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First documentation of Nepticulidae feeding on Gondwanan relict *Nothofagus* from Andean Patagonia and the unexpected discovery of morphologically similar pygmy moth species from distant Central America

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The trophic association of Nepticulidae with *Nothofagus* in Andean Patagonia has been speculated about but never conclusively demonstrated. This study provides the first definitive evidence that the species of the *Stigmella purpurimaculae* group are leaf miners of *Nothofagus* spp., with documented mines and male genital structure analysis of two species reared from *Nothofagus*. Additionally, we describe three new *Stigmella* species from Honduras, which, despite the geographic distance from Andean Patagonia, share key genital traits with the *S. purpurimaculae* group. While these species exhibit some external differences, their morphological similarities raise intriguing questions about potential evolutionary connections.

Keywords: Ando-Patagonian region, Argentina, Honduras, host plant, leaf mines, Neotropical region, pygmy moths

INTRODUCTION

***Nothofagus* from a biogeographical perspective.** *Nothofagus* Blume, commonly known as the southern beeches, is an iconic genus in austral biogeography studies. It is the sole genus within the family Nothofagaceae Kuprian., considered a monophyletic group and a sister taxon to other members of the order Fagales (Hill, Read, 1991). Molecular studies, consistent with fossil-based

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estimates, indicate that Nothofagaceae diverged from other Fagales approximately 93–83.5 million years ago (Cook, Crisp, 2005).

Currently, southern beeches are found in temperate forests of the Southern Hemisphere, with 35 extant species classified into four subgenera, distinguished by morphology and DNA analysis: *Fuscospora*, found in New Zealand, Tasmania, and southern South America; *Lophozonia*, in New Zealand, Australia, and southern South America; *Nothofagus* (sensu stricto), in southern South America; and *Brassospora*, in New Guinea and New Caledonia (Hill, 2001). Heenan and Smissen (2013) argue that the morphological and molecular distinctions among these subgenera are significant enough to warrant their recognition as four separate clades of generic rank. This distribution pattern around the southern Pacific Rim suggests that the spread of *Nothofagus* can be traced back to the ancient supercontinent Gondwana, when present-day Antarctica, Australia, Africa, and South America were connected as a common landmass approximately 80–90 million years ago (Swenson et al., 2001).

Extensive fossil evidence, including that from Antarctica, supports the hypothesis that *Nothofagus* originated in western Gondwana (Taylor et al., 2024), was not found in Africa, and was a significant component of the primordial vegetation on Gondwanan landmasses over a long period during the late Cretaceous and Cenozoic eras, before the supercontinent broke apart (Swenson et al., 2001; Cook, Crisp, 2005). According to the widely accepted theory of tectonic plate drift, the breakup of Gondwana – where Antarctica, Australia, New Zealand, New Caledonia, New Guinea, and South America separated – is thought to have contributed to many of the disjunct biogeographic patterns observed today in Southern Hemisphere biota (Swenson et al., 2001).

Notably, biogeographic analyses by Swenson et al. (2001) and the panbiogeographical evidence presented by Heads (2006) align with a full vicariance scenario, suggesting that tectonic drift primarily explains the current distribution of *Nothofagus*. Nevertheless, different biogeographic analyses have produced conflicting interpretations. Debate persists regarding the relative contributions of vicariance, terrestrial dispersal prior to Gondwana's breakup, and post-breakup oceanic dispersal (Cook, Crisp, 2005). Several authors (Linder, Crisp, 1995; Swenson et al., 2001; Sanmartín, Ronquist, 2004; Cook, Crisp, 2005; Knapp et al., 2005) have argued that the sister-group relationships between Australia and New Zealand in subgenera *Lophozonia* and *Fuscospora* are incongruent with the pattern expected under a vicariance model. They reject the all-vicariance scenario, noting that the radiation of the *Nothofagus* crown group is too recent. The independent divergences between Australian and New Zealand taxa in subgenera *Lophozonia* and *Fuscospora* may have occurred less than 50 million years ago (and possibly much more recently), which is more than 30 million years after the opening of the Tasman Sea. Conversely, the molecular dates for divergences between Australasian and South American taxa align with the rifting events that separated Australia, Antarctica, and South America between 50 and 30 million years ago (Cook, Crisp, 2005).

In summary, while *Nothofagus* was traditionally thought to have limited dispersal capability (Crisci et al., 2003), current evidence suggests that both vicariance and dispersal processes have influenced the genus's present-day distribution patterns (Cook, Crisp, 2005). This dual influence of vicariance and dispersal adds complexity to the biogeographical history of *Nothofagus* and highlights the intricate processes shaping Southern Hemisphere biota.

***Nothofagus* in Andean Patagonia.** The temperate regions of the Southern Hemisphere lack direct analogs to the broadleaf deciduous forests of the Northern Hemisphere. Instead, these areas, under a humid subtropical climate, are characterised by mixed evergreen forests composed of both broadleaf and needleleaf species. These forests are of significant biogeographic interest due to the presence of Gondwanian relicts, including *Araucaria* pines (found in South America and Australia), *Podocarpus* species (present in South America, Africa, and Australia), and the evergreen southern beech, *Nothofagus* (native to South America, Australia, and New Zealand) (Rogers, 2004).

Nothofagus first appeared in southern South America during the late Campanian period and was particularly abundant in southern Patagonia during the Palaeocene and Eocene epochs. Its distribution peaked during the Miocene but began retreating westward in the late Miocene as aridification increased across Patagonia (Pujana et al., 2021). Today, the northernmost extent of the genus is found at La Campana National Park and the Vizcachas Mountains in central Chile.

The striking morphological similarity among *Nothofagus* species across Southern Hemisphere landmasses, along with their persistence in comparable habitats, provides compelling evidence that these trees have remained largely unchanged since the breakup of Gondwana (Rogers, 2004).

While modern *Nothofagus* species predominantly inhabit cool, isolated, high-altitude environments at temperate and tropical latitudes, fossil records reveal that the genus once thrived in significantly warmer climates (Carpenter et al., 2012).

Currently, South America is home to twelve species of *Nothofagus* (POWO, 2025): *N. alessandrii* Espinosa (Central Chile), *N. alpina* (Poepp. & Endl.) Oerst. (Southern Argentina, Central and Southern Chile), *N. antarctica* (G. Forst.) Oerst. (Southern Argentina, Central and Southern Chile), *N. betuloides* (Mirb.) Oerst. (Southern Argentina, Southern Chile), *N. dombeyi* (Mirb.) Oerst. (Southern Argentina, Central and Southern Chile), *N. glauca* (Phil.) Krasser (Central Chile), *N. macrocarpa* (A.DC.) F. M. Vázquez & R. A. Rodr. (Central Chile), *N. nitida* (Phil.) Krasser (Southern Chile), *N. obliqua* (Mirb.) Oerst. (Southern Argentina, Central and Southern Chile), *N pumilio* (Poepp. & Endl.) Krasser (Southern Argentina, Central and Southern Chile), *N. rutila* Ravenna (Central Chile), and *N.* × *leoni* Espinosa (Central Chile).

Nothofagus forests, forming part of the Andean-Patagonian woodlands, are ecologically isolated from other major South American forests, creating island-like ecosystems with high levels of endemism. These forests are critically endangered, confined to a narrow, 60-kilometer-wide strip along the Andean foothills that extends intermittently for 1,500 kilometres, from Neuquén Province in Argentina to Tierra del Fuego (Rogers, 2004).

Phytophagous insects on *Nothofagus*. Extensive research has been conducted on phytophagous insects associated with *Nothofagus*. Notably, McQuillan (1993) reported that *Nothofagus* supports insects from at least 30 genera in New Zealand. The sap-sucking insect fauna inhabiting *Nothofagus* in Chile, Australia, and New Zealand was reviewed by Carrillo-Li & Cerda (1987).

The insect fauna associated with *Nothofagus* in Andean Patagonia has been the focus of several studies, including those by Gentili and Gentili (1988) and Welch (1988). Among significant contributions, Claire Margaret McDonald's dissertation, *Herbivory in Antarctic Fossil Forests and Comparisons with Modern Analogues in Chile* (McDonald, 2009), stands out as a thorough and invaluable resource, albeit not taxonomic in focus. Gall-inducing insects in Andean Patagonia represent an especially rich component of the local insect fauna, with approximately 43 morphospecies across at least five insect orders identified (Quintero et al., 2014).

Some insect species associated with *Nothofagus* have been recognised as pests. For example, the Saturniidae moth *Ormiscodes amphimone* is a phytophagous species whose caterpillars, during massive outbreaks, can completely defoliate *Nothofagus pumilio* stands in Chilean part of Andean Patagonia (Carrillo-Li, Cerda, 1987; Altmann, 2011; Huerta-Fuentes et al., 2011; Paritsis et al., 2010; Piper, Fajardo, 2014).

Nothofagus-mining lepidopteran families were reviewed by McQuillan (1993) and McDonald (2009). Of particular phylogenetic and ecological significance is the genus *Heterobathmia*, discovered in Andean Patagonia. This genus is trophically linked to *Nothofagus* and represents a phylogenetically very archaic lineage of Lepidoptera (Kristensen, Nielsen, 1983; Kristensen, 1999). *Heterobathmia* is the only genus in the family Heterobathmiidae and the sole representative of the suborder Heterobathmiina, endemic to the region. Adult *Heterobathmia* moths feed on the pollen of *Nothofagus*, while their larvae mine the leaves of *Nothofagus obliqua*, *N. antarctica*, and *N. pumilio* (Kristensen, Nielsen, 1983; Kristensen, 1999; Wagner, 2013).

In Andean Patagonia, *Nothofagus dombeyi* is mined by another phylogenetically primitive family, the Incurvariidae, specifically by *Basileura elongata* Nielsen & Davis, a species from the monotypic moth genus found in Argentina and described by Ebbe Nielsen and Donald R Davis (Nielsen, Davis, 1981). Incurvariidae moths of the genus *Plesiozela* (originally classified as Heliozelidae) have also been described from *Nothofagus* forests by Karsholt & Kristensen (2003).

Among the most intriguing discoveries of phylogenetically primitive moths feeding on Patagonian *Nothofagus* is *Notiopostega atrata* Davis (Opostegidae), which exhibits an outstanding biology. In general, the biology of Opostegidae is extremely poorly known worldwide (Puplesis, Robinson, 1999; Davis, Stonis, 2007). Biological data on the life cycle of the Patagonian *N. atrata* originally came from an unpublished thesis submitted to the Universidad Austral de Chile, Valdivia in 1975 (Biología del Minador del Cambium de *Nothofagus dombeyi* (Mirb.) Oerst., 1–59 pp., by P. Carey Briones). A summary of this study was later published by Carey Briones et al. (1978). The host plant of *N. atrata* is *Nothofagus dombeyi* (Mirbel) Oerst. Upon hatching from the egg, the larva of *N. atrata* enters the leaf, mines into the petiole, and then the cambium layer of the terminal branch. The larva eventually reaches the main trunk, producing a characteristic zig-zag gallery under the bark, extending up to seven metres down the trunk (Davis, Stonis, 2007). Pupation occurs in a flattened, oval cocoon amidst the leaf litter and above the soil (Carey Briones et al., 1978; Davis, Stonis, 2007).

Nepticulidae (pygmy moths), a sister family to Opostegidae, is also one of the basal phylogenetic clades of Lepidoptera. According to molecular dating analyses, this family likely originated around 130 million years ago (Doorenweerd et al., 2016). The oldest known fossils of Nepticulidae species are from the 102-million-year-old strata of the Dakota Formation (USA), corresponding to the latest Albian Stage of the Early Cretaceous (Doorenweerd et al., 2015). The larvae of pygmy moths are predominantly leaf miners with a cosmopolitan geographical distribution. To date, no fossil evidence of Nepticulidae leaf mines has been reported on *Nothofagus* (see Sohn et al., 2012, and the most comprehensive review to date by Doorenweerd et al., 2016). McQuillan (1993) observed that many leaf-mining Lepidoptera, mainly from the Cretaceous, are not reliant on nectar during the adult stage and, as a result, would not be disadvantaged by the primitive anemophily of *Fagales*.

While revising the extant Nepticulidae fauna of New Zealand, Hans Donner and Christopher Wilkinson (Donner, Wilkinson, 1989) re-described and illustrated *Stigmella lucida* (Philpott, 1919), a pygmy moth species whose larvae mine the leaves of the evergreen *Nothofagus menziesii* in New Zealand. According to Donner and Wilkinson (1989), '*Nothofagus menziesii* is the only southern beech species with a nepticulid miner'.

