Phylogeny, evolution and speciation of *Choristoneura* and Tortricidae (Lepidoptera)

by

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Abstract

Leafrollers moths are one of the most ecologically and economically important groups of herbivorous insects. These Lepidoptera are an ideal model for exploring the drivers that modulate the processes of diversification over time. This thesis analyzes the evolution of *Choristoneura* Lederer, a well known genus because of its pest species, in the general context of the evolution of Tortricidae. It takes an inductive view, starting with analysis of phylogenetic, biogeographic and diversification processes in the family Tortricidae, which gives context for studying these processes in the genus *Choristoneura*. Tectonic dynamics and niche availability play intertwined roles in determining patterns of diversification; such drivers explain the current distribution of many clades, whereas events like the rise of angiosperms can have more specific impacts, such as on the diversification rates of herbivores.

Tortricidae are a diverse group suited for testing the effects of these determinants on the diversification of herbivorous clades. To estimate ancestral areas and diversification patterns in Tortricidae, a complete tribal-level dated tree was inferred using molecular markers and calibrated using fossil constraints. The time-calibrated phylogeny estimated that Tortricidae diverged ca. 120 million years ago (Mya) and diversified ca. 97 Mya, a timeframe synchronous with the rise of angiosperms in the Early-Mid Cretaceous. Ancestral areas analysis supports a Gondwanan origin of Tortricidae in the South American plate. Analysis detected an increase in speciation rate that coincided with the peak of angiosperm diversification in the Cretaceous, which was probably further heightened by continental colonization of the Paleotropics near the end of the Late Cretaceous.

Taking advantage of the usefulness of mitogenomes as markers for phylogenetic studies across a range of taxonomic levels, a second part of the thesis focused on mitogenome variation

across *Choristoneura* and particularly the spruce budworm *Choristoneura fumiferana* (Clemens) species complex, a notorious pest group of North American conifer forests. Phylogenetic relationships of Tortricidae were analyzed using 21 mitogenomes, including six newly-sequenced haplotypes in the spruce budworm complex, mitogenomes for three additional *Choristoneura* species, and 12 published mitogenomes. Phylogenetic informativeness of the mitogenome was evaluated by comparing its accuracy for recovering clades reconstructed in the previous chapter using different markers (nuclear genes) and the barcode fragment, and a time-calibrated tree was reconstructed using mitochondrial genes and fossil calibrations. Analysis of all protein-coding plus ribosomal genes together provided an efficient marker for reconstructing phylogenies at any taxonomic rank. The time-calibrated phylogeny showed evolutionary convergence of conifer feeding within *Choristoneura*, with the Nearctic spruce budworm complex and the Palearctic species *Choristoneura murinana* (Hübner) shifting onto conifers during the late Miocene from angiosperms after the expansion of boreal forest. Haplotype diversification within the spruce budworm complex was estimated at 3.5 Mya, and may be linked to the initial cooling cycles of the Northern Hemisphere in the Pliocene.

Using the ages estimated in the previous chapters, I then focused on the genus *Choristoneura*, which is part of the species-rich tribe Archipini. Delimitation of *Choristoneura* has remained unresolved and taxonomic confusion has been generated by the transfer of *Archips occidentalis* (Walsingham) to *Choristoneura*, creating a homonym with *Choristoneura occidentalis* Freeman, an important defoliator of Nearctic forests. To define the limits of the genus, I reconstructed a phylogeny using published and new gene sequences of mitochondrial COI and ribosomal 28S for 23 species of *Choristoneura*, complemented by a large sample of outgroups. I also generated a time-calibrated tree using fossil and secondary calibrations to infer biogeographic and diversification processes in *Choristoneura*. The analysis recovered the genus

as paraphyletic, with the tropical and subtropical species *Archips occidentalis* and *Choristoneura simonyi* (Rebel) and the Palearctic species *Choristoneura evanidana* (Kennel) excluded from the stem of genus. Consequently, *Choristoneura* is restricted primarily to species with a northern hemisphere distribution. An analysis of ancestral areas supported a Holarctic origin of *Choristoneura* about 23 Mya, followed by early colonization of the Palearctic. The main diversification occurred at the crown (16 Ma) when two clades diverged, one Nearctic and another mostly Palearctic. Cladogenesis was almost synchronous and related to herbivorous specialization, with each clade divided into coniferophagous or polyphagous lineages. The analyses support nomenclatural changes including transfers of *Cudonigera houstonana* Grote to *Choristoneura*; *Archips occidentalis* Walsingham to *Cacoecimorpha* Obraztsov; *Choristoneura evanidana* to *Archips* Hübner; and *Choristoneura simonyi* to *Xenotemna* Powell.

Preface

A version of Chapter 2 of this thesis has been published as: Fagua, G., Condamine, F.L., Horak, M., Zwick A., Sperling, F.A.H., 2017. Diversification shifts in leafroller moths linked to continental colonization and the rise of angiosperms. Cladistics. DOI: 10.1111/cla.12185. Corrigendum (accepted June 12, 2017) will appear in a subsequent issue of Cladistics. I contributed to the experimental design, mining of data, analysis, and manuscript preparation. The experimental design was largely supported by Fabien L. Condamine, who contributed to manuscript editing and revisions. Marianne Horak contributed by corroborating fossil morphology and identification. Andreas Zwick contributed to generating sequences of Australian species and discussion about some phylogenetic analysis. Felix Sperling contributed to manuscript editing, experimental design, revisions, and sequencing of Australian species.

Dedication

       To my ladies, Monica and Suanti, and to my family.

Acknowledgements

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Chapter 1: General Introduction

Tortricid moths, also known as leafroller moths (Tortricidae), are the fifth most species-rich family of Lepidoptera and one of the most diversified lineages of herbivorous insects (van Nieukerken et al. 2011). Included in the microlepidoptera, or "small moths", leafrollers are mostly cryptic in coloration and remain unnoticed until reaching formidable population sizes (Pureswaran et al. 2016). In effect, this group contains species that can modulate forest dynamics through cyclic outbreaks that affect millions of hectares of temperate ecosystems (MacLean 2016). Our knowledge about leafrollers has been principally limited to pest species, which comprise just over a hundred of the almost 11000 species of tortricids described (Gilligan and Epstein 2014). Fifteen percent of leafroller species are included in Archipini, one of the 22 tribes of the family (Horak and Brown 1991). Several plesiomorphic lineages of Archipini are Gondwanan and the tribe has lower diversity in the Neotropics; yet, members of the tribe are recorded around the world, making it cosmopolitan (Horak 1999; Brown 2005; Regier et al. 2012).

Choristoneura is a well known genus of Archipini with some species that are major defoliators of the boreal forest. The systematics and phylogeny of the genus remains under debate (Gilligan and Brown 2014) and *Choristoneura* is a good example of the generally problematic taxonomy of Tortricidae. Although the circumscription of the family is stable, the homogeneous external morphology of larvae and adults contrasts with the extraordinary variability of adult genitalic morphology. This combination has made it challenging to resolve phylogenetic relationships within the family. By default, estimation of divergence times or inferences of biogeographic and diversification patterns in the family have been limited to expressions of the personal views of researchers who proposed hypotheses based on their years of experience. Resolution of the phylogeny of *Choristoneura,* and the evolutionary processes by which it arose, has been constrained by a lack of information about fossils, divergence times, biogeography and diversification patterns for Tortricidae. I have endeavoured to generate this information as a series of studies that comprise my PhD thesis.

1.1. *Phylogeny and general patterns of diversity of Tortricidae and* Choristoneura

Tortricidae is a well differentiated clade of Lepidoptera (Horak 1999). Despite controversy about the position of the family in the clade Apodytrisia (Kristensen and Skalski

1999; Regier 2013; Wahlberg et al. 2013) or its relationship with the families Galacticidae and Heliocosmidae (Bazinet et al. 2013; Regier et al. 2013; Wahlberg et al. 2013; Heikkilä et al. 2015), the family is widely recognized as a monophyletic and morphologically homogeneous taxon. The divergence of Tortricidae from other Lepidoptera has been estimated as ca. 133 Ma by Wahlberg et al. (2013) in the first work to include leafrollers in time estimations. Morphological phylogenies proposed for Tortricidae have changed the status and composition of the contained groups below the family rank depending on the species used in the sample (Powell 1964; Kuznetsov and Stekolnikov 1973, 1984, 2001; Razowski 1976; Safonkin 2007). These topologies generated different suprageneric arrays that remained under debate until the taxonomic study of Horak and Brown (1991), who used morphology to stabilize the arrangement of 22 tribes distributed in three subfamilies: Tortricinae, Olethreutinae and Chlidanotinae. Intuitive phylogenies based on morphology show a stable group comprised of current Olethreutinae as the sister group of an unresolved array of Chlidanotinae and Tortricinae tribes (Powell 1964; Kuznetsov and Stekolnikov 2001; Razowski 1976; Safonkin 2007). Major differences between these studies occur in the position of some tribes of Tortricinae (Cochyliini, Sparganothini, Hilarographini, Schoenotenini) and, especially, the position of Chlidanotinae tribes (Chlidanotini, Hilarographini and Polyorthini). Later, Safonkin (2007), based on the topology of Kuznetsov and Stekolnikov (2001), generated an analysis of the evolution of pheromone composition in Tortricidae. Regier et al. (2012), based on molecular data, analyzed the most complete sample to date including 19 of the 22 tribes recognized by Horak and Brown (1991). In this work, Regier et al. (2012) generated a robust phylogeny that recovered Chlidanotinae as a basal and paraphyletic group, where Polyorthini was the earliest clade to diverge in Tortricidae, and Chlidanotini + Hilarographini were the sister group of other tortricids. Regier et al. (2012) compared numbers of species per tribe and their geographical distributions, and based on these data, suggested a Gondwanan origin for the family; however, Regier remarked on the lack of fossils for calibrations to test their hypothesis.

Pest species are widely distributed among leafrollers, with genera such as *Cydia*, *Grapholita*, *Bactra,* and *Acleris* being frequent targets in crop management (Gilligan and Epstein 2014). Archipini is not an exception, the tribe includes pest species in *Adoxophyes*, *Epiphyas*, *Homona,* among other genera (Dombroskie and Sperling 2013), but *Choristoneura* is, without doubt, the most studied genus in the tribe. Although Archipini has some taxonomic and

nomenclatural studies that have been generated as part of general or local reviews of Tortricidae (e.g. Freeman 1958; Razowski 1997), very little phylogenetic work has been published. Only two studies are available to date, a phylogeny based on morphological data focused on Japanese species (Jinbo 2000), and another based on molecular data with species from around the world but mostly the Nearctic (Dombroskie and Sperling 2013). Species of *Choristoneura* were recovered as derived terminals and paraphyletic in both studies. Paraphyly is a frequent result in phylogenetic analyses of Tortricidae genera since the cryptic coloration, high number of species, variability in morphology of genitalia and difficulty of including a wide sample of species in reviews have contributed to the limits of several genera being poorly defined (Gilligan and Brown 2014). A good example of this problem is the group composed of *Choristoneura*, *Archips*, *Cudonigera*, *Homona,* and *Meridemis*, genera that are similar in male genitalic morphology (Dang 1992, Razowski 2002, Gilligan and Brown 2014). *Choristoneura* was described by Lederer in 1859 based on the "longer hair" of the scape, a common character in tortricids; *Choristoneura diversana* (Hübner) was designated as the type species without a complete description. Razowski (2002) redefined the genus and his autapomorphy for the genus as "position of the uncus, which is convex, situated on tegumen dorsally", an equivalent character to Freeman (1958) but shared with *Homona* and *Meristis* (Dang 1992).

Only two studies have dealt with global reviews of *Choristoneura*: the taxonomic comments of Razowski (1992) and the morphological study of male genitalia of Dang (1992). These works described a genus with 41 species distributed mainly in Holarctic regions. After these, some species have been synonymized (*C. disparana* (Kennel), *C. lappona* (Tengstrom), *C. seminolana* Kearfott) or transferred back to their original genus (*Homona issikii* Yasuda, *Homona magnanima* Diakonoff). Others have been described from Palearctic regions (*C. chapana* Razowski, *C. colyma* Razowski, *C. expansiva* Wang & Yang, *C. improvisana* Kuznetzov, *C. irina* Dubatolov & Syachina) and some that are more tropical and subtropical in range (*C. africana* Razowski, *C. bracatana* (Rebel), *C. heliaspis* (Meyrick), *C. palladinoi* Razowski & Trematerra, *C. simonyi* (Rebel), and *C. psoricodes* (Meyrick)) have been described in or transferred to *Choristoneura* by Razowski, based on his views on the existence of tropical species of the genus (Razowski 2008). Brown (2005) recognized 38 species; yet, the most current list includes 46 species (Gilligan et al. 2014). Despite these efforts, the delineation of the genus

remains uncertain because a stable phylogeny is lacking; no phylogeny includes species endemic to Africa, and the type species of the genus, *Choristoneura diversana*, is often omitted.

Several taxonomic issues remain to be resolved in *Choristoneura*; the case of *Archips occidentalis* (Walsingham, 1891) may have the highest impact. Originally described as *Cacoecia occidentalis* from specimens collected in Gambia (West Africa), Razowski (2008) placed this taxon in *Choristoneura* based on limited morphological evidence (Gilligan and Brown 2014). This nomenclatural change created confusion about *Choristoneura occidentalis* Freeman, 1967, the Western spruce budworm, a North American conifer-feeding species, because the African name (*Archips occidentalis*) has priority (ICZN 1999). This taxonomic act necessitated a name change for one of the most studied forest defoliators in America (Johns et al. 2016), and Razowski (2008) accordingly proposed the replacement name *Choristoneura freemani*. As recommended by Gilligan and Brown (2014), a comprehensive phylogenetic analysis to identify the position of Walsingham's taxon is the best solution to resolve the problem.

No studies about the biogeography and diversification of *Choristoneura* have yet been published. Since species traditionally assigned to the genus are arctic, temperate or Mediterranean in distribution (Brown 2005; Gilligan et al. 2014), the inclusion of tropical and subtropical species is in need of discussion. Generally, *Choristoneura* species with host plant records (Brown et al. 2008) are major herbivores of core Rosids (Angiospermae) or specialists on conifers, both of which are common groups of plants in temperate ecosystems. Several *Choristoneura* species are polyphagous herbivores, including the type species of the genus, *C. diversana*. Since so little previous work has been done, the biogeography, host plants, and diversification patterns of the genus are all in need of study.

