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Three new species of the genus Argyresthia Hübner, [1825] from Guatemala, with notes on host plant evolution and Nearctic taxa (Lepidoptera: Argyresthiidae)

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Abstract

Neotropical species of the genus Argyresthia Hübner, [1825] represent a reservoir of undescribed biodiversity and are the most poorly known members of this cosmopolitan genus. From a series of Guatemalan material, three new species are described: Argyresthia quetzaltenangonella Gorneau & Dombroskie, sp. nov., Argyresthia guatemala Gorneau & Dombroskie, sp. nov., Argyresthia guatemala Gorneau & Dombroskie, sp. nov., representing the first Neotropical species to be described in over a century, and the first from Central America. A phylogeny is inferred using the barcode gene cytochrome c oxidase subunit I (COI), representing an initial foray into the internal relationships of the family. For species with known host plants and available molecular data, a stochastic character mapping analysis was conducted to estimate character states at internal nodes. Furthermore, this phylogeny allows for preliminary insights into the monophyly of the subgenus Blastotere Ratzeburg 1840. Systematic work on Argyresthia remains particularly salient as species in the genus run the gamut from being pests to being considered extinct. Furthermore, notes are provided regarding the status of select Nearctic species, such as the ongoing confusion in North America between Argyresthia goedartella (Linnaeus, 1758) and A. calliphanes Meyrick 1913. Focusing taxonomic efforts on Argyresthia of the Neotropics will lay the foundation for future work regarding biodiversity, ecology, and biogeography of the family.

Keywords: Lepidoptera, Argyresthiidae, new species, host plants, phylogenetics, Guatemala.

Tres nuevas especies del género Argyresthia Hübner, [1825] de Guatemala, con notas sobre la evolución de la planta nutricia y taxas Neárticas (Lepidoptera: Argyresthiidae)

Resumen

Las especies neotropicales del género *Argyresthia* Hübner, [1825] (Lepidoptera: Argyresthiidae) representan un reservorio de biodiversidad no descrita y son los miembros menos conocidos de este género cosmopolita. A partir de una serie de material guatemalteco se describen tres nuevas especies: *Argyresthia quetzaltenangonella* Gorneau & Dombroskie, sp. nov., *Argyresthia guatemala* Gorneau & Dombroskie, sp. nov., *argyresthia quetzaltenangonella* Gorneau & Dombroskie, sp. nov., representando la primera especie neotropical descrita en más de un siglo y la primera de América Central. Se infiere una filogenia utilizando el gen del código de barras citocromo c oxidasa subunidad I (COI), lo que representa una incursión inicial en las relaciones internas de la familia. Para especies con plantas nutricias conocidas y datos moleculares disponibles, se realizó un análisis de mapeo de caracteres estocásticos para estimar los estados de caracteres en los nodos internos. Además, esta filogenia permite obtener información preliminar sobre la monofilia del subgénero *Blastotere* Ratzeburg 1840. El trabajo sistemático sobre *Argyresthia*

sigue siendo particularmente destacado ya que las especies del género van desde ser plagas hasta considerarse extintas. Además, se proporcionan notas sobre el estado de especies neárticas seleccionadas, como la confusión actual en América del Norte entre *Argyresthia goedartella* (Linnaeus, 1758) y *A. calliphanes* Meyrick 1913. Centrar los esfuerzos taxonómicos en *Argyresthia* del Neotrópico sentará las bases para el trabajo futuro con respecto a la biodiversidad, ecología y biogeografía de la familia.

Palabras clave: Lepidoptera, Argyresthiidae, nuevas especies, plantas nutricias, filogenética, Guatemala.

Introduction

The enigmatic genus *Argyresthia* Hübner, [1825] belongs to the superfamily Yponomeutoidea and is the sole lineage of the family Arguresthiidae, totaling just over 200 described species (Lewis & Sohn, 2015; Liu et al. 2017). While small in size, species of *Argyresthia* exhibit a variety of forewing patterns ranging from high-contrast metallics to dull silvers, to mottled browns, and are sometimes colloquially referred to as "shiny head-standing moths" for their resting posture. Currently, most species are Palearctic in distribution (Lewis & Sohn, 2015; Liu et al. 2017). Although it has been suggested by Heppner (2008) that the total diversity of the family may "exceed 450 species", the recent description of forty-three new species from China alone indicates this is likely to be a lower estimate (Liu et al. 2017). The subgenus *Blastotere* Ratzeburg, 1840 was more formally characterized by Liu et al. (2017) and represents the sole subgenus aside from the nominate subgenus. It contains twenty-five species (Table I), in accordance with Bengtsson & Johansson (2011) and Liu et al. (2017).

Table I. Species currently described formally in subgenus *Blastotere* Ratzeburg 1840.

Species	Authority		
Argyresthia (Blastotere) affinicineretra	Liu, Wang & Li, 2017		
A. (B.) albaureola	Liu, Wang & Li, 2017		
A. (B.) amiantella	(Zeller, 1847)		
A. (B.) anthocephala	Meyrick, 1936		
A. (B.) arceuthina	Zeller, 1839		
A. (B.) aureola	Liu, Wang & Li, 2017		
A. (B.) bergiella	(Ratzeburg, 1840)		
A. (B.) chalcocausta	Meyrick ,1936		
A. (B.) cineretra	Liu, Wang & Li, 2017		
A. (B.) densa	Liu, Wang & Li, 2017		
A. (B.) dilectella	Zeller, 1847		
A. (B.) dolichocoremata	Liu, Wang & Li, 2017		
A. (B.) glabratella	(Zeller, 1847)		
A. (B.) idiograpta	Meyrick, 1935		
A. (B.) illuminatella	Zeller ,1839		
A. (B.) kulfani	Bengtsson & Johansson, 2011		
A. (B.) laevigatella	Herrich-Schäffer, 1855		
A. (B.) longipenella	Liu, Wang & Li, 2017		
A. (B.) ornatipennella	Moriuti, 1974		
A. (B.) praecocella	Zeller, 1839		
A. (B.) punctireticulata	Liu, Wang & Li, 2017		
A. (B.) sporadolepis	Liu, Wang & Li, 2017		
A. (B.) svenssoni	Bengtsson & Johansson, 2011		
A. (B.) trifasciata	Staudinger, 1871		

As larvae, species in the genus Argyresthia are miners and borers on gymnosperms and angiosperms. Host plant records currently exist for approximately one-third of the species in the genus

(Friese, 1969; Bengtsson & Johansson, 2011; Lewis & Sohn, 2015). Of these sixty-one species, forty-two of them feed on gymnosperms, and sixteen on Rosaceae (Friese, 1969; Bengtsson & Johansson, 2011; Lewis & Sohn, 2015). Three are cited as polyphagous (Lewis & Sohn, 2015). Liu et al. (2017) have suggested that the evolution of this group in China may be closely related to the diversity of gymnosperms in the region, noting the geographic similarities with areas of high *Argyresthia* diversity to high gymnosperm diversity, but this has yet to be evaluated in a phylogenetic context.

