 28829

There are three North American, Rhamnaceae-feeding species in *Tischeria* with uncertain taxonomic positions within Tischeriidae: *T. ceanothi* Walsingham, 1890; *T. ambiqua* Braun, 1915; *T. immaculata* Braun, 1915 (**stat. restored**, previously synonymized with *T. ceanothi* by Diškus & Puplesis 2003). These species do not fit into the current concept of the genus *Tischeria* or the recently erected genus *Dishkeya*. Here, we provide the first morphological documentation for *T. ceanothi* and *T. immaculata* (Figs 562–569) based on our studies of NHMUK material. As a result, we designate a new species group, the *T. ceanothi* group, for all three species listed above. Because of the uncertainty of their taxonomic position, we temporarily leave this species group in the genus *Tischeria*.

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