



Zootaxa 3729 (1): 001–062
www.mapress.com/zootaxa/

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Monograph

ISSN 1175-5326 (print edition)

ZOOTAXA

ISSN 1175-5334 (online edition)

<http://dx.doi.org/10.11646/zootaxa.3729.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:CA0C1355-FF3E-4C67-8F48-544B2166AF2A>

ZOOTAXA

3729

Phylogeny of the tribe Archipini (Lepidoptera: Tortricidae: Tortricinae) and evolutionary correlates of novel secondary sexual structures

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Magnolia Press
Auckland, New Zealand

Accepted by J. Brown: 2 Sept. 2013; published: 25 Oct. 2013

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(*Zootaxa* 3729)

62 pp.; 30 cm.

25 Oct. 2013

ISBN 978-1-77557-288-6 (paperback)

ISBN 978-1-77557-289-3 (Online edition)

FIRST PUBLISHED IN 2013 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

<http://www.mapress.com/zootaxa/>

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Table of contents

Abstract	3
Material and methods	6
Results	18
Discussion	23
Conclusions	33
Acknowledgements	33
Literature cited	34
APPENDIX 1.	38
APPENDIX 2.	44
Additional References for Appendices 1 & 2	49
APPENDIX 3.	51
APPENDIX 4.	52
APPENDIX 5.	53
APPENDIX 6.	54
APPENDIX 7.	55
APPENDIX 8.	56
APPENDIX 9.	57
APPENDIX 10.	58
APPENDIX 11.	59
APPENDIX 12.	60

Abstract

We reconstructed a preliminary phylogeny for the economically important tribe Archipini (Lepidoptera: Tortricidae: Tortricinae) based on 135 exemplar species (including four outgroups) and a combined analyses of 28S rDNA and COI DNA using maximum parsimony, maximum likelihood, and Bayesian analyses. A summary tree was produced as the majority rule consensus tree by first assembling all clades that were present in more than 50% of analyses. Based on the results of the analyses, several taxonomic changes are suggested. After mapping secondary sexual characters (SSCs), host plant breadth, and geographic distribution onto the phylogeny, we examined correspondences among these traits using two-by-two χ^2 tests and ancestral character state reconstructions. Absence of SSCs was associated with decreased host plant breadth and colonization of the New World, but was not significantly associated with the presence of other SSCs. There is a strong likelihood of an Australasian origin for Archipini. We propose the synonymy of *Archebandemis* Mutuura with *Pandemis* Hübner (**new synonymy**); the synonymy of *Cudonigera* Obraztsov & Powell with *Choristoneura* Lederer (**new synonymy**); and elevation of *Anaphelia* Razowski, *Sacaphelia* Razowski, and *Zelotheres* Lederer to genera from subgenera of *Aphelia* Hübner (**revised status**). *Epiphyas* Turner, may be subordinate within *Clepsis* Guenée, but further study is needed to confirm this.

Key words: *Aphelia*, *Archebandemis*, *Choristoneura*, *Clepsis*, *Cudonigera*, *Epiphyas*, *Pandemis*

Introduction

The tortricid tribe Archipini includes many economically important species worldwide such as the smaller tea tortrix, *Adoxophyes honmai* Yasuda, 1998; the summer fruit tortrix, *Adoxophyes orana* (Fischer von Röslerstamm, 1834); the fruit tree leafroller, *Archips argyrospila* (Walker, 1863); the orange tortrix, *Argyrotaenia franciscana* (Walsingham, 1879); the spruce budworm, *Choristoneura fumiferana* (Clemens, 1865) species complex; the obliquebanded leafroller, *C. rosaceana* (Harris, 1841); the carnation worm, *Epichoristodes acerbella* (Walker, 1864); the light brown apple moth, *Epiphyas postvittana* (Walker, 1863); the greater tea tortrix, *Homona coffearia* (Nietner, 1861); the tea tortrix, *H. magnanima* Diakonoff, 1948; the green-headed leafrollers, *Planotortrix* spp.; and many others (Timm *et al.* 2010, Lee *et al.* 2005, Liu & Li 2002, Razowski 2002a, Freeman 1958). The tribe is found worldwide, although it has lower diversity in the Neotropics (Horak 1999). There are 187 genera and 1,709 species currently recognized (Baixeras *et al.* 2010), although this number is undoubtedly low since many undescribed species are known in collections and there has been limited collecting in large parts of the tropics (Razowski 2004). In Canada and the United States, there are 18 genera and 123 species (Pohl 2006).

Archipini were initially recognized by Pierce & Metcalfe (1922) based on the presence of an elongate signum and a bulbous capitulum in the female genitalia. However, several of the taxa placed in the tribe by Pierce and

Metcalf (1922) lacked this character, and their circumscription of the group was based solely on the British fauna. Common (1956) subsequently had difficulty applying Pierce and Metcalfe's (1922) tribal arrangement to the Australian tortricids, which led him to broaden Archipini to include several additional taxa lacking the signum and/or capitulum. Horak (1984, 1999) postulated that Common's concept of Archipini was polyphyletic and divided the tribe into three groups typified by *Archips*, *Clepsis*, and *Planotortrix*. Razowski (1987) briefly expanded the tribe to include the tribe Euliini but then removed the latter, as well as transferring taxa with a well sclerotized costa of the valve of the male genitalia into a new tribe, Ramapesiini (Razowski 1993). Jinbo (2000) conducted the only phylogenetic analysis of Archipini to date, based on morphology of the Japanese species, and found Ramapesiini to be paraphyletic to a monophyletic Archipini *s. s.* In our study we use Brown's (2005) concept of Archipini which includes the Ramapesiini. "*Dichelias*" *clarana* (Meyrick, 1881) is in quotation marks because it does not belong in that genus and is placed in "new genus 1" following Brown (2005). The authors disagree on the use of *Choristoneura freemani* Razowski, 2008a as a replacement name for the Nearctic species *C. occidentalis* Freeman, 1967; however, we chose to use it here to be consistent with Baixeras *et al.* (2010) with the knowledge that further study is needed to clarify the generic position of *C. occidentalis* (Walsingham, 1891).

Coexistence among closely related and ecologically similar species requires mechanisms that reduce gene flow and maintain species boundaries. Secondary sexual characters (SSCs) are specific pre-mating stimuli that are not directly involved in copulation (Savalli 2001). In most animals they are most obviously developed in males (Savalli 2001). These characters can serve as a prezygotic barrier, allowing closely related and ecologically equivalent species to live in sympatry while maintaining their genomic integrity (Lande 1981). Such divergence of SSCs has been proposed as an important mechanism in speciation (Parzer & Moczek 2008, Panhuis *et al.* 2001, Phelan & Baker 1987, Carson & Bryant 1979). However, SSCs can be energetically expensive (Møller & de Lope 1994), and it is reasonable to assume that they will tend to be lost when they are not needed as a pre-zygotic barrier between related species. If the latter is true, the loss of SSCs should potentially be associated with at least three different scenarios: 1) reduced ecological overlap among sympatric species due to physical separation despite sympatry (e.g. via a host plant shift or narrowing of host range as proposed by Phelan & Baker (1987)); 2) intraspecific SSC redundancy due to the evolution of novel structures that are presumably either less expensive to develop or more efficient as a prezygotic boundary; or 3) expansion into a habitat or geographic region unoccupied by other related species.

Archipini is an ideal group to examine these processes because it includes a mix of oligophagous and polyphagous species, a high frequency of apparent gains and losses of SSCs among its members, and a seemingly recent radiation into the New World, which is associated with relatively low generic diversity in North and South America.

Like ornamentation in male mammals and elaborate courtship displays in birds (Savalli 2001), SSCs in archipine moths probably function in contest competition or as signals. Chemical communication by males using close range pheromones are the most widespread signals in Lepidoptera and many structural modifications are known to be associated with the dissemination of these pheromones (Scoble 1992, Hallberg & Poppy 2003). In Tortricidae, the most widespread of these structures is the costal fold (CF) (Fig. 1), which is located near the base of the male dorsal forewing and conceals modified scent-disseminating scales (Brown & Miller 1983). In the few tortricid species that have been studied, there are one or two dense tufts of long scales, frequently referred to as "hair pencils," tucked underneath the fold and lying against an adjacent glanduliferous area of the wing. Microstructural features of these scales allow them to wick the gland product and subsequently disseminate it when the hair pencils are everted from the fold (Grant 1978). Structural variation within the CF can be found even within a genus. For example, *Archips argyrospila* (Walker, 1863) and *A. mortuana* (Kearfott, 1907) have a CF that curls in on itself, while *A. rosana* (Linnaeus, 1758) has one set of hair pencils that originates adjacent to glandular tissue (Grant 1978). An even more impressive modification can be found in *Cryptoptila australana* (Lewin, 1805) in which the fold conceals a broad expansion from the subcostal vein that forms a double pocket (Horak 1984). The overall size of the CF varies widely within the Archipini, ranging from a broad structure in *Adoxophyes negundana* (McDunnough, 1923) to a slender fold in *Archips rileyana* (Grote, 1868), and vestigial non-functional remnants that are open and lack associated glands as in *Choristoneura rosaceana* (Harris, 1841) (see Grant 1978) (Fig. 2).

Other potential gland-related SSCs are common among tortricids, although they tend to be more restricted in taxonomic breadth. These structures can be found in a variety of locations but most often occur on the antennae, thorax, hindlegs, forewing or hindwing surface, or various places on the pre-genitalic abdomen (Razowski 2008b). The male genitalia themselves often have elaborate ornamentation or scaling that suggests a pheromone dispensing role. However, such structures are much more difficult to examine, as most species have at least some scales or setae present on the genitalia, and normal genitalic preparations typically remove most deciduous scales (JJD *pers. obs.*).



FIGURES 1–2. Morphological characters of Archipini. 1. Male *Archips eleagnana* (McDunnough, 1923) with arrow indicating costal fold. CAN: AB: Kootenay Plains E. R.: 20 viii 2009. ©JJD. 2. Male *Choristoneura rosaceana* with arrow indicating vestigial costal fold. USA: MS: Delta N. F.: 01 vii 2008. ©JJD.

Although the exact function of SSCs in tortricids is poorly known due to limited histological study of only a few species of *Archips* (Grant 1978) and one of *Episimus* (Barth 1957), we can extrapolate their function from better studied and structurally similar SSCs in other moths where these structures deliver an indirect or direct mating stimulus through pheromone dissemination (Hallberg & Poppy 2003). For example, in *Epiphyas postvittana* (Walker, 1863), the male directs the costal fold towards the female's antennae as he rapidly fans his wings (Bartell 1977). Hair pencils likely serve a similar role in species such as *Grapholita molesta* (Busck, 1916), where the male reveals the hair pencils as a pre-mating stimulus (Cardé *et al.* 1975). It is also likely that the pheromones have varying functions, like enticing the female not to take flight or stimulating female abdominal extension (Scoble 1992).

The aim of this study is to develop a preliminary phylogeny of Archipini and determine whether divergences of novel SSCs are associated with other biological characteristics that implicate evolutionary tradeoffs. We examined specimens and literature sources for: 1) the presence of structures likely to function as SSCs, like the costal fold; 2) ecological overlap with other species, as indicated by similarity in larval host and geographic range; or 3) expansion and diversification into new geographic regions lacking their congeners. A phylogenetic framework was used to examine the relationships between novel SSCs and the CF, SSCs and host plant breadth, and SSCs and zoogeography. The phylogeny of Jinbo (2000) is not appropriate for this purpose since it examines only 20 genera and, due to relatively few parsimony informative characters, his bootstrap values are low. In this study we analyse 134 species in 33 genera representing all major zoogeographic regions except the Neotropics, using a phylogeny derived from up to 1542 bp of the mitochondrial COI gene and up to 902 bp of a nuclear gene, 28S rDNA. Our sampling includes 67% of species and all genera known from the Nearctic except for "*Durangarchips*" Powell. We then use our Archipini phylogeny to test whether: a) the presence of SSCs is linked to polyphagy (an indicator of greater opportunity for overlap of female calling locations (Young 1997)); b) existing SSCs are lost when novel SSCs evolve (as expected if there is redundancy between them); and c) SSCs are more likely to be lost after new areas like the Nearctic are colonized.

Material and methods

DNA was sequenced from 91 species including four outgroups; collection records are listed in Table 1. Ceracini, Cnephasiini, Sparganothini, and Tortricini were used as outgroup taxa, and *Epitymbia alaudana* Meyrick, 1881 was treated as an ingroup. Our sampling was guided by results from Zwick *et al.* (unpublished presentation at 2007 annual meeting of the Lepidopterists' Society, MS, USA) who showed the first three tribes as close sister taxa and the Epitymbiini as subordinate within the Archipini. All sequences are available on GenBank, while specimen vouchers are deposited in the Cornell University Insect Collection and extracted DNA is stored in the Sperling Lab at the University of Alberta. Published COI sequences were obtained from GenBank for 44 additional species and several unpublished sequences were generously shared by L. Lumley, A. Zwick, M. Horak, M. San Jose, and D. Rubinoff (Table 2).

For most specimens we removed two legs soon after the moths were killed and stored the legs in 95% ethanol at -20°C. Legs were removed later for a few specimens, either from specimens collected directly into ethanol or live frozen. DNA was extracted using QIAamp Mini Kits (Qiagen, Canada) and eluted in three steps into a 150 µl volume. The whole COI gene was sequenced because of its ease of amplification, phylogenetic utility, and widespread use across Lepidoptera (Caterino *et al.* 2000, Silva-Brandão *et al.* 2005), which allowed many published sequences to be used in this study (see refs. in Table 2). Attempts to also amplify EF-1α and CAD met with consistent difficulties in obtaining clean sequences. Consequently the D2 and D3 expansion regions of 28S rDNA were used instead, because of the greater ease of amplification of this gene region and its documented potential to show a stronger phylogenetic signal than COI for phylogenetically deeper nodes (Mardulyn & Whitfield 1999). PCR reactions for COI followed Lumley & Sperling (2010), except that 4 µl of DNA template was used. PCR reactions for 28S rDNA were similar but used 3 µl of MgCl₂ and cycle sequencing followed that of Wiegmann *et al.* (2000). Primers used in our study are listed in Table 3. PCR purification was performed either with a QIAquick PCR purification kit (Qiagen) or ExoSAP-IT (USB Corporation, Cleveland, OH), and sequencing was done with BigDye Terminator version 3.1 cycle sequencing (Applied Biosystems, Foster City, CA). Sequences were purified using ethanol precipitation and sequencing reactions were run on an ABI Prism 3730 DNA analyser of the Molecular Biology Facility at the University of Alberta Department of Biological Sciences.

TABLE 1. Specimens sequenced for this study.

Species	DNA #	Location	latitude / longitude	date	collectors	COI (bp)	Genbank numbers	
							28S (bp)	COI
<i>Adoxophyes negundana</i>	4567	Canada: AB: Lethbridge	49.689 -112.827	02 vi 2008	M. Vankosky	1516	JF703014	JF702925
<i>Ad. Orana</i>	4599	România: CT: Canarau Fetii	44.068 27.645	17 v 2009	JJD, A. Sandor	1542	JF703015	JF702926
<i>Aphelia alleniana</i>	2999	Canada: AB: Porcupine Hills	49.972 -114.087	31 vii 2007	JJD, <i>et al.</i>	1515	JF703016	JF702927
<i>Ap. ochreana</i>	4600	România: TL: Macim Mountains, Suluclu	45.234 28.194	14 v 2009	JJD, A. Sandor	1541	JF703017	JF702928
<i>Ap. Unitana</i>	6302	România: BV: Stațiunea Sâmbăta	45.674 24.791	22 v 2009	JJD, <i>et al.</i>	1516	JF703018	JF702929
<i>Archeopandemis coniferana</i>	4571	Canada: AB: EMEND	56.751 -118.330	11 vii 2007	E. Kamunya	1510	JF703021	JF702932
<i>Archips alberta</i>	2960	Canada: AB: Kootenay Plains Ecol. Res.	51.999 -116.496	27 vii 2006	JJD, B. C. Schmidt	1518	JF703019	JF702930
<i>Archips cerasivorana</i>	2970	Canada: AB: Waterton Lakes	49.056 -113.915	15 viii 2006	JJD, <i>et al.</i>	1521	JF703020	JF702931
<i>Archips elegana</i>	2914	Canada: AB: Kootenay Plains Ecol. Res.	52.003 -116.465	27 vii 2006	JJD, B. C. Schmidt	1542	JF703022	JF702933
<i>Archips fervidana</i>	3000	United States: AR: Crawford Co.: Ozark-St. Francis Nat. For.	35.702 -94.296	16 vi 2008	JJD, D. Lawrie	1533	JF703023	JF702934
<i>Archips negundana</i>	2912	Canada: AB: Edmonton	53.525 -113.492	20 vii 2006	JJD, A. Rose	1542	JF703024	JF702935
<i>Archips packardiana</i>	2947	Canada: AB: Jasper Nat. Pk., Jasper Lake	53.097 -118.003	27 vi 2006	B. C. Schmidt, G. Anweiler	1542	JF703025	JF702936
<i>Archips podana</i>	4557	Denmark: LFM: Mandemarle	54.967 12.491	14-17 vii 2007	O. Karsholt	1515	JF703026	JF702937
<i>Archips purpurana</i>	6306	Canada: AB: Blindloss	50.901 -110.294	22 vii 2008	JJD, B. Proshok	1541	JF703027	JF702938
<i>Archips rosana</i>	4563	Denmark: LFM: Mandemarle	54.967 12.491	14-17 vii 2007	O. Karsholt	1538	JF703028	JF702939
<i>Archips siriana</i>	2945	Canada: AB: Jasper Nat. Pk., The Palisades	52.963 -118.058	27 vi 2006	B. C. Schmidt, G. Anweiler	1492	JF703029	JF702940
<i>Archips xylosteana</i>	4559	Canada: NL: St. John's	47.575 -52.738	2006	B. C. Schmidt	1539	JF703030	JF702941
<i>Argyrotaenia alisellana</i>	2905	United States: VA: Fairfax Co.: Fairfax City	38.847 -77.295	31 v 2006	J. W. Brown	1542	JF703031	JF702942
<i>Arg. coloradana</i>	4501	United States: UT: Cache Nat. For.: Logan Canyon	41.780 -111.139	06 vii 2007	JJD, <i>et al.</i>	1542	JF703032	JF702943
<i>Arg. dorsalana</i>	4502	Canada: BC: Tranquille Ecol. Res.	50.755 -120.589	15 viii 2007	JJD	1519	JF703033	JF702944
<i>Arg. floridana</i>	6328	United States: FL: Marion Co.: Ocala Nat. For., Delancey Lake	29.427 -81.789	22 vi 2006	JJD, <i>et al.</i>	1542	JF703034	JF702945
<i>Arg. franciscana</i>	Afran13	United States: CA: Sonoma Co.: Bodega Bay Mar. Res.	38.306 -123.066	24 v 1996	B. Landry	-	Table 2	JF702946
<i>Arg. graceana</i>	4526	United States: CA: Ventura Co.: Los Padres Nat. For.: Mt. Pinos	34.812 -119.099	15 vii 2007	JJD, <i>et al.</i>	1542	JF703035	JF702947

TABLE 1. (Continued)

Species	DNA #	Location	latitude / longitude	date	collectors	Genbank numbers	
						COI	28S
<i>Arg. franciscana</i>	Afran13	United States: CA: Sonoma Co.: Bodega Bay Mar. Res.	38.306 -123.066	24 v 1996	B. Landry	Table 2	JF702946
<i>Arg. griseana</i>	4526	United States: CA: Ventura Co.: Los Padres Nat. For.: Mt. Pinos	34.812 -119.099	15 vii 2007	JJD, <i>et al.</i>	JF703035	JF702947
<i>Arg. kimballi</i>	2940	United States: FL: Baker Co.: Osceola Nat. For.	30.384 -82.331	18 vi 2006	JJD, <i>et al.</i>	JF703036	JF702948
<i>Arg. lautana</i>	4527	United States: CA: Ventura Co.: Los Padres Nat. For.: Mt. Pinos	34.812 -119.099	16 vii 2007	JJD, <i>et al.</i>	JF703037	JF702949
<i>Arg. jungiana</i>	6310	France: Mormoiron: near Mormoiron	44.090 5.235	17 vi 2009	T. M. Gilligan		899
<i>Arg. mariana</i>	4528	Canada: AB: Buck Lake	54.656 -112.522	31 v 2007	M. Schwarzfeld		900
<i>Arg. occuliana</i>	4529	Canada: AB: Jasper Nat. Pk., Jasper Lake	53.097 -118.003	27 vi 2006	B. C. Schmidt, G. Anweiler	JF703040	JF702952
<i>Arg. provana</i>	4530	United States: OR: Wasco Co.: Mt. Hood Nat. For.	45.232 -121.627	26 vii 2007	JJD, <i>et al.</i>	JF703041	JF702953
<i>Arg. quadrifasciana</i>	4585	Canada: AB: Bindloss	50.901 -110.294	23 vii 2008	JJD, B. Proshok		897
<i>Arg. quercifoliana</i>	2938	United States: VA: Fairfax Co.: Fairfax City	38.847 -77.295	03 vi 2006	J. W. Brown		828
<i>Arg. repertana</i>	2934	Canada: AB: Wagner Bog	53.565 -113.832	15 v 2006	JJD, <i>et al.</i>	JF703044	JF702956
<i>Arg. tabulana</i>	6308	United States: AR: Pulaski Co.: Little Rock	34.826 -92.459	16 vi 2008	JJD, <i>et al.</i>	JF703045	JF702957
<i>Arg. velutinana</i>	2909	United States: VA: Fairfax Co.: Fairfax City	38.847 -77.295	03 vi 2006	J. W. Brown		877
<i>Cacoecimorpha pronubana</i>	6329	Spain: Catalonia: Sant Fost de Campsentelles	41.515 2.235	1 vii 2009	T. Gilligan & V. Santo Montey	JF703047	JF702959
<i>Capta vulgana</i>	4554	Denmark: LFM: Mandemarke	54.967 12.491	01 vi 2007	O. Karsholt		845
<i>Choristoneura albaniana</i>	2948	Canada: AB: Jasper Nat. Pk., Jasper Lake	53.097 -118.003	27 vi 2006	B. C. Schmidt, G. Anweiler	JF703050	JF702962
<i>Ch. argentifasciata</i>	2942	United States: FL: Baker Co.: Osceola Nat. For.	30.384 -82.331	19 vi 2006	JJD, <i>et al.</i>	JF703051	JF702963
<i>Ch. biennis</i>	2616	Canada: AB: Peter Lougheed Prov. Pk.	50.618 -115.122	05 vii 2005	L. M. Lumley, A. Roe		898

.....continued on the next page

TABLE 1. (Continued)

Species	DNA #	Location	latitude / longitude	date	collectors	COI (bp)	28S (bp)	
							COI	28S
<i>Ch. parallela</i>	2941	United States: FL.: Baker Co.: Osceola Nat. For.	30.384 -82.331	19 vi 2006	JJD, <i>et al.</i>	1542	JF703054	JF702971
<i>Ch. pinus</i>	3568	Canada: AB: Redwater Nat. Area	53.937 -112.952	17-25 vii 2006	L. M. Lumley	-	Table 2	JF702972
<i>Ch. retiniana</i>	4835	United States: CA: Madera Co.: Bass Lake	37.505 -119.410	10 vii 2007	L. M. Lumley, <i>et al.</i>	-	Table 2	JF702973
<i>Ch. rosaceana</i>	2937	United States: VA: Fairfax Co.: George Washington Mem. Pkwy	38.817 -77.228	04 vi 2006	J. W. Brown	1542	JF703055	JF702974
<i>Ch. zapilata</i>	4533	Canada: AB: Pakowki Dunes	49.397 -110.875	16 viii 2006	JJD, <i>et al.</i>	1542	JF703056	JF702975
<i>Clepsis anderslaneyii</i>	6330	United States: AZ: Cochise Co.: SW Res. Sta., Chiricahua Mtns.	31.881 -109.207	9 viii 2010	J. W. Brown	1516	JF703057	JF702976
<i>Cl. clemensiana</i>	2913	Canada: AB: Edmonton	53.525 -113.492	23 vii 2006	JJD, A. Rose	1542	JF703058	JF702977
<i>Cl. consimilana</i>	6332	France: Massif des Maures: near La Londe-les-Maures	43.169 6.215	19 vi 2009	T. M. Gilligan	859	JF703059	JF702978
<i>Cl. ficana</i>	6315	United States: CA: Alameda Co.: Berkeley	37.872 -122.273	03 v 1995	J. A. Powell	1511	JF703060	JF702979
<i>Cl. melaleucana</i>	4534	Canada: AB: Edmonton	53.545 -113.434	15 vi 2007	G. Anweiler	1537	JF703061	JF702980
<i>Cl. penetralis</i>	4544	Canada: AB: Jasper Nat. Pk., The Palisades	52.963 -118.058	27 vi 2006	B. C. Schmidt, G. Anweiler	1541	JF703062	JF702981
<i>Cl. peritana</i>	2906	United States: VA: Fairfax Co.: Fairfax City	38.847 -77.295	31 v 2006	J. W. Brown	1540	JF703063	JF702982
<i>Cl. persicana</i>	2910	Canada: AB: Jasper Nat. Pk., The Palisades	52.963 -118.058	27 vi 2006	B. C. Schmidt, G. Anweiler	1542	JF703064	JF702983
<i>Cl. rurinana</i>	6317	Italia: LOM: Samerate	45.621 8.798	05 vi 2009	JJD, D. Lawrie	1519	JF703065	JF702984
<i>Cl. siciliana</i>	6318	Spain: CAS: Pobra de Benifassa, Latemaia Form del Vidre	40.669 0.212	25 vi 2009	T. M. Gilligan, <i>et al.</i>	859	JF703066	JF702985
<i>Cl. spectrana</i>	4558	Denmark: LFM: Mandemarke	54.967 12.491	07-13 vii 2007	O. Karsholt	1540	JF703067	JF702986
<i>Cl. virescana</i>	2956	Canada: AB: Waterton Lakes Nat. Pk., Bellevue Hill	49.099 -113.905	15 viii 2006	JJD, <i>et al.</i>	1521	JF703068	JF702987
<i>Cudonigera houstonana</i>	4546	United States: AR: Logan Co.: Ozark-St. Francis Nat. For.	35.193 -93.645	19 vi 2008	JJD, <i>et al.</i>	1514	JF703069	JF702988
<i>Dichelia histriana</i>	4556	Denmark: LFM: Mandemarke	54.967 12.491	27-28 vii 2007	O. Karsholt	1534	JF703070	JF702989
<i>Diedra intermontana</i>	4548	United States: UT: Lander Co.: Toiyabe Nat. For.	39.225 -117.139	08 vii 2007	JJD, <i>et al.</i>	1542	JF703071	JF702990