Knowledge of the systematics of this family is important to help understand pest management, climate change, and conservation. Some species are invasive pests of ornamental plants and fruit crops. Argyresthia thuiella (Packard, 1871) has been introduced from North America to Europe multiple times, where it has wreaked havoc on ornamental cupressaceous plants, such as that of Thuja occidentalis Linnaeus (Csóka, 2001). Argyresthia trifasciata, though native to Europe, appears to be spreading and has established itself as a pest in Hungary (Tiborne & Kálmán, 2000). Other species, such as A. conjugella Zeller, 1839, and A. pruniella (Clerck, 1759) are demonstrated pests of rosaceous fruit crops (Lampa, 1905; Shreyner, 1906; Schøyen, 1913; Ahlberg, 1927; Stapley, 1934; Belosel's Kaya, 1963; Korchagin, 1988; Sharma et al. 1988; Wimshurst, 1928; Alford, 1978; Carter, 1984; Alford, 2007; Jaastad, 2007; Loone et al. 2017). Climate change may have resulted in intensified outbreaks of A. retinella Zeller, 1839, a native birch (Betula spp.) feeder in northwestern Norway that until the 1990's was not known to exhibit an outbreak (Tenow et al. 1999). Conversely, one species, A. castaneella Busck, 1915, whose recorded host plant is the critically endangered American Chestnut (Castanea dentata (Marsh.) Borkh.), is now presumed extinct (World Conservation Monitoring Centre, 1996; Stritch, 2018). The relevance of this group to agricultural, horticultural, and natural systems makes applied and basic work on the Argyresthiidae integral.

While the genus *Argyresthia* is well-studied in other regions of the world, particularly in Europe and Asia, a comprehensive review of the group in the Americas has not been completed in over one-hundred years, necessitating the taxonomic study of this group in the New World (Zeller, 1877; Bisck, 1907). Only seven species have been described from the Neotropics (Lewis & Sohm, 2015): *A. biruptella* Zeller, 1877, *A. carcinomatella* Zeller, 1877, *A. diffractella* Zeller, 1877, *A. ochridorsis* Zeller, 1877, and *A. percussella* Zeller, 1877 from Bogotá, Colombia; *A. conspersa* Butler, 1883 from Cauquenes, Chile; and *A. melitaula* Meyrick, 1918 described from La Cumbre, Colombia. Incidentally, no Central American *Argyresthia* species have been described or noted.

The goal of this work is to describe the Guatemalan holdings of *Argyresthia* in the Cornell University Insect Collection (CUIC) and to infer a phylogeny of the group based on the barcode gene, cytochrome oxidase c subunit I (COI). From this phylogeny, stochastic character mapping will be used to provide some preliminary insights into the evolution of host plant associations in the family. This study will also evaluate evidence for phylogenetic support of the subgenus *Blastotere* based on the COI inference. Lastly, some notes on the taxonomy of Nearctic species will be provided. Due to the estimated magnitude of unexplored diversity in this family and its worldwide distribution, this work also serves as a call-to-action for more to study the systematics of this family.

Materials and Methods

Specimens were collected by JJD, Tim McCabe, and JMS in early 2014. Specimens and genitalia were photographed using Canon EOS 6D with a Macropod Pro photo-stacking setup and images were automatically stacked using ZereneStacker. Photos were post-processed using Adobe Photoshop.

Dissections were made by removing the abdomen with fine forceps and placing it in a 1.5 mL plastic tube with approximately 1 mL of 10% potassium hydroxide (KOH) solution. The tube was then placed in a heat block at 81°C and was checked at twenty-minute intervals until the abdomen was translucent. The abdomen was then removed from the heat and placed in a Syracuse watch glass with 70% ethanol. A small brush was used to remove scales that were not digested by KOH. Once the abdomen was brushed clean of scales, the specimen was soaked in chlorazol black for one full minute,

and then placed in eosin Y, microwaved for four seconds, and then left to sit in the microwaved eosin y dye for at least 10 minutes afterwards to ensure adequate setting of the dye. Terminology used for descriptions is in accordance with Liu et al. (2017), which largely follows Moriuti (1977).

For data not generated by this study, 130 sequences of the DNA barcoding region, COI, were downloaded from GenBank and the Barcode of Life Database (BOLD, Table S1). Single legs from a total of seven specimens were sent to BOLD (Centre for Biodiversity Genomics, Guelph, ON, CA) for sequencing of COI, and one additional sample was sequenced through the Cornell Genomics Facility (Ithaca, NY, USA). All sequences were submitted to GenBank through the BOLD interface. For all samples, the standard HCO2198/LCO1490 primer set was used (Folmer et al. 1994). Sequence accession information for those containing data generated by this study are available in Table II.

Genus	Species	JD Accession	GenBank Accession	BOLD Voucher
Argyresthia	quetzaltenangonella sp. nov.	JD23247	OM158441	CUICA018-19
Argyresthia	guatemala sp. nov.	JD13161	OM158438	CUICA010-19
Argyresthia	guatemala sp. nov.	JD17039	OM158444	CUICA014-19
Argyresthia	guatemala sp. nov.	JD17808	OM158442	CUICA016-19
Argyresthia	guatemala sp. nov.	JD16994	OM158437	CUICA012-19
Argyresthia	guatemala sp. nov.	JD17474	N/A	CUICA015-19
Argyresthia	iridescentia sp. nov.	JD22454	OM158440	CUICA017-19
Argyresthia	sp. nov.	JD13196	OM158439	CUICA011-19
Argyresthia	sp. nov.	JD17038	OM158443	CUICA013-19

Table II. Sequence information generated in this study with accession numbers.

Sequences were then aligned using the program MAFFT using the L-INS-i method (Katoh & Standley, 2013). Sequences were then manually examined and alterations to the MAFFT alignment were made as necessary in the program Mesquite (version 6.0) to ensure no stop codons were present in the alignment (Maddison & Maddison, 2018). A maximum likelihood phylogeny was inferred using IQ-TREE, a maximum likelihood phylogeny was inferred with 10,000 replicates and UFBoot values as nodal supports (Nguyen et al. 2015; Kalyaanamoorthy et al. 2017; Hoang et al. 2018). Using another method to examine convergence, a NEXUS block partitioned by codon position was exported from Mesquite for use in MrBayes. The analysis ran for 100,000,000 generations, with a burn in of 25%, following an inverse gamma distribution, with four chains. The phytools function cophylo was used to examine similarity among inferences.

