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Dvidulopsis gen. nov., a rare Neotropical genus of pygmy moths (Nepticulidae) endemic to lowland humid forests, a biome of conservation priority

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Abstract

This publication describes *Dvidulopsis* Stonis & Diškus, **gen. nov.**, and a new species, *D. diviantis* Stonis & Remeikis, **sp. nov.**, along with new distribution data for *D. latipennata* (Puplesis & Robinson) from Honduras. The study identifies *Dvidulopsis* **gen. nov.** as a distinct taxon, characterized by notable characters of the male genitalia, including a typically divided uncus and gnathos, and three elongated apical carinae of the phallus. Molecular evidence from new mtDNA COI-5' sequences further supports the genus description.

The new genus, comprising eight species, is endemic to lowland tropical humid forests, typically found at elevations of 10–400 m. Half of the known species inhabit equatorial regions, specifically the humid forests of the Amazon Basin, while the other half are found in the humid forests of Central America. The study also summarizes distribution data on Nepticulidae from the conservation-priority lowland tropical humid forests of the Neotropics, currently encompassing 57 species, representing approximately 30% of the described Nepticulidae fauna in the Neotropical region (*sensu stricto*).

The article is illustrated with a chart depicting Nepticulidae occurrence in the lowland tropical humid forests of the Americas, a species distribution map, photographs of *Dvidulopsis* adults and male genitalia, and two molecular NJ trees distinguishing the new genus from similar taxa, such as *Acalyptris* Meyrick, 1921; *Fomoria* Beirne, 1945; and other Nepticulidae.

Key words: Neotropics, Neotropical fauna, Nepticulidae, new genus, pygmy moths, species distribution, taxonomy, tropical humid forests, tropical moist forests

Introduction

Pygmy moths or pigmy moths? The terms "pygmy moths" and "pigmy moths" are often used interchangeably, but "pygmy" is the more widely accepted term in scientific literature. The word "pygmy" derives from Greek and correctly conveys the tiny size of these moths, aligning with standard entomological nomenclature. Therefore, we recommend using "pygmy moths" to ensure clarity and consistency with the majority of the literature.

Pygmy moths are true "micro marvels" or "tiny wonders" due to their exceptionally small size and unique biology. Their intricate wing patterns, vibrant hues, and occasional iridescence or metallic sheens contribute to their aesthetic appeal and highlight their biological importance. Despite their diminutive stature, making some of them the smallest moths globally, these moths represent one of the phylogenetically basal clades of Lepidoptera, which probably originated approximately 130 million years ago in the Early Cretaceous (Doorenweerd *et al.* 2016). This can provide valuable insights into evolutionary processes, giving us a tool to study ecological interactions across various ecosystems, and overall biodiversity. For detailed descriptions of Nepticulidae morphology, biology, and both early and current taxonomy, we recommend reviewing Johansson *et al.* (1990), Puplesis (1994), Puplesis & Robinson (2000), Puplesis & Diškus (2003), van Nieukerken *et al.* (2016b), and Stonis *et al.* (2022).

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The global number of species and their distribution. The number of Nepticulidae species is rapidly increasing. In 2003, the catalogue by Diškus & Puplesis listed 780 species. In 2016, the global catalogue by van Nieukerken *et al.* reported 862 extant species. Just five to six years later, while analyzing the global dynamics of species descriptions, Dobrynina *et al.* (2022) reported the milestone of 1,000 species. Currently, the family Nepticulidae comprises 1,020 extant species globally. According to our database of the latest publications on Nepticulidae (Stonis *et al.* 2022, 2024), nearly one-fifth of the world's Nepticulidae fauna (191 species) is now recorded exclusively from the Neotropical region (*sensu stricto*, i.e., excluding the temperate Ando-Patagonian region; see Stonis *et al.* 2016). This includes species such as *A. podenasi* Stonis, Dobrynina & Remeikis, *A. palpiformis* Stonis, Remeikis & Diškus, and *A. tortoris* Stonis, Diškus & Dobrynina, which were recently described from tropical dry forests (Stonis *et al.* 2024), as well as *Dvidulopsis diviantis* Stonis & Remeikis, **sp. nov.**, described in the present paper.

Nepticulidae are distributed worldwide, inhabiting a wide range of terrestrial ecosystems—from tundra (Kozlov *et al.* 2023) and alpine mountainous habitats (Tokár *et al.*, 2017) to temperate forests, arid boreal or subtropical deserts (Scoble 1983; Puplesis 1994), and diverse tropical habitats, including lowland humid forests (rainforests). They can be found at elevations up to 4,700 meters in the northern Andean bush and grass páramo and the central Andean puna (Stonis *et al.* 2016). Additionally, according to our observations, they are common in anthropogenic habitats, even in green areas of cities. Therefore, research on pygmy moths not only deepens our understanding of biodiversity and phylogenetics but also has practical implications for agriculture, horticulture, and forestry. Their remarkable, yet partially uncovered, diversity—alongside their ecological and morphological adaptations—continues to be of significant interest to the scientific community. However, despite previous research efforts, the Nepticulidae fauna of the Neotropics, including those in lowland tropical forests, remains insufficiently and unevenly explored. Addressing this knowledge gap is particularly important for investigating tropical humid forests, which are classified as "high conservation priority biomes" due to their exceptional biodiversity, critical ecosystem services, and the severe threats they face.