As for South America, no reliable data had been published on *Nepticulidae* mining *Nothofagus* in Andean Patagonia. However, the late Ebbe S Nielsen hypothesised that *Nothofagus* in Andean Patagonia could host unidentified *Stigmella* species or possibly represent a new genus. This hypothesis was likely based on his personal experience during the research expeditions of the 'Misión Científica Danesa' to Patagonia in 1978 and 1981. During these expeditions, Danish entomologists Ebbe S. Nielsen and Ole Karsholt collected a substantial amount of material from the southern Andes (Argentina and Chile). However, all material from the *Nothofagus* forests was collected either using light traps or by sweeping with nets during the day, and no host associations were established. Thanks to Ole Karsholt and the late Prof. Niels P. Kristensen DSc (ZMUC), all the collected material was transferred to the three first authors of this article for taxonomic identification and was later published in a series of scientific papers.

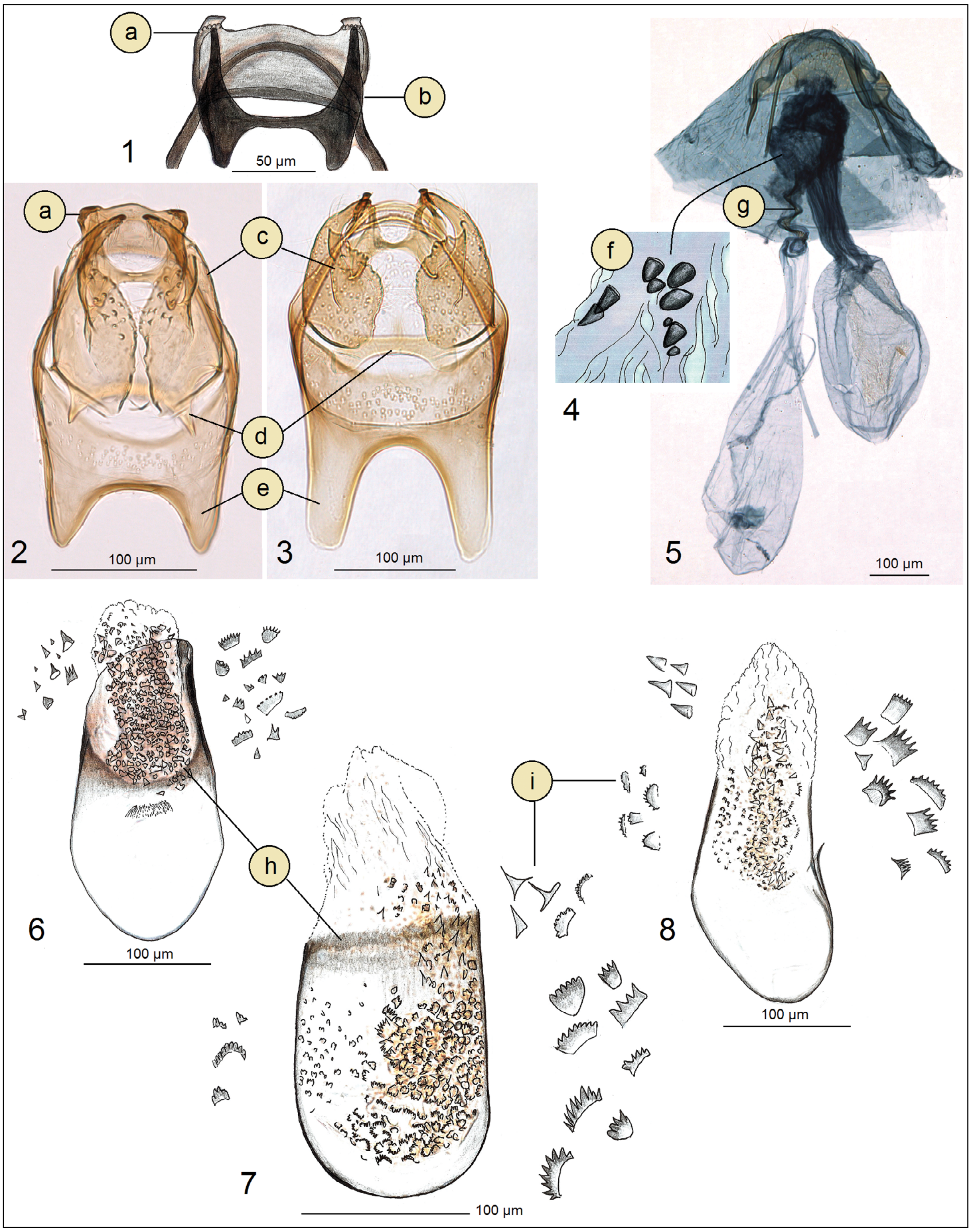
In the paper 'Ten new species [...] belonging to a newly designated *Stigmella purpurimaculae* group' by Jonas R. Stonis, Andrius Remeikis, and the late Donald R. Davis (Stonis et al., 2014), several species were described, with their adults collected from *Nothofagus* forests. Among these species, seven were included in the newly established *purpurimaculae* group: *Stigmella purpurimaculae* Remeikis & Stonis, *S. cana* Remeikis & Stonis, *S. truncata* Remeikis & Stonis, *S. sceptra* Remeikis & Stonis, *S. concreta* Remeikis & Stonis, *S. pseudoconcreta* Remeikis & Stonis, and *S. quadrata* Remeikis & Stonis. These species exhibited distinctive morphological features previously unknown among other *Stigmella* species. Notably, many species of the new group displayed a 'partial reduction' of the phallus, dentate cornuti (in the male genitalia), and a strongly developed utriculus, which in the female genitalia could be equal to or longer than the corpus bursae. Furthermore, some of these closely related species were collected near *Nothofagus pumilio* (Poepp. & Endl.) Krasser. In the biology descriptions provided in the paper, it was noted for *Stigmella purpurimaculae*, *S. cana*, and *S. truncata* that 'some specimens are collected around *Nothofagus pumilio*, but there is insufficient proof that this plant is the host plant of the species' (Stonis et al., 2014). Despite this, it was hypothesised that if the species are flying near *Nothofagus* trees, their larvae might be mining *Nothofagus*. As a result, it was suggested that the *purpurimaculae* group, or at least some of its species, might be trophically associated with Nothofagaceae. However, in the absence of collected or documented leaf mines, this hypothesis could not be confirmed, and the paper emphasised the need for stronger evidence beyond speculation.

Defining the *Stigmella purpurimaculae* group (Figs 1–8). The original diagnosis of the *Stigmella purpurimaculae* group, whose members were hypothesised to be *Nothofagus* feeders, was provided by Stonis et al. (2014). The group is characterised by the following morphological traits: forewings often featuring an apical purple spot; absence of androconial scales; a frontal tuft that varies from fuscous brown to orange; in the male genitalia, a gnathos that is often broadly U-shaped (with lacking anterior processes) or H-shaped (with short anterior processes), and partial thickening of the phallus tube (a partial reduction or partial chitinization); a vesica with numerous small dentate cornuti; and absence of the manica. In the female genitalia, a weakly defined accessory sac, a strongly chitinised ductus spermathecae, and an unusually developed utriculus, which can sometimes be longer than the corpus bursae, are present. Unique short, thickened spines may occur in the distal part of the corpus bursae, and signa are absent.

At the time of the group's designation, its biology was entirely unknown. Over 16 male and female adult specimens from three species of the *purpurimaculae* group were collected near *Nothofagus pumilio* (Poepp. & Endl.) Krasser, but there was insufficient evidence to confirm that *Nothofagus* serves as the host plant (Stonis et al., 2014). When the group was first described, it included seven species found in the southern Andes (Argentina and Chile).

MATERIALS AND METHODS

Materials. The research materials from Honduras were obtained by the first author. Since 2023, Prof. Dr Jonas R. Stonis, Senior Researcher at NRC, has been visiting the Delegation of the European Union to Honduras and conducting voluntary research on the biological diversity of Honduran forests (Stonis et al., 2024). This initiative is part of two long-term programmes between the European Union and Honduras: the Memorandum of Understanding between the Republic of Honduras and the European Union ('Forest Partnership') and the Multiannual Indicative Programme of the European Union for Honduras (2021–2024), which includes Priority Area 1: 'Sustainable Management of Natural Resources and Climate Change', with the participation of the Honduran Institute of Forest Conservation, Protected Areas, and Wildlife (ICF).



Figs 1–8. Diagnostics of the *Stigmella purpurimaculae* species group (after Stonis et al., 2014). 1 – uncus and gnathos, *S. sceptra* Remeikis & Stonis; 2 – male genitalia, capsule, *S. truncata* Remeikis & Stonis; 3 – same, *S. concreta* Remeikis & Stonis; 4 – thickened spines, *S. cana* Remeikis & Stonis; 5 – female genitalia, *S. sceptra*; 6 – phallus and cornuti, *S. pseudoconcreta* Remeikis & Stonis; 7 – same, *S. truncata*; 8 – same, *S. concreta*.

Diagnostic characters: a – broadly separated lateral lobes of uncus; b – H-shaped or U-shaped gnathos; c – valva with papillated inner lobe and prominent apical process; d – band-shaped transtilla with tiny or no sublateral processes; vinculum with usually well-developed lateral lobes; f – bursa with thickened spines; g – ductus spermathecae with thickened coils and long utriculus; h – tube of the phallus thickened only in basal 1/3–2/3; I – cornuti, at least some are dentate

The materials used in this paper will be deposited in the collection of the Museum für Naturkunde (MfN), Berlin, Germany, following publication.

The materials from Argentina were neither collected nor deposited; all data for the current paper come from field observations by the second author, Assoc. Prof. Dr Arūnas Diškus, who visited Argentina in February 2019 (Figs 9–14). The field observations in Argentina led to the discovery of Nepticulidae

Figs 9–14. Habitats, along the approximately 450-km-long route from north of San Carlos de Bariloche (in the Province of Rio Negro) to the Province of Neuquén, starting from the localities along the southern and eastern side of Lago Nahuel Huapi, then in between Lago Correntoso and Lago Espejo Grande, up to the northern tip of Lago Traful; 9 – forest of *Nothofagus dombeyi* (Mirb.) Oerst.; 10–13 – various localities along the route; 14 – co-author Arūnas Diškus at fieldwork

leaf mines on *Nothofagus*, which were photographed but not collected or preserved. Two genitalia mounts, which emerged from two pupae and represent two undescribed, new *Stigmella* species (microscope slide nos AD750 and AD757), are held by the Biosystematic Research Group (BRG), currently based at the State Research Institute Nature Research Centre, Vilnius, Lithuania.

Methods. In the current study, we employed the collecting and specimen dissection methods outlined in Puplesis & Diškus (2003), Diškus & Stonis (2022), and Stonis et al. (2022a, 2022b, 2024). During our fieldwork in Honduras, we attracted moths to a white screen using fluorescent lanterns powered by flashlight batteries, as well as the LepiLED lamp powered by power bank batteries with a voltage of 5–13 V DC (Brehm, 2017). Male genital capsules were removed after macerating the abdomen in 10% KOH, followed by cleaning, and then mounted with the ventral side facing up. In many cases, the phallus was removed and mounted separately alongside the genital armature. Abdominal pelts were not preserved in this study. Permanent microscope slide preparations were photographed and examined using a Leica DM2500 microscope equipped with a Leica DFC420 digital camera (Stonis et al., 2022c). Adults were measured and examined under a Lomo stereoscopic microscope (MBS-10), and images were captured with a Leica S6D stereoscopic microscope paired with a Leica DFC290 digital camera. For illumination of the adult specimens, we used a stereomicroscope ring light LED 60, which was attached directly to the stereomicroscope lens. The light intensity was adjustable, and the colour temperature ranged from 7000 to 11000 K, with a maximum illumination of 8000 Lux at a distance of 100 mm. Leaf mine and host plant photographs were taken using an Olympus TG-2 camera, while habitat photos were captured with a Samsung A-52 smartphone.

The molecular study follows the methods detailed in Stonis et al. (2024). All new sequences have been deposited in GenBank, and their accession codes are provided in the molecular trees presented below along the new species descriptions.