Stochastic character mapping of host plants was implemented in RStudio (2022) using the packages phytools, corHMM, and geiger (Revell 2012; Pennell et al. 2014; Boyko & Beaulieu, 2021). The phylogeny was trimmed to species for which host plant data were available. While it is customary to include only one representative for each species in comparative phylogenetic analyses, multiple representatives were included for paraphyletic species. The tree was converted to an ultrametric topology to eliminate the bias of branch lengths on the inference. Model selection for host plant stochastic character mapping was conducted with the fitMk function for the equal rates, symmetric rates, and all rates different models. The equal rates model was selected via Akaike information criterion (AIC) values. Stochastic map trees were generated under the equal rates model using the function make.simmap for 1000 generations using a Markov Chain Monte Carlo approach with sampling every 10 generations, for a total of 100 stochastic map trees. From these 100 trees, posterior probabilities were calculated for all nodes. While there is likely less plasticity necessary for a host plant change from gymnosperm to gymnosperm versus a change between gymnosperm and angiosperm host plants, to not over parameterize the dataset, which already has limited resolution due to the single locus nature of this study, no further assumptions were made beyond that of the equal rates model. The character matrix, with corresponding character states is available in Table SII. Code avalable from https://doi.org/10.5281/zenodo.6865177.

Results

Argyresthia quetzaltenangonella, Gorneau & Dombroskie, sp. nov. (Figure 1)

Type material: Holotype, &, Guatemala: Quetzaltenango, Fuentes Georginas, 14.750, -91.480; 26-II-2014; J. J. Dombroskie, T. McCabe & J. Monzón leg.; MV/UV light: 2439 m; JD23247 (CUIC).

Description: Male adult (Figure 1A): Head with vertex white and roughly scaled. Frons creamcolored and smoothly scaled, becoming slightly whiter toward the proboscis. Labial palpus with first segment cream-colored, second segment distinctly whiter, and held freely, not erect in an upright position. Antenna with white eyecap obscuring approximately one-fourth of the eye; flagellum ground color white, striped with alternating dark brown scales. Thorax white, tegula golden orange. Forewing length 6.5 mm (n = 1). Forewing ground color just slightly off-white, with first two-thirds of wing from costa toward inner margin lightly reticulated with slightly off-white squares outlined in brownish-gold and interrupted basally by a thick golden orange band parallel to inner margin and costa which tapers distally about one-third of the way toward apex of wing; towards inner margin, ground color slightly whiter than elsewhere and interrupted at about same place where the golden orange band tapers by a broken light brown fascia which penetrates slightly into reticulated region of forewing, last one-fifth of wing near apex mottled golden brown with a series of dark scales marking apex before fringe, which are all dark grayish-brown. Hindwing length 5.0 mm (n = 1). Hindwing gray, becoming darker toward apex and inner margin a grayish-yellow color. Foreleg entirely dark brown ventrally, banded dorsally, predominantly white in ground color with dark brown bands occurring at the joints; midleg banded dorsally, as in foreleg, with this pattern slightly fainter ventrally; hindleg as in midleg. Abdomen pearly and with light grayish-white ground color. Coremata present and occupying approximately two-thirds of the abdomen in length (Figure 1B).

Male genitalia (Figure 1C-D): Socius covered with approximately 20 elongate scale-like setae, with three or four additional elongate setae on inner side of socius (Figure 1C). Tube analis tapering and subequal to width of valva. Valva rotund, with very few hairs. Phallus (Figure 1D) kinked basally, with cornutus visible in apical third; cornutus with seven small notches.

Female: Unknown.

Diagnosis: Similar to *Argyresthia biruptella* Zeller, 1877, described from Bogotá, Colombia, but with less maculation throughout the forewing, a faded reticulated pattern on the first two-thirds of the wing from the costa, and the presence of a golden orange band which runs parallel to the inner margin and costa extending about one-third of the way down the wing.

Distribution: One male specimen known from a cool high elevation forest in Quetzaltenango, Guatemala (2439 m).

Biology: See further discussion under Stochastic Character Mapping, but likely gymnosperm-feeding, as the ancestral state for the clade this species is inferred to belong to is Cupressaceae-feeding. *Cupressus lusitanica* Miller is present in the vicinity of this location.

Etymology: It is so named for the Quetzaltenango Department in Guatemala, where the type was found.

Argyresthia guatemala Gorneau & Dombroskie, sp. nov. (Figure 2)

Type material: Holotype ♀, Guatemala, Alta Verapaz, Posada del Guardabarranco 15.300, -90.317; 02-III-2014; J. J. Dombroskie, T. McCabe & J. Monzón leg.; MV/UV light: 1549 m; JD13161 (CUIC).

Paratypes $(2\ \ensuremath{\circlearrowleft}\ \ensuremath{\hookrightarrow}\ \ensuremath{\hookrightarrow}$

Description: Female adult (Figure 2A): Head with vertex white and roughly scaled. Frons white to light beige and smoothly scaled. Labial palpus uniformly beige, sometimes darker than that of the frons, and held freely, not in an upright position. Antenna with white eyecap obscuring approximately one-fourth of the eye; flagellum ground color white, striped with alternating dark brown scales. Thorax white, tegula a light purplish brown. Forewing length 4.0 - 4.3 mm (n = 3). Forewing ground color cream colored, forewing from costa a mottled brown which becomes lightly reticulated toward the inner margin. About halfway down the inner margin, a small dark brown patch is present, with a smaller patch just opposite this on the costa. There are two more patches between the others, one located apically relative to the midpoint between the first two patches, and one located basally relative to the midpoint between the first two patches. Another patch about one-sixth of the way from the base of the wing that may just appear as a darker reticulation near the inner margin and another patch just slightly apical to that in the about halfway between the inner margin and the costa. Another dark patch on the apex of the wing. Hindwing length 3.3 - 3.5 mm (n = 3). Hindwing a uniform silver. Foreleg entirely dark brown ventrally, banded dorsally, predominantly white in ground color with dark brown bands occurring at the joints. Midleg banded dorsally, as in foreleg, with this pattern slightly fainter ventrally; hindleg as in midleg. Abdomen uniform silver as in hindwing.

Female genitalia (Figure 2B-C): Ductus bursae elongate, roughly 2.3 times the length of corpus bursae, and widening anteriorly approximately halfway to the corpus bursae (Figure 2B). Corpus bursae (Figure 2B) ovate and tapered distally as it nears the ductus bursae, with few maculations. Basal plate of signum ovoid and denticulate, with strongly sclerotized horn on either side of this plate slightly curved posteriorly. Horn of signum serrated regularly. Anterior to the horn of the signum, the basal plate remains ovoid but smaller in surface area, covering approximately one-third of the area of the basal posterior to the horn. Antrum and posterior apophyses visible in dissection image but damaged and indistinct image as ductus bursae separated from last abdominal segment in dissection process (Figure 2C).