Lowland tropical humid forests. Tropical forests, in general, represent some of the most biodiverse and ecologically important ecosystems on Earth. They play a crucial role in regulating global climate patterns, maintaining atmospheric moisture, and providing habitats for countless organisms. Tropical forests account for over half of the world's vegetation carbon (Saatchi *et al.* 2021). The biological features of tropical forests have been discussed in a vast array of publications (e.g., Richards 1996; Saw 2004; Lewis 2006; Hartshorn 2013; Butler 2020; Vancutsem *et al.* 2021).

Tropical forests vary from dry to humid and occur at elevations ranging from sea level to montane heights. Several different types of tropical forests have been identified, with their terminology and classification varying slightly (e.g., see Saw 2004; Faber-Langendoen 2014; and Butler 2020). In the current study, we follow the classification by the Hierarchy Revisions Working Group, Federal Geographic Data Committee (Faber-Langendoen 2014, 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 categorized as a formation, along with tropical montane humid forest, tropical flooded & swamp forest, mangrove forest, and tropical dry forest & woodland formations. However, in our publication, we emphasize the lowland criterion first and use the term "Lowland Tropical Humid Forest" instead of "Tropical Lowland Humid Forest". This term is also frequently used in ecological literature and suggests that the primary distinction lies in the lowland regions, mirroring the montane tropical humid forest.

According to Faber-Langendoen (2014), lowland tropical humid forests occur in regions where rainfall is abundant and well-distributed throughout most or much of the year (i.e., aseasonal to moderately seasonal). Notably, these forests include both moist semi-evergreen and wet evergreen forests (often referred to as tropical rainforests), as well as a striking variant known as heath forests (Richards 1996; Whitmore 1998).

Lowland tropical forests can be found from sea level up to approximately 1,000 meters, although elevation may vary (Butler 2020). The boundary between lowland and montane forests occurs at different elevations due to the "Massenerhebung effect" (Richards 1996), and may extend up to 1,200 meters. Lowland tropical humid forests are dominated by broad-leaved evergreen trees, often with multiple complex strata (Faber-Langendoen 2014). When primary, these forests (relatively unaffected by human activities and existing in their original condition) are usually characterized by five or more forest tier levels, are typically taller and more diverse than montane forests, and have a greater diversity of fruiting trees. This results in more animals specially adapted to feed on fruits and a higher density of large mammals (Butler 2020).

All tropical forests are increasingly threatened by human activities and environmental stressors, including droughts and fires (Lewis 2006). They are being lost at an alarming rate due to deforestation and degradation: since the early 1990s, approximately 15% to 20% of tropical humid forests have been cleared, with at least an additional 10% experiencing degradation (Vancutsem *et al.* 2021). In some respects, forests in the Americas are particularly vulnerable to stressors (Saatchi *et al.* 2021). Moreover, lowland tropical forests, the biome central to this study, are even more threatened than montane forests due to their accessibility, more suitable soils for agriculture, and the value of hardwoods as timber. In many areas, virtually all lowland primary forest has been lost, while montane forests remain intact (Butler 2020).

Prehistory of the current taxonomic study. The genus *Acalyptris* Meyrick is widespread across the Nearctic, Palaearctic, Oriental, and Afrotropical regions. From the early stages of research, it has been recognized as a prolific Nepticulidae genus in the tropical lowlands of the Neotropics (Puplesis & Robinson 2000; Puplesis *et al.* 2002a; van Nieukerken *et al.* 2016b; Stonis *et al.* 2020, 2022, 2024). *Acalyptris* exhibits significant morphological and molecular diversity, particularly in the Neotropics. In the Eastern Hemisphere, three informal units, or species groups, have been established (Puplesis 1994; Diškus & Puplesis 2003, van Nieukerken *et al.* 2016a), while Neotropical species—demonstrating a remarkable range of morphological structures in the male genitalia—have recently been divided into nine distinct species groups (Stonis *et al.* 2020).