1.2. *Estimation of divergence time and fossil record in Lepidoptera*

Molecular clock theory maintains that molecular evolution occurs at a uniform rate over time (Kumar 2005); consequently, the number of genetic changes accumulated between molecular sequences is proportional to the time of species divergence (Yang 2015). Methods for divergence time estimation are based on the molecular clock principle; these methods generate trees where branch lengths are proportional to time (Drummond et al. 2003, 2006; Kumar 2005, Heat 2015). However, molecular sequence changes only provide a relative timescale and need an external source of information to calibrate the rate of changes and convert them into absolute

geological time (Shaul and Graur 2002; Drummond et al. 2003; Rieux and Balloux 2016). Two general methodological approximations exist to generate external references: assignment of dates to tips using the ages of the sequenced samples to calibrate the phylogeny (known as tip calibrated phylogenies; Rieux and Balloux 2016); or assignment of dates to internal nodes between lineages (the most recent common ancestors, MRCA) using external age estimation obtained from the fossil record, known geological time of separation by geographical barriers (Rieux and Balloux 2016) or equivalent ages obtained from independent analysis (secondary calibrations; Heat 2015). Tip dating methods are used for data sets of numerous sampled sequences and a fast mutation rate (Drummond et al. 2003), which is not the case for Tortricidae; consequently, I focus on methods to date internal nodes by external calibrations. Different programs have been created to estimate time-dated trees using methods such as maximum likelihood (ML), least squares, distance base, or a combination of several methods (e.g. *PHYSHER*, Fourment and Holmes 2014; *TipDate*, Rambaut 2000; *DAMBE*, Xia 2013; *R8s*, Sanderson 1997; Rieux and Balloux 2016).

Currently, Bayesian divergence time estimations are the most frequently used method to construct time-dated trees (Zhu et al. 2015). Bayesian methods infer the total posterior probability in a tree of the branch rates of substitutions and times, given the set of sequences and calibration information, generating probability distributions for the prior on the rates and for the prior on the times (Heat 2015); the marginal probability of data is estimated using Markov chain Monte Carlo (MCMC) methods. Different models of rate variation among branches can be used for the inference, including a general strict clock with a constant rate of substitution for all branches of the tree, or an uncorrelated relaxed clock variable between branches, where the rate of each branch is drawn from a single underlying exponential or log-normal parametric distribution (between other models; Drummond et al. 2006, 2012; Ho and Duchêne 2014; Heat 2015). Since Bayesian estimations under relaxed molecular clock models incorporate uncertain fossil calibrations, some programs like *mcmctree* (Inoue et al. 2010), *BEAST* (Drummond et al. 2012) or *DPPDiv* (Heath et al. 2014) have implemented different priors for rates and times and different strategies for incorporating fossil calibrations and may use age bounds to calibrate the molecular tree (Zhu et al. 2015). Density of the posterior probability of the best age between these bounds can follow different distributions: *uniform* with equal probability along the interval of exploration, *normal* with a most probable age and symmetrical decreasing exploration until

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bounds, or *exponential* with the younger bound baring the highest probability and posterior decreasing of exploration, between other distributions (Ho and Phillips 2009). Several other priors must be defined in a time date tree analysis (e.g. substitution model per partition, base frequencies, clock type and distribution, mean rate, among others), depending on the program. BEAST is the most versatile program to explore different possibilities on the priors (Drummond et al. 2012). Two kinds of priors, among several others, modulate results of the analysis: the tree prior and the age of the root and node priors. The tree prior, or the branching process prior, describes the lineage diversification process in the tree; it assumes that cladogenesis occurs uniquely on the tree and a birth rate must be set in the process (Yule process) or assumes that birth and death (extinction) occur on the tree (Birth-death process) and rate of birth and rate of death must be set (Heat 2015). The age of the root is the prior for exploring the time of origin of the tree, while node priors explore times for the MRCA; these priors require external references for calibration (fossil or secondary) and an interval between bounds to explore the posterior probability of ages, following a kind of distribution.

As described above, fossil calibrations are a key component of the construction of time calibrated trees. However, the fossil record for Lepidoptera is poor in comparison with other insects (Kristensen and Skalski 1999; Shon et al. 2012, 2015). Fossil specimens are dispersed among collections around the world and frequently their identification is not accurate due to the difficulty of observing key morphological characteristics (Razowsky 2008). A major problem is that no world catalogue of such fossils was available before Sohn et al. (2012) and this dearth constrained the construction of time-dated trees for Lepidoptera for many years since some groups have a particularly poor fossil record. Sohn et al. (2012, 2015) reported 4561 body and trace fossils of Lepidoptera with known geological ages. Only 82 of Sohn's fossils are associated with Tortricoidea at the level of family and just eight can be included in some of the extant subfamilies. Of these, six specimens were described with a complete species name and fewer had good illustrations of specimens: *Polyvena horatis* Poinar and Brown (Chlidanotinae), *Electresia zalesskii* Kusnezov, *Tortricibaltia diakonoffi* Skalski, *Tortricidrosis inclusa* Skalski, *Retinia resinella* Linnaeus (Olethreutinae), and *Spatalistiforma submerga* Skalski (Tortricinae). This list includes at least one specimen for each subfamily of leafrollers, allowing their use in the construction of a time-dated tree specifically for Tortricidae. The ages of such a time-dated tree can be use as secondary calibrations in the construction of other trees such as within Tortricinae

and Archipini. Another issue with fossil calibrations is the identification of accurate geological times and substrates. The international reference for defining geological times is the study of Cohen et al. (2013); however, confidence in the identification of geological substrates and date of a fossil is frequently debatable. Fortunately, tortricid fossils are limited principally to inclusions in amber and other plant resins (Kristensen and Skalski 1999, Sohn et al. 2015) and these are very well studied. These fossils are from Baltic amber dated to the Lutetian (Labandeira 2014) or from Dominican amber dated to the Burdigalian (Poinar and Poinar 2006).

1.3. *Probabilistic inference tools for biogeography and biological diversification*

Classical narrative studies that make comments about biogeographic or diversification processes on a phylogenetic tree have slowly been replaced by more falsifiable methods (Crisp et al. 2010). Panbiogeography, cladistic biogeography, ancestral state methods or multistate character methods have increased the level of complexity in biogeography analyses (Matzke 2013). Probabilistic biogeography and diversification analyses allow exploration of evolutionary hypotheses like classical dispersal-vicariance (diva), dispersal-extinction cladogenesis (dec) or founder-event speciation linked with tectonic changes and estimation of ancestral areas on a time calibrated phylogeny (Buerki et al. 2011; Almeida et al. 2012; Condamine et al. 2013; Matzke 2013). The principal input for this kind of analysis is a time-dated tree; reconstruction of processes and hypothesis tests are contrasted against the calibrated phylogeny. Different tests using the aforementioned methodologies in programs such as DIVA (Ronquist 1997), LAGRANGE (DEC, Ree 2005, Ree and Smith 2008) or BayArea (Landis et al. 2013) have been developed recently in BioGeography with Bayesian (and likelihood) Evolutionary Analysis in R Scripts (BioGEOBEARS; Matzke 2013). This is a program for testing models and estimating ancestral states for inference of historical biogeography that, additionally, includes independent tests for founder-event speciation, a process that has received increasing study in speciation (Maztke 2013). Equivalent programs such as RASP (Yu et al 2015) have started a new trend of probabilistic biogeography studies. A similar trend can be observed in the creation of programs for diversification analyses. Traditionally, analysis of temporal diversification is limited to groups with a rich fossil record and extended phylogeny for long time periods (Rabosky 2014). The availability of time dated trees has enhanced the use of different methods and programs to estimate changes in diversification through a time date tree. Currently, some of the most used

approaches are Modeling Evolutionary Diversification Using Stepwise Akaike Information Criterion (MEDUSA; Alfaro et al. 2009), TreePar (Stadler 2011), both ML programs, and Bayesian Analysis of Macroevolutionary Mixture (BAMM; Rabosky 2014) a Bayesian program. BAMM is defined as a more flexible program but results with both are equally efficient (Laurent et al. 2015). BAMM additionally has a more versatile interface of graph generation.

1.4. *Mitogenomes in insects*

Aerobic respiration generates ATP for eukaryote cells; this reaction liberates energy from glycolysis through the oxidative phosphorylation enzyme pathway (Steward 2005). In eukaryotes, this process occurs in the mitochondrion, a small and specialized double membranous organelle that contains its own genetic system and DNA, the mitogenome, an independent system from the nuclear genome (Gissi et al. 2008). The mitogenome is a small molecule that encodes a series of four to five protein complexes (Steward 2005). Its small size and absence of introns make the mitogenome a very useful system for comparative studies (Cameron 2014). Additionally, rates of evolution of mitochondrial genes and regions are considerably faster than rates in nuclear genes (Ho et al. 2005).

The insect mitogenome is a double helical and circular molecule 15 to18 kb in length that usually contains 13 protein encoding genes, 22 tRNA genes and the small (12S) and large (16S) ribosomal RNAs, with 37 genes in total (Babbucci et al. 2014; Cameron 2014). The mitogenome contains very few dispersed non-coding sites plus a major non-coding control region (Fenn et al. 2007). More than 600 insect mitogenomes have been published (Cameron 2014). Recent papers have focused on the evolution of the mitogenome in Lepidoptera (Timmermans et al. 2014; Ramirez-Rios et al. 2016; Wu et al. 2016). Leafroller moths have been frequent objects of study of the mitogenome, since several of them are pest species. Mitogenomes of 11 tortricid species of Olethreutinae (tribes Eucosmini, Grapholitini) and Tortricinae (tribes Archipini and Tortricini) are deposited in GenBank, including the mitogenome of *Choristoneura longicellana*, an economically important orchard pest from China, Japan, Korea, and Russia (Byun et al. 1998; Wu et al. 2016). These 11 mitogenomes allow estimation of the rate of evolution of the mitochondrial genome throughout the family and between tribes, as well as application of this rate of change in species groups of the genus *Choristoneura*.

1.5. *Objectives and outline*

The general objective of this thesis was to analyze the evolution of the genus *Choristoneura* in the context of the general evolution of Tortricidae, including biogeographical and diversification patterns. Chapter 2 inferred a new and complete tribal-level phylogeny for Tortricidae, documenting times of divergence along with diversification and global dispersal patterns of the tenth most speciose family of phytophagous insects. Using new tools for biogeographical and diversification analyses, I associated the origin and radiation of this insect lineage with the rise to dominance of angiosperms in the Cretaceous. Chapter 3 examined mitogenomes across the Tortricidae, with an emphasis on *Choristoneura* and the spruce budworm (SBW) species complex. It estimated their phylogenetic relationship based on the whole mitogenome, and compared it to relationships recovered using single mitochondrial genes and estimated divergence times of the coniferophagous pest species of *Choristoneura* and the major mitochondrial lineages within the SBW complex. Chapter 4 presented a more comprehensive sampling of *Choristoneura* species to reconstruct a phylogeny of the genus, placing it within a large outgroup array of Archipini to define the limits of the genus, generate a time-dated tree and examine biogeographic and diversification processes. I also defined the phylogenetic relationship between *Archips occidentalis* Walsingham and the genus *Choristoneura*. General findings are detailed and discussed in chapter 5.

Note: To facilitate reading of the text, complete scientific names of species with descriptors and years of description are presented in the appendices of material studied (Appendices 2.1, 3.1 and 4.2).

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Chapter 2: Diversification shifts in leafroller moths linked to continental colonization and the rise of angiosperms

2.1. Introduction

    Southern hemisphere distributions of clades are frequently presented as classic examples of biogeographic vicariance in ancient Gondwanan continents (Sanmartín and Ronquist 2004; Almeida et al. 2012). However, vicariance is not the only plausible explanation; using parsimony-based analyses of diverse plants and animals, Sanmartín and Ronquist (2004) identified dispersal events as an important explanation for biogeographic patterns in Gondwanan biota. Long-distance dispersal (de Queiroz 2005), including founder-event speciation (Matzke 2014) can explain the current patterns of some Gondwanian plant clades. Founder-event speciation is increasingly recognized as a plausible but difficult to test phenomenon in plants (Sanmartín and Ronquist 2004) and flying insects (Chapman et al. 2011; Condamine et al. 2013; Rota et al. 2016; McColloch et al. 2016). Fortunately, the design of biogeographic analyses based on hypothesis testing allows exploration of evolutionary processes like dispersal and founder-event speciation that can be linked to ancestral areas estimated on a time calibrated phylogeny, facilitating the identification of the hypothesis with the best likelihood (Buerki et al. 2011; Almeida et al. 2012; Condamine et al. 2013).

    Aside from their biogeographic consequences, tectonic plate reconfigurations have often been associated with drastic environmental changes (Chaboureau et al. 2014). After the beginning of the Cretaceous, ca. 139 million years ago (Ma), world climate began a gradual increase in global surface temperature and moisture with higher oxygen concentrations and reduced carbon dioxide that continued until the Palaeocene-Eocene thermal maximum (Chumakov et al. 1995; Scotese et al. 1999; Zachos et al. 2008). These climatic changes coincided with the appearance and rapid diversification of flowering plants that became dominant in the mid-Cretaceous (Crane 1987; Lidgard and Crane, 1988; Vakhrameev, 1991; Lupia et al. 1999). Their rise to dominance characterized the "angiosperm revolution", also known as the "Cretaceous terrestrial revolution" (KTR) (Lloyd et al. 2008, de Boer et al. 2012; Labandeira and Currano 2013).

    Understanding the reciprocal effects of angiosperms and herbivore groups represents an important field of research, especially for insect clades (Labandeira 1994, 2007; Hunt et al. 2007; Labandeira and Currano 2013). With new leaf types and chemical defenses (Labandeira 1998,

2007; Boyce et al. 2009; de Boer et al. 2012), angiosperms were able to foster (as a new ecological niche) or inhibit (as competitors with gymnosperms and other plants) the diversification of certain animal clades. Some groups have benefitted, like mammals (Meredith et al. 2011), Hymenoptera (Grimaldi and Engel 2005; Cardinal and Danforth 2012) or Lepidoptera (Wahlberg et al. 2013), while others like tenebrionid beetles (Kergoat et al. 2014) may have been negatively affected. In Lepidoptera, Wahlberg et al. (2013) detected significant increases in diversification rates at the base of Dytrisia (150 Ma), the base of Apoditrysia (120 Ma) and in Noctuoidea (70 Ma), a pattern supported by Condamine et al. (2016) in a global macroevolutionary analysis of insect families. However, we still know little about the effect of the angiosperm revolution on the small-bodied "microlepidoptera" that make up half of the diversity of the order and include its most ancient lineages.