RESULTS

Documentation of discovered Nepticulidae leaf mines on *Nothofagus*

During an extensive survey conducted along an approximately 450-km-long route from San Carlos de Bariloche (Province of Río Negro) to the northern tip of Lago Traful (Province of Neuquén), the following five different types of leaf mines of Nepticulidae were discovered and are documented below for the first time.

Species A (Figs 15–22):

Initial part of the leaf mine: fully filled with greenish-brown frass (Fig. 17).

Main gallery: characterised by a wide line of blackish-brown frass, often arranged in a spiral pattern (coiled and forming contorted arcs), with slender to medium-wide unfilled margins along the gallery track (Figs 18, 19, 21, 22).

Final part of the leaf mine: marked by a slender line of black frass with wide unfilled margins (Figs 19, 22).

Larva: bright yellow with a dark green intestine (Figs 19, 20).

Host plant: *Nothofagus antarctica* (G. Forst.) Oerst. (Figs 15, 16).

Species B (Figs 24–27):

Initial part of the leaf mine: with brownish-black frass and slender unfilled margins.

Main gallery: characterised by a slender to medium-wide line of black frass, often arranged in a spiral pattern (coiled and forming contorted arcs), with wide or medium wide unfilled margins along the gallery track (Figs 25, 27).

Final part of the leaf mine: marked by a slender line of black frass with wide unfilled margins (Fig. 27).

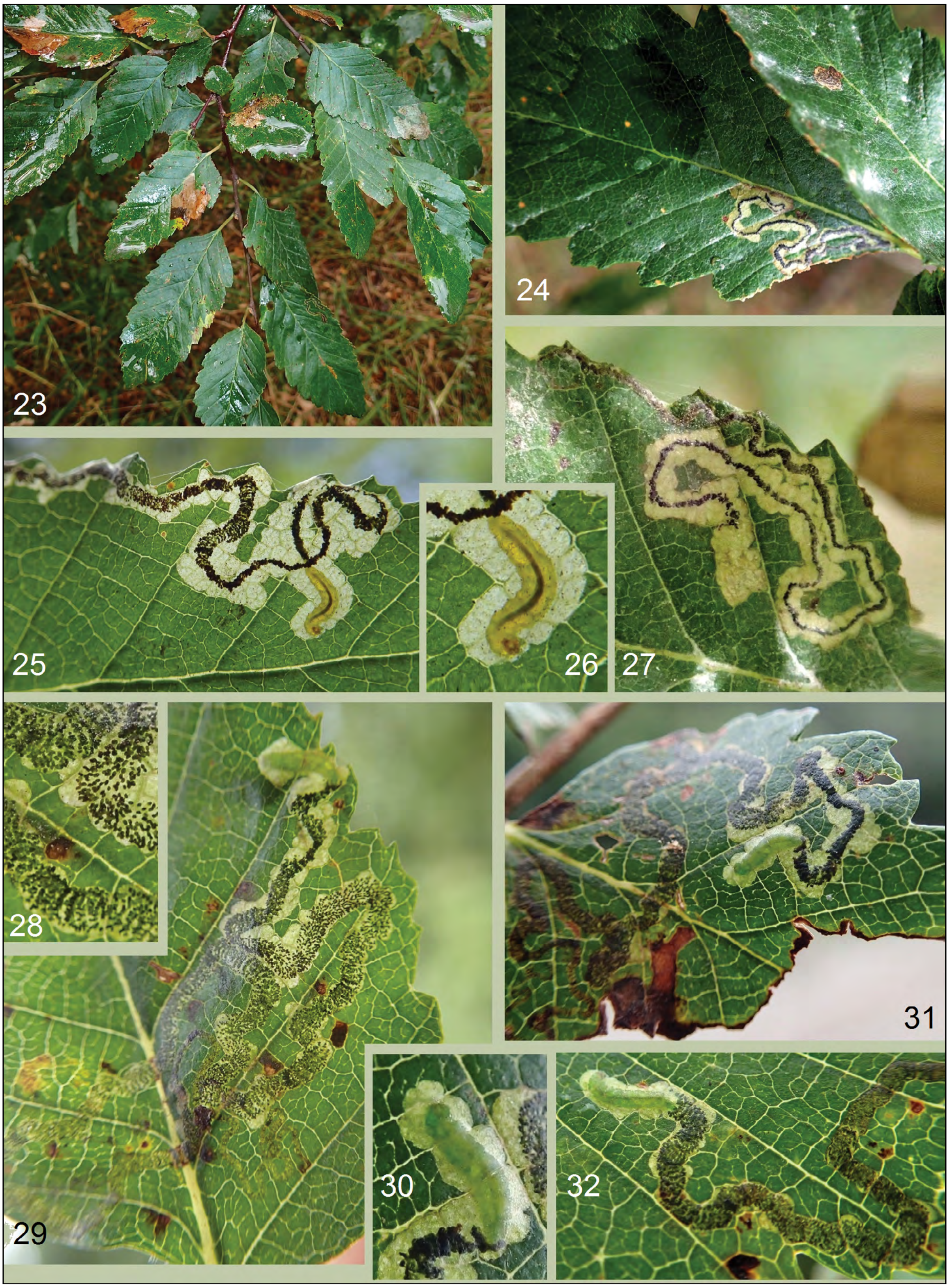
Larva: greenish yellow with a dark brown-green intestine (Fig. 26).

Host plant: *Nothofagus obliqua* (Mirb.) Oerst. (Figs 23, 24).

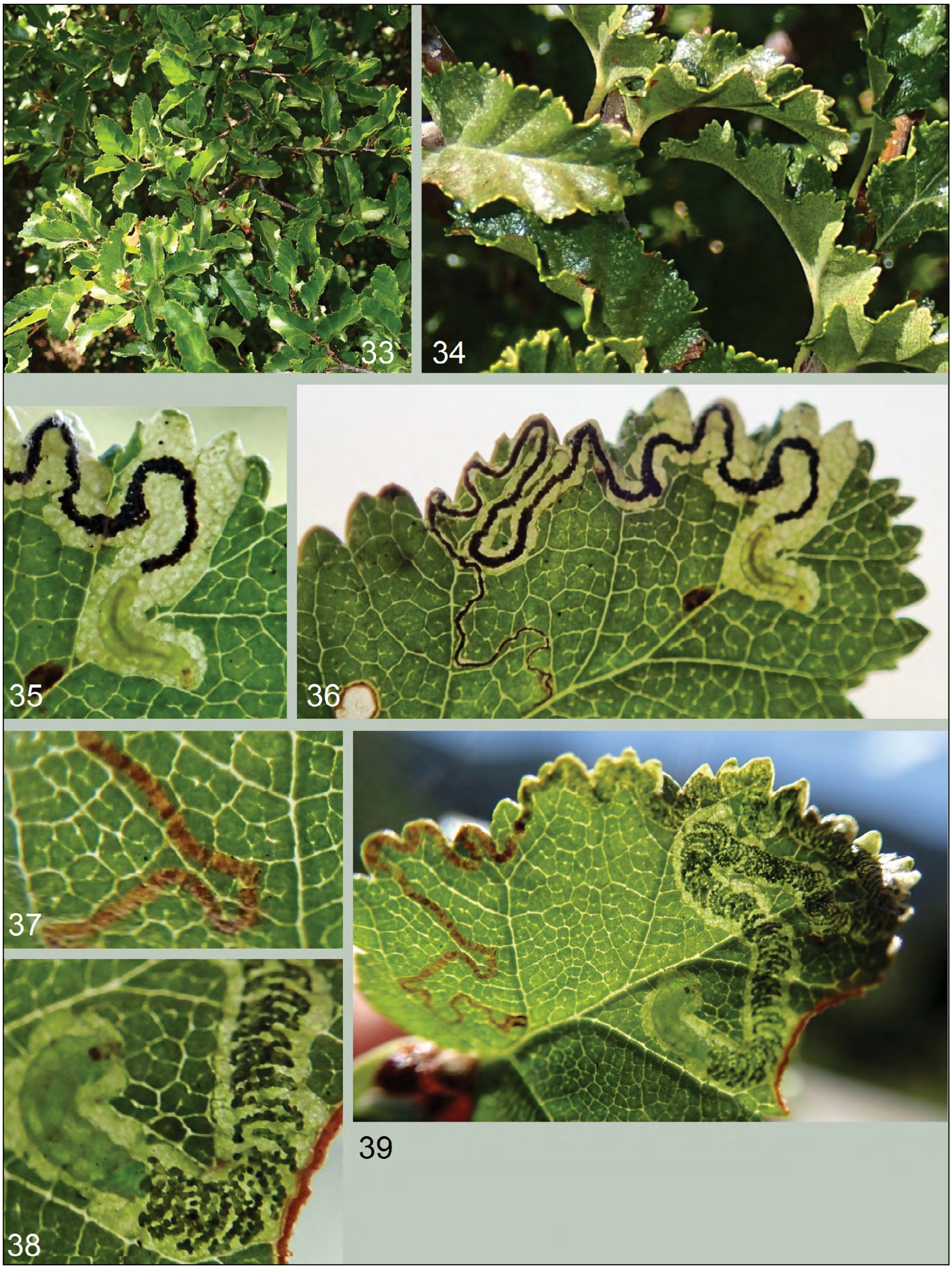
Species C (Figs 28–32):

Initial part of the leaf mine: fully filled with green-brown frass.

Figs 15–22. Detected Nepticulidae leaf mines on the deciduous Antarctic beech or ñire, *Nothofagus antarctica* (G. Forst.) Oerst. 15, 16 – host plant; 17–22 – species A, leaf mines (vacant and with feeding larvae), approximately 250 km N of San Carlos de Bariloche, 40°29'0"S, 71°36'37"W – 40°9'8"S, 71°34'25"W, 845 m, 17–19.ii.2019, A. Diškus



Figs 23–32. Detected Nepticulidae leaf mines on the deciduous Patagonian oak or roble pellín, *Nothofagus obliqua* (Mirb.) Oerst. 23 – host plant; 24–27 – species B, leaf mines (vacant and with feeding larvae), 40°9'9"S, 71°34'23"W, 690 m, 18.ii.2019, A. Diškus; 28–32 – species C, leaf mines with feeding larvae, 40°8'48"S, 71°37'29"W, 660 m



Figs 33–39. Detected Nepticulidae leaf mines on the deciduous Antarctic beech or ñire, *Nothofagus antarctica* (G. Forst.) Oerst. 33, 34 – host plant; 35, 36 – species D, leaf mines with a feeding larva, about 250 km N of San Carlos de Bariloche, 40°29'2"S, 71°36'36"W, 845 m, 19.ii.2019, A. Diškus; 37–39 – species E, leaf mines with a feeding larva, about 250 km N of San Carlos de Bariloche, 40°29'4"S, 71°36'33"W, 19.ii.2019, A. Diškus

Main gallery: fully or almost fully filled with dark green frass, often arranged in a spiral pattern (coiled and forming contorted arcs), sometimes with very slender unfilled margins (Figs 28, 29, 32).

Final part of the leaf mine: marked by a medium-wide line of dark green to black frass with medium-wide unfilled margins along the gallery track (Figs 29, 31).

Larva: green with a green intestine (Fig. 30).

Host plant: *Nothofagus obliqua* (Mirb.) Oerst. (Figs 23, 24).

Species D (Figs 33–39):

Initial part of the leaf mine: the beginning of the gallery is very slender, almost fully filled with black frass, and has slender unfilled margins (Fig. 36).

Main gallery: characterised by a slender line of black frass with wide unfilled margins along the gallery track (Fig. 36).

Final part of the leaf mine: marked by a slender line of black frass with very wide unfilled margins (Fig. 35).

Larva: pale green with a pale brown-green intestine (Fig. 35).

Host plant: *Nothofagus antarctica* (G. Forst.) Oerst. (Figs 15, 16, 33, 34).

Species E (Figs 33, 34, 37–39):

Initial part of the leaf mine: fully filled with ochreous brown frass (Figs 37, 39).

Main gallery: fully filled with dark green or blackish green frass arranged in a spiral pattern (coiled and forming contorted arcs), with slender unfilled margins along the gallery track (Fig. 39).

Final part of the leaf mine: almost fully filled with dark green or blackish green frass arranged in a spiral pattern, with slender unfilled margins (Fig. 38).

Larva: green with a green intestine (Fig. 38).

Host plant: *Nothofagus antarctica* (G. Forst.) Oerst. (Figs 15, 16, 33, 34).