Male adult (Paratypes): As in female, but with forewing length 3.5 mm and hindwing length 3.0 mm (n = 2). Genitalia damaged and unavailable for dissection.

Diagnosis: Looks most similar to *Argyresthia deletella* Zeller, 1873 (Figure 3A-C), described from Texas, USA, but without the brown fascia occasionally present in *A. deletella*, and a more overall mottled appearance. Ground color is overall much whiter than that of *Argyresthia deletella*, which has an overall browner ground color with whitish regions just nearer the inner margin. The signum is strongly serrated in *A. guatemala* but smooth to lightly serrated in *A. deletella*. Furthermore, while both species have a lightly sclerotized plate that is medially located on the signum, the signum in *A. guatemala* is larger and bisected by this structure, while the signum in *A. deletella* remains strongly sclerotized and is not bisected by this structure (Figure 3C).

Distribution: Three specimens (two female, one male) from Atitlan Reserve in Suchitepéquez, Guatemala, and two specimens (one female, one male) from Posada Del Guardabarranco, Alta Verapaz, Guatemala. Both locations are moderate in elevation, from 1549 - 1561 m.

Biology: See further discussion under Stochastic Character Mapping, but host plant ambiguous based on phylogenetic placement and known host plants for related species.

Etymology: It is so named for the country in which this species has been recorded.

Argyresthia iridescentia Gorneau & Dombroskie, sp. nov. (Figure 4)

Type material: Holotype, ♂, Guatemala: Quetzaltenango, Fuentes Georginas 14.750 -91.480; 26-II-2014; J. J. Dombroskie, T. McCabe & J. Monzón leg.; MV/UV light: 2439 m; JD22454 (CUIC).

Description: Male adult (Figure 4A): Head with vertex grayish white and roughly scaled. Frons uniformly light gold and smoothly scaled. Labial palpus uniformly light gold and held freely, not in an upright position. Antenna with white eyecap obscuring approximately one-fourth of the eye. Flagellum grayish white and striped with alternating gold scales. Thorax and tegula gold. Forewing length approximately 3.5 mm. Forewing ground color metallic gold at basal fifth of the wing and fading in

color apically, to match the pale gray-gold of hindwing. Gold ground color of wings can appear as a plumbeous brown when examined at certain angles or photographed. Four broken fasciae a darker metallic gold in coloration. First fascia appears one-fifth from the base of the wing at the inner margin and extends about halfway to the costa. Second fascia also originates from the inner margin, about halfway from the base of the wing and splits into two branches about one-third of the way from the inner margin toward the costa, as to create a V-shape. This fascia fades into the brownish-lead costa about three-fourths of the way from the inner margin. Third fascia originates at the inner margin where the fringe of scales on the forewing also begins and extends diagonally toward the apex and threefourths of the way to the costa. Fourth fascia originates from the costa about halfway to the inner margin and appears much like a triangle. All fasciae may become worn, and appear as a few distinct spots, as in the left wing of the holotype. The apex of the wing has a small patch of five to ten very dark brown scales on the edge of the inner margin. These scales can be reduced to just a few scales from wear. Hindwing length 3.0 mm. Hindwing uniformly light gray-gold. Foreleg entirely dark brown ventrally, predominantly cream colored with slightly darkened bands at the joints dorsally. Midleg banded dorsally, as in foreleg, with this pattern slightly fainter ventrally. Hindleg as in midleg. Abdomen a pearly grayish white. Coremata not present.

Male genitalia (Figure 4B-C): socius covered with elongate scale-like setae (Figure 4B). Tuba analis stout, tapering and subequal to width of valva, valva rotund, and apparently hairless. Phallus kinked basally, with apical third of phallus containing cornutus (Figure 4C). Cornutus with seven small notches.

Female: Unknown.

Diagnosis: Looks most similar to *Argyresthia flexilis* Freeman, 1960, especially in that the wings can appear dull brown at one angle, and near gold in another. The general ground color of the wings is more plumbeous than that of *A. flexilis* and has noticeable maculations and fasciae, where *A. flexilis* is more uniformly patterned. *Argyresthia iridescentia* also has a patch of distinctly dark brown scales at the apex of the forewing.

Distribution: One male specimen known from a cool high elevation forest in Quetzaltenango, Guatemala (2439 m).

Biology: See further discussion under Stochastic Character Mapping, but likely gymnosperm-feeding, as the ancestral state for the clade this species is inferred to belong to is Pinaceae-feeding. *Abies guatemalensis* Rehder and several *Pinus* species can be found in the vicinity of this site.

Etymology: It is so named for the iridescent appearance of the wings which make them appear a pale lead brown at some angles, but golden at others.

Phylogenetic Inference

A monophyletic Argyresthiidae with convergent topologies was supported in both the maximum likelihood and Bayesian inferences (Figure 6, UFBoot = 99; Figure S1, posterior probability = 1.00). While higher-level relationships were not consistent between the inferences, most species-level groupings were (Figure S2). The new species described in this paper were all recovered as distinct (in the case of Argyresthia quetzaltenangonella and A. iridescentia, with single representatives) or monophyletic where there were multiple representatives. Eleven out of twenty-five representatives were included from the subgenus Blastotere, which was recovered as paraphyletic. Argyresthia goedartella (Linnaeus 1758) and A. calliphanes Meyrick, 1913 formed a monophyletic group but were rendered paraphyletic in the groups examined here. Despite this, two representatives from Europe identified as Argyresthia goedartella formed a monophyletic group, Western North American representatives identified as A. calliphanes formed a monophyletic group, and Eastern North American representatives of A. goedartella and A. calliphanes formed a monophyletic group. Argyresthia cupressella Walsingham 1890, Argyresthia trifasciae Braun, 1910, A. abies Freeman, 1972, A. glabratella, A. illuminatella, A. quadristrigella Zeller, 1873 were all rendered paraphyletic in both inferences.

Stochastic Character Mapping

The results of the stochastic character mapping, while inconclusive suggest a potentially Betulaceae-feeding origin for the family (Figure 7). There appear to be two predominant lineages within the Argyresthiidae, one ancestrally Rosaceae-feeding and one ancestrally Cupressaceae-feeding. Within the latter, there are two lineages ancestrally Pinaceae-feeding and one apparent evolution of angiosperm feeding in *Argyresthia glaucinella* Zeller, 1839. Sister to the clade ancestrally Cupressaceae-feeding *Argyresthia* is a grade of Betulaceae-feeding *Argyresthia*.

The results of the stochastic character mapping allow for some broad inferences about host plant use for species that do not currently have a recorded host plant (Figure 7). Species lacking a recorded host plant which fall into the gymnosperm-feeding clade include: *Argyresthia ruidosa* Braun, 1940, *A. austerella* Zeller, 1873, and *A. deletella* Zeller, 1873. Species which fall into the angiosperm-feeding clade include *A. atlanticella* Rebel, 1940, *A. notoleuca* (Turner, 1913), *A. assimilis* Moriuti, 1977, *A. pulchella* Lienig & Zeller, 1846, *A. chalcochrysa* Meyrick, 1913, *A. submontana* Frey, 1870.