Among these diverse species groups, the *latipennata* group, originally designated by Puplesis *et al.* (2002b) and later included in the global fauna catalogue (Diškus & Puplesis 2003), has always been a subject of some uncertainty. Species in this group are characterized by their relatively wide forewings with a distinctive pattern and unusual male genitalia, featuring a divided uncus and gnathos. Van Nieukerken *et al.* (2016a) subtly questioned their placement within the genus *Acalyptris*, a doubt later echoed by Stonis & Diškus (2018). These authors, while acknowledging the *latipennata* group as a highly unusual subset of *Acalyptris*, raised the possibility that it might belong to an as-yet-undescribed taxon related to *Acalyptris* and/or *Fomoria* Beirne. Interestingly, *latipennata*, the species that gave its name to the group, was originally described as a species of *Fomoria* by Puplesis & Robinson (2000) and was only later transferred to *Acalyptris* (Puplesis *et al.* 2002b).

Consequently, Stonis & Diškus (2018) called for urgent further research, particularly in Central America or the western part of the Amazon Basin, to reassess the justification for placing this remarkable group within the genus *Acalyptris*. At that time, molecular data for this group were entirely unavailable.

Recognizing the need for further studies, we conducted targeted fieldwork in Honduras from January to early May in both 2023 and 2024, marking the first focused study of Nepticulidae in this Central American country. Unlike many *Acalyptris* species, specimens of the so-called *latipennata* group were extremely rare at light traps. However, during our fieldwork, we collected some material, and further dissection of the male genitalia allowed us to identify two species (including one new) and, for the first time, study these remarkable moths molecularly.

The primary goal of this publication is to describe a previously overlooked but highly specialized new genus, along with a distinct new species. As the new genus represents a notable example of the endemic fauna inhabiting lowland forests, we also aim to provide a concise analysis of the distribution of Nepticulidae currently known from the lowland tropical humid forests of the Neotropics. We hope that this publication will stimulate further research on the diversity of these fascinating moths in the Neotropics and contribute to a more comprehensive understanding of the Neotropical lowland humid forests as a biodiversity hotspot of conservation priority.

Material and Methods

Material. The material for this study was obtained by the first author, who has been visiting the Delegation of the European Union to Honduras since 2023 and conducting voluntary research contributing to two long-term programs between the European Union and Honduras. These programs included the initiative "Sustainable Management of Natural Resources and Climate Change", with the participation of the Honduran Institute of Forest Conservation, Protected Areas, and Wildlife (ICF). The material used in this study will be deposited in the collection of the Museum für Naturkunde (MfN), Berlin, Germany, following publication. Holotypes and paratypes of all previously described species currently attributed to the new genus were studied, including those deposited at the Natural History Museum, London (NHMUK), and the Zoological Museum, Natural History Museum of Denmark, Copenhagen (ZMUC).

Collecting methods, specimen dissection, and documentation. We employed the collecting and specimen dissection methods outlined in Puplesis & Diškus (2003) and Stonis *et al.* (2022). During our research in Honduras, moths were attracted to a white screen using fluorescent lanterns powered by flashlight batteries, as well as a LepiLED lamp powered by a power bank with a voltage range of 5–13 V DC (Brehm, 2017). Male genital capsules were removed after macerating the abdomen in 10% KOH. Permanent microscope slide preparations were photographed and examined using a Leica DM2500 microscope equipped with a Leica DFC420 digital camera. Photographs of adults were taken using a Leica S6D stereoscopic microscope paired with a Leica DFC290 digital camera.

Molecular analysis. The hindlegs of the three (one fresh and two one-year-old) air-dried specimens were used for DNA extraction according to the protocol of the GeneJet Genomic DNA Purification Kit (Thermo Fisher Scientific Baltics). During the polymerase chain reaction (PCR), 709 base pair (bp) long sequences of mitochondrial DNA cytochrome c oxidase subunit 1 (mtDNA CO1-5') were amplified with the universal primers, LCO1490 (5'ggtcaacaaatcataaagatattgg-3') and HCO2198 (5'-taaacttcagggtgaccaaaaaatca-3') for a broad range of metazoan invertebrates (European and Mediterranean Plant Protection Organization, 2016, 2021). Thermocycler settings were as follows: 5 min at 95°C; 45 cycles of 40 s at 94°C, 40 s at 45°C, and 1 min at 72°C; followed by 5 min at 72°C. The PCR mixture in a total volume of 25 µL consisted of 12.5 µL of 2× DreamTag PCR Master Mix (Thermo Fisher Scientific Baltics), 2 μ L of 10 pmol/ μ L of each primer, 6.5 μ L of deionised water, and 2 μ L of extracted DNA. The PCR products were electrophoresed on 1.5% agarose gel (Thermo Fisher Scientific Baltics) with 10000× GelRed (Biotium) and purified following the protocol of exonuclease I and FastAP thermosensitive alkaline phosphatase (Thermo Fisher Scientific Baltics). They were sent to the automatic Sanger sequencing with the ABI 3730xl 96capillary DNA analyzer (Applied Biosystems) in BaseClear B.V. (Leiden, The Netherlands). The successfully obtained nucleotide sequences were aligned with the BioEdit v.7.2.5 software (Hall, 1999) and deposited in the NCBI GenBank database (Benson et al. 2013) under the accession numbers PV121131-PV121133. In addition, the mtDNA CO1-5' fragments of the related genera (Acalyptris Meyrick species from our previous studies (Stonis et al. 2020) as well as Ectoedemia Busck, 1907, and Fomoria Beirne) were included in the analysis from the Barcode of Life Data System (BOLD) platform (Ratnasingham & Hebert 2007) or the GenBank database. The pairwise distances were estimated and the most likely nucleotide substitution model was selected from the list of 24 available models using MEGA v.7 (Kumar et al. 2016). The phylogenetic trees were constructed by the Maximum Likelihood (ML) algorithm and the general time reversible model with gamma distribution evolutionary rates, applying four discrete categories, and a fraction of invariable sites (GTR+G+I) by the same program. The node support was assessed using bootstrapping with 10,000 replicates.