Leafroller moths (Lepidoptera: Tortricidae) feed mostly on angiosperms (Brown, 2005; Brown et al. 2008) and represent one of the most species-rich families of Lepidoptera (Kristensen and Skalski 1999; van Nieukerken et al. 2011). With ca. 11,000 described species (Gilligan et al. 2014a), this microlepidopteran family includes highly destructive pest species worldwide (Brown et al. 2008) as well as major modulators of temperate forest dynamics (Cooke et al. 2007), with some species reaching massive populations and using wind currents for long-distance dispersion (Sturtevant et al. 2013). Tortricidae feed on a variety of plants, particularly species of the orders Rosales and Asterales, and may be polyphagous, oligophagous or monophagous. These moths are cosmopolitan but have numerous plesiomorphic Gondwanan lineages (Horak 1999; Brown 2005; Regier et al. 2012). The divergence of Tortricidae from other Lepidoptera has been estimated as ca. 133 Ma (Wahlberg et al. 2013), which is very close to the major diversification events estimated for the angiosperm crown (Magallón et al. 2015, Silvestro et al. 2015).

Several morphological phylogenies proposed for Tortricidae (Powell 1964; Kuznetsov and Stekolnikov 1973; Razowski 1976; Safonkin 2007) have recently been unified by a robust molecular phylogeny (Regier et al. 2012) that includes 19 of 22 recognized tribes (Horak and Brown 1991). Regier et al. (2012) suggested a Gondwanan radiation but lacked fossil calibrations to test their hypothesis. The lack of a time-calibrated phylogeny for leafroller moths also hampers understanding of the potential role played by the angiosperm radiation. The simultaneous publication of a catalogue of Lepidoptera fossils (Sohn et al. 2012), including several tortricids assigned to extant groups, provides an opportunity to construct such a time-calibrated phylogeny.

Building on Regier et al. (2012) and Sohn et al. (2012), we used the most frequently available genes for Tortricidae in GenBank. The genes span a gradient of rates of evolution useful for phylogenetic studies in Tortricidae and Lepidoptera. We included species from all tribes not analyzed by Regier et al. (2012) to infer a new and complete tribal-level tree for Tortricidae. Our main objective was to document the diversification and global dispersal of this important herbivorous clade, which is the tenth most species-rich family of phytophagous insects (Condamine et al. 2016). Using recently developed tools for biogeographic and diversification analyses, we reconstructed the origin and radiation of this herbivorous lineage during the rise to dominance of angiosperms in the Cretaceous. Since Tortricidae are closely associated with angiosperms (Brown et al. 2008) and both taxa are estimated to have originated in the Early Cretaceous (Wahlberg et al. 2013; Magallón et al. 2015), we expected that speciation rates and colonization processes of tortricids were positively affected by the angiosperm evolution. Given their worldwide distribution and early-diverging Gondwanan clades, we also expected that ancient vicariance coupled to dispersal processes explain the current distribution pattern of the family. Furthermore, the combination of these drivers could have had a synergistic effect on tortricid speciation since new niches were opened up at a time of major tectonic changes. A separate objective of the study was to provide gene-specific molecular clock rates based on the fossil-calibrated molecular dating. Such rates could be secondarily used for phylogenetic analyses of recent clades (e.g. genera) that lack relevant information to estimate their divergence times.

2.2. Material and methods

2.2.1. *Taxon sampling*

We used 62 terminal taxa in our phylogenetic analyses, including 56 species of Tortricidae (as the ingroup) and six outgroups comprising one species of each of Heliocosmidae, Galacticidae, Cossidae, Lacturidae, Limacodidae, and Sesiidae (Appendix 2.1). We included at least one representative of each of the 22 tortricid tribes proposed by Horak and Brown (1991), including three tribes, Gatesclarkeanini, Schoenotenini and Epitymbiini, which had not previously been analyzed in molecular phylogenies. This covered all tribes recognized in the family in recent classifications (Powell 1983; Horak and Brown 1991; Horak 2006). Outgroups included species from the two families (Galacticidae, Heliocosmidae) that Regier et al. (2013)

found to be most closely related to Tortricidae, as well as three superfamilies that were close to Tortricoidea (Zygaenoidea, Cossoidea, Sesioidea). Taxon sampling is detailed in Appendix 2.1.

2.2.2. *Molecular dataset*

Based largely on Regier et al. (2012, 2013) and GenBank (NCBI) accessions of Zwick et al. (2012, not published), we searched for genes that were best represented in the 62 taxa used to infer a tribal-level phylogeny for Tortricidae. We selected regions of five nuclear genes and one mitochondrial gene to build a molecular dataset comprising 7479 bp. The nuclear genes were: carbamoyl-phosphate synthetase II (CAD, 2935 bp), dopa decarboxylase (DDC, 1286 bp), enolase (Eno, 1137 bp), period (PER, 1058 bp), wingless (WG, 405 bp), and the mitochondrial gene was the barcode fragment of cytochrome oxidase subunit I (COI, 658 bp; Hebert et al. 2003) (Appendix 2.1). This COI fragment is widely used for reconstructing recent divergences but is less effective for recovering deep nodes when used alone (Dupuis et al. 2012). Thus, the nuclear genes mainly serve to provide resolution at the subfamily and tribal levels, while the mitochondrial fragment is a link between sequences of different sources as well as resolution between closer terminals. Since our objective was to compare subfamilies and tribes, we used the barcode sequence of another species of the same genus in 12 cases where the species did not have a barcode sequence available (Appendix 2.1); in these cases, we selected sequences of the type species of a genus when available. We retrieved 309 GenBank accessions, principally from Regier et al. (2012, 2013) (77% of total) complemented with other studies (Buchsbaum and Miller 2002; Hebert et al. 2010; Gilligan et al. 2014b; Brown et al. 2014; Huemer et al. 2014) and the unpublished submissions of Hebert et al. (2010, 2013), Zwick et al. (2012), Mitter (2013), Mitter and Mitter (2013), Mitter et al. (2013), Mutanen et al. (2012), BOLD project (2011, 2012), and iBOL (2012) (see Appendix 2.1 for GenBank accession numbers).

2.2.3. *Phylogenetic analyses*

We first obtained the best alignment for each gene over the complete molecular dataset (7479 bp; Appendix 2.2) using MUSCLE 3.8 (Edgar, 2004) implemented in the EMBL-EBI server (Lopez et al. 2014). Maximum parsimony (MP) analysis of the MUSCLE alignment was done using PAUP* 4.0b (Swofford et al. 2003) with unordered, equal weight characters and settings for heuristic search using parsimony and random addition of sequences (1000 replicates,

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nchuck = 1000, chuckscore = 1, hold = 1) after checking the phylogenetic signal of the data (g1 skewness statistics and PTP test with 100 replicates). Maximum parsimony bootstrap (BS) analysis using PAUP* 4.0b was performed using 1000 replicates; clades were considered supported when the nodal support had BS ≥ 75%.

For parametric phylogenetic analysis, we first determined the best scheme of partitions using the MUSCLE alignment in PartitionFinder 1.1.1 (Lanfear et al. 2012). We tested models of nucleotide substitution with partitions representing codon position and genes in independent runs using the mrbayes set of models and beast set of models with branch lengths linked, greedy search, and Bayesian Information Criterion (BIC) model selection with other settings at default. In both cases partitions by codon position presented better likelihood values and a 13-partitions scheme was selected. Partitions were made using Geneious 9.0 (Kearse et al. 2012) and implemented in IQ-TREE 1.3.11.1 (Nguyen et al. 2015), MrBayes 3.2.6 (Ronquist et al. 2012) and BEAST 1.8.3 (Drummond et al. 2012) analyses. Maximum Likelihood (ML) analysis was implemented using the 13-partition scheme in IQ-TREE 1.3.11.1 with default settings and by obtaining SH-aLRT support (SH) and ultrafast bootstrap support (UFBS) after 1000 replicates. Clades were considered supported when the nodal support had SH/UFBS ≥ 75%.

Bayesian analyses were performed using MrBayes 3.2.6 (Ronquist et al. 2012) with reversible-jump Markov Chain Monte Carlo (MCMC) and allowing molecular partitions to evolve under different models across the entire substitution rate model space (Huelsenbeck et al. 2004); the parameters governing evolutionary rates were unlinked. Bayesian searches were executed using 2 independent runs and 8 chains (1 cold and 7 heated, temperature of 0.1) to obtain an average standard deviation of split frequencies close to 0.001 after 20 million MCMC generations and sampling trees every 2000 generations. Convergence and mixing of runs were verified by: (i) checking that values of the Potential Scale Reduction Factor (PSRF) were close to 1.0 and Effective Sample Size (ESS) was over 200 for all parameters, and (ii) visual convergence of the analyses using Trace plots (Tracer 1.6, Rambaut et al. 2013). The first 25% of the trees prior to stationarity of the log-likelihood values were discarded as burn-in. A 50% majority-rule consensus tree was constructed from the remaining trees to estimate posterior probabilities (PP). Clades were considered strongly supported when the nodal support had PP ≥ 0.95.

2.2.4. *Fossil calibrations and secondary calibrations*

We used three fossils to calibrate internal nodes in the Tortricidae tree, and a secondary calibration for the maximum age of the tree root. Fossils and their date information were selected from Sohn et al. (2012) and original descriptions (Skalski 1992; Poinar and Brown 1993) using the ages of stratigraphic boundaries of Gradstein et al. (2012) and dates of Poinar and Poinar, (2006; Burdigalian) and Labandeira (2014; Lutetian). We selected three fossils with good morphological support to calibrate the crown ages of the three recognized subfamilies of Tortricidae as follows:

(i) †Tortricibaltia diakonoffi Skalski, 1992 (Lutetian, middle Eocene 41.2–47.8 Ma; Sohn et al. 2012) assigned to Olethreutinae Walsingham, 1895, in agreement with Sohn et al. (2012), due to the presence of forewing (FW) veins M-stem and stem of R4+5. Although this character is only a plesiomorphy found among today's Tortricidae nearly exclusively in Olethreutinae, we consider it on balance justified to retain the assignment of Sohn et al. (2012) based on this trait.

(ii) †Spatalistiforma submerga Skalski, 1992 (Lutetian, middle Eocene 41.2–47.8 Ma; Sohn et al. 2012) assigned to Tortricinae Latreille, 1803, in agreement with Skalski (1992) and Sohn et al. (2012), because veins M3 and Cu1 are stalked in both wings, a diagnostic characteristic of extant Spatalistis Meyrick, 1907 (Tortricinae: Tortricini) and relatives (Skalski 1992);

(iii) †Polyvena horatis Poinar & Brown, 1993 assigned to Chlidanotinae (Burdigalian, early Miocene 15.97–20.44 Ma; Sohn et al. 2012), in agreement with the description and Sohn et al. (2012), by the presence of widely distant M2 and M3 in the hindwing (HW), raised scale tufts on the FW, and large valvae without a corresponding large tegumen (Poinar and Brown 1993).

We performed analyses using exponential and uniform distributions for each fossil calibration set on the most recent common ancestor of each subfamily. We did not use the lognormal prior because this distribution is biased towards the fossil age and because the fossil record of tortricids is sparse. The younger bound (upper limit of the prior) is the estimated age of each fossil as the lower value (41.3 Ma for Olethreutinae and Tortricinae, 15.97 Ma for Chlidanotinae) and the older bound (lower limit of the prior) is the origin of angiosperms estimated with molecular dating (153 Ma, Magallón et al. 2015, which corresponds to the older bound of the confidence interval of the angiosperm origin) and the age of the estimated split of Apoditrysia (sensu Wahlberg et al. 2013). The tree root height (age of the root) was estimated

using a normal distribution with average at the oldest limit of the diversification of angiosperms (153 Ma, Magallón et al. 2015) and standard deviation of 10.

2.2.5. *Molecular dating*

A time-calibrated tree was reconstructed from molecular partitions identified by PartitionFinder (as explained above) using BEAUti and BEAST 1.8.3 (Drummond et al. 2012) and the three fossil calibrations described above. The BEAST approach implemented the relaxed molecular clock model (Drummond et al. 2006). We performed analyses contrasting Yule versus birth-death process for the branching process prior (Condamine et al. 2015) assuming an uncorrelated lognormal distribution clock model (UCLD). We used the following: uniform priors between 0 to 10 with starting value of 0.1 for both Yule and birth-death mean growth rate; uniform prior between 0 to 1 with starting value of 0.5 for the birth-death relative death rate; an exponential prior with mean one-third on the standard deviation of the UCLD model; and a uniform prior between 0 and 1 on the mean of the UCLD model. Fossil calibrations were set using exponential and uniform distributions as described above in Fossil calibrations. MCMC analyses were run for 200 million generations sampled every 20,000 generations. We discarded the first 25% of trees from the 10,000 trees obtained. All BEAST analyses were performed on the computer cluster CIPRES Science Gateway 3.3 (Miller et al. 2015). We ensured good convergence of the Bayesian runs by checking the ESS values of all parameters, considering values above 200 to indicate good mixing, using Tracer 1.6 (Rambaut et al. 2013).

To estimate rates of evolution per gene in Tortricidae as a reference for further studies within Tortricidae, an additional time-calibrated tree was reconstructed using the PartitionFinder best scheme for genes. This scheme defined five independent partitions corresponding to: CAD, DDC+Eno, PER, WG, and COI. We used one molecular clock per partition and the same contrasting analyses and parameters described above, including comparison between Yule and birth-death processes, and comparison between exponential and uniform distribution for fossil calibrations.

2.2.6. *Ancestral range reconstruction*

We used the R-package BioGeoBEARS 0.2.1 (BioGeography with maximum likelihood and Bayesian Evolutionary Analysis in R Scripts; Matzke 2014) to test the six different models

implemented in BioGeoBEARS including, or not, founder-event speciation, denoted as the jump (J) dispersal parameter. We thus applied Dispersal–Extinction–Cladogenesis (DEC; Ree and Smith 2008), DIVA-like (a likelihood implementation of dispersal-vicariance analysis, Ronquist 1997), and BayArea-like (a likelihood implementation of BayArea, Landis et al. 2013) analyses. We built species distribution matrices for each sampled tortricid species (Appendix 2.3) by coding presence/absence in biogeographic regions taken from classical Wallace's biogeographical regions (Kreft and Jetz 2010) but dividing the Nearctic and Palaearctic regions into East and West entities. Nine regions were considered as follows: AF, Africa (including Madagascar); AU, Australasia; IN, India; NT, Neotropics; EN, East Nearctic; WN, West Nearctic; EP, East Palearctic; WP, West Palearctic; and SA, Southeast Asia (Appendix 2.3).

The time-calibrated tree selected in BEAST analyses (outgroups removed) was the input for all BioGeoBEARS analyses. A time-stratified palaeographic model was constructed taking into account changes in continental plate distribution for each of the following six time intervals: 0-5.33, 5.33-23.03, 23.03-33.9, 33.9-56, 56-66, 66-100.5 Ma. We also built connectivity matrices through time describing how the aforementioned areas were (or not) adjacent and connected to each other over time (Appendix 2.4). No dispersal rate matrices were used given the low objectivity in assigning probability values of dispersal. In all analyses and models, the maximum number of areas allowed was set to nine. To select which model best described the biogeography of the group, a model testing approach was performed using the corrected Akaike Information Criterion (AIC). We compared models with two-parameters (without J parameter) against models with three-parameters (with J parameter). The biogeographic model with the lowest AIC was considered to be the best fit (Matzke 2014).

