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# What are the smallest moths (Lepidoptera) in the world?

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## Abstract

The world's smallest moths in Lepidoptera (Insecta) and the complexity in making such a determination are examined and discussed. The forewing length and wingspan of 650 species were measured and the same data were retrieved from published papers to determine which species and family have the smallest moths in the world. The minimal recorded forewing length was found to be around 1.2–1.3 mm and the wingspan around 2.6–2.8 mm in two families, the Gracillariidae and Nepticulidae. Among Lepidoptera, the following species have the smallest moths globally: the European *Johanssoniella acetosae* (Stainton), the Peruvian *Simplimorpha kailai* Stonis & Diškus, the Mexican *Stigmella maya* Remeikis & Stonis, the Mediterranean *S. diniensis* (Klimesh), the Mediterranean *Parafomoria liguricella* (Klimesh) (Nepticulidae), the South East Asian *Porphyrosela alternata* Kumata, and the Central African *P. desmodivora* De Prins (Gracillariidae). Additionally, in the Nepticulidae, we provide a measurement update for *Stigmella maya* Remeikis & Stonis, one of the tiniest species with a forewing length of 1.3 mm and wingspan of 2.8 mm, and describe a new species, *Stigmella incaica* Diškus & Stonis, sp. nov., with a forewing length of 1.75 to 1.95 mm and a wingspan of 3.8 to 4.3 mm.

**Key words:** Gracillariidae, Opostegidae, Nepticulidae, Tischeriidae, pygmy moths, small-size record holders

## Introduction

This publication was inspired by a discussion at the science portal ResearchGate.net (García-Barros *et al*. 2016). Enrique García-Barros (Universidad Autónoma de Madrid, Spain) raised the question: "What is the smallest moth in the world?". He wrote that we are "more impressed by the higher figures (the oldest tree, the heaviest vertebrate…) than by the minima" and often we "read about the largest moths, *Thysania*, *Attacus*" (García-Barros *et al*. 2016), but not the smallest moths.

In the specialized literature on Lepidoptera, the superfamily Nepticuloidea comprises some of the smallest Lepidoptera known (Davis 1999; Davis & Stonis 2007; Stonis *et al*. 2020d). Moreover, in Nepticulidae, or pygmy moths, their size has been emphasized, i.e., containing "some of the smallest lepidopterans" (Scoble 1983) or calling nepticulids "the smallest lepidopterans in the world" (Puplesis 1994; Diškus & Stonis 2012; Stonis *et al*. 2020c). Recently, David C. Lees (The Natural History Museum, London) in a published interview stated that the Mexican *Stigmella maya* Remeikis & Stonis and the smallest British nepticulid species, *Johanssoniella acetosae* (Stainton), are the smallest moths (Pavid 2016).

For the record, we provide a measurement update for *Stigmella maya*, discuss the world's tiniest moths, and, as an example of pygmy moths, describe one new species, *Stigmella incaica* Diškus & Stonis, **sp. nov.**, an Andean nepticulid species with a forewing length that ranges from 1.75 to 1.95 mm (and wingspan from 3.8 to 4.3 mm).

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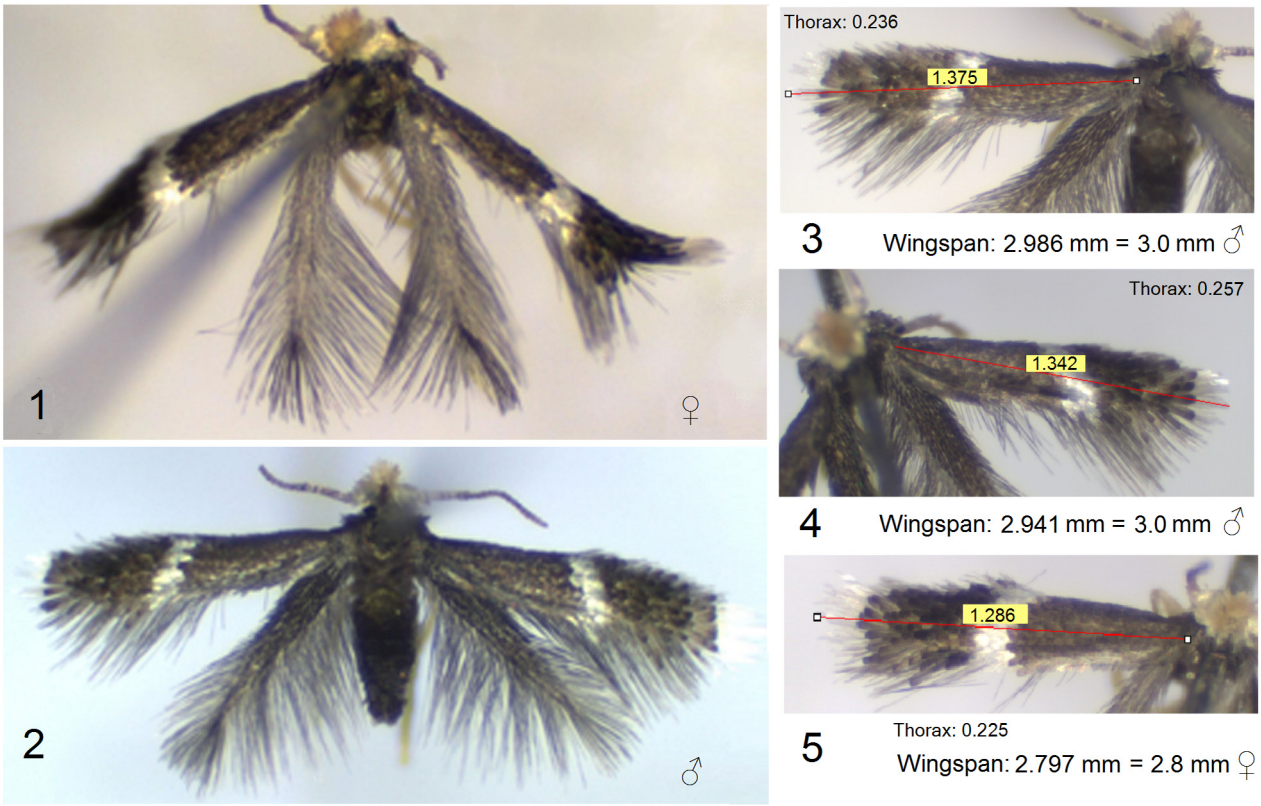
## Material and Methods

The description of the new species, *Stigmella incaica* sp. nov., is based on a series of ten specimens collected by a Quechua collector in Peru and deposited in the collection of Zoological Institute of the Russian Academy of Sciences (ZIN), St. Petersburg, Russia. The measurement update of *Stigmella maya* Remeikis & Stonis was conducted with specimens located in the collection of the Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark (ZMUC).

Prior to our current paper, during a decades-long preparatory period, we measured forewing length and wingspan for about 2800 specimens of the smallest moths belonging to approximately 650 species. For the forewing measurements, adults were measured from the very base of the forewing to the end of the apical cilia; for the wingspan measurements, the thorax was measured across, then, to have the full expanse of the moths, one forewing length was doubled and added to the thorax measurement. Adults of *S. maya* were measured using a Lomo MBS-10 stereomicroscope and repeated for confirmation of the measurements by a Leica S6D stereoscopic microscope with an attached Leica DFC290 digital camera.

Preparation of permanent micro-mounts of genital structures in Euparal were undertaken following the conventional method described by Stonis *et al.* (2014a). Permanent slides were photographed and studied using a Leica DM2500 microscope and Leica DFC420 digital camera.

In order to clarify our terminology regarding the word "small", we created the following key to indicate different size categories of small moths in this paper: medium small (wingspan > 6.0 mm); small (wingspan = 5.0–6.0 mm); very small (wingspan = 4.0–4.9 mm); and extremely small (wingspan < 4.0 mm) (also includes small-size record holders).