Description of a new genus and new species

Dvidulopsis Stonis & Diškus, gen. nov.

urn:lsid:zoobank.org:act:73AC80A1-AA68-4104-9A72-00CA9505F628 (Figs 1–31)

Type species: Dvidulopsis amazonensis (Stonis & Diškus, 2018) comb. nov. (deposited at NHMUK).

Diagnosis. Adult moths are characterized by wide forewings with a distinct oblique, dark, postmedian or subapical pseudofascia. The genus is easily distinguishable, including from the most similar *Fomoria* Beirne and *Acalyptris* Meyrick, by the following unique combination of male genitalia characteristics: the uncus and gnathos are fully divided (paired) or at least partially divided; the valva possesses an inner (median) process or lobe; the phallus lacks cornuti but has three distinctive, elongated carinae; and the phallus tube is constricted basally. In all cases, the clade of *Dvidulopsis* **gen. nov.** consistently appeared as a distinct, separate phylogenetic entity (see the subchapter "Molecular considerations").

Description. *External characters* (Figs 1–6). The forewing is relatively wide, in contrast to most Nepticulidae species, which typically have more slender forewings. The scaling of the forewing is often yellowish cream and always features a distinct oblique, dark, postmedian or subapical fascia-like marking. While some *Acalyptris* species also exhibit an oblique postmedian marking, it is generally less distinctive and persistent compared to that in *Dvidulopsis* **gen. nov.** The forewing venation (illustrated in Puplesis & Diškus, 2018: Figs. 10–12) resembles that of *Acalyptris* and is similar to that of the Central American *A. bovicorneus* Puplesis & Robinson (see illustrated in Puplesis & Robinson, 2000: Fig. 65). A closed cell is formed by an indistinct, and possibly rudimentary, vein Rs+M.



FIGURES 1–6. Adults of *Dvidulopsis* gen.nov. 1, 2, *D. latipennata* (Puplesis & Robinson, 2000) comb. nov., Honduras, 7.5 km SE of La Ceiba, right bank of Rio Cangrejal, 100 m, 15°43′34″N, 86°44′26″W, 14.iv.2023 (new distribution); 3, *D. diviantis* Stonis & Remeikis, sp. nov., Honduras; 4, *D. amazonensis* (Stonis & Diškus, 2018) comb. nov. (type species of the genus), Ecuador; 5, 6, *D. ecuadoriana* (Puplesis & Diškus, 2002) comb. nov., Ecuador (4–6, after Stonis & Diškus 2018).



FIGURES 7–20. Diagnostic characters of male genitalia of *Dvidulopsis* gen. nov. 7, uncus, *D. onorei* (Puplesis & Diškus); 8, same, *D. amazonensis* (Stonis & Diškus); 9, same, *D. ecuadoriana* (Puplesis & Diškus), 10, gnathos, *D. onorei*; 11, same, *D. amazonensis*; 12, same, *D. ecuadoriana*; 13, valva, *D. ecuadoriana*; 14, same, *D. onorei*; 15, genitalia capsule, *D. latipennata*, Honduras (new distribution), slide no. RA1224 (MfN); 16, same, *D. ecuadoriana*, Ecuador, paratype, slide no. AD325 (NHMUK); 17, carinae, *D. ecuadoriana*; 18, same, *D. onorei*; 19, 20, phallus, *D. amazonensis*.