Discussion

This study represents preliminary work to describe the diversity of the genus *Argyresthia* in the Neotropics and describes the first species of this family in Central America. All species described are from moderate- to high- elevation areas 1549 m to 2439 m in elevation. Due to the lack of data regarding *Argyresthia* in the Neotropics and the cooler habitat these specimens were collected in, it was necessary to ensure these specimens indeed represented new species and were not part of a range extension for Nearctic conspecifics or were agricultural invasions. Evidence from the phylogenetic inferences using COI supports the monophyly of Argyresthiidae, which has been demonstrated with fewer taxa in past work (Sohn et al. 2013). Both the IQ-TREE maximum likelihood and Bayesian phylogenetic inferences have multiple regions of uncertainty due to soft polytomies representing the inability of the well-conserved COI to resolve all internal relationships in the group. While the topology appears more branching in nature in the IQ-TREE inference, the support is generally low and does not provide additional insight where the Bayesian inference recovered polytomies. Despite this, most species for which there were more than one exemplar were recovered as monophyletic.

Of particular interest is the paraphyly of both Argyresthia calliphanes and A. goedartella. Meyrick (1913), in the original description, characterized A, calliphanes as having a white thorax and Argyresthia goedartella a golden one. Forbes (1923) in his Lepidoptera of New York series seconds Meyrick's notes on distinguishing the two species saying of A. calliphanes: "Head white, thorax white, wing markings exactly like those of A. goedartella", and of A. goedartella "thorax bright golden, fore wing white and coppery golden". He also states the range for A. goedartella to be "Europe; reported from some places in the United States, in part, at least, in error for A. calliphanes". Furthermore, Lewis & Sohn (2015) also note: "This species has been confused with A. goedartella L. It is still unclear if both A. calliphanes and A. goedartella are present in North America. Therefore, some Nearctic records of A. goedartella may be due to confusion with A. calliphanes. A careful revision of these records is necessary." Pohl et al. (2018) only considered individuals as Argyresthia calliphanes if from the type locality of Toronto, Ontario, Canada, but noted concerns by Forbes (1923) and Covell (1984). There are currently no Nearctic specimens in the Cornell University Insect Collection identified as either with a gold/yellowish thorax, which at face value would indicate Forbes' supposition as true. Some examples photographed from Western North America appear to have a gold thorax, but this is difficult to evaluate given cuticle wear often presents itself in images as gold-appearing thoraces. If they do indeed have a gold thorax, this may indicate a movement into North America potentially associated with Beringia. Based on existing taxonomic works, it is prudent to refer to North American specimens identified as Argyresthia goedartella as A. calliphanes until further treatment of the group which may represent a species complex, as at least three lineages were identified in the phylogenetic inference. Resolving this taxonomic issue will require extensive sampling across the Nearctic but focused on northeastern North America, southwestern North America, and northwestern North America.

Argyresthia cupressella was rendered paraphyletic in both inferences, with one clade, consisting entirely of specimens collected in the District of Columbia, United States of America, coming out sister to A. glaucinella, and a clade consisting entirely of specimens from British Columbia, Canada coming out as sister to A. canadensis Freeman 1972 + (A. aureoargentella Brower, 1953 + A. deletella). Considering A. cupressella is a western species (type locality Los Angeles, California), and that the representatives from BOLD listed as A. cupressella do not resemble A. cupressella, this likely represents a misidentification and should not call the species into question. Since most sequences were downloaded from either GenBank or BOLD, and were thus not examined, it is unclear for most species whether species recovered as paraphyletic were due to misidentifications, poor molecular resolution, or indeed represent paraphyletic lineages. Further analysis using a broader Sanger dataset, or ideally, a high-throughput sequencing approach, is preferred to elucidate the relationships of this family more clearly.

The stochastic character mapping suggests that the evolution of this family is closely tied to host plant associations, particularly a grade from angiosperm feeding Argyresthia to Argyresthia that feed on gymnosperms. Only two species in the clade of primarily Cupressaceae-feeding Argyresthia had a reversal to angiosperms-A. subreticulata (Sapindaceae) and A. glaucinella (multiple angiosperm hosts). No reversals to a gymnosperm host were observed in the angiosperm clade. While the stochastic character mapping should be viewed with some caution due to the lack of resolution provided by a single-locus phylogeny, the consistency of these traits suggests that better resolution will support these initial findings. The ancestral state for the family is hypothesized to potentially Betulaceae-feeding. The ancestral state for the primarily angiosperm clade is Rosaceae-feeding, but there are angiospermfeeders ancestrally Betulaceae-feeding that grade into a primarily Cupressaceae-feeding clade. While this is a preliminary investigation into host plant associations in these families, the phylogenetic implications of conserved host plant evolutions are notable-there may be a potential to predict host plants for new species or species for which we do not currently have host plant information from with a reasonable degree of confidence. For example, while the newly described species here A. guatemala groups ambiguously among Betulaceae- and gymnosperm-feeding Argyresthia, A. quetzaltenangonella and A. iridescentia group with the clade containing the gymnosperm-feeding Argyresthia, A. quetzaltenangonella more specifically within a clade ancestrally Cupressaceae-feeding, and A. iridescentia within an ancestrally Pinaceae-feeding. The stochastic character mapping likely oversimplifies host plant evolution since the Mk1 model posits equally likely changes for all character states and biologically, it is more likely that host plant switches occur within gymnosperms versus within angiosperms. Similarly, the inclusion of multiple specimens for paraphyletic species also influences the stochastic character mapping yet is also expected to not influence the results broadly.

The following representatives of the subgenus *Blastotere* were included in the phylogenetic inference: *Argyresthia (Blastotere) amiantella; A. (B.) arceuthina; A. (B.) bergiella; A. (B.) dilectella; A. (B.) glabratella; A. (B.) illuminatella; A. (B.) laevigatella, A. (B.) kulfani, A. (B.) praecocella; A. (B.) svenssoni; A. (B.) trifasciata. These representatives were recovered as paraphyletic, though a few species groups are monophyletic (Figure 6). More phylogenetic and morphological work is necessary to delineate whether the members of this clade that render <i>Blastotere* paraphyletic are also members of *Blastotere*, meaning *Blastotere* is monophyletic, or if *Blastotere* represents a paraphyletic lineage.

The species descriptions of *Argyresthia* in this paper are by no means exhaustive but rather represent a relatively high degree of diversity returned from a small sample size. There is no doubt that additional sampling in Guatemala, as well as other locales in Central and South America, will bring more species of *Argyresthia* to light.