**FIGURES 1–5.** *Stigmella maya* Remeikis & Stonis, SE Mexico, Yucatán (ZMUC). 1, female paratype; 2, male paratype with black androconia on the hindwings; 3–5, a measurement update

## A measurement update for the record-small *Stigmella maya*, Nepticulidae

We found that *Stigmella maya* Remeikis & Stonis (Figs 1, 2), described from Yucatán, SE Mexico (Stonis *et al.* 2013c), is among the smallest moths described in the Nepticulidae. In this study, we made additional, more consistent measurements of adult specimens comprising of two males and one female (Figs 3–5), and we can confirm that

earlier published measurements of the forewing and wingspan (Stonis *et al*. 2013c) are correct. In this study, the forewing length varied from 1.29 (Fig. 5) to 1.38 mm (Fig. 3), and the wingspan from 2.8 to 3.0 mm. The difference between the early and current measurements is insignificant, and is probably due to sample size, i.e., we had access to only three specimens of the six specimens included in the *S. maya* primary type series for our original study.

### What Nepticulidae species "look like" sizewise

According to our database, the family Nepticulidae, or pygmy moths, is comprised of 995 described species globally, including 11 recently described species from Asia (Stonis *et al*. 2020c). About a dozen additional species are documented, but unnamed.

Although Nepticulidae are especially famous for their small-sized or minuscular moths, adults of some species are real "monsters" among the pygmy moths. Notably, a few North American *Ectoedemia* Busck species have wingspans exceeding 8 mm. The wingspan of *E. grandisella* (Chambers) was reported to be about 10 mm (Wilkinson 1981), in *E. heinrichi* Busck the wingspan ranges from 8 to 10.5 mm, and in *E. phleophaga* Busck from 8.3 to 10.6 mm (Wilkinson & Newton 1981). The largest-size record probably belongs to two documented, but unnamed North American *Ectoedemia* specimens: "specimen 170" with a very large wingspan of 11 mm and "specimen 180" with a reported wingspan of 12.5 mm (Wilkinson 1981). Some examples of genera from the Palaearctic with large-sized pygmy moths are *Ectoedemia*, *Fomoria* Beirne, *Trifurcula* Zeller, *Etainia* Beirne, and *Bohemannia* Stainton (van Nieukerken 1985b; Johansson *et al*. 1990; Puplesis 1994), and a few large *Glaucolepis* Braun and *Simplimorpha* Scoble were recently described from Chile and Argentina (Stonis *et al*. 2017d, 2018c).

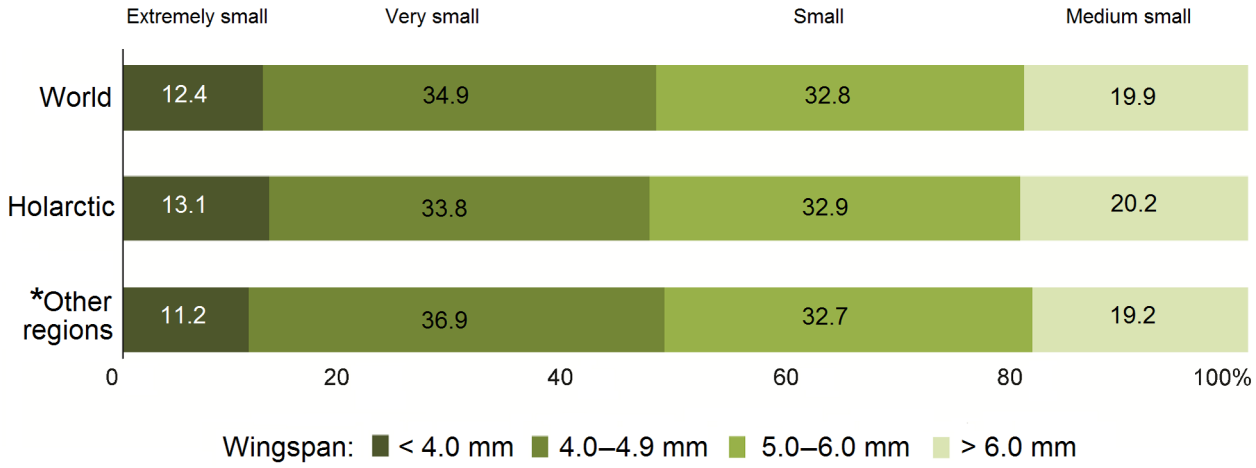



**FIGURE 6.** Number of Nepticulidae species with different parameters of wingspan in the world, Holarctic, and other, mostly tropical and subtropical regions (in %)

Note that species with moths distinctly in two size categories were counted for both corresponding categories, e.g., the North American *Stigmella villosella* (Clemens) with the wingspan range of 2.8 mm to 4.6 mm was counted twice, in the category "<4.0" and in category "4.0–4.9 mm";

*—The Holarctic includes the Palaearctic and Nearctic, with predominantly boreal and some subtropical habitats, while "other regions" in the graph are mostly represented by tropical and subtropical habitats, and include the following biogeographical regions: Neotropical, Afrotropical, Oriental, Australian, and Pacific

To investigate what portion of the Nepticulidae is comprised of very small and extremely small moths, we recorded measurements for about 85% of the currently known global fauna. The actual data were retrieved from our exhaustive species database with measurements, as well as from published references. A few of them are listed further in the text, and a small, freely selected portion of further uncited references are provided here as principally important papers for the current study: Wilkinson (1979); Wilkinson & Scoble (1979); Newton & Wilkinson (1982); Scoble (1983); Kemperman & Wilkinson (1985); Donner & Wilkinson (1989); van Nieukerken (1985a, 1990, 2007a, 2007b, 2019); Hoare *et al*. (1997); Hoare (2000a, 2000b); Puplesis & Robinson (2000); van Nieukerken & Liu (2000); van Nieukerken *et al.* (2010); Stonis & Rocienė (2013); Rocienė & Stonis (2013); and Hoare & van

Nieukerken (2013). Recently, based on new discoveries of Nepticulidae in the Neotropics, many new measurement data became available because Stonis *et al*. (2013a, 2013b, 2016, 2017a, 2017b, 2017c, 2018a, 2018b, 2018c, 2020b); Remeikis & Stonis (2015); Stonis & Remeikis (2015, 2017, 2018), and many others (a few are cited further in the text).

We estimate that in the global fauna of Nepticulidae, many species have a wingspan ranging either from 4.0 to 4.9 mm (34.9%) or from 5.0–6.0 mm (32.8%), accounting for a combined 68% of the world nepticulid fauna (Fig. 6). The extremely small species, with a forewing length of less than 1.8 mm or a wingspan less than 4.0 mm comprise about 12% of the world fauna.

Erik J. van Nieukerken in García-Barros *et al*. (2016) stated that "the smallest are tropical species, usually unnamed ones." Indeed, we found many to be some of the smallest moths in our extensive studies of material collected in the Caribbean, Central America and tropical South America. However, we found that there was no difference in the forewing and wingspan length between the Holarctic species found primarily in boreal habitats and species from other regions with predominantly tropical and subtropical habitats ($\chi 2 = 3.23$, df = 3, p = 0.36). Therefore, a slightly higher share of the moths with a wingspan < 4.0 mm in the Holarctic (13.1%), compared to 11.2% in other regions (Fig. 6), is not enough to support the hypothesis that smaller species predominate in tropical regions. Additional, different studies comparing taxa with strictly separated tropical fauna from the boreal regions may be necessary. On the other hand, our considerable studies in tropical areas of the world show that there is still a lot of hidden species diversity in the tropics that has yet to be discovered.