First documented proof of Nepticulidae from *Nothofagus* in Andean Patagonia based on examination of the male genitalia of two reared species

During our search, no reared adults were obtained; however, two fully developed pupae were found in a mixed leaf-mine sample. Dissection of the male genitalia of these pupae revealed two different but closely related *Stigmella* species (Figs 40–46). Upon examination of the morphological structures of the genital capsule and phallus, it was evident that these species belong to the *S. purpurimaculae* group (as characterised in Figs 1–8).

In the studied genitalia, the uncus exhibits broadly separated lateral lobes (Figs 41, 45); the gnathos is either H-shaped (Fig. 45) or transitional between H-shaped and U-shaped (Fig. 41); the valvae possess strongly papillated inner lobes (Fig. 44) and prominent apical processes (Figs 40, 45); the transtilla is band-shaped, with tiny or no sublateral processes (Figs 42, 45); the vinculum features well-developed lateral lobes (Figs 42, 45); the phallus tube is inequal in thickness (Figs 43, 46), with many dentate cornuti (Figs 43, 46).

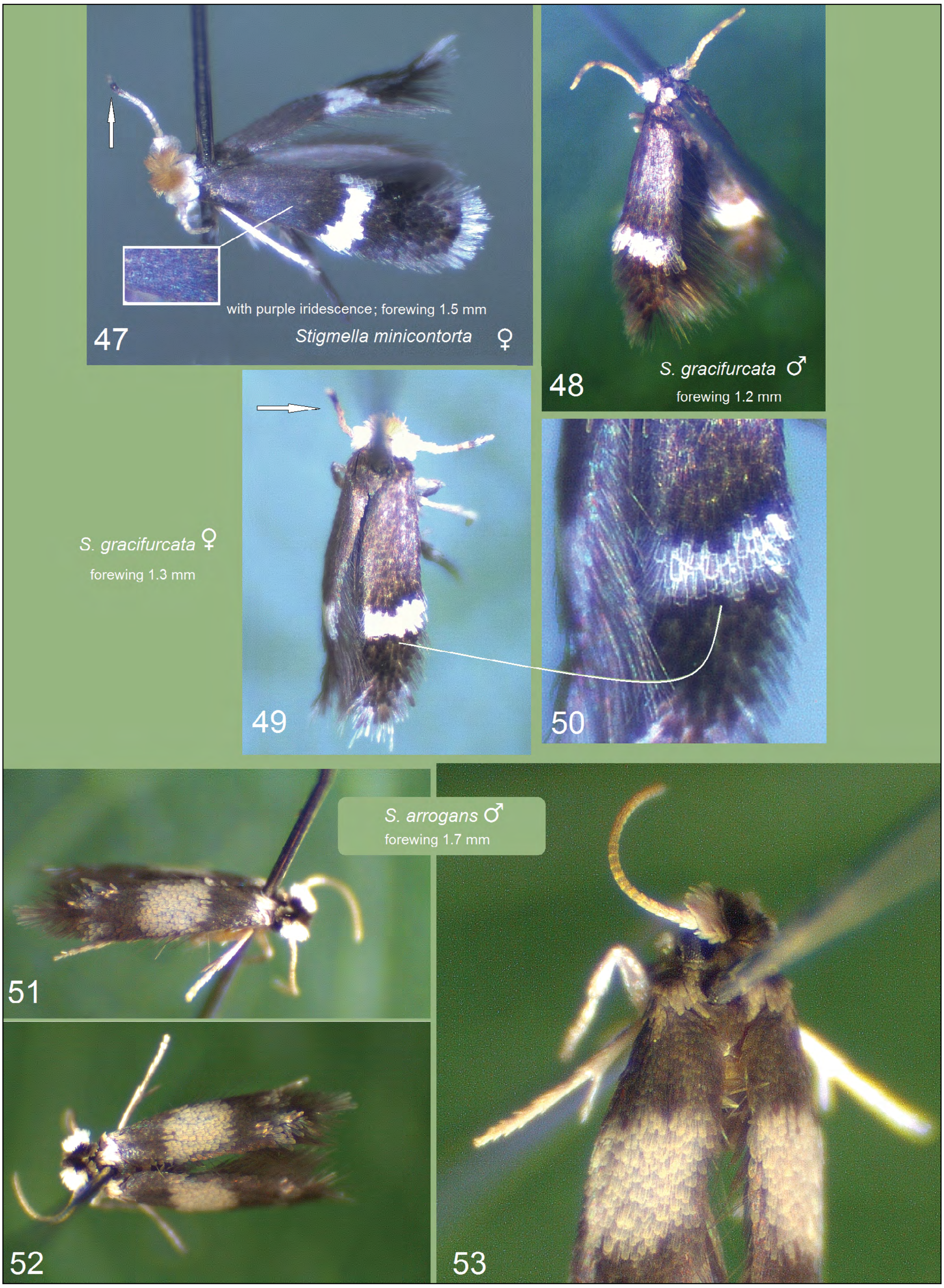
A detailed comparison of the studied genitalia with those of previously described species from South America (Stonis et al., 2014, 2022c) indicates that both species reared from *Nothofagus* represent new, yet undescribed taxa. While they belong to the *S. purpurimaculae* group, the specific combination of uncus, valva, vinculum, and phallus does not exactly match any previously described members of this group. Given the insufficient adult material, we refrain from formally naming the new species shown in Figs 40–43 and Figs 44–46.

Discovery of *Stigmella* species from distant Central America morphologically resembling the *Nothofagus*-feeding *S. purpurimaculae* group

Focused research in Honduras, conducted by the first author, has yielded unexpected discoveries. Sampling in various habitats of the tropical dry and humid forests using luminescent lanterns and LepiLED lamps produced taxonomically diverse material. Dissection of male genitalia of *Stigmella* species revealed three new taxa, each showing an unexpected morphological resemblance to the Patagonian *S. purpurimaculae* group. These three new *Stigmella* species (*S. minicontorta* Stonis,

Figs 40–46. Male genitalia of Nepticulidae species proven to mine leaves of *Nothofagus*. 40–43 – *Stigmella* sp. AD750 (BRG), a new species (left unnamed); 44–46 – *Stigmella* sp. AD757, another unnamed new species (BRG)

Remeikis & Diškus, sp. nov.; *S. gracifurcata* Stonis & Remeikis, sp. nov.; and *S. arrogans* Stonis & Diškus, sp. nov.) are described and named below (Figs 47–53). Due to the morphological resemblance of their male genitalia to those of the *S. purpurimaculae* group, all three new species from Honduras are considered as satellite species of the *S. purpurimaculae* group.



Figs 47–53. Adults of new *Stigmella* species from Honduras, Central America, considered here as satellite species of the *S. purpurimaculae* group. 47 – *S. minicontorta* Stonis, Remeikis & Diškus, sp. nov.; 48–50 – *S. gracifurcata* Stonis & Remeikis, sp. nov.; 51–53 – *S. arrogans* Stonis & Diškus, sp. nov.

Stigmella minicontorta Stonis, Remeikis & Diškus, sp. nov.

urn:lsid:zoobank.org:act:D1E7759C-6210-4A32-B37B-F07CDC8697F5

(Figs 47, 54–65)

Diagnosis. *Stigmella minicontorta* sp. nov. is considered a satellite species of the *S. purpurimaculae* group. Externally, adults of this new species resemble some other *Stigmella* species with a shiny transverse fascia on the forewing, but differ from all previously described species of the *S. purpurimaculae* group from Andean Patagonia, none of which possess such a fascia. In the male genitalia, *S. minicontorta* sp. nov. is easily distinguishable from all other *Stigmella* species (including the Patagonian members of the *S. purpurimaculae* group), but not from the closely related Honduran *S. gracifurcata* sp. nov., by the unique combination of long, slender lateral lobes of the vinculum, a single valval apical process, angular transtilla, and U-shaped gnathos. The new species can be further distinguished from *S. gracifurcata* sp. nov. by the distinct basal thickening of the phallus tube (which is less pronounced in *S. gracifurcata*) and the wide transverse plate of the gnathos. In the female genitalia, *S. minicontorta* sp. nov. differs from *S. gracifurcata* sp. nov. by weakly developed spines on the accessory sac, absence of lateral vaginal thickening, and wider coils of the ductus spermathecae.

Barcodes. We barcoded the male and female paratype specimens; the sequences are available in GenBank under the voucher/sample IDs: PV213457 and PV213458.

Male. Forewing length 1.1–1.2 mm; wingspan 2.5 mm (*n* = 2). Head: frons and palpi golden cream to brownish cream; frontal tuft bright orange to pale orange; collar and scape golden cream. Antenna shorter than half the length of the forewing; flagellum with about 18 segments, beige cream to cream, with 4–5 subapical segments being grey-black. Thorax, tegulae, and basal part of the forewing brown with purple iridescence; fascia of the forewing silvery shiny; apical part of the forewing coarsely scaled, blackish brown. Forewing underside brown, without spots or androconia. Hindwings grey to grey-brown on both upper side and underside, without androconia. Legs beige cream to cream, with brown to dark brown scales on the upper side. Abdomen dark brown on both upper and underside.

Female (Fig. 47). Forewing length 1.4–1.5 mm; wingspan 3.3–3.4 mm (*n* = 9). Flagellum with about 14–16 segments. Abdomen dark brown on the upper side, cream on the underside. Otherwise as in male.

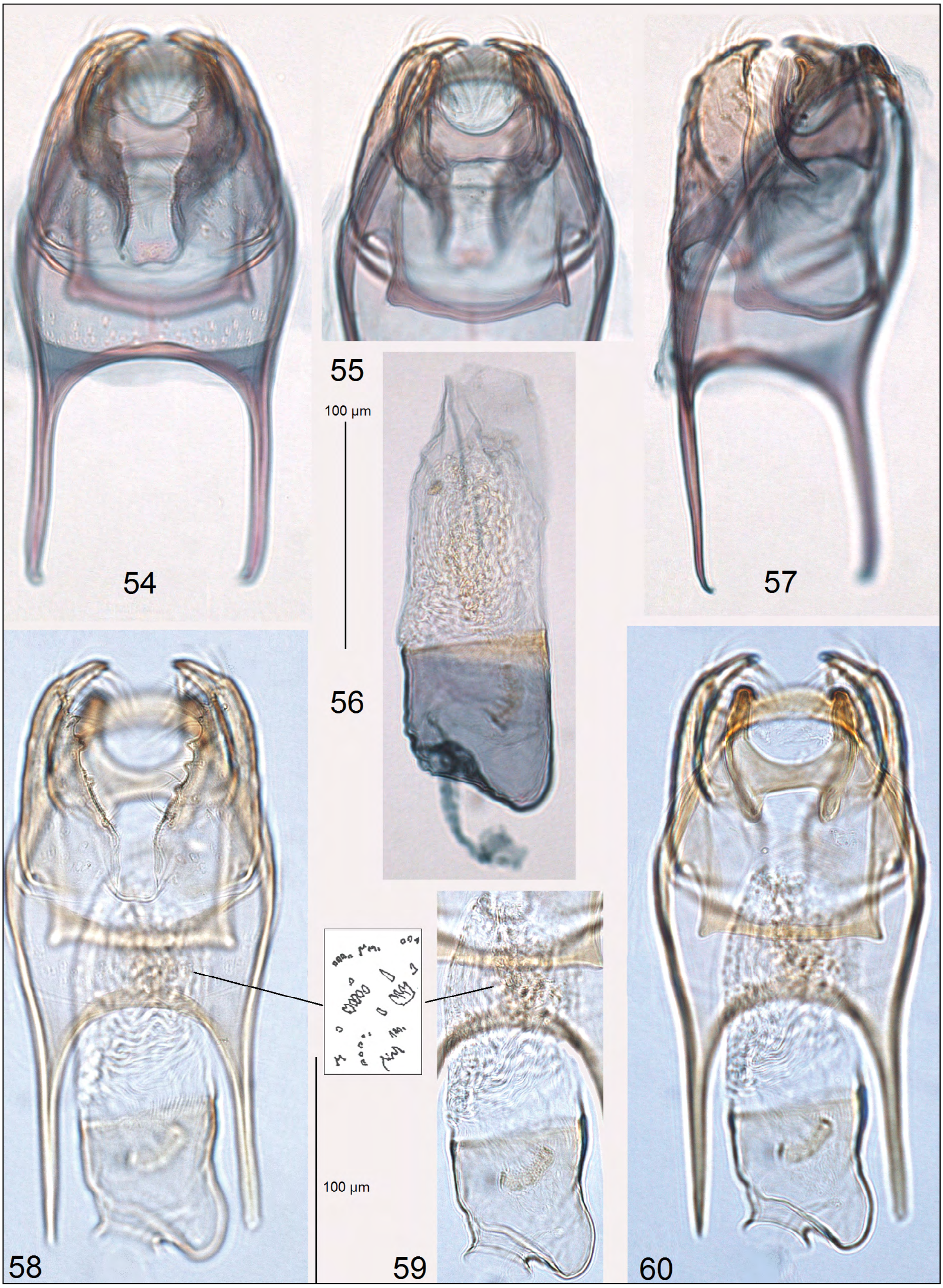
Male genitalia (Figs 54–60). Capsule much longer (240–250 μm) than wide (115–120 μm). Vinculum with two long and slender lateral lobes. Uncus broadly rounded medially, with short lateral lobes. Gnathos U-shaped, with a large transverse (central) plate. Valva triangular, 100–105 μm long, with inner lobe heavily papillated and pointed apical process; transtilla angular, without sublateral processes. Phallus 160–195 μm long, 65–70 μm wide; the phallus tube is thickened only in the basal part (50–70 μm), while the remaining part of the tube lacks thickening; vesica with numerous small irregular cornuti, some of them pecten-like or dentate. Manica absent.