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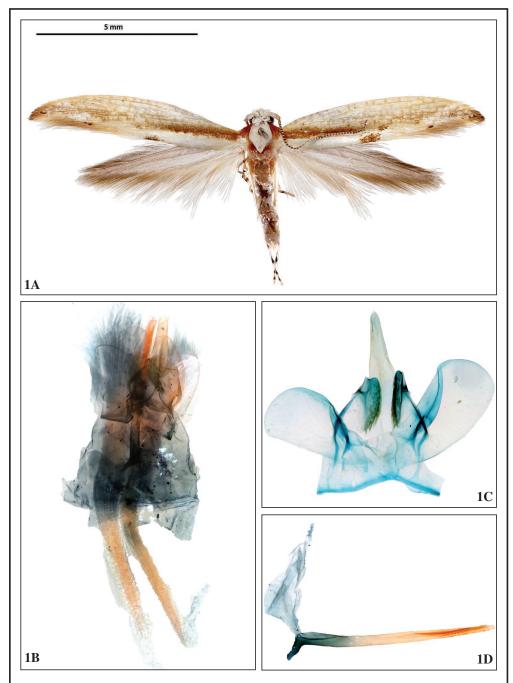
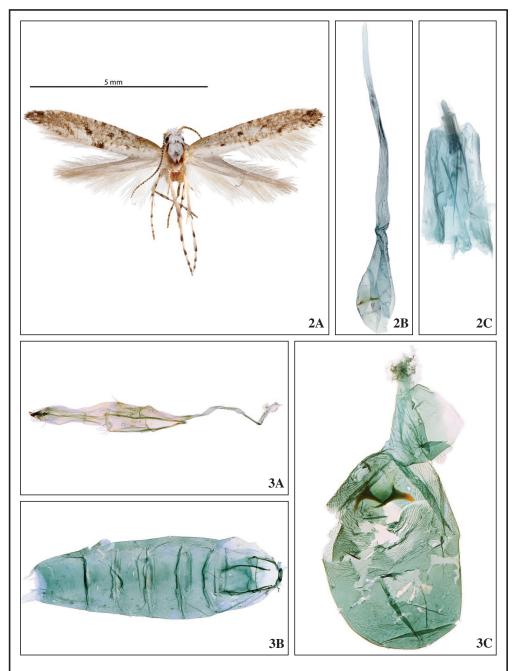
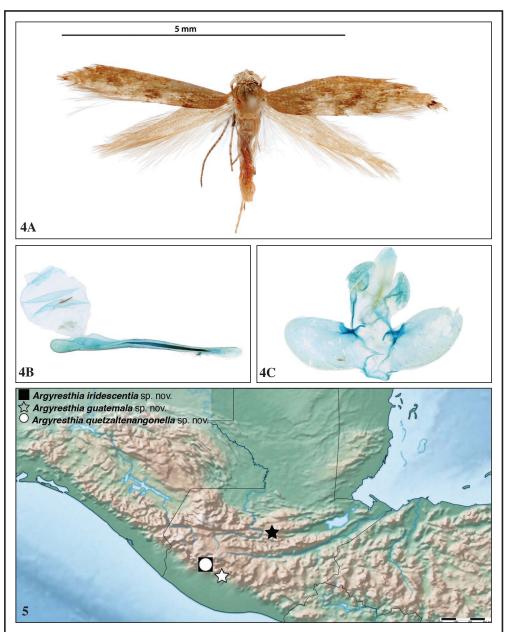


Figure 1. Argyresthia quetzaltenangonella Gorneau & Dombroskie, sp. nov., holotype, \eth . A. Adult. B. Coremata of abdomenov. C. Male genitalia with phallus removed. D. phallus.



Figures 2-3. 2. Dorsal habitus (A), ductus bursae and corpus bursae (B); and genital capsule (C) of holotype *Argyresthia guatemala* Gorneau & Dombroskie, sp. nov. **3.** Genital capsule, ductus bursae (A); abdomen (B); and corpus bursae (C) of slide of dissected female *Argyresthia deletella* (USNM 76603).



Figures 4-5. 4. Dorsal habitus (A), phallus (B), and genital capsule with valves spread (C) of holotype *Argyresthia iridescentia* Gorneau & Dombroskie, sp. nov. **5.** Maps with holotype localities of new *Argyresthia* species made using SimpleMappr (SHORTHOUSE 2010). Holotype locality of *Argyresthia iridescentia* Gorneau & Dombroskie, sp. nov. in black square, of *A. guatemala* Gorneau & Dombroskie, sp. nov. in black star, and of *A. quetzaltenangonella* Gorneau & Dombroskie, sp. nov. in white circle. Paratype locality of *A. guatemala* Gorneau & Dombroskie, sp. nov. in white star.

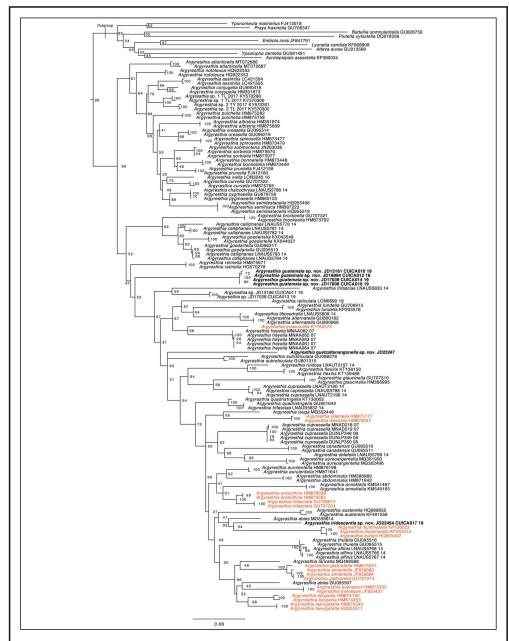


Figure 6. Maximum likelihood phylogeny of Argyresthiidae inferred in IQ-TREE. Phylogeny of Argyresthiidae with Yponomeutoidea outgroup indicated by hash mark. Species described as new are bolded and species considered within subgenus *Blastotere* are in red. Nodal labels represent support values as ultrafast bootstrap replicates (UFBoot, described in MINH et al. 2013). Scale bar at bottom with value 0.06 indicates branch lengths.

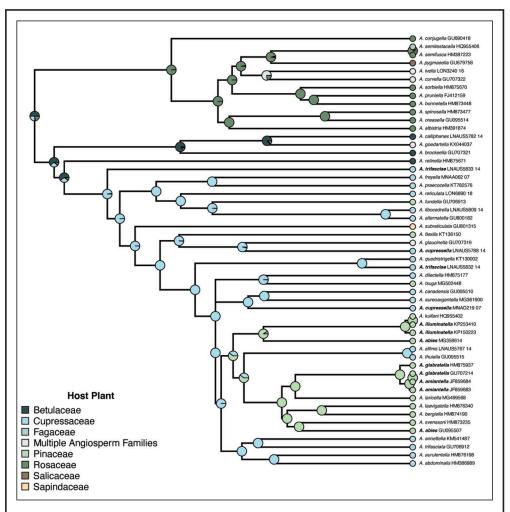


Figure 7. Stochastic Character Mapping. Posterior probabilities of stochastic character mapping of known host plants for species of *Argyresthia* for which barcodes and records exist. Bold indicates species not recovered as monophyletic.