Our study revealed that more than a hundred species have a minimal wingspan of less than 4.0 mm. These species are characteristic of various genera of Nepticulidae, and are particularly abundant in *Stigmella* Schrank, less so in *Acalyptris* Meyrick, *Johanssoniella* Borkowski, *Simplimorpha* Scoble, *Ozadelpha* van Nieukerken, *Ectoedemia* Busck, *Paraformoria* van Nieukerken, and a few other genera. Twenty extremely small Nepticulidae species and their measurements are provided in Table 1.

## Range of the forewing and wingspan measurements

Based on the data provided in Tables 1 and 2, we provide wingspan ranges of the smallest Nepticulidae and Gracillariidae (Fig. 7). The average size of the series (*n*) on which the wingspan ranges were estimated is relatively small: both in Nepticulidae and Gracillariidae n = 12. Because primary descriptions and current knowledge about some small-sized moths were based on a single specimen, there is no wingspan range for several species, e.g., *Simplimorpha kailai*, *Stigmella dominicanus*, *Acalyptris amazonius, Hyloconis luki, Porphyrosela homotropha, Phyllonorycter lantanae, Phyllocnistis kawakitai,* and *P. norak.*

Wingspan ranges among the species of the smallest Nepticulidae and Gracillariidae vary strongly. We designated the range between 2.6 mm (the minimal recorded wingspan) and 3.2 mm as the category for small-size record holders (In Fig. 7, it is marked in red). Six species of Gracillariidae and 14 species of Nepticulidae fall into this category. However, although some species (*Simplimorpha kailai*, *Stigmella maya*, *S. diniensis*, *S. condiliafoliella*, *S. gossypi*, *Acalyptris amazonius*, *Hyloconis luki*, *Porphyrosela desmodivora*, and *P. homotropha*) fully fit within this category of small-size record holders, four have an unknown range because each is known only from a single specimen. Some species from the category of small-size record holders have an upper limit of the wingspan range that is relatively high (including *Johanssoniella acetosae*, *Stigmella semiaurea*, *Ectoedemia picturata*, *Porphyrposela dorinda,* and particularly *Parafomoria liguricella*, *Porphyrposela alternata*, and *P. gautegi*).

The ranges of wingspan (or forewing length) seem very important in the general understanding of size in an entire species because upper and lower limits of individual measurements can be misleading. Sample size is important to determine whether the species is one of the smallest moth species because variation can be significant among specimens. For example, in a series of about 50 specimens of *Johanssoniella acetosae*, bred by an independent researcher Thomas Sobczyk, the measurement of the forewing ranged from 1.13 mm to 1.9 mm (Table 1). If the measurement 1.9 mm is the common length in Nepticulidae, the measurement of 1.13 mm of some specimens of *J. acetosae* may make it appear as if *J. acetosae* is the smallest ever recorded pygmy moth or Lepidoptera.

**TABLE 1.** Measurements of selected smallest Nepticulidae

| Species | Forewing (mm) | Wingspan (mm) | References |
|---|---|---|---|
| *Johanssoniella* acetosae* (Stainton), Europe | 1.13–1.9 | 2.65–4.1<br>3.0–4.0 | García-Barros *et al.* 2016**<br>García-Barros *et al.* 2016*** |
| *Simplimorpha kailai* Stonis & Diškus, Peru | 1.3 | 3.0 | Stonis *et al.* 2018c |
| *Stigmella maya* Remeikis & Stonis, Mexico | 1.3–1.5<br>1.3–1.4 | 2.8–3.2<br>2.8–3.0 | Stonis *et al.* 2013<br>Our current study |
| *Stigmella diniensis* (Klimesch), Europe | 1.3–1.6 *** | 3.0–3.1<br>3.0 | Klimesch 1985, van Nieukerken 1983<br>García-Barros *et al.*, 2016**** |
| *Stigmella condaliafoliella* (Busck), U.S.A. | | 2.8–3.1 | Newton & Wilkinson 1982 |
| *Stigmella gossypii* (Forbes & Leonard), U.S.A. | | 3.0–3.2 | Newton & Wilkinson 1982 |
| *Stigmella juglandifoliella* (Clemens), U.S.A. | | 3.0–3.4 | Wilkinson & Scoble 1979 |
| *Stigmella himalayai* Puplesis & Diškus, Nepal | 1.4–1.6 | 3.0–3.5 | Puplesis & Diškus 2003 |
| *Stigmella scintillans* (Braun), U.S.A., Canada | | 3.2–3.4 | Wilkinson & Scoble 1979 |
| *Stigmella foreroi* Stonis & Vargas, Colombia | 1.4–1.6 | 3.2–3.6 | Stonis *et al.* 2019a |
| *Stigmella semiaurea* Puplesis, Central Asia | 1.4–1.9 | 3.0–4.0 | Puplesis 1994 |
| *Stigmella pruinosa* Puplesis & Robinson, Central and South America | 1.5–1.7 | 3.4–3.9 | Stonis *et al.* 2019b |
| *Ozadelpha guajavae* (Puplesis & Diškus), Ecuador | 1.4–1.6 | 3.1–3.6 | Remeikis *et al.* 2014 |
| *Acalyptris amazonius* Puplesis & Diškus, Ecuador | 1.5 | 3.3 | Puplesis *et al.* 2002 |
| *Acalyptris egidijui* Puplesis, Central Asia | 1.3–1.6 | 2.9–3.5 | Puplesis 1994 |
| *Acalyptris brevis* Puplesis, Central Asia | 1.5–1.9 | 3.3–4.2 | Puplesis 1994 |
| *Acalyptris dominicanus* Remeikis & Stonis, Dominica | 1.6–1.7 | 3.7–3.8 | Stonis & Remeikis 2015 |
| *Acalyptris minimus* Diškus and Stonis, Ecuador | 1.6–1.8 | 3.7–4.0 | Stonis *et al.* 2018d |
| *Ectoedemia picturata* Puplesis, East Asia | 1.4–1.8 | 3.1–4.1 | Puplesis 1994 |
| *Parafomoria liguricella* (Klimesch), Mediterranean | 1.3–2.2 | | van Nieukerken 1983 |

*—for a discussion on the taxonomic status of *Johanssoniella* Koçak and recent attribution of *acetosae* to *Johanssoniella*, see Stonis *et al*. 2018b; **—data provided by Thomas Sobczyk; ***—by Erik J. van Nieukerken; ****—by David C. Lees (♂ paratype of *Stigmella diniensis*, NHMUK)