Female genitalia (Figs 61–65). Total length about 350 μm. Ovipositor short but slender. Anterior apophyses longer than posterior apophyses. Vestibulum without thickening. Corpus bursae elongated, weakly thickened, without signa or pectinations, with some slender thickened spines in the area where the folded part of the bursae extends into the accessory sac. Accessory sac oval-shaped, with indistinct spines; ductus spermathecae with numerous heavily contorted slender coils and lobe-like coils extending into a large oval-shaped vesicle and further into a long, membranous utriculus.

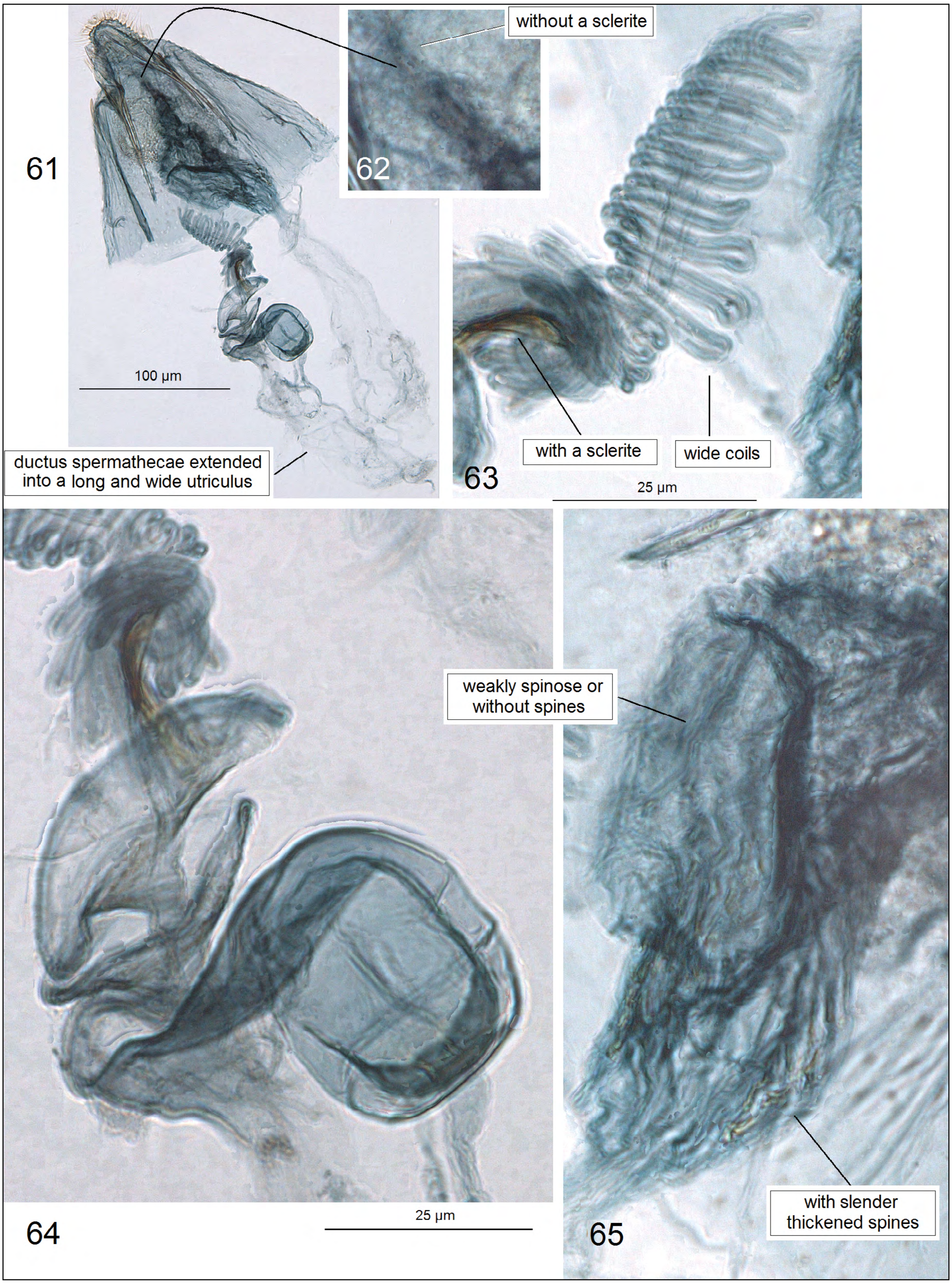
Bionomics. Adults fly in February–March, during the peak of the dry season. Otherwise, the biology is unknown.

Distribution. The new species occurs in the tropical dry forests along the Pacific coast of Honduras, including the nearby islands, at elevations of 10–40 m.

Type material. Holotype: ♂, HONDURAS, the Pacific, San Lorenzo, 1.5 km E by Pan American Hwy (left side), approx. 40 m,



Figs 54–60. Male genitalia of *Stigmella minicontorta* Stonis, Remeikis & Diškus, sp. nov. from Honduras. 54–57 – holotype, genitalia slide RA1214 (MfN); 58–60 – paratype, genitalia slide AD1161 (MfN)



Figs 61–65. Female genitalia of *Stigmella minicontorta* Stonis, Remeikis & Diškus, sp. nov. from Honduras. 61 – general view; 62–65 – details, paratype, genitalia slide RA1230 (MfN)

13°25'59.2"" N, 87°25'24.7"W, 6–7.ii.2023, leg. J. R. Stonis, genitalia slide no. RA1214♂ (MfN). Paratypes (3 ♂, 8 ♀): 1 ♂, Isla Zacate Grande, El Moray (near Terra Mar), 25 m, 13°21'28.5"N, 87°36'06.5""W, 11–12.ii.2023, leg. J. R. Stonis, genitalia slide no. AD1161♂ (MfN); 7 ♀, Isla Zacate Grande, El Moray (Restaurante Terra Mar), 20 m, 13°21'28.5"N, 87°36'06.5"W, 15–16 February 2023, leg. J. R. Stonis, genitalia slide no. RA1229♀ (MfN); 1 ♂, Isla del Tigre, Amapala, approx. 10 m, 13°17'41.3"N, 87°38'40.6"W, 17.iii.2023, leg. J. R. Stonis, genitalia slide no. RA1233♂ (only genitalia, adult taken for DNA study) (MfN); 1 ♀, Isla del Tigre, Amapala, Playa Grande, approx. 40 m, 13°16'32.3"N 87°39'37.5"W, 8.ii.2023, leg. J. R. Stonis, genitalia slide no. RA1230♀ (MfN); 1 ♂, Isla del Tigre, Amapala, Playa Caracol, approx. 20 m, 13°16'41,1"N, 87°39'29.5"W, 18.ii.2023, leg. J. R. Stonis, genitalia slide no. RA1235♂ (MfN).

Etymology. The species name is derived from the Latin *minimus* (smallest) and *contortus* (twisted or contorted), referring to the small size of the adults and the heavily contorted ductus spermathecae in the female genitalia of *Stigmella minicontorta* sp. nov.

Stigmella gracifurcata Stonis & Remeikis, sp nov.

urn:lsid:zoobank.org:act:62C1C61A-4383-4223-B2F6-167AA808534A

(Figs 48–50, 66–71)

Diagnosis. *Stigmella gracifurcata* sp. nov. is considered a satellite species of the *S. purpurimaculae* group. Externally, adults of the new species resemble a few other species of *Stigmella* with a shiny transverse fascia on the forewing but differ from all previously known species of the *S. purpurimaculae* group from Andean Patagonia, all of which lack a fascia. In the male and female genitalia, *S. gracifurcata* sp. nov. closely resembles the related Honduran species *S. minicontorta* sp. nov. (described above). It differs from the latter by the absence of a distinct basal thickening of the phallus tube (in *S. minicontorta* sp. nov., the basal part of the phallus tube is distinctly thickened, while the remaining part lacks this thickening) and by the slender transverse plate of the gnathos. In the female genitalia, *S. gracifurcata* sp. nov. differs from *S. minicontorta* sp. nov. by the distinctly spined accessory sac, lateral vaginal thickenings, and slightly more slender coils of the ductus spermathecae.

Barcode. We barcoded the male paratype specimen; the sequence is available in GenBank under the voucher/sample ID PV213456.

Male (Fig. 48). Forewing length 1.2–1.3 mm; wingspan 2.7–3.0 mm ($n = 2$). Thorax and basal part of the forewing dark brown (darker than in *S. minicontorta* sp. nov.), with little or no purple iridescence. Otherwise, as in *S. minicontorta* sp. nov. (see the description above).

Female (Figs 49, 50). Forewing length 1.3–1.4 mm; wingspan 3.0–3.3 mm ($n = 3$).

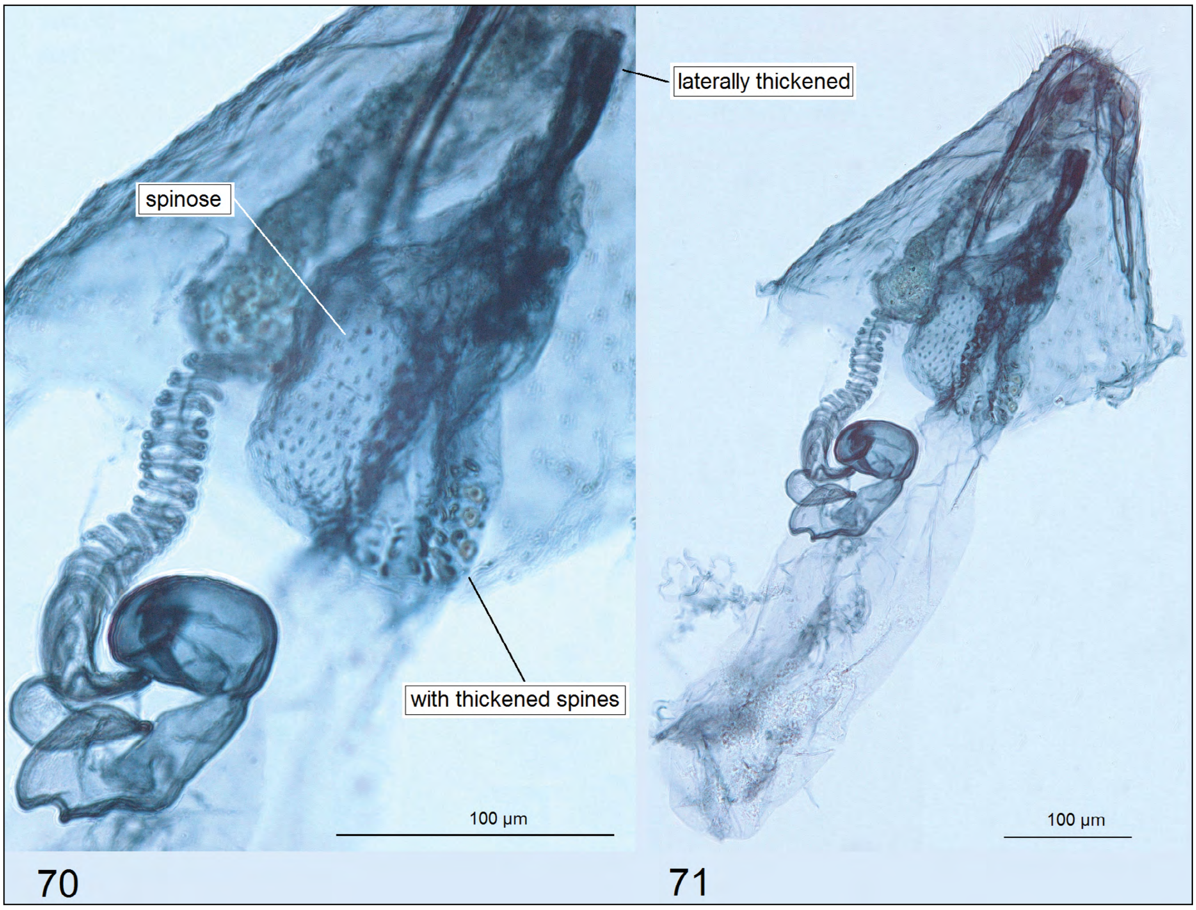
Male genitalia (Figs 66–69). Capsule much longer (230–270 μm) than wide (110–115 μm). Vinculum with two long and slender lateral lobes. Uncus broadly rounded medially, with short lobes laterally. Gnathos U-shaped, with a slender transverse bar (central plate). Valva triangular, 100 μm long, with an inner lobe slightly papillated and a pointed apical process; transtilla almost angular, with minuscule sublateral processes. Phallus 170–200 μm long, 55 μm wide; the phallus tube is irregularly thickened in the distal part; vesica with numerous minuscule irregular cornuti, some of which are pecten-like or dentate. Manica absent.