TABLE 1. (Continued)

Species	DNA #	Location	latitude / longitude	date	collectors	COI (bp)	Genbank numbers	
							COI	28S
<i>Epagoge grotiana</i>	4555	Denmark: LFM: Mandemarle	54.967 12.491	07-13 vii 2007	O. Karsholt	1542	JF703074	JF702993
<i>Epiphyas ashworthana</i>	6320	Australia	-		T. Gilligan	1541	JF703075	JF702994
<i>Epi. caryotis</i>	6321	Australia	-		T. Gilligan	1541	JF703076	JF702995
<i>Epi. postvittana</i>	6333	United States: CA: Alameda Co.: Berkeley	37.872 -122.273	10-18 v 2010	J. A. Powell	1541	JF703077	JF702996
<i>Lozotaenia hesperia</i>	2949	Canada: AB: Jasper Nat. Pk., Jasper Lake	53.097 -118.003	27 vi 2006	B. C. Schmidt, G. Anweiler	1531	JF703079	JF702998
<i>Lozotaeniodes cupressana</i>	6323	Spain: CAS: Pobl. de Benifassa, Latemaia Form del Vidre	40.669 0.212	24 vi 2009	T. M. Gilligan, et al.	1541	JF703078	JF702997
<i>Pandemis canadana</i>	2911	Canada: AB: Edmonton	53.545 -113.434	30 vii 2006	G. Anweiler	1542	JF703080	JF702999
<i>Pa. cerasana</i>	4539	Denmark: LFM: Mandemarle	54.967 12.491	09 vi 2007	O. Karsholt	1542	JF703081	JF703000
<i>Pa. cinnamomeana</i>	4561	Denmark: LFM: Mandemarle	54.967 12.491	07-13 vii 2007	O. Karsholt	1540	JF703082	JF703001
<i>Pa. corylana</i>	4594	Italia: LOM: Samarate	45.621 8.798	05 vi 2009	JJD, D. Lawrie	1542	JF703083	JF703002
<i>Pa. dumetana</i>	4553	Denmark: LFM: Mandemarle	54.967 12.491	07-13 vii 2007	O. Karsholt	1542	JF703084	JF703003
<i>Pa. heparana</i>	4590	România: GJ: Cheile Sohodolului	45.139 23.139	01 vi 2009	JJD, D. Lawrie	1542	JF703085	JF703004
<i>Pa. lamprosana</i>	4573	United States: MD: Prince George's Co.: Patuxent W. R.	39.027 -76.798	xii 1997	J. A. Powell	1538	JF703086	JF703005
<i>Pa. limitata</i>	2907	United States: VA: Fairfax Co.: Fairfax City	38.847 -77.295	31 v 2006	J. W. Brown	1542	JF703087	JF703006
<i>Pa. pyrusana</i>	4551	United States: CA: Modoc Co.: Modoc Nat. For.	41.519 -120.233	23 vii 2007	JJD, et al.	1541	JF703088	JF703007
<i>Ptycholoma lecheana</i>	4536	Denmark: NEZ: Copenhagen	55.676 12.568	31 v-06 vi 2007	O. Karsholt	1542	JF703090	JF703009
<i>Ptycholomoides aeriferana</i>	4564	Denmark: LFM: Mandemarle	54.967 12.491	25-26 vii 2007	O. Karsholt	1512	JF703089	JF703008
<i>Syndemis afflictana</i>	2933	Canada: AB: Dunvegan Prov. Pk.	55.926 -118.594	10 v 2006	JJD, et al.	1541	JF703092	JF703011
<i>Xenotemma pallorana</i>	4547	Canada: AB: Pakowki Dunes	49.397 -110.875	08 vii 2008	JJD, A. Rose	1541	JF703093	JF703012

TABLE 2. Sequences used in this study from GenBank and other researchers.

Species	GenBank haplotype number	source	COI (bp)	28S (bp)
<i>Acropolitis hedista</i>	KC315441	Zwick, Sperling, & Horak <i>unpublished</i>	1536	901
<i>Adoxophyes furcatana</i>	GU089610	Hebert, <i>et al.</i> 2010	658	-
<i>Adoxophyes honmai</i>	DQ073916	Lee, <i>et al.</i> 2006	1542	-
<i>Adoxophyes</i> sp. nr. <i>marmarogodes</i>	EF432743	Hulcr, <i>et al.</i> 2007	658	-
<i>Adoxophyes</i> sp. nr. <i>orana</i>	FJ499909	Craft, <i>et al.</i> 2010	658	-
<i>Adoxophyes thoracica</i>	FJ499942	Craft, <i>et al.</i> 2010	658	-
<i>Aphelia paleana</i>	GU828404	Mutanen, <i>et al.</i> 2010	803	-
<i>Archips argyrospila</i>	AF308931	Kruse & Sperling 2001	1536	-
<i>Archips fuscocupreana</i>	AF441272	Kruse & Sperling 2002	820	-
<i>Archips georgiana</i>	AF441275	Kruse & Sperling 2002	820	-
<i>Archips goyerana</i>	AF309509	Kruse & Sperling 2001	820	-
<i>Archips grisea</i>	AF441277	Kruse & Sperling 2002	820	-
<i>Archips infumatana</i>	AF441280	Kruse & Sperling 2002	820	-
<i>Archips magnoliana</i>	AF441276	Kruse & Sperling 2002	820	-
<i>Archips nigriplagana</i>	AF309510	Kruse & Sperling 2001	820	-
<i>Archips rileyana</i>	AF441281	Kruse & Sperling 2002	820	-
<i>Archips semiferana</i>	AF441273	Kruse & Sperling 2002	820	-
<i>Argyrotaenia franciscana</i>	AF093681	Landry, <i>et al.</i> 1999	1536	-
<i>Argyrotaenia juglandana</i>	GU089664	Hebert, <i>et al.</i> 2010	658	-
<i>Argyrotaenia niscana</i>	AF309513	Landry, <i>et al.</i> 1999	799	-
<i>Argyrotaenia pinatubana</i>	GU096226	Hebert, <i>et al.</i> 2010	659	-
<i>Choristoneura biennis</i>	DQ792587	Lumley & Sperling 2010	1536	-
<i>Choristoneura freemani</i>	L19094	Sperling, <i>et al.</i> 1994	1536	-
<i>Choristoneura fumiferana</i>	GQ890278	Lumley & Sperling 2010	1542	-
<i>Choristoneura murinana</i>	GQ890294	Lumley & Sperling 2010	1542	-
<i>Choristoneura orae</i>	DQ792586	Roe & Sperling 2007	1536	-
<i>Choristoneura pinus</i>	L19095	Sperling, <i>et al.</i> 1994	1536	-
<i>Choristoneura retiniana</i>	HM223218	Lumley & Sperling 2011	1536	-
<i>Clepsis listerana</i>	GU096279	Hebert, <i>et al.</i> 2010	658	-
<i>Clepsis moeschleriana</i>	GU096722	Hebert, <i>et al.</i> 2010	658	-
<i>Cryptoptila australana</i>	KC315447	Zwick, Sperling, & Horak <i>unpublished</i>	1536	849
<i>Ctenopseustis filicis</i>	AF016466	Newcomb & Gleeson 1998	472	-
<i>Ctenopseustis fraterna</i>	AF016467	Newcomb & Gleeson 1998	472	-
<i>Ctenopseustis herana</i>	AF016468	Newcomb & Gleeson 1998	472	-
<i>Ctenopseustis obliquana</i>	AF016481	Newcomb & Gleeson 1998	472	-
<i>Ctenopseustis servana</i>	AF016471	Newcomb & Gleeson 1998	472	-
" <i>Dichelia</i> " <i>clarana</i>	KC315449	Zwick, Sperling, & Horak <i>unpublished</i>	1530	896
<i>Epichoristodes acerbella</i>	EU031651	Timm, <i>et al.</i> 2010	429	-
<i>Epitymbia alaudana</i>	KC315453	Zwick, Sperling, & Horak <i>unpublished</i>	1536	878
<i>Homona aestivana</i>	EF070743	Hulcr, <i>et al.</i> 2007	658	-

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TABLE 2. (Continued)

Species	GenBank haplotype number	source	COI (bp)	28S (bp)
<i>Homona auriga</i>	EF070825	Hulcr, <i>et al.</i> 2007	658	-
<i>Homona mermerodes</i>	EF070749	Hulcr, <i>et al.</i> 2007	661	-
<i>Homona salaconis</i>	GU440205	Miller, <i>et al.</i> 2010	658	-
<i>Homona spargotis</i>	EF070839	Hulcr, <i>et al.</i> 2007	658	-
<i>Homona trachyptera</i>	EF070863	Hulcr, <i>et al.</i> 2007	466	-
<i>Leucotenes coprosmae</i>	AF016473	Newcomb & Gleeson 1998	472	-
<i>Planotortrix avicenniae</i>	AF016474	Newcomb & Gleeson 1998	472	-
<i>Planotortrix excessana</i>	AF016475	Newcomb & Gleeson 1998	472	-
<i>Planotortrix flammea</i>	AF016476	Newcomb & Gleeson 1998	472	-
<i>Planotortrix notophaea</i>	AF016477	Newcomb & Gleeson 1998	472	-
<i>Planotortrix octo</i>	AF016478	Newcomb & Gleeson 1998	472	-
<i>Planotortrix octoides</i>	AF016479	Newcomb & Gleeson 1998	472	-
<i>Planotortrix puffini</i>	AF016480	Newcomb & Gleeson 1998	472	-
<i>Syndemis musculana</i>	-	San Jose & Rubinoff <i>unpublished</i>	1483	-
<i>Thrincochora lignigerana</i>	GU828783	Mutanen, <i>et al.</i> 2010	670	-
<i>Xenothictis gnetivora</i>	AY313944	Brown, <i>et al.</i> 2003	639	-

TABLE 3. Primers used in this study.

	primer name	sequence	source
COI	Jerry	CAACATTTATTTTGATTTTTTGG	Simon, <i>et al.</i> 1994
	Pat2	TCCATTACATATAATCTGCCATATTAG	Sperling, <i>et al.</i> 1994
	K525	ACTGTAAATATATGATGAGCTCA	Simon, <i>et al.</i> 1994
	K698	TACAATTTATCGCCTAAACTTCAGCC	Sperling, <i>et al.</i> 1994
28S rDNA	28SD2fwtort	ACGYGCACGCGTTCWTAC	Sperling, <i>unpublished</i>
	28SD2rctort	GACTCCTTGGTCCGTTTC	Sperling, <i>unpublished</i>
	A1	TCKGKTKTTCAAGACGGGGTC	Whiting, <i>et al.</i> 1997
	A335	TCGGARGGAACCAGCTACTA	Whiting, <i>et al.</i> 1997
	D2R	TTGGTCCGTGTTTCAAGACGG	Campbell, <i>et al.</i> 1994
	S1	GACCCGTCTTGAAMCAMGGA	Whiting, <i>et al.</i> 1997
	S3660	GAGAGTTMAASAGTACGTGAAAC	Dowton & Austin, 1998
	WF&LD2F	GTGGGTGGTAAACTCCATCTAAG	Zwick, <i>unpublished</i>

Chromatograms were examined with SeqMan Pro version 7.2.0 (DNASTAR) and since indels were minimal, sequences were easily aligned by eye in Mesquite version 2.73 (Maddison & Maddison 2010). Because each different phylogenetic algorithm has its own strengths and weaknesses (Felsenstein 2004), we used multiple analyses employing maximum parsimony, maximum likelihood, and Bayesian methods. PAUP* 4.0 (Swofford 2003) was employed for maximum parsimony analyses using default settings. Likelihood analyses were carried out using Garli (Zwickl 2006) with default settings and the GTR + I + G model of evolution as determined by Modeltest (Posada & Crandall 1998). MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) was used for Bayesian analyses, with default settings as determined by MrModeltest (Nylander 2004). Two sets of 14 million generations were sampled at a frequency of 1000, except for the 28S rDNA analyses which ran for 10 million generations. Indels were treated as 5th characters in PAUP*, and as missing data in Garli and Mr. Bayes. All three analyses were conducted for COI, 28S rDNA, and combined COI + 28S rDNA datasets.

The resulting trees were condensed into one tree for further analyses based on support and topological concordance between analyses. This summary tree was produced as the majority rule consensus tree by first assembling all clades that were present in more than 50% of analyses. Then, in the few cases where conflicting clades occurred in equal frequency, morphology was used as an additional source of information to select the clade. The morphological characters and clades that were chosen conformed to previous phylogenetic hypotheses of the relationships of the genera and species groups in question; all are justified and discussed in greater detail in Appendix 2. In general, both the number of morphological characters and an informal assessment of their evolutionary lability were considered in judging whether these characters justified support for a particular topology. In addition, we favored established hypotheses of relationship in order to minimize taxonomic disruption.

Our approach to integrating different molecular and morphological sources of evidence to produce a summary tree is philosophically Bayesian, in that hypotheses are sequentially evaluated and adjusted using new evidence. The currently more common phylogenetic practice of using a single combined analysis to provide the best tree-like summary of a character matrix is more compatible to a frequentist approach. This latter approach is vulnerable to the validity of a variety of assumptions about character distributions, such as the equality of support from different character types that have been fitted to a common, procrustean grid. Our use of a more traditional mode of integrating distinct kinds of evidence is itself vulnerable to the confining influence of prior hypotheses; nonetheless, we use it in the spirit of providing the most evidence-rich hypothesis currently available for a group still at the early stages of phylogenetic exploration.

The majority of non-molecular characters (Table 4) were recorded as binary variables to facilitate analyses. Geographic distribution was determined by examining native ranges for individual species from published literature (Appendix 1). Based on the previous hypothesis of Horak (1999), these taxa were divided into three unordered categories (0=New World, 1=Old World, and 2=Australasian) to examine the overall zoogeographic trends. To determine the correlation between radiation into new regions and SSCs, the data were further broken down into binary data of New World and Old World to facilitate analyses. The radiation from Australasia to the rest of the Old World was not examined due to poor generic coverage (19% of Australasian genera) compared to the Nearctic coverage (93% of genera).

TABLE 4. Non-molecular characters used in analyses from specimens examined and from the literature. ? = missing data; for zoogeography 0 = New World, 1 = Old World, 2 = Australasian; for hosts 0 = monophagous/oligophagous, 1 = polyphagous; for all others 0 = absent, 1 = present; for specimen source L = literature, S = specimen.

species	zoogeography	hosts	costal fold	antennal notch	anterior thoracic scale tufts	coxal hair pencil	hindwing pouch	basal abdominal scales	pregenital sternite modification	specimen source
<i>Acropolitis hedista</i>	2	1	1	?	?	?	0	0	?	L
<i>Adoxophyes furcatana</i>	0	0	1	0	0	0	0	0	0	S
<i>Adoxophyes honmai</i>	1	0	1	0	?	?	0	0	0	L
<i>Adoxophyes near marmaryodes</i>	2	?	?	?	?	?	0	0	0	L
<i>Adoxophyes near orana</i>	1	?	?	?	?	?	0	0	0	L
<i>Adoxophyes negundana</i>	0	0	1	0	0	0	0	0	0	S
<i>Adoxophyes orana</i>	1	1	1	0	0	0	0	0	0	S
<i>Adoxophyes thoracica</i>	2	?	1	?	?	?	0	0	0	L

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TABLE 4. (Continued)

species	zoogeography	hosts	costal fold	antennal notch	anterior thoracic scale tufts	coxal hair pencil	hindwing pouch	basal abdominal scales	pregenital sternite modification	specimen source
<i>Aphelia alleniana</i>	0	1	0	0	0	0	0	0	0	S
<i>Aphelia ochreana</i>	1	0	0	0	0	0	0	0	0	S
<i>Aphelia paleana</i>	1	0	0	?	?	?	0	0	0	L
<i>Aphelia unitana</i>	1	0	0	0	0	0	0	0	0	S
<i>Archepandemis coniferana</i>	0	0	0	0	0	?	0	0	0	L
<i>Archips alberta</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips argyrospila</i>	0	1	1	0	0	0	0	0	0	S
<i>Archips cerasivorana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips eleagnana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips fervidana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips fuscocupreana</i>	1	1	1	0	0	?	0	0	0	L
<i>Archips georgiana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips goyerana</i>	0	0	1	0	0	?	0	0	0	L
<i>Archips grisea</i>	0	1	1	0	0	0	0	0	0	S
<i>Archips infumatana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips magnoliana</i>	0	0	1	0	0	?	0	0	0	L
<i>Archips negundana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips nigriplagana</i>	0	?	1	0	0	?	0	0	0	L
<i>Archips packardiana</i>	0	0	0	0	0	0	0	0	0	S
<i>Archips podana</i>	1	1	1	0	0	0	0	0	0	S
<i>Archips purpurana</i>	0	1	1	0	0	0	0	0	0	S
<i>Archips rileyana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips rosana</i>	1	1	1	0	0	0	0	0	0	S
<i>Archips semiferana</i>	0	1	1	0	0	0	0	0	0	S
<i>Archips striana</i>	0	0	1	0	0	0	0	0	0	S
<i>Archips xylosteanana</i>	1	1	1	0	0	0	0	0	0	S
<i>Argyrotaenia alisellana</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia coloradana</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia dorsalana</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia floridana</i>	0	?	0	0	0	0	0	0	0	S
<i>Argyrotaenia franciscana</i>	0	1	0	0	?	0	0	0	0	S
<i>Argyrotaenia graceana</i>	0	?	0	0	0	0	0	0	0	S
<i>Argyrotaenia juglandana</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia kimballi</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia lautana</i>	0	0	0	0	0	0	0	0	0	S

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TABLE 4. (Continued)

species	zoogeography	hosts	costal fold	antennal notch	anterior thoracic scale tufts	coxal hair pencil	hindwing pouch	basal abdominal scales	pregenital sternite modification	specimen source
<i>Argyrotaenia ljugiana</i>	1	1	0	0	0	0	0	0	0	S
<i>Argyrotaenia mariana</i>	0	1	0	0	0	0	0	0	0	S
<i>Argyrotaenia niscana</i>	0	0	0	0	0	?	0	0	0	L
<i>Argyrotaenia occultana</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia pinatubana</i>	0	0	0	0	0	?	0	0	0	S
<i>Argyrotaenia provana</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia quadrifasciana</i>	0	0	0	0	?	0	0	0	0	S
<i>Argyrotaenia quercifoliata</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia repertana</i>	0	1	0	0	?	0	0	0	0	S
<i>Argyrotaenia tabulana</i>	0	0	0	0	0	0	0	0	0	S
<i>Argyrotaenia velutinana</i>	0	1	0	0	0	0	0	0	0	S
<i>Cacoecimorpha pronubana</i>	1	1	0	0	0	0	0	0	?	S
<i>Capua vulgana</i>	1	0	1	0	?	0	0	0	0	L
<i>Choristoneura albaniana</i>	1	0	0	0	0	0	0	0	0	S
<i>Choristoneura argentifasciata</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura biennis</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura conflictana</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura freemani</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura fumiferana</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura hebenstreitella</i>	1	1	0	?	?	?	0	0	0	L
<i>Choristoneura murinana</i>	1	0	0	?	?	?	0	0	0	L
<i>Choristoneura orae</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura parallela</i>	0	1	0	0	0	0	0	0	0	S
<i>Choristoneura pinus</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura retiniana</i>	0	0	0	0	0	0	0	0	0	S
<i>Choristoneura rosaceana</i>	0	1	0	0	0	0	0	0	0	S
<i>Choristoneura zapulata</i>	0	1	0	0	0	0	0	0	0	S
<i>Clepsis anderslaneyii</i>	0	?	1	0	0	0	0	0	0	S
<i>Clepsis clemensiana</i>	0	1	1	0	0	0	0	0	0	S
<i>Clepsis consimilana</i>	1	1	1	0	0	0	0	0	0	S
<i>Clepsis fucana</i>	0	1	0	?	?	?	0	0	0	L
<i>Clepsis listerana</i>	0	?	0	0	0	?	0	0	0	L
<i>Clepsis melaleucana</i>	0	1	1	0	0	0	0	0	0	S
<i>Clepsis moeschleriana</i>	1	?	0	?	?	?	0	0	0	L
<i>Clepsis penetralis</i>	0	?	0	0	0	0	0	0	0	S

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TABLE 4. (Continued)

species	zoogeography	hosts	costal fold	antennal notch	anterior thoracic scale tufts	coxal hair pencil	hindwing pouch	basal abdominal scales	pregenital sternite modification	specimen source
<i>Clepsis peritana</i>	0	1	0	0	0	0	0	0	0	S
<i>Clepsis persicana</i>	0	1	1	0	0	0	0	0	0	S
<i>Clepsis rurinana</i>	1	1	1	0	0	0	0	0	0	S
<i>Clepsis siciliana</i>	1	?	1	0	0	0	0	0	0	S
<i>Clepsis spectrana</i>	1	1	1	?	?	?	0	0	0	L
<i>Clepsis virescans</i>	0	0	1	0	0	0	0	0	0	S
<i>Cryptoptila australana</i>	2	1	1	?	0	?	0	0	?	L
<i>Ctenopseustis filicis</i>	2	0	1	?	?	?	0	0	0	L
<i>Ctenopseustis fraterna</i>	2	0	1	?	?	?	0	0	0	L
<i>Ctenopseustis herana</i>	2	1	1	?	?	?	0	0	0	L
<i>Ctenopseustis obliquana</i>	2	1	1	?	0	?	0	0	0	L
<i>Ctenopseustis servana</i>	2	1	1	?	?	?	0	0	0	L
<i>Cudonigera houstonana</i>	0	0	0	0	0	0	0	0	0	S
<i>Dichelia histrionana</i>	1	0	1	0	1	?	0	0	0	L
" <i>Dichelia</i> " <i>clarana</i>	2	?	1	?	?	?	0	0	?	L
<i>Diedra intermontana</i>	0	0	0	0	0	0	0	0	0	S
<i>Ditula angustiorana</i>	1	1	1	0	0	0	0	0	0	S
<i>Epagoge grotiana</i>	1	1	0	0	0	?	0	0	?	L
<i>Epichoristodes acerbella</i>	1	1	0	?	0	?	0	0	?	L
<i>Epiphyas ashworthana</i>	2	0	1	0	0	?	0	0	0	L
<i>Epiphyas caryotis</i>	2	1	?	?	?	?	0	0	0	L
<i>Epiphyas postvittana</i>	2	1	1	0	0	0	0	0	0	S
<i>Epitymbia alaudana</i>	2	0	1	1	0	?	1	0	?	L
<i>Homona aestivana</i>	2	1	0	?	0	?	0	0	?	L
<i>Homona auriga</i>	2	?	?	?	?	?	0	0	?	L
<i>Homona mermerodes</i>	2	1	?	?	?	?	0	0	?	L
<i>Homona salaonis</i>	1	1	0	0	0	?	0	0	?	L
<i>Homona spargotis</i>	2	1	?	?	?	?	0	0	?	L
<i>Homona trachyptera</i>	2	1	1	?	?	?	0	0	?	L
<i>Leucotenes coprosmae</i>	2	0	0	?	?	?	0	0	?	L
<i>Lozotaenia hesperia</i>	0	?	0	0	0	1	0	0	0	S
<i>Lozotaeniodes cupressana</i>	1	0	0	0	0	0	0	0	0	S
<i>Pandemis canadana</i>	0	1	0	1	0	0	0	1	1	S
<i>Pandemis cerasana</i>	1	1	0	1	0	0	0	1	1	S
<i>Pandemis cinnamomeana</i>	1	1	0	1	0	0	0	1	1	S

.....continued on the next page

TABLE 4. (Continued)

species	zoogeography	hosts	costal fold	antennal notch	anterior thoracic scale tufts	coxal hair pencil	hindwing pouch	basal abdominal scales	pregenital sternite modification	specimen source
<i>Pandemis corylana</i>	1	1	0	1	0	0	0	1	1	S
<i>Pandemis dumetana</i>	1	1	0	0	0	?	0	1	1	L
<i>Pandemis heparana</i>	1	1	0	1	0	0	0	1	1	S
<i>Pandemis lamprosana</i>	0	1	0	1	0	0	0	0	1	S
<i>Pandemis limitata</i>	0	1	0	1	0	0	0	1	1	S
<i>Pandemis pyrusana</i>	0	1	0	1	0	0	0	1	1	S
<i>Planotortrix avicenniae</i>	2	0	1	?	?	?	0	0	?	L
<i>Planotortrix excessana</i>	2	1	1	0	0	?	0	0	?	L
<i>Planotortrix flammea</i>	2	0	1	?	?	?	0	0	?	L
<i>Planotortrix notophaea</i>	2	1	1	?	?	?	0	0	?	L
<i>Planotortrix octo</i>	2	1	1	?	?	?	0	0	?	L
<i>Planotortrix octoides</i>	2	1	1	?	?	?	0	0	?	L
<i>Planotortrix puffini</i>	2	0	1	?	?	?	0	0	?	L
<i>Ptycholoma lecheana</i>	1	1	1	0	0	0	0	0	0	S
<i>Ptycholomoides aeriferana</i>	1	0	1	0	0	?	0	0	?	L
<i>Syndemis afflictana</i>	0	1	1	0	1	0	0	0	0	S
<i>Syndemis musculana</i>	1	1	1	0	1	0	0	0	0	S
<i>Thrincoptera lignigerana</i>	2	0	1	0	0	?	0	0	?	L
<i>Xenotemna pallorana</i>	0	1	0	0	0	0	0	0	?	S

Host plant breadth was determined from the tortricid host plant database of Brown *et al.* (2008), and supplemented by Prentice (1965) and Dugdale (1990). Species were judged to be monophagous or oligophagous (0) if they have been recorded from two or fewer plant families as primary hosts, or polyphagous (1) if they were regularly recorded from three or more plant families.