**TABLE 2.** Measurements of selected smallest Gracillariidae

| Species | Forewing (mm) | Wingspan (mm) | References |
|---|---|---|---|
| *Cameraria palawanensis* Kumata, South East Asia | 1.7–1.8 | 3.9–4.1 | Kumata 1995 |
| *Cameraria sokoke* De Prins, East Africa | 1.9 | | De Prins & Kawahara 2012 |
| *Cameraria pongamiae* Kumata, South East Asia | 1.8–2.3 | 3.8–4.8 | Kumata 1993 |
| *Cameraria trizosterata* Kumata, South East Asia | 1.7–2.3 | 3.7–4.9 | Kumata 1993 |
| *Cremastobombycia kipepeo* De Prins, East Africa | 1.76 | | De Prins & Kawahara 2012 |
| *Hyloconis luki* De Prins, Central Africa | 1.55* | | De Prins & Kawahara 2012 |
| *Neolithocolletis nsengai* De Prins, Central Africa | 1.69–2.01 | | De Prins & Kawahara 2012 |
| *Porphyrosela alternata* Kumata, South East Asia | 1.2–2.0* | 2.6*–4.3 | Kumata 1993 |
| *Porphyrosela desmodivora* De Prins, Central Africa | 1.15*–1.45 | | De Prins & Kawahara 2012 |
| *Porphyrosela dorinda* (Meyrick), South East Asia | 1.4–1.8 | 3.0–4.1 | Kumata 1993 |
| *Porphyrosela homotropha* Vári, East Africa | 1.45 | | De Prins & Kawahara 2012 |
| *Porphyrosela gautengi* De Prins, South Africa | 1.9–2.7 | | De Prins & Kawahara 2012 |
| *Phyllonorycter lantanae* (Váry), East and South Africa | 1.9 | 4.0 | Váry 1961<br>De Prins & Kawahara 2012 |
| *Phyllonorycter mida* De Prins, East Africa and West Asia | 1.82–2.07 | | De Prins & Kawahara 2012 |
| *Phyllonorycter mwatawalai* De Prins, East Africa | 1.7 | | De Prins & Kawahara 2012 |
| *Phyllocnistis dichotoma* Turner, Australia | | 4.0 | Turner 1947 |
| *Phyllocnistis hyperpersea* Davis & Wagner, North America | 1.9–2.2 | | Davis & Wagner 2011 |
| *Phyllocnistis kawakitai* Brito & Lopez-Vaamonde, South America | 1.78 | | Brito *et al.* 2017 |
| *Phyllocnistis norak* Brito & Lopez-Vaamonde, South America | 1.73 | | Brito *et al.* 2017 |
| *Phyllocnistis petronellii* Brito & Lopez-Vaamonde, South America | 1.75 | | Brito *et al.* 2017 |

*—these data should be re-examined, the forewing may appear by 0.02 mm longer; see Discussion

For comparison, species with a wingspan of less than 4.0 mm were significantly less common in the doubly speciose family Gracillariidae (see De Prins & De Prins 2012–2020 for data on gracillariid diversity). Specifically,

in this group, moths with a wingspan of less than 4.0 mm occurred in eight genera of the 110 genera known globally: *Cameraria* Chapman, *Cremasrobombycia* Braun, *Hyloconis* Kumata, *Neolithocolletis* Kumata, *Porphyrosela* Braun, *Phyllonorycter* Hübner, *Phyllocnistis* Zeller, and *Corythoxestis* Meyrick. Twenty extremely small Gracillariidae species and their measurements were provided in Table 2.

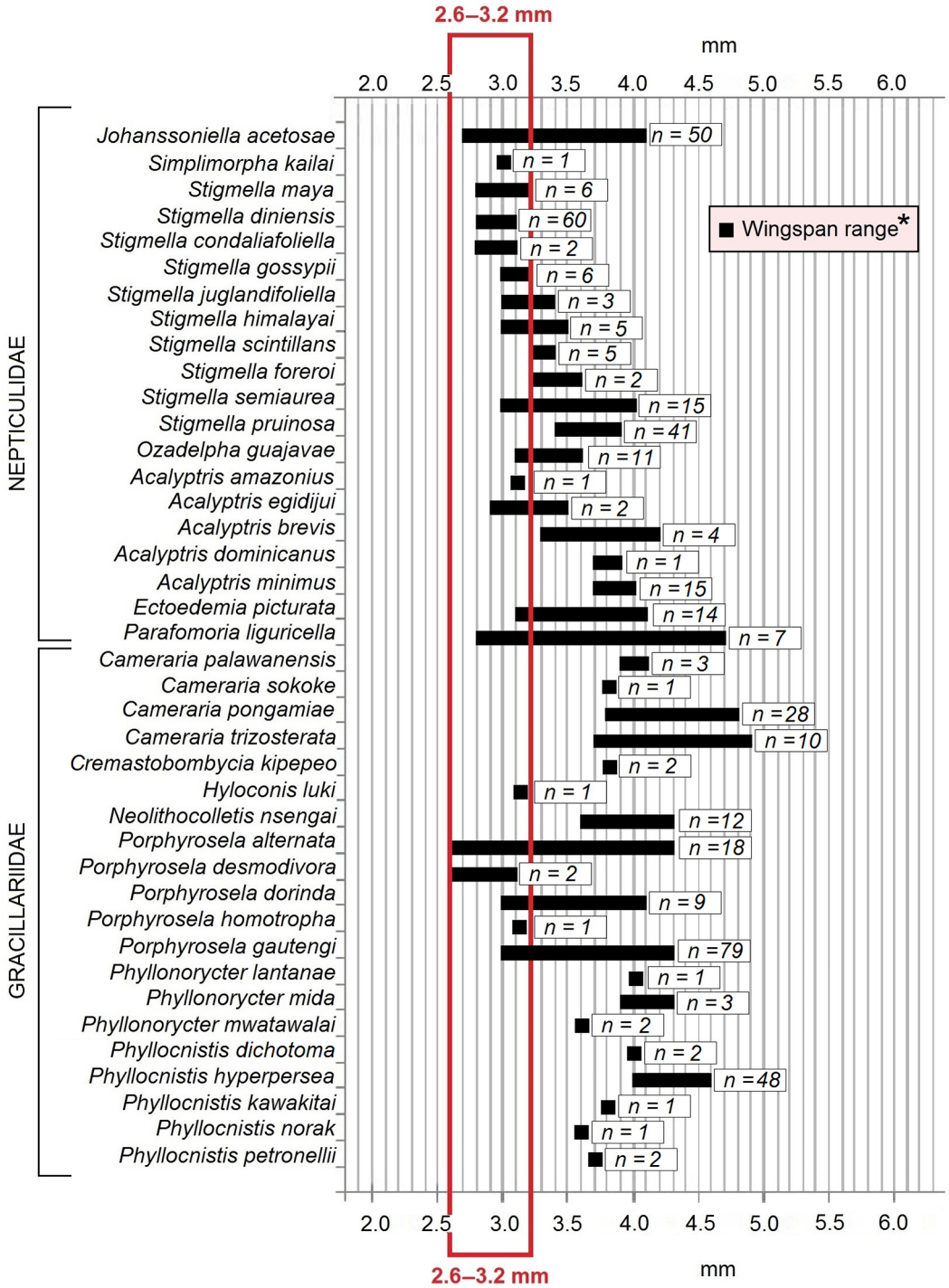



**FIGURE 7.** Wingspan ranges of the smallest Nepticulidae and Gracillariidae (based on the data provided in Table 1 and Table 2)

*—approximate data: in some cases, particularly in Gracillariidae, the wingspan data were unavailable, and therefore they were calculated from the doubled forewing length by adding an average measurement of the thorax

It can be noticed from the examples provided above that in some species the measured series (and available wingspan ranges) are not sufficient for a firm conclusion. However, the presence of the phenomenon is obvious.

Below, based on a series of ten specimens, we describe a new species of pygmy moth, *Stigmella incaica* Diškus & Stonis, sp. nov., which is characterized by a very small or extremely small size, and size variation of the series, i.e., significant range of the forewing length (not correlated with gender). In this new species, specimens vary significantly, but not so markedly as in the case of a studied large series of *Johanssoniella acetosae* (see above).

Various causes for extremely small size in moths have been suggested. For example, extremely small size might be correlated with leaf size of a food plant. Some host plants, such as the needle sunrose, *Fumana* (Dunel) Spach, Cistaceae, have very small, narrow leaves. "S. *diniensis* is a rare species, but on average it is much smaller than *acetosae*. Once more specimens are reared smaller specimens will surely turn up. The reason it is smaller, is because the *diniensis* caterpillar only has the very small leaf of *Fumana*, whereas *acetosae* can use a much larger *Rumex* leaf" (E. J. van Nieukerken, in García-Barros *et al*. 2016) (Table 1). The larvae of pygmy moths, with very rare exceptions (see Johansson *et al*. 1990), cannot leave the mine and move to another leaf, so they must live all their larval stages in a single leaf, and it is not dependent on how much food resource is available. However, our recent field observations of *Tischeria ptarmica* (Meyrick) in Laos suggest that only a small percentage of the entire leaf area is consumed by one larva. For example, the larva of *T. ptarmica*, the smallest species among Tischeriidae, consumes only about 4–5% of the host leaf. The same has been observed with other minuscular species such as the Mexican *Stigmella maya*, a small-size record holder: its larva consumes on average only about 5–6% of the host leaf.