2.2.6. *Diversification in Tortricidae*

The temporal pattern of tortricid diversification was estimated with the best time-calibrated tree inferred with BEAST (outgroups removed). We used BAMM 2.5 (Bayesian Analysis of Macroevolutionary Mixtures: Rabosky et al. 2013), which makes inferences of speciation and extinction rates as well as the possible shifts of speciation across clades and through time. We performed several runs of BAMM for 5 million generations, using default parameters, and a burn-in of 25%. Because priors potentially affect posteriors (Moore et al. 2016; http://bamm-project.org/prior.html), we implemented a series of analysis with a gradient of

values for the prior governing the number of rate shifts (the compound Poisson process); it was tested from 1.0 (the default, higher probability of no rate shift) to 0.1 (higher probability of several shifts) with a step of 0.1. We selected the best-fit run with the highest posterior probability for the number of shifts. We used the R-package BAMMtools 2.1 (Rabosky et al. 2014) to check for good convergence and mixing of the MCMC for each BAMM analysis. For the best-fit analysis we plotted the estimate of speciation rates and the best shift configuration.

2.3. Results

2.3.1. *Phylogenetic analyses*

The MP, ML and Bayesian analyses showed very similar topologies with high support (i.e. BS/UFBS/SH ≥ 75; PP ≥ 0.95; Table 2.1) for the majority of clades (46% of total nodes for MP, 88% for ML and 80% for Bayesian, Appendices 2.5-2.8). Some differences were observed in the positions of *Phricanthes, Gatesclarkeana* and *Oxysemaphora*, and the topology of clades comprising Archipini, *Epitymbia, Cerace*, and *Cornuticlava+Proselena* (Appendices 2.5 to 2.9); all these clades were recovered with low nodal support (i.e. BS/UFBS/SH < 75; PP < 0.9). Detailed description and phylogenetic discussion is presented in Appendix 2.5.

We selected the 13-partition Bayesian scheme as the best for downstream analyses (dating, diversification and biogeography) as it had the highest LnL values and strong support for most clades (LnL = -134,848.17; Appendix 2.8). This topology indicates monophyly for Tortricidae and subfamilies Olethreutinae and Tortricinae while subfamily Chlidanotinae is paraphyletic with two lineages. Within Olethreutinae, Microcorsini is the sister group of the remaining Olethreutinae and Enarmoniini is sister to Olethreutini, a clade with strong support that includes Bactrini, Endotheniini and Gatesclarkeanini, but not *Oxysemaphora*. Within Tortricinae, Phricanthini+Schoenotenini are basal, Ceracini is sister to Archipini+Epitymbiini, Atteriini is sister to Sparganothini, Cnephasiini is sister to Tortricini, and Cochylini is part of Euliini.

2.3.2. *Molecular dating*

The time-calibrated tree with the highest LnL and ESS values was reconstructed using the 13-partition scheme, Yule process as tree prior, fossil calibrations set with uniform distribution, and an exponential distribution for the UCLD mean (Fig. 2.1). In this tree, Tortricidae diverged at 120.48 Mya (Table 2.1; node 7, Fig. 2.1) from the stem of Tortricoidea and remains a single

branch for 25 million years (My). The crown age of Tortricidae is estimated at the beginning of the Late Cretaceous, with one branch of paraphyletic Chlidanotinae diverging first (Polyorthini, 96.99 Mya; node 8) followed by the rest of Chlidanotinae five My later (92.26 Mya; node 10). Olethreutinae and Tortricinae, the most speciose subfamilies of Tortricidae, did not diverge from each other until 20 My later in the Late Cretaceous at 72.42 Mya (node 12). However, the crowns of both subfamilies diversified soon afterward in the Paleogene, at 65.77 Mya for Tortricinae (node 37) and 58.95 Mya for Olethreutinae (node 13). Divergence of most tribes in both subfamilies occurred before 40 My, especially during the Eocene and Oligocene. Some clades diverged more recently (Gatesclarkeanini, Endotheniini, Bactrini, Epitymbiini, Cochylini, non-Australian Archipini) and/or were derived in the midst of older tribes that thereby became paraphyletic (Fig. 2.1).

Bayesian analysis with gene partitions also allowed estimation of substitution rates for Tortricidae. Estimated rates of evolution for each gene are presented in Table 2.2 with statistical parameters (coef. variation, covariance, ucld.mean, ucld.stdev) that support the use of independent uncorrelated relaxed lognormal clocks for each gene-partition. As expected, the fastest evolving gene was mitochondrial COI, which was at least 2.5 times faster than nuclear genes. The barcode fragment of COI facilitates reconstruction of recent divergences but does not as consistently allow recovery of deep nodes if used alone. The fastest evolving nuclear gene was PER while WG was the slowest. These selected gene regions provided a gradient of evolutionary rates (Table 2.2) that allowed confidence in most phylogenetic and time date estimates from the level of family to tribe.

2.3.3. *Ancestral range reconstruction*

The DEC+*J* model was selected as the best fit for Tortricidae (highest LnL = -177.22; Table 2.3, Fig. 2.2). All models were almost identical in their estimates of ancestral areas per node when speciation founder effect was included (Fig. 2.2, Appendix 2.10), and all models including the founder effect were significantly better than models without the founder effect (p-values column; Table 2.3). In all cases, parameter founder-event speciation (*J*) played an important role in Tortricidae biogeographic models, increasing dispersal (d) and extinction (e) parameters and likelihood scores on models without the *J* parameter (d = 0.047, e = 0.043, j = 0, lnL = -357.63) versus models with the *J* parameter (d = 0.01, e ≈ 0, j = 0.074, lnL = -177.22;

Table 2.3). DEC and DIVA-like biogeographic founder effect analyses, based on the current distribution of selected species, strongly support a Gondwanan origin of Tortricidae (node 7) with the South American plate as primary center of origin (Appendix 2.10). Models DEC (j = 0) and DIVA-like (j = 0) support a Gondwanan origin too; however, they show India+Australia as primary dispersal region with India as an ancestral bridge to other areas after the Eocene (37 Mya), when a massive extinction of clades occurred in both Australia and India (Appendix 2.10). The selected model (DEC+*J*, Fig. 2.2) shows a founder effect with some South American Chlidanotinae colonizing Australia; then the diaspora radiated on this continent before the end of the Cretaceous. This was followed by the divergence of Tortricinae (node 37) and Olethreutinae (node 13) in Australia after the Cretaceous and dispersal on other Gondwanan continents. After that, both clades started colonization of northern lands during the early Eocene (nodes 16, 25, 41, 48). Colonization of other regions was principally through founder events. The South American plate is the putative ancestral area of Chlidanotinae and its tribes, and also for Sparganothini (node 50), Euliini (node 56), and Cochylini (node 60; Tortricinae). Australia is the ancestral area of Tortricinae and Olethreutinae and several of its tribes (nodes 13, 15, 37, 38), while the Palearctic can be the ancestral area for Grapholitini, Eucosmini (node 26), Cnephasiini and Tortricini (node 53; Fig. 2.2).

2.3.4. *Diversification in Tortricidae*

BAMM analyses always inferred a diversification model with the highest probability of only one major shift in the rate of speciation in Tortricidae (Table 2.4, Fig. 2.3), even when modifying values for the prior governing the number of rate shifts (the Poisson process). We selected the run with the Poisson process fixed at 0.6 as the best fit with the highest posterior probability for the number of shifts (PP = 0.76 for a single shift; Table 2.4). This analysis showed an initial high rate of diversification (Fig. 2.4a) that decreased gradually over time for Chlidanotinae tribes (Figs 2.4b, c). However, the clade Tortricinae+Olethreutinae (node 12) started a new diversification regime 78 Mya with a positive shift that reaches its highest peak of speciation between 72-73 Mya (Fig 4a; Appendix 2.11), when Tortricinae and Olethreutinae diverged (Appendix 2.11). After that, rates of diversification decreased gradually in both branches (Fig 4d, e). Speciation and extinction rates decreased through time from starting values

of $\lambda = 0.2707$ and $\mu = 0.0154$ until almost 0. We found that the K-Pg event had a small effect on the trend of speciation in tortricids (Appendix 2.11).

2.4. Discussion

2.4.1. *Tribal relationships within Tortricidae*

Our phylogenetic analyses supported the results of Regier et al. (2012), including the monophyly of Tortricidae and the paraphyly of Chlidanotinae (MP, ML and Bayesian; node 7-10; Appendices 2.6-2.9; Table 2.1). These results did not change with full sampling of all tortricid tribes (three more tribes, four more species), the addition of the COI barcode fragment, and different outgroups. Tortricinae and Olethreutinae were recovered as monophyletic groups in all analyses (nodes 14-13, 38-37; Appendices 2.6-2.9; Table 2.1). Phylogenetic relationships between genera within tribes generally supported the topology of Regier et al. (2012). The principal difference between the analyses was the phylogenetic position of Phricanthini. MP analysis recovered Phricanthini as sister group of Tortricinae+Olethreutinae with low support (node 12, BS 53; Appendix 2.6), while ML and Bayesian analyses recovered Phricanthini close to or within Schoenotenini, also with low support (nodes 38, 39; Appendices 2.7-2.9). The position of Phricanthini in the MP topology may be a case of long branch attraction affecting node support for deep relationships (Tortricinae: BS < 50%, and Olethreutinae: 54%; Appendix 2.6). Both subfamilies were better supported in ML and Bayesian analyses (Appendices 2.7-2.9; Table 2.1). We cannot currently resolve the topology; further studies should include more species of Phricanthini and Schoenotenini to potentially reduce long branch attraction and increase node supports. The Bayesian time-calibrated tree (Fig. 2.1) recovered the early divergence of only Phricanthini as sister group of other Tortricinae with low support (PP= 0.7), but in the same position recovered by Regier et al. (2012). An extended phylogenetic discussion is presented in Appendix 2.5.

Of the tribes not analyzed by Regier et al. (2012), Gatesclarkeanini (Olethreutinae) was recovered inside Olethreutini in all analyses and with strong support in ML and Bayesian (node 21, 20; Appendices 2.7-2.9; Table 2.1), which indicates that its tribal status is not supported. As in Regier et al. (2012), our results also do not support the tribal status of Bactrini and Endotheniini (Appendix 2.5; Table 2.1) because both are part of Olethreutini. Olethreutini is a speciose tribe of leaf-rollers (1077 species) whereas Bactrini, Endotheniini and Gatesclarkeanini

may represent groups of mainly specialized borers (Horak 2006) better characterized with the status of subtribes or genus groups, as foreshadowed in Horak (2006) based on morphology. Bactrini is a lineage of specialized herbivores of Poaceae; the implication of this association is discussed below.

The positions of Schoenotenini and Epitymbiini, the remaining Tortricinae tribes not included in Regier et al. (2012), were unstable between phylogenetic analyses. In both cases, only CAD and COI barcode sequences were available, which may explain part of their instability. Schoenotenini either includes Ceracini, with this clade forming the sister group of Epitymbiini+Archipini (node 44; Appendix 2.6), or Schoenotenini is a paraphyletic group with the addition of Phricanthini, and is located at the base of Tortricinae (node 38; Appendices 2.7-2.9); all these positions had low support values, precluding any firm conclusions. Epitymbiini was recovered as either the sister group of Archipini (node 43; Appendix 2.8) or inside Archipini (Appendices 2.6, 2.7, 2.9). The clade *Dichelia+Epitymbia* was one of the topologies recovered by Dombroskie and Sperling (2013) in an analysis of Archipini. Based on our results and those of Dombroskie and Sperling (2013), we consider Epitymbiini to be part of Archipini.

2.4.2. *A time-calibrated phylogeny for tortricids*

Estimating a time-calibrated tree for Tortricidae is challenging. Until now, no study has provided such a temporal framework for the family, perhaps due to the paucity of fossil specimens preserved in good condition for unambiguous taxonomic assignment (Razowsky 2008). Tortricid fossils are limited principally to inclusions in plant resins (Kristensen and Skalski 1999). Fossil calibrations give the uppermost boundary (minimum age) for dating analysis (Heads 2005). The fossils used in our study are the most conservative and unambiguous data for fossil calibration in the tortricid subfamilies. Every dated phylogeny provides an evolutionary hypothesis that can be tested using other fossils and more comprehensive molecular data and taxon sampling.

The time-calibrated tree that was obtained (Fig. 2.1) produced slightly different but compatible divergence time estimations compared to previous work that relied on completely different sets of fossils and genes for Lepidoptera. For instance, Wahlberg et al. (2013) estimated the divergence of Tortricidae at 132.6 Mya (±11.5 My); an age older than the 120.5 Mya (±20.6 My) recovered in this study but both dates are from the Early Cretaceous. Furthermore, Wahlberg

et al. (2013) estimated more recent divergences between subfamilies: Chlidanotinae (Polyorthini) diverged from Tortricinae+Olethreutinae 68 Mya (±17.5 My), and Tortricinae diverged from Olethreutinae 53 Mya (±8 My). Instead we found older divergences: 97 Mya (±21.04 My) for Chlidanotinae (Polyorthini) and 72.4 Mya (±14.7 My) for Tortricinae/Olethreutinae. Differences were expected because of our taxonomically broader sampling of tortricids, the addition of the closely related outgroups, and the internal fossil calibrations.

The main divergence events in Tortricidae occurred during transitions between geological periods (Fig. 2.2): (i) the divergence of Polyorthini (Chlidanotinae) during the Early/Late Cretaceous, when the increase in global temperature transformed the Late Cretaceous into a "Hot House" (Chumakov et al. 1995; DeConto et al. 2000; Royer et al. 2004); (ii) the divergence between Tortricinae and Olethreutinae during the warmest and last stage of the Cretaceous; and (iii) both Tortricinae and Olethreutinae began to radiate in the aftermath of the Cretaceous-Paleogene mass extinction, an event that did not seem to severely affect leaf-rollers (Appendix 2.11), contrasting with the near-demise of another herbivorous lineage, the Nymphalidae (Wahlberg et al. 2009). Another interesting result is the origin of the family (120.48 Mya), 20 million years after the origin of angiosperms (139.35-136 Mya *sensu* Magallón et al. 2015). The tortricid crown age was concurrent with the radiation of Rosidae and Asteridae (64.31% of all angiosperms; Magallón et al. 2015), which are very important components of current biomes. The synchronicity of the origin and rise to dominance of the main angiosperm clades with the origin and main diversification period of Tortricidae is a robust and interesting finding in this study. Our study also adds insight to previous phylogenetic studies that supported the hypothesis of a positive role of the angiosperm revolution on some insect groups (Hedges et al. 1996; Grimaldi, 1999; Wahlberg et al. 2013).