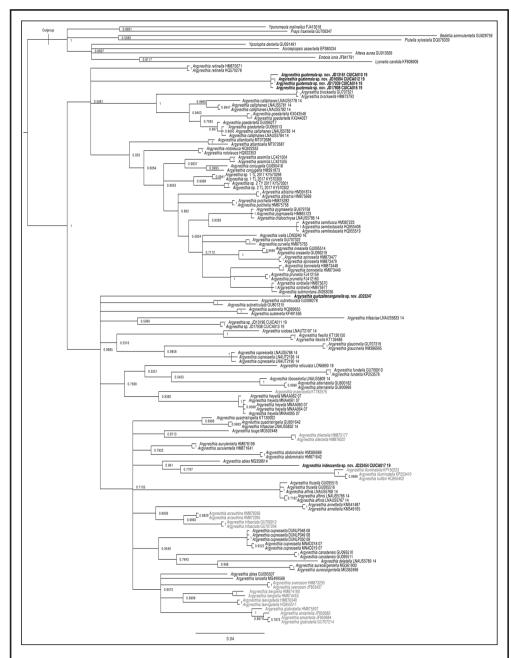
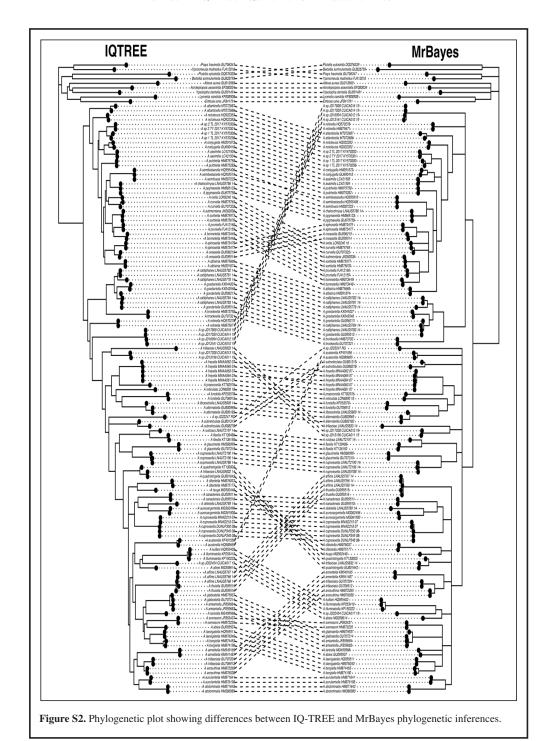


Figure S1. Bayesian phylogeny of Argyresthiidae inferred in MrBayes. Phylogeny of Argyresthiidae with Yponomeutoidea outgroup indicated by hash mark. Species described as new are bolded and species considered within subgenus *Blastotere* are in red. Nodal labels represent support values as posterior probability values. Scale bar at bottom with value 0.04 indicates branch lengths.



Supplementary Material

Table SI. Sequences downloaded from GenBank and BOLD for analysis.

Taxon	GenBank Accession(s)	BOLD Voucher(s)
Argyresthia abdominalis Zeller, 1839	HM386989, HM871642,	-
Argyresthia abies Freeman, 1972	GU095507, MG358614	-
Argyresthia abies Freeman, 1972	MG358614	-
Argyresthia affinis Braun, 1940	-	LNAUS5768-14, LNAUS5767-14, LNAUS5766-14
Argyresthia albistria (Haworth, 1828)	HM391874, HM875669	-
Argyresthia alternatella Kearfott, 1908	GU800182, GU800969	-
Argyresthia amiantella (Zeller, 1847)	JF859683, JF859684	-
Argyresthia annettella Busck, 1907	KM541487, KM549165	-
Argyresthia arceuthina Zeller, 1839	HM876038, HM872265	-
Argyresthia assimilis Moriuti, 1977	LC421504, LC421505	-
Argyresthia atlanticella Rebel, 1940	MT072686, MT072687	-
Argyresthia aureoargentella Brower, 1953	MG361900, MG362496	-
Argyresthia aurulentella Stainton, 1849	HM876198, HM871641	-
Argyresthia austerella Zeller, 1873	HQ989655, KF491556	-
Argyresthia bergiella (Ratzeburg, 1840)	HM874190, HM874453	-
Argyresthia bonnetella (Linnaeus, 1758)	HM873448, HM873449	-
Argyresthia brockeella (Hübner, [1813])	GU707321, HM873792	-
Argyresthia calliphanes Meyrick, 1913	-	LNAUS5784-14, LNAUS5783-14, LNAUS5782-14, LNAUS5781-14, LNAUS5778-14
Argyresthia canadensis Freeman, 1972	GU095510, GU095511	-
Argyresthia chalcochrysa Meyrick, 1918	-	LNAUS5786-14
Argyresthia conjugella Zeller, 1839	GU690418, HM391873	-
Argyresthia cupressella Walsingham, 1891	-	MNAD219-07, MNAD218-07, LNAUT2196-14, LNAUT2190-14, LNAUS5788-14, DUNLP350-08, DUNLP349-08, DUNLP348-08
Argyresthia curvella (Linnaeus, 1764)	GU707322	-
Argyresthia curvella (Linnaeus, 1764)	HM875765	-
Argyresthia deletella Zeller, 1873	-	LNAUS5789-14
Argyresthia dilectella Zeller, 1847	HM875177, HM876037	-
Argyresthia flexilis Freeman, 1960	KT136150, KT139486	-
Argyresthia freyella Walsingham, 1891	-	MNAA065-07, MNAA064-07, MNAA063-07, MNAA062-07, MNAA061-07
Argyresthia fundella Fischer von Röslerstamm, 1834	GU706913, KP253578	-
Argyresthia glabratella (Zeller, 1847)	GU707214, HM875937	-
Argyresthia glaucinella Zeller, 1839	GU707319, HM386995	-
Argyresthia goedartella (Linnaeus, 1758)	GU095513, GU096217, KX043548, KX044037	-
Argyresthia illuminatella Zeller, 1839	KP150223, KP253410	-
Argyresthia ivella (Haworth, 1828)	-	LON3240-16
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Argyresthia kulfani Bengtsson & Johansson, 2012	HQ955402	-