On the other hand, it was observed that when the leaf with the *Phyllonorycter* (Gracillariidae) mine dries up, the larva has to pupate before it has been fully fed, resulting in smaller adults (O. Karsholt *pers. comm*).

Size usually correlates with gender. Although there are some species where both males and females do not differ significantly in size, more often females are larger than males. Based on the actual data published by us earlier, we state here an inverse case when females are significantly smaller than males within some Neotropical Nepticulidae; most of these species are from the Andes. Smaller females and larger males are characteristic for the Caribbean *Acalyptris caribbicus* Diškus & Stonis (male wingspan 3.9–4.3 mm, n = 2, female wingspan 3.7–3.9 mm, n = 2) (Stonis *et al*. 2013a); the northern Andean *Stigmella lamiacifoliae* Remeikis & Stonis (male wingspan 6.1–6.5 mm, n = 13, female wingspan 5.1–5.5 mm, n = 8) (Stonis *et al*. 2017b), *S. robleae* Remeikis & Stonis (male wingspan 5.2 mm, n = 1, female wingspan 4.8 mm, n = 1) (Remeikis & Stonis 2015); the equatorial Andean *S. lachemillae* Diškus & Stonis (wingspan 4.9–6.6 mm, n = 10, female wingspan 4.7–5.0 mm, n = 5) (Stonis *et al*. 2016), the central Andean *S. pandora* Remeikis & Stonis (male wingspan 9.7–10 mm, n = 6, female wingspan 8.6 mm, n = 3), *S. auriargentata* Remeikis & Stonis (male wingspan 6.4–6.5 mm, n = 3, female wingspan 5.7 mm, n = 1) (Stonis *et al*. 2016), *S. expressa* Remeikis & Stonis (male wingspan 6.5 mm, n = 1, female wingspan 5.5 mm, n = 2), *S. acalyphae* Diškus & Stonis (male wingspan 4.8 mm, n = 1, female wingspan 4.3 mm, n = 2) (Stonis *et al*. 2017a); the southern Andean *S. torosa* Remeikis & Stonis (male wingspan 5.7 mm, n = 1, female wingspan 5.1–5.2 mm, n =3), *S. monstrata* Remeikis & Stonis (male wingspan 5.3–5.6 mm, n = 7, female wingspan 4.9 mm, n = 2) (Stonis *et al*. 2017c); the Patagonian *S. lilliputica* Remeikis & Stonis (male wingspan 4.1 mm, n = 6, female wingspan 3.9–4.0 mm, n = 2) (Stonis & Remeikis 2017).

## Description of a new pygmy moth species with a wingspan of 3.8–4.3 mm

### *Stigmella incaica* Diškus & Stonis, sp. nov.

urn:lsid:zoobank.org:act:AC1D62F5-881A-45C9-A782-B77A58E38460

**Type material.** Holotype ♂, PERU: Cusco Region, La Convención Province, Cerro Quintalpata, 13°0'22"S, 72°36'44"W, elevation 1270 m, mining larva 23.vi.2018, ex pupa vii.2018, leg. Arotaype-Puma, genitalia slide no. AD1030♂ (ZIN). Paratypes: 3 ♂, 6 ♀, same label data as holotype, genitalia slide nos AD1029♂ (from adult in pupal skin, no moths preserved), AD1028♀ (ZIN).

**Diagnosis.** This species belongs to the *Stigmella nivea* group (see Stonis *et al*. 2017a for group diagnosis). In the male genitalia, the combination of the gnathos with two well-separated caudal processes, the wide uncus with four distinctive caudal papillae, and a unique set of four clusters of sizewise different cornuti in the phallus easily distinguishes *S. incaica* **sp. nov.** from all members of the *S. nivea* group, including the most similar Ecuadorian *S. apicibrunella* Diškus & Stonis, described and illustrated in Stonis *et al*. (2017c).

