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Four new adelgid (Hemiptera: Adelgidae) species from Bhutan, including the first legless species of Aphidomorpha

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Abstract

A new subgenus and four new species of *Adelges* (Hemiptera: Adelgidae) are described from Bhutan. To support their taxonomic placement, we provide a phylogeny of Adelgidae reconstructed using mitochondrial and nuclear DNA sequence data. *Cassiadelges* **subgen. nov** is distinguished by the combination of feeding on *Larix* secondary hosts, having tergites of the head and pronotum fused into a cephaloprothoracic shield, and having only acuminate setae on the terminal abdominal segments. *Adelges* (*Cassiadelges*) *coccipus* **sp. nov.** feeds on *Larix griffithii.* This remarkable species is the only known member of Aphidomorpha that is lacking legs. The first instar nymph has legs, while the second instar to adult have vestigial legs present as small cuticular protrusions with clusters of setae. Its discovery presents an exciting opportunity to examine the evolutionary development of insect limb formation from a new perspective. *Adelges* (*Cholodkovskya*) *changaphuensis* **sp. nov.** feeds and forms galls on *Picea spinulosa*. *Adelges* (*Aphrastasia*) *densae* **sp. nov.** feeds on *Abies densa*. This may be the same as what was reported on this host in 1985 as *Chermes abietispiceae* Stebbing (*nomen dubium*). *Adelges* (*Annandina*) *lepsimon* **sp. nov.** feeds on *Tsuga dumosa*. It is separated from the only other member of its subgenus, *Adelges* (*Annandina*) *tsugae* Annand, by first instar exules having a pair of prominent anterior cephalic wax glands. It feeds between the needles on twigs in a similar fashion to *A.* (*An.*) *tsugae* Annand, which is also found in Bhutan, making it difficult to distinguish them in the field.

Key words: Eastern Himalayas, apodal, apodous, gall, hemlock, fir, larch, pine, spruce

Introduction

Adelgidae (Hemiptera: Aphidomorpha) is a small group of approximately 65 species (Favret *et al*. 2015b; Favret 2024) that feed exclusively on members of the conifer genera *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga* (Pinaceae). Adelgidae includes two genera: *Adelges* Vallot, 1836, with seven subgenera and 37 species, and *Pineus* Shimer, 1869, with two subgenera and 28 species (Favret *et al.* 2015b; Favret 2024). Holocyclic adelgid species alternate between primary host species in *Picea*, where they produce galls and have a sexual generation, and secondary hosts in one of the other host genera (Havill & Foottit 2007). They can also exhibit anholocycles with entirely asexual reproduction on only primary or only secondary hosts. Adelgids are endemic to regions in the northern hemisphere where Pinaceae naturally grow. Some species have invaded regions outside of their native ranges and have become devastating pests (Havill *et al.* 2016, 2021).

In the Himalayan region, adelgid species have been described from India and Pakistan (Schneider-Orelli & Schneider 1954, 1959; Ghani & Rao 1966; Yaseen & Ghani 1971; Ghosh 1983), and Southwest China (Zhang *et al*. 1980). Our current knowledge of adelgids in Bhutan is limited. The only documented records come from Schmutzenhofer (1985), who reported *Chermes abietispiceae* Stebbing, 1903 (considered *nomen dubium*, discussed below) collected on *Abies densa*, and an unidentified *Pineus* species collected on *Pinus wallichiana*.

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Prompted by the discovery of adelgids damaging *Picea spinulosa* in a conifer nursery in Changaphu in western Bhutan, a survey of Adelgidae across the country was conducted by members of the Bhutan Department of Forest and Park Services between 2020 and 2021. From the specimens collected during this survey, we describe four new species whose taxonomic placement is supported by phylogenetic reconstruction using mitochondrial and nuclear DNA sequences.

Materials and Methods

Molecular phylogeny

Our phylogenetic analyses include the 20 adelgid species previously included in the phylogeny of Havill *et al.* (2007), plus 18 additions. These additions include the four species described here, plus: *Adelges* (*Adelges*) *karamatsu* Inouye, 1945, undescribed *Adelges* (*Annandina*) nr. *tsugae* from central China [considered *Adelges* (*Annandina*) *tsugae* Annand, 1928 in Havill *et al.* (2016)], undescribed *Adelges* (*Cassiadelges* **subgen. nov.**) nr. *coccipus*, *Adelges* (*Cholodkovskya*) *oregonensis* Annand, 1928, *Adelges* (*Cholodkovskya*) *viridanus* (Cholodkovsky, 1896), *Adelges* (*Dreyfusia*) *joshii* (Schneider-Orelli & Schneider, 1959), *Adelges* (*Dreyfusia*) *knucheli* (Schneider-Orelli & Schneider, 1954), *Pineus* (*Pineodes*) *pinifoliae* Fitch, 1858, *Pineus* (*Pineus*) *boerneri* Annand, 1928, *Pineus* (*Pineus*) *harukawai* Inouye, 1945, *Pineus* (*Pineus*) *konowashiyai* Inouye, 1945, and *Pineus* (*Pineus*) *wallichianae* Yaseen & Ghani, 1971. "*Adelges* sp. A" from Havill *et al.* (2007) has since been determined as *Adelges* (*Sacchiphantes*) *kitamiensis* (Inouye, 1963) (Sano *et al.* 2011), but *Adelges* sp. B from Havill *et al.* (2007) has not yet been determined. We also included data from new specimens of *A.* (*An.*) *tsugae*, *Adelges* (*Gilletteella*) *glandulae* (Zhang, 1980), and *Pineus* (*Pineus*) *armandicola* Zhang, Zhong & Zhang, 1992, collected from our survey in Bhutan for comparison to specimens previously collected from western China.

Voucher information for samples used in the phylogeny are listed in Table 1. Some sequences were previously published in Havill *et al.* (2007), Foottit *et al.* (2009), and/or Havill *et al.* (2016). Two species of Phylloxeridae (Hemiptera: Aphidomorpha) were included as an outgroup. Species were determined using a variety of sources (Annand 1928; Inouye 1945, Börner & Heinze 1957; Yaseen & Ghani 1971; Zhang *et al.* 1980; Binazzi 1984; Pashchenko 1988; Blackman & Eastop 2024). For new sequences, DNA was extracted non-destructively by piercing specimens with a sterilized insect pin and retaining the cuticle after proteinase K digestion. Extraction was performed using the ABI MagMAX DNA Multi-Sample Ultra Kit (Thermo Fisher Scientific) on a KingFisher instrument (Thermo Fisher Scientific). The 658 bp DNA barcoding portion of the mitochondrial cytochrome c oxidase subunit I gene (COI) was amplified using primers LepF1 and LepR1 (Hebert *et al.* 2004), a 380 bp region of mitochondrial cytochrome b (cytb) was amplified using primers AdelCytbF1 and AdelCytbR1 (Havill *et al.* 2006), and a 661 to 680 bp region of nuclear elongation factor-1 α (EF1α) was amplified using primers AdelEF1F1 and AdelEF1R2 (Havill *et al.* 2007). Sequencing was performed on an Applied Biosystems 3730 automated sequencer (Applied Biosystems, Foster City, California) at the Keck DNA Sequencing Facility at Yale University, New Haven, Connecticut. Sequences were edited and aligned using Geneious Prime 2023.2.1 (https://www.geneious.com). All new sequences generated for this study were deposited in GenBank (Table 1). For EF1α, the intron was excluded from the analysis because it is difficult to align among divergent taxa. This left 595 bp of EF1α for the analysis. Maximum likelihood analysis was performed using IQ-TREE v.2.1.3 (Nguyen *et al.* 2015) with separate substitution models for each gene region, and with node support assessed using 1,000 UFBoot and SH-aLRT support replicates. Bayesian analysis was performed using MrBayes 3.2.7a (Ronquist *et al*. 2012) using default priors, unlinked GTR + I + G substitution models for each gene region, four incrementally heated Markov chains and two runs of 2,000,000 generations sampled every 10,000 generations. The first 25% burnin trees were discarded.

Morphological description

Specimens were slide-mounted in Canada balsam after clearing, either with proteinase K during DNA extraction or overnight in 10% KOH. Specimens were observed under optical microscopes to describe morphological features. Selected specimens were photographed with a DP28 digital camera mounted on an Olympus BX53 microscope.

TABLE 1. Collection and voucher information for specimens included in the phylogenetic analysis. Vouchers are deposited at the Canadian National Collection of Insects, Arachnids & Nematodes, Agriculture & Agri-Food Canada, Ottawa, Ontario, Canada (CNC), or Yale Peabody Museum (YPM).

Species	Specimen Accession	Collection data	COI GenBank Accession	Cytb GenBank Accession	EF1 GenBank Accession
Phylloxera caryaecaulis (Fitch, 1855)	CNC#HEM017791	CANADA; Ontario, Ottawa; lat. 45.3925, long. -75.717; 4 September 1997; Coll. Eric Maw	EF073060	EF073184	EF073222
Daktulosphaira vitifoliae (Fitch, 1855)	CNC#HEM054242	USA; California, University of California at Davis; 7 September 2004; Coll. Jeffrey Grannett	EF073059	EF073183	EF073221
Adelges sp. B NPH2007	CNC#HEM053359	CHINA; Yunnan, Yulong County, Lijiang, Bai Shui He; lat. 27.1296, long. 100.2582; 1 June 2004; Coll. Nathan Havill, Yu Guoyue; on *Larix*	EF073103	EF073211	EF073251
Adelges (*Adelges*) *karamatsu* Inouye, 1945	CNC#HEM056246	JAPAN; Hyogo, Kobe, Kobe Municipal Arboretum; lat. 34.7403, long. 135.1771; 8 May 2006; Coll. Shigehiko Shiyake, Michael E. Montgomery; on *Larix*	FJ502492	PQ038015	PQ038031
Adelges (*Adelges*) *japonicus* (Monzen, 1929)	CNC#HEM054839	JAPAN; Hokkaido, Lake Horokayantô, Bansei, Taiki; lat. 42.527, long. 143.479; 7 July 2005; Coll. Shigehiko Shiyake; on *Larix kaempferi*	FJ502414	N/A	PQ038029
Adelges (*Adelges*) *lariciatus* (Patch, 1909)	CNC#HEM040004	CANADA; Alberta, Erith, Hwy 47; lat. 53.4119, long. -116.668; 8 August 2001; Coll. Eric Maw, Robert Foottit; on *Picea glauca*	EF073075	N/A	EF073231
Adelges (*Adelges*) *laricis* Vallot, 1836	CNC#HEM053183	USA; Massachusetts, Suffolk County, Jamaica Plain, Arnold Arboretum; lat. 42.296, long. -71.126; 23 June 2003; Coll. Nathan Havill; on *Larix decidua*	EF073076	N/A	EF073232
Adelges (*Annandina*) *lepsimon* Havill & Brunet, **sp. nov.**	YPM#ENT594618	BHUTAN; Mongar, Sengor; lat. 27.3711, long. 91.0234; 7 April 2022; Coll. Kaka Tshering; on *Tsuga dumosa*	PQ014111	PQ038016	PQ038033
Adelges (*Annandina*) nr. *tsugae*	CNC#HEM056232	CHINA; Guizhou, Guiyang, Shanping; lat. 26.2579, long. 106.8019; April 2006; Coll. Yu Guoyue; on *Tsuga chinensis*	KU659174	PQ038018	PQ038035
Adelges (*Annandina*) *tsugae* Annand, 1924	YPM#ENT594219	BHUTAN; Wangdue Phodrang, Dradraphu; lat. 27.4543, long. 90.0235; 26 April 2022; Coll. Choney Yangzom; on *Tsuga dumosa*	PQ014107	PQ038019	PQ038037
Adelges (*Annandina*) *tsugae* Annand, 1924	CNC#HEM053351	CHINA; Yunnan, Yulong County, Lijiang; lat. 26.8121, long. 100.1798; 31 May 2004; Coll. Nathan Havill, Yu Guoyue; on *Tsuga forrestii*	EF073089	EF073198	EF073241

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TABLE 1. (Continued)

Species	Specimen Accession	Collection data	COI GenBank Accession	Cytb GenBank Accession	EF1 GenBank Accession
Adelges (*Annandina*) *tsugae* Annand, 1924	CNC#HEM053369	JAPAN; Nagano, Norikura Skyline, Kamitakara-mura; lat. 36.16313, long. 137.52752; 10 June 2004; Coll. Nathan Havill, Yu Guoyue, Shigehiko Shiyake; on *Tsuga diversifolia*	EF073094	EF073203	EF073245
Adelges (*Annandina*) *tsugae* Annand, 1924	CNC#HEM053432	JAPAN; Shizuoka, Yugashima, Izu-shi; lat. 34.883, long. 138.917; 19 March 2005; Coll. Shigehiko Shiyake; on *Tsuga sieboldii*	EF073095	EF073204	EF073246
Adelges (*Annandina*) *tsugae* Annand, 1924	CNC#HEM053427	TAIWAN; Taichung County, Tayuling; lat. 24.183, long. 121.342; 23 December 2004; Coll. H.Y. Wang; on *Tsuga chinensis*	EF073091	EF073200	EF073242
Adelges (*Annandina*) *tsugae* Annand, 1924	CNC#HEM053161	USA; Washington, Clark County, Ridgefield; lat. 45.7382, long. -122.6435; 5 May 2003; Coll. Nathan Havill; on *Tsuga heterophylla*	EF073098	EF073207	EF073247
Adelges (*Aphrastasia*) *pectinatae ishiharai* (Inouye, 1936)	CNC#HEM053377	JAPAN; Nagano, Norikura Skyline, Kamitakara-mura; lat. 36.1665, long. 137.5220; 10 June 2004; Coll. Nathan Havill, Yu. Guoyue, Shigehiko Shiyake; on *Abies veitchii*	EF073081	EF073191	EF073236
Adelges (*Aphrastasia*) *pectinatae pectinatae* (Cholodkovsky, 1888)	CNC#HEM054110	POLAND; Warsaw, Sowinski Park, Wola Street; 25 June 2005; Coll. Nathan Havill, Cezary Bystrowski; on *Abies concolor*	EF073084	EF073193	EF073238
Adelges (*Cassiadelges*) *coccipus* Havill & Brunet, **sp. nov.**	YPM#ENT996709	BHUTAN; Mongar, Sengor; lat. 27.3642, long. 91.0328; 27 March 2022; Coll. Namgay Sacha, Kaka Tshering; on *Larix griffithii*	PQ014095	PQ038011	PQ038026
Adelges (*Cassiadelges*) nr. *coccipus*	CNC#HEM053400	CHINA; Yunnan, Shangri-La, Diqing; lat. 27.7, long. 99.7; 3 June 2004; Coll. Nathan Havill, Yu Guoyue; on *Larix*	PQ038005	PQ038017	PQ038034
Adelges (*Cholodkovskya*) *changaphuensis* Havill & Brunet, **sp. nov.**	YPM#ENT594251	BHUTAN; Thimphu, Changaphu Forest Nursery; lat. 27.4997, long. 89.7176; 22 May 2022; Coll. Kaka Tshering; on *Picea spinulosa*	PQ014145	PQ038010	PQ038025
Adelges (*Cholodkovskya*) *oregonensis* Annand, 1928	YPM#ENT594000	USA; Montana, Lincoln County, Kootenai Natioanal Forest; lat. 48.9256, long. -115.7513; 11 October 2020; Coll. Gina Davis; on *Larix occidentalis*	PQ038004	N/A	PQ038036