Characters of the male genitalia (Figs 7–20). The phallus is characterized by three large, horn-like carinae apically-a unique and likely apomorphic feature not found in the resembling Acalyptris. Lobe-like or lateral carinae are absent. The phallus tube is often constricted at the basal part, particularly in the informal and undescribed D. onorei species complex, a feature not characteristic of Acalyptris and possibly an apomorphy of Dvidulopsis gen. nov., or at least of the D. onorei species complex. The uncus is clearly paired and, in the D. onorei species complex, strongly developed, which seems to be an apomorphic character. In Neotropical Acalyptris, the uncus is unpaired, typically forming an inverted V or Y shape. The gnathos is paired and often partially reduced, with exceptions in two species: D. latipennata (Puplesis & Robinson), which has an unpaired gnathos with one caudal process and distinctive lateral arms, and D. diviantis sp. nov., which has a slightly different, still bilobed gnathos. In contrast, the majority of Neotropical Acalyptris species have a stout gnathos with one caudal process. The valva features a large inner (median) process, except in D. ecuadoriana (Puplesis & Diškus). Few Neotropical Acalyptris species have a valva with an inner process, and when present, it is not morphologically homologous to that of *Dvidulopsis* gen. nov. The sublateral processes of the valva are always long or very long, whereas only some Neotropical Acalyptris species have rather long sublateral processes. The transtilla always has a transverse bar, unlike most Acalyptris, where the absence (rather than the presence) of a transverse bar is more typical. The juxta usually present but small. The vinculum is large or very large, except in D. ecuadoriana, which has a moderately large vinculum. The posterior margin of the vinculum usually has either two short, rounded lobes or one short, rounded lobe.

The lateral apodemes, unique structures characteristic of the male genital capsule of *Acalyptris*, are usually absent in *Dvidulopsis* gen. nov.

Female genitalia. Known from an illustrated *D. latipennata* specimen by Puplesis & Robinson (2000); however, this specimen was excluded from the type series by later authors, and therefore, because of some uncertainty, the female genitalia are not discussed here.

Biology. The host plant is known only for the type species, *D. amazonensis* (Stonis & Diškus, 2018). Larvae of the latter species mine leaves of *Psychotria* L. (Rubiaceae). The leaf mine (illustrated in Stonis & Diškus, 2018) is a sinuous to very contorted gallery, with dark green to black-green or brown-green frass variously deposited at certain stages of development. Exit slits of the type species are on the upper side of the leaf; the cocoon is round, 2 mm long, 1.5 mm wide, yellowish beige, and not glossy (matte) (Stonis & Diškus, 2018).

Distribution: The species of this genus are known exclusively from lowland tropical forests of the Neotropics, from southwestern Mexico, Belize and Honduras (Fig. 26) in the north to equatorial Ecuador in the south (Figs 27, 28).

Taxonomic composition. The following species are included in the genus *Dvidulopsis* gen. nov.: *D. latipennata* (Puplesis & Robinson, 2000), comb. nov.: Belize (Chiquibul forest) and Honduras, 2 ♂, 7.5 km SE of La Ceiba, right bank of Rio Cangrejal, 100 m, 15°43′34″N, 86°44′26″W, 14.iv.2023, leg. J.R. Stonis, genitalia slide nos RA1224♂, RA1223♂ (MfN) (new distribution); *D. dividua* (Puplesis & Robinson, 2000), comb. nov.: Belize (Chiquibul forest); *D. paradividua* (Šimkevičiūtė & Stonis, 2009), comb. nov.: Mexico (Pacific coast) (Šimkevičiūtė et al. 2009); *D. ecuadoriana* (Puplesis & Diškus, 2002), comb. nov.: Ecuador (Región amazónica); *D. onorei* (Puplesis & Diškus, 2002), comb. nov.: Ecuador (Región amazónica); *D. insolentis* (Puplesis & Diškus, 2002), comb. nov.: Ecuador (Región amazónica); *D. diviantis* Stonis & Remeikis, sp. nov.: Honduras (Atlantída Department) (described below).

Etymology. The new genus name *Dvidulopsis* is a noun of neutral gender. It is a unique combination of Lithuanian and Greek elements, crafted to emphasize the genus's distinctive morphological characteristics. The prefixes "Dvi-" (feminine) and "du" (masculine) means "two" in Lithuanian. This deliberate combination of "dvi" and "du" underscores the dual nature of the genus, specifically referring to the two structures of the male genitalia, the uncus and gnathos, each fully or partially divided into two lobes (or processes). The suffix "-opsis" is from the Greek word "opsis", meaning "appearance" or "resemblance".

Dvidulopsis diviantis Stonis & Remeikis, sp. nov. urn:lsid:zoobank.org:act:11055433-CA46-4A13-8369-B060F08285E5 (Figs 3, 21–26)



FIGURES 21–25. Male genitalia of *Dvidulopsis diviantis* Stonis & Remeikis, **sp. nov.**, Honduras, holotype, genitalia slide no. RA1222 (MfN). 21, 23–25, enhanced details; 22, photographic image of the genitalia slide.



FIGURES 26–28. Habitats of *Dvidulopsis* gen. nov. 26, habitat of *D. diviantis* Stonis & Remeikis, sp. nov., Honduras, the Caribbean coast, Atlantída Department, Tela, elevation approx. 10 m; 27, 28, habitat of the type species *D. amazonensis* (Stonis & Diškus), comb. nov., Ecuador, Región amazónica, Misahualli, approx. 400 m.