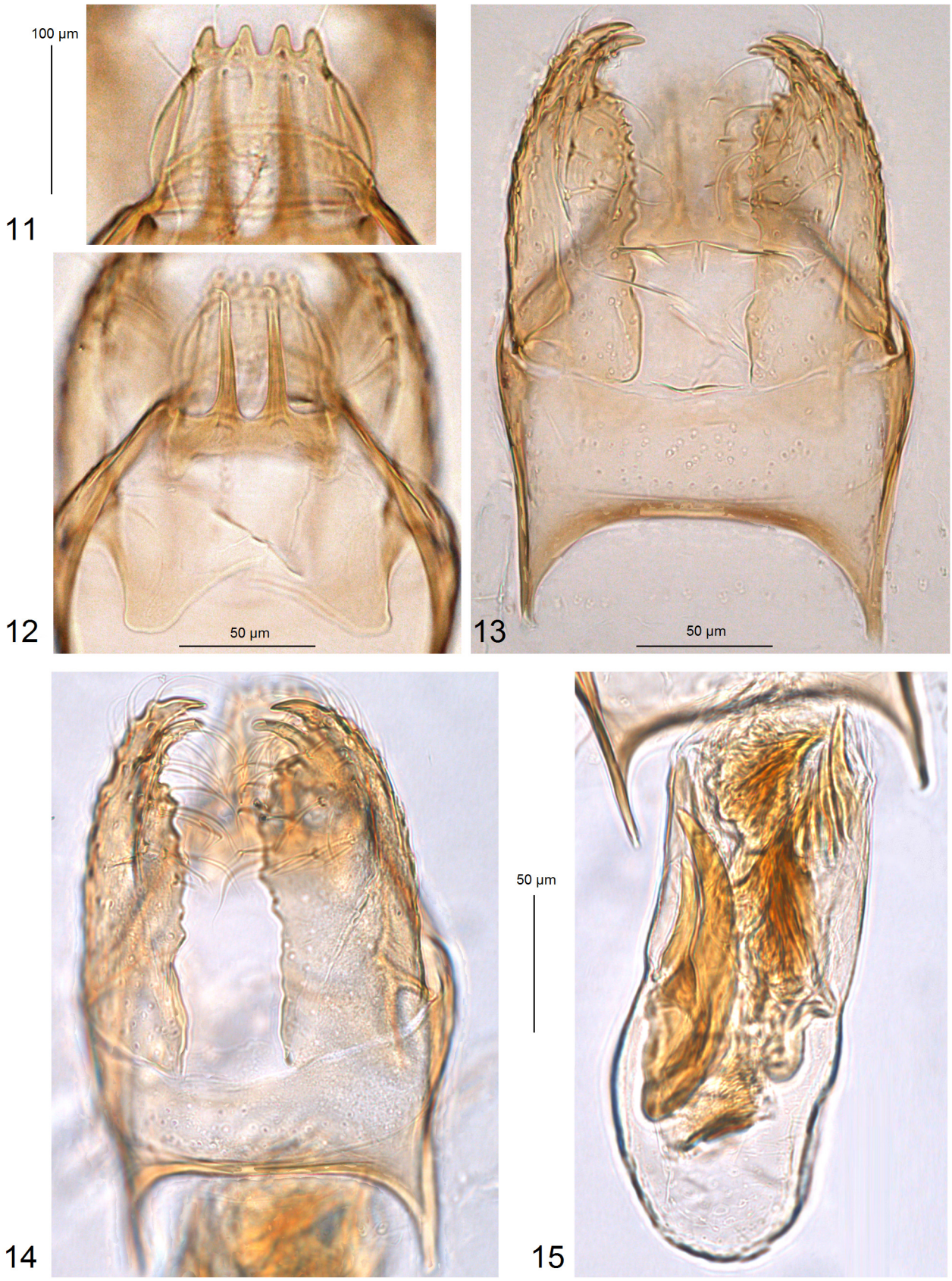

forewing: 1.92 mm, wingspan: 4.21 mm


forewing: 1.75 mm, wingspan: 3.82

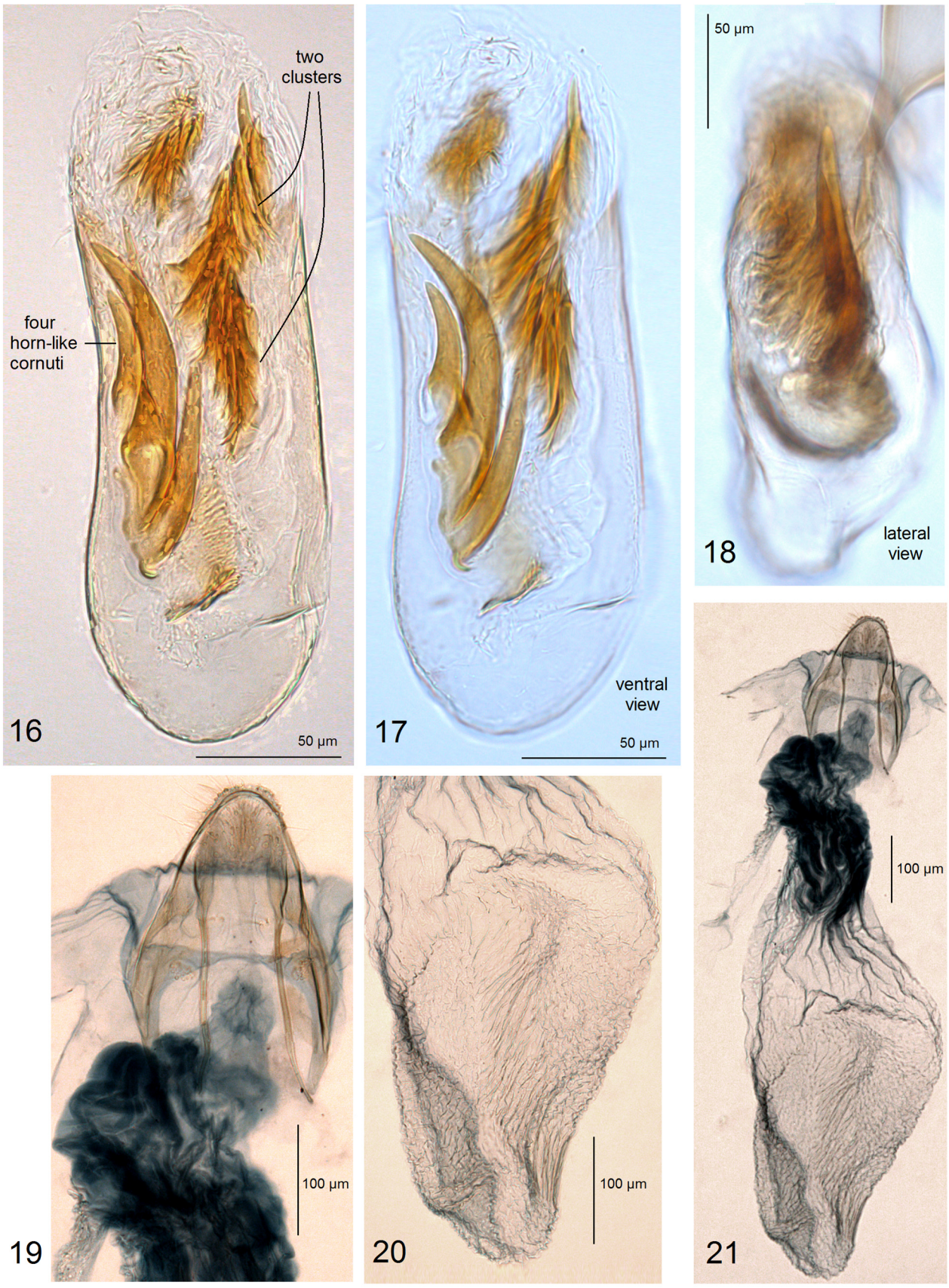
Note the size difference


forewing: 1.75 mm, wingspan: 3.83 mm

**FIGURES 8–10.** Adults of *Stigmella incaica* Diškus & Stonis, **sp. nov.** 8, female, paratype; 9, another female, paratype; 10, male, paratype (ZIN)




**FIGURES 11–15.** Male genitalia of *Stigmella incaica* Diškus & Stonis, **sp. nov.** 11, paratype, genitalia slide no. AD1029, uncus; 12, same, gnathos and transtilla; 13, same, capsule with phallus removed, ventral view; 14, holotype, genitalia slide no. AD1030, capsule, with phallus partially removed, ventral view; 15, same, phallus (ZIN)




**FIGURES 16–21.** Genitalia of *Stigmella incaica* Diškus & Stonis, **sp. nov.** 16, 17, male genitalia, paratype, genitalia slide no. AD1029, phallus; 18, same, lateral view; 19–21, female genitalia, paratype, genitalia slide no. AD1028 (ZIN)

In the female genitalia, *S. incaica* **sp. nov.** is very similar to *S. apicibrunella*, but differs in the presence of only a few indistinctive spines in the ductus spermathecae that in *S. apicibrunella* is heavily spined.

Externally, *S. incaica* **sp. nov.** may be easily distinguished from all species of the *S. nivea* group, except *S. apicibrunella*, by the distinctly dark apex of the generally pale forewing (also see Remarks).

**Male** (Fig. 10). Forewing length 1.75–1.87 mm (n = 3, average mean = 1.83); wingspan 3.83–4.09 mm (n = 3, average mean = 4 mm). Head: palpi golden cream; frontal tuft orange-ochre; collar large, comprised of lamellar, golden cream to ochreous yellow scales; scape golden cream to ochreous yellow; antenna shorter than half the length of forewing; flagellum with about 22–23 segments, grey to dark grey, golden glossy, with some purple iridescence. Thorax and tegula smoothly scaled, golden cream with some blue and purple iridescence. Forewing golden cream to ochreous yellow, with some blue and purple iridescence, but apically and narrowly along costal margin brown-black with purple iridescence; fringe grey, golden glossy, with some purple or blue iridescence; underside of forewing dark grey to black-grey except a cream, small, elongated spot at base, without androconia. Hindwing and its fringe grey to blackish grey, without spots or androconia. Legs golden glossy, yellow cream, on upper side covered with blackish grey scales with purple iridescence. Abdomen dark metallic grey to black-grey on upper side and laterally, golden cream to almost grey on underside; genital plates golden cream; anal tufts absent (or indistinctive).

**Female** (Figs 8, 9). Forewing length 1.75–1.95 mm (n = 5, average mean = 1.87); wingspan 3.82–4.27 mm (n = 5, average mean = 4.09 mm). Similar to male. Antenna 1/3 length of forewing; flagellum with about 18 segments. The brown-black apex of the forewing with stronger purple iridescence than male.

**Male genitalia** (Figs 11–18). Capsule longer (210–215 μm) than wide (140–155 μm). Uncus wide, with four distinctive papillae caudally (Fig. 11). Gnathos with two very slender and well separated caudal processes and angular central plate. Valva 130–135 μm long, with two slender and sharp apical processes; transtilla without sublateral processes, lobe-like laterally. Juxta membranous, indistinctive. Vinculum with small pointed lateral lobes, and medium short ventral plate. Phallus (Figs 15–18) 220–260 μm long, 60–85 μm wide; vesica with a wide, distinctly interrupted band of cornuti comprised of four clusters: three clusters of large spine-like cornuti and one cluster of very large, horn-like cornuti.