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TABLE 1. (Continued)

Species	Specimen Accession	Collection data	COI GenBank Accession	Cytb GenBank Accession	EF1 GenBank Accession
Adelges (*Cholodkovskya*) *viridanus* (Cholodkovsky, 1896)	YPM#ENT996678	JAPAN; Gifu, Gero, Nigorigo; lat. 35.9239, long. 137.4504; 15 June 2022; Coll. Shigehiko Shiyake; on *Picea jezoensis*	OQ607732	N/A	OQ607127
Adelges (*Dreyfusia*) *densae* Havill & Brunet, **sp. nov.**	YPM#ENT996705	BHUTAN; Bumthang, Tangsibi; lat. 27.4972, long. 90.8699; 6 April 2022; Coll. Kaka Tshering; on *Abies densa*	PQ014124	PQ038012	PQ038027
Adelges (*Dreyfusia*) *joshii* (Schneider-Orelli & Schneider, 1959)	CNC#HEM076512	PAKISTAN; Punjab, Jhika Gali; lat. 33.914, long. 73.415; 10 September 2014; Coll. Riaz Mahmood, Khalid Rashid; on *Abies pindrow*	PQ038003	PQ038014	PQ038030
Adelges (*Dreyfusia*) *knucheli* (Schneider-Orelli & Schneider, 1954)	YPM#ENT594942	PAKISTAN; Punjab, Murree; lat. 33.92, long. 73.39; 15-16 July 2014; Coll. Riaz Mahmood, Khalid Rashid; on *Abies pindrow*	PQ038009	N/A	PQ038032
Adelges (*Dreyfusia*) *piceae* (Eckstein, 1890)	CNC#HEM053155	USA; Maine, Knox County, Owls Head State Park; lat. 44.0907, long. -69.0460; 17 May 2002; Charlene Donahue; on *Abies balsamea*	EF073085	EF073194	EF073239
Adelges (*Dreyfusia*) *nordmannianae* (Eckstein, 1890)	CNC#HEM053420	SLOVAKIA; Špania Dolina; lat. 48.8058, long. 19.1317; 5 November 2004; Coll. Jozef Vakula; on *Abies alba*	EF073080	EF073190	EF073235
Adelges (*Gilletteella*) *cooleyi* (Gillette, 1907)	CNC#HEM054135	USA; Alaska, Sitka; 8 June 2005; Coll. M. Schultz; on *Pseudotsuga menziesii*	EF073065	EF073185	EF073224
Adelges (*Gilletteella*) *glandulae* (Zhang, 1980)	YPM#ENT594010	BHUTAN; Thimphu, Changaphu Forest Nursery; lat. 27.4997, long. 89.7176; 26 March 2020; Coll. Kaka Tshering; on *Abies densa*	PQ013992	PQ038013	PQ038028
Adelges (*Gilletteella*) *glandulae* (Zhang, 1980)	CNC#HEM053358	CHINA; Yunnan, Yulong County, Lijiang; lat. 27.1296, long. 100.2582; 1 June 2004; Coll. Nathan Havill, Yu Guoyue; on *Abies*	EF073069	EF073187	EF073228
Adelges (*Sacchiphantes*) *abietis* (Linnaeus, 1758)	CNC# HEM053176	USA; Massachusetts, Suffolk County, Jamaica Plain, Arnold Arboretum; lat. 42.296, long. -71.126; 23 June 2003; Coll. Nathan Havill; on *Picea abies*	EF073061	N/A	EF073223
Adelges (*Sacchiphantes*) *kitamiensis* (Inouye, 1963)	CNC#HEM053415	JAPAN; Yamanashi, Yamanaka, Yamanakako; lat. 35.4454, long. 138.8522; 11 June 2004; Coll. Shigehiko Shiyake; on *Picea torano*	EF073102	EF073210	EF073250

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TABLE 1. (Continued)

Species	Specimen Accession	Collection data	COI GenBank Accession	Cytb GenBank Accession	EF1 GenBank Accession
Adelges (*Sacchiphantes*) *viridis* (Ratzeburg, 1843)	CNC#HEM053419	SLOVAKIA; Špania Dolina; lat. 48.8058, long. 19.1317; 5 November 2004; Coll. Jozef Vakula; on *Larix decidua*	EF073101	N/A	EF073249
Pineus (*Pineodes*) *pinifoliae* Fitch, 1858	YPM#ENT980683	USA; New Hampshire, Hillsborough County, Hillsboro, Fox State Forest; lat. 43.1331, long. -71.9326; 23 May 2019; Coll. Jennifer Weimer; on *Pinus strobus*	PQ038008	PQ038024	PQ038042
Pineus (*Pineus*) *armandicola* Zhang, Zhong & Zhang, 1992	YPM#ENT594950	BHUTAN; Trashi Yangtse, Womina; lat. 27.6764, long. 91.5280; 18 May 2021; Coll. Kaka Tshering; on *Pinus bhutanica*	PQ013995	PQ038020	PQ038038
Pineus (*Pineus*) *armandicola* Zhang, Zhong & Zhang, 1992	CNC#HEM053097	CHINA; Shaanxi, Ningshan County, Huoditang Forest Farm; lat. 33.45856, long. 108.4555; 13-18 October 2002; Coll. Nathan Havill, Yu Guoyue, Michael E. Montgomery; on *Pinus* (5-needle)	EF073106	EF073212	EF073253
Pineus (*Pineus*) *boerneri* Annand, 1928	CNC#HEM056339	CHINA: Beijing; 12 May 2006; Coll. Michael E. Montgomery; on *Pinus tabulaeformis*	FJ502627	PQ038021	PQ038039
Pineus (*Pineus*) *cembrae cembrae* (Cholodkovsky, 1888)	CNC#HEM053433	POLAND; Masovian, Warsaw, Powsin; 8 March 2005; Coll. Cezary Bystrowski; on *Pinus cembra*	EF073109	EF073213	EF073254
Pineus (*Pineus*) *cembrae pinikoreanus* Zhang & Fang, 1981	CNC#HEM054240	RUSSIA; Sakhalin, near Lake Krestonoshka, near Lake Tunaycha; 29 July 2005; Coll. Shigehiko Shiyake; on *Pinus pumila*	EF073111	EF073214	EF073255
Pineus (*Pineus*) *coloradensis* (Gillette, 1907)	CNC#HEM053182	USA; Massachusetts, Suffolk County, Jamaica Plain, Arnold Arboretum; lat. 42.296, long. -71.126; 23 June 2003; Coll. Nathan Havill; on *Pinus monticola*	EF073112	N/A	EF073256
Pineus (*Pineus*) *harukawai* Inouye,1945	CNC#HEM056294	JAPAN; Nagano, Ina, Mibu Valley; lat. 35.6437, long. 138.1613; 10 May 2006; Coll. Shigehiko Shiyake, Michael E. Montgomery; on *Pinus parviflora*	PQ038006	PQ038022	PQ038040
Pineus (*Pineus*) *konowashiyai* Inouye, 1945	CNC#HEM056252	JAPAN; Nagano, Fujimi, Mt. Yatsugatake; lat. 35.9399, long. 138.3156; 11 May 2006; Coll. Shigehiko Shiyake, Michael E. Montgomery; on *Pinus koraiensis*	PQ038007	PQ038023	PQ038041

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TABLE 1. (Continued)

Species	Specimen Accession	Collection data	COI GenBank Accession	Cytb GenBank Accession	EF1 GenBank Accession
Pineus (*Pineus*) *orientalis* (Dreyfus, 1888)	CNC#HEM054108	POLAND; Łódź, Rogow Arboretum; lat. 51.490, long. 19.510; 25-Jun-2005; Coll. Nathan Havill, Cezary Bystrowski; on *Picea orientalis*	EF073113	EF073215	EF073257
Pineus (*Pineus*) *strobi* (Hartig, 1839)	CNC#HEM054239	USA; Maine, Georgetown; lat. 43.8150, long. -69.7288; 6-Aug-2005; Coll. Nathan Havill; on *Pinus strobus*	EF073118	EF073218	EF073261
Pineus (*Pineus*) *similis* (Gillettte, 1907)	CNC#HEM054844	CANADA; British Columbia, Saanichton; lat. 48.60, long. -123.42; 18 June 2002; Coll. R. Bennett; on *Picea sitchensis*	EF073116	EF073217	EF073259
Pineus (*Pineus*) *wallichianae* Yaseen & Ghani, 1971	YPM#ENT996690	BHUTAN; Trashigang, Yonphula; lat. 27.2522, long. 91.5199; 23 March 2022; Coll. Namgy Sacha; on *Pinus wallichiana*	PQ014084	N/A	PQ038043

Image stacking was performed using the automatic acquisition z-stack function in the Olympus CellSens v. 3.2 software. For some larger images, x-y stitching was performed with the photomerge function in Adobe Photoshop v. 23.3.2. Differential interference contrast (DIC) photographs were acquired using an Olympus BH-51 compound microscope with a Teledyne Lumenera Infinity 3 digital camera with positioning and focus controlled by Objective Imaging Surveyor v. 9.4.0.5 software, after which images were stitched together on x, y, and z axes using Helicon Focus Pro v. 8.2.0. Measurements were taken from slide mounted specimens with the BX53 microscope using CellSens software. Measurements are indicated as ranges with means in parentheses.

The morphological terminology in the descriptions is consistent with Sano *et al.* (2008) and Sano *et al.* (2011). Material from this study was deposited at the National Biodiversity Centre (NBC), Ministry of Agriculture and Livestock, Thimphu, Bhutan, Yale University Peabody Museum of Natural History (YPM), New Haven, Connecticut, USA, Canadian National Collection of Insects, Arachnids and Nematodes (CNC), Ottawa, Ontario, Canada, and United States National Museum of Natural History (USNM), Beltsville, Maryland, USA. Host plant names are according to World Flora Online (https://www.worldfloraonline.org/). This paper and the nomenclatural acts it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:724CDD58-8DA7-4205-9C8D-AA402DDFB774.

Results and discussion

Molecular phylogeny

The topologies of the maximum likelihood tree (Fig. 1) and Bayesian 50% majority-rule consensus tree were identical, except that the Bayesian tree placed *P.* (*Pd.*) *pinifoliae* sister to the rest of Adelgidae with low support

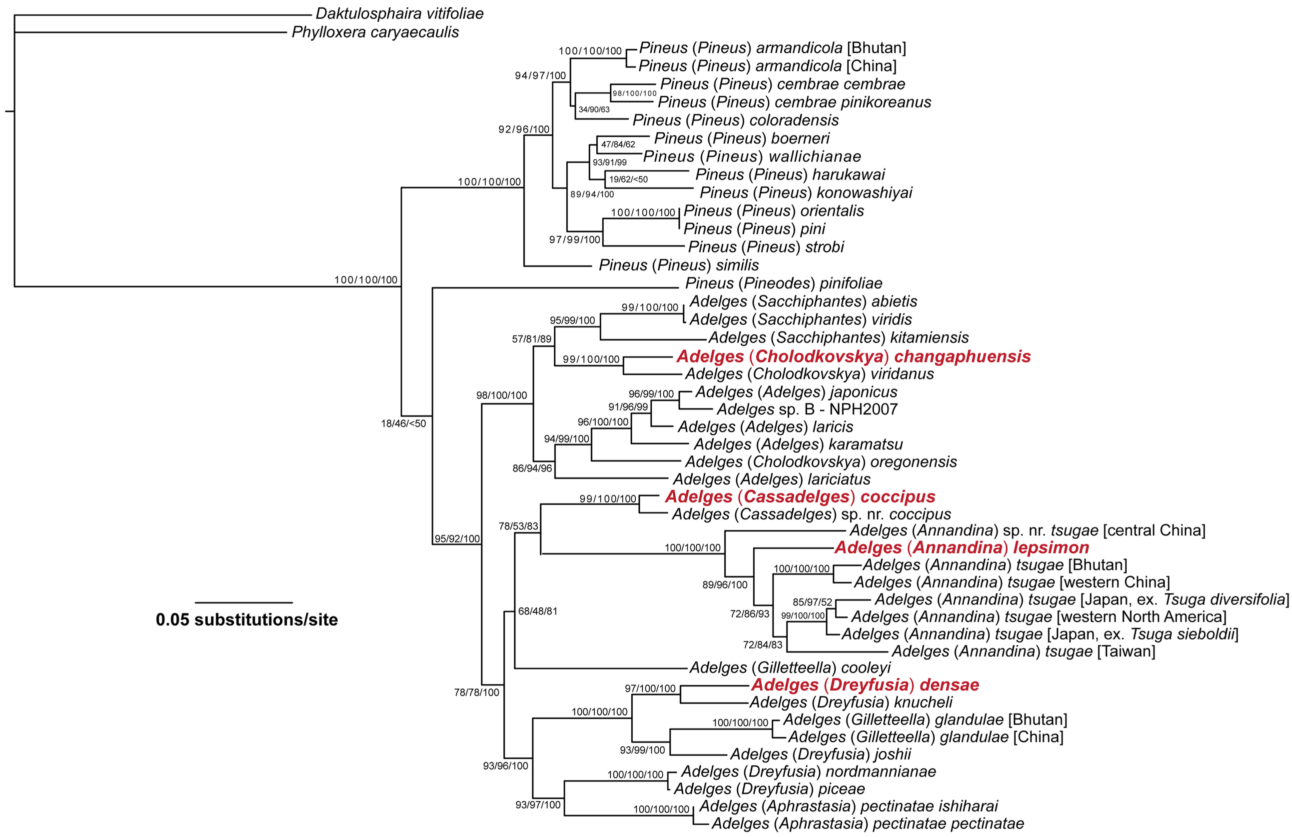

FIGURE 1. Phylogeny of Adelgidae reconstructed using mitochondrial COI and cytb, and nuclear EF1α DNA sequence data. The topology shown is from maximum likelihood analysis with IQ-TREE. Specimen data is shown in Table 1. The new species are highlighted in red. For species with multiple specimens, the country of origin and sometimes the host plant are shown in square brackets to indicate different sources. SH-aLRT and ultrafast bootstrap support from the maximum likelihood analysis, followed by posterior probability from the Bayesian analysis are shown for each clade.