Presence (1) or absence (0) of the costal fold and other SSCs was determined by examining between one and five male specimens and at least one female. Data were derived from examination of specimens in the personal collection of JJD or the published literature (Brown *et al.* 2003, Diakonoff 1941a, Dugdale 1990, Franclemont 1986, Green & Dugdale 1982, Hulcr *et al.* 2007, Jinbo 2000, Lee *et al.* 2005, Mutuura 1978, Newcomb & Gleason 1998, Obraztsov 1961, Powell 1962, 1964, Razowski 1977, 1978, 1981, 1987, 2002a) (Table 4). All SSCs were considered to be novel structures except for the CF, which may be pleisiomorphic for Tortricidae (Horak 1984). Specimens were examined under a Wild Heerbrugg dissecting microscope at 25X and 50X power to look for external SSCs. For abdominal characters, the abdomen was removed and dissections were prepared as described by Brown & Powell (1992) with diluted chlorazol black as a stain. The entire pelt and genital capsule were then examined in glycerol under the same dissecting microscope at 50X power.

Whole specimens were photographed inside an Aristo DA-10 light box with a Canon G11 digital camera with an external Canon Speedlite 270EX attached by TTL cable. External characters were photographed with a Nikon Coolpix 8400 camera mounted on an Olympus SZX16 dissecting microscope with illumination from an Olympus LG-PS2 light source. Images were stacked and assembled in CombineZP (Hadley 2010). Genitalic and abdominal

characters were photographed using the previous system in a single shot, and the specimens were mounted in glycerol on a slide under a coverslip.

The character correlation of 1) the costal fold versus combined novel SSCs (where presence of any novel SSCs is coded as present), 2) host breadth versus total SSCs, and 3) zoogeography versus SSCs, was tabulated comparing correlated changes within clades based on ancestral character state reconstructions. Ambiguous character state reconstructions were treated conservatively to give the least number of changes. Polytomies were treated as independent changes. For example, in comparing the loss of the CF versus the evolution of novel SSCs, clade 73 would support the null hypothesis that there is no correlation, while clade 76 would support the alternate hypothesis that novel SSCs evolve more frequently when the CF is lost as happens with the *Lozotaenia* Stephens lineage. Pagel's (1994) test of correlated discrete character evolution was not appropriate to use since the tree had several polytomies. Sample sizes were too small to run a χ^2 contingency analysis. To test for total correlation of the previous character pairs in terminal taxa, a two-by-two χ^2 test was conducted with the summary data. Zoogeographic origins were mapped onto the summary tree using ancestral character state reconstruction under a likelihood optimality criterion. Parsimony was the optimality criterion used for mapping the SSCs and host breadth characters.

Results

We obtained sequences from 91 species (see Tables 1 & 2 for genes and sequence lengths). Maximum parsimony, maximum likelihood, and Bayesian methods were used on each of three datasets (28S rDNA, COI, and combined 28S rDNA+COI), resulting in nine trees with similar tree topologies (summarized in Figs. 3–9). Alignment of 28S rDNA sequence was unproblematic due to the presence of only 22 indels of at most two base pairs (available on TreeBASE). However, there were only 136 parsimony informative nucleotides (667 invariant, 128 autapomorphic) and all three analyses that used only 28S rDNA sequence resulted in poorly resolved phylogenies. Nonetheless, there was higher bootstrap and posterior probability support for clades at the tribal level. COI had much more variation with 555 parsimony informative characters (867 invariant, 120 autapomorphic). Most of the nucleotide changes were synonymous substitutions (471 versus 125 nonsynonymous substitutions), and the resulting trees had much more resolution and higher support values than 28S rDNA. Likelihood, on the other hand, produced several long branches in the core Archipini that were usually found elsewhere in the other analyses and unsupported by morphology. With the exception of these long branches, the supported clade topology is consistent with the trees from maximum parsimony and Bayesian analyses. Combining 28S rDNA and COI data resulted in a Bayesian tree with good support values in clades higher in the tree but a large polytomy at the base of Archipini. Maximum parsimony and likelihood analysis of the same data produced weak support and also placed some of the basal archipines as terminal taxa and the combined parsimony had almost no support for deeper nodes. Overall the COI and combined 28S rDNA+COI analyses agreed well with each other.

A final tree (the whole tree is summarized in partitions, Figs. 3–9) was assembled based upon all of the analyses (Appendix 3–11). Support values are given for COI and combined COI+28S rDNA analyses, but not for those from 28S rDNA sequence alone due to the poor resolution it provided at levels shallower than tribe. Where there were topological conflicts between trees, the clade that was best supported, as judged by the relative frequency of the clade among the six trees as well as its support values, was chosen for the summary tree. In a few cases where there was very little support, we relied on morphological characters to resolve any conflicts. Justifications for, and explanation of, the resolution for most nodes is explored in Appendix 2. In the final summary tree Archipini inclusive of Epitymbiini was found to be monophyletic. The basal Archipini group is recovered as a sister to the remainder of the Archipini, referred to henceforth as the core Archipini. *Adoxophyes* Meyrick, *Thrincoptora* Meyrick, and *Cryptoptila* Meyrick are found to be sister groups of the remainder of the core Archipini, which in turn forms a large polytomy. There is some support for a sister group relationship for the *Archips* Hübner and *Choristoneura* Lederer groups, while *Ptycholoma* Stephens, *Ptycholomoides* Obraztsov, and two species of *Homona* form another group. Most genera are found to be monophyletic, with some notable exceptions. Paraphyletic relationships included *Leucotenes* Dugdale within *Planotortrix* Dugdale, *Thrincoptora* Meyrick within *Adoxophyes*, *Archebandemis* within *Pandemis*, *Diedra* Rubinoff & Powell within *Argyrotaenia* Stephens, *Epiphyas* Turner within *Clepsis*, and *Cudonigera* Obraztsov & Powell within *Choristoneura*. Both *Aphelia* and *Homona* were polyphyletic.

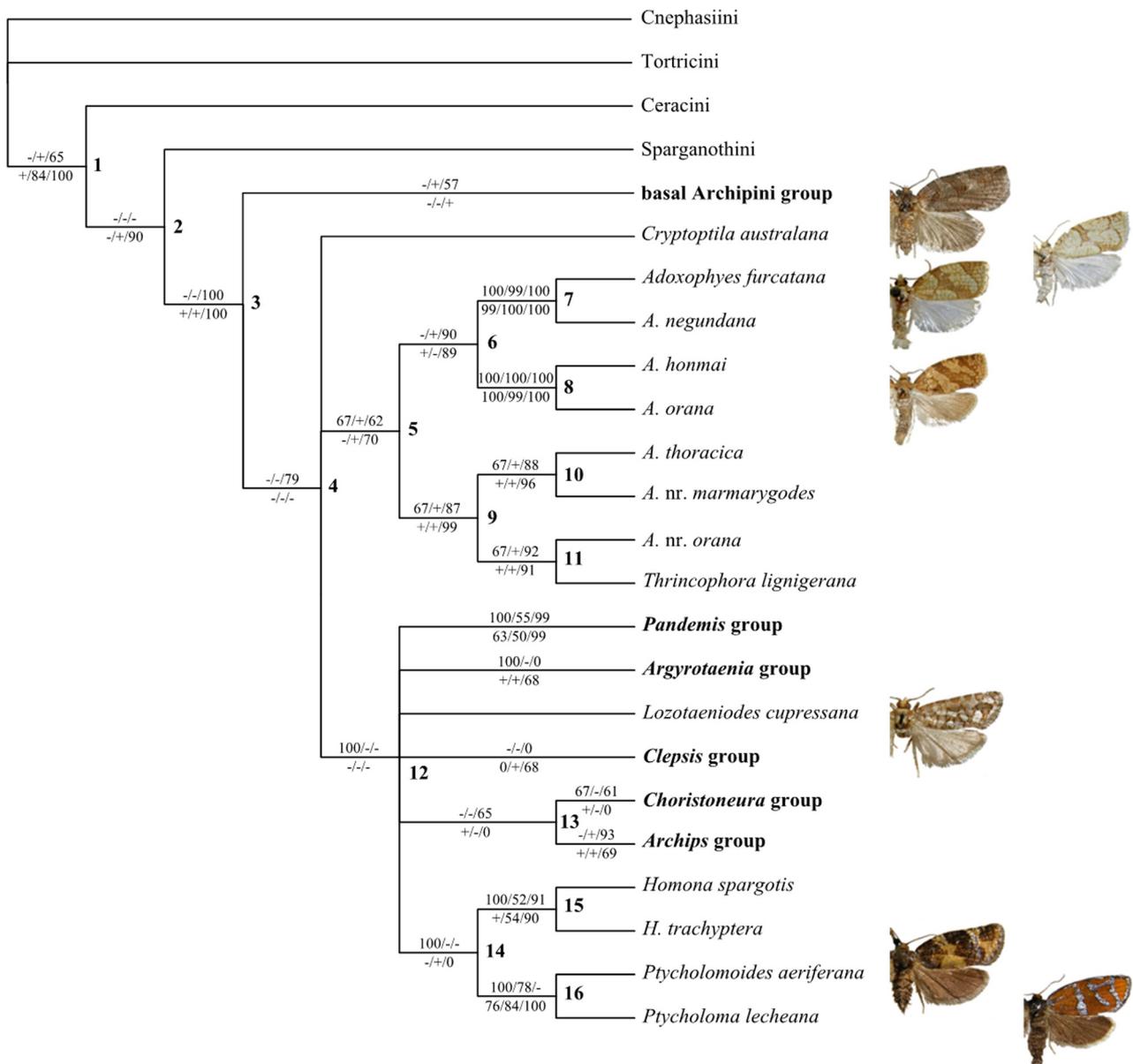


FIGURE 3. Summary tree of phylogenetic analyses. Clades are numbered in bold to the right of their respective nodes. Numerical values above and below branches are maximum parsimony bootstrap, maximum likelihood bootstrap, and Bayesian posterior probabilities, respectively (COI above, COI+28S rDNA below). "+" = a clade with less than 50% bootstrap support or posterior probability, "0" = a clade is part of a polytomy, and "-" = a clade contradicted by tree topology. Bolded terminal taxa are expanded in the following trees. Specimen photos are absent when no specimens were available for examination.

Six SSCs in addition to the CF were examined in males, both by direct observation in specimens and from published descriptions. The CF was scored as present if there was at least some noticeable folding on the basal half of the forewing of the male. This usually could be corroborated by the presence of a few elongate scales projecting from beneath it. The only exception to this was *C. rosaceana* which has a unique small triangular costal fold with a median scale tuft (Fig. 2) that has been described as degenerate and non-functional by Grant (1978) as it lacks glandular tissue and hair pencils. The CF is widespread across Tortricidae and has traditionally been considered plesiomorphic to the group (Horak 1984). It is lost at many taxonomic levels, most notably for all members of *Argyrotaenia* and multiple times within *Clepsis* (Fig. 10). The antennal notch (Fig. 11) was present in *Epitymbia alaudana* (Horak & Common, 1985) and in all *Pandemis* species except *P. dumetana* (Treitschke, 1835) (Razowski

1978). A possible degenerate antennal notch was found in *Archebandemis coniferana* Mutuura, 1978, but it was coded as absent since its presence was ambiguous (Dombroskie & Sperling 2012). A series of long flowing thoracic scales (Fig. 12) was found in both *Syndemis* species examined and in *Dichelia histrionana* (Frölich, 1828) (J. W. Brown *pers. comm.*), and Svensson (2006) mentions it as a unifying character in both *S. musculana* (Hübner, 1796) and *D. histrionana* (Frölich, 1828). A distinct hair pencil between the pro- and mesocoxae (Fig. 13) was observed only in *Lozotaenia hesperia* Powell, 1962, as mentioned in the original description (Powell 1962). A distinct pouch in the hindwing was not directly observed, but its presence is mentioned in *E. alaudana* by Horak & Common (1985). Distinct broad dark scales set into pouches in the basal abdominal sternites (Fig. 14) were found in all examined *Pandemis* species (Razowski 1978) except *P. lamprosana* (Robinson, 1869). All examined *Pandemis* species also had the pregenital sternite modified into distinct sclerotized structures with elaborate slender deciduous scales (Fig. 15) called “coremata” by Freeman (1958) and Jinbo (2000).

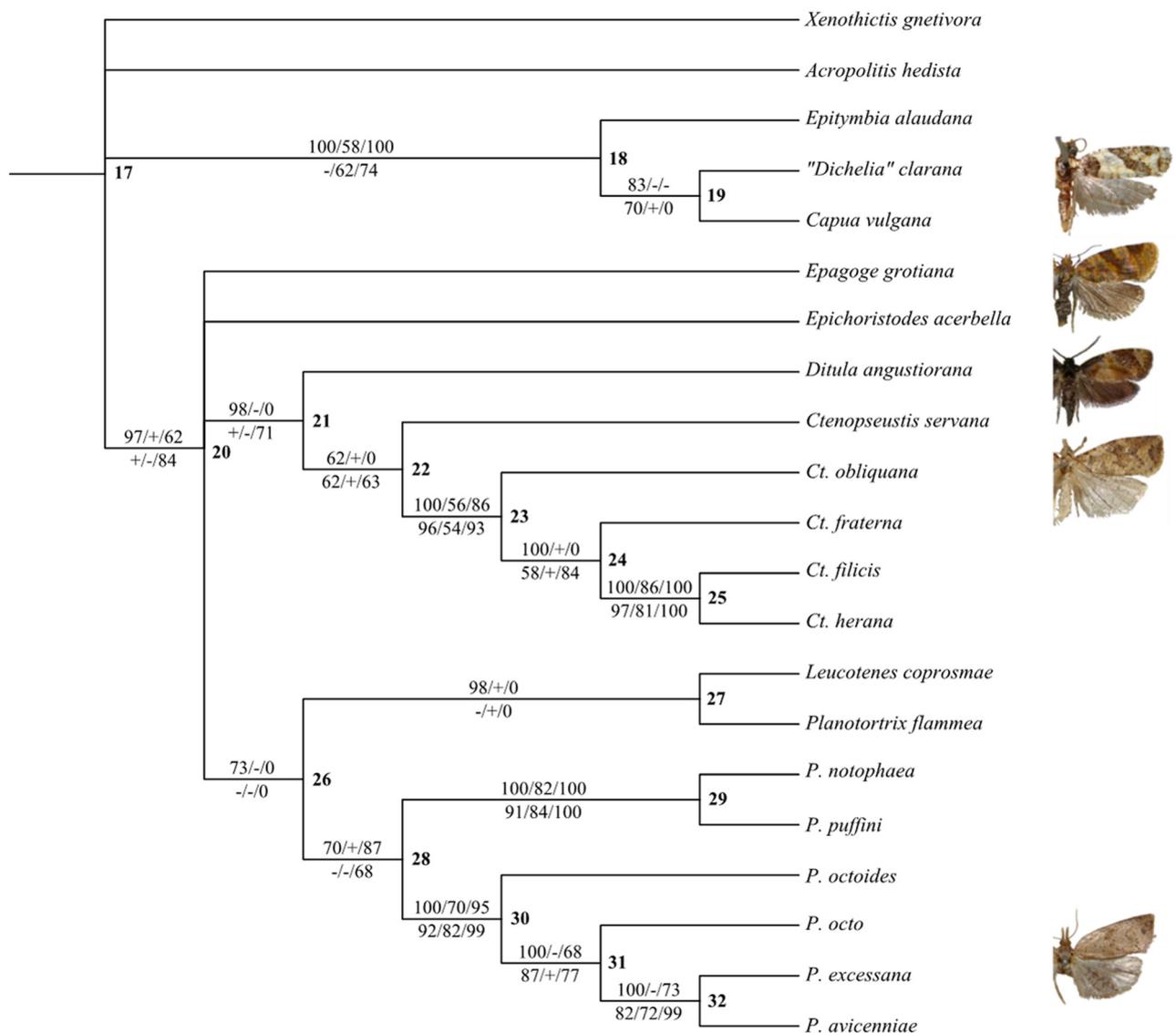


FIGURE 4. Basal Archipini group summary tree of phylogenetic analyses. Clades are numbered in bold to the right of their respective nodes. Numerical values above and below branches are maximum parsimony bootstrap, maximum likelihood bootstrap, and Bayesian posterior probabilities, respectively (COI above, COI+28S rDNA below). "+" = a clade with less than 50% bootstrap support or posterior probability, "0" = a clade is part of a polytomy, and "-" = a clade contradicted by tree topology. Specimen photos are absent when no specimens were available for examination.

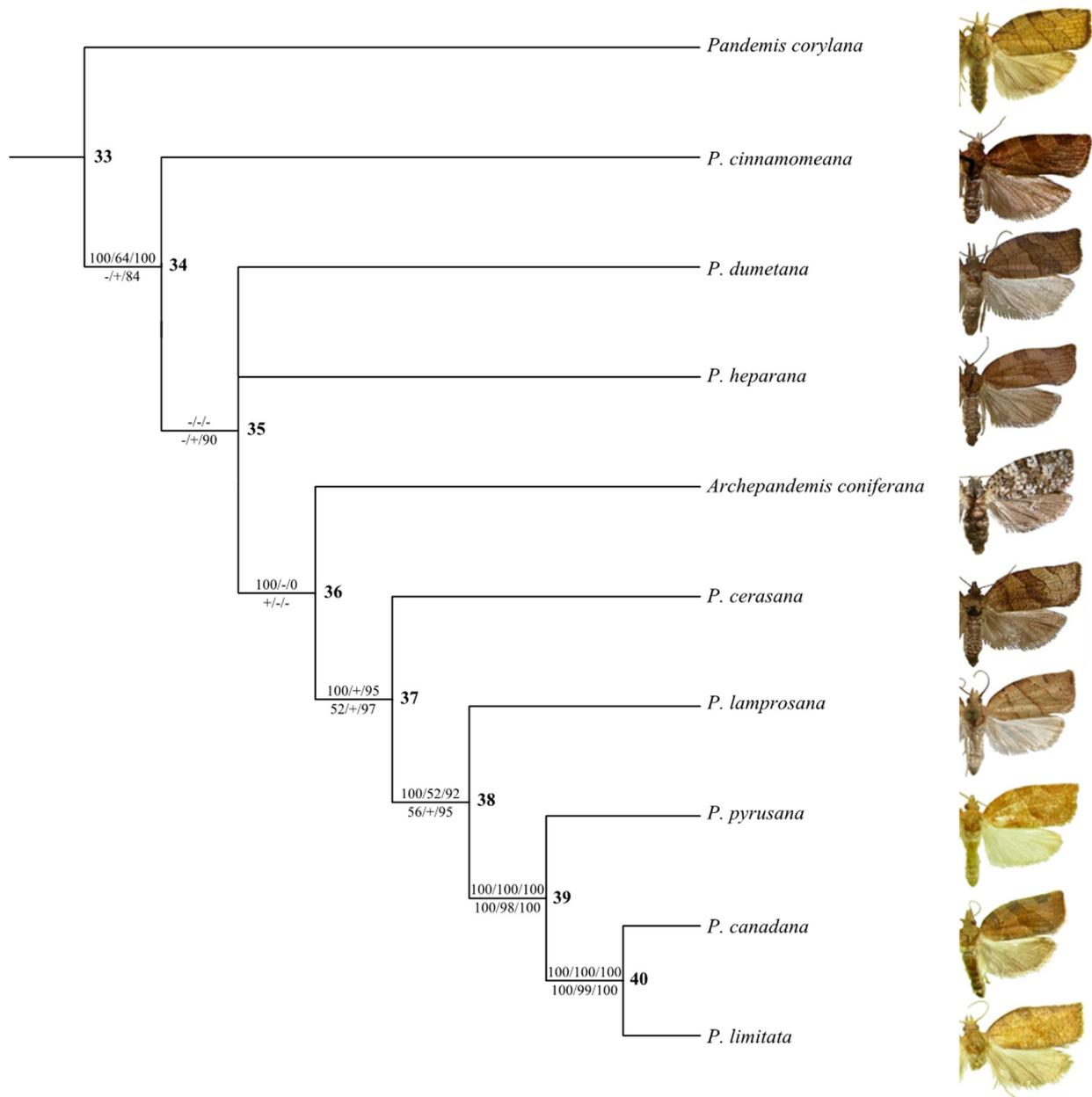


FIGURE 5. *Pandemis* group summary tree of phylogenetic analyses. Clades are numbered in bold to the right of their respective nodes. Numerical values above and below branches are maximum parsimony bootstrap, maximum likelihood bootstrap, and Bayesian posterior probabilities, respectively (COI above, COI+28S rDNA below). "+" = a clade with less than 50% bootstrap support or posterior probability, "0" = a clade is part of a polytomy, and "-" = a clade contradicted by tree topology.

Several characters were not used due to variation and/or ambiguity. All core Archipini are reported to have the pregenital sternite modified with long setae or scales (Jinbo 2000). Upon examination it became clear that this character varied from an almost obsolete bar with short setae, as in *Adoxophyes* and most *Argyrotaenia*, to a broad plate with longer setae as in *Archips mariana* (Fernald, 1882) (JJD *pers. obs.*; Razowski 1990), and extreme modification in *Pandemis* as mentioned above. Because of this ambiguity and the rarity of references to this structure in the literature, we chose to code only the extreme modification as seen in *Pandemis* as a SSC. Razowski (1987) reported abdominal scent organs in *Epiphyas* and in some *Clepsis* species, but this was not easily observed using traditional dissection methods, so this character was excluded. Elongate setae are present on the valve of the male genitalia, and in some species of *Clepsis* they are modified to such extremes that they seem likely to be used

as a mating stimulus, not just the primary mechanical act of mating. This is most obvious in *Clepsis consimilana* (Hübner, 1822), which has enlarged scales (Fig. 16). These scales are often deciduous, vary greatly in density, and frequently are lost in genitalic preparations (JJD *pers. obs.*). Because of the difficulty of consistent observation, the fact that genitalic drawings produced by some artists lack indications of setae (e.g. Freeman 1958), and that they are arguably primary sexual characters since they are on the genitalia, we have excluded them as a character. Finally the pecten on the CuP vein of the hindwing were noticeably longer and denser in *Choristoneura parallela* (Robinson, 1869) (Fig. 17) than in other examined archipines, although this character was excluded because it is usually found in both sexes, is difficult to characterize, and is rarely reported in the literature.