**Female genitalia** (Figs 19–21). Total length about 950 μm. Anterior and posterior apophyses equal in length; anterior apophyses slender only distally, gradually widened proximally; posterior apophyses very slender all their length. Vestibulum narrow, without sclerites. Corpus bursae with a very large and wide, heavily folded part and a large, about 400 μm long, 280 μm wide basal body; pectinations distinctive, forming a band-like structure somehow resembling a weakly developed signum (see Fig. 20). Accessory sac indistinctive, very small, folded; ductus spermathecae wide but with few indistinctive spines proximally, with a lobe-like vesicle, without coils. Abdominal apex tapered into relatively slender, but distally rounded ovipositor.

**Bionomics** (Figs 22–26). Host plant is unknown (unidentified, possibly *Acalypha* sp., Euphorbiaceae) (Fig. 22). Larva pale greyish green with a dark green intestine and dark brown head; mines in leaves in June. Leaf mine (Figs 23–26) starts as a very slender sinuous or contorted gallery with a slender line of black, occasionally black-brown frass; further on, the gallery gradually widens and frass is dispersed; at the final part of the gallery, the frass is collected in a slender, central line. Larval exit slit on upper side of the leaf. Adults fly in July.

**DNA Barcode**. One whole female specimen of the type series was COI barcoded, but not the holotype; sequences are available in GenBank under voucher/sample no. MW438869.

**Distribution**. This species occurs on the eastern slopes of the Peruvian Andes (Peru, Cusco Region) at altitudes about 1300 m.

**Etymology**. The species name is derived from the Spanish *incaico* or *incásico* (pertaining to the Incas; feminine) referring to the locality where the species was collected by our Quechua counterpart in the historical centre of the ancient Inca Empire in the Lucumayo river valley with close proximity to Machu Picchu.

**Remarks.** Note that *S. apicibrunella* (see Stonis *et al*. 2017c) is larger than *S. incaica* in all size parameters: the wingspan and male or female genitalia. Based on molecular data, the exact position of *S. incaica* in the *S. nivea* group will be discussed separately (Stonis *et al. in prep.*).


**FIGURES 22–26.** Bionomics of *Stigmella incaica* Diškus & Stonis, **sp. nov.** 22, host plant (unidentified); 23–26, leaf mines, Peru, Cusco Region, La Convención Province, Cerro Quintalpata, 13°0’22”S, 72°36’44”W, elevation 1270 m

## Discussion

In Lepidoptera the families informally classified as Microlepidoptera are comprised of some of the smallest moths known to exist on the planet. This includes Tineidae and Bucculatricidae with forewings as small as 2.5 mm (Davis & Robinson 1999). Another family of small-size moths is the Lyonetiidae with medium small and occasionally very small moths. It includes well-known species such as the very small coffee leaf miner *Perileucoptera coffeella* (Guérin-Méneville) (also widely known as *Leucoptera coffeella*) with a wingspan of around 4.5 mm (Guérin-Méneville & Perrottet 1842; CSALOMON 2014) and the medium small apple leaf miner *Lyonetia clerkella* (Linnaeus) with a wingspan of the aestival form of about 6–7 mm, and the autumnal form of about 8–9 mm (Kuroko 1964).

The family of grass-miner moths, Elachistidae, also possesses some very small moths. Competition for the title of the smallest elachistid is tight. Several *Urodeta* Stainton species have a forewing length of 2.3 mm (L. Kaila *pers. comm*.). However, the smallest described species is probably *Elachista elaphria* Kaila from Australia (Kaila 2011). Its forewing length is 2 mm, and wingspan is about 4.2 mm. In addition, it is much more narrow-winged than the *Urodeta* species, but still a rather big moth compared to some extremely small nepticulids (L. Kaila *pers. comm*).

The families Opostegidae, Tischeriidae and Heliozelidae should be discussed separately: Heliozelidae was specifically mentioned in a recent discussion in ResearchGate (García-Barros *et al*. 2016) because it includes some very small and extremely small moths, while Opostegidae and Tischeriidae were already indicated as the families among the smallest Lepidoptera in some earlier published works (Davis 1999; Davis & Stonis 2007; Diškus & Stonis 2012; Stonis *et al*. 2020a). Forewings of Heliozelidae often range from 1.7 to 7.0 mm (Davis 1999); the extremely small European *Holocacista rivillei* (Stainton) has a wingspan of about 3.5–4.0 mm (van Nieukerken *et al*. 2012). The recently described East Asian *Antispila kunyuensis* Liu is 1.7–2.1 mm in forewing length, and another East Asian species, *A. uenoi* Kuroko, possesses forewings 1.6–1.8 mm in length (Wang *et al*. 2018). Small-sized moths are common in *Coptodisca* Walsingham; e.g., forewing length of *C. juglandiella* (Chambers) and *C. lucifluella* (Clemens) is around 1.75–1.95 mm and an undescribed *Coptodisca* species from Texas, USA, has a forewing length of only 1.45 mm (Bernardo *et al*. 2015).

Among Opostegidae, the majority of species have a wingspan between 5.8 and 6.8 mm and forewing length range from 2.8 to 3.1 mm. The smallest known opostegid species are around 4.0–4.7 in wingspan (or 1.8–2.2 mm in the forewing length). Such very small Opostegidae include the Caribbean *Pseudopostega colognatha* Davis & Stonis, Central American *P. mexicana* Remeikis & Stonis, *P. lateriplicata* Davis & Stonis, *P. latiplana* Remeikis & Stonis, also *P. kempella* (Eyer) known from Florida, USA, and a couple species with wider distributions in the Neotropics: *P. rotunda* Davis & Stonis and *P. atenuata* Davis & Stonis (Davis & Stonis 2007). The smallest-ever opostegid might be *P. mexicana*, with the published forewing length of 1.7–1.8 mm (Remeikis *et al.* 2009); if calculated, it would make a range from about 3.7 to 4.0 mm in wingspan. However, measurements are based on only two specimens that may have not been measured precisely because of the relatively poor condition of specimens that were not field-pinned, but were pinned and prepared years later with possible damage to the fringe. On the other hand, some opostegids are relatively "giant" species in comparison to the majority of opostegids. In a category of species which can reach above 10 mm in wingspan are the Oriental *Opostegoides tetroa* (Meyrick) with a wingspan of 11.6–13.0 mm, *O. pelorrhoa* (Meyrick) with a wingspan of 9.0–10.7 mm, *O. nephelozona* (Meyrick) with a wingspan of 10.1 mm (Puplesis & Robinson 1999); the Neotropical *Pseudopostega protomochla* (Meyrick) with a forewing length of 3.5–5.0 mm and wingspan about 7.5–10.6 mm, *Pseudopostega trinidadensis* (Busck) with a forewing length 4.3–4.8 mm and wingspan about 9.0–10.2 mm, *P. acrodicra* Davis & Stonis with a forewing length 5.0–5.6 mm and wingspan about 10.4–11.7 mm, *P. perdigna* (Walsingham) with a forewing length about 6 mm and wingspan about 12.7 mm; the Nearctic *Pseudopostega quadristrigella* (Chambers) with a forewing length 4.4–5.2 mm and wingspan about 9.2–11 mm, *P. albogaleriella* (Clemens), in which some specimens can occasionally reach up to 6.0 mm in forewing lenghth and approximally 12.6 in wingspan (Davis & Stonis 2007). The maximal opostegid size globally was recorded in *Notiopostega atrata* Davis from Chile with the forewing range 5.0–8.3 mm in males and 6.4–8.3 mm in females (Davis 1989), and make the approximate maximal figure of the wingspan above 17 mm.