(64% posterior probability) and placed *P.* (*Pi.*) *harukawai* sister to a clade containing *P.* (*Pi.*) *konowashiyai*, *P.* (*Pi.*) *boerneri*, and *P.* (*Pi.*) *wallichianae* with high support (99% posterior probability).

The phylogeny was broadly consistent with Havill *et al.* (2007), having species that use the same secondary host genus forming separate clades, with two exceptions. *Pineus* (*Pd.*) *pinifoliae*, which was not included in Havill *et al.* (2007), was not in the clade with the rest of *Pineus* spp. that also feed on *Pinus* secondary hosts. Its weak placement outside of *Pineus* in both the maximum likelihood and Bayesian trees might be affected by long branch attraction and its relationship could be better resolved with additional data. The members of the new subgenus *Cassiadelges*, which feed on *Larix*, were sister to the *Tsuga*-feeding species rather than in the clade with other *Larix*-feeding species, but this relationship is also rather poorly supported and could also be better resolved with additional data.

The new samples of *A*. (*An*.) *tsugae*, *A*. (*G*.) *glandulae*, and *P*. (*Pi*.) *armandicola* from Bhutan were all very closely related to their counterparts from western China. Additional information about these collections will be detailed in a separate publication.

Of the subgenera represented by multiple taxa, *Annandina* Favret, Blackman & Stekolschchikov, 2015, *Cassiadelges*, *Pineus*, and *Sacchiphantes* Curtis, 1844 were monophyletic, but *Adelges*, *Cholodkovskya* Börner, 1909, *Dreyfusia* Börner, 1908, and *Gilletteella* Börner, 1930 were not monophyletic indicating that a combination of taxonomic revision and reconstruction of a more robust molecular phylogeny are needed. We did not include an identification key for the new species described below pending completion of these analyses.

Taxonomic account

Cassiadelges **Havill & Brunet, subgen. nov.**

Type species. *Adelges* (*Cassiadelges*) *coccipus* Havill & Brunet, by present designation.

Etymology. A noun in apposition stemming from the Latin *cassida*, meaning "helmet," in reference to the prominent cephaloprothoracic shield in adult exules.

Diagnosis. *Adult exulis*. Feeds on *Larix* secondary hosts. Head and pronotum completely covered with plates fused into a cephaloprothoracic shield. Ventral spiracles present on abdominal segments II–VI. Only acuminate setae on abdominal segments VIII–IX.

Remarks. Monotypic, including only *A*. (*Ca*.) *coccipus* at present, pending the description of an additional species, *A*. (*Ca*.) nr. *coccipus*, collected from *Larix* in Sichuan, China (Table 1). This additional species has fully developed legs in the adult stage, so lacking legs is not a diagnostic character of *Cassiadelges*. *Annandina* is the only other subgenus in *Adelges* with a complete cephaloprothoracic shield in the adult exulis stage. *Cassiadelges* differs from *Annandina* in feeding on *Larix* vs. *Tsuga* secondary hosts and by *Annandina* having knobbed setae on the distal abdominal segments.

Adelges **(*Cassiadelges*)** ***coccipus*** **Havill & Brunet, sp. nov.**
(Fig. 2A–J)

Etymology. A noun in apposition stemming from the Greek *κόκκος* meaning "berry" and *πούς*, meaning "foot," in reference to the round vestigial legs. Also, in reference to the developmental similarity to many scale insects (Coccomorpha).

Type material. HOLOTYPE: 1 adult exulis, **BHUTAN, Bumthang, Shingnyer**, lat. 27.4595, long. 90.8690, 5-IV-2022, on *Larix griffithii*, Kaka Tshering (USNM). PARATYPES: 1 first instar progrediens, same data (CNC#5338333-15). 1 adult exulis, same data (CNC#5338333-8). 1 first instar progrediens, same data (USNM). 1 adult exulis, same data (YPM#ENT594747). 1 adult exulis, **BHUTAN, Mongar, Sengor**, lat. 27.3642, long. 91.0328, 27-III-2022, on *Larix griffithii*, Namgay Sacha, Kaka Tshering (CNC#5338328-4). 1 nymph exulis, same data (NBC). 1 second instar exulis, same data (USNM). 1 first instar sistens, **BHUTAN, Mongar, Sengor**, lat. 27.3652, long. 91.0346, 27-III-2022, on *Larix griffithii*, Namgay Sacha, Kaka Tshering (CNC#5338325-12). 1 second instar exulis, same data (YPM#ENT594677). 1 adult exulis, 1 first instar sistens, same data (NBC). 1 first instar progrediens, **BHUTAN, Mongar, Sengor**, lat. 27.3683, long. 91.0127, 7-IV-2022, on *Larix griffithii*, Kaka Tshering (CNC#5338330-10). 1 first instar progrediens, same data (NBC). 1 first instar sistens, same data (USNM). 1 first instar sistens, same data (YPM#ENT594732). 1 first instar progrediens, same data (YPM#ENT594731). 1 adult exulis, **BHUTAN, Bumthang, Tangsibi**, lat. 27.4891, long. 90.8625, 6-IV-2022, on *Larix griffithii*, Kaka Tshering (CNC#5338331-5).

Additional specimens examined. BHUTAN: Bumthang: Shingyner: 1 egg, 4 first instar progredientes, 12 adult exules (CNC), 1 first instar progrediens, 2 adult exules (NBC), 1 first instar progrediens, 2 adult exules (USNM), 2 first instar progredientes, 2 adult exules (YPM), lat. 27.4595, long. 90.8690, 5-IV-2022, on *Larix griffithii*, Kaka Tshering. **Mongar: Sengor**: 1 late instar nymph exulis, 19 adult exules (CNC), 3 adult exules (NBC), 1 late instar nymph exulis, 5 adult exules (USNM), 3 first instar sistentes, 6 late instar nymph exules, 26 adult exules (YPM), lat. 27.3642, long. 91.0328, 27-III-2022, on *Larix griffithii*, Namgay Sacha, Kaka Tshering. 1 first instar sistens, 2 late instar nymph exules, 24 adult exules (CNC), 1 first instar sistens, 1 late instar nymph exulis (NBC), 4 first instar sistentes, 6 late instar nymph exules, 37 adult exules (USNM), 14 first instar sistentes, 2 first instar sistens exuviae, 11 late instar nymph exules, 6 adult exules (YPM), lat. 27.3652, long. 91.0346, 27-III-2022, on *Larix griffithii*, Namgay Sacha, Kaka Tshering. 3 eggs, 5 first instar progredientes, 1 late instar nymph exulis, 6 adult exules (CNC), 3 first instar progredientes (USNM), 19 first instar progredientes, 9 adult exules (YPM), lat. 27.3683, long. 91.0127, 7-IV-2022, on *Larix griffithii*, Kaka Tshering. **Bumthang: Tangsibi**: 1 egg, 3 first instar progredientes, 1 late instar nymph exulis, 4 adult exules (CNC), 1 adult exulis (NBC), 3 first instar progredientes, 1 late instar nymph exulis, 3 adult exules (USNM), 1 first instar progrediens, 9 adult exules (YPM), lat. 27.4891, long. 90.8625, 6-IV-2022, on *Larix griffithii*, Kaka Tshering.

Diagnosis. *Adelges* (*Ca*.) *coccipus* lacks developed legs in all exulis stages after the first instar. The general wax gland structure in the neosistens is similar to *Sacchiphantes* and *Cholodkovskya* in that the facets are arranged in a rosette pattern around a central seta, but they are more tightly packed than in the other subgenera. The abdominal spiracles in adult exules are very small and without sclerotization making them difficult to see except at high magnification. The strongly sclerotized cephaloprothoracic shield resembles many *Pineus* species, but having five pairs of abdominal spiracles and molecular phylogeny places this species definitively within *Adelges* (Fig. 1).

Description. *Neosistens* (Fig. 2A). Body length: $n = 7$, 0.359–0.451 (0.406) mm. Body width: $n = 6$, 0.202–0.293 (0.260) mm. Dorsal wax glands generally on lightly sclerotized plates with 3–6 facets, often triangular, sometimes rhomboidal to circular, with a granular appearance, arranged in tightly packed rosettes around a central seta.

Head and pronotum with lightly sclerotized dorsal plates, separated from each other and along mid-line by narrow sutures. Each cephalic dorsal plate with five or six wax glands, one apical often folded ventrally in slide-mounted specimens, two anterior arranged transversely, two mesad to ocelli arranged longitudinally, sometimes one postero-spinal. Generally, 2–7 facets per cephalic gland. Postero-spinal gland, when present, with fewer facets than the others. The largest wax gland facets on head approximately half the diameter of ocellus. Antennae 3-segmented, segment III imbricated, with length [$n = 8$, 0.041–0.052 (0.045) mm] 3.1x its width at midpoint [$n = 8$, 0.013–0.016 (0.015) mm], and approximately 1.4x longer than segments I [$n = 8$, 0.015–0.026 (0.020) mm] and II [$n = 8$, 0.016–0.024 (0.020) mm] combined. Two primary rhinaria on antennal segment III, one subapical and one approximately ½ the segment length from the apex, each with a small thumb-like projection. A few accessory rhinaria adjacent to the subapical primary rhinarium. Processus terminalis with five setae, the apical seta length [n = 6, 0.046–0.056 (0.051) mm] approximately 3–4x longer than the rest. Rostrum reaching past hind coxae, with ultimate segment length [n = 7, 0.033–0.040 (0.037) mm] subequal to width of segment III at midpoint [$n = 7$, 0.036–0.045 (0.042) mm]. Stylet length: $n = 6$, 1.314–1.728 (1.579) mm, approximately 3.9x body length.

Coxae, femorotrochanters, and tibiae smooth, second tarsal segments weakly imbricated. Pair of long dorso-subapical setae on foreleg. Pairs of subequal dorso-subapical setae on mid- and hindlegs. Wax glands anterior to coxae lacking. Hind femorotrochanter length: n = 7, 0.045–0.057 (0.049) mm.

Pronotum with one antero-lateral and sometimes one postero-lateral wax gland on each plate. Mesonotum with one lateral wax gland. Metanotum with one lateral wax gland, usually with fewer facets than on pro- and mesonotum, sometimes lacking. Raised ventral spiracles on meso- and metanotum bearing facets on basal surface. Abdominal wax glands lacking. Abdominal spiracles minute, hardly visible. Acuminate ventral setae in lateral, pleural, and spinal positions on abdominal segments I–VI, in lateral and spinal positions on abdominal segment VII, in a lateral position on abdominal segment VIII, and a pair of long setae on the apex of abdominal segment IX. Abdominal setae not always apparent.