Argyresthia laricella Kearfott, 1908	MG499568	-
Argyresthia libocedrella Busck, 1916	-	LNAUS5809-14
Argyresthia notoleuca (Turner, 1913)	HQ922352, HQ922353	-
Argyresthia oreasella Clemens, 1861	GU095514, GU096219	-
Argyresthia praecocella Zeller, 1839	KT782576	-
Argyresthia pruniella (Clerck, 1759)	FJ412159, FJ412160	-
Argyresthia pulchella Lienig & Zeller, 1846	HM875282, HM875758	-
Argyresthia pygmaeella ([Denis & Schiffermüller], 1775)	GU679758, HM865123	-
Argyresthia quadristrigella Zeller, 1873	GU801642, KT130002	-
Argyresthia reticulata Staudinger, 1877	-	LON6890-18
Argyresthia retinella Zeller, 1839	HM875671, HQ570278	-
Argyresthia ruidosa Braun, 1940	-	LNAUT3197-14
Argyresthia semifusca (Haworth, 1828)	HM387223	-
Argyresthia semitestacella (Curtis, 1833)	HQ955406, HQ955519	-
Argyresthia sorbiella (Treitschke, 1833)	HM875670, HM875977	-
Argyresthia spinosella Stainton, 1849	HM873477, HM873479	-
Argyresthia submontane Frey, [1871]	-	-
Argyresthia subreticulata Wlsingham, 1882	GU088278, GU801315	-
Argyresthia svenssoni Bengtsson & Johansson, 2011	HM873235, JF853437	-
Argyresthia thuiella (Packard, 1871)	GU095515, GU095516	-
Argyresthia trifasciae Braun, 1910	-	LNAUS5832-14, LNAUS5833-14
Argyresthia trifasciata Staudinger, 1871	GU706912, GU707204	-
Argyresthia tsuga Freeman, 1972	MG502448	-
Argyresthia sp. 1 TL-2017	KY570298, KY570300	-
Argyresthia sp. 2 TL-2017	KY570301, KY570302	-
Embola ionis (Clarke, 1952)	JF841791	-
Lyonetia candida Braun, 1916	KF808908	-
Ypsolopha dentella (Fabricius, 1775)	GU0914191	-
Acrolepiopsis assectella (Zeller, 1839)	EF380034	-
Atteva aurea (Fitch, 1856)	GU013569	-
Bedellia somnulentella (Zeller, 1847)	GU828759	-
Plutella xylostella (Linnaeus, 1758)	DQ076339	-
Yponomeuta malinellus Zeller, 1838	FJ413018	-
Prays fraxinella (Bjerkander, 1784)	GU706347	-

Table SII. Matrix used in ancestral state reconstruction with host information from Lewis and Sohn (2015) reduced to family level or listed as multiple angiosperm families if species feeds on multiple families. Multiple representatives retained from original phylogenetic analysis for specimens that were not recovered as monophyletic. Accession information kept for efficient retrieval of specific specimen information.

Taxon	Accession Number(s)	Host Family
Argyresthia abdominalis Zeller, 1839	HM386989	Cupressaceae
Argyresthia abies Freeman, 1972	GU095507, MG358614	Pinaceae
Argyresthia affinis Braun, 1940	LNAUS5767-14	Cupressaceae
Argyresthia albistria (Haworth, 1828)	HM391874	Rosaceae
Argyresthia alternatella Kearfott, 1908	GU800182	Cupressaceae
Argyresthia annettella Busck, 1907	KM541487	Cupressaceae
Argyresthia arceuthina Zeller, 1839	HM876038	Cupressaceae

Argyresthia aureoargentella Brower, 1953	MG361900	Cupressaceae	
Argyresthia aurulentella Stainton, 1849	HM876198	Cupressaceae	
Argyresthia bonnetella (Linnaeus, 1758)	HM873448	Rosaceae	
Argyresthia brockeella (Hübner, [1823])	GU707321	Betulaceae	
Argyresthia calliphanes Meyrick, 1913	LNAUS5782-14	Betulaceae	
Argyresthia canadensis Freeman, 1972	GU095510	Cupressaceae	
Argyresthia conjugella Zeller, 1839	GU690418	Rosaceae	
Argyresthia cupressella Walsingham, 1891	LNAUS5788-14,		
	MNAD219-07	Cupressaceae	
Argyresthia curvella (Linnaeus, 1761)	GU707322	Multiple Angiosperm Families	
Argyresthia dilectella Zeller, 1839	HM875177	Cupressaceae	
Argyresthia flexilis Freeman, 1960	KT136150	Pinaceae	
Argyresthia freyella Walsingham, 1891	MNAA062-07	Cupressaceae	
Argyresthia fundella Fischer von Röslerstamm, 1834	GU706913	Pinaceae	
Argyresthia glabratella Zeller, 1847	HM875937	Pinaceae	
Argyresthia glaucinella Zeller, 1839	GU707319	Multiple Angiosperm Families	
Argyresthia goedartella (Linnaeus, 1758)	KX044037	Multiple Angiosperm Families	
Argyresthia illuminatella Zeller, 1839	KP150223	Pinaceae	
Argyresthia ivella (Haworth, 1828)	LON3240-16	Multiple Angiosperm Families	
Argyresthia laevigatella (Herrich-Schäffer, 1855)	HM876340	Pinaceae	
Argyresthia laricella Kearfott, 1908	MG499568	Pinaceae	
Argyresthia libocedrella Busck, 1916	LNAUS5809-14	Cupressaceae	
Argyresthia oreasella Clemens, 1861	GU095514	Rosaceae	
Argyresthia praecocella Zeller, 1839	KT782576	Cupressaceae	
Argyresthia pruniella (Clerck, 1759)	FJ412159	Rosaceae	
Argyresthia pygmaeella ([Denis &			
Schiffermüller], 1775)	GU679758	Salicaceae	
Argyresthia quadristrigella Zeller, 1873	KT130002	Cupressaceae	
Argyresthia reticulata Staudinger, 1877	LON6890-18	Cupressaceae	
Argyresthia retinella Zeller, 1839	HM875671	Betulaceae	
Argyresthia semifusca (Haworth, 1828)	HM387223	Rosaceae	
Argyresthia semitestacella (Curtis, 1833)	HQ955406	Fagaceae	
Argyresthia sorbiella (Treitschke, 1833)	HM875670	Rosaceae	
Argyresthia spinosella Stainton, 1849	HM873477	Sapindaceae	
Argyresthia subreticulata Walsingham, 1882	GU801315	Cupressaceae	
Argyresthia thuiella (Packard, 1871)	GU095515	Cupressaceae	
Argyresthia trifasciae Braun, 1910	LNAUS5832-14,		
	LNAUS5833-14	Cupressaceae	
Argyresthia trifasciata Staudinger, 1871	GU706912	Cupressaceae	
Argyresthia tsuga Freeman, 1972	MG502448	Pinaceae	