2.4.3. *Biogeographic and diversification patterns*

Angiosperms started their initial diversification in the Early Cretaceous (Magallón et al. 2015; Silvestro et al. 2015). Pollen fossil data show that angiosperms were distributed worldwide about 125 Mya (Hochuli and Feist-Burkhardt, 2013), but were diverse and abundant only in the Northern Gondwanan tropical areas (Schrank and Mahmoud, 2002). Prior to angiosperm dominance, a massive forest composed of gymnosperms covered India, Antarctica and Australia at least until 140 Mya (Vakhrameev 1991; Anderson et al. 1999; Peralta-Medina and Falcon-

Lang 2012). However, the Earth climate shifted to a warming period in the mid-Cretaceous and angiosperms diversified rapidly (113 Mya), becoming the dominant plant group in the Late Cretaceous, 100 Mya (Crane 1987; Lidgard and Crane 1988; Lupia et al. 1999). Our inferred stem and crown ages for tortricids coincide with this floristic turnover (Fig. 2.4; Appendix 2.11). Remarkably, the diversification analyses indicated an early tortricid radiation, characterized by a high net diversification rate that subsequently declines with time (Figs 2.3, 2.4a). The time of the tortricid origin and their high initial rates of diversification suggest that angiosperms were a dominant macroevolutionary driver of their diversification. Moreover, we inferred a positive shift in speciation (78 Mya, Appendix 2.11) when angiosperms are reported to have reached their ecological dominance in Gondwana (80 Mya; Anderson et al. 1999). This speciation shift resulted in the origin and radiation of the two species-rich subfamilies. A similar shift was also noted by Wahlberg et al. (2013) in Lepidoptera 90 Mya, suggesting a very robust pattern in the rate of diversification of the order.

Like their main host-plant group, the angiosperms (Brown et al. 2014), Tortricidae originated in the South American plate during the angiosperm radiation (Appendix 2.11). Although this inference may be biased by our low taxon sampling, additional data supports the hypothesis of a South American origin: (i) all 'basal' lineages of Tortricidae are principally Neotropical in distribution, and (ii) most Chlidanotinae species are Neotropical (281 of 370, 76%) and only 9% have a non-Gondwanan distribution. Polyorthini and its sister group probably originated in South America, 100 Mya, then both dispersed to other Gondwanan regions through the Antarctic Peninsula, which was geologically connected and had a warmer climate during this period (Lawer et al. 1992; Chaboureau et al. 2014).

At the beginning of Late Cretaceous, tortricid lineages would have been confined to their respective regions, the South American plate for Chlidanotini+Hilarographini and Antarctic-Australasia for Tortricinae+Olethreutinae. They occurred in a warmer climate and inhabited a massive forest composed of new angiosperms as potential resources (Peralta-Medina and Falcon-Lang 2012); then Tortricinae+Olethreutinae exhibited a peak of diversification ca. 72 Mya, probably mediated by continental colonization that opened new niches and eventually culminated in the divergence of Tortricinae and Olethreutinae 73 Mya (Appendix 11). This hypothesis explains the current Australasian distribution of early-diverging clades of Tortricinae and Olethreutinae. After an initial diversification, Olethreutinae tribes and non-Australian Archipini,

Ceracini, Schoenoteninii, Phricanthini (Tortricinae) would have reached the Northern Hemisphere through Southeast Asia, Africa and India during the late Eocene, while Cochylini, Euliini and Sparganothini (Tortricinae) could have dispersed through Central America at the early Eocene (Fig 2.1; Appendix 2.11). A similar pattern of colonization of the Northern Hemisphere was proposed by Wahlberg et al. (2009) for Nymphalidae. This last colonization event is coincident with a behavioural change in Tortricinae that could have facilitated the expansion within northern landmasses: early divergent lineages are mainly oligophagous (Phricanthini), but recently diverging lineages are mainly polyphagous (Powell 1964, Regier et al. 2012). The change to polyphagy could have facilitated colonization and establishment, and a change from laying single eggs to laying egg masses (Powell 1964) could have further increased the fitness of migrants. In contrast, the pattern of herbivory for Olethreutinae tribes is different; most of these tribes are oligophagous (Regier et al. 2012). Within the polyphagous Olethreutini, the Bactrini are feeders on grasses of the family Poaceae. Bactrini diverged and radiated 19.4 Mya (Fig 2.1; Table 2.1), whereas the major diversification of Poaceae occurred at the Miocene, when Panicoideae and Chloridoideae radiated (Bouchenak-Khelladi et al. 2014; Spriggs et al. 2014) during the expansion of grasslands (Edwards et al. 2010; Strömberg 2011). The radiation of Bactrini may be associated with radiation of an Olethreutini clade specialized in grasses, given its synchronous radiation with the formation of grasslands in the Northern Hemisphere. A similar association has been proposed for the subfamily Satyrinae (Nymphalidae), a specialist in grasses (Peña and Wahlberg 2008). Another possible transition from polyphagous to a more specialized diet may have occurred in Cochylini, which are mostly specialized on Asteraceae. In our study, Cochylini diverged 43.1 Mya, few million years after the divergence of Asteraceae (Panero and Funk 2008; Magallón et al. 2015).

The hypothesis of a South American origin and subsequent dispersal through the Southern Hemisphere continents with a strong effect of founder-event speciation (Table 2.3) is congruent with a biogeographical pattern of exchange between South America and Australia via the trans-Antarctic dispersal route (Sanmartín and Ronquist 2004). Long-distance dispersal events are an important process for colonizing southern continents in plant lineages, which is likely associated with the most resistant stage of plants (seeds/spores). Although not comparable to seeds, moths use wind currents for dispersal (Cardé 2008), a well-known phenomenon in forestry (Greenbank et al. 1980). Studies of *Choristoneura fumiferana* (Tortricinae: Archipini) estimated a potential

flying distance of 43.2 km per day without wind assistance; however, a maximum of 450 km per day with wind assistance has been recorded during outbreaks (Sturtevant et al. 2013). Longer distances can be reached in consecutive journeys (Cardé, 2008) or by using prevailing wind currents, including jet streams (Rota et al. 2016). Wind dispersal has been proposed even for weak flyers like stoneflies (McCulloch et al. 2016).

In contrast, the hypothesis of India+Australia ($j = 0$) as origin requires a complex combination of biological events that reduce its viability. It shows worldwide dispersal through India, then extinction in Australia of early-diverged Polyorthini and extinction in India of several clades. This hypothesis represents a combination of low probability events and had lower statistical support; therefore, we consider a South American origin plus founder-event speciation as the best hypothesis with robust biological and statistical support.

The pattern of diversification in Tortricidae shows an initial high rate of speciation that decreased with time (Figs 2.3, 2.4), congruent with the hypothesis of gradual saturation of available niches (i.e. angiosperm lineages). A second peak of angiosperm diversity (70 Mya; Appendix 2.11) may represent a new set of available niches for tortricids during the colonization of Southern Hemisphere continents. The strong increase in tortricid speciation rates could thus be due to the synergistic effect of both the angiosperm revolution and landmass colonization.

Horak and Brown (1991) proposed a detritivore-fungivore larva as the original condition for tortricids. However, all species of Chlidanotinae with host plant records (Brown et al. 2008) and early diverged tribes of Tortricinae and Olethreutinae are almost exclusively angiosperm feeders. Moreover, host plants for Galacticidae and Heliocosmidae, the closest families to Tortricidae (Regier et al. 2013), are exclusively angiosperms (Robinson et al. 2010), supporting an ancestral larval condition as angiosperm feeder even for Tortricoidea. Just a few million years after the early angiosperm radiation, leaf rollers moths would first have been able to take advantage of the herbaceous species in the initial phase of radiation of angiosperms (Peralta-Medina and Falcon-Lang 2012). Later, after 78 Mya, when angiosperms replaced conifers as the predominant trees (Crane 1983; Vakhrameev 1988), tortricids would have reached the forest canopy to become one of the most successful herbivorous clades, the tenth most diversified family of phytophagous lineages.

2.4. Conclusion

Our time-calibrated phylogenetic tree has reconstructed the divergence of Tortricidae from other Lepidoptera as occurring during the mid-Cretaceous (ca. 120 Mya), and our biogeographic analysis supports the hypothesis of a Gondwanan center of origin in the South American plate. The origin of Tortricidae was thus synchronous with the rise of angiosperms, and the increase in speciation rate of the family during the Cretaceous agrees with the angiosperm revolution hypothesis. Worldwide colonization occurred between the late Cretaceous and the early Paleogene, mainly through dispersal-vicariance and founder events. Our study also quantifies a gradient of substitution rates for several genes (nuclear WG, Eno, DDC, CAD, PER, and mitochondrial COI barcode fragment) that are potentially also useful for estimating time-calibrated trees for taxa without fossils.

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Table 2.1. Estimated mean ages of divergence of Tortricidae taxa (in Mya) with the stem of the clade taken as origin. Tribes proposed by Horak and Brown (1991) and selected other clades are shown with their 95% highest posterior density (HPD) interval for dates of divergence and posterior probability (PP) for monophyly. Clade names in the first column refer to Fig. 1. Underlined taxa are not recovered as formal tribes in this study. Sister tribes or subfamilies are separated by commas and have the same divergence ages. Support values obtained in MP, ML, and Bayesian analyses are presented in columns six to eight. Abbreviations: NA= not applicable since there is a single terminal, *s.s.* = *sensu stricto*, Enar. = Enarmoniini, Ole. = Olethreutini, End. = Endotheniini, Bac. = Bactrini, Gat. = Gatesclarkeanini. SH-aLRT = Shimodaira Hasegawa- approximate Likelihood Ratio Support, UFBS = Ultra-Fast Bootstrap support. (Table continues in next page)

Clade names	Estimated divergence time	95% HPD	Clade # in Fig. 1	PP of clade in Fig. 1	BS of clade in MP	SH-aLRT / UFBS of clade in ML	PP of clade in Bayesian
Tortricidae	120.48	99.29 - 140.48	7	1	91	100/100	1
Polyorthini	96.99	75.90 - 117.98	8	1	94	100/100	1
Hilarographini+Chlidanotini	92.26	72.22 - 112.73	10	1	91	100/100	1
Hilarographini, Chlidanotini	67.29	50.66 - 83. 49	10, 11	NA, 1	91, 97	NA, 100/100	NA, 1
Olethreutinae, Tortricinae	72.42	58.40 - 87.74	13, 37	1, 1	60[1], <50[2]	100/100, 100/100	1, 0.73
Microcorsini	58.95	46.23 - 71.76	14	1	100	100/100	1
Enar.+Ole.+End.+Bac.+Gat.	50.99	39.52 - 61.53	16	0.97	----	56/72[15]	0.73
Enarmoniini, Olethreutini *s.s.*	48.36	37.15 - 58.21	17,18	1, 1	74, <50[3]	82/85[16], 99/99[17]	0.99, 0.99
Gatesclarkeanini	26.14	16.00 - 35.78	20	NA	NA	NA	NA
Endotheniini, Bactrini	19.40	14.35 - 24.18	23, 24	NA, 1	NA, 100[4]	NA, 100/100[18]	NA, 1

Eucosmini+Grapholitini	48.18	37.59 - 58.77	26	1	87[5]	100/100	1
Grapholitini, Eucosmini	42.18	32.40 - 50.71	27, 32	1, 1	93[6], 71[7]	100/100, 98/99	1,1
Phricanthini	65.77	50. 75 - 79.51	37	NA	NA	NA	NA
Schoenotenini	54.27	41.66 - 66.44	40	0.82	<50[8]	85/54[19]	0.79[22]
Ceracini, Archipini	49.67	38.27 - 60.51	41	NA, 1	---	NA, 100/98[20]	NA, 0.54[23]
Epitymbiini	34.27	25.36 - 43.30	43	NA	NA	NA	NA
non-Australian Archipini	32.89	25.44 - 40.51	45	1	98[9]	100/100[21]	1[24]
Atteriini+Sparganothini	57.85	45.61 - 69.99	49	0.99	<50[10]	100/95	1
Atteriini, Sparganothini	51.30	39.94 - 62.56	49, 50	NA, 1	NA, 95[11]	NA, 99/100	NA, 1
Cnephasiini+Tortricini	54.31	42.02 - 65.76	53	1	66[12]	100/100	1
Tortricini, Cnephasiini	46.48	35.75 - 56.73	54,55	1, 1	100[13], 99[14]	100/100, 100/100	1,1
Euliini+Cochylini	49.99	38.76 - 60.74	56	1	61	100/100	1
Cochylini	43.10	33.32 - 52.72	60	1	98	100/100	1

[1] Node 14 in Appendix_S6. [2] Node 38 in Appendix_S6. [3] Node 19 in Appendix_S6. [4] Node 25 in Appendix_S6. [5] Node 27 in Appendix_S6. [6] Node 28 in Appendix_S6. [7] Node 33 in Appendix_S6. [8] Node 51 in Appendix_S6. [9] Node 48 in Appendix_S6. [10] Node 53 in Appendix_S6. [11] Node 54 in Appendix_S6. [12] Node 39 in Appendix_S6. [13] Node 40 in Appendix_S6. [14] Node 41 in Appendix_S6.

[15] Node 17 in Appendix_S7. [16] Node 18 in Appendix_S7. [17] Node 19 in Appendix_S7. [18] Node 25 in Appendix_S7. [19] Node 38 in Appendix_S7. [20] Node 42 in Appendix_S7. [21] Node 46 in Appendix_S7.

[22] Node 39 in Appendix_S8. [23] Node 44 in Appendix_S8. [24] Node 46 in Appendix_S8.

Table 2.2. Estimated rates of evolution (substitutions per site per million years) for the six genes used in Tortricidae. Average rates and rate statistics are presented for each gene; they correspond to the results of the BEAST analyses with uniform prior for the fossil constraint and independent molecular clocks per gene-partition. DDC and Eno were grouped in the same partition by PartitionFinder. Abbreviations: stdev = standard deviation, ucld = uncorrelated lognormal distribution, coef. = coefficient.