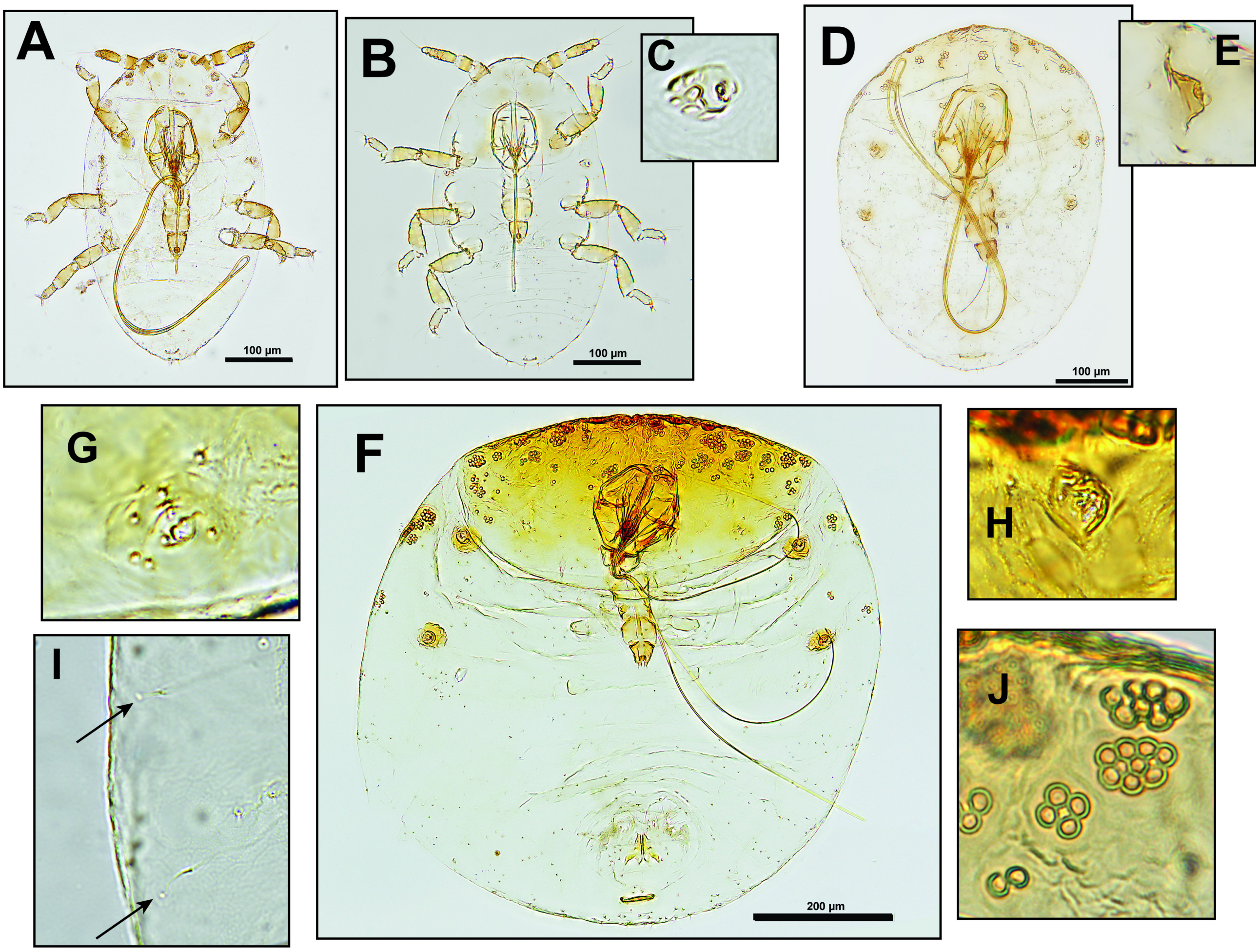

FIGURE 2. *Adelges* (*Cassiadelges*) *coccipus*. A. Sistens, first instar (paratype USNM): habitus; B—C. Progrediens, first instar (paratype, USNM): habitus (B), thoracic spiracle (C); D—E. Exulis, second instar (paratype, USNM): habitus (D), antenna (E); F—J. Exulis, adult (holotype, USNM): habitus (F), prothoracic vestigial leg (G), antenna (H), abdominal spiracles (I), cephalic wax glands (J).

Neoprogrediens (Fig. 2B–C). Body length: *n* = 12, 0.415–0.482 (0.451) mm. Body width 0.244–0.295 (0.265) mm. Body lacking wax glands.

Head and pronotum with very lightly sclerotized plates, separated from each other and along mid-line by narrow sutures. Each dorsal cephalic plate with six setae, one postero-spinal, one postero-lateral, one antero-spinal, two antero-lateral, one apical. A pair of ventro-spinal setae between antennae. Antennae 3-segmented, segment III imbricated, length [*n* = 13, range 0.044–0.062 (0.052) mm] approximately 3.1x its width at midpoint [*n* = 13, 0.014–0.020 (0.017) mm], and subequal to segments I [*n* = 13, range 0.019–0.030 (0.024) mm] and II [*n* = 13, range 0.022–0.031 (0.026) mm] combined. Two primary rhinaria on segment III, one subapical and one approximately ½ the segment length from the apex, each with a small thumb-like projection. A few accessory rhinaria adjacent to the subapical primary rhinarium. Processus terminalis with five setae, the apical seta length [*n* = 12, 0.038–0.051 (0.044) mm] approximately 3x longer than the rest. Rostrum reaching just anterior to hind coxae. Stylets short [*n* = 13, 0.411–0.680 (0.477) mm], approximately 1.0x body length.

Coxae, femorotrochanters, and tibiae smooth, second tarsal segments imbricated. Pair of dorso-subapical setae on foreleg, one capitate seta approximately 2x longer than the other acuminate one. Pairs of subequal dorso-subapical setae of mid- and hindlegs. Wax glands anterior to coxae lacking. Hind femorotrochanter length: *n* = 13, 0.053–0.065 (0.058) mm.

Prominent, raised ventral spiracles on the meso- and metanotum bearing facets on basal surface (Fig. 2C). Abdominal spiracles not apparent. Acuminate ventral setae in lateral, pleural, and spinal positions on all thoracic segments and abdominal segments I–VI, in lateral and spinal positions on abdominal segment VII, in a lateral position on abdominal segment VIII, and a pair of long setae on the apex of abdominal segment IX.

Adult exulis (Fig. 2F–J). Body length: *n* = 21, 0.631–1.044 (0.802) mm. Body width: *n* = 21, 0.579–0.877 (0.752) mm. Pronotum width: *n* = 21, 0.484–0.698 (0.600) mm. Body shape transverse oval to nearly round. Dorsal wax glands generally with one to approximately 20 contiguous or nearly contiguous small round pores.

Head and prothorax strongly sclerotized on dorsal and ventral surfaces. Dorsal plates of head and pronotum completely fused into cephaloprothoracic shield with distinctly wrinkled surface. Anterior half of cephaloprothoracic shield bearing numerous small wax glands with usually less than 10 thick-walled, round to ovoid, tightly packed facets (Fig. 2J). Wax glands on both dorsal and ventral surfaces of cephaloprothoracic shield. Wax glands less numerous (often absent), smaller, and with fewer facets on posterior half of cephaloprothoracic shield. The largest wax facets on the head approximately half the diameter of ocellus. Antennae greatly reduced, appearing as a narrow ridge with no apparent segmentation (Fig. 2H). Rostrum with ultimate segment length [*n* = 13, 0.031–0.042 (0.038) mm] approximately 0.7x width of segment III at midpoint [*n* = 13, 0.047–0.059 (0.052) mm].

Vestigial legs present as slightly raised cuticular protrusions on pro-, meso-, and metanotum with clusters of approximately 8–15 setae (Fig. 2G). Vestigial legs on meso-, and metanotum unsclerotized. Anterior base of vestigial legs with 0–5, usually 1–2, small wax glands with one to approximately 12 round facets.

Meso- and metanotum, and abdominal segments I–II usually with 1–9 small lateral wax glands with approximately 1–20 facets each. Mesonotum with pleural wax glands, or an irregular transverse row of 0–4 small wax glands consisting of 2–8 facets. Prominent, strongly sclerotized and raised ventral spiracles on meso- and metanotum. Rarely, a single small lateral wax gland with a 1–14 minute facets on some of abdominal segments III–VII. Minute unsclerotized spiracles on abdominal segments II–VI (Fig. 2I), often not apparent but sometimes recognizable if internal trachea leading to them are preserved in the specimen. Acuminate setae abundant on abdominal segment IX. Ovipositor short, with length of gonapophyses [*n* = 10, 0.029–0.059 (0.043) mm] approximately 0.9x the width across apodemes [*n* = 10, 0.034–0.061 (0.044) mm].

Host and Distribution. *Larix griffithii* in Bhutan (Mongar and Bumthang) (Fig. 3).

Remarks. *Adelges* (*Ca.*) *coccipus* feeds at the base of the buds and needle whorls, and on the bark on twigs of *Larix griffithii*. Similar to many other adelgid species, *A.* (*Ca.*) *coccipus* has morphologically dissimilar sistens and progrediens forms in the first instar, with sistentes having stronger sclerotization and longer rostral stylets (Havill & Foottit 2007). All but one of the first instars collected on March 27 were sistens forms, while all the first instars collected on April 5–7 were progrediens forms. The neosistentes on the earlier date were likely the remnants of the overwintering generation that had not developed because all of the specimens in our possession were damaged to some degree. The progredientes collected later were alive and abundant. This could indicate the presence of a longer generation of overwintering sistens individuals with an intervening series of short generations of progredientes individuals. We did not observe a dichotomy among the adults that would indicate morphologically distinct sistens and progrediens, nor did we collect sexupara adults into which a proportion of progrediens nymphs often develop in other species. In addition, their DNA sequences did not match any specimens on *Picea*, so there is no indication at this point that *A.* (*Ca.*) *coccipus* can complete a holocycle.

This is the first known legless species in the Aphidomorpha. The nymph illustrated in Fig. 2D–E was confirmed as a second instar because it was found emerging from its first instar exuvium. This confirms that all but the first instar lacks legs and have reduced antennae (Fig. 2E). We are not aware of any other completely legless species within Aphidomorpha, but some species, scattered throughout Aphididae have reduced leg structures. For example, *Colopha hispanica* Nieto Nafría & Mier Durante, 1987 (Aphididae: Eriosomatinae), some *Quadrartus* species (Aphididae: Hormaphidinae) (Takahashi 1958; Sorin 2001), *Mastopoda pteridis* Oestlund, 1886 (Aphidinae: Macrosiphini), and *Atarsos grindeliae* Gillette, 1911 (Aphidinae: Macrosiphini) all have shortened legs with some segments missing or fused.

Being nested well into the Adelgidae, *A.* (*Ca.*) *coccipus* represents an independent evolution of the apodous trait commonly found in scale insects (Hemiptera: Sternorrhyncha: Coccomorpha). In scale insects, legs can be entirely missing, or represented by a variety of reduced morphologies (Gullan & Kosztarab 1997). The morphology of *A.* (*Ca.*) *coccipus* leg vestiges as clusters of setae is similar to some species of flat grass scales (Hemiptera: Acleridae; McConnell 1953) and legless mealybugs (Hemiptera: Pseudococcidae: Pseudococcinae: Serrolecanini; Hendricks & Kosztarab 1999).

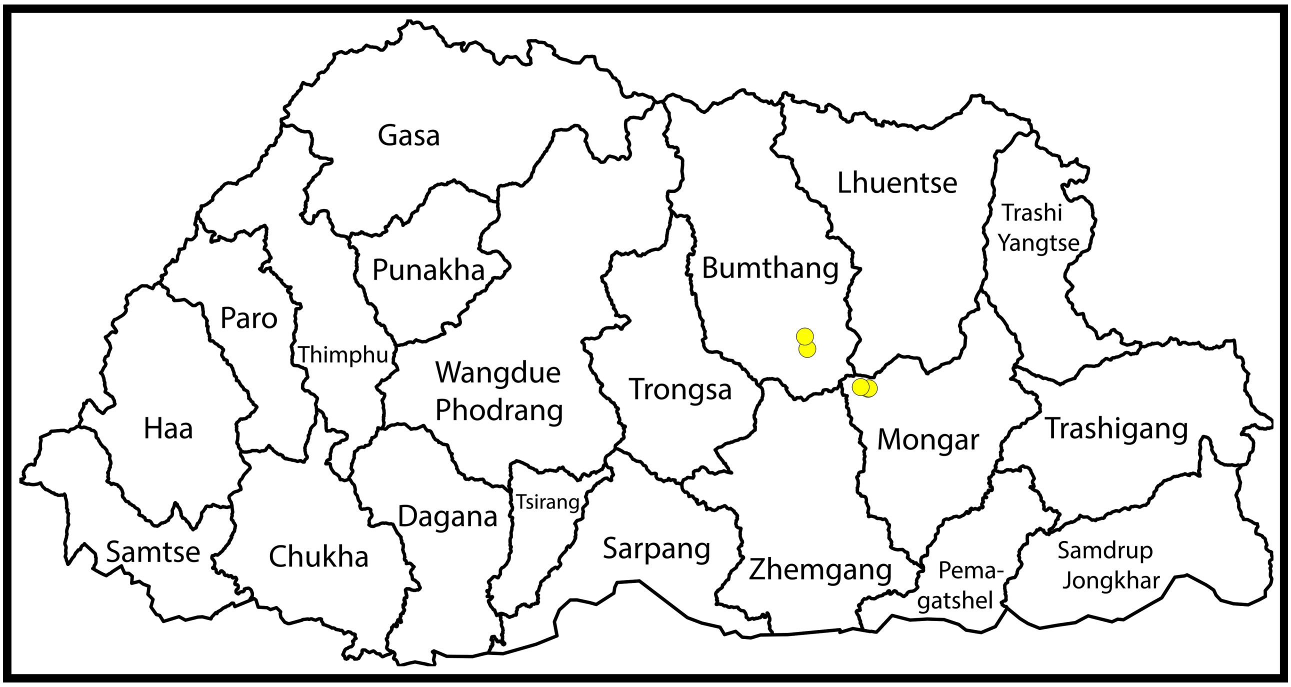

FIGURE 3. Map of Bhutan showing collection locations for *Adelges* (*Cassiadelges*) *coccipus.*

The phylogeny (Fig. 1) places *A.* (*Ca.*) *coccipus* sister to an undescribed species from China that will be dealt with in a subsequent publication when more specimens are available for a full description. This other species has all of the features of *Cassiadelges*, but unlike *A.* (*Ca.*) *coccipus*, it has fully developed legs. Comparison between *Adelges* (*Ca.*) *coccipus* and *A.* (*Ca.*) nr. *coccipus* presents an exciting opportunity to examine the evolutionary development of insect limb formation from a new perspective.

***Adelges* (*Cholodkovskya*) *changaphuensis* Havill & Brunet, sp. nov.**
(Fig. 4A–E)

Etymology. From *Changaphu*, the locality in Bhutan where spruce trees were found to be heavily infested by this species.

Type material. HOLOTYPE: 1 adult fundatrix, **BHUTAN, Thimphu, Changaphu Forest Nursery**, lat. 27.4997, long. 89.7176, 2-IV-2020, on *Picea spinulosa*, Kaka Tshering (USNM). PARATYPES: 1 first instar fundatrix, 1 adult fundatrix, same data (NBC). 1 first instar fundatrix, 1 nymph fundatrix, same data (USNM). 1 first instar fundatrix, same data (YPM#ENT594814). 1 nymph fundatrix, same data (YPM#ENT594815). 1 adult fundatrix, same data (YPM#ENT594816). 2 adult gallicolae, **BHUTAN, Thimphu, Changaphu**, lat. 27.5022, long. 89.7156, 29-VII-2021, on *Picea spinulosa*, Kaka Tshering (CNC#5338320-6, CNC#5338321-9). 1 adult gallicola, same data (NBC). 1 adult gallicola, same data (USNM). 1 adult gallicola, same data (YPM#ENT594826).