Tischeriidae also comprises some small or even very small moths. Recently it was stated by Kobayashi *et al*. (2016) that "this lepidopteran family [is] compris[ed of] some of the smallest moths, with a wing expanse of only 5–11 mm". In a family overview, Davis (1999) stated that the tischeriid forewing length is 2.7–5.0 mm. According our estimates, the majority of Tischeriidae range from 3.1 to 3.4 mm in forewing length and 6.5 to 7.3 mm in wingspan and, using our terminology of size categories (see Methods), tischeriids can be called medium small moths. The East

Asian *Coptotriche minuta* Diškus & Stonis with a forewing length 2.8–3.3 mm and wingspan about 6.1–7.1 mm (Stonis *et al*. 2014b) is also among the category of medium small moths. Only the smallest known tischeriid species fall between the categories of small and very small moths. The smallest Tischeriidae are the Caribbean *Coptotriche pulverea* (Walsingham) with a minimal male forewing length of 2.2–2.5 mm and wingspan of 4.9–5.3 mm (Stonis *et al*. 2008) and the South Asian *Tischeria ptarmica* Meyrick with a previously published forewing length of 2.2 mm and wingspan ca. 4.9 mm (van Nieukerken 2010). Recently, upon measuring our series of *T. ptarmica* from Laos, it revealed an even smaller minimal size: male forewing length 2.0–2.75 mm (n = 3, average mean = 2.5 mm); male wingspan 4.35–5.93 mm (n = 3, average mean = 5.40 mm); female forewing length 1.92–2.95 mm (n = 3, average mean = 2.55 mm); female wingspan 4.06–6.33 mm (n = 3, average mean = 5.47 mm). With a minimal wingspan of 4.06 mm, *T. ptarmica* is the smallest described species among the family, however, the maximal recorded wingspan is bigger than in another tiny species, *C. pulverea*.

There are also some Tischeriidae species that are above the average tischeriid size: the European *Tischeria ekebladella* (Bjerkander, 1795) (wingspan 8–11 mm), the Mediterranean *T. ekebladoides* Puplesis & Diškus (forewing length 3.2–4.4 mm, wingspan 8.2–10.1 mm) (Puplesis & Diškus 2003), the Caucasian *T. caucasica* Klasiński & Stonis (forewing length 4.2– 4.8 mm, wingspan 9.1–10.1 mm) (Klasiński *et al*. 2020), the East African *Coptotriche kenyensis* Mey (forewing length 4 mm, wingspan 10 mm (Mey 2010), the South East Asian *Coptotriche imperator* Puplesis & Diškus (forewing length about 5.0 mm, wingspan 10.8–10.9 mm) (Puplesis & Diškus 2003), the Andean *Astrotischeria chilei* Puplesis & Diškus (forewing length 4.4–4.8 mm, wingspan 9.0–10.6 mm), *A. pallens* Puplesis & Diškus (forewing length 3.7–4.7 mm, wingspan 7.9–10.2 mm) (Puplesis & Diškus 2003), and one species of currently uncertain generic position with wingspan 10.5–11 mm (Braun 1972).

Two families, the Gracillariidae and particularly the Nepticulidae, stand out among all other Lepidoptera as having the smallest moths. Although Nepticulidae is not a homogeneous family sizewise, approximately half of the species globally have a forewing length of less than 2.2 mm and a wingspan of less than 5 mm (i.e., belong to categories of very small and extremely small moths respectively). The family is also very rich in small-size record holders; the lower limit for a known forewing length is 1.13–1.3, and a minimal wingspan is 2.7–2.8 mm (Table 1). Many small-sized species are also characteristic for Gracillariidae (Table 2). However, proportions differ: in Nepticulidae, species with a wingspan less than 4 mm (extremely small species) comprise about 12% of the family, while in Gracillariidae, such extremely small species are not as abundant. There are fewer small-size record holders in Gracillariidae when compared to Nepticulidae. However, at least one or two gracillariid species, *Porphyrosela alternata* Kumata and *P. desmodivora* De Prins, may surpass the record of Nepticulidae (this should be re-examined, see asterisk in Table 2).

We have taken into account that small-sized species may be widespread differently in a family: either in some phylogenetically close genera or widespread among most of the family‘s taxa. Understandably, Nepticulidae, in which extremely small species with the wingspan of less than 4 mm are found in many and phylogenetically diverse genera, is a testament to the small size of the family as a whole rather than a phenomenon. Extremely small Gracillariidae species with a wingspan of less than 4 mm are known only in a minority of gracillariid genera.

Previously stated species size records may have been imprecise because specimens of the same species show great variation in wing length, especially in a large series. But often the smallest species are known only from singletons, and so a range of the forewing length and wingspan from multiple specimens is unavailable. Not all measurements, especially those of the smallest specimens, are the same because they are made by different researchers, using different measurement equipment. We found that significant differences in measurement may occur when the same moth is measured with microscopes from different manufacturers (see Methods) or using different software. We also paid particular attention to the forewing length and the internal scale of the photograph of some published papers that included specimens of the smallest moths. Sometimes the smallest moths appeared to be bigger (approximately by 0.02 mm) than stated in the original description. Occasionally, we also noticed obvious discrepancies when, for example, a wingspan range of a species was published as 4.0–4.6 mm, but the forewing length was stated as 2.0–2.4 mm (i.e, arithmetically measurement data on the minimal and maximal wingspan do not correspond with the data of the wingspan). Unfortunately, we also found a few of our previously published works with this discrepancy.

Simonsen & Kristensen (2003) discovered a positive correlation between wing length and lepidopteran scale length: the minimal individual scale length (40 μm) was observed in Nepticulidae, while the maximum (about 500 μm) was found in Castniidae. The authors supposed that scale size variation probably reflects variation in the size of scale-forming trichogen cells; the latter may at least partially reflect difference in genome size (Simonsen & Kristensen 2003).

It should be noted that all lepidopteran families comprising small-sized moths and mentioned in this paper, except for Tineidae, are plant miners (predominantly leaf miners). The correlation of moth size of various lepidopteran families with the living and feeding of their larvae within assimilatory (photosynthetic) tissues of plants was evidently shown in a graph by Ivinskis *et al*. (1985). Information about the specialized life of Nepticulidae can be found in, for example, Johansson *et al*. (1990); Puplesis (1994); Remeikis *et al*. (2016); on Gracillariidae, in Davis & Deschka (2001); Davis & Wagner (2011), etc. This successful ecological adaptation is widespread not only among moths, but also among other insect groups (e.g., Hespenheide 1991; Diškus & Stonis 2012).

Summarizing, although other families, notably the Gracillariidae, have adult moth sizes that can also be surprisingly small and include small-size record holders (the South East Asian *Porphyrosela alternata* Kumata and Central African *P. desmodivora* De Prins), we found that the Nepticulidae should be recognized as having the largest portion of smallest moths in the world. It also has a high number of extremely small species, including many small-size record holders like the European *Johanssoniella acetosae* (Stainton), Central American *Stigmella maya* Remeikis & Stonis, and Mediterranean *S. diniensis* (Klimesh), and wide distribution of small-sized species in phylogenetically very different genera.

Among Lepidoptera, the smallest-known species globally, with the minimal recorded forewing length around 1.2–1.3 mm and the wingspan around 2.6–2.8 mm, are as follows: the European *Johanssoniella acetosae*, the Peruvian *Simplimorpha kailai* (Stonis & Diškus), the Mexican *Stigmella maya*, the Mediterranean *S. diniensis*, the Mediterranean *Parafomoria liguricella* (Klimesh) (Nepticulidae), the South East Asian *Porphyrosela alternata* Kumata, and the Central African *P. desmodivora* De Prins (Gracillariidae). It is expected that there are probably many more extremely small species in the tropics, and upon further study of the world fauna of leaf-mining moths, we hope these small-size records may be shattered upon the discovery of new species.

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