Gene partition	mean rate	coef. variation	covariance	ucld.mean	ucld.stdev
COI (658 bp)	$1.03 \times 10^{-2} \pm 1.61 \times 10^{-3}$	0.6294 ± 0.078	0.0682 ± 0.090	$1.060 \times 10^{-2} \pm 1.79 \times 10^{-3}$	0.6110 ± 0.076
PER	$4.14 \times 10^{-3} \pm 4.03 \times 10^{-4}$	0.3159 ± 0.033	0.0395 ± 0.085	$4.337 \times 10^{-3} \pm 4.44 \times 10^{-4}$	0.3156 ± 0.036
CAD	$2.84 \times 10^{-3} \pm 2.64 \times 10^{-4}$	0.3290 ± 0.028	-0.0134 ± 0.086	$2.894 \times 10^{-3} \pm 2.83 \times 10^{-4}$	0.3275 ± 0.032
DDC & Eno	$2.42 \times 10^{-3} \pm 2.30 \times 10^{-4}$	0.2635 ± 0.026	0.0612 ± 0.083	$2.468 \times 10^{-3} \pm 2.44 \times 10^{-4}$	0.2661 ± 0.031
WG	$2.15 \times 10^{-3} \pm 2.28 \times 10^{-4}$	0.3378 ± 0.097	-0.0319 ± 0.089	$2.240 \times 10^{-3} \pm 3.10 \times 10^{-4}$	0.3299 ± 0.091

Table 2.3. Likelihood scores and model comparison of six biogeographical scenarios estimated using BioGeoBEARS. Values of parameters of dispersal (d), extinction (e), and founder effect (j) are detailed. Chi-square tests between models were performed allowing (alternative hypothesis: *alt*) or not allowing (null hypothesis: null) founder effect (+*J*). Abbreviations: lnL = likelihood scores, DF = degrees of freedom, AIC = Akaike information criterion, ΔAIC = Delta Akaike information criterion (difference within AIC values with the best fit score).

Model	k	d	e	j	lnL	DF null vs *alt.*	P-value	AIC	ΔAIC	Akaike weight
DEC null	2	0.0486	0.0439	0.0	-360.74	1	9.7×10^{-80}	725.5	355.6	6.3×10^{-78}
DEC+ J alt.	3	0.0096	1×10^{-12}	0.0667	-181.97			369.9	0.0	1
DIVA-like null	2	0.0459	0.0395	0.0	-360.32	1	2.4×10^{-79}	724.7	353.8	1.5×10^{-77}
DIVA-like + J alt.	3	0.0099	1×10^{-12}	0.0643	-182.45			370.9	0.0	1
BAYAREA-like null	2	0.0623	0.0674	0.0	-359.69	1	1.0×10^{-65}	723.4	291.2	5.8×10^{-64}
BAYAREA-like + J alt.	3	0.0008	0.0259	0.0062	-213.09			432.2	0.0	1

    *Selected model

Table 2.4. Summary of models compared across a gradient of values for priors governing the number of rate shifts (the Poisson process) using BAMM 2.5 and BAMMtools 2.1 (Rabosky, 2014). * Selected model according to the highest posterior distribution per number of shifts. Abbreviations: ESS = effective sample size, lnL = likelihood, NA = not applicable.

Poisson rate prior	ESS N shifts	ESS lnL	Posterior distribution per number of shifts								
			0	1	2	3	4	5	6	7	8
0.1	2030.255	519.599	0.04	0.42	0.33	0.14	0.046	0.014	0.0023	0.0005	0.0001
0.2	2628.844	530.371	0.06	0.58	0.28	0.074	0.012	0.0016	0.0001	NA	NA
0.3	1592.380	493.907	0.05	0.68	0.22	0.044	0.0060	0.0008	0.0001	NA	NA
0.4	170.037	30.046	0.08	0.70	0.19	0.028	0.0031	0.00013	NA	NA	NA
0.5	560.557	219.551	0.33	0.52	0.13	0.016	0.0013	NA	NA	NA	NA
*0.6	1857.729	612.815	0.09	*0.76	0.13	0.013	0.0013	0.0004	NA	NA	NA
0.7	1060.434	575.678	0.41	0.50	0.08	0.076	0.0004	NA	NA	NA	NA
0.8	481.279	258.554	0.43	0.50	0.06	0.0052	0.00053	NA	NA	NA	NA
0.9	515.676	287.479	0.24	0.66	0.09	0.0069	0.00053	NA	NA	NA	NA
1	57.637	28.713	0.32	0.59	0.08	0.0060	0.0004	NA	NA	NA	NA

* Selected model *sensu* highest posterior distribution per number of shifts for the Poisson rate prior.
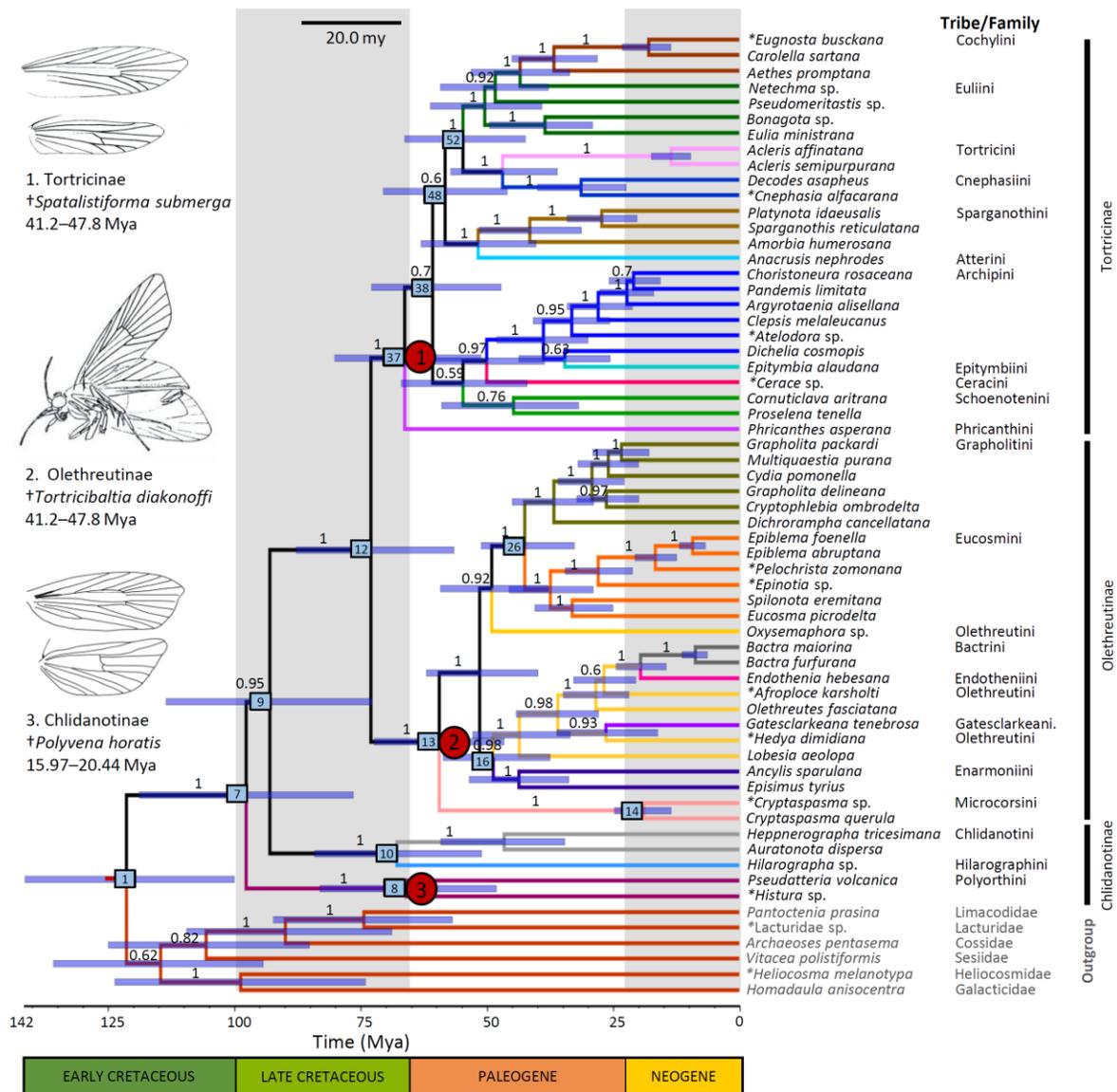
Figure 2.1. Time-calibrated phylogeny of Tortricidae, using BEAST. Species from the same tribe are represented by branches of the same color (outgroups in red). Numbers on branches denote their posterior probability, and node bars show 95% posterior density for divergence dates. The three fossils used to calibrate the molecular clock are depicted on the left, and their phylogenetic assignment is represented by red-filled circles. Drawings of fossils are original figures from descriptions (Skalski, 1992; Poinar and Brown, 1993) used with permission. Selected node numbers are in blue-filled squares. Asterisk indicates a taxon that includes sequence for the barcode fragment (COI) for a substitute species of the same genus (see Appendix 2.1).
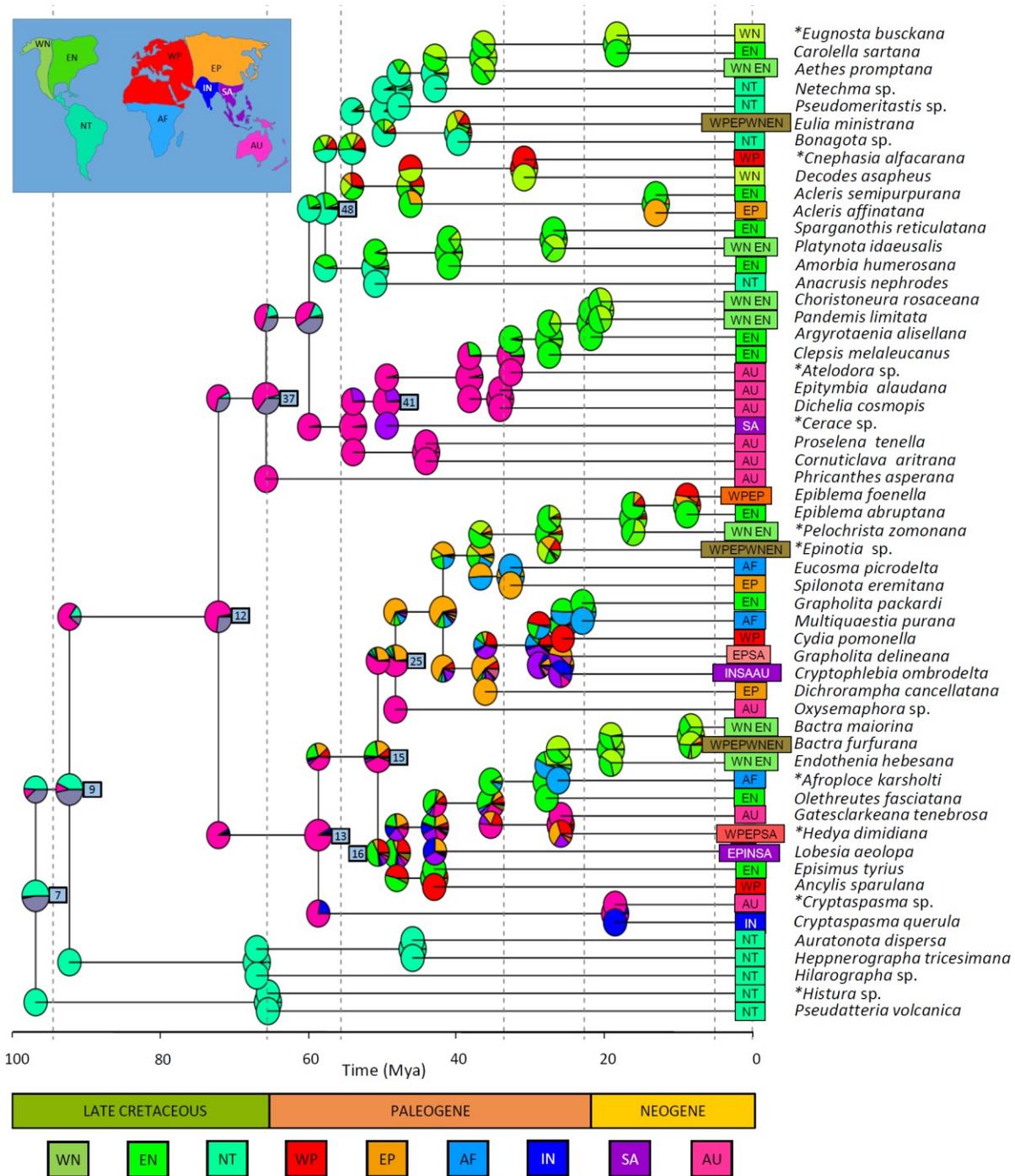
Figure 2.2. Historical biogeography of Tortricidae using BioGeoBEARS. The best time-stratified palaeographic model was used, with founder effect (DEC+*J*). Selected node numbers are in blue-filled squares. Gray vertical dashed lines refer to time intervals used in the analysis. Colored boxes identify biogeographical regions: WN = West Nearctic, EN = East Nearctic, NT = Neotropic, WP = West Palearctic, EP = East Palearctic, (*legend Fig. 2.2 continues next page*)

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AF = Africa (including Madagascar), IN = India, SA = Southeast Asia, and AU = Australasia. Pie charts show relative probabilities of ancestral areas. Species distributions with more than one area have combined letters for biogeographical regions and alternate color boxes. Asterisk indicates a taxon that includes sequence for the barcode fragment (COI) for a substitute species of the same genus (see Appendix 2.1).
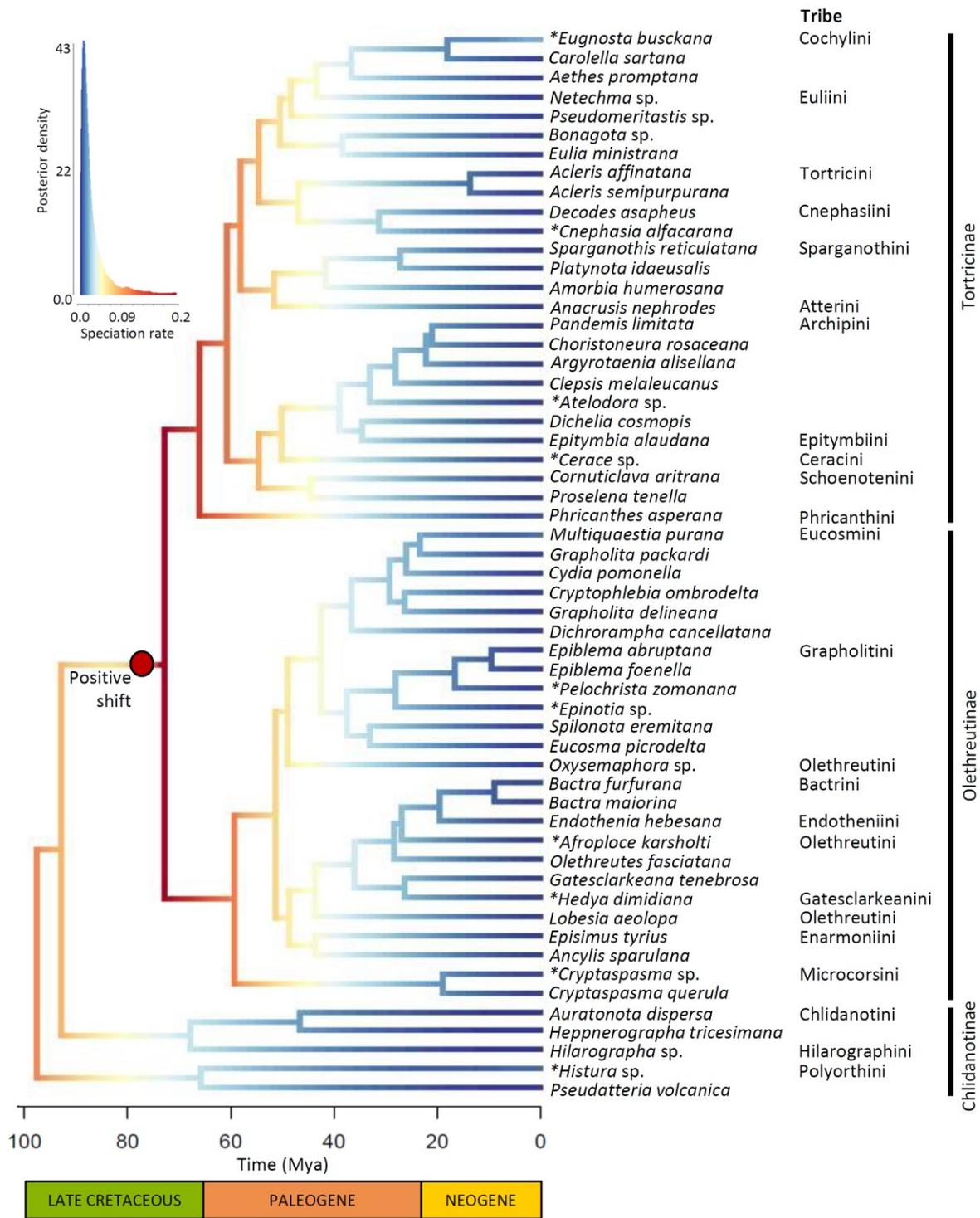
Figure 2.3. Speciation pattern of Tortricidae inferred with BAMM. Colors on branches show speciation rates ranging from almost 0 (dark blue) to 0.2 (red), based on the best macroevolutionary model. BAMM estimated a significant (*legend Fig. 2.3 continues next page*)