Additional material examined. BHUTAN: Bumthang: Khandopang: 2 adult fundatrices, 3 fundatrix exuviae (YPM), 27.4262, 90.9063, 8-IV-2022, on *Picea spinulosa*, Kaka Tshering. **Thimphu: Changaphu Forest Nursery**: 11 late instar nymph fundatrices (CNC), 1 first instar fundatrix exuvium, 4 late instar nymph fundatrices, 2 adult fundatrices (USNM), 1 first instar fundatrix exuvium, 5 late instar nymph fundatrices, 3 adult fundatrices (YPM), lat. 27.4997, long. 89.7176, 2-IV-2020, on *Picea spinulosa*, Kaka Tshering. 9 fourth instar nymph gallicolae, 17 adult gallicolae (CNC), 1 adult gallicola (NBC), 2 late instar nymph gallicolae, 5 adult gallicolae (USNM), 1 nymph gallicola, 15 adult gallicolae (YPM), lat. 27.4997, long. 89.7176, 29-VII-2021, on *Picea spinulosa*, Kaka Tshering. 16 first instar gallicolae (CNC), 15 galls (YPM), lat. 27.4997, long. 89.7176, 22-V-2022 on *Picea spinulosa*, Kaka Tshering.

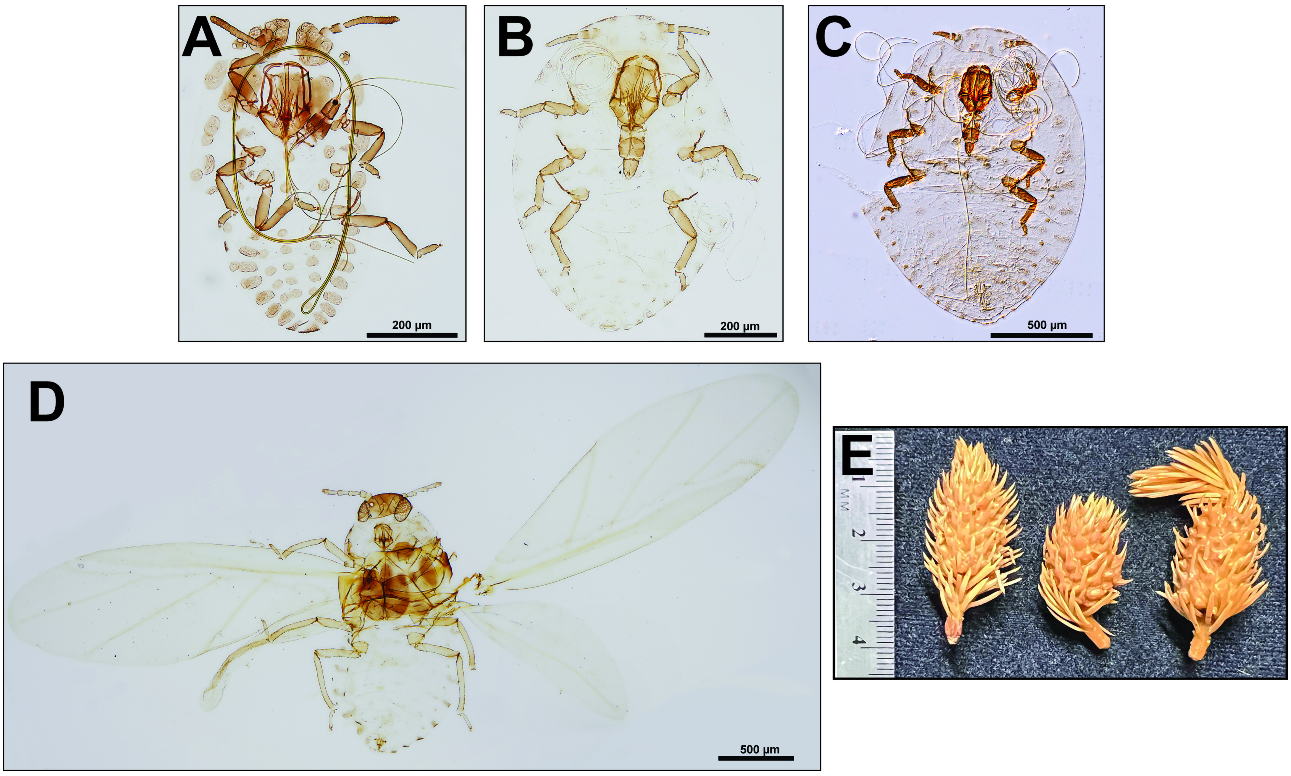

FIGURE 4. *Adelges* (*Cholodkovskya*) *changaphuensis*. A—C. Fundatrices: neofundatrix (paratype, USNM) (A), late instar nymph (paratype, USNM) (B), adult (holotype, USNM) (C); D. Gallicola adult (paratype, USNM); E. Galls.

Diagnosis. The neofundatrix of *A.* (*Ch.*) *changaphuensis* (Fig. 4A) is similar to the neosistens of *A.* (*Ch.*) *viridanus* (Börner 1909; Inouye 1945) in having a wide spinal fissure bisecting the cephalic and prothoracic plates, spinal, pleural, and lateral wax glands on the meso- and metathoracic and first six abdominal segments, and wax glands with facets surrounding a central seta. The *A.* (*Ch.*) *changaphuensis* neofundatrix differs from the *A.* (*Ch.*) *viridanus* neosistens in having separate longitudinal lateral prothoracic plates and differs from all other members of *Cholodkovskya* in having larger lateral abdominal wax glands arranged around two setae instead of around one seta. The neofundatrix of *A.* (*Ch.*) *viridanus* has not been described to allow direct comparison with the same morph in *A.* (*Ch.*) *changaphuensis*. The general appearance of the wax glands is also similar to neosistentes and neofundatrices in species of *Sacchiphantes*. The adult fundatrix of *A.* (*Ch.*) *changaphuensis* (Fig. 4C) is similar to that of *A.* (*Ch.*) *viridanus* (Havill *et al*. 2023) but *A.* (*Ch.*) *changaphuensis* lacks wax glands antero-lateral to forecoxae. Late instar nymphs (Fig. 4B) are similar in morphology to the adult but lack an ovipositor. The adult gallicola of *A.* (*Ch.*) *changaphuensis* (Fig. 4D) differs from *A.* (*Ch.*) *viridanus* because it does not have anterior and posterior wax glands on each side of the head united. Unlike the gallicolae of other *Adelges*, the medial vein on the hindwings of *A.* (*Ch.*) *changaphuensis* are either faint or lacking entirely. Also note, that the sexuparae of *Adelges* (*Gilletteella*) *cooleyi* (Gillette, 1907) and *Adelges* (*Dreyfusia*) *nordmannianae* (Eckstein, 1890) lack the medial vein on the hindwing, so *A.* (*Ch.*) *changaphuensis* is not the only alate *Adelges* with this character.

Description. *Neofundatrix* (Fig. 4A). Body length: $n = 4$, 0.604–0.722 (0.665) mm. Body width: $n = 4$, 0.374–0.437 (0.404) mm. Dorsal wax glands generally on strongly sclerotized plates, and with 3–6 round to ovoid facets with a granular appearance, loosely packed and arranged around a central stout seta, sometimes merged with neighboring glands to include up to approximately 20 facets arranged around two or three setae.

Head and pronotum with strongly sclerotized spinal and lateral plates, separated from each other and along mid-line by wide fissures. Ocelli borne on small lateral plates. Each spinal cephalic plate with five large wax glands, three apical and two postero-lateral, a sixth slightly raised postero-spinal area with a central seta, usually lacking facets, occasionally with one or several facets. The largest dorsal wax gland facets on the head are slightly smaller than ocellus. Large ventral wax glands on moderately sclerotized sternites posterior to base of antennae with approximately 30 small, round, tightly packed facets. Antennae 3-segmented, segment III distinctly imbricated, very long and slender [*n* = 6, 0.125–0.132 (0.129) mm], 7.3x its width at midpoint [*n* = 6, 0.017–0.019 (0.018) mm], approximately 2.3x longer than segments I [*n* = 4, 0.019–0.034 (0.025) mm] and II [*n* = 4, 0.020–0.033 (0.027) mm] combined. Two primary rhinaria on segment III, one subapical and one approximately 1/3 the segment length from the apex, each with a small thumb-like projection. A few accessory rhinaria adjacent to the subapical primary rhinarium. Processus terminalis with five setae, the apical seta length [*n* = 4, 0.035–0.041 (0.038) mm] approximately 2x the rest. Rostrum reaching past hind coxae, with ultimate segment as long [*n* = 5, 0.053–0.061 (0.057) mm] as width of segment III at midpoint [*n* = 4, 0.051–0.056 (0.054) mm]. Stylets very long [*n* = 2, 3.353–3.467 (3.410) mm], approximately 5.1x body length.

Coxae and femorotrochanters smooth, with tibiae weakly imbricated, and second tarsal segments distinctly imbricated. Pair of dorso-subapical capitate setae of fore- and midlegs with one of the pair approximately 2x as long as the other, subequal on hindleg. Mid- and hind-coxae with basal wax glands with approximately 8–12 moderately packed round to ovoid facets. Hind femorotrochanter length: n = 5, 0.096–0.105 (0.101) mm.

Pronotum with wax glands on the four corners of each spinal plate, each gland with 1–4 facets. Lateral plates of pronotum extended longitudinally with two wax glands, each with approximately 5–12 facets. Meso- and metanotum with dorsal spinal, pleural, and lateral plates, each with a single wax gland. Spinal and pleural wax glands round and arranged around one seta, lateral wax glands oval-shaped along longitudinal axis usually arranged around two setae. Abdominal segments I–VI with dorsal spinal, pleural, and lateral plates, segment VII with spinal and lateral plates, and segment VIII with lateral plates. Abdominal segment IX with a transversely extended plate in central position. Each abdominal plate with a single wax gland. Lateral wax glands of abdominal segments I–VIII transverse oval-shaped with 7–20 facets usually arranged around two setae. Pleural and spinal wax glands of abdominal segments I–VI and spinal glands of segment VII round to oval with 3–7 facets arranged around a single seta. Ventral spiracles on abdominal segments II–VI. All abdominal segments with a ventro-spinal pair of fine acuminate setae, those on segment IX especially long and slender.

Adult fundatrix (Fig. 4C). Body length: *n* = 6, 1.343–1.903 (1.644) mm. Body width: *n* = 6, 1.042–1.226 (1.111) mm. Color in life light green. Dorsal wax glands generally on very lightly sclerotized plates, and with small round, tightly packed facets with borders only slightly darker than the surrounding cuticle.

Sclerotized plates on head and pronotum lacking. Head with 8–10 small anterior wax glands between ocelli, each gland with approximately 3–20 loosely packed facets, the largest of which are approximately half the diameter of the ocellus. Ventral wax glands at base of antennae with approximately 30–40 very small tightly packed facets. Antennae 3-segmented, segment III [*n* = 6, 0.074–0.097 (0.083) mm], approximately 3.6x its width at midpoint [*n* = 6, 0.019–0.026 (0.023) mm], longer than segments I [*n* = 6, 0.024–0.037 (0.031) mm], and II [*n* = 6, 0.027–0.033 (0.032) mm] combined. Rostrum reaching to hind coxae, with ultimate segment length [(n = 4, 0.068–0.091 (0.079) mm] approximately 0.9x width of segment III at midpoint [n = 4, 0.076–0.099 (0.084) mm].

Coxae, femorotrochanters, and tibiae smooth, second tarsal segments weakly imbricated. Mid- and hind-coxae with transversely oval wax glands bearing 10–25 facets. Hind femorotrochanter length: n = 6, 0.125–0.224 (0.171) mm.

All thoracic segments and abdominal segments I–VI with spinal, pleural, and lateral wax glands, abdominal segment VII with lateral and spinal wax glands, segment VIII with lateral wax glands. Spiracles on abdominal segments II–VI strongly sclerotized and conspicuous. Numerous acuminate setae on abdominal segments VIII and IX. Ovipositor with length of gonapophyses [*n* = 4, 0.117–0.157 (0.130) mm] approximately 1.2x the width across apodemes.

Adult gallicola (Fig. 4D). Body length: *n* = 16, 1.772–2.610 (2.058) mm. Pronotum width: *n* = 15, 0.587–0.812 (0.676) mm. Abdomen width: *n* = 16, 0.839–1.221 (0.960) mm. Color in life light green when newly emerged. Dorsal wax glands generally with round, tightly packed facets interspersed with minute setae.

Head with a pair of anterior and a pair of posterior irregular-shaped wax glands with approximately 10–30 facets. Posterior glands may be subdivided into small groups of facets around setae. Antenna distinctly five segmented, *n* = 12, 0.336–0.434 (0.381) mm long, segments II–V imbricated. Length of antennal segment III: *n* = 12, 0.075–0.088 (0.080) mm, IV: *n* = 12, 0.080–0.109 (0.093) mm, *n* = 12, V: 0.101–0.137 (0.115) mm. Ratio of length of antennal segments III:IV:V 1.00:1.16:1.43. Antennal segment III tapering sharply towards the base, segments IV and V with a gradual taper below rhinarium. Rhinaria on antennal segments III–V oval, subapical, often with sinuate margins, sometimes appearing triangular in profile. Rhinarium occupying approximately 1/3 of each segment: III: *n* = 10, 0.25–0.41 (0.34), IV: *n* = 10, 0.25–0.40 (0.33), V: *n* = 10, 0.30–0.40 (0.34). Processus terminalis with four or five acuminate setae, with apical seta length [*n* = 10, 0.015–0.022 (0.017) mm] approximately 1.9x as long as the rest. Ultimate segment of rostrum length [(*n* = 14, 0.055–0.080 (0.064) mm] 0.9x the width of segment III at midpoint [*n* = 14, 0.058–0.083 (0.072) mm].