Female genitalia (Figs 70–71). Total length about 650 μm. Ovipositor short and truncated. Anterior apophyses slightly longer than posterior apophyses. Vestibulum thickened laterally. Corpus bursae elongated, weakly thickened, without signa or pectinations, with distinctive short thickened spines where the folded part of the bursae extends into the accessory sac. Accessory sac oval-shaped, distinctly spinose; ductus spermathecae heavily contorted, comprised of numerous slender coils and lobe-like coils extending into a large oval-shaped vesicle (the utriculus is likely broken and lost in Fig. 00).

Bionomics. Adults fly in April. Otherwise, the biology is unknown.

Distribution. The new species occurs in the tropical humid forests along the Caribbean

Figs 66–69. Male genitalia of *Stigmella gracifurcata* Stonis & Remeikis, sp. nov. from Honduras, holotype, genitalia slide RA1228 (MfN). 66–68 – capsule; 69 – phallus



Figs 70, 71. Female genitalia of *Stigmella gracifurcata* Stonis & Remeikis, sp. nov. from Honduras, paratype, genitalia slide RA1227 (MfN). 70 – enlarged view of accessory sac and ductus spermathecae; 71 – general view

Sea on the Atlantic coast of Honduras, at elevations of 10–30 m.

Type material. Holotype: ♂, HONDURAS, the Caribbean Coast, Tela (Las Palmas), approx. 30 m, 15°46'09.62"N, 87°23'15.49"W, 14–19.iv.2024, leg. J. R. Stonis, genitalia slide no. RA1228♂ (MfN). Paratypes: 2 ♂, 3 ♀, same label data as holotype, genitalia slide nos RA1227♀, RA1232♂ (adult taken for DNA examination), RA1234♂ (MfN).

Etymology. The species name is derived from the Latin *gracilis* (slender) and *furcatus* (forked or branched), referring to the distinctive, long, and slender lateral lobes of the vinculum in the male genitalia, which form a ‘fork’ shape.

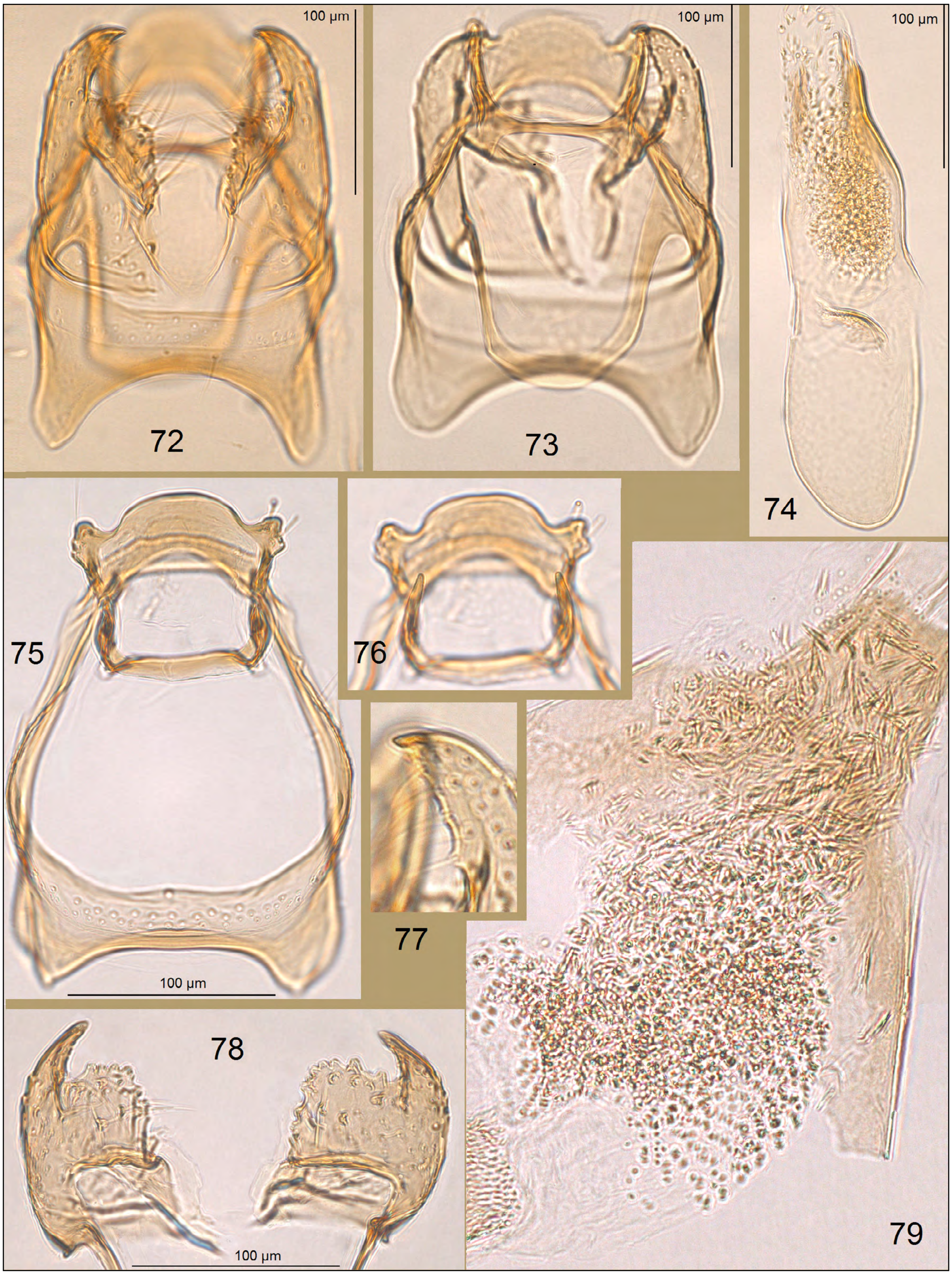
Stigmella arrogans Stonis & Diškus, sp. nov.

urn:lsid:zoobank.org:act:18F984CC-E9BD-4C4E-9F56-B2ED3E3D9487

(Figs 51–53, 72–79)

Diagnosis. *Stigmella arrogans* sp. nov. is considered a satellite species of the *S. purpurimaculae* group. Externally, the new species is distinguished by its unique scaling pattern: a dark grey forewing with blue and purple iridescence, featuring a wide median fascia composed of cream white scales and a slender, interrupted apical fascia of milky white scales (Fig. 51). The thorax and tegula are predominantly cream white, accented with distinctive patches of blackish grey scales (Fig. 53). In the male genitalia, *Stigmella arrogans* is characterised by a distinctive combination of morphological traits, including a large, rounded transtilla, robust valvae, and a wide uncus with pronounced sublateral lobes.

Barcode. We barcoded the male paratype specimen; the sequence is available in GenBank under the voucher/sample ID PV213455.



Figs 72–79. Male genitalia of *Stigmella arrogans* Stonis & Diškus sp. nov. from Honduras. 72 – holotype, capsule, genitalia slide AD1200 (MfN); 73, 74, 77 – paratype, capsule and phallus, genitalia slide AD1170 (MfN); 75, 76, 78 – paratype, dissected capsule, genitalia slide AD1171 (MfN); 79 – same, torn and squashed phallus with cornuti displayed

Male (Figs 51–53). Forewing length 1.6–1.7 mm; wingspan 3.8–4.0 mm. Head: palpi cream white; frontal tuft black to grey-black; collar dark grey, large, comprised of lamellar scales; scape cream white, large; antenna significantly shorter than half the length of the forewing; flagellum with 25–26 segments, glossy beige-cream, appearing pale grey at certain angles. Thorax and tegula predominantly cream white but with large patches of blackish grey scales. Forewing dark grey with blue and purple iridescence, wide median fascia composed of cream white scales, and slender, interrupted apical fascia of milky white scales; occasionally with a small cream white basal spot along the costal edge; fringe grey to white apically; forewing underside densely covered with blackish grey or grey scales. Hindwing grey on upper side and underside, without androconia; fringe pale grey. Legs glossy cream white, upper side covered with glossy grey scales with purple iridescence.

Female: Unknown.

Male genitalia (Figs 72–79). Capsule longer (245–255 μm) than wide (170–190 μm). Uncus wide, broadly rounded, with pronounced sublateral lobes (Fig. 81). Gnathos broadly U-shaped, with two slender caudal processes and small corners anteriorly; central plate of gnathos as a slender transverse bar. Valva 140–150 μm long, with a large, inwardly pointed apical process; inner lobe wide, heavily papillated. Transtilla large, rounded, without sublateral processes. Vinculum with a relatively short ventral plate and two wide but short lateral (anterior) lobes. Phallus 260–315 μm long, 70–90 μm wide; sclerotisation of the phallus tube unequal. Vesica with an apical patch of numerous small, slender, spine-like cornuti and a patch of tiny, irregular cornuti, some of which are dentate. Manica absent.

Bionomics. Adults were collected in tropical dry forests in February and March, during the peak of the dry season. Otherwise, the biology remains unknown.

Distribution. The new species occurs on the Pacific coast of Honduras, at elevations of 10–40 m.

Type material. Holotype: ♂, HONDURAS, the Pacific, Isla del Tigre, Amapala, Playa Grande, elevation approx. 40 m, 13°16'32.3"N 87°39'37.5"W, 13–14.iii.2023, leg. J. R. Stonis, genitalia slide no. AD1200 (MfN). Paratypes: 1 ♂, HONDURAS, the Pacific, Isla del Tigre, Amapala, elevation approx. 10 m, 13°17'41.3"N, 87°38'40.6"W, 17.iii.2023, leg. J. R. Stonis, genitalia slide no. AD1170 (MfN); 1 ♂, Amapala, Playa Caracol, elevation approx. 20 m, 13°16'41,1"N, 87°39'29.5"W, 18.ii.2023, leg. J. R. Stonis, genitalia slide no. AD1171 (MfN).

Etymology. The species name *arrogans* (Latin for 'arrogant' or 'proud') refers to the striking and distinguished appearance of the adult moth, as well as the prominent morphological characters of the male genitalia. The name highlights the 'outstanding' nature of the species and aligns with our preference for memorable and catchy names for new species.

DISCUSSION

Until now, it had only been speculated, but not conclusively known, that Nepticulidae mine the leaves of *Nothofagus* in Andean Patagonia. In this article, it is demonstrated for the first time with certainty that species of the *Stigmella purpurimaculae* group are leaf miners of *Nothofagus*: not only were various mines documented, but the male genital structures of two species reared from *Nothofagus* were also examined.