Type material. Holotype: ♂, HONDURAS, Atlantída Department (the Caribbean coast), Tela, approx. 10 m, 15°45′56.78″N, 87°21′06.97″W, at light (25C), 3.iii.2024, leg. J.R. Stonis, genitalia slide no. RA1222♂ (MfN).

Diagnosis. Externally, *Dvidulopsis diviantis* **sp. nov.** can be confused with the similar, cream-scaled *D. dividua*, *D. paradividua*, and *D. ecuadoriana*. However, in the male genitalia, the new species differs from all currently known species of the genus by at least three unique characters: the massive, bilobed gnathos; the basally pointed phallus; and the short, widely triangular inner lobe of the valva.

Barcodes. We barcoded the male holotype specimen; the sequence is available in GenBank under the voucher/ sample ID: PV121131.

Male (Fig. 3). Forewing length 2.0 mm; wingspan 4.4 mm. (n = 1). Head: palpi and frons glossy cream; frontal tuft pale beige-orange; collar very indistinct, comprised of piliform scales; scape large, golden cream; antenna unknown (broken in the holotype). Thorax and tegula golden cream, glossy, with some scattered brown scales. Forewing golden cream, sparsely speckled with brown scales, with oblique subapical pseudofascia composed of blackish brown scales; fringe greyish cream on the tornus, golden cream apically; fringe-line absent; forewing underside densely speckled with brown to dark brown scales, without androconia. Hindwing and its fringe grey. Legs glossy cream, densely speckled with dark brown scales on the upper side.

Female. Unknown.

Male genitalia (Figs 21–25). Capsule significantly longer (300 μ m) than wide (180 μ m). Uncus clearly bilobed. Gnathos partially divided, with thickened slender lateral arms and a two-lobed main plate. Valva 160 μ m long, with two lobe-like processes: median and smaller basal; transtilla with a slender transverse bar; sublateral processes long, slender, and straight. Juxta absent. Vinculum with large lateral lobes, anteriorly with a deep, round excavation. Phallus 225 μ m long, strongly constricted basally, with three elongated carinae apically; vesica without cornuti.

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

Distribution. This species is known from the lowland humid (moist) forests of northern Honduras (Caribbean coast, Atlántida Department), at an elevation of 10 m (Fig. 26).

Etymology. The name of the new species is an adjective derived from the combination of the Latin prefix "divi-" (related to the concept of division or separation) and the Latin suffix "-antis" (an ending commonly used to form adjectives that describe a state or action related to the root). The species name *diviantis* refers to the uniquely divided gnathos in the male genitalia of the new species.

Molecular considerations of Dvidulopsis gen. nov.

For our molecular analysis, we successfully obtained three new mtDNA CO1-5' sequences for *Dvidulopsis diviantis* **sp. nov.** and *D. latipennata* (Puplesis & Robinson). The latter was originally described from the tropical humid forests of Belize as *Fomoria latipennata* (Puplesis & Robinson, 2000). Two years later, it was transferred to *Acalyptris* Meyrick and became the eponymous species of the former *Acalyptris latipennata* group (Puplesis *et al.* 2002b). In the current study, this group was excluded from *Acalyptris* and due to its striking morphology, the *latipennata* group was elevated to a taxonomic rank, resulting in the creation of the new genus *Dvidulopsis* **gen. nov.** This is why, to justify the phylogenetic status of the new genus and its species, our current molecular analysis included several species from the morphologically similar genera *Acalyptris* Meyrick and *Fomoria* Beirne.

In all of our reconstructed phylogenetic trees, the two sequenced species of *Dvidulopsis* gen. nov. clearly differed from *Acalyptris* species and consistently clustered together with a high degree of reliability (ML probability value of 87%) (Fig. 29). When we included the morphologically resembling genus *Fomoria* Beirne in the analysis, *Dvidulopsis* gen. nov. still diverged from both *Acalyptris* and *Fomoria*, appearing as a sister clade to *Acalyptris* + *Fomoria* (ML probability value of 87%). Additionally, we included *Ectoedemia*, which is closely related to *Fomoria* and *Acalyptris* (see Fig. 4 in Doorenweerd *et al.* 2016). It is interesting that some *Ectoedemia* species, *Ectoedemia* formed a distinct clade with an ML probability value of 85% (Fig. 30). In this tree, *Dvidulopsis* gen. nov. also showed clear distinction, forming a well-supported dichotomy with *Fomoria* + *Acalyptris* + *Ectoedemia* (ML probability value of 94%).

In all cases, the clade of *Dvidulopsis* gen. nov. consistently appeared as a distinct, separate phylogenetic entity. These results align well with the unique morphology of the genus *Dvidulopsis* gen. nov. and its species, supporting the erection of this new genus.