Coxae and femorotrochanters smooth, tibiae very weakly imbricated, and second tarsal segments distinctly imbricated. Hind femur with approximately 15–20 long fine acuminate setae along ventral surface. Length of longest setae on hind femur: *n* = 15, 0.028–0.039 (0.034) mm. Hind femorotrochanter length: *n* = 15, 0.314–0.408 (0.350) mm.

Each side of pronotum with several small, antero-lateral oval-shaped glands with 2–50 facets, a very large postero-lateral band of approximately 120–150 facets, and a narrow irregular row, 2–5 facets thick, along the posterior edge. Mesonotum with a pair of spinal oval-shaped wax glands bearing approximately 50–60 facets between mesothoracic lobes. Metanotum with a pair of wax glands with approximately 30–60 facets towards the posterior half of the spinal lobes. Forewing length: *n* = 16, 2.286–3.023 (2.661) mm. Hindwing length: *n* = 16, 1.377–1.892 (1.588) mm. Forewing with medial, cubital, and anal veins straight or only slightly curved back towards the body, leaving the radial sector at acute angles. Hindwing with medial vein faint or lacking.

Abdomen with spinal, pleural, and lateral wax glands on segments I–VI, lateral and pleural wax glands on segment VII, only lateral wax glands on VIII, and a post-anal gland on IX. Lateral glands on abdominal segments I–VII transverse, often crescent-shaped. Spinal glands decrease in size posteriorly. Distinct sclerotized spiracles on abdominal segments II–VI. Abdominal segments VII–VIII with numerous ventral fine acuminate setae, some long and slender. Ovipositor with gonapophyses [*n* = 11, 0.106–0.126 (0.114) mm] approximately 1.3x longer than width across apodemes [*n* = 11, 0.072–0.101 (0.086) mm].

Gall (Fig. 4E). Light green in color, strobile-shaped. Usually occurring singly per node on terminal and lateral buds of new shoots. Consists of swollen needle bases, fused at the axis of the shoot. Chambers internally unconnected. Gall length [n = 9, 21–34 (24.6) mm] approximately 1.9x the width (n = 9, 10–16 (12.7) mm]. Usually without a distal shoot, but occasionally with a distal tuft of shortened needles or short shoot. Distal ends of the needles on gall narrow and sharp, extending approximately 2–5 mm from the surface.

Hosts and distribution. *Picea spinulosa* in Bhutan (Bumthang, Thimphu) (Fig. 5).

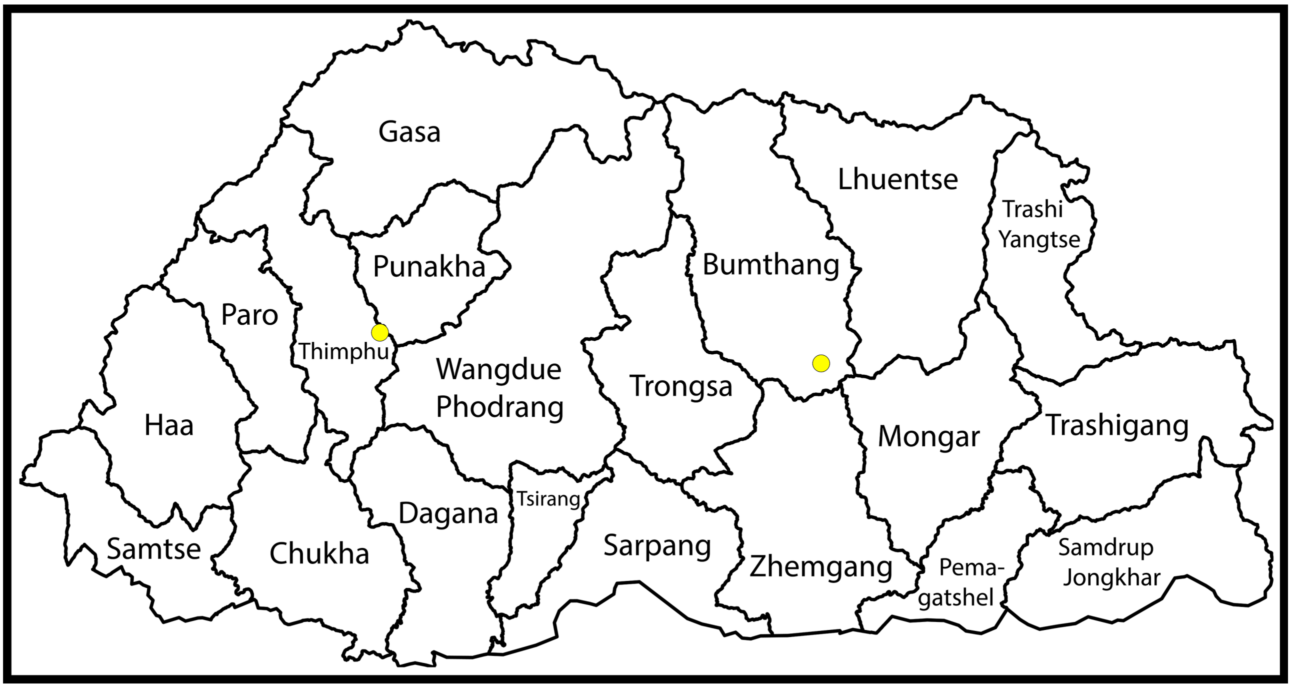

FIGURE 5. Map of Bhutan showing collection locations for *Adelges* (*Cholodkovskya*) *changaphuensis.*

Remarks. The morphological similarities to *A.* (*Ch.*) *viridanus* (Börner, 1909), and the sister relationship with *A.* (*Ch.*) *viridanus* in the phylogeny (Fig. 1) supports the placement of *A.* (*Ch.*) *changaphuensis* in subgenus *Cholodkovskya*. The life cycle of *A.* (*Ch.*) *changaphuensis* cannot be determined from our collections. There is no evidence of host alternation because our survey did not yield specimens with matching DNA barcodes from potential secondary hosts. Galls collected on May 22, 2022 were mature and close to opening. This species could be anholocyclic on *Picea*, or since in the molecular phylogeny (Fig. 1) it is nested well within a clade of species that use *Larix* species as secondary hosts, it may alternate between *Picea* and *Larix*. The other members of *Cholodkovskya*, *A.* (*Ch.*) *viridanus*, *Adelges* (*Cholodkovskya*) *viridulus* (Cholodkovsky, 1911), and *A.* (*Ch.*) *oregonensis*, all feed on species of *Larix*. *Adelges* (*Ch.*) *viridanus* has an anholocyclic life cycle in Europe and China with a generation of wingless sistentes that settle on the bark, followed by a series of generations of alates that settle on the needles (Cholodkovsky 1911; Li & Tsai 1973). In Japan, the fundatrix adult and gallicola nymph of *A.* (*Ch.*) v*iridanus* were recently described, indicating that in that region the species can either be holocyclic, alternating between *Larix* and *Picea*, or includes recently diverged anholocyclic populations on *Picea* (Havill *et al.* 2023). The life cycle of *A.* (*Ch.*) v*iridulus* is anholocyclic on *Larix* but has only one annual generation of sistens on the bark and no known alate forms. The life cycle of *A.* (*Ch.*) *oregonensis* is unknown, as the species is only known from wingless forms that feed on the needles and the base of needles of *Larix* in western North America (Annand 1928). Note that *A.* (*Ch.*) *oregonensis* is not sister to *A.* (*Ch.*) *viridanus* or *A. (Ch.) changaphuensis* in the molecular phylogeny (Fig. 1), so it may not belong in this subgenus. A more detailed morphological analysis of the adelgid species feeding on *Larix*, and a more robust phylogeny of the family could help to resolve a more informative delimitation of *Cholodkovskya*.

***Adelges* (*Dreyfusia*) *densae* Havill & Brunet, sp. nov.**
(Fig. 6A–C)

Etymology. Genitive derived from its host plant, *Abies densa.*

Type material. HOLOTYPE: 1 adult exulis, **BHUTAN, Bumthang, Tangsibi**, lat. 27.4972, long. 90.8699, 6-IV-2022, on *Abies densa*, Kaka Tshering (USNM). PARATYPES: 1 first instar exulis (CNC#5338332-12), same data. 2 late instar nymph exules, same data (NBC). 1 first instar exulis, 2 late instar nymph exules, same data (USNM). 1 first instar exulis, same data (YPM#ENT594781). 2 late instar nymph exules, same data (YPM# ENT594788).

Additional material examined. BHUTAN: Bumthang: Tangsibi: 2 first instar exules, 11 late instar nymph exules (CNC), 1 first instar exulis, 2 first instar exulis exuviae, 10 late instar nymph exules (NBC), 4 first instar exules, 6 first instar exulis exuviae, 2 late instar nymph exules (USNM), 8 first instar exules, 17 first instar exulis exuviae, 14 late instar nymph exules, 2 late instar nymph exulis exuviae (YPM), lat. 27.4972, long. 90.8699, 6-IV-2022, on *Abies densa*, Kaka Tshering.

Diagnosis. The first instar exulis of *A.* (*D.*) *densae* (Fig. 6A) is similar to *Adelges* (*Aphrastasia*) *pectinatae* (Cholodkovsky, 1888), *A.* (*Ap.*) *pindrowi* Yaseen & Ghani, 1971, *A.* (*D.*) *nordmannianae*, and *Adelges* (*D.*) *piceae* (Ratzeburg, 1844) in having compound wax glands with emarginated clusters of many small facets. It differs from these species in the structure of the wax glands, and that the first instar exulis has wax glands in pleural and lateral positions. Late instar exulis nymphs (Fig. 6B) are similar to the adult (Fig. 6C) but lack an ovipositor.

Description. *First instar exulis.* (Fig. 6A). Body length: n = 10, 0.431–0.588 (0.494) mm. Body width: n =11, 0.271–0.457 (0.335) mm. Dorsal wax glands generally on strongly sclerotized plates. Glands consist of 2–6 round, oval, or polygonal delineated areas arranged around a central seta, each area containing approximately 6–50 very small round, oval, or polygonal facets, sometimes glands merged, arranged around two or more setae.

Head and pronotum with moderately to strongly sclerotized and reticulated spinal and lateral plates, separated from each other and along mid-line by wide fissures. Ocelli borne on separate lateral plates. Each spinal cephalic plate with six large wax glands, two spinal, two lateral, two apical, together filling most of the area of the plate. Ventral wax glands at base of antennae lacking. A pair of spinal flagellate setae on head slightly less than half the distance from apex. Antennae 3-segmented, segment III imbricated, length [n = 13, 0.076–0.089 (0.083) mm], approximately 5.2x its width at midpoint [n = 13, 0.013–0.020 (0.016) mm], and approximately 2.1x longer than segments I [n = 12, 0.016–0.028 (0.021) mm] and II [n = 12, 0.017–0.022 (0.019) mm] combined. Two primary rhinaria on segment III, one subapical and one approximately ½ the segment length from the apex, each with a small thumb-like projection. Several accessory rhinaria adjacent to subapical primary rhinarium. Processus terminalis with five setae, the apical seta length [n = 5, 0.033–0.037 (0.034) mm] approximately 3.0x longer than the rest. Rostrum reaching hind coxae, with ultimate segment 0.7x as long [n = 11, 0.033–0.038 (0.036) mm] as width of segment III at midpoint [n = 11, 0.045–0.052 (0.050) mm]. Stylet length [n = 4, 1.811–1.959 (1.888) mm] approximately 3.8x body length.

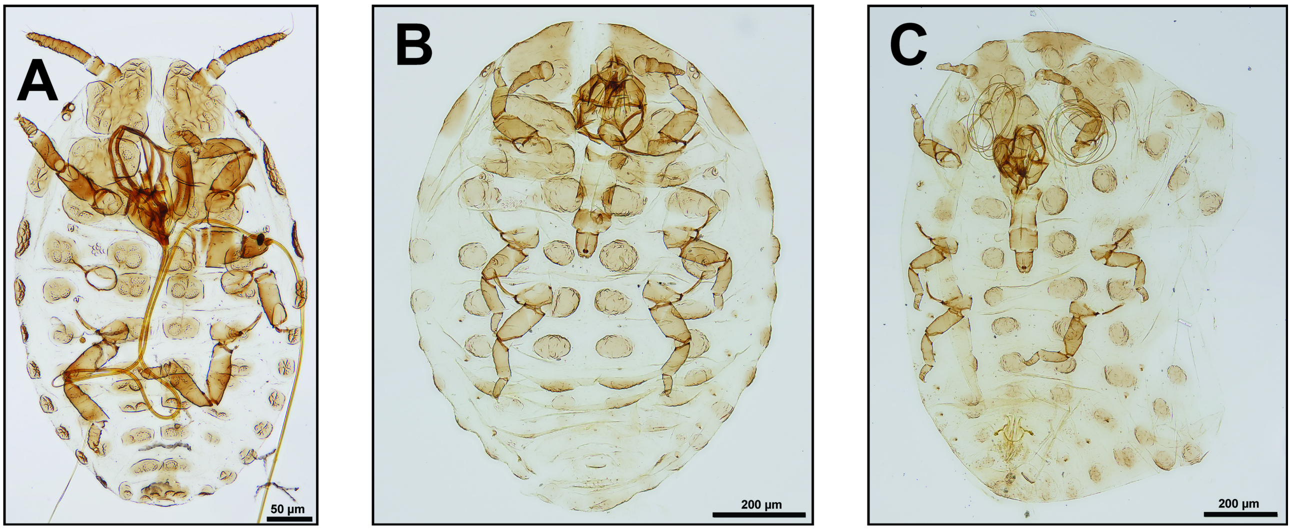

FIGURE 6. *Adelges densae*. A—C. Exules: first instar (paratype, USNM) (A), late instar (paratype, USNM) (B), adult (holotype, USNM) (C).

Coxae and femorotrochanters smooth, with tibiae and second tarsal segments weakly imbricated. Pair of dorso-subapical capitate setae, subequal in length, on tarsal segment II of fore-, mid- and hindlegs. Wax glands antero-lateral to mid-coxae with approximately 7–12 round to oval facets. Hind femorotrochanter length: *n* = 13, 0.056–0.068 (0.063) mm.