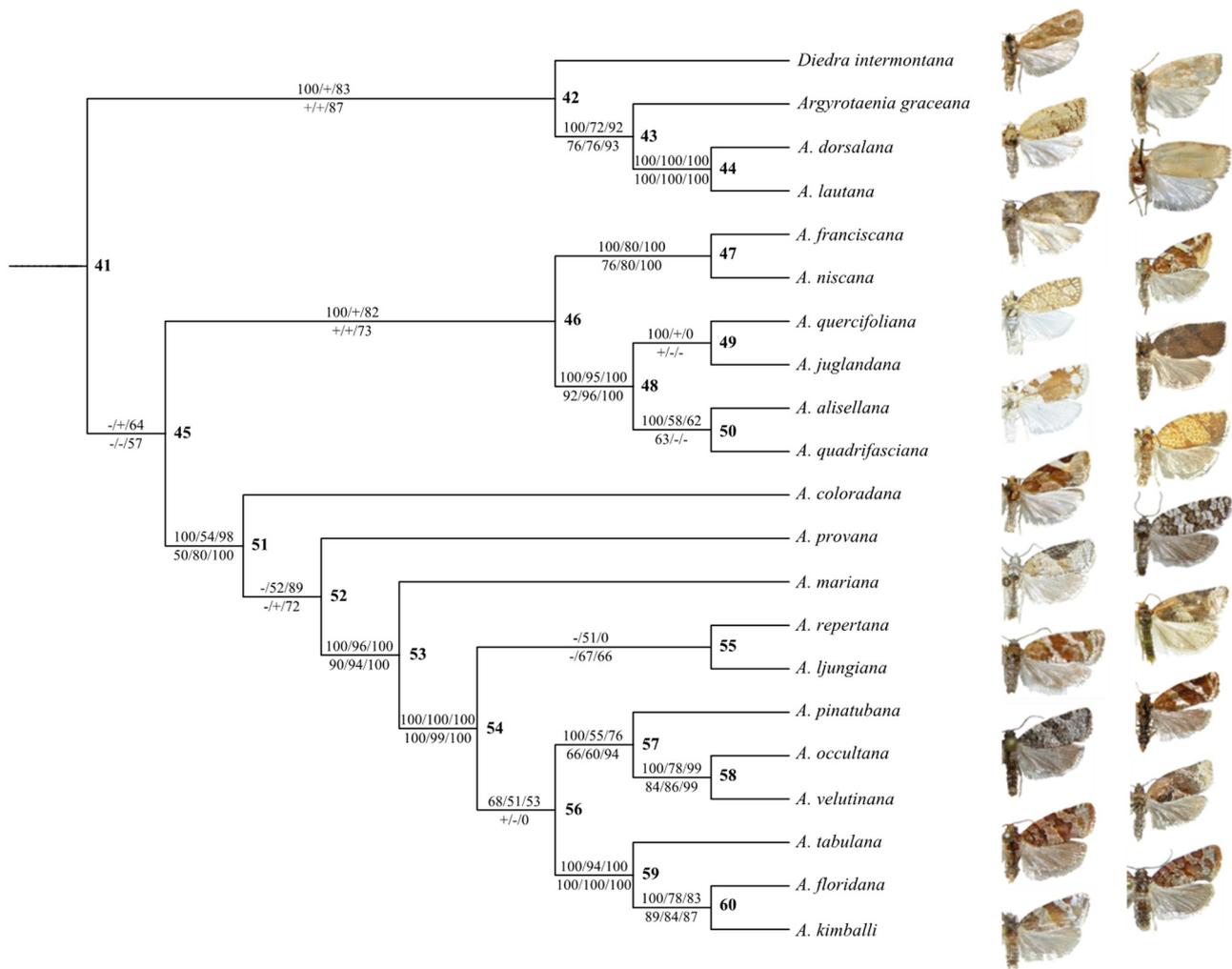


FIGURE 6. *Argyrotaenia* group summary tree of phylogenetic analyses. Clades are numbered in bold to the right of their respective nodes. Numerical values above and below branches are maximum parsimony bootstrap, maximum likelihood bootstrap, and Bayesian posterior probabilities, respectively (COI above, COI+28S rDNA below). "+" = a clade with less than 50% bootstrap support or posterior probability, "0" = a clade is part of a polytomy, and "-" = a clade contradicted by tree topology.

No strong association was noted between any of the three hypotheses tested when correlations of individual evolutionary events were compared (Table 5), although sample sizes were too small for statistical tests. χ^2 values of character correlation among terminal taxa returned a strong correlation between SSCs and host plant breadth ($p = 0.0045$) and SSCs and zoogeography ($p = 0.00039$), but no significant correlation was found between CF and novel SSCs ($p = 0.13$).

Ancestral character state reconstruction of zoogeographic distribution (Fig. 18) shows a strong likelihood for an Australasian origin of the Archipini, the basal Archipini group, *Adoxophyes*, and the core Archipini (Appendix 12). Strong likelihood values were also obtained for an Old World origin for the *Pandemis* group, the *Clepsis* group, *Cacoecimorpha*+*Choristoneura*+*Cudonigera*, and the *Archips* group. The only major group likely to have originated in the New World is *Argyrotaenia*, although the origin of the *Choristoneura* group is ambiguously placed between the Old and New Worlds.

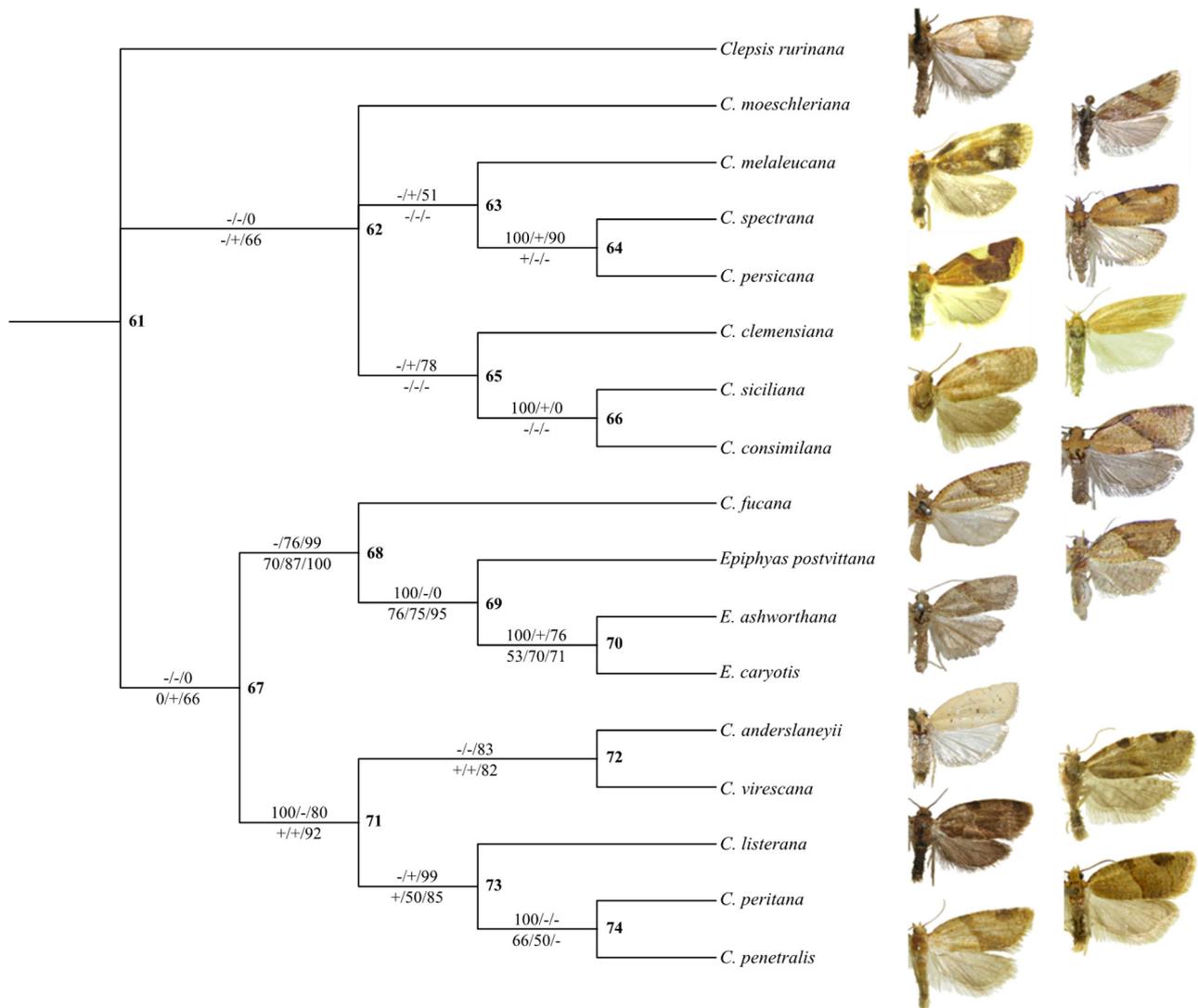


FIGURE 7. *Clepsis* group summary tree of phylogenetic analyses. Clades are numbered in bold to the right of their respective nodes. Numerical values above and below branches are maximum parsimony bootstrap, maximum likelihood bootstrap, and Bayesian posterior probabilities, respectively (COI above, COI+28S rDNA below). "+" = a clade with less than 50% bootstrap support or posterior probability, "0" = a clade is part of a polytomy, and "-" = a clade contradicted by tree topology. Specimen photos are absent when no specimens were available for examination.

Discussion

Comparison of bootstrap and posterior probability support values was straightforward for most clades, since clades were often consistently well supported by most analyses. We generally considered a value of 95 or more as strong bootstrap support for maximum parsimony and maximum likelihood analyses, and a value of 70 or more as strong posterior probability with Bayesian analyses, as discussed in Alfaro *et al.* (2003). Several of the deeper clades were more challenging to resolve since support was much weaker; consequently we often relied upon ad hoc consideration of morphology when molecular data were ambiguous or scarce. The large polytomy within the core Archipini made ancestral character state reconstructions more difficult, but this lack of resolution may reflect historically rapid radiation of these lineages. Clade justifications are discussed in Appendix 2.

Taxonomic implications. The resulting phylogeny has many interesting taxonomic implications that are thoroughly discussed in Appendix 2. The genus *Aphelia* is recovered as paraphyletic, with *Xenotemna* Powell, *Lozotaenia*, *Dichelia* Guenée, and *Syndemis* Hübner, interrupting its monophyly (Fig. 8). Obraztsov (1954) originally treated *Aphelia* as having three subgenera (*Aphelia s. s.*, *Djakonovia* Obraztsov, and *Zelothereses*), and he (1959) later elevated his three subgenera to generic level. Razowski (1981) subsequently synonymised *Djakonovia* under *Zelothereses* and described two other subgenera, *Anaphelia* and *Sacaphelia*. Razowski (1981, 2002a) argued for maintenance of all four taxa as subgenera until all archipine genera are revised. Despite the lack of synapomorphies for *Zelothereses* (Razowski 1987), the other remaining subgenera have distinct characters in the male genitalia that separate them, and these characters are good candidates for synapomorphies. We were unable to examine specimens of *Anaphelia* or *Sacaphelia* due to their restricted east Palaearctic distribution; however, the genitalia figures and descriptions in Razowski (1981) are of excellent quality. *Anaphelia* has paired dentate processes in the center of the transtilla, *Aphelia s. s.* has dentate lateral processes on the transtilla, and *Sacaphelia* has large dentate processes at the base of the valve, fused with the dentate transtilla. For a thorough discussion of these characters, see Razowski (1981). Because of these distinct differences, we propose that *Anaphelia*, *Sacaphelia*, and *Zelothereses* be raised to generic status separate from *Aphelia s. s.* (**revised status**).

TABLE 5. Tables of correlated changes. The total correlation values refer to separate χ^2 analyses of terminal taxa.

	novel SSC			oligophagy			Nearctic	
	0	+		0	+		0	+
loss of CF	13	2	loss of SSCs	5	7	loss of SSCs	7	8
	CF			SSCs			SSCs	
	0	-		0	-		0	-
gain novel SSC	3	4	gain oligo	10	8	Nearctic	7	8
total correlation, p = 0.13			total correlation, p = 0.0045			total correlation, p = 0.00039		

With a few exceptions, *Pandemis* is well defined morphologically with a modified pregenital sternite (Fig. 15), basal ventral abdominal scale tufts (Fig. 14), and antennal notch (Fig. 11) (Dombroskie & Sperling 2012). *Arche pandemis* is very similar in venation and genitalia to *Pandemis*, but lacks the defining SSCs present in most species (Mutuura 1978). This is likely due to a loss of these characters, a phenomenon that is frequent in certain *Pandemis* species (Fig. 10), and is supported by the presence of a subtle antennal notch present in *Arche pandemis*. Maintaining *Arche pandemis* as a valid taxon would require the erection of many genera with few synapomorphies from basal *Pandemis* species. Based on DNA sequence, similar morphology, presence of a partial antennal notch, and nomenclatural stability, we synonymize *Arche pandemis* with *Pandemis* (**new synonymy**).

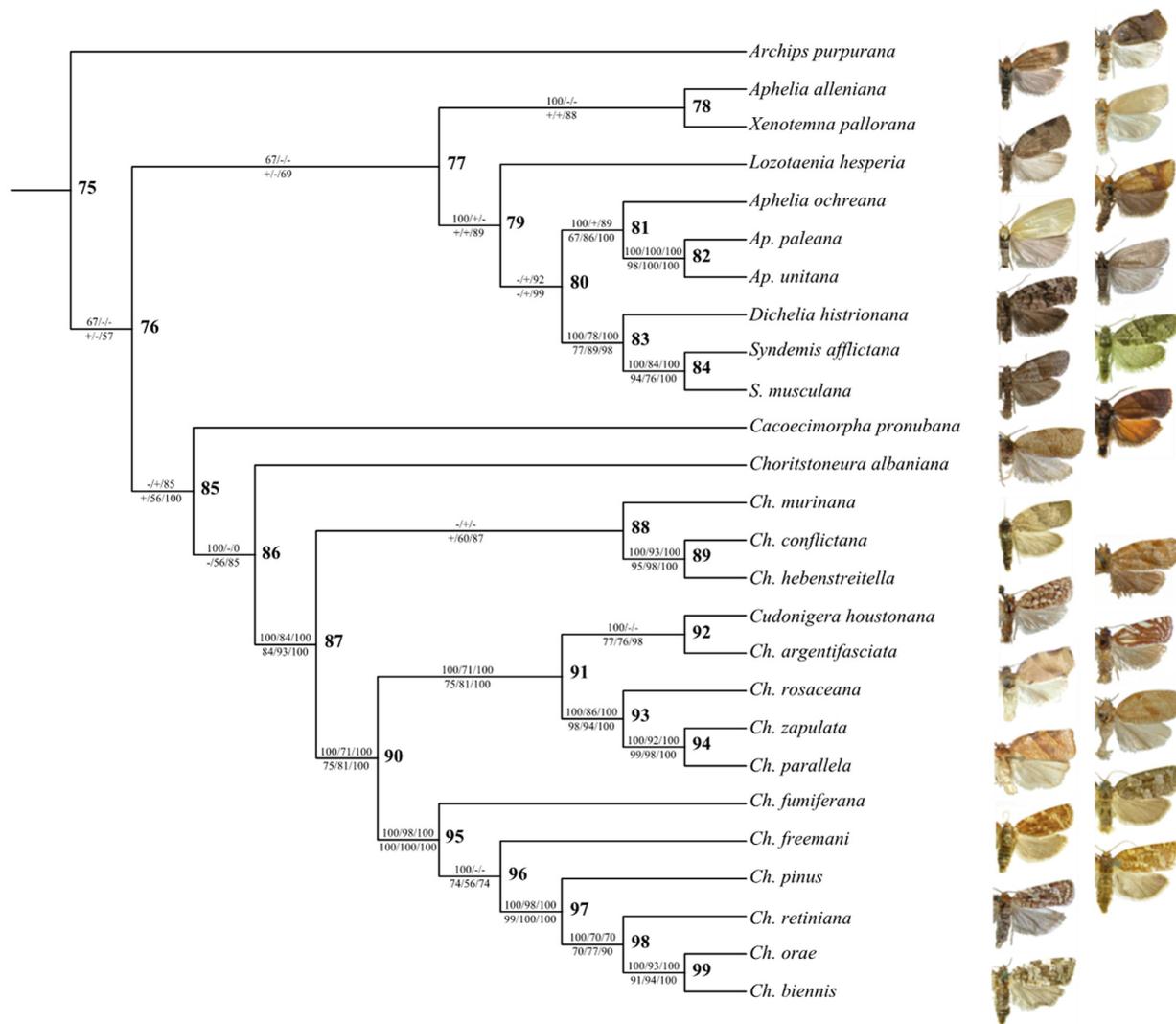


FIGURE 8. *Choristoneura* group summary tree of phylogenetic analyses. Clades are numbered in bold to the right of their respective nodes. Numerical values above and below branches are maximum parsimony bootstrap, maximum likelihood bootstrap, and Bayesian posterior probabilities, respectively (COI above, COI+28S rDNA below). "+" = a clade with less than 50% bootstrap support or posterior probability, "0" = a clade is part of a polytomy, and "-" = a clade contradicted by tree topology. Specimen photos are absent when no specimens were available for examination.

While the characters that define the monotypic genus *Cudonigera* are convincing, this taxonomic treatment would render the genus *Choristoneura* polyphyletic according to our analyses. Powell & Obrachtsov (1977) state that *Cudonigera houstonana* is derived from *Choristoneura*, but they suspected that it would fit closely with MacKay's (1962) *Choristoneura* group 2 (clade 95 in our analyses), whereas our analyses place it confidently in group 3 (clade 91 in our analyses). *Cudonigera* is strongly supported as being within *Choristoneura* in clades 87, 90, and 91. Therefore, rather than divide *Choristoneura* into several genera, we synonymise *Cudonigera* with *Choristoneura* (**new synonymy**).

Our analyses strongly support *Epiphyas* within *Clepsis*, which is also supported by the total replacement of *Clepsis* in Australia by *Epiphyas* and their male genitalic similarity (JJD *pers. obs.*). *Epiphyas* also has nearly identical glands in the male abdomen to those found in the *C. peritana* group (Razowski 1987). Molecular results place *Epiphyas* within *Clepsis*, and there are no reliable morphological characters to separate the genera (JJD *pers. obs.*). Therefore, either *Epiphyas* should be synonymised with *Clepsis*, or *Clepsis* should be split up into several genera to maintain generic monophyly. However, until more species are examined to determine the generic boundaries of *Clepsis*, we choose to maintain the status quo for the sake of nomenclatural stability in the widespread literature on these major pest species.

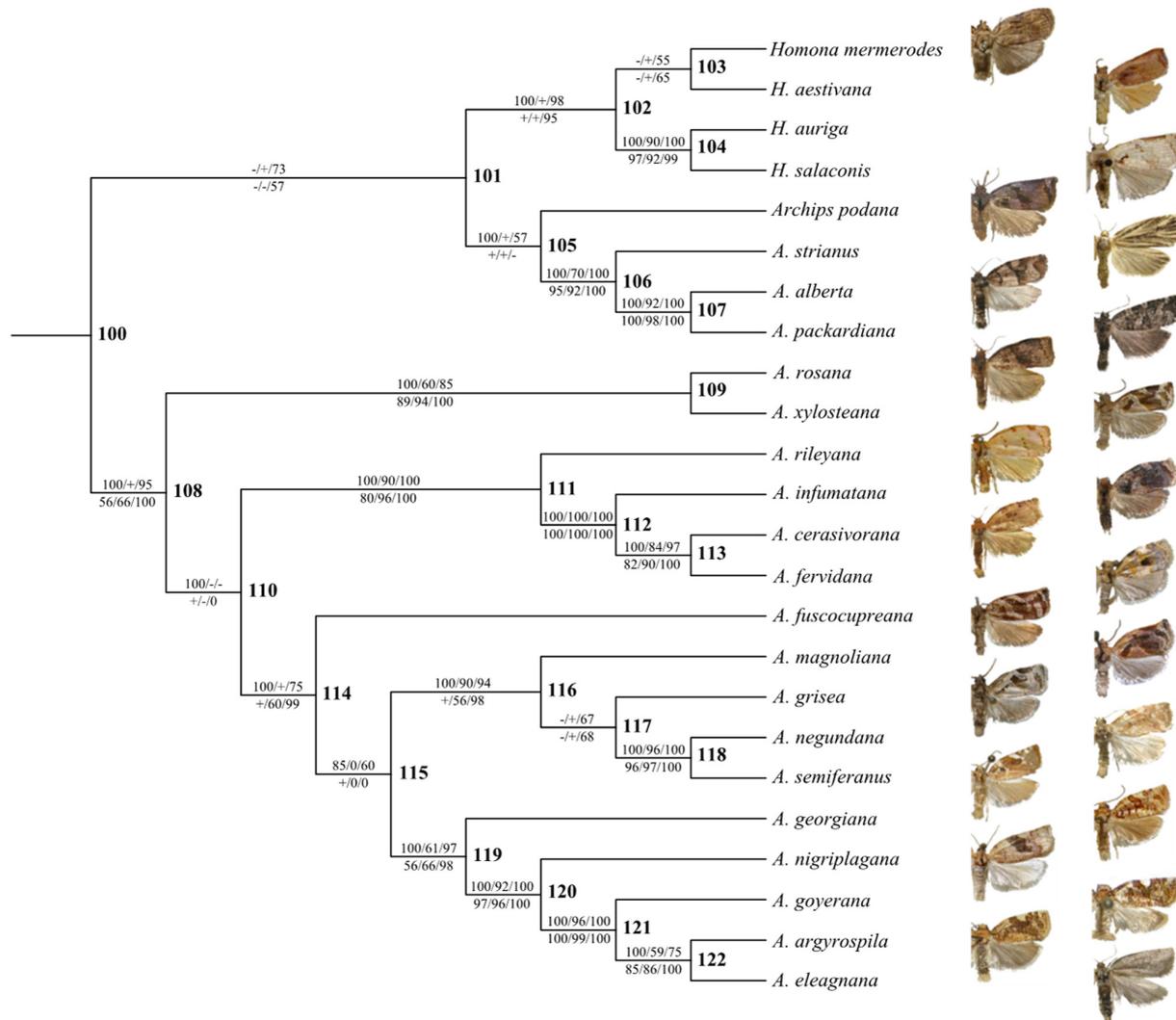


FIGURE 9. *Archips* group summary tree of phylogenetic analyses. Clades are numbered in bold to the right of their respective nodes. Numerical values above and below branches are maximum parsimony bootstrap, maximum likelihood bootstrap, and Bayesian posterior probabilities, respectively (COI above, COI+28S rDNA below). "+" = a clade with less than 50% bootstrap support or posterior probability, "0" = a clade is part of a polytomy, and "-" = a clade contradicted by tree topology. Specimen photos are absent when no specimens were available for examination..

Secondary sexual characters and correlations. The complexity and unknown utility of most of the SSC's examined here make it difficult to treat them as binary characters for phylogenetic analyses since we do not know if they are used as mating stimuli. While most of the broad costal folds seem undoubtedly functional, some of the smaller ones are of questionable utility. Greater certainty of their functionality could be derived by conducting histological examinations because some of the most slender costal folds are apparently fully functional with hairpencils and associated glands (Grant 1978). There was often no clear distinction between regular elongate scales and distinctive SSCs. The modified pregenital sternite that is common to all core Archipini examined is a prime example. To more fully understand its function, the histology of this sternite needs to be examined across a range of its variation. However, it is clear that the relatively extreme modification of this pregenital sternite, which is found in most *Pandemis* species, qualifies as a SSC (Fig. 15). It is generally referred to as "coremata" (Freeman 1958; Jinbo 2000); however, we prefer to restrict this term to intersegmental inflatable tube-like organs as in Birch *et al.* (1990).