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diversification increase at the divergence of Tortricinae from Olethreutinae (denoted by red circle). Asterisk indicates a taxon that includes sequence for the barcode fragment (COI) for a substitute species of the same genus (see Appendix 2.1).
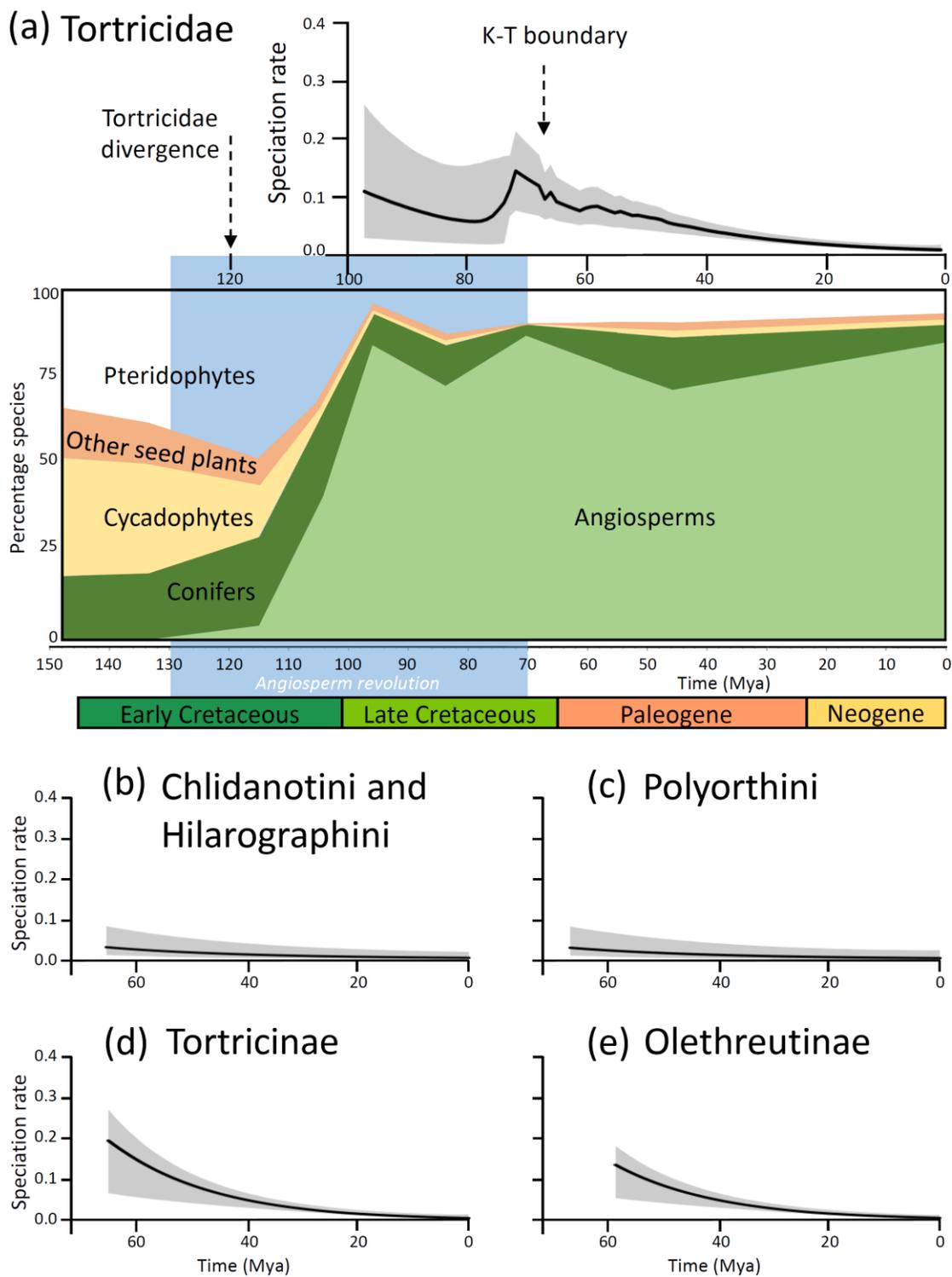
Figure 2.4. Tortricid speciation rates and plant diversity through time. Rates for Tortricidae as a whole are above the percentage of plant species per group along the geological record (redrawn from Crane, 1983; de Boer et al. 2012). (*legend Fig. 2.4 continues next page*)

The period known as the 'angiosperm revolution' is highlighted in blue. Rates of speciation through time are shown for: (a) Tortricidae as a whole, (b) Chlidanotini and Hilarographini, (c) Polyorthini, (d) Tortricinae, and (e) Olethreutinae, with grey area representing the 95% HPD interval of the speciation rates.

Chapter 3: Mitogenomes reveal convergent herbivory on conifers by *Choristoneura* moths after boreal forest formation

3.1. Introduction

Mitogenomes are receiving increasing attention in phylogenetic and evolutionary research on insects, including Lepidoptera (e.g. Cameron 2014; Timmermans et al. 2014; Ramírez-Ríos et al. 2016; Wu et al. 2016); however, no study has use mitogenomes to analyze evolutionary patterns in a family clade of this order. The small molecular size and absence of introns have made mitogenomes convenient and useful markers for phylogenetic studies across insects (Cameron 2014), with 4126 full mitogenome sequences now published for 1527 insect species (GenBank, accessed May 2017; Clark et al. 2016). Insect mitogenomes are composed of 37 genes (13 protein-coding, 22 tRNAs, and two rRNAs), a few short non-coding regions, and a long and highly variable control region (Babbucci et al. 2014; Cameron 2014).

Leafroller moths (Tortricidae) are a diverse family of about 11,000 recognized species (Gilligan et al. 2014a). They include several destructive pest species (Brown et al. 2008), as well as some major modulators of temperate forest dynamics (Cooke et al. 2007; Nealis 2016) that have cyclic outbreaks and use wind currents for long-distance dispersal (Sturtevant et al. 2013). Various molecular studies have focused on the evolution, phylogenetic relationships and origin of this family (e.g. Regier et al. 2012; Gilligan et al., 2014b; Razowski and Tarcz 2014). Recently, Fagua et al. (2017) estimated a time-calibrated tree for all recognized tribes of Tortricidae (sensu Horak and Brown 1991), using six genes and fossil calibrations. However, tortricid evolution has not yet been studied with full mitogenome sequences. To date, mitogenomes for eleven tortricid species have been published, including taxa from four tribes in the two largest subfamilies: Olethreutinae (tribes Eucosmini and Grapholitini) and Tortricinae (tribes Archipini and Tortricini) (Wu et al. 2016).

Within the tribe Archipini, *Choristoneura* is one of the most economically and ecologically important tortricid genera (Silk and Eveleigh 2016). Only one mitogenome is available for this genus: *Choristoneura longicellana*, a generalist orchard pest from temperate East Asia (Byun et al. 1998; Wu et al. 2016). No mitogenome is published yet for the most well-studied species of Archipini, several of which are in the *Choristoneura fumiferana* species complex, also known as the spruce budworm (SBW) species complex. The SBW complex includes eight (Brunet et al. 2017; Dupuis et al. 2017) or nine (Brown 2005; Gilligan et al. 2014a)

coniferophagous species of *Choristoneura* in North America. In addition to major impact on forestry by the SBW complex in North America (Alfaro and Fuentealba 2016), *C. murinana* is an important conifer pest in Europe (Sarýkaya and Avcý 2005), while *Choristoneura rosaceana* and *C. conflictana,* are pests in orchards and aspen forest in North America (Reissig 1978; Holsten and Hard 1985). Consequently, understanding of diversification processes in *Choristoneura* has implications for both evolutionary biology and resource management.

The variability and accessibility of short mitochondrial DNA sequences have led to their use in several studies on the SBW species complex. Sperling and Hickey (1994, 1995), followed by Lumley and Sperling (2010, 2011a,b), found 169 mitochondrial haplotypes clustered into five major lineages (named f, p, o, bβ, and oβ) distributed among the species of the SBW complex. Most SBW species were non-monophyletic with respect to these mitochondrial lineages but the f and p lineages each had most of their haplotype variation restricted to a single species: *C. fumiferana* and *C. pinus*, respectively (Lumley and Sperling 2011a).

Despite the economic importance of *Choristoneura*, its diversification remains poorly studied, with only general comments in taxonomic and phylogenetic studies of the genus or Archipini (Razowski 1987, 1992, 2002, 2008; Dang 1992; Jinbo 2000; Wang and Yang 2008; Dombroskie and Sperling 2013). However, work on the diversification of the SBW complex has generated contrasting hypotheses. Volney (1985) proposed that the current distribution of western and eastern species is the result of recent changes in the composition and distribution of boreal forests during the Holocene. Powell and De Benedictis (1995) proposed a similar hypothesis for the western species but attributed their divergences to changes in forest distribution during the Pliocene, more than 2.5 million years ago (Ma). No rigorous time estimates were available for *Choristoneura* or the SBW complex to test these competing hypotheses.

In this study, we examine mitogenomes across Tortricidae, emphasizing *Choristoneura* and the SBW complex, to estimate: (i) phylogenetic relationships based on single mitochondrial genes compared to whole mitogenomes; (ii) rates of mitochondrial DNA evolution in Tortricidae, and (iii) divergence times of coniferophagous species of *Choristoneura* and major mitochondrial lineages in the SBW complex. We sequenced new mitogenomes for three non-SBW species of *Choristoneura* and all five major mitochondrial lineages of the SBW complex, then estimated phylogenetic relationships and divergence times using fossil and secondary calibrations.

3.2. Material and methods

3.2.1. *Samples, library prep, and sequencing*

Mitochondrial genomes for 12 Lepidoptera species were obtained as accessions in GenBank (Clark et al. 2016), including 11 Tortricidae (*Acleris fimbriana*, *Adoxophyes honmai*, *Adoxophyes orana*, *Choristoneura longicellana*, *Cydia pomonella*, *Epiphyas postvittana*, *Grapholita dimorpha*, *Grapholita molesta*, *Spilonota lechriaspis*, *Retinia pseudotsugaicola*, and *Rhyacionia leptotubula*) and a member of the Cossidae as outgroup (*Eogystia hippophaecolus*) (Lee et al. 2006; Son and Kim 2011; Zhao et al. 2011, 2016; Zhu et al. 2012; Shi et al. 2013; Wu et al. 2013, 2016; Gong et al. 2014; Timmermans et al. 2014; Niu et al. 2016).

Additionally, nine mitogenome sequences were obtained via library preparation and high-throughput sequencing, four of them at the Institut de Biologie Intégratives et des Systèmes (IBIS) at Laval University and the McGill University and Genome Quebec Innovation Centre (*C. fumiferana* [East] f lineage*, Choristoneura occidentalis occidentalis* o lineage, *Choristoneura pinus* p lineage, and *Choristoneura occidentalis biennis* bβ lineage) and five at the Molecular Biology Service Unit at the University of Alberta (*Choristoneura fumiferana* [West] f lineage, *Choristoneura occidentalis occidentalis* oβ lineage, *Choristoneura conflictana*, *Choristoneura murinana* and *Choristoneura rosaceana*). See Appendix S3.1 for all collection and accession information.

Sequence for the *C. fumiferana* (East) mitochondrial genome was obtained from DNA extracted from a pool of male pupae (Insect Production Services, Natural Resources Canada, Sault Ste. Marie, Canada). This DNA was used to generate both a shotgun and a 6 kb paired-end library for sequencing on a Roche 454 GS-FLX sequencer. Newbler version 2.6 (Roche) was used for genome assembly. The eight other new mitogenome sequences were generated from ethanol precipitated DNA samples extracted from entire thoraces using DNeasy Blood & Tissue Kits (Qiagen®). DNA quantity and quality were assessed using the Qubit® dsDNA BR Assay and Nanodrop® 1000 protocols (Thermofisher Scientific).

Single-end libraries were prepared for three of the eight samples (*C. o. biennis* bβ, *C. pinus* p and *C. occidentalis* o) using an Illumina TruSeq® DNA Library Preparation kit (Illumina®) and sequenced on a HiSeq 2000 platform (read length of 32 to 100 bp). Paired-end libraries were prepared for the other five samples (*C. fumiferana* (West) f, *C. occidentalis* oβ, *C.*

conflictana, *C. murinana* and *C. rosaceana*) using an Illumina Nextera® DNA Library Preparation kit and sequenced on a NexSeq 550 platform (Illumina) (read length of 32 to 75 bp). Morphological and DNA voucher specimens are stored at -20° C.