Pronotum with wax glands on the four corners of each spinal plate, each gland with 4–6 facet areas. Lateral prothoracic plates longitudinal oval-shaped, each with 2 wax glands, each gland with 5–6 facet areas. Meso- and metathorax with separate lateral, pleural, and spinal plates, lateral plates with wax gland with 5–6 facet clusters arranged around 1–2 setae, pleural and spinal plates each with a single wax gland with 4–5 facet clusters arranged around one seta.

Each abdominal plate generally with a single wax gland with 2–4 faceted areas surrounding a seta. Abdominal segments I–V with separate lateral, pleural, and spinal wax plates, segment VI–VII with lateral and spinal plates, spinal plates touching or fused at the midline, segment VIII with very small lateral plates lacking wax glands, segment IX with apical plate lacking wax glands. Abdominal segments VII–IX tend to collapse telescopically when slide mounted, making these segments easier to see in exuviae. Lateral abdominal plates ovoid to square, pleural and spinal plates transverse oval. Abdominal segment IX with a pair of flagellate setae at the tip.

Adult exulis. (Fig. 6C). Body length: *n* = 1, 1.305 mm. Body width: *n* = 1, 0.770 mm. Moderately to strongly sclerotized dorsal plates generally bearing large, strongly sclerotized hemispheroid protuberant spinal and pleural plates with 1–3 stout setae on the surface and bearing no apparent wax glands.

Head and pronotum with lightly sclerotized large spinal and small lateral plates, separated from each other and along mid-line by fissures. Ocelli borne on lateral plates. Each spinal cephalic plate with three protuberances: two posterior and one apical. Antennae 3-segmented, segment III (*n* = 1, 0.060 mm), approximately 1.3x longer than segments I (*n* = 1, 0.028 mm) and II (*n* = 1, 0.019 mm) combined. Segment III with a subapical primary rhinarium with a few adjacent accessory rhinaria. Processus terminalis with 3 stout setae. Rostrum reaching past mid coxae, with ultimate segment as long (*n* = 1, 0.062 mm) as 0.7x the width of segment III at its midpoint (*n* = 1, 0.080 mm).

Coxae and femorotrochanters, and tibiae smooth, distitarsi weakly imbricated. Wax glands with approximately 20–40 loosely packed facets antero-lateral to all coxae. Hind femorotrochanter length: *n* = 1, 0.096 mm.

Pronotum with protuberant plates on the four corners of each spinal plate. Meso- and metanotum and abdominal segments I–IV with separate lateral, pleural, and spinal wax plates, each borne on a large protuberance. Abdominal segments V–VIII with only lateral plates with the protuberance becoming less pronounced and less sclerotized posteriorly. Abdominal segment IX with a lightly sclerotized transversely extended post-anal plate with a pair of long acuminate setae. Very lightly sclerotized sternites with wax glands with 4–12 loosely packed facets and 3–4 setae mesad to the spiracles on abdominal segments IV–VI. Acuminate setae abundant ventrally on segment VIII and dorsally on segment IX, and in a single spinal pair on each of the other abdominal segments. Ovipositor with length of gonapophyses ($n = 1$, 0.125 mm) 1.2x width across apodemes ($n = 1$, 0.108 mm).

Hosts and Distribution. *Abies densa* in Bhutan (Bumthang) (Fig. 7).

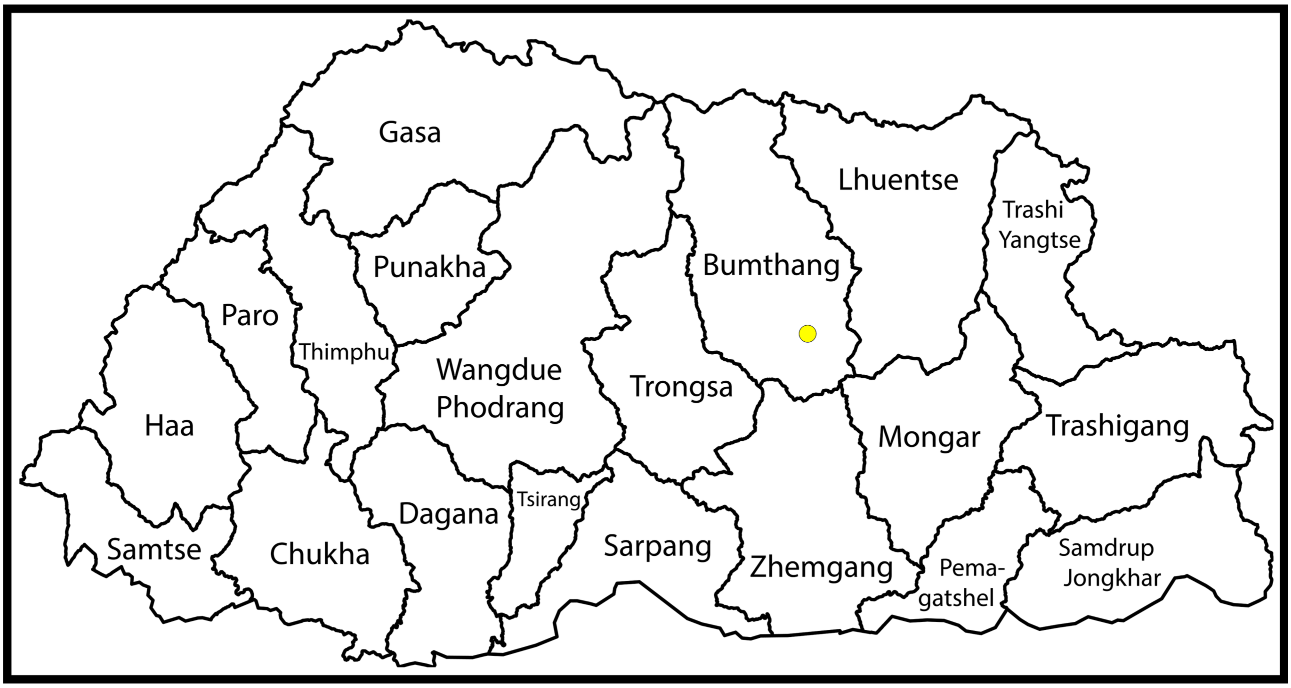

FIGURE 7. Map of Bhutan showing collection locations for *Adelges* (*Dreyfusia*) *densae.*

Remarks. This species was collected from *Abies densa* in densely congregated colonies on the bark of the main stem and on the underside of lateral branches on twigs. On the twigs, the stylets were inserted mostly into the bark, and occasionally into the base of needles.

We tentatively place *A.* (*D.*) *densae* in *Dreyfusia* because it is sister to *A.* (*D.*) *knucheli* in the molecular phylogeny (Fig. 1). It has some morphological similarities to *A.* (*D.*) *pindrowi*, and both *A.* (*D.*). *pindrowi* and *A.* (*D.*) *densae* have morphological similarities to *A.* (*Ap.*) *pectinatae*, which with its two subspecies, is the only member of *Aphrastasia* Börner, 1909. *Adelges* (*D.*). *pindrowi* was placed in *Dreyfusia* by Havill & Foottit (2007) and Favret *et al.* (2015b). However, Yaseen & Ghani (1971) remarked that *A.* (*D.*) *pindrowi* closely resembles *Adelges* (*Aphrastasia*) *pectinatae ishiharai* (Inouye, 1936), and Blackman & Eastop (2024) also remarked that *A.* (*D.*) *pindrowi* is "in the pectinatae group." It might be appropriate to place *A.* (*D.*). *pindrowi* and *A.* (*D.*) *densae* in *Aphrastasia*; however *A.* (*D.*) *densae* is not sister to *A.* (*Ap.*) *pectinatae* in our molecular phylogeny. A more detailed morphological analysis of the adelgid species feeding on *Abies*, and a more robust phylogeny of the family could help to resolve a more informative delimitation of *Aphrastasia*.

It is possible that either *A.* (*D.*) *densae* or *A.* (*G.*) *glandulae* is the same as what Schmutzenhofer (1985) recorded as "*Chermes abietis-piceae*" on *Abies densa* at Thumsingla (= Phrumsengla). In our survey, both *A.* (*D.*) *densae* and *A.* (*G.*) *glandulae* were collected from *Abies densa* within 16 km of this locality. *Chermes abietispiceae* was originally described from northern India, alternating between *Picea smithiana* and *Abies spectabilis* (Stebbing 1903a, b). It was later renamed *Chermes himalayensis* by Stebbing (1910) and given a more detailed description, but this name is an unavailable synonym of the earlier name. *Chermes abietispiceae* is currently considered a *nomen dubium* (Favret 2024) because neither of Stebbing's descriptions provide enough information about the appearance and arrangement of the wax glands to confirm its identity (Schneider-Orelli & Schneider 1954). Our sample of *A.* (*D.*) *densae* was collected from the stem, not from the needles as described by Schmutzenhofer (1985), who observed their feeding causing a downward twisting of the needles. However, it is possible that, similarly to *A.* (*D.*) *nordmannianae* (Pschorn-Walcher & Zwölfer 1958), *A.* (*D.*) *densae* includes progredientes that feed on the needles that we did not sample. Ghani & Rao (1966) also speculated that *A.* (*D.*) *knucheli* could be the same as *Chermes abietispiceae*. Additional sampling in the region could resolve this.

***Adelges* (*Annandina*) *lepsimon* Havill & Brunet, sp. nov.**
(Fig. 8A–D)

Etymology. Invariant combination of the Dzongkha noun, *lep*, meaning "brain" and *Psimon* the supervillain from the DC Comics Universe, whose brain is visible through a clear dome on his head. Both are in reference to the large wax glands on the head, that superficially resemble the lobes of a vertebrate brain.

Type material. HOLOTYPE: 1 adult exulis, **BHUTAN, Mongar, Sengor**, lat. 27.3394, long. 91.0295, 8-IV-2022, on *Tsuga dumosa*, Kaka Tshering (USNM). PARATYPES: 1 first instar exulis exuvium, same data (CNC#5338329-10). 1 adult exulis, same data (CNC#5338329-7). 1 late instar nymph exulis, 1 adult exulis, same data (NBC). 1 first instar exulis, 2 first instar nymph exulis exuviae, 1 late instar exulis, same data (USNM). 1 late instar exulis, same data (YPM#ENT594636). 1 adult exulis, same data (YPM#ENT594641). 1 first instar exulis exuvium, **BHUTAN, Mongar, Sengor**, lat. 27.3711, long. 91.0234, 7-IV-2022, on *Tsuga dumosa*, Kaka Tshering (NBC). 1 late instar nymph sexupara, same data (USNM). 2 first instar exulis exuviae, same data (YPM#ENT594634). 1 first instar exulis, **BHUTAN, Wangdue Phodrang, Dungdungnyesa**, lat. 27.5377, long. 90.1851, 12-XI-2021, on *Tsuga dumosa*, Kaka Tshering (CNC#5338322-9). 1 adult exulis, same data (CNC#5338322-4). 3 first instar exules, 1 first instar exulis exuvium, same data (USNM).

Additional material examined. BHUTAN: Mongar: Sengor: 2 late instar nymph exules (USNM), 1 first instar exulis, 6 first instar exulis exuviae, 10 late instar nymph exulis exuviae, 12 late instar nymph exules, 3 late instar nymph sexuparae (YPM), lat. 27.3711, long. 91.0234, 7-IV-2022, on *Tsuga dumosa*, Kaka Tshering. 2 first instar exules exuviae, 1 late instar nymph sexupara, 6 adult exules (CNC), 1 first instar exulis, 9 first instar exulis exuviae, 2 late instar nymph exulis exuviae, 9 late instar nymph exules (USNM), 1 first instar exulis, 16 first instar exulis exuviae, 12 late instar nymph exulis exuviae, 11 late instar nymph exules, 1 late instar nymph sexupara, 12 adult exules (YPM), lat. 27.3394, long. 91.0295, 8-IV-2022, on *Tsuga dumosa*, Kaka Tshering. **Wangdue Phodrang: Dungdungnyesa**: 1 egg, 3 first instar exules, 3 adult exules (CNC), 2 first instar exules, 1 adult exulis (NBC), 3 first instar exules, 2 first instar exulis exuviae, 1 late instar nymph exulis exuvium, 1 adult exulis (USNM), 4 first instar exules, 2 first instar exulis exuviae, 3 late instar nymph exulis exuviae, 6 adult exules (YPM), lat. 27.5377, long. 90.1851, 12-XI-2021, on *Tsuga dumosa*, Kaka Tshering.

Diagnosis. *Adelges* (*An*.) *lepsimon* is placed in *Annandina* by phylogenetic relatedness (Fig. 1), and by the combination of characters outlined in Favret *et al.* (2015a): feeding on *Tsuga*, having the first instar exulis with head and pronotum almost completely covered by plates, with margins lined with wax gland facets, four plates on the mesothorax, and six on the metathorax and first five abdominal segments, the adult with a completely fused cephaloprothoracic shield containing many small facets, and by having capitate setae on the ultimate abdominal segments (Annand 1924; Havill *et al*. 2022). In *A.* (*An*.) *lepsimon*, the spinal and pleural mesothoracic plates are not always fused, so the diagnosis for *Annandina* should be amended to specify four or six plates on this segment. The first instar exulis of *A.* (*An*.) *lepsimon* differs from *A.* (*An*.) *tsugae* by having round to oval wax glands proximal to the lateral rows of facets on the head and each thoracic segment, and abdominal segments I–VI with dorso-spinal plates each with a wax gland in the center with 1–4 facets. The adult exulis of *A.* (*An*.) *lepsimon* resembles *A.* (*An*.) *tsugae*, which includes a diversity of genetic lineages in different regions of Asia and North America (Havill *et al.* 2016). A future paper will address morphological differences among these lineages compared to *A.* (*An*.) *lepsimon.*

Description. *First instar exulis* (Fig. 8A–B). Body length: n = 10, 0.314–0.423 (0.355) mm. Pronotum width: n = 11, 0.171–0.211 (0.193) mm. Body width: n = 11, 0.189–0.271 (0.220) mm. Dorsal wax glands generally on strongly to moderately sclerotized plates, with facets either arranged as anterior, lateral, or spinal longitudinal lines of individual pores, or as clusters of two to approximately 13 tightly packed, often overlapping pores.