FIGURE 29. The phylogenetic relationships of *Dvidulopsis* **gen. nov.** and *Acalyptris* Meyrick species based on the 657 bp mtDNA CO1-5' sequences. The Maximum Likelihood algorithm with 10,000 replicates and the GTR+G+I model were applied. Bootstrap values below 50 are not shown. Three Tischeriidae species were included as an outgroup.

Discussion

It was previously believed that pygmy moths, although very diverse in temperate habitats, were probably uncommon in tropical humid forests—especially in lowland tropical humid forests (Puplesis & Robinson, 2000). However, recent studies have shown a different trend. In preparing the current paper, we created a distribution map for the species currently recorded from the lowland tropical humid forests (Fig. 31) of the mainland of Central and South America (i.e., excluding islands).

The study of Nepticulidae in the lowland tropical humid forests of the Neotropics began in 2000 and continues today. Before this period, only a few Nepticulidae species were described from this biome, such as *Stigmella eurydesma* (Meyrick, 1915), *Enteucha cyanochlora* Meyrick, 1915, and *Manoneura basidactyla* (Davis, 1978). Our review revealed that a great number of Nepticulidae species in the Neotropical region (*sensu stricto*, excluding the temperate Ando-Patagonian fauna) were discovered in montane areas above 1,000 m, with the highest recorded elevation being 4,700 m (*Stigmella nivea* Remeikis & Stonis, as described by Stonis *et al.* 2016) (Fig. 32). However, the lowland Nepticulidae fauna in the Neotropics appears to be just as rich as the montane fauna. Currently, the Nepticulidae fauna of the lowland tropical humid forests in the Neotropics consists of about 57 species, representing roughly 30% of the total currently described Neotropical fauna (*sensu stricto*).



FIGURE 30. The phylogenetic relationships of *Dvidulopsis* **gen. nov.**, *Acalyptris* Meyrick, *Ectoedemia* Busck, and *Fomoria* Beirne species based on the 657 bp mtDNA CO1-5' sequences. The Maximum Likelihood algorithm with 10,000 replicates and the GTR+G+I model were applied. Bootstrap values below 50 are not shown. Three Tischeriidae species were included as an outgroup.

Despite the dramatic destruction of natural habitats in lowland areas, the diversity of lowland tropical Nepticulidae remains high, and studies in these regions often lead to the discovery of exotic-looking, phylogenetically basal, or even endemic taxa.

The genus *Dvidulopsis* gen. nov. is distinct not only in its species morphology but also in its geographical distribution. It is an endemic genus of the lowland tropical humid forests in the Neotropical region. All species of this genus, whether from Central or South America, are exclusively found in humid forests much below 1,000 m, with their typical elevation range being between 10 and 400 m, including the Amazon rainforest.

The species of *Dvidulopsis* gen. nov. are rare in entomological collections. For instance, during sampling in Honduras, many Nepticulidae specimens were collected, with some species found in large numbers (in the hundreds), but the specimens belonging to *Dvidulopsis* gen. nov. were surprisingly few. During the relatively intense four-month collecting effort in Honduras in 2023, only two specimens of a single *Dvidulopsis* species were captured, and during three months of collecting in 2024, only one specimen of another *Dvidulopsis* species was found. Therefore, it is not surprising that out of the eight currently described *Dvidulopsis* species, four have been described from singletons. The remaining species were described from only a few specimens: *D. onorei* (Puplesis & Diškus) from two specimens, *D. ecuadoriana* (Puplesis & Diškus) and *D. dividua* (Puplesis & Robinson) from three specimens each, and *D. insolentis* (Puplesis & Diškus) from four specimens (Puplesis *et al.* 2002).

The reasons for the rarity of *Dvidulopsis* gen. nov. are unclear. It is possible that *Dvidulopsis* moths do not fly well to light and, as a result, are rarely encountered. Additionally, leaf mines also appear to be uncommon; so far, leaf mines of only a single species, *D. amazonensis* (Stonis & Diškus), have been discovered. We believe that *Dvidulopsis* species occur in low densities and can truly be considered rare, which further reduced the chances of finding these "exotic-looking" moths.