3.2.2. *Mitogenome assembly and annotation.*

Single-end sequences from the HiSeq 2000 were trimmed of universal and indexing adapter sequences at a length greater than 8 bases, and subsequently filtered to retain lengths greater than five bases after trimming, remove sequencing artefacts consisting of mononucleic sequence, and remove sequences with base qualities less than Q20 over the entire sequence length using the FASTX-Toolkit 0.0.13 (http://hannonlab.cshl.edu/fastx_toolkit/index.html; accessed 17.02.03). Sequences were then aligned against the reference mitogenomes of *C. fumiferana* (East) and *Choristoneura longicellana* (Wu et al. 2016) using the Burrows-Wheeler Aligner 'aln' algorithm ('bwa'; Li and Durbin 2010), and compiled into final sequences using SAMtools (Li et al. 2009). Paired-end sequences from the NexSeq platform were aligned to the *C. fumiferana* and *C. longicellana* mitogenome references directly using the 'mem' algorithm of bwa, and subsequently compiled into final sequences using SAMTools.

Sequences for each specimen (including the 12 GenBank mitogenomes) were aligned using MUSCLE 3.8 (Edgar 2004) as implemented in the EMBL-EBI server (Lopez et al. 2014). Primer 3 (Untergasser et al. 2012) was used to design 13 primer pairs (Table A.3.1) to verify the presence of insertions or deletions (indels) in mitogenomes using Sanger sequencing. Once validated, consensus sequences were mapped and annotated for mitochondrial genes using the MITOS WebServer (Bernt et al. 2013; http://mitos.bioinf.uni-leipzig.de/help.py).

3.2.3. *Phylogenetic analyses*

The control region and tRNA genes were excluded from phylogenetic analyses since the observed high variability and frequent insertions, even at the intraspecific level, of the control region and the almost invariant sequences of the tortricid's tRNAs. Datasets were then analyzed comprising the entire sequence of all protein and ribosomal genes (i.e. 15 genes combined) and independent sequences for each protein or ribosomal gene (i.e. each gene tree). The best partitioning schemes per codon position and gene from the alignment for subsequent

phylogenetic analyses were defined with PartitionFinder 1.1.1 (Lanfear et al. 2012). Independent runs of the '*mrbayes*' and '*beast*' models were used with branch lengths linked and the *greedy* algorithm with the Bayesian Information Criterion for model selection, while maintaining other settings as default. Descriptive characteristics of sequences, genetic distances, and partitions were made using Geneious 9.0 (Kearse et al. 2012) and Phylip 3.695 (Felsenstein 1989).

Phylogenetic analyses were first performed under maximum likelihood using IQ-TREE 1.5.3 (Nguyen et al. 2015; Trifinopoulos et al. 2016) running the Shimodaira Hasegawa-approximate Likelihood Ratio Support (SH-aLRT) and Ultra-Fast Bootstrap Support (UFBS) with 1000 replicates. We considered clades to be well supported when nodes had SH/UFBS values greater than or equal to 90%. Bayesian analyses were then performed using MrBayes 3.2.6 with reversible jump Markov Chain Monte Carlo (MCMC) and allowing molecular partitions to evolve under different models across the entire substitution model space (Huelsenbeck et al. 2004). Partitions were allowed to evolve under different rates of evolution; the parameters governing evolutionary rates were *unlinked*. Bayesian searches were executed using two independent runs consisting of eight chains (one cold and seven hot) to obtain an average standard deviation of split frequencies close to 0.001 and potential scale reduction factor (PSRF) close to 1.0. We performed analyses for the full mitogenome dataset with runs of 20 million generations sampled every 2000th generation, and analyses for individual genes with runs of 5 million generations sampled every 500th generation. The first 25% of samples were discarded as burn-in. Convergence and mixing of runs were verified by values of PSRF, values for effective sample size (ESS, above 200) for all parameters, and visual convergence of the analyses using '*Trace Plots*' in Tracer 1.6 (Rambaut et al. 2013). A 50% majority-rule consensus tree was constructed from the remaining trees to estimate posterior probabilities (PP). Clades were considered strongly supported when nodes had a PP greater than or equal to 0.95.

A topological comparison was used to test the monophyly of the Nearctic and Palearctic coniferophagous taxa within *Choristoneura*: the SBW complex and *C. murinana,* respectively. We compared a topology without constraints (Model 1) against one that constrained *C. murinana* as the sister group of the SBW complex (Model 2). Marginal likelihoods of the two models were estimated from 10 million generations (100 steps and 10000 generations per step) of stepping-stone sampling (Xie et al. 2011). Marginal likelihood allowed computation of Bayes factors, for

which a value above 10 was considered to be very strong evidence in favor of the best model (Kass and Raftery 1995).

3.2.4. *Molecular dating analyses*

A time-calibrated tree was estimated using BEAST 1.8.3 (Drummond et al. 2012) relying on molecular partitions identified by PartitionFinder and the clock was calibrated using two fossils. The MCMC analysis was run for 100 million generations sampled every 10,000 generations. We discarded the first 25% of the 10,000 trees obtained. Internal nodes for Tortricidae were calibrated using two fossils selected based on Sohn et al. (2012) and original descriptions: †*Tortricibaltia diakonoffi* Skalski, 1992 (Lutetian, middle Eocene: 41.3–47.8 Ma) for Olethreutinae Walsingham, 1895; and †*Spatalistiforma submerga* Skalski 1992 (also from the Lutetian, middle Eocene) for Tortricinae Latreille, 1803.

The BEAST analyses explored credibility intervals for divergence times by comparing uniform and normal distributions for each fossil calibration based on the most recent common ancestor of each subfamily and for the tree root height (age of the root). The upper limits of the uniform distribution were defined using the younger boundary of the geological period in which each fossil was found (i.e. 41.3 Ma for Olethreutinae and Tortricinae), while the lower limits were set by the estimated divergence time of 120 Ma for Tortricidae recently estimated by Fagua et al. (2017). For the analysis set with a normal distribution, we relied on secondary calibrations based on age estimates for Olethreutinae and Tortricinae estimated by Fagua et al. (2017) with mean of 72 Ma and standard deviation of 10. Tree root height was constrained using the estimation of 158 Ma for the age of Apoditrysia by Wahlberg et al. (2013). For the analysis with uniform distribution, a lower limit and upper limit of 80 and 160 Ma were set, respectively, while in the analysis with normal distribution, a mean of 120 Ma and standard deviation of 20 was used. Convergence of the runs was confirmed by checking the ESS values of all parameters using *Tracer* and accepting good convergence with ESS values above 200.

3.3. Results and discussion

3.2.1. *Mitogenome phylogeny and evolution of Tortricidae and spruce budworms*

The mitogenomes obtained for our study, all from the genus *Choristoneura*, had the same gene arrangement as that reported for *Choristoneura longicellana* and other Lepidoptera (Wu et

al. 2016), including the tRNA gene re-arrangement of Met-Ile-Gln (MIQ) proposed as synapomorphic for Dytrisia by Timmermans et al. (2014). Species studied in Lepidoptera mostly have the Dytrisian arrangement; however, see Liu et al. (2016) and Park et al. (2016) for different arrangements in Limacodidae, Gelechiidae and others. The new mitogenomes had few nucleotide substitutions in their 13 protein-coding genes, two ribosomal RNAs and 22 tRNAs, giving an average genetic distance (F84) of 0.04 (±0.02) expected mutations per nucleotide site among specimens. As with other insect mitogenomes (Cameron 2014), the AT-rich control region (D-loop) was highly variable and difficult to align, and so was excluded from further phylogenetic analyses. Comparison of *Choristoneura* mitogenomes from our study to *C. longicellana* showed larger differences, including substitutions, indels and a long repeat (TA$_{28}$) near the end of the 16S region (Appendix S2, Fig. A.3.1). This repeat accounts for Wu *et al.* (2016)'s finding that *C. longicellana* has the longest 16S region in Lepidoptera and the highest AT content in Tortricoidea.

All the major mitochondrial genes showed increasing genetic distance (F84) with higher taxonomic ranks (Fig. 3.1). Genetic distance among haplotypes of the SBW complex was less than 0.02 for all protein-coding genes and 0.01 for the two ribosomal genes. Except for 12S rDNA, genetic distances among different species within genera (counting the SBW group only once) ranged from 0.03 to 0.09. The genus level included comparisons within *Choristoneura* as well as *Grapholita* and *Adoxophyes*. Except for low values for 12S and high divergences in ND6, distances within genera were clearly different from distances at higher taxonomic ranks for each gene (Fig. 3.1). Most genetic distances between genera within tribes, tribes within subfamilies, and subfamilies of Tortricidae ranged from 0.09 to 0.16. There were no consistent differences in genetic distances between ranks above the level of genus. Some genes showed slightly higher means between tribes within subfamilies than between subfamilies (e.g. ND1), reflecting variation in rates of divergence among tortricid clades (Regier et al. 2012; Fagua et al. 2017)

Phylogenetic relationships among tortricid mitogenomes are shown in Fig. 3.2 and Appendix S3. Maximum likelihood and Bayesian analyses of the combined protein-coding and ribosomal genes recovered almost the same topology as that of Fagua et al. (2017) at the tribal level (Appendix S3), except that the mitogenome phylogeny showed Eucosmini as paraphyletic. The low number of species included in our study, variation in divergence rates, and early

divergence of *Spilonota* at the base of Eucosmini (Regier et al. 2012; Fagua et al. 2017) may explain the lack of monophyly of Eucosmini in our analyses.

Gene-tree topologies for separate protein or ribosomal genes are summarized in Table 3.1 and shown in Appendix S4. Four of the nine genes that were >700 bp in length (COIII, ND2, ND4, and 16S) recovered, in both ML and Bayesian analyses, four or more of the six suprageneric clades that were supported by Fagua et al. (2017) and Regier et al. (2012). In contrast only one (ND6) of eight shorter genes or fragments recovered four or more of these clades. At the generic and infrageneric level, six genes were effective for both species differentiation and recovering monophyly of genera and higher clades found in the reference tree (COI, COII, ND1, ND2, ND4, and ND6). Only one gene, ND2, consistently recovered the same topology as Fagua et al. (2017) at all levels; curiously, ND2 is one of the least used mitochondrial markers in Lepidoptera. In general, any of these six genes was an efficient marker in phylogenetic analysis involving species belonging to closely related genera. Our results are in general agreement with Mandal et al. (2014) regarding the most useful mitochondrial genes for phylogenetic studies of insects. However, COI was not the best marker among these six genes.

Our finding that individual mitochondrial genes do not usually support suprageneric relationships well coincides with other work on Lepidoptera and other organisms (Brower 2006; Wiemers and Fiedler 2007; Wilson 2010; Mitchell and Gopurenko 2016; Trunz et al. 2016). However, the full set of protein-coding and ribosomal genes was more useful for reconstructing phylogenies up to the level of family in Tortricidae. Our results complement other current work on Lepidoptera (Timmermans et al. 2014; Ramírez-Ríos et al. 2016; Wu et al. 2016), Coleoptera (Timmermans et al. 2010) and Neuropterida (Wang et al. 2017), indicating the usefulness of mitogenomes in phylogenetic reconstructions at higher taxonomic ranks.

3.2.2. *Rates of mitochondrial evolution and origin of the spruce budworm complex*

Rates of molecular evolution estimated for each mitochondrial protein-coding or ribosomal gene are presented in Table 3.2. Ribosomal genes showed the slowest rates (9.38×10^{-4} substitutions per site per million years, smy, for 12S and 1.53×10^{-3} smy for 16S). In contrast, rates were generally faster for protein-coding genes (1.93×10^{-3} to 3.63×10^{-3} smy). Three groups may be defined: (1) ATP8, ND1, ND4, ND5 with rates close to 2.0×10^{-3} smy; (2) COI, ATP6, ND4L, ND2 around 2.5×10^{-3} smy; and (3) COIII, ND3, ND6, COII, COB around 3.5×10^{-3} smy.

Rates for protein-coding genes were generally higher than the expected "standard" mitochondrial DNA clock, estimated at 1.15×10^{-3} by Brower (1994; see also Papadopoulou et al. 2010). Higher values may be associated with a higher proportion of recently diverging species (e.g. the SBW complex), (Ho et al. 2005). However, fossil calibrations (or secondary calibrations) and substitution models (GTR+Γ+I for all genes) for uncorrelated relaxed clock analyses should allow such biases to be reduced (Papadopoulou et al. 2010).

Our Bayesian dating analyses showed moderate variability in ages estimated using different priors. The 95% credibility intervals of our age estimate also overlapped with the ages recovered by Fagua et al. (2017), a dating study that was based on both mitochondrial and nuclear information (Table 3.3). Our new divergence times were based on >95% independent molecular data (barcode fragment versus 13 protein-coding and 2 ribosomal mitochondrial genes) and taxonomic sampling (19 different species) but were consistent with the estimates of Fagua et al. (2017; see Table 3.3). We consider the results of the dated tree obtained using a uniform distribution for root and calibrations to be the best estimate for divergence times in *Choristoneura* and the SBW complex (Fig. 3.2) since this analysis is based on the most conservative exploration of priors. The stem age of Tortricidae (tree root age) was estimated to be 126 Ma using mitogenomes; this older age was expected because of the deeper phylogenetic separation between the Cossidae (outgroup) and the Tortricidae in comparison with the outgroups used in Fagua et al. (2017). More interestingly, the Bayesian mitogenome dating estimated the time of divergence between Olethreutinae and Tortricinae at 63.85 (crown age of Tortricidae in this study), younger than the reference, which is probably a consequence of the absence of mitogenomes for Chlidanotinae, the first subfamily to branch off in Tortricidae and included in Fagua et al. (2017). Incomplete sampling at the tribal level would explain differences between both estimates. At the subfamily and tribal level (Table 3.3), all age estimates nonetheless overlapped with the credibility intervals of Fagua et al. (2017), demonstrating that time-calibrated trees reconstructed using mitogenomes yield similar divergence times to those estimated with both mitochondrial and nuclear data.

We estimated the age of the *Choristoneura* crown to be in the early Miocene at 18.19 Ma. Interestingly, we found that divergence of the Palearctic coniferophagous species (*C. murinana*), at 10.66 Ma, is synchronous with the divergence of the Nearctic coniferophagous SBW complex in the middle Miocene, at 11.04 Ma (Table 3.3). The cluster of haplotypes at the SBW crown

diversified far later, in the Pliocene at 3.53 Ma. All three dating analyses show very similar divergence times for *C. murinana*, the SBW stem, and for the crown of the SBW complex. Their specialization as conifer feeders is a major shift in these moths; most *Choristoneura* species are polyphagous, with very few specialized on a single hostplant family (Brown et al. 2008; Robinson et al. 2010). However, incomplete taxon sampling for *Choristoneura* could hide the phylogenetic signal of a topology in which the coniferophagous species, the SBW complex and *C. murinana*, might