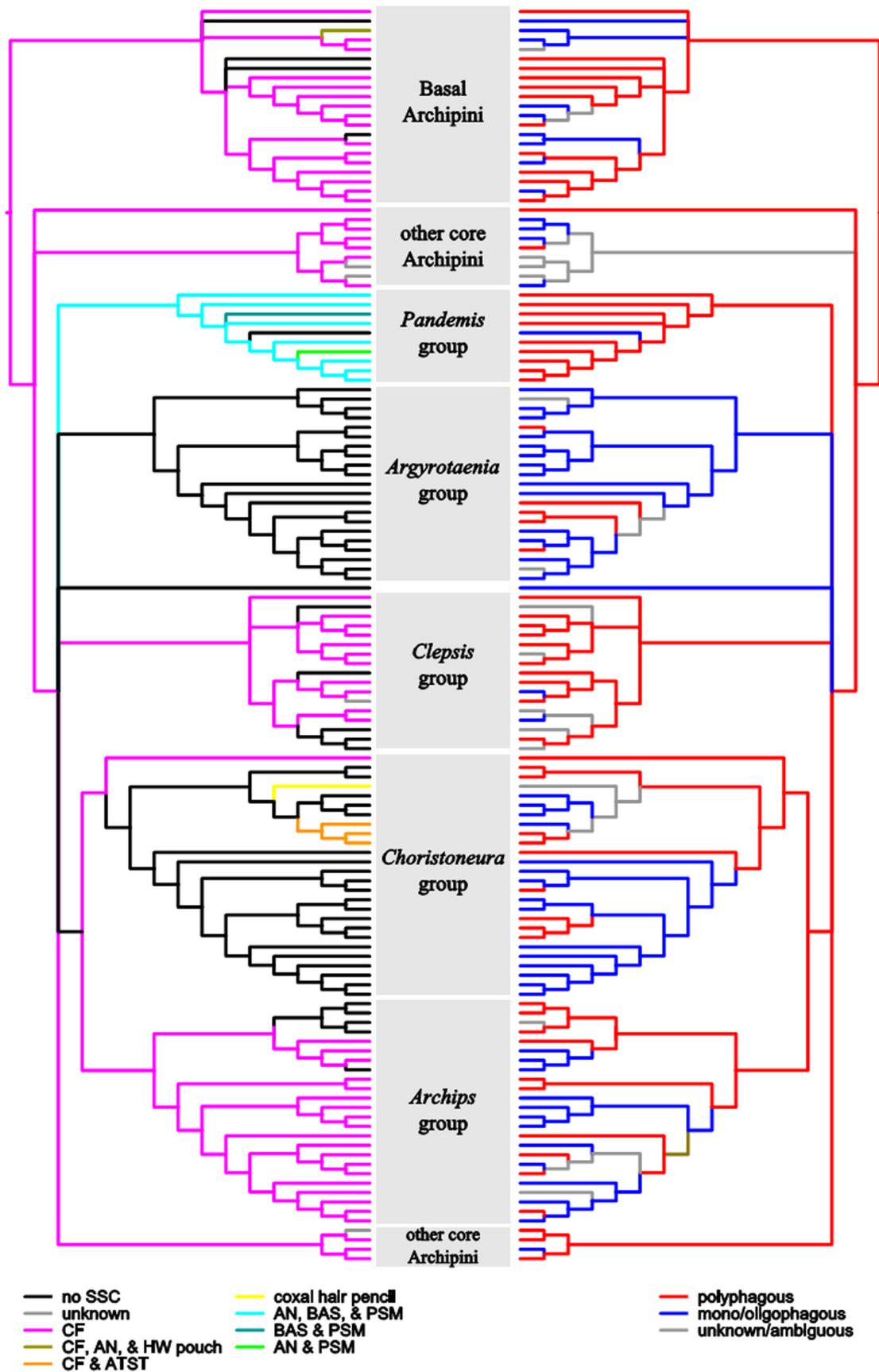
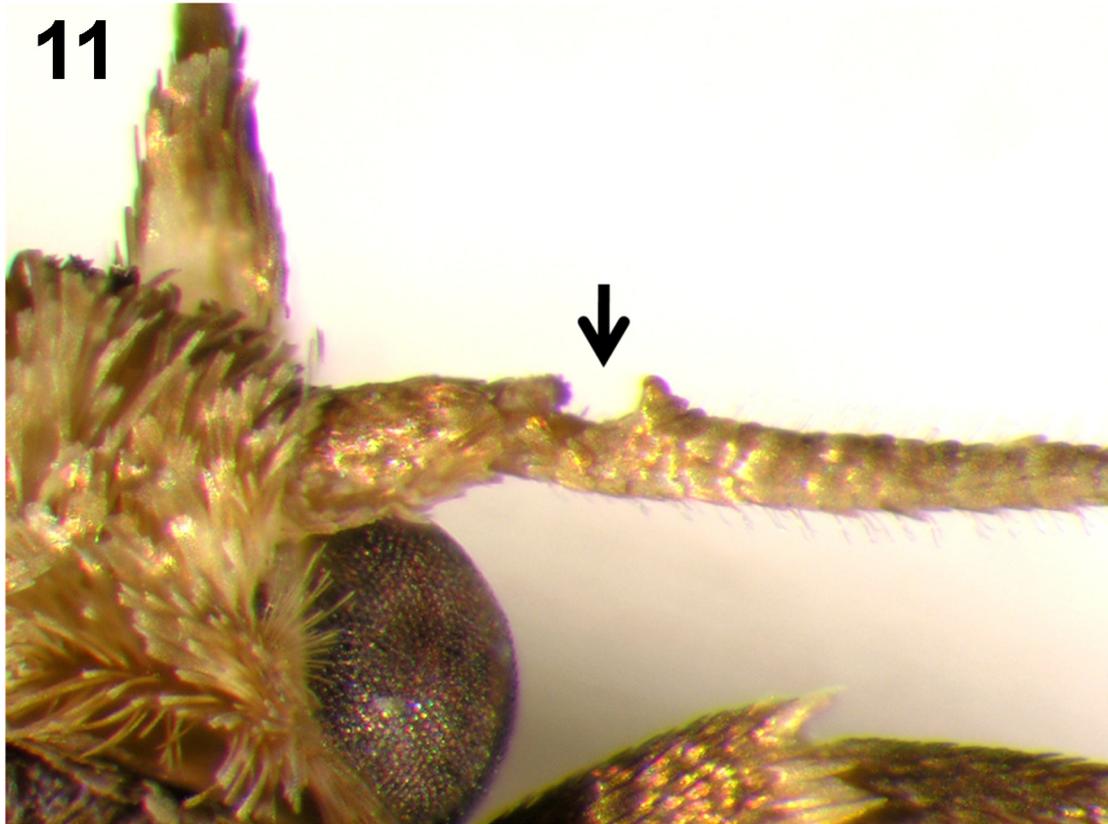
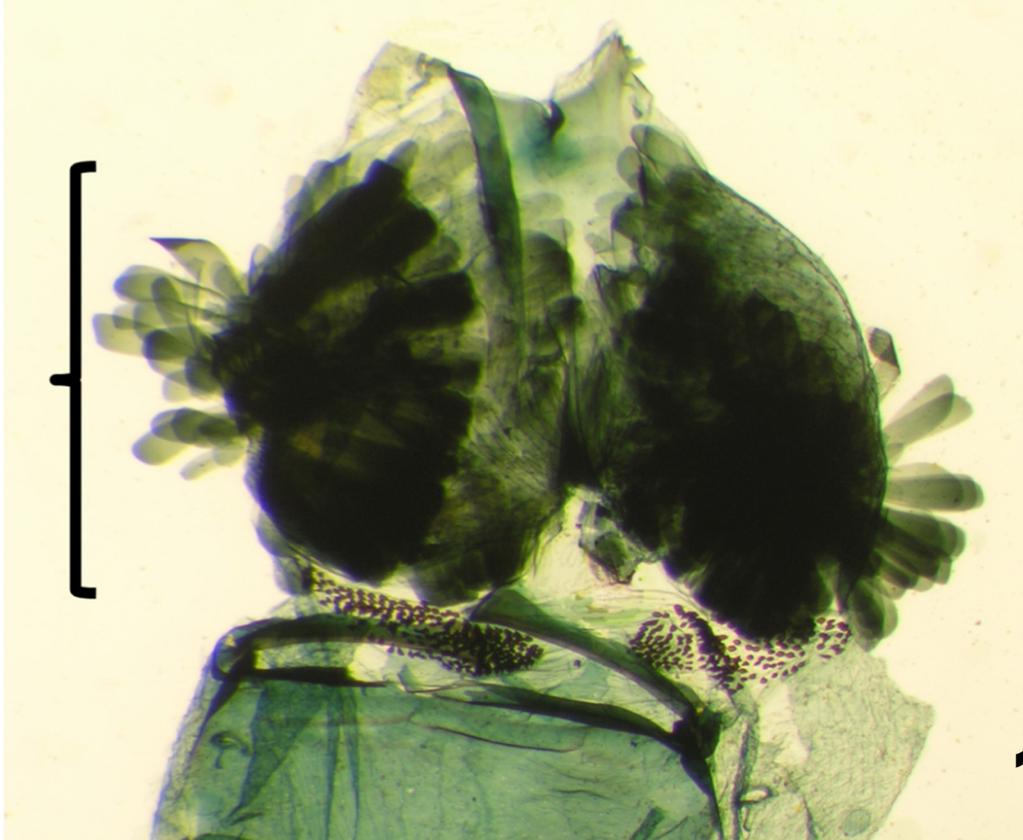
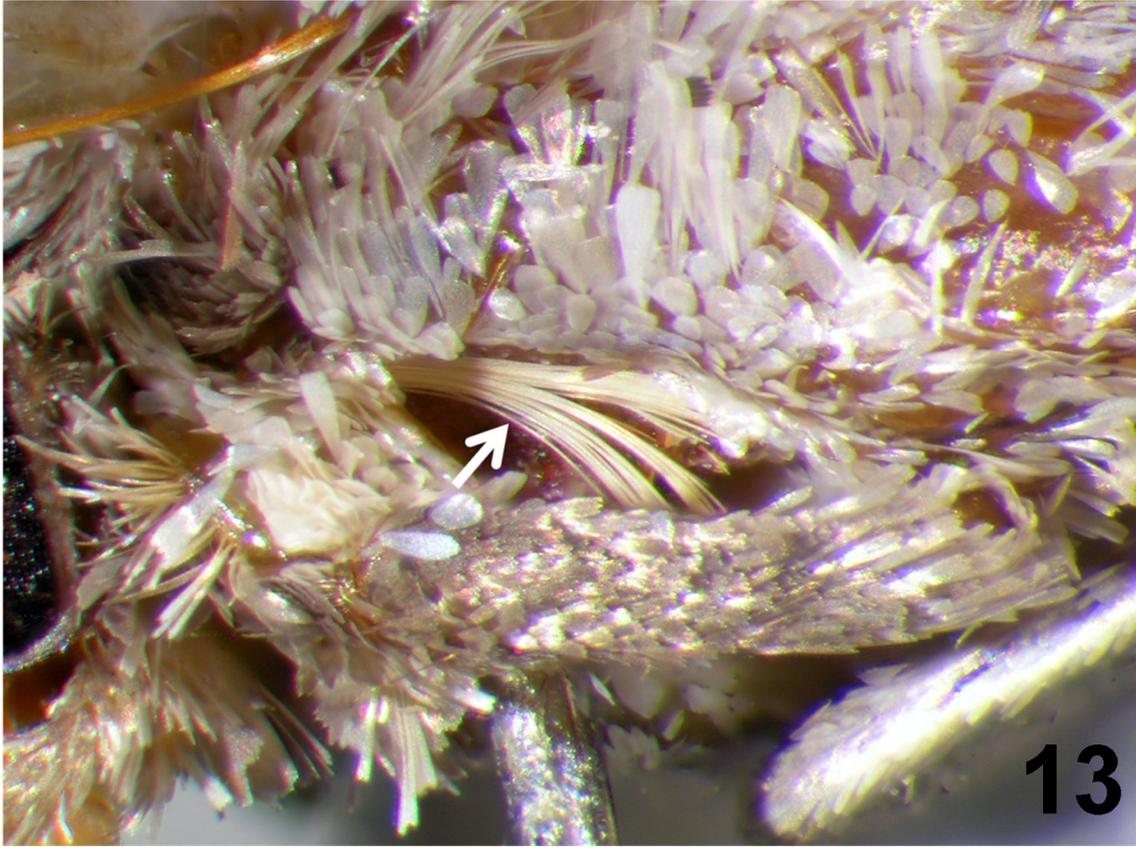


FIGURE 10. Trees with mapped parsimonious ancestral character state reconstructions. The left tree is of SSCs and the right is host plant breadth. AN = antennal notch, HW = hind wing, ATST = anterior thoracic scale tuft, BAS = modified basal abdominal scales, PSM = pregenital sternal modification.



FIGURES 11–12. Morphological features of Archipini. 11. Antennal notch of male *Pandemis canadana* Kearfott, 1905 indicated by arrow. JD6757: CAN: AB: Edmonton: 01 viii 2009: JJD, *et al.* 12. Anterior thoracic scale tufts of male *Syndemis afflictana* indicated by arrows. JD4282: CAN: AB: North Cooking Lake: 17 v 2008: JJD, *et al.*



FIGURES 13–14. Morphological features of Archipini. 13. Hair pencil posterior of procoxa in male of *Lozotaenia hesperia*. JD1047: CAN: AB: Jasper N. P.: 27 vi 2006: B. C. Schmidt & G. A. Anweiler. 14. Base of male abdomen of *Pandemis canadana* showing modified scales. JD6054: CAN: AB: Bindloss: 23 vii 2008: JJD & B. Proshek.



FIGURES 15–16. Morphological features of Archipini. 15. Male genitalia and modified pregenital sternite (indicated by arrow) of *Pandemis canadana*. JD6054: CAN: AB: Bindloss: 23 vii 2008: JJD & B. Proshek. 16. Male genitalia of *Clepsia consimilana* with arrows indicating modified socketed scales (s) and incomplete dentate transtilla (t). FRANCE: Massif des Maures: 19 vi 2009: T. M. Gilligan

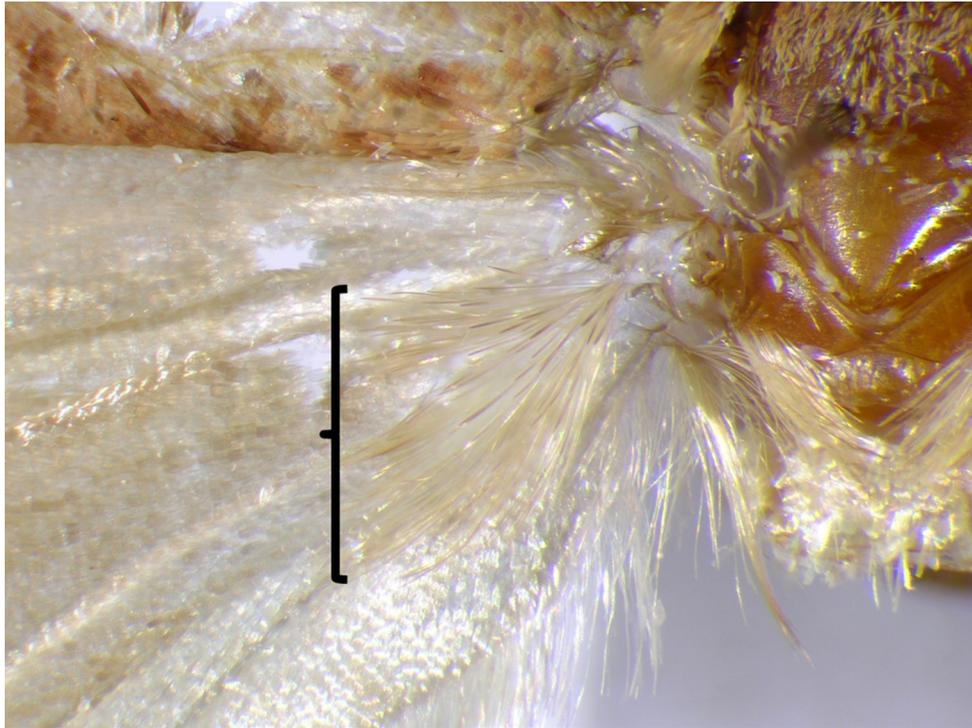


FIGURE 17. Hindwing base of male *Choristoneura parallela* showing modified scales. JD0600: USA: FL: Osceola N. F.: 19 vi 2006: JJD, *et al.*

We hypothesize that the CF should be lost more frequently in clades that have evolved novel SSCs. Since there were only seven independent origins of novel SSCs, the sample size was too small to test for statistical significance (Table 5), but nonetheless, is unsupported by χ^2 analysis of terminal taxon character correlation. This may be due to under-representation or unrepresentative sampling of the low number of novel SSCs used in our analyses. The correlation between the presence of the CF and SSCs may be stronger within certain clades like the *Pandemis* group, but is not evident in others like *Dichelia* and *Syndemis*.

We hypothesize that monophagous and oligophagous species should be more likely to lose SSCs. The χ^2 analysis shows a strong non-random distribution and a correlation between presence of SSCs and polyphagy. These results are similar to those of Phelan & Baker (1987), even though for the Tortricidae they restrict their definition of SSCs to only the CF. We could potentially obtain a more accurate estimate of correlations through more refined determination of SSCs. For example, clade 93 in *Choristoneura* consists of three polyphagous species that are often found together: *C. rosaceana*, *C. parallela*, and *C. zapulata* (Robinson, 1869). This clade has strong support in both of our analyses and the species are morphologically similar as both adults (Freeman 1958) and larvae (MacKay 1962). Geographically they overlap broadly and the larvae are polyphagous. In our analyses we coded them as having no SSCs since none appear to have a functional costal fold. Therefore these species contradict our hypothesis that closely related polyphagous species are more likely to have SSCs. However, in some of these species there is more than the normal amount of scaling on the valve of the genitalia and on the male hindwing, which is best exemplified by *C. parallela*. Histological investigation is needed to determine whether these modified scales are associated with any glandular structures.

The diversity of archipine genera by zoogeographic region is as follows (with genera endemic to that region in brackets): Australasian 81 [63], Indomalayan 50 [23], Palearctic 40 [20], Afrotropical 44 [31], Nearctic 14 [5], and Neotropical 15 [12] (Appendix 1). Two distinct patterns are visible: 1) a group of genera in common between the Australasian and Indomalayan regions that are a mix of the basal and core Archipini, and 2) genera in common with the rest of the regions that are in the core Archipini (Appendix 1). This fits well with the ancestral character state reconstruction for zoogeography (Fig. 18) and agrees with Horak (1999). An Australasian origin of the Archipini has the highest likelihood, which is borne out by the preponderance of the basal Archipini in this region and by that region harbouring more archipine genera than any other region. It is also likely that the core Archipini and *Adoxophyes* originated there as well. Because of the large polytomy in the core Archipini, it is difficult to say

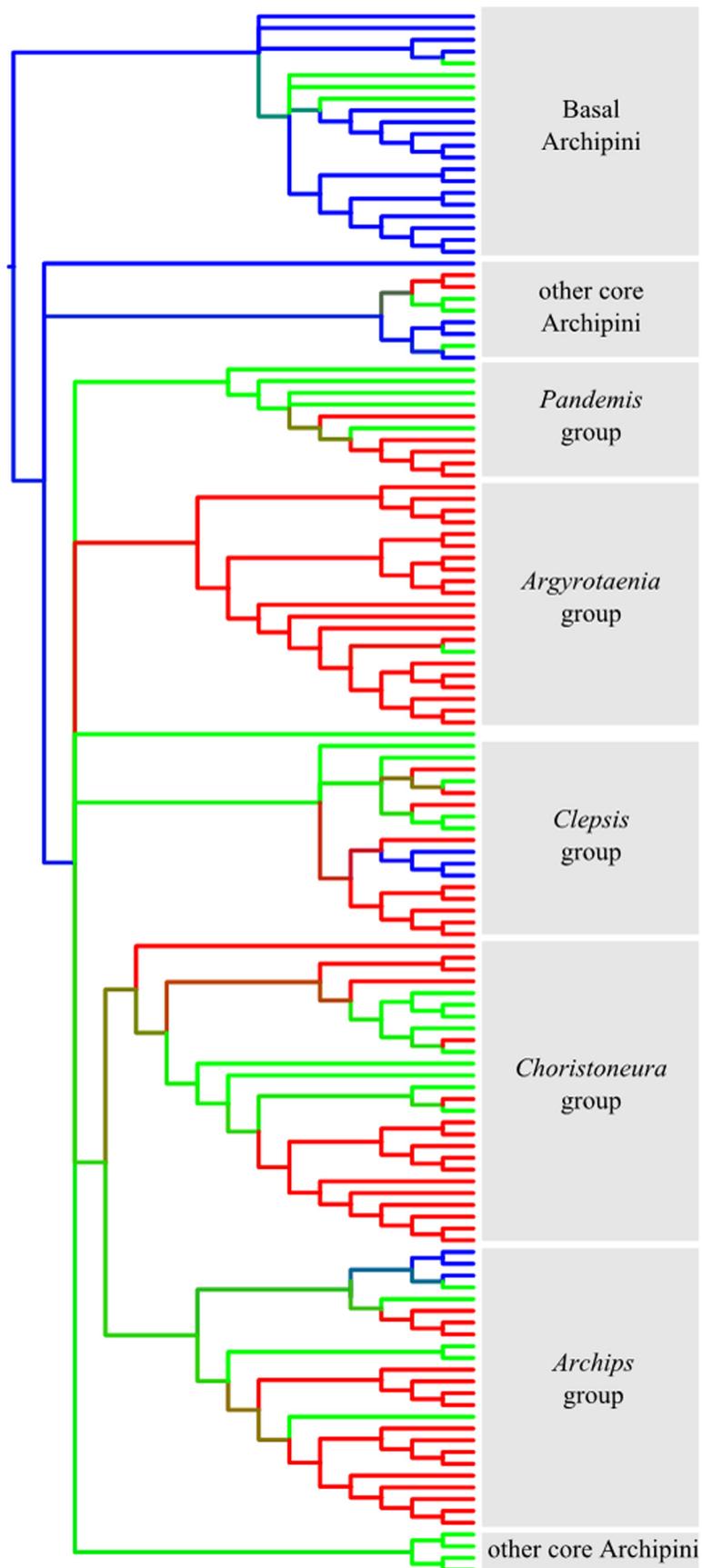


FIGURE 18. Tree with zoogeography mapped under likelihood ancestral character state reconstructions. Branch colours represent relative likelihoods of zoogeographic origin.

where most major lineages originated, although it appears that they radiated from the Palaearctic, except for the primarily New World *Argyrotaenia* group. It is difficult to determine where the Afrotropical region fits into this pattern because only one genus from this continent was used in our phylogeny (*Epichoristodes*), but the affinities of Afrotropical genera are primarily considered to be with genera within the core Archipini that are found broadly through the Palaearctic (Razowski 2002b, 2004, Razowski *et al.* 2010). The genus *Argyrotaenia* is supported as having radiated in the Nearctic, though it is also very diverse in the Neotropical region. The remainder of the Nearctic genera have close affinities with the northern Palaearctic, but are much less diverse (Razowski 1997). Most of the endemic Nearctic genera were phylogenetically close to existing Holarctic genera in our analyses (*Arche pandemis* within *Pandemis*, *Cudonigera* within *Choristoneura*, *Diedra* with *Argyrotaenia*, and *Xenotemna* with *Aphelia s. s.*). The Neotropical region also has a few genera in common with most of the rest of the world, and most of the few endemic genera are probably very close to *Argyrotaenia* and *Clepsis* (Razowski & Becker 2000).

The correlation between a supposed recent radiation into the Nearctic and the loss of SSCs, has a significant χ^2 value. This agrees with the original hypothesis that SSCs should be lost more frequently when radiating into regions previously uninhabited by congeners, and the pattern is most obvious in the *Argyrotaenia* group and the main Nearctic radiation in *Choristoneura* (clade 90) (Fig. 18).

Conclusions

Based on multiple analyses of sequences of COI supplemented by 28S rDNA, with some resolution of ambiguous clades using classical morphological characters, our preliminary phylogeny of the Archipini has a topology that is largely congruent with recent systematic work by other workers on various component groups. However, our analysis produced a large polytomy within the core Archipini. Nonetheless, some parts of the phylogeny were well supported, and on this basis we propose the following generic changes: 1) *Anaphelia*, *Aphelia s. s.*, *Sacaphelia*, and *Zelothereses* should be raised from subgenera within *Aphelia s. l.*, to full genera; 2) *Arche pandemis* should be synonymised with *Pandemis*; 3) *Cudonigera* should be synonymised with *Choristoneura*, and 4) *Epiphyas* is subordinate within *Clepsis* as currently defined, but the generic boundaries of these two require further study since any taxonomic change would be more disruptive than for the other genera. There were frequent gains and losses of SSC's, although the CF was most widespread. There was no significant correlation between the presence or absence of the CF and the development of other SSCs. There was a strong correlation between host plant breadth and SSCs using a χ^2 approach, although this was not apparent when looking at correlation of individual evolutionary events. Ancestral character state reconstruction supports an Australasian origin for the Archipini and limited radiation into the New World. This New World colonization was correlated with a greater frequency of loss of SSCs. Exploration and testing of these fundamental patterns has contributed to an improved understanding of the evolution of this economically important group of tortricid moths.

Acknowledgements

We would like to thank a number of people for assisting with fieldwork and obtaining specimens, notably, J. Adams, G. Anweiler, S. Bromilow, J. W. Brown, M. Djernaes, T. M. Gilligan, E. Kamunya, O. Karsholt, D. Lawrie, L. Lumley, D. Macaulay, J. A. Powell, B. Proshek, A. Roe, A. Rose, A. Sandor, B. C. Schmidt, M. Schwarzfeld, T. Simonsen, M. Vankosky, and K. Zocchi. Several unpublished sequences were generously shared by L. Lumley, A. Zwick, M. Horak, M. San Jose, and D. Rubinoff. Input on early versions of the manuscript, help with analyses, lab work, and translation were provided by S. Bromilow, B. Brunet, J. Dupuis, C. Jaeger, S. Leo, Y. Li, L. Lumley, G. Pohl, C. Schmidt, M. Schwarzfeld, and T. Simonsen. C. Lockerbie, W. Nordstrom, and C. Smith facilitated permits in protected areas and provincial and federal parks. We would also like to thank R. Brown, L. Dossall, A. Murray, H. Proctor, and two anonymous reviewers for providing valuable input on later versions of the manuscript. This study was funded by Alberta Conservation Association Grants in Biodiversity and a Discovery Grant from the National Sciences and Engineering Research Council of Canada to Felix Sperling.