FIGURE 31. Distribution map of Neotropical Nepticulidae species currently recorded from lowland tropical humid forests on the mainland of Central and South America (i.e., excluding islands). 1-Simplimorpha (Myrtinepticula) kailai Stonis & Diškus, 2018, Peru; 2-Johanssoniella hilli (Puplesis & Robinson, 2000), Belize; 3-J. contracolorea (Puplesis & Robinson, 2000), Belize; 4-J. acuta (Puplesis & Diškus, 2002), Ecuador; 5-Enteucha cyanochlora Meyrick, 1915, Guyana; 6-E. snaddoni Puplesis & Robinson, 2000, Belize; 7-Manoneura basidactyla (Davis, 1978), USA: Florida, Belize, Cuba, Dominica, French Guiana, Ecuador, and Colombia; 8-M. trinaria Puplesis & Robinson, 2000, Venezuela; 9-Ozadelpha guajavae (Puplesis & Diškus, 2002), Ecuador; 10-Stigmella kimae Puplesis & Robinson, 2000, Belize; 11-S. barbata Puplesis & Robinson, 2000, Belize; 12-S. maya Remeikis & Stonis, 2013, Mexico: Yucatán; 13-S. eurydesma (Meyrick, 1915), Guyana; 14-S. albilamina Puplesis & Robinson, 2000, Belize; 15-S. fuscilamina Puplesis & Robinson, 2000, Belize; 16-S. venezuelica Remeikis & Stonis, 2017, Venezuela; 17-S. pruinosa Puplesis & Robinson, 2000, Mexico: Pacific Coast, Belize, Guatemala, and Colombia; 18-Ectoedemia fuscivittata Puplesis & Robinson, 2000, Belize and Ecuador; 19-Hesperolyra diskusi (Puplesis & Robinson, 2000), Belize; 20-H. robinsoni Stonis, 2017, Belize; 21-H. repanda (Puplesis & Diškus, 2002), Ecuador; 22-Fomoria tabulosa Puplesis & Diškus, 2002, Ecuador; 23-Acalyptris minimus Diškus & Stonis, 2018, Ecuador; 24-A. marmor Stonis & Diškus, 2020, Peru; 25-A. barbudo Stonis & Remeikis, 2020, Peru; 26-A. hispidus Puplesis & Robinson, 2000, Belize and Ecuador; 27-A. jareki Stonis & Diškus, 2020, Belize; 28-A. novenarius Puplesis & Robinson, 2000, Belize; 29-A. trifidus Puplesis & Robinson, 2000, Belize; 30-A. laxibasis Puplesis & Robinson, 2000, Belize; 31-A. rotundus Puplesis & Diškus, 2002, Ecuador; 32-A. hilli Stonis & Diškus, 2020, Peru; 33-A. amazonius Puplesis & Diškus, 2002, Ecuador; 34-A. miranda (Diškus & Stonis, 2017), Ecuador; 35-A. lascuevella Puplesis & Robinson, 2000, Belize, Mexico, and Honduras; 36-A. bifidus Puplesis & Robinson, 2000, Belize, and Colombia; 37-A. yucatani Remeikis & Stonis, 2013, Mexico: Yucatán and Colombia; 38-A. argentosa (Puplesis & Robinson, 2000), Belize; 39-A. unicornis Puplesis & Robinson, 2000, Belize; 40-A. peteni Diškus & Stonis, 2013, Guatemala; 41-A. solaris Remeikis & Stonis, 2018, Venezuela; 42-A. fortis Puplesis & Robinson, 2000, Belize; 43-A. martinheringi Puplesis & Robinson, 2000, Belize; 44-A. basihastatus Puplesis & Diškus, 2002, Ecuador; 45-A. pseudohastatus Puplesis & Diškus, 2002, Ecuador; 46-A. articulosus Puplesis & Diškus, 2002, Ecuador; 47-A. platygnathos Puplesis & Robinson, 2000, Belize; 48-A. basicornis Remeikis & Stonis, 2013, Guatemala; 49-A. bovicorneus Puplesis & Robinson, 2000, Belize; 50-Dvidulopsis latipennata (Puplesis & Robinson, 2000), Belize and Honduras (new distribution record); 51-D. dividua (Puplesis & Robinson, 2000), Belize; 52-D. ecuadoriana (Puplesis & Diškus, 2002), Ecuador; 53-D. onorei (Puplesis & Diškus, 2002), Ecuador; 54-D. insolentis (Puplesis & Diškus, 2002), Ecuador; 55-D. paradividua (Šimkevičiūtė & Stonis, 2009), Mexico; 56-D. amazonensis (Stonis & Diškus, 2018), Ecuador; 57-D. diviantis Stonis & Remeikis, sp. nov., Honduras.



FIGURE 32. Comparison of the number of Neotropical Nepticulidae species recorded in lowland tropical habitats (below 1,000 m) and montane habitats (above 1,000 m), highlighting the Andean *Stigmella nivea* Remeikis & Stonis (Stonis *et al.* 2016) as a species discovered at record-high altitudes globally. Notes: The total number of Nepticulidae species in the Neotropical region (*sensu stricto*; see Stonis *et al.* 2016) is calculated as 191 species, comprising 57 from lowland tropical humid forest habitats, 34 from other lowland habitats, and 100 recorded from montane habitats. This illustrative representation of Neotropical ecosystem diversity, conceptualized by J. R. Stonis, is stylized and idealized, without aiming for precise depiction of the actual components (ecosystems or habitats) of the Neotropical biota

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