Stigmella lucida (Philpott), found in New Zealand, is also a leaf miner of *Nothofagus*. Therefore, it would be logical to assume that it might also belong to the *S. purpurimaculae* group. Indeed, the gnathos, valvae, and transtilla of this species align with the concept of the *S. purpurimaculae* group. However, the distinctly bilobed uncus and large, spine-like cornuti in the male genitalia, as well as the strongly folded and densely pectinate female genitalia, for now, do not provide sufficient grounds to include this species into the *S. purpurimaculae* group.

The current article also describes three new *Stigmella* species from Honduras. Two of these species, *S. minicontorta* sp. nov. and *S. gracifurcata* sp. nov., are characterised by particularly long and slender lateral lobes of the vinculum (a distinctive feature of the male genitalia) and distally darkened antennae. These two species are very closely related, differing only in some details of the male and female genitalia and slightly in external appearance. Interestingly, they are found in markedly different ecosystems: *S. gracifurcata* sp. nov. in humid forest, and *S. minicontorta* sp. nov. (like *S. arrogans* sp. nov., the third new species described in the article) in dry forest (Figs 80–84). Since all these species exhibit major traits clearly consistent with the *S. purpurimaculae* group, they have been assigned as satellite species of the *S. purpurimaculae* group.

While mentioning *S. minicontorta* sp. nov. and *S. gracifurcata* sp. nov. from Honduras, which in this article are linked with the *S. purpurimaculae* group, it is also worth noting *S. elegantiae* Puplesis & Diškus 2003, described from Nepal (Puplesis & Diškus, 2003). This species is currently assigned by us to the small *S. incognitella* group, but like the Honduran *S. minicontorta* sp. nov. and *S. gracifurcata* sp. nov., it exhibits long, slender lateral lobes of the vinculum and partial thickening of the phallus tube in the male genitalia, as well as a strongly elaborated ductus spermathecae in the female genitalia. However, in *S. elegantiae*, the female corpus bursae is adorned with prominent scaphoid-like pectinations, while the male uncus is not bilobed (instead, it is a single rectangular plate). Additionally, the valvae have two apical processes, the gnathos is H-shaped and highly elaborate, and the juxta is present. Therefore, despite the initial similarity, the Himalayan *S. elegantiae* likely should not be associated with the *S. purpurimaculae* group.

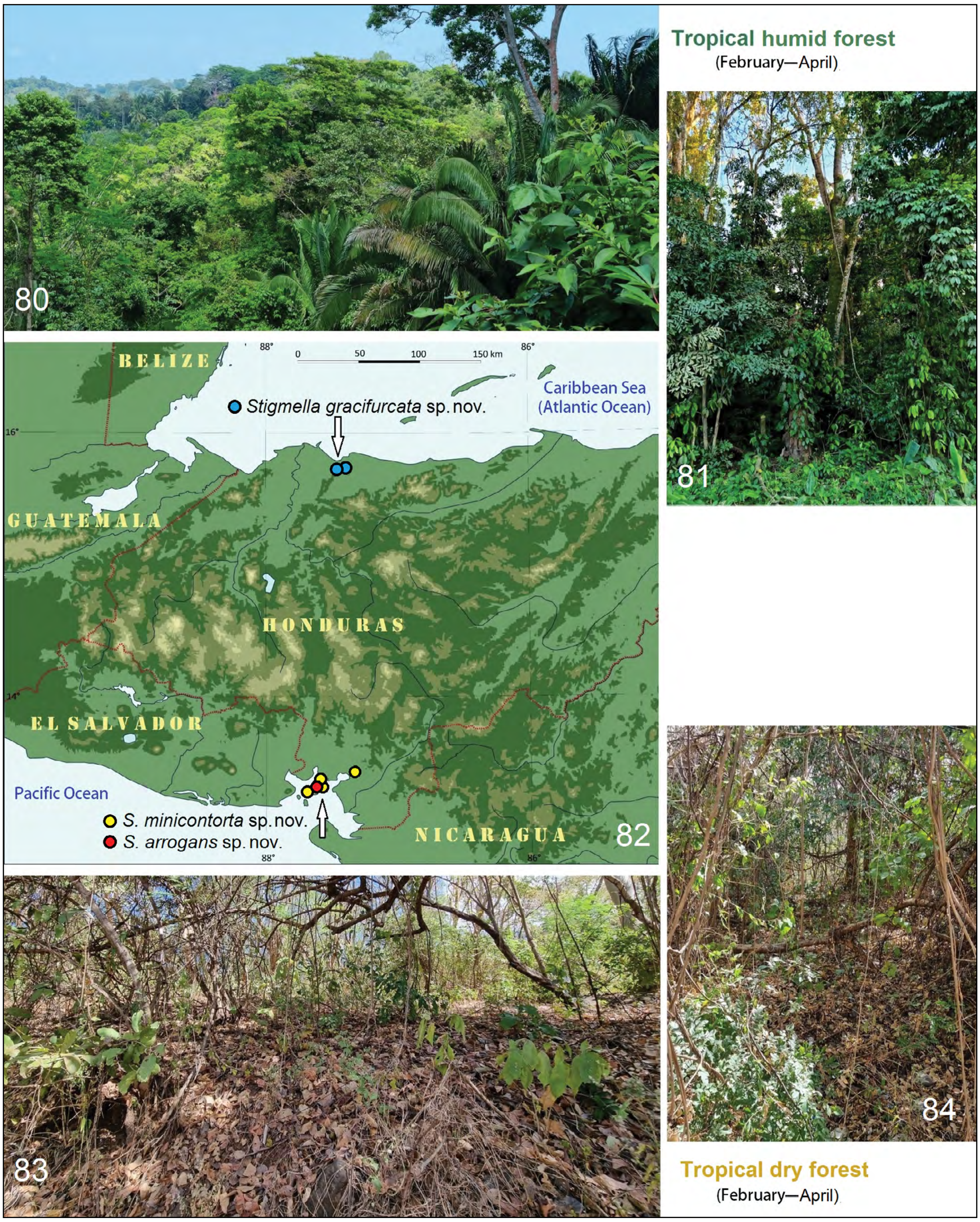
The discovery of three new species from Honduras, currently linked to the *S. purpurimaculae* group, not only enhances our understanding of Nepticulidae diversity in Central America but also raises an intriguing question: is the morphological resemblance of their male genitalia to those of the Patagonian *S. purpurimaculae* group incidental, or does it indicate a significant evolutionary connection?

In Central America, which is geographically very distant from Andean Patagonia (Fig. 85), *Nothofagus* does not grow and has never grown. However, in the male morphology, the three new *Stigmella* species discovered in Honduras fundamentally align with the concept of the *S. purpurimaculae* group based on genital characteristics. On the other hand, it should also be noted that externally, the new species from Honduras are not completely identical to the species from Andean Patagonia. Unlike the Patagonian species, the Honduran species are characterised by a fascia on the forewings and distally darkened antennae.

A particularly distinctive scale pattern is exhibited by *S. arrogans* sp. nov.; externally (but not in genital structures), this species somewhat resembles the species of the North and Central American *S. saginella* group, which are leaf miners of oaks (*Quercus*). Given that Honduras has a diverse flora of *Quercus*, it could be speculated that *S. arrogans* sp. nov., or perhaps even all three new *Stigmella* species from Honduras, are potentially trophically associated with Fagaceae, which, like Nothofagaceae, belong to the same order, Fagales. It is noteworthy that Siniscalchi et al. (2023) proposed that Nothofagaceae, unknown from the North American fossil record, may have dispersed from North America to South America in a single event before 45 Ma. Conversely, we rely on evidence presented by Vento et al. (2022), which identifies Antarctica as the origin of *Nothofagus*.

The results of our molecular analysis became available only after the submission of the article; therefore, they have been included here, in the Discussion. First and foremost, our molecular study clearly differentiated two closely related species, *S. minicontorta* and *S. gracifurcata*, and naturally confirmed the distinctiveness of *S. arrogans*.

When all three new species from Honduras were analysed together, they grouped with American species that are trophically associated with *Quercus*. In most cases, *S. minicontorta* and *S. gracifurcata* clustered within the American *Quercus*-feeding groups as a sister clade to the North American *S. procrastinella* + *S. quercipulchella* groups. Meanwhile, the Honduran *S. arrogans* typically



Figs 80–84. Habitats and a distribution map of three new species of the *Stigmella purpurimaculae* group from Honduras, Central America. 80–81 – tropical humid forest, habitat of *S. gracifurcata* Stonis & Remeikis, sp. nov.; 82 – distribution map; 83–84 – tropical dry forest, habitat of *S. minicontorta* Stonis, Remeikis & Diškus, sp. nov. and *S. arrogans* Stonis & Diškus, sp. nov.

Note: In the current study, we follow the classification by the Hierarchy Revisions Working Group, Federal Geographic Data Committee (Faber-Langendoen et al. 2016). According to this classification, within the subclass of Tropical Forest & Woodland, the Tropical Lowland Humid Forest (code 1.A.2/F020) is categorised as a formation, along with tropical montane humid forest, tropical flooded & swamp forest, mangrove forest, and tropical dry forest & woodland formations.

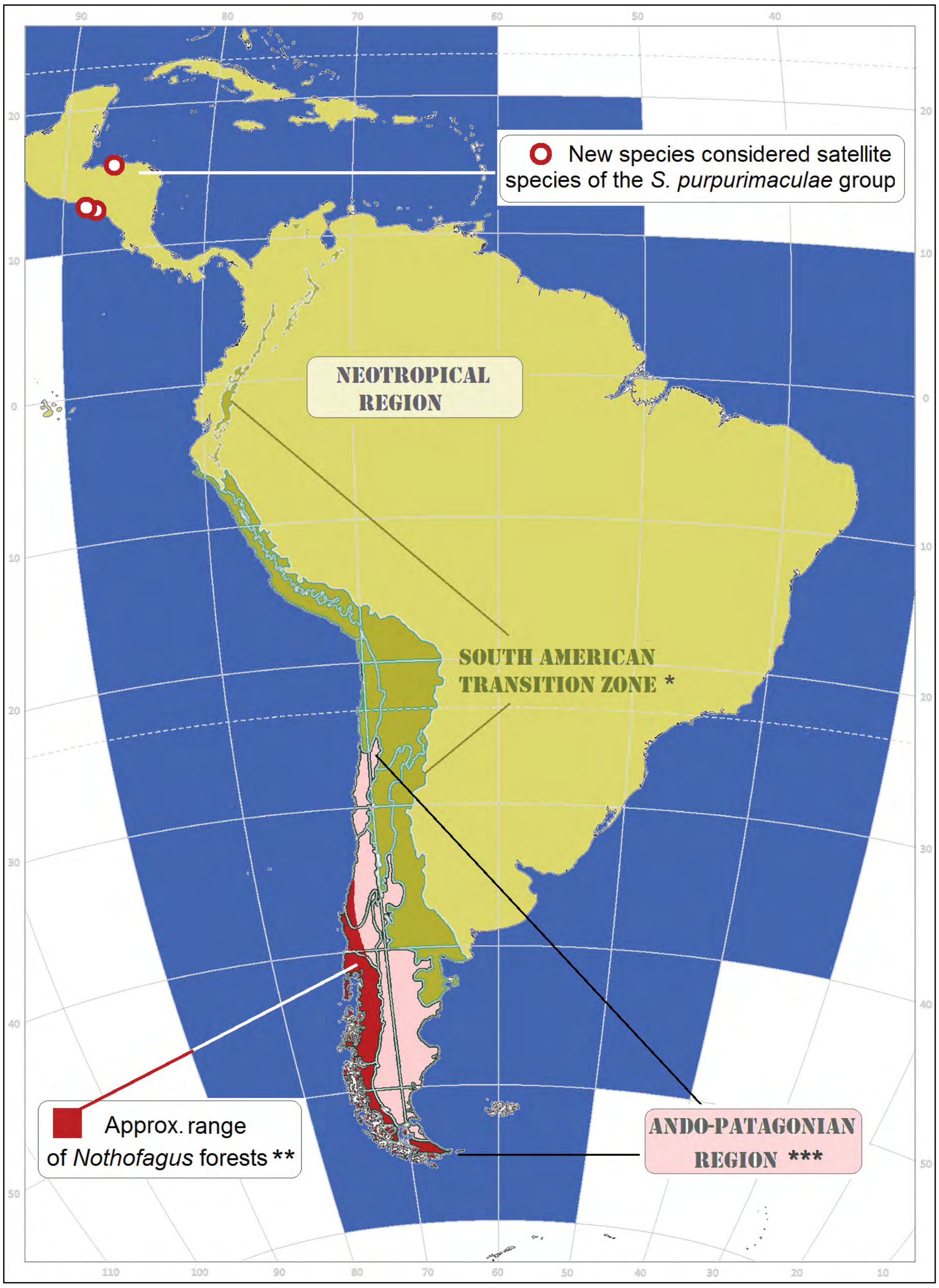


Fig. 85. Schematic map of the Neotropical and Ando-Patagonian regions showing the approximate distribution range of *Nothofagus*, host plants for species of the *Stigmella purpurimaculae* group, and the distribution of three newly discovered species from distant Honduras, Central America.