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APPENDIX 1. Zoogeography of Archipini genera.

genus	number of spp.	Nearctic	Neotropical	Palearctic	Afrotropic	Indomalaysian	Australian/Oceania	References
<i>Abrepagoge</i>	1			X				Razowski 2001; 2002a
<i>Acroceuthes</i>	2						X	Brown 2005
<i>Acropolitis</i>	9						X	Brown 2005
<i>Adoxophyes</i>	50	X		X	X	X	X	Brown 2005; Byun <i>et al.</i> 2003; Diakonoff 1939; 1941a; 1941b; 1941c; 1941d; 1951; 1952; 1957; 1960; 1961; 1967; 1976; 1982; Freeman 1958; Hulcr <i>et al.</i> 2007; Lee <i>et al.</i> 2005; Liu and Li 2002; Razowski 2001; Robinson <i>et al.</i> 1994
<i>Allodemis</i>	6						X	Brown 2005; Diakonoff 1939; 1941; Robinson <i>et al.</i> 1994
<i>Ancyroclepsis</i>	2						X	Brown 2005; Diakonoff 1976; Liu and Li 2002
<i>Aneuxanthis</i>	1			X				Razowski 2002a
<i>Anisotenes</i>	21						X X	Brown 2005; Diakonoff 1941; 1953; Liu and Li 2002
<i>Anthophrys</i>	1				X			Diakonoff 1960; 1973
<i>Antiphrastris</i>	1						X	Diakonoff 1939
<i>Aphelia</i>	36	X		X	X			Brown 2005; Byun <i>et al.</i> 2003; Gaedike 1990; Jürivete and Ōunap 2008; Liu and Li 2002; Obraztsov 1959; Razowski 1981; 2001; 2002a; Trematerra 2010b
<i>Aphthonocosma</i>	1						X	Brown 2005
<i>Arche pandemis</i>	3	X						Freeman 1965; Mutuura 1978
<i>Archidemis</i>	1						X	Diakonoff 1967
<i>Archips</i>	108	X	X	X	X	X		Brown 2005; Byun <i>et al.</i> 1998; 2003; Chapman 1973; Diakonoff 1941c; 1951; 1952; 1976; 1982; Duncan 2006; Franclemont 1986; Freeman 1958; Hoebeke <i>et al.</i> 2008; Jinbo 2006; Kruse 2000; Kruse and Sperling 2001; Liu and Li 2002; MacKay 1962; Maier 2003; Razowski 1977; 2000; 2001; Robinson <i>et al.</i> 1994; Trematerra 2010a; 2010b
<i>Argyrotaenia</i>	99	X	X	X				Brown and Cramer 1999; Brown 2005; Chapman 1973; Chapman and Lienk 1971; Duncan 2006; Freeman 1944; 1958; Heppner 1989; Liu and Li 2002; MacKay 1962; Obraztsov 1961; 1962; Powell 1960; 1964; Razowski 2001; Razowski and Becker 2000; Trematerra 2010b; Trematerra and Brown 2004
<i>Aristocosma</i>	1						X	Brown 2005
<i>Arizelana</i>	2						X	Brown 2005
<i>Ascerodes</i>	1						X	Meyrick 1905
<i>Asteriognatha</i>	2						X	Brown 2005
<i>Atelodora</i>	2						X	Brown 2005
<i>Authomaema</i>	3						X	Brown 2005
<i>Avaria</i>	2			X				Brown 2005; Razowski 2002a
<i>Balioxena</i>	1				X			Diakonoff 1960; 1973
<i>Battalia</i>	21						X	Brown 2005; Diakonoff 1953
<i>Borboniella</i>	16				X			Brown 2005; Diakonoff 1957; 1961

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APPENDIX 1. (Continued)

genus	number of spp.	Nearctic	Neotropical	Palearctic	Afrotropic	Indomalaysian	Australian/Oceania	References
<i>Borneogena</i>	1					X		Diakonoff 1941d
<i>Brachyvalva</i>	1				X			Diakonoff 1960
<i>Bradleyella</i>	5						X	Brown 2005
<i>Cacoecimorpha</i>	1			X				Razowski 2001
<i>Callibryastis</i>	1					X		Diakonoff 1939
<i>Capua</i>	22			X	X	X	X	Brown 2005; Diakonoff 1967; 1976; Jürivete and Öunap 2008; Liu and Li 2002; Razowski 2001
<i>Carphomigma</i>	1						X	Brown 2005
<i>Catamacta</i>	5				X		X	Brown 2005; Diakonoff 1939; Diakonoff 1941d
<i>Ceramea</i>	1					X		Diakonoff 1951
<i>Ceritaenia</i>	1		X					Razowski and Becker 2000
<i>Chionothremma</i>	29						X	Brown 2005
<i>Chiraps</i>	4					X		Brown 2005; Liu and Li 2002; Robinson <i>et al.</i> 1994
<i>Choanograptis</i>	15			X		X	X	Brown 2005; Diakonoff 1941d; 1948
<i>Choristoneura</i>	46	X		X	X	X		Bradley <i>et al.</i> 1973; Brown 2005; Byun <i>et al.</i> 2003; Dang 1992a; 1992b; Duncan 2006; Freeman 1958; Heppner 1989; Liu and Li 2002; Lumley and Sperling 2010; Obraztsov 1962; Razowski 2001; 2002a; 2008a; Razowski and Trematerra 2010; Trematerra 2010b
<i>Claduncaria</i>	2		X					Brown 2005; Razowski and Becker 2000
<i>Clepsis</i>	150	X	X	X	X	X		Brown 2005; Chapman and Lienk 1971; Clifton 2007; Dang <i>et al.</i> 1996; Diakonoff 1957; 1976; Dombroskie and Brown 2009; Duncan 2006; Freeman 1958; Jürivete and Öunap 2008; Kearfott 1907; Liu and Li 2002; MacKay 1962; Obraztsov 1962; 1968; Razowski 1979a; 1979b; 2001; 2002a; 2004; Razowski <i>et al.</i> 2010; Trematerra 2010a; Wang <i>et al.</i> 2003
<i>Coeloptera</i>	3						X	Brown 2005
<i>Cornips</i>	2				X			Razowski <i>et al.</i> 2010
<i>Cornuclepsis</i>	1		X					Razowski and Becker 2000
<i>Cornusaccula</i>	1				X			Diakonoff 1960
<i>Cosmiophrys</i>	2				X			Diakonoff 1960; 1970
<i>Cryptomelaena</i>	1					X		Brown 2005
<i>Cryptoptila</i>	4						X	Brown 2005; Diakonoff 1953
<i>Ctenopseustis</i>	6				X		X	Brown 2005; Green and Dugdale 1982; Newcomb and Gleeson 1998
<i>Cudonigera</i>	1	X						Freeman 1958; Powell and Obraztsov 1977
<i>Cununcus</i>	1		X					Razowski and Becker 2000
<i>Cuspidata</i>	10				X			Diakonoff 1960; 1963; 1970; 1973
<i>Daemilus</i>	2			X				Byun <i>et al.</i> 1998; Jinbo 2000; Liu and Li 2002
<i>Dentisociaria</i>	1			X				Jinbo 2000
<i>Dicanticinta</i>	1			X				Brown 2005

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APPENDIX 1. (Continued)

genus	number of spp.	Nearctic	Neotropical	Palearctic	Afrotropic	Indomalaysian	Australian/Oceania	References
<i>Dicellitiss</i>	3					X	X	Brown 2005; Diakonoff 1939; 1941b; 1952; 1976
<i>Dichelia</i>	4			X		X		Brown 2005; Křenek 2000; Razowski 2001; 2002a
<i>Dichelopa</i>	50						X	Brown 2005
<i>Diedra</i>	5	X						Rubinoff and Powell 1999
<i>Digitosa</i>	6				X			Diakonoff 1960; 1970; 1973
<i>Diplocalyptis</i>	6			X		X		Brown 2005; Byun <i>et al.</i> 2003; Diakonoff 1976; 1982; Liu and Li 2002; Razowski 2000
<i>Ditula</i>	2			X				Razowski 2002a
<i>Droceta</i>	1				X			Brown 2005
<i>Durangarchips</i>	1	X						Brown 2005
<i>Dynatocephala</i>	1					X		Robinson <i>et al.</i> 1994
<i>Ecclitica</i>	4						X	Brown 2005; Meyrick 1905
<i>Egogepa</i>	2			X				Brown 2005
<i>Electraglaia</i>	4					X		Brown 2005; Diakonoff 1976
<i>Epagoge</i>	8			X		X	X	Brown 2005; Baixeras and Dominguez 1993; Diakonoff 1941b; 1941c; 1941d; 1948; Razowski 2001
<i>Epalxiphora</i>	1						X	Brown 2005
<i>Epichorista</i>	32				X		X	Brown 2005; Diakonoff 1939; 1941a
<i>Epichoristodes</i>	15				X			Brown 2005; Diakonoff 1960; 1970; 1973; Razowski 2002a; Razowski <i>et al.</i> 2010; Timm <i>et al.</i> 2010
<i>Epiphyas</i>	40						X	Brown 2005; Newcomb and Gleeson 1998; Razowski 2002a
<i>Ericodesma</i>	14						X	Brown 2005; Meyrick 1905
<i>Eurythecta</i>	8						X	Brown 2005; Meyrick 1905
<i>Exorstaenia</i>	2		X					Razowski and Becker 2000
<i>Furcataenia</i>	5		X					Razowski and Becker 2000
<i>Gelophaula</i>	9						X	Brown 2005
<i>Geogepa</i>	8			X		X		Brown 2005; Jinbo 2000; Liu and Li 2002
<i>Gephyraspis</i>	3				X			Diakonoff 1960; 1973
<i>Glyphidoptera</i>	2						X	Brown 2005
<i>Gnorismoneura</i>	24			X		X		Brown 2005; Byun <i>et al.</i> 1998; 2003; Liu and Li 2002
<i>Gongylotypa</i>	1					X		Brown 2005
<i>Goniotorna</i>	36				X			Brown 2005; Diakonoff 1960; 1963; 1970; 1973
<i>Harmologa</i>	13						X	Brown 2005; Diakonoff 1939
<i>Hectaphelia</i>	6				X			Brown 2005
<i>Heterochorista</i>	20						X	Brown 2005; Diakonoff 1953
<i>Hiceteria</i>	3						X	Brown 2005
<i>Homona</i>	34			X		X	X	Brown 2005; Byun <i>et al.</i> 1998; Diakonoff 1941a; 1941b; 1941c; 1941d; 1948; 1952; 1967; 1982; Hulcr <i>et al.</i> 2007; Liu and Li 2002; Miller <i>et al.</i> 2010; Razowski 2008a; Robinson <i>et al.</i> 1994

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APPENDIX 1. (Continued)

genus	number of spp.	Nearctic	Neotropical	Palearctic	Afrotropic	Indomalaysian	Australian/Oceania	References
<i>Homonoides</i>	1				X			Diakonoff 1960
<i>Homonopsis</i>	4			X				Brown 2005; Byun <i>et al.</i> 1998; Liu and Li 2002
<i>Hypsidracon</i>	1				X			Brown 2005
<i>Idolatteria</i>	11		X					Brown 2005
<i>Isochorista</i>	10						X	Brown 2005; Diakonoff 1939
<i>Isodemis</i>	4					X		Brown 2005; Diakonoff 1976; Liu and Li 2002; Robinson <i>et al.</i> 1994
<i>Isotenes</i>	24					X	X	Brown 2005; Diakonoff 1939; 1941a; 1941c; 1941d; 1948; 1952; 1953; 1960; Liu and Li 2002; Robinson <i>et al.</i> 1994
<i>Labidosa</i>	2				X			Brown 2005; Diakonoff 1960
<i>Leontochroma</i>	5					X		Brown 2005; Diakonoff 1976; Liu and Li 2002
<i>Leptochroptila</i>	1						X	Diakonoff 1939; 1952
<i>Leucotenes</i>	1						X	Newcomb and Gleeson 1998
<i>Lozotaenia</i>	24	X		X	X			Brown 2005; Byun <i>et al.</i> 1998; Franclemont 1986; Jinbo 2000; Liu and Li 2002; Obratsov 1962; Powell 1962b; Razowski 2001; 2002a; Razowski and Trematerra 2010; Razowski <i>et al.</i> 2010
<i>Lozotaeniodes</i>	3			X				Bradley <i>et al.</i> 1973; Brown 2005; Razowski 2002a
<i>Lumaria</i>	10				X	X		Brown 2005; Diakonoff 1941; 1948; Razowski 2002b; Razowski <i>et al.</i> 2010; Robinson <i>et al.</i> 1994
<i>Mantua</i>	1						X	Brown 2005
<i>Meridemis</i>	11				X	X		Brown 2005; Diakonoff 1976; 1979; 1982; Robinson <i>et al.</i> 1994; Razowski 2008a; Razowski <i>et al.</i> 2010
<i>Merophyas</i>	10						X	Brown 2005; Patrick and Dugdale 1994
<i>Mesocalyptis</i>	2						X	Brown 2005
<i>Metamesia</i>	21				X			Brown 2005; Diakonoff 1960; 1973; Razowski and Trematerra 2010
<i>Midaellobes</i>	1				X			Diakonoff 1960
<i>Minutargyrotoza</i>	2			X		X		Brown 2005; Diakonoff 1976; 1982
<i>Neocalyptis</i>	29			X		X	X	Brown 2005; Byun <i>et al.</i> 2003; 2007; Diakonoff 1941d; 1948; 1951; 1967; Liu and Li 2002; Razowski 2000; Robinson <i>et al.</i> 1994; Wang <i>et al.</i> 2003
<i>Niphothixa</i>	4				X			Brown 2005; Diakonoff 1960; 1970
<i>Notiocleipsis</i>	1					X		Brown 2005
<i>Ochetarcha</i>	1						X	Brown 2005
<i>Ochrotaenia</i>	1		X					Razowski and Becker 2000
<i>Orilesa</i>	2				X			Brown 2005
<i>Panaphelix</i>	2						X	Brown 2005; Diakonoff 1957
<i>Pandemis</i>	63	X		X	X	X		Brown 2005; Byun <i>et al.</i> 2003; Chapman and Lienk 1971; Diakonoff 1960; 1963; 1970; 1973; Liu and Li 2002; MacKay 1962; Mutuura 1980; Razowski 1978 2001; Trematerra 2010a; 2010b

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APPENDIX 1. (Continued)

genus	number of spp.	Nearctic	Neotropical	Palearctic	Afrotropic	Indomalaysian	Australian/Oceania	References
<i>Paradichelia</i>	8						X	Brown 2005; Diakonoff 1941
<i>Paramesia</i>	4			X				Brown 2005; Razowski 2001; 2002a
<i>Paramesiodes</i>	5				X			Brown 2005; Diakonoff 1960
<i>Paraphasis</i>	1						X	Brown 2005
<i>Pararrhaptica</i>	19						X	Brown 2005
<i>Periclepsis</i>	2			X				Brown 2005; Křenek 2000; Razowski 2001
<i>Peteliacma</i>	1				X			Diakonoff 1960
<i>Petridia</i>	1					X		Brown 2005
<i>Phaenacropista</i>	2					X		Brown 2005; Diakonoff 1941a; 1941b; 1941c; 1941d
<i>Philedone</i>	1			X				Bradley <i>et al.</i> 1973; Razowski 2001
<i>Philedonides</i>	3			X				Bradley <i>et al.</i> 1973; Razowski 2001; 2002a
<i>Philocryptica</i>	1						X	Brown 2005
<i>Phlebozemia</i>	1				X			Brown 2005
<i>Planostochoa</i>	4					X	X	Brown 2005; Byun <i>et al.</i> 1998; Diakonoff 1941; Liu and Li 2002
<i>Planotortrix</i>	7						X	Newcomb and Gleeson 1998
<i>Platyhomopsis</i>	1			X				Brown 2005
<i>Platysemaphora</i>	1				X			Diakonoff 1960
<i>Procalyptis</i>	3						X	Brown 2005; Diakonoff 1939
<i>Procrica</i>	14				X			Brown 2005; Diakonoff 1960; 1963; Razowski 2008a; Razowski and Trematerra 2010
<i>Pseudeulia</i>	1			X				Liu and Li 2002; Razowski 2002a
<i>Pteridoporthis</i>	1						X	Brown 2005
<i>Pternozyga</i>	4					X	X	Brown 2005; Diakonoff 1939; 1941
<i>Ptycholoma</i>	5			X				Brown 2005; Byun <i>et al.</i> 2003; Liu and Li 2002; Razowski 2001; 2002a
<i>Ptycholomoides</i>	1			X				Liu and Li 2002; Razowski 2001
<i>Pyrgotis</i>	12					X	X	Brown 2005
<i>Pysarcha</i>	1					X		Brown 2005
<i>Saetotaenia</i>	1		X					Brown 2005
<i>Scotiophyes</i>	3					X		Brown 2005; Liu and Li 2002; Robinson <i>et al.</i> 1994
<i>Snodgrassia</i>	4					X	X	Brown 2005; Diakonoff 1941; 1967
<i>Sorensenata</i>	1						X	Brown 2005
<i>Spheterista</i>	17						X	Brown 2005
<i>Spinotaenia</i>	1		X					Razowski and Becker 2000
<i>Sychnochlaena</i>	1					X		Brown 2005
<i>Sychnovalva</i>	4		X					Razowski 1997; Razowski and Becker 2000
<i>Syndemis</i>	10	X		X		X	X	Brown 2005; Diakonoff 1948; 1953; Liu and Li 2002; Razowski 2001; Trematerra 2010b

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APPENDIX 1. (Continued)

genus	number of spp.	Nearctic	Neotropical	Palearctic	Afrotropic	Indomalaysian	Australian/Oceania	References
<i>Tacertaenia</i>	1		X					Razowski 1997
<i>Terricula</i>	5			X		X		Brown 2005; Jinbo 2000
<i>Terthreutis</i>	11					X		Brown 2005; Diakonoff 1951; 1976; Liu and Li 2002
<i>Thrincophora</i>	14						X	Brown 2005; Diakonoff 1939; 1952; 1953
<i>Tosirips</i>	2			X				Byun <i>et al.</i> 2003; Liu and Li 2002; Razowski 2002a
<i>Tremophora</i>	6						X	Brown 2005; Diakonoff 1953
<i>Tuckia</i>	2				X			Brown 2005
<i>Ulodemis</i>	5					X		Diakonoff 1941c; 1941d; 1976; Liu and Li 2002; Robinson <i>et al.</i> 1994
<i>Vialonga</i>	2				X			Diakonoff 1960; 1973
<i>Viettea</i>	1				X			Diakonoff 1960
<i>Williella</i>	2						X	Brown 2005
<i>Worcesteria</i>	1				X			Brown 2005
<i>Xeneda</i>	1						X	Diakonoff 1961
<i>Xenophylla</i>	1				X			Diakonoff 1960
<i>Xenotemma</i>	1	X						Chapman and Lienk 1971; Razowski 1981
<i>Xenothictis</i>	6						X	Brown <i>et al.</i> 2003
<i>Zacorisca</i>	30					X	X	Brown 2005; Diakonoff 1941a; 1941d; 1948; 1967; Robinson <i>et al.</i> 1994
new genus 1	8						X	Brown 2005
new genus 2	10						X	Brown 2005
new genus 3	1						X	Brown 2005
new genus 4	3						X	Brown 2005
new genus 5	6						X	Brown 2005
new genus 6	19						X	Brown 2005
new genus 7	9						X	Brown 2005
new genus 8	2						X	Brown 2005
new genus 9	18						X	Brown 2005
new genus 10	14						X	Brown 2005
new genus 11	1						X	Brown 2005
new genus 12	13						X	Brown 2005
new genus 13	1						X	Brown 2005
new genus 14	1						X	Brown 2005
new genus 15	6						X	Brown 2005
new genus 16	1						X	Brown 2005
unplaced	20		X	X	X	X		Brown 2005
total	1709	14	15	40	44	50	81	

APPENDIX 2. Clade justifications, only clades with weak support or additional morphological comments are discussed.

Archipini summary tree (Fig. 3)

- 2— The clade of Sparganothini plus Archipini is poorly supported, although it is in agreement with Powell's (1964) phylogenetic hypothesis.
- 3— The monophyly of Archipini inclusive of Epitymbiini (represented by *Epitymbia alaudana*) is strongly supported by Bayesian analyses and not contradicted by other analyses of combined sequence data. Parsimony and likelihood analyses of COI do not support this clade, placing Ceracini near *Xenothictis* and *Clepsis*, respectively, neither of which are supported morphologically (JJD *pers. obs.*).
- 4— The core Archipini are weakly supported, potentially due to the variable positioning of basal Archipini. This group is morphologically well supported by obsolete costal sclerotization of the male genitalia (Horak 1999) (Figs. 15, 16), but see comments for clades 17 and 20 for *Cryptoptila* and *Epichoristodes*.
- 5— Monophyly of *Adoxophyes* is weakly supported if *Thrincoptora* is included. While *Thrincoptora* has an obviously enlarged point on the sacculus that is lacking in *Adoxophyes* (Diakonoff, 1939), the transtilla is obsolete in the middle and dentate at the base, which is similar to that in *Adoxophyes* (JJD *pers. obs.*). We do not suggest any generic changes pending a broader sampling of the large genus *Adoxophyes*.
- 7— The very strong molecular support for this clade is supported by morphological similarity between these two species (Freeman 1958).
- 8— This pair of *Adoxophyes* species is also well supported by both morphology and DNA (Lee *et al.* 2005).
- 13— The relationship between the *Choristoneura* and *Archips* groups is weakly supported, but both have overall similar male genitalia (Razowski 1987) and a typically very long ductus bursae and prominent cestum in the female genitalia (JJD *pers. obs.*).
- 15— These two *Homona* species have good support as sister taxa, which agrees with Hulcr *et al.* (2007). They are isolated from other *Homona* species within the genus *Archips*, which agrees with Razowski's (1987) concept of *Homona* as polyphyletic.
- 16— These two genera have strong support as sister taxa, which is also well supported by morphology (Razowski 2002a).

Basal Archipini (Fig. 4)

- 17— There is weak support for the basal Archipini group, potentially due to the uncertain placement of *Xenothictis* and *Cryptoptila*. These two genera, along with the other genera in this group, all have a partially sclerotized costa of the valve in the male genitalia, although this may be plesiomorphic (Horak & Brown 1991; Razowski 1987). *Xenothictis* fits well in this group based on male genitalia (Brown *et al.* 2003), but together with *Acropolitis*, there is uncertainty over what their nearest relatives are. We chose to exclude *Cryptoptila* from the basal Archipini and placed it in the core Archipini near *Adoxophyes* and *Thrincoptora*, based on similarity with the latter genus in their male genitalia, as noted by Common (1956) (see also comments on clade 5). Also included in this group are the Epitymbiini, represented in these analyses by *Epitymbia alaudana*. This agrees with the morphological similarity between Epitymbiini and Archipini (Common 1956). See clade 20 for comments on *Epichoristodes*.
- 20— This clade is well supported by our analyses, although with a basal polytomy. *Epichoristodes* has usually been placed in the core group of Archipini based on the reduced costa of the valve (Razowski 2002a). Diakonoff (1960) suggested that *Epichoristodes* was similar to *Epichorista* (not examined in our analyses) which also has obsolete costal sclerotization (Diakonoff 1939); implicating it as belonging to the basal Archipini. This may be a convergent reduction as the overall valve shape is less plicate and Dugdale (1990) places it in the basal Archipini.
- 22— The monophyly of *Ctenopseustis* is weakly supported but agrees with the molecular phylogeny of Newcomb & Gleason (1998) and the morphological characters of Dugdale (1990).
- 26— This poorly supported clade disagrees with Dugdale's (1990) suggestion that *Leucotenes* is closer to *Ctenopseustis* based upon overall appearance and phallus shape, which are often variable characters. *Leucotenes* appears closer to *Planotortrix* if consideration is given to both of these genera having cubital pecten on the hindwing, which is a rare character in the Archipini (Freeman 1958). The status of *Leucotenes* will remain unresolved until more DNA or morphological work is done to supplement the 472 bp of CO1 available in our analyses.
- 27— This clade is variably supported, but agrees with parsimony analysis of this data by Newcomb and Gleason (1998). See also clade 26.
- 29— This clade is well supported by all analyses and agrees with the parsimony analysis of this data by Newcomb & Gleason (1998).
- 30— This clade is well supported by all analyses and agrees with the parsimony analysis of this data by Newcomb & Gleason (1998).

Pandemis group (Fig. 5)

- 33— *Pandemis*, with a few exceptions, is well defined morphologically with a modified pregenital sternite (Fig. 15), basal ventral abdominal scale tufts (Fig. 14), and antennal notch (Fig. 11) (Dombroskie & Sperling 2012). *Arche pandemis* is very similar in venation and genitalia to *Pandemis*, but lacks the defining SSCs present in most species (Mutuura 1978). This is likely due to a loss of these characters, a phenomenon that is frequent in certain *Pandemis* species (Fig. 10), and is

supported by the presence of a subtle antennal notch present in *Archebandemis*. Maintaining *Archebandemis* as a valid taxon would require the erection of many genera with few synapomorphies from basal *Pandemis* species. Based on DNA sequence, similar morphology, presence of a partial antennal notch, and nomenclatural stability, we chose to synonymize *Archebandemis* with *Pandemis*.

- 34—The position of *Pandemis corylana* (Fabricius 1794) as sister to the remainder of the *Pandemis* group is well supported in these analyses, although this conflicts with other analyses (Dombroskie & Sperling, 2012) using COI and ITS2, which place it as a well supported sister clade to *P. cinnamomeana* (Treitschke 1830). Arguments could be made for either clade since *P. corylana* has reduced basal abdominal scale tufts (Razowski 1987). Treating *P. corylana* as basal to the other *Pandemis* is supported if it is assumed to have a pleisiomorphic weak development of this SSC. Placing it as sister to *P. cinnamomeana* is supported if the SSC is assumed to be secondarily reduced. We chose the first scenario based on the stronger bootstrap values and posterior probabilities of that grouping.
- 35—This clade is weakly supported but we chose it based partially on the basis of these species having a noticeably straighter sacculus relative to *P. corylana* and *P. cinnamomeana* (JJD pers. obs.).
- 36—The phylogenetic position of *Archebandemis* within the *Pandemis* group is well supported.
- 37—This clade and the clades within it are well supported by all analyses.