Head and pronotum almost completely covered by moderately to strongly sclerotized plates, separated from each other and along mid-line by a narrow fissure. Each cephalic plate lined with a row of single wax gland facets along the lateral, anterior, and spinal margins. Facets along the spinal margin indistinct, often more visible in exuviae (Fig. 8B) than intact nymphs (Fig. 8A). Each cephalic plate with a prominent round to oval wax gland with approximately 6–13 tightly packed facets, proximal to anterior row of facets. Ventral wax glands at base of antennae with approximately 3–4 facets. Antenna 3-segmented, segment III distinctly imbricated, length [n = 12, 0.055–0.062 (0.059) mm], approximately 3.8x its width at midpoint [n = 12, 0.013–0.018 (0.015) mm], and approximately 1.6x longer than segments I [n = 12, 0.017–0.022 (0.020) mm] and II [n = 12, 0.015–0.020 (0.018) mm] combined. Two primary rhinaria on segment III, one subapical and one approximately 1/2 the segment length from the apex, each with a small thumb-like projection. Several accessory rhinaria adjacent to subapical primary rhinarium. Processus terminalis with 5 setae, the apical seta length [*n* = 11, 0.028–0.040 (0.036) mm] approximately 3x the rest. Rostrum reaching past hind coxae with ultimate segment 0.8x as long [*n* = 9, 0.028–0.039 (0.034) mm] as width of segment III at midpoint [*n* = 9, 0.037–0.044 (0.041) mm]. Stylet length [*n* = 4, 0.630–0.773 (0.704) mm] approximately 2.0x body length.

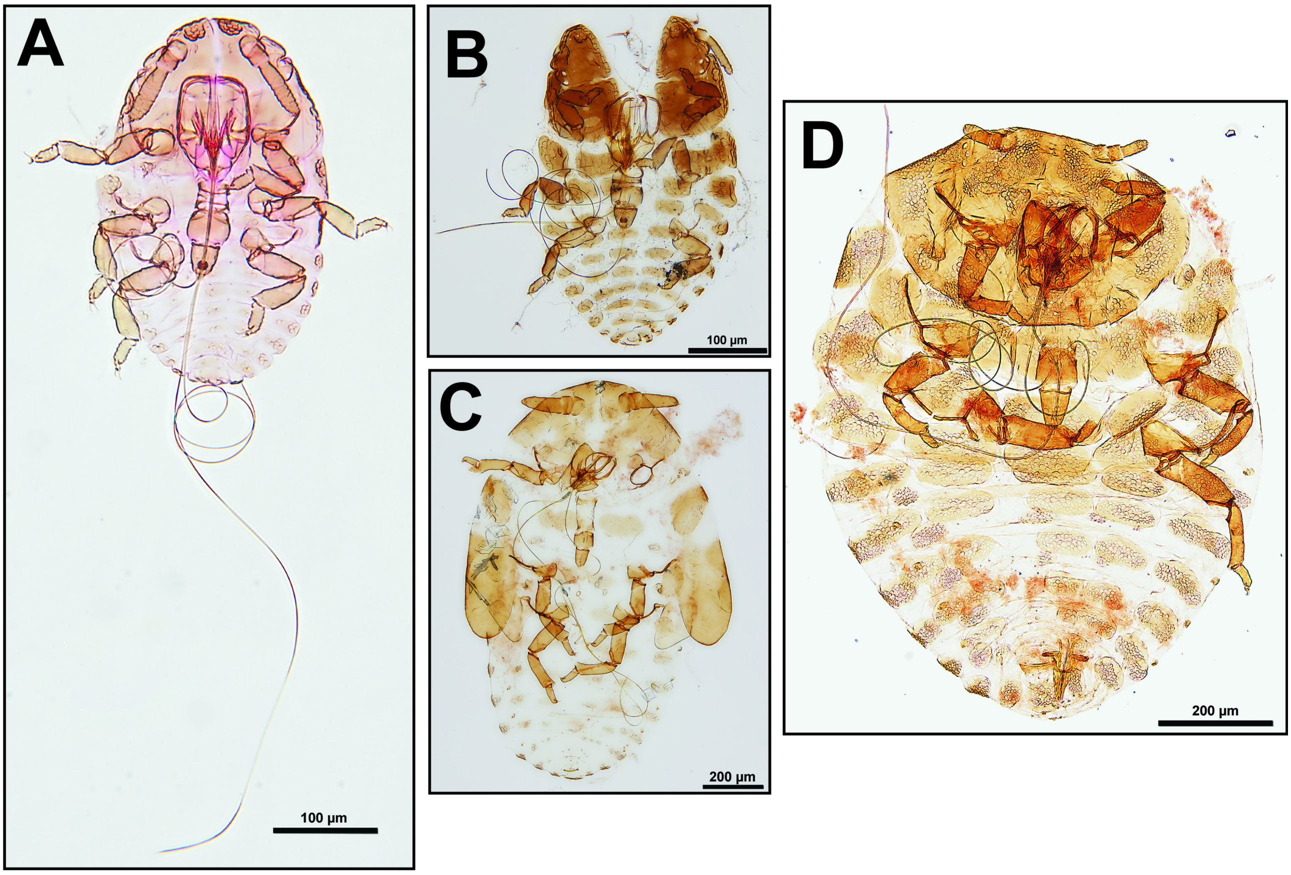

FIGURE 8. *Adelges* (*Annandina*) *lepsimon*. A—D. Exules: first instar (paratype, USNM) (A), first instar exuvium (paratype, USNM) (B), sexupara nymph (paratype, USNM) (C), adult (holotype, USNM) (D).

Coxae smooth. Femorotrochanters smooth to weakly imbricated, tibiae and second tarsal segments weakly imbricated. Pair of dorso-subapical setae on foreleg, one capitate seta approximately 2x longer than the other acuminate one. Pairs of subequal dorso-subapical capitate setae on mid- and hindlegs. Wax glands antero-lateral to mid- and hindcoxae with approximately 1–6 round to oval facets. Hind femorotrochanter length: n = 12, 0.046–0.054 (0.050) mm.

Each thoracic segment lined with a row of single wax gland facets along the lateral, margin, and a round to oval anterior cluster of approximately 2–13 wax gland facets, just proximal to lateral row. Meso- and metanotum with spinal and pleural plates, each plate with a single seta and a single row of 1–5 indistinct spinal and 0–5 lateral wax gland facets. Spinal and pleural plates of the mesothorax often fused. Metathoracic spinal plate sometimes with a central cluster of 1–5 wax gland facets. Abdominal segments I–V with separate lateral, pleural, and spinal wax plates, segment VI–VII with lateral and spinal plates, segment VIII with lateral plates, segment IX lacking plates. Abdominal segments I–VI dorso-spinal plates each with wax gland in the center consisting of a cluster of 1–4 facets. Abdominal segments I–III with pleural plates usually lacking wax gland facets. Abdominal segments IV–V with pleural plates with 1–3 wax facets. Abdominal segments I–VI with lateral plates each with 1–3 lateral facets and a small proximal wax gland with 1–5 facets. Abdominal spiracles minute, hardly visible. Pairs of small, ventro-spinal acuminate setae on abdominal segments I–VIII. Pair of dorso-lateral setae on abdominal segment VIII. Abdominal segment IX with two short acuminate dorsal setae anterior to anus, two longer acuminate ventral setae, and two long capitate setae at apex.

Adult exulis (Fig. 8D). Body length: n = 13, 0.764–1.251 (0.980) mm. Pronotum width: n = 14, 0.402–0.626 (0.523) mm. Body width: n = 13, 0.502–0.883 (0.726) mm. Dorsal wax glands generally on moderately to strongly sclerotized plates with numerous, up to more than 200, contiguous to nearly contiguous small round granular facets.

Head and pronotum with sclerotized plates completely fused into cephaloprothoracic shield with largely smooth surface that extends ventrally to surround the base of antennae. Head with very large anterior wax glands with a lateral area mesad to ocelli curling towards, and sometimes touching posterior cephalic wax glands. Pair of cephalic postero-lateral, oval or irregularly shaped wax glands with approximately 25–50 facets. Largest diameter of facets on head subequal to the diameter of the ocellus. Large ventral wax glands on head with approximately 60–110 small round facets on surface at base of antennae. Antenna 3-segmented, segment III [n = 13, 0.029–0.056 (0.041) mm] approximately 2.0x its width at midpoint [n = 13, 0.016–0.022 (0.020) mm], approximately 0.9x the length of segments I [n = 13, 0.016–0.033 (0.025) mm] and II [n = 13, 0.014–0.029 (0.020) mm] combined. Segment III with subapical primary rhinarium with a few adjacent accessory rhinaria. Processus terminalis with five or six stout setae. Rostrum reaching to anterior margin of hind coxae, with ultimate segment [n = 13, 0.041–0.091 (0.064) mm] 0.7x the width of segment III at midpoint [n = 13, 0.050–0.076 (0.063) mm].

Coxae, femorotrochanters, and tibiae smooth, with second tarsal segment weakly imbricated. Large wax glands antero-lateral to coxae with approximately 50–100 loosely packed facets. Hind femorotrochanter length: n = 13, 0.064–0.144 (0.104) mm.

Pronotum with very large lateral wax glands consisting of bands of up to 200 or more facets, and with postero-pleural and postero-spinal irregularly shaped wax glands with 20–70 facets. Meso- and metathoracic segments and abdominal segments I–V with spinal, pleural, and lateral wax glands, circular or elliptical with numerous tightly packed facets. Plates on meso- and metanotum sometimes fused or touching. Abdominal segments VI–VII with lateral and spinal wax glands, segment VIII with lateral wax glands. Abdominal segment IX with large post-anal wax gland. Abdominal segments II–VI with distinct ventral spiracles. Abdominal segments VIII and IX with numerous capitate setae. Ovipositor with gonapophyses [n = 11, 0.075–0.115 (0.094) mm] approximately 1.4x longer than width across apodemes [n = 11, 0.057–0.083 (0.067) mm].

Hosts and Distribution. *Tsuga dumosa* in Bhutan (Mongar, Wangdue Phodrang) (Fig. 9).

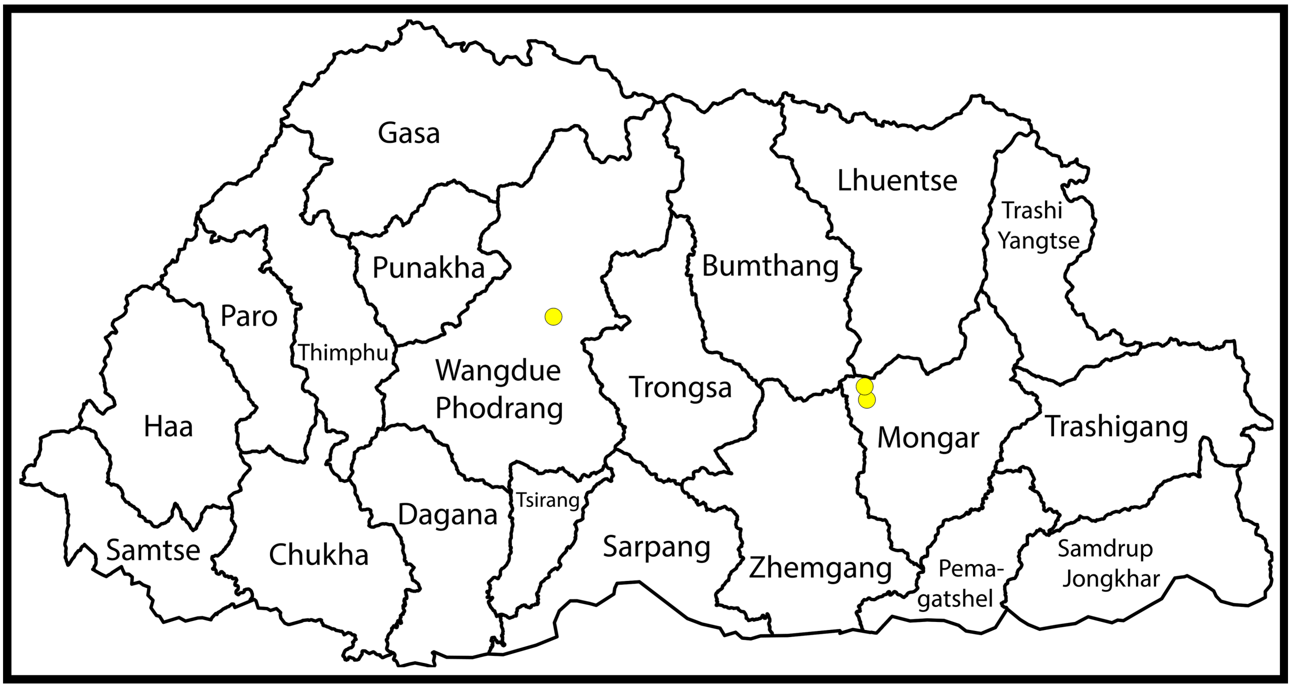

FIGURE 9. Map of Bhutan showing collection locations for *Adelges* (*Annandina*) *lepsimon.*

Remarks. *Adelges* (*An.*) *lepsimon* feeds between the needles on *Tsuga dumosa* twigs, in a similar fashion to *A.* (*An.*) *tsugae*, which feeds on *T. dumosa* and other *Tsuga* species (Havill *et al.* 2016). The two species were collected together at two sites on different trees, so distinguishing them in the field may be difficult. *Adelges* (*An.*) *lepsimon* was collected more rarely than *A.* (*An.*) *tsugae*, which was also collected in Bumthang, Paro, and Thimphu Districts. In addition to exules of *A.* (*An.*) *lepsimon*, we also collected sexupara nymphs with wing pads (Fig. 8C), so it is likely that this species migrates to *Picea* where it completes a holocycle.

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