* after Morrone, 2015 and Stonis et al., 2022c; ** after Swenson et al., 2001; *** after Morrone, 2015, but with a new name by Stonis et al., 2016

appeared as a separate, basal lineage to all American *Quercus*-feeding groups (Fig. 86). Only in some instances did *S. arrogans* cluster closely with *S. minicontorta* + *S. gracifurcata* (Fig. 87). However, in these cases, the molecular trees were poorly resolved and exhibited

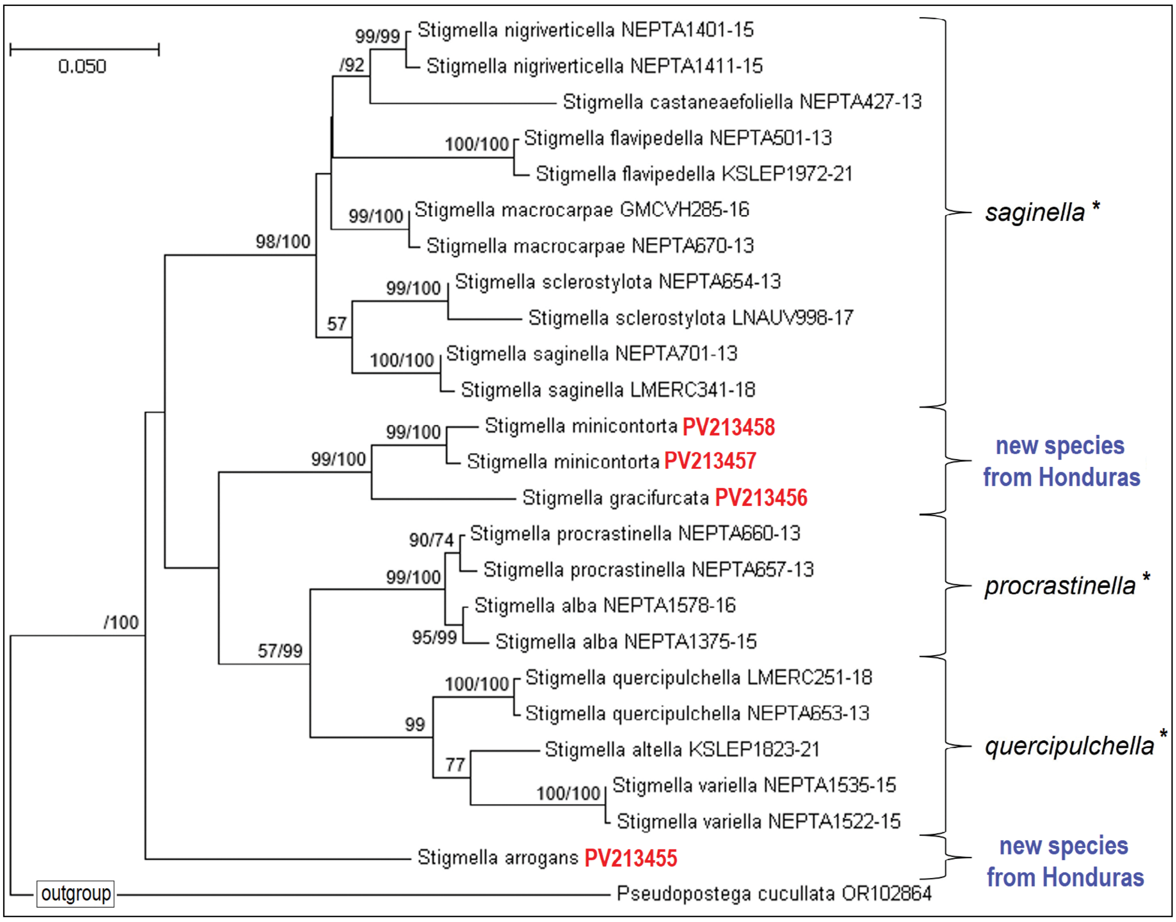


Fig. 86. Phylogenetic tree of *Stigmella minicontorta* Stonis & Remeikis, sp. nov., *S. gracifurcata* Stonis & Remeikis, sp. nov., and *S. arrogans* Stonis & Diškus, sp. nov. in relation to the recognised American *Quercus*-feeding groups (marked with *), based on 657 bp mtDNA COI-5' sequences. Statistics of branches: maximum likelihood probability (10,000 bootstrap replicates) / Bayesian posterior probability (10,000,000 generations) in % (values below 50 are not shown). *Pseudopostega cucullata* (Opostegidae) was included as an outgroup.

comb-like branching. Considering this, along with the distinct external morphology of *S. arrogans* compared to *S. minicontorta* and *S. gracifurcata*, we conclude that *S. arrogans* should not be included in the same species group as *S. minicontorta* and *S. gracifurcata*.

Moreover, the molecular study revealed that none of the newly described Honduran species, whose male genitalia resemble those of the Patagonian *S. purpurimaculae* group, belong to any of the currently known *Quercus*-feeding groups. While they are closely related to the American groups trophically associated with *Quercus* (and are presumably *Quercus*-feeding in Honduras), the Honduran species may represent two distinct species groups, one of which could be either the *S. purpurimaculae* group itself or a closely related lineage. However, for the time being, this hypothesis remains unresolved as no molecular data are currently available for the Patagonian *S. purpurimaculae* group. In any case, the discovery of the Honduran species, which exhibit male genitalia similar to those of the *S. purpurimaculae* group, provides further evidence of an evolutionary link between the Patagonian *Nothofagus*-feeding *S. purpurimaculae* group and the North American *Quercus*-feeding species.

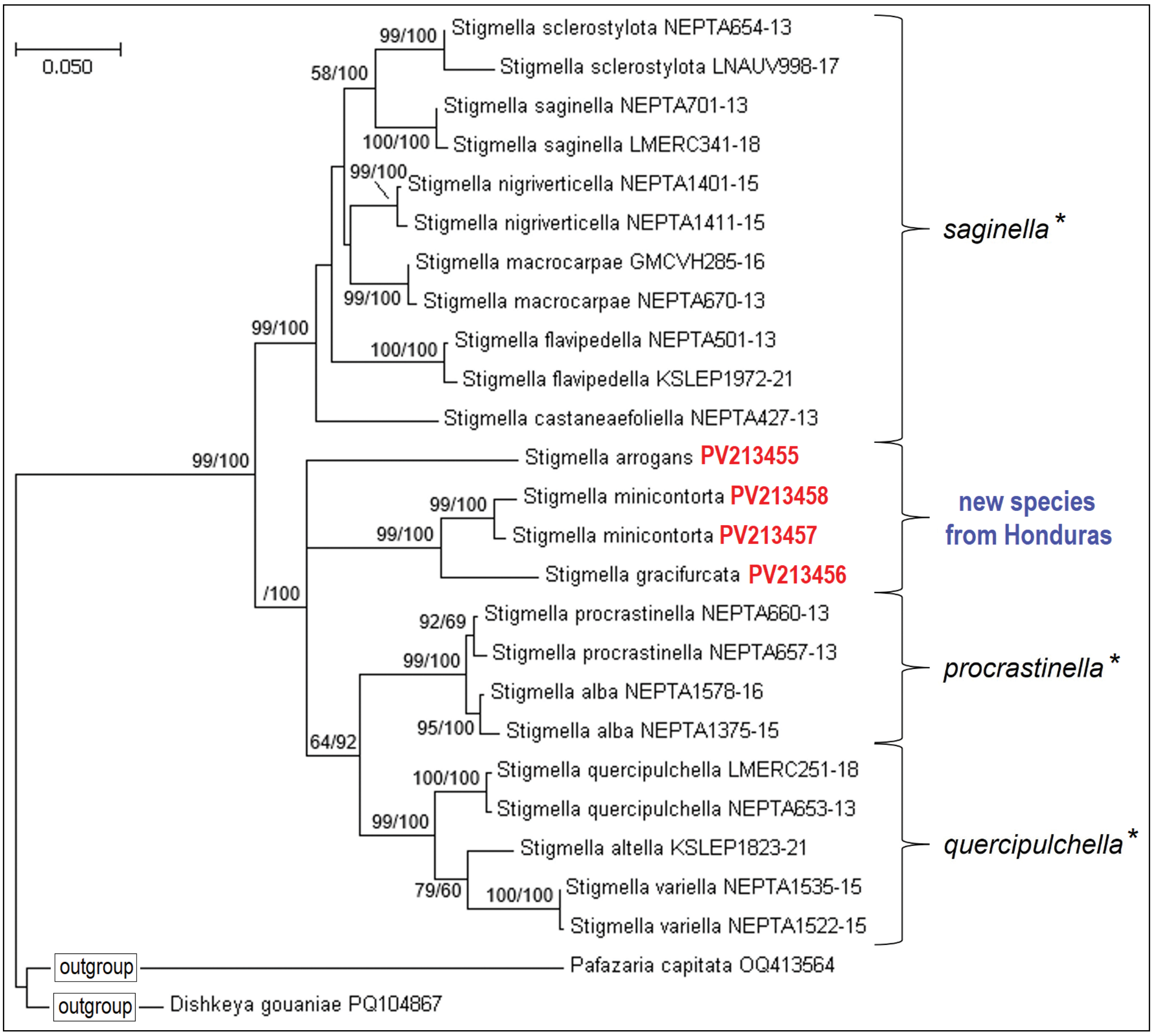


Fig. 87. Alternative phylogenetic tree of *Stigmella minicontorta* Stonis & Remeikis, sp. nov., *S. gracifurcata* Stonis & Remeikis, sp. nov., and *S. arrogans* Stonis & Diškus, sp. nov. in relation to the recognized American *Quercus*-feeding groups (marked with *), based on 657 bp mtDNA COI-5' sequences. Statistics of branches: maximum likelihood probability (10,000 bootstrap replicates) / Bayesian posterior probability (10,000,000 generations) in % (values below 50 are not shown). *Pafazaria capitata* and *Dishkeya gouaniae* (Tischeriidae) were included as an outgroup.

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PIRMĄ KARTĄ NUSTATYTA, KAD ANDŲ PATAGONIJOJE NEPTICULIDAE MINUOJA RELIKTINIUS GONDVANOS *NOTHOFAGUS*, MORFOLOGIŠKAI PANAŠIŲ MAŽŲJŲ GAUBTAGALVIŲ RŪŠIŲ APTIKTA IR TOLIMOJE CENTRINĖJE AMERIKOJE

Santrauka

Šiame straipsnyje pirmą kartą pateikiami įrodymai apie mažųjų gaubtagalvių (Nepticulidae) mitybinius ryšius su reliktiniais *Nothofagus* Patagonijoje, Pietų Amerikoje. Aprašytos Nepticulidae minos ir dokumentuotos dviejų naujų *Stigmella purpurimaculae* grupės rūšių, minuojančių *Nothofagus* lapus, genitalinės struktūros. Taip pat aprašomos trys naujos *Stigmella* rūšys iš Hondūro, kurios, nepaisant geografinio atstumo nuo Patagonijos, pasižymi tomis pačiomis genitalijų morfologijos ypatybėmis kaip ir *S. purpurimaculae* grupės rūšys Pietų Amerikoje. Tai kelia klausimų apie galimus evoliucinius ryšius tarp reliktinius *Nothofagus* minuojančių *S. purpurimaculae* grupės rūšių ir morfologiškai panašių *Stigmella* rūšių Centrinėje Amerikoje.

Raktažodžiai: Andų ir Patagonijos regionas, Argentina, Hondūras, lapų minos, mažieji gaubtagalviai, mitybiniai augalai, neotropinis regionas