Argyrotaenia group (Fig. 6)

- 41—The monophyly of the *Argyrotaenia* group (Fig. 3) varies in support and has deep divisions between the two main clades. Based on genitalic similarity among these two clades, they are likely monophyletic (Freeman 1958).
- 42—This clade is present in all analyses, though only with good support for the COI parsimony analysis and both Bayesian analyses. *Diedra* was described based on five very similar species with several distinct synapomorphies, including a relatively sclerotized valve and basal flange on the phallobase (Rubinoff & Powell 1999). These species were traditionally considered to be *Argyrotaenia* (Powell 1964), and their placement inside *Argyrotaenia*, as sister group to a southwest Nearctic clade, is supported by their similarly thickened sacculus (JJD pers. obs.). The simplest solution to dealing with the paraphyly of *Argyrotaenia* would be to synonymise *Diedra*; however, we are reluctant to do this since the support for maintaining clade 42 within *Argyrotaenia* is weak. Other solutions are to either broaden the definition of *Diedra* to include clade 43, or erect a new genus or subgenus for clade 43. Until further SW Nearctic species in this group are examined, we chose to maintain the nomenclatural status quo.
- 43—This clade is fairly well supported. Although it has been stated that *Argyrotaenia* genitalia are invariant (Freeman, 1944), these three species can be separated from the other main *Argyrotaenia* lineage by the much broader sacculus in the male genitalia (JJD pers. obs.).
- 44—The close relationship of these two species is well supported by our molecular analyses and by genitalic morphology (Powell 1960; 1964).
- 45—The position of this clade is weak with half of the analyses placing clade 46 as sister to clade 42. They are positioned here based on the Bayesian analyses which consistently produced high posterior probabilities, and by a similar slender sacculus compared to clade 42.
- 47—This clade is well supported by all analyses and agrees with parsimony analysis of COI sequence data in Landry *et al.* (1999).
- 48—This clade is strongly supported by these analyses and by similar herbivory of most species on Fagales (Brown *et al.* 2008), despite *A. juglandana* (Fernald, 1879) being treated as an entirely separate group by MacKay (1962) based on larval morphology. However, the clades within it are weakly supported and contradict each other or lack resolution in some analyses.
- 51—This clade is also well supported by some molecular analyses as well as by genitalia which are barely morphologically distinguishable from each other in the included species (JJD pers. obs.).
- 52—*Argyrotaenia provana* (Kearfott, 1907) is recovered as basal to *A. coloradana* (Fernald, 1882) in both parsimony analyses, though with weak support, but is placed here as sister to the remaining *Argyrotaenia* on the basis of higher support from ML and Bayesian analyses.
- 54—This strongly supported group is also supported by wing patterns that can be scarcely distinguishable between species, and nearly identical genitalia among the included species (JJD pers. obs.).
- 55—This weakly supported clade was contradicted in both parsimony analyses, which placed *A. repertana* Freeman, 1944 as basal to *A. ljungiana* (Thunberg, 1797), but with no support. The topology in Fig. 6 is supported, however, by both species being polyphagous on predominantly marsh-inhabiting shrubs (Brown *et al.* 2008), and adults being found in boggy habitats for *A. repertana* (JJD pers. obs.) and moors and mires for *A. ljungiana* (Svensson 2006).

Clepsis group (Fig. 7)

- 61—A potential reason for the weak support for the *Clepsis* group, and many clades within it, is the placement of basal Archipini, *Cacoecimorpha*, or *Lozotaeniodes* within this clade in some analyses. There are no good morphological characters supporting the first two inclusions (JJD pers. obs.), and these are unsupported by other analyses. The inclusion of *Lozotaeniodes* has some merit since it has the incomplete and dentate transtilla of the male genitalia typical of *Clepsis* (Fig. 16) (Razowski 1987). In three of the analyses the genus appears within *Clepsis*, though never in a stable position and with a long branch. In two analyses the species is placed as sister to some of the basal Archipini, which is unsupported by

morphology. Because of this uncertainty, we have kept *Lozotaeniodes* outside of *Clepsis* as part of the large polytomy of the core Archipini (Fig. 3). *Clepsis* is considered to have no reliable synapomorphies (Razowski 1979a) as it is currently defined since many of the characters that are traditionally used are found in some form in a variety of other genera (JJD pers. obs.). However, Razowski (1979a; 1987) is confident of its monophyly. For comments on the inclusion of *Epiphyas*, see clade 68.

- 62—This clade is recovered as a mix of the *C. rogana* (*C. clemensiana* & *C. moeschleriana* in our analyses) and *C. pallidana* (*C. consimilana*, *C. melaleucana*, *C. persicana*, *C. siciliana* & *C. spectrana* in our analyses) species groups (Razowski 1979a) with neither being monophyletic. The tree topology in Fig. 7 was selected due to the presence of this clade in both likelihood and Bayesian analyses using combined sequence data, and since no anomalous taxa are included within this clade.
- 67—This clade unites two well supported groups, although with weak support values for similar reasons to those mentioned for clade 61. See clade 68 for a potential synapomorphy.
- 68—*Clepsis fucana* (Walsingham 1879) is strongly supported as sister to *Epiphyas*, which is also supported by the total replacement of *Clepsis* in Australia by *Epiphyas* and their male genitalic similarity (JJD pers. obs.). *Epiphyas* also has nearly identical glands in the male abdomen to those found in the *C. peritana* group (Razowski 1987). Molecular results squarely place *Epiphyas* within *Clepsis*, and there are no reliable morphological characters to separate the genera (JJD pers. obs.), however we are reluctant to propose that *Epiphyas* be synonymised with *Clepsis* until more species are examined.
- 69—The genus *Epiphyas* is usually recovered as monophyletic with strong support values, which is also supported by genitalic characters and its zoogeographic restriction to Australia (Razowski 2002a).
- 71—This clade is usually well supported and agrees with the *C. peritana* group (*sensu* Razowski 1979b). See also clade 72 comments.
- 72—*Clepsis anderslaneyii* Dombroskie & Brown, 2009 has moderate support as sister to *C. virescana* (Clemens 1865). This conflicts with Dombroskie & Brown (2009) where it was considered closest to *C. fucana* based on male genitalia. However, except for the much broader uncus, it can reasonably be placed in the *C. peritana* group based on the similar sacculus bulge and prolonged valval apex (JJD pers. obs.).
- 73—This clade is well supported by Bayesian analyses, although the position of *C. listerana* (Kearfott 1907) is unclear. In the COI likelihood, and both Bayesian analyses it is recovered as monophyletic with *C. penetralis* Razowski 1979, which would be reasonable if *C. listerana* has at least a partially coiled ductus bursae. This sequence was obtained through GenBank; however, JJD has examined this specimen so the identity is not in doubt. Unfortunately however, the genitalia of this rarely encountered species are undescribed and the only mention of its morphology in the literature is from the original description by Kearfott (1907).
- 74—This clade is supported in half of the analyses, but the topology shown here agrees with the overall similarity in the genitalia and wing pattern of these two species (JJD pers. obs.). See also comments on clade 73.

Choristoneura group (Fig. 8)

- 75—The *Choristoneura* group has weak support, perhaps due to the uncertain placement of *Archips purpurana*. We chose to put it basally in the *Choristoneura* group rather than the *Archips* group because the support for this topology was overall slightly higher. *Archips purpurana* is problematic, and despite placing it within the *A. xylosteana* group Razowski (1977) commented on its anomalous placement. Its valve shape is unique within *Archips*, with the sacculus margin not prominently bulging below the sacculus, a much shorter uncus, and overall appearance and lack of dorsal abdominal pits (JJD pers. obs.). Therefore it likely does not belong in *Archips*.
- 76—This clade has weak support, though these genera are considered to be closely related (Razowski 1987).
- 77—While this group has weak support in our analyses, its members have enough genitalic similarities that their placement together by Razowski (1987) is reasonable. There is also strong support to elevate two of the subgenera in *Aphelia* (*Aphelia s. s.* clade 78, and *Zelothereses* clade 81) to genera to maintain generic monophyly according to these analyses. Synapomorphies for clades 78 and 83 are discussed below. *Aphelia* (*Zelothereses*) and *Lozotaenia* do not have known synapomorphies (Razowski 1987). Obraztsov (1954) originally treated *Aphelia* as having three subgenera (*Aphelia s. s.*, *Djakonovia*, and *Zelothereses*), and he (1959) later elevated his three subgenera to the genus level. Razowski (1981) later synonymised *Djakonovia* under *Zelothereses* and described two other subgenera, *Anaphelia* and *Sacaphelia*. Razowski (1981; 2002a) argued for maintenance of all four taxa as subgenera until all archipine genera are revised. Despite the lack of synapomorphies for *Zelothereses*, the other remaining subgenera have distinct characters in the male genitalia that separate them and are good candidates for synapomorphies. We were unable to examine specimens of *Anaphelia* or *Sacaphelia* due to their restricted east Palaearctic distribution; however, the genitalia figures and descriptions in Razowski (1981) are of excellent quality. *Anaphelia* has paired dentate processes in the center of the transtilla, *Aphelia s. s.* has dentate lateral processes on the transtilla, and *Sacaphelia* has large dentate processes at the base of the valve, fused with the dentate transtilla. For a thorough discussion of these characters, see Razowski (1981). The dentate processes on the transtilla or valve are a potentially unifying character for *Anaphelia*, *Aphelia s. s.*, *Lozotaenia*, *Sacaphelia*, and *Xenotemna*. For this reason and the non-monophyly of *Aphelia* according to our analyses, we propose that *Anaphelia*, *Sacaphelia*, and *Zelothereses* be raised to generic status separate from *Aphelia s. s.* See also Clade 81.

- 78—This clade is variably supported. Likelihood and Bayesian analyses of COI conflict with this topology and place *A. purpurana* (Clemens, 1865) and *A. alleniana* (Fernald, 1882) in a weakly supported monophyletic group, with *X. pallorana* (Robinson, 1869) basal to them. Both species have traditionally been included in the genus *Aphelia* because they have a dentate gnathos that is probably a synapomorphy for *Aphelia s. s.* (Razowski 1987), and the larvae are similar (MacKay 1962). Curiously, MacKay also finds the larvae similar to *Clepsis*, and this may have influenced *X. pallorana* being placed in that genus in Chapman & Lienk (1971). While *X. pallorana* has distinct male and female genitalia, no justification has been published for the erection of the genus *Xenotemna*. The name was first published in Powell (1964) who variably treated it as “*Tortrix*” and *Xenotemna*. Because of the very large, dentate gnathos and dentate spines in the center of the valve in the male genitalia, and the pointed eighth tergite and broad dentate signum in the female, we choose to maintain *X. pallorana* in its monotypic genus. See also comments on *Aphelia* under clade 77.
- 81—This well supported clade agrees with the subgenus *Zelothereses* of *Aphelia* (Razowski 1981; 1987). Its phylogenetic placement is also supported by the unmodified transtilla of *Zelothereses* which is more similar to *Dichelia* and *Syndemis* than to other *Aphelia* subgenera (JJD pers. obs.). See comments for clade 77.
- 82—This clade is well supported in our analyses and supported by the close similarity of the two species (Razowski 1981).
- 83—This clade is strongly supported and is united by the male having a pair of long tufts of modified scales anteriorly on the thorax (Fig. 12). The genera are also similar enough that Svensson (2006) lumps them both into *Syndemis*. Until more species of both *Dichelia* and *Syndemis* are examined, we choose to maintain them as separate genera for nomenclatural stability.
- 84—These two *Syndemis* species are morphologically virtually inseparable (Freeman 1958) and have excellent support in our analyses.
- 85—This clade is well supported by both Bayesian analyses, and even though *Cacoecimorpha* has such divergent genitalia that it is difficult to compare to typical *Choristoneura*, there are genitalic similarities in valve shape to the enigmatic *Ch. lafauryana* (Ragonot 1875) (JJD pers. obs.). *Choristoneura lafauryana* was unfortunately not obtained for our molecular analyses.
- 86—The monophyly of *Choristoneura* inclusive of *Cudonigera* has weak but fairly consistent support. However, in two of the trees, *C. albaniana* (Walker, 1863) is found as sister to *Cacoecimorpha* with weak support. Our retention of *C. albaniana* within *Choristoneura* is supported by its lack of synapomorphies for *Cacoecimorpha* (Razowski 1987), and the dorsal raised area on the uncus in the male genitalia that place it in *Choristoneura* (Dang 1992a; Razowski 1987). See also note for clade 92.
- 88—Both parsimony and Bayesian analyses of COI placed *C. murinana* (Hübner, 1799) as basal to the remainder of clade 87, but with weak support.
- 89—This clade is well supported and agrees with the male genitalic similarity of these two species (Razowski 2002a).
- 91—This well supported clade is also unified by the broad uncus in the male genitalia (JJD pers. obs.).
- 92—This clade has support from four of the analyses, although both likelihood and Bayesian analyses of COI place *C. argentifasciata* Heppner, 1989 as basal to the remainder of clade 91. While the host plant of *C. argentifasciata* is unknown, it is strongly suspected to be *Taxodium distichum* (Heppner 1989). This would link both taxa as specialized Cupressaceae feeders and support this tree topology. While the characters that define the monotypic genus *Cudonigera* are convincing, this taxonomic treatment would render the genus *Choristoneura* polyphyletic according to our analyses. Powell & Obraztsov (1977) state that *C. houstonana* is derived from *Choristoneura*, but they suspected that it would fit closely with MacKay’s (1962) *Choristoneura* group 2 (clade 95 in our analyses), while our analyses place it confidently in group 3 (clade 91 in our analyses). *Cudonigera* is strongly supported as being within *Choristoneura* in clades 87, 90, and 91 and, rather than divide *Choristoneura* into several genera, we synonymise *Cudonigera* with *Choristoneura*.
- 93—This well supported clade agrees with the overall similarity of these species as adults and larvae, corresponding to *Choristoneura* group 3 (MacKay 1962).
- 95—It is not surprising that the conifer-feeding *Choristoneura* group (group 2 of MacKay 1962) is well supported since the included species are often very difficult to distinguish. These species often share haplotypes across species (Lumley & Sperling 2010) and our analyses only used a single representative of each species, so the specific tree topology should be taken as a generalization only.

Archips group (Fig. 9)

- 100—The *Archips* group is well supported only by Bayesian analysis of COI, although most analyses also support it weakly (Fig. 3). The exclusion of *A. purpurana* from this group is consistent with the molecular analyses of Kruse & Sperling (2002) which had similar taxon coverage. See also clade 75.
- 101—This clade is weakly supported, and in those analyses that disagree, the four *Homona* species in this clade are placed as basal to the core Archipini, usually with weak support. Though these *Homona* lack the costal fold typical of *Archips*, they are genitally similar in both males and females, including the long ductus bursae with prominent cestum common to both *Archips* and *Choristoneura* groups (JJD pers. obs.). *Homona salacensis* (Meyrick, 1912) has previously been placed in *Archips* by Diakonoff (1967). Razowski (2004) commented on the similarities between *Choristoneura*, *Homona*, and other genera. Due to the weak support for the inclusion of these four *Homona* species within *Archips* and our sampling of only six of the 34 total described species, we maintain them in their existing genus. However, it is clear that that *Homona* is polyphyletic if *H. spargotis* and *H. trachyptera* are included in the genus (Fig. 3: clade 15). Examining sequence data from *H. coffearia*, the type species of *Homona* (as *H. fasciculana* Walker, 1863) may help resolve which taxa belong to this genus.

- 102**—This clade is strongly supported and consistent with the same data used in Hulcr *et al.* (2007).
- 103**—While this clade has very weak support, it is consistent with the same weakly supported node in the NJ tree of Hulcr *et al.* (2007).
- 104**—This clade is strongly supported by all analyses and is also supported both molecularly and morphologically by Miller *et al.* (2010).
- 105**—This clade is present in most trees, and although usually weakly supported it is consistent with the phylogeny of Razowski (1977).
- 106**—The strong support for this clade agrees with the similar genitalia (Razowski 1977) and larval morphology of its members (MacKay 1962). This is also consistent with the concept of *Archippus* (Freeman 1958) and agrees with the molecular analysis of COI by Kruse & Sperling (2002).
- 108**—This strongly supported clade corresponds well with the concept of the *A. xylosteana* group (Razowski 1977). It disagrees slightly with the phylogeny of Kruse & Sperling (2002) due to their placement of the *A. packardiana* group as sister to the *A. cerasivorana* group, a placement that had weak bootstrap support in their analyses.
- 109**—While strongly supported in our analyses, this conflicts with the views of Razowski (1977) who, without clear justification, grouped *Archips rosana* as closer to the main Nearctic clade than to *A. xylosteana* (Linnaeus, 1758).
- 110**—The placement of clade 111 has some uncertainty. Where analyses disagree with this topology, clade 111 is either placed as sister to clade 109 or basal to 109 + 114. See also comments under clade 109 and 114.
- 111**—This well supported clade agrees with the adult morphology since the adults of all four species lack the dorsal abdominal pits typical of most *Archips* (Freeman 1958), the larval communal habits and morphology, which are distinct from other *Archips* (MacKay 1962).
- 113**—This clade is well supported, but conflicts with the phylogeny of Kruse & Sperling (2002), who place *A. infumatana* (Zeller, 1875) and *A. fervidana* (Clemens, 1860) as sister taxa. However, they used a smaller segment of COI (820 bp) was used in their analysis, and the clade had weak bootstrap support.
- 114**—This clade is well supported but conflicts with Razowski's (1977) view that *A. rosana* is closer to the main Nearctic clade, although he gives little justification for it. It is also inconsistent with a weakly supported portion of the tree of Kruse & Sperling (2002) (see comment for clade 109).
- 115**—This clade has weak support perhaps due to the uncertain position of *A. fuscocupreana* Walsingham, but was present in all analyses.
- 117**—Both parsimony analyses place *Archips grisea* (Robinson, 1869) and *A. magnoliana* (Fernald, 1892) in a monophyletic group, which is consistent with Kruse & Sperling (2002). The remainder of the analyses weakly support *A. grisea* as sister to *A. negundana* (Dyar, 1902) and *A. semifera* (Walker, 1863). I use the latter arrangement, due to the genitalic similarity of these three species (Razowski 1977).
- 118**—The relationship of these two closely related species is also supported by very similar genitalia (Freeman 1958).
- 119**—While this clade is supported by all analyses and agrees with the analysis of COI by Kruse & Sperling (2002), it conflicts with the suggestion by Razowski (1977) that *A. georgiana* (Walker, 1863) and *A. grisea* are closely related because of their very similar male genitalia.
- 120**—This clade and the more terminal clades are consistent with both mtDNA analyses by Kruse & Sperling (2001; 2002).
- 122**—These two species have overlapping morphological variation and COI sequences (Dombroskie & Sperling *unpublished*) and *A. eleagnana* (McDunnough, 1923) may be a host plant race of the polymorphic species *A. argyrospila*.

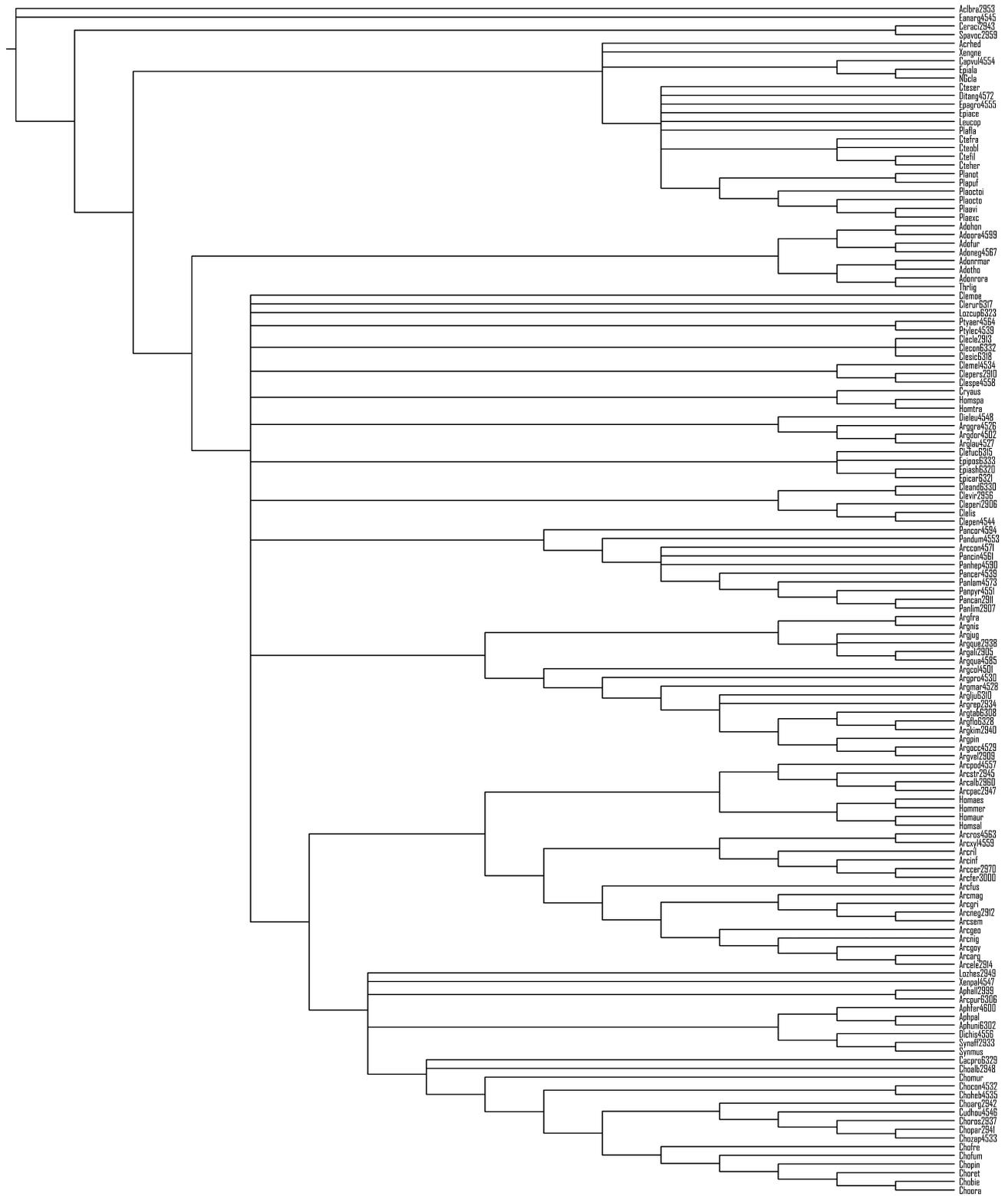
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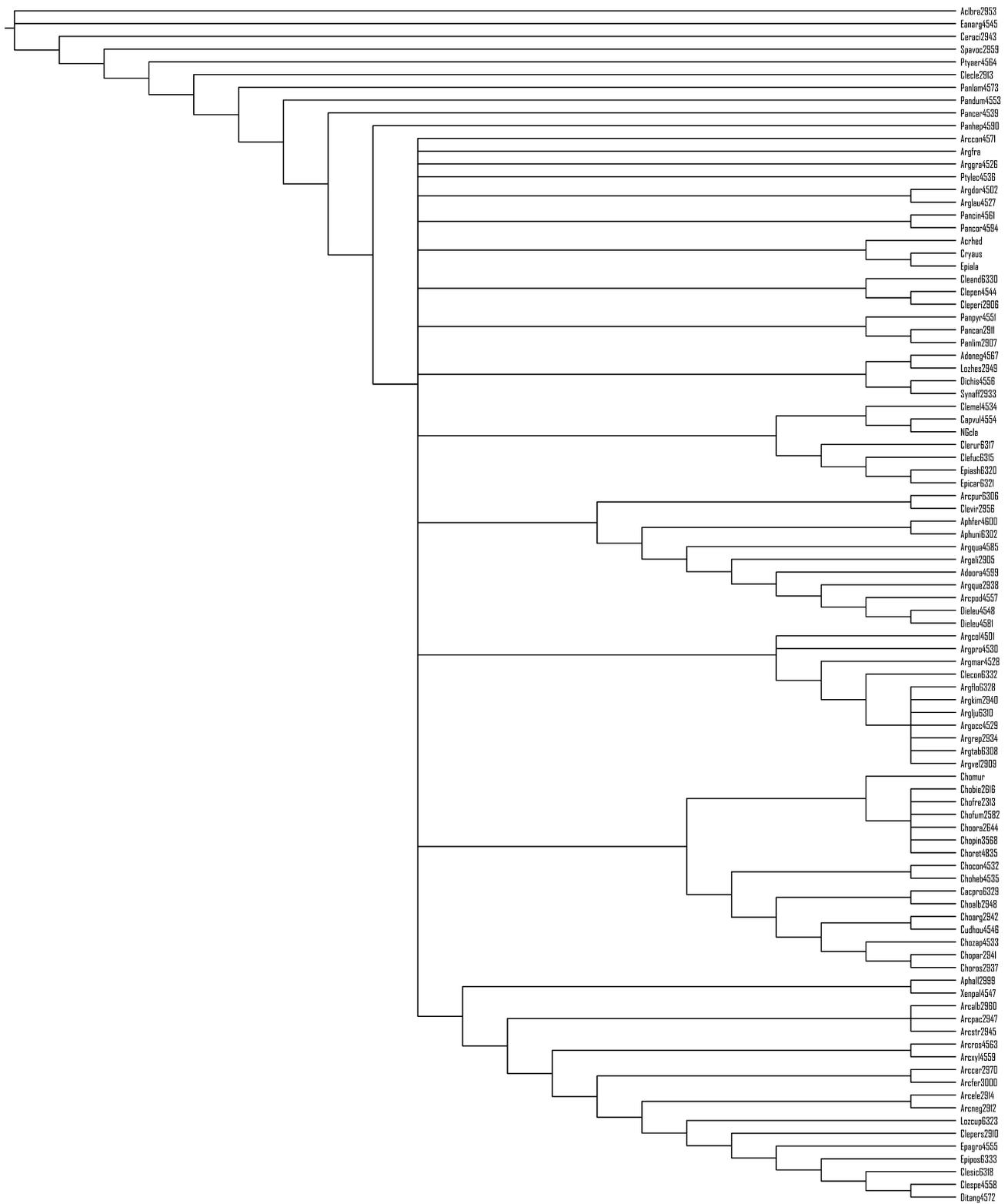
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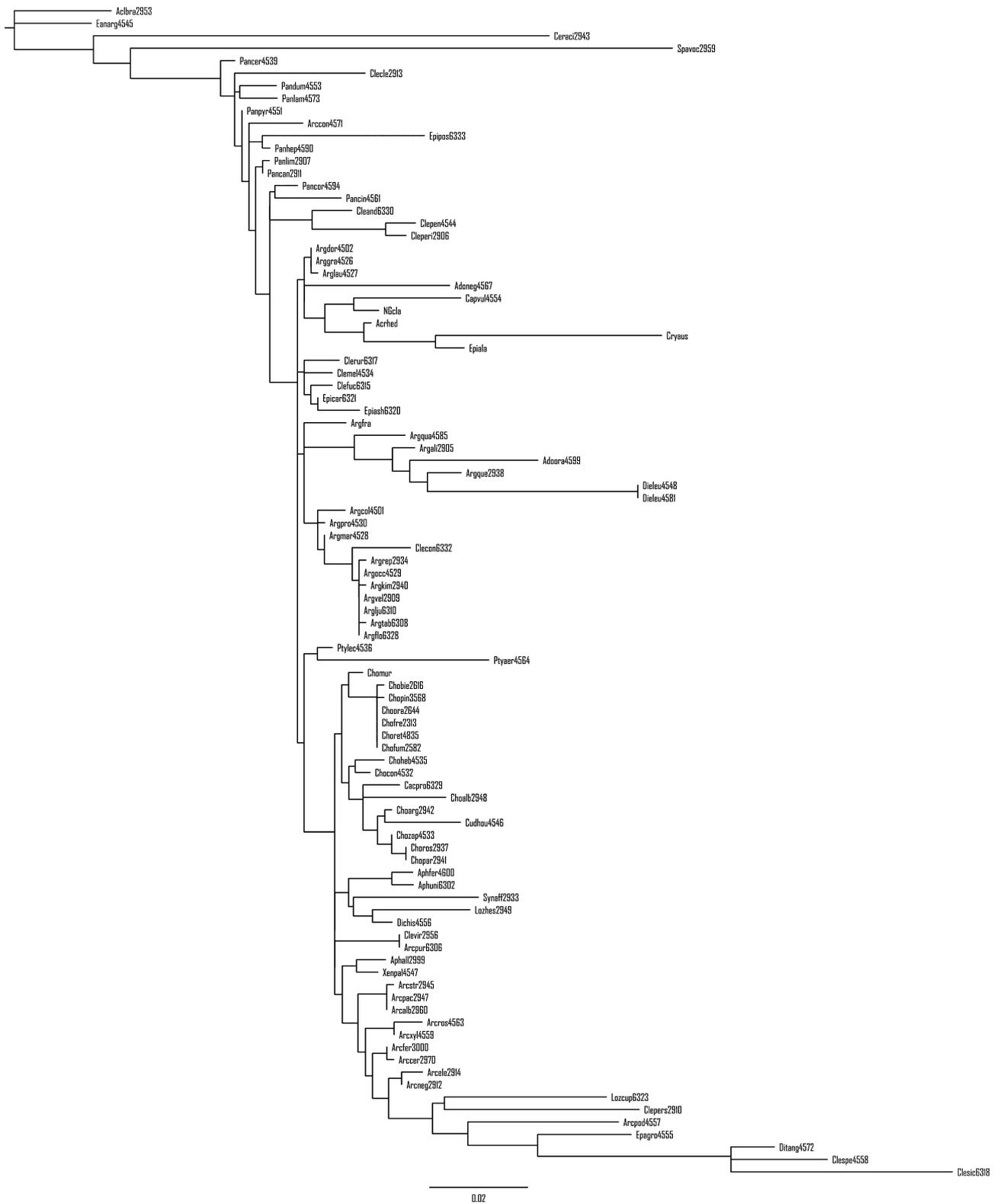
APPENDIX 3.



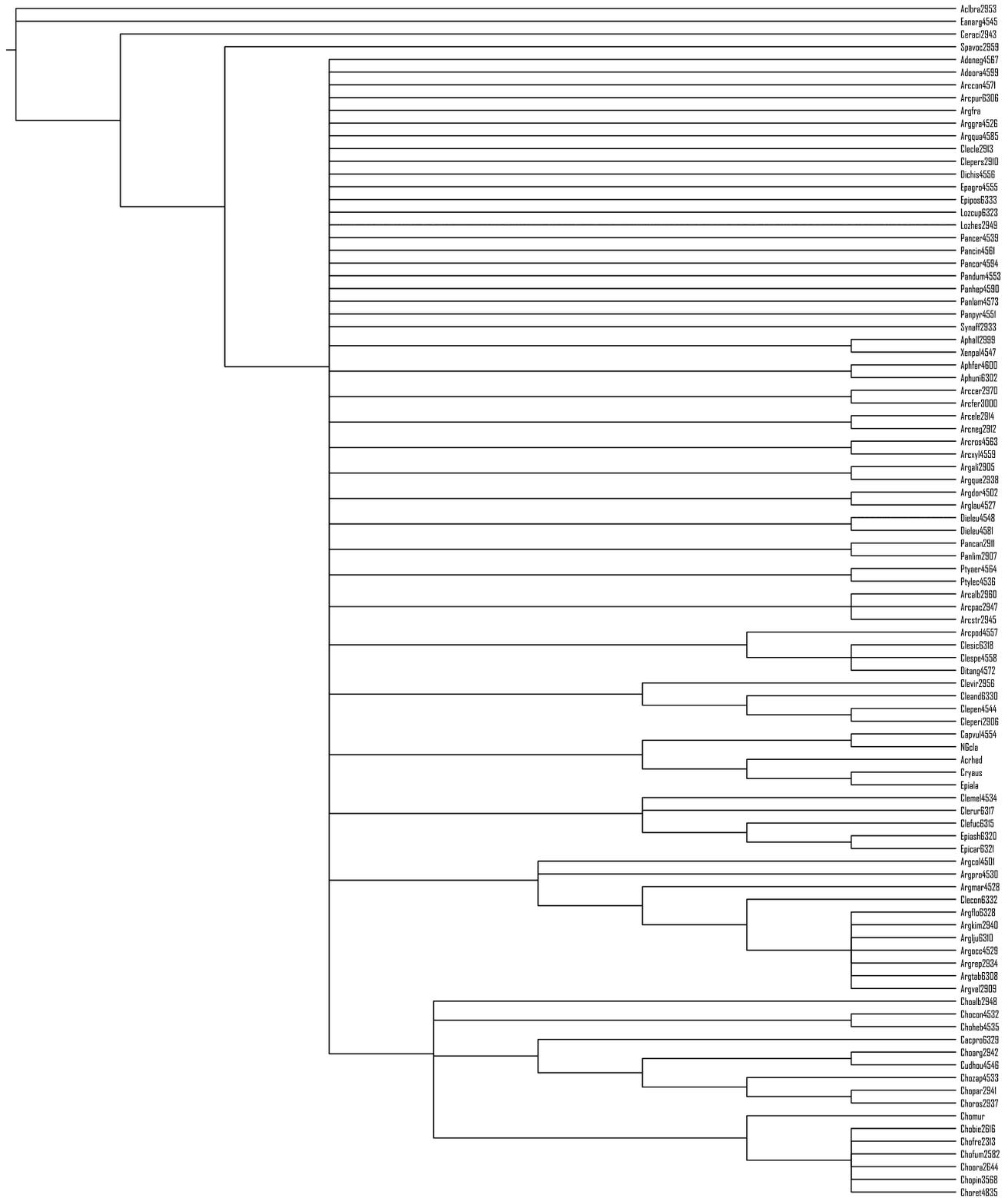
APPENDIX 4.



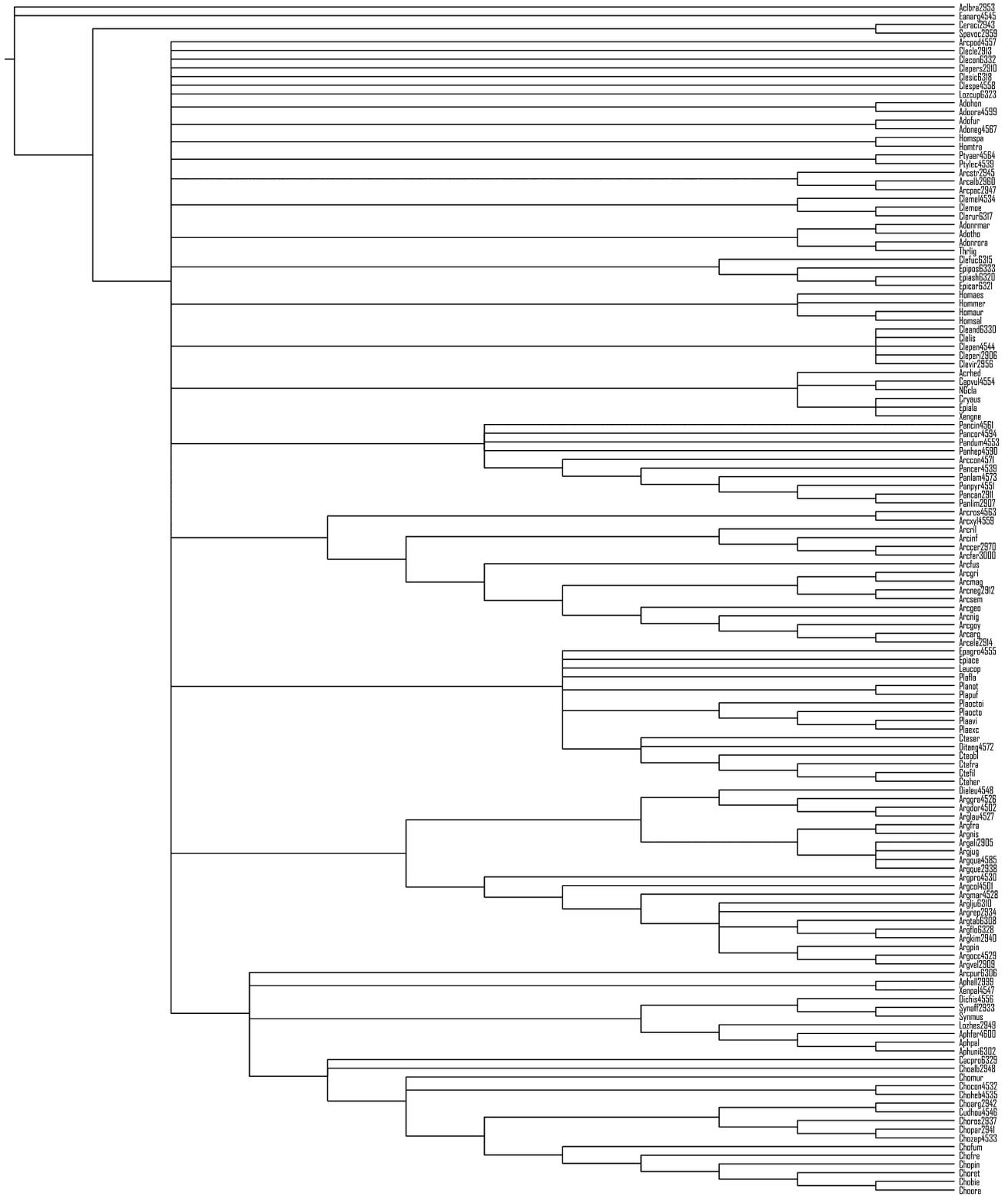
APPENDIX 5.



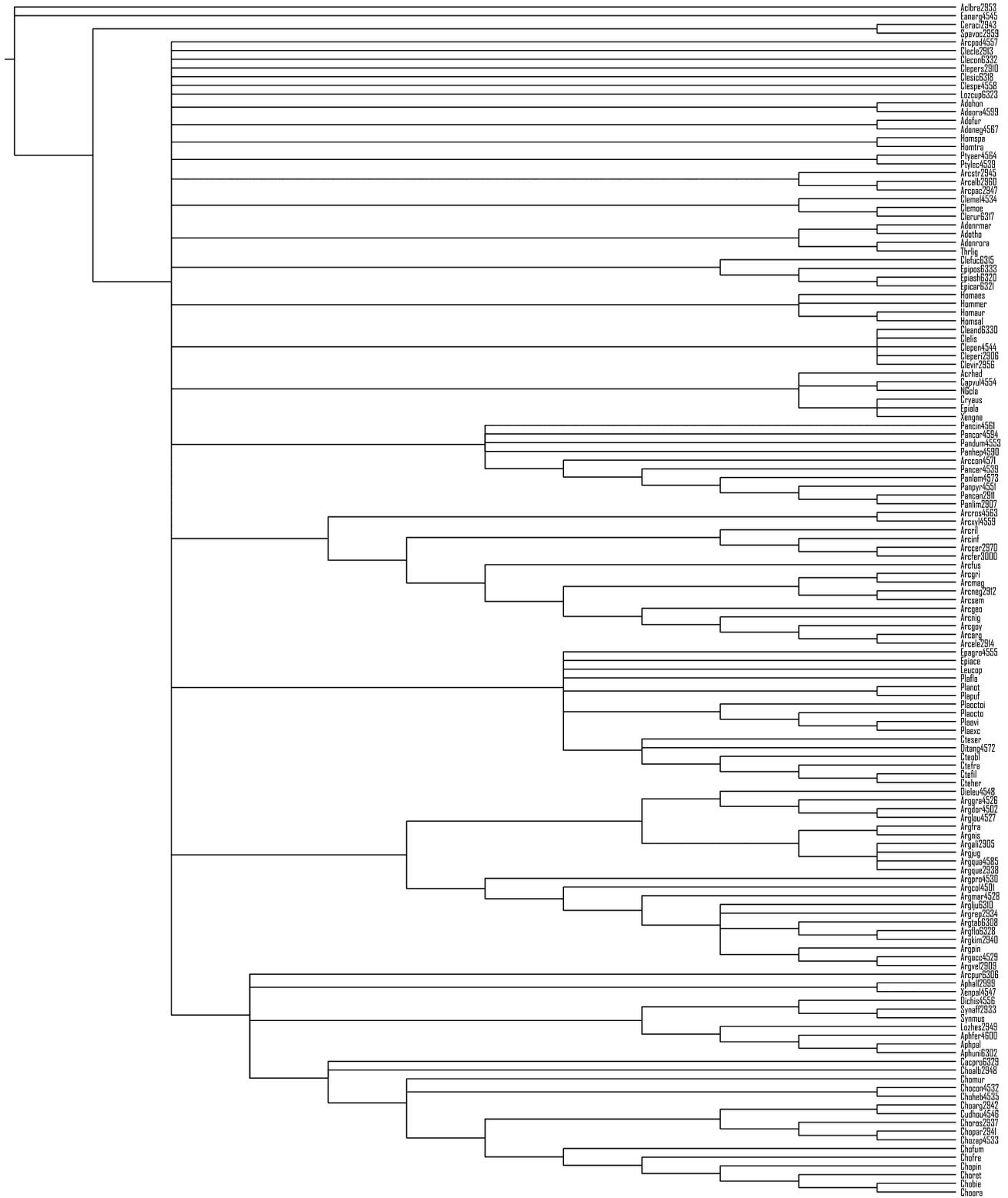
APPENDIX 6.



APPENDIX 7.



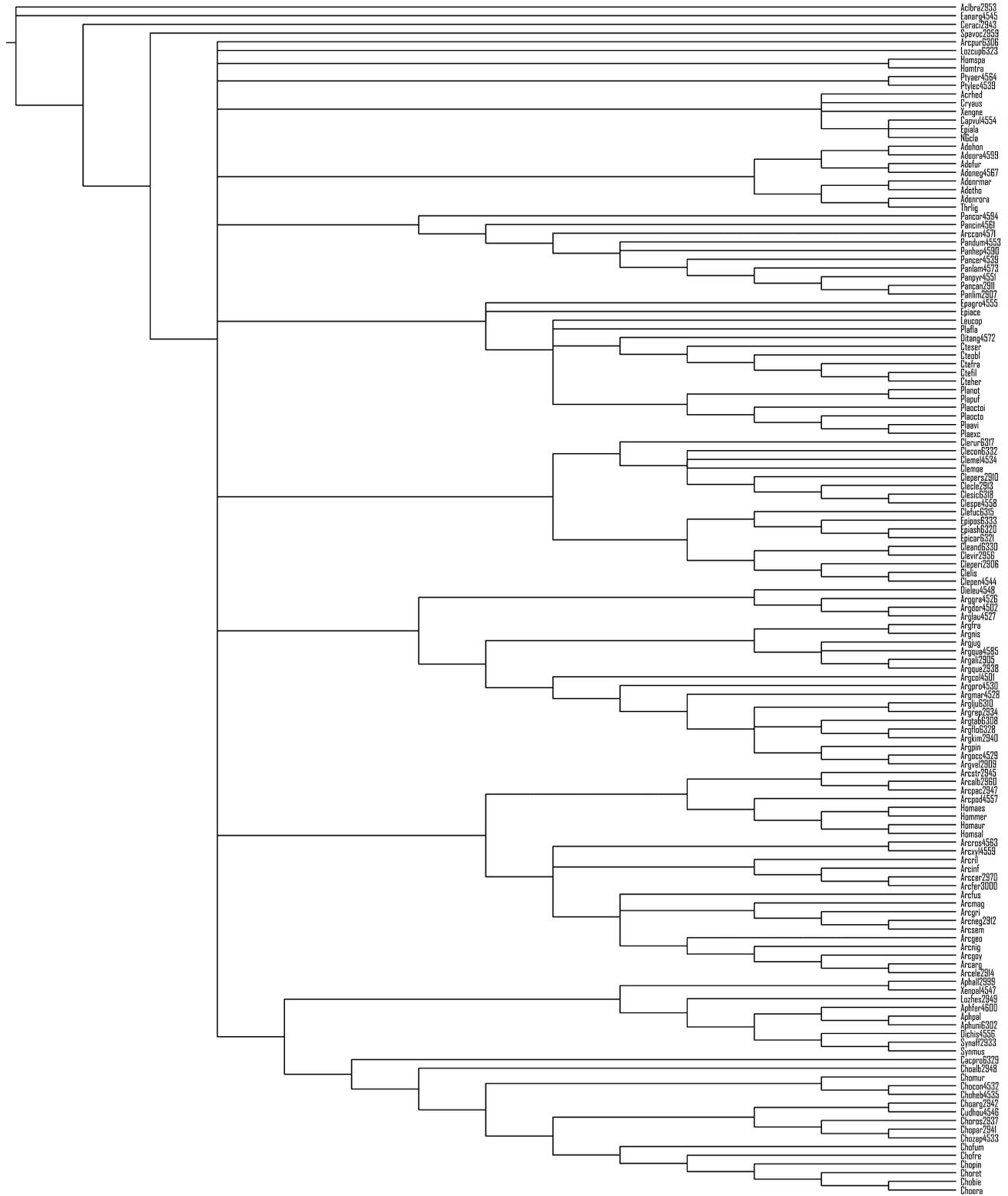
APPENDIX 8.



APPENDIX 9.



APPENDIX 10.



APPENDIX 11.

APPENDIX 12. Ancestral zoogeographic character reconstruction and proportional likelihoods.

Clade #	proportional likelihoods		
	New World	Old World	Australasian
3	0.0118	0.0591	0.9290
4	0.0066	0.1070	0.8865
5	0.0371	0.1381	0.8248
6	0.3117	0.3982	0.2901
7	0.9486	0.0292	0.0223
8	0.0232	0.9549	0.0218
9	0.0085	0.0784	0.9131
10	0.0014	0.0058	0.9928
11	0.0080	0.1385	0.8535
12	0.0157	0.9815	0.0028
13	0.1605	0.8289	0.0106
14	0.0110	0.9134	0.0756
15	0.0055	0.0633	0.9312
16	0.0015	0.9928	0.0057
17	0.0000	0.0049	0.9950
18	0.0012	0.0080	0.9908
19	0.0056	0.0763	0.9181
20	0.0006	0.5420	0.4574
21	0.0056	0.5388	0.4556
22	0.0036	0.0405	0.9559
23	0.0009	0.0035	0.9956
24	0.0005	0.0007	0.9988
25	0.0005	0.0005	0.9991
26	0.0035	0.0439	0.9526
27	0.0009	0.0035	0.9957
28	0.0010	0.0040	0.9950
29	0.0005	0.0007	0.9988
30	0.0005	0.0008	0.9987
31	0.0005	0.0005	0.9990
32	0.0005	0.0005	0.9991
33	0.0017	0.9976	0.0007
34	0.0008	0.9987	0.0005
35	0.0030	0.9968	0.0003
36	0.4801	0.5120	0.0078
37	0.4769	0.5151	0.0080
38	0.9576	0.0387	0.0037
39	0.9958	0.0033	0.0009
40	0.9989	0.0007	0.0005
41	0.9142	0.0796	0.0062
42	0.9923	0.0064	0.0013
43	0.9985	0.0009	0.0006

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APPENDIX 12. (Continued)

Clade #	proportional likelihoods		
	New World	Old World	Australasian
44	0.9991	0.0005	0.0005
45	0.9916	0.0069	0.0014
46	0.9983	0.0011	0.0006
47	0.9990	0.0005	0.0005
48	0.9989	0.0006	0.0005
49	0.9991	0.0005	0.0005
50	0.9991	0.0005	0.0005
51	0.9984	0.0010	0.0006
52	0.9989	0.0006	0.0005
53	0.9985	0.0010	0.0006
54	0.9920	0.0066	0.0014
55	0.9192	0.0752	0.0056
56	0.9983	0.0010	0.0006
57	0.9990	0.0005	0.0005
58	0.9991	0.0005	0.0005
59	0.9990	0.0005	0.0005
60	0.9991	0.0005	0.0005
61	0.0464	0.9523	0.0014
62	0.0775	0.9216	0.0009
63	0.5349	0.4577	0.0073
64	0.5293	0.4631	0.0076
65	0.1409	0.8533	0.0058
66	0.0101	0.9884	0.0015
67	0.7802	0.1630	0.0568
68	0.7862	0.0602	0.1536
69	0.0588	0.0089	0.9323
70	0.0045	0.0013	0.9942
71	0.9803	0.0138	0.0059
72	0.9977	0.0014	0.0009
73	0.9975	0.0015	0.0010
74	0.9990	0.0005	0.0005
75	0.4950	0.4967	0.0084
76	0.4631	0.5295	0.0074
77	0.7360	0.2580	0.0061
78	0.9798	0.0182	0.0021
79	0.7110	0.2818	0.0072
80	0.0991	0.8954	0.0055
81	0.0078	0.9908	0.0014
82	0.0010	0.9985	0.0005
83	0.0544	0.9429	0.0027
84	0.1165	0.8774	0.0061

.....continued on the next page

APPENDIX 12. (Continued)

Clade #	proportional likelihoods		
	New World	Old World	Australasian
85	0.0770	0.9190	0.0039
86	0.0567	0.9406	0.0027
87	0.1679	0.8252	0.0069
88	0.0883	0.9084	0.0034
89	0.1457	0.8480	0.0063
90	0.9274	0.0670	0.0056
91	0.9928	0.0059	0.0013
92	0.9986	0.0008	0.0005
93	0.9985	0.0009	0.0006
94	0.9991	0.0005	0.0005
95	0.9933	0.0055	0.0012
96	0.9986	0.0009	0.0006
97	0.9990	0.0005	0.0005
98	0.9990	0.0005	0.0005
99	0.9991	0.0005	0.0005
100	0.1516	0.8249	0.0235
101	0.1489	0.7392	0.1118
102	0.0316	0.3906	0.5778
103	0.0044	0.0274	0.9681
104	0.0155	0.4120	0.5724
105	0.2196	0.7374	0.0430
106	0.9375	0.0551	0.0074
107	0.9946	0.0042	0.0012
108	0.1658	0.8232	0.0110
109	0.0119	0.9862	0.0020
110	0.5486	0.4425	0.0089
111	0.9633	0.0333	0.0034
112	0.9962	0.0029	0.0009
113	0.9989	0.0006	0.0005
114	0.5352	0.4564	0.0084
115	0.9592	0.0371	0.0037
116	0.9959	0.0032	0.0009
117	0.9988	0.0007	0.0005
118	0.9991	0.0005	0.0005
119	0.9959	0.0032	0.0009
120	0.9988	0.0007	0.0005
121	0.9990	0.0005	0.0005
122	0.9991	0.0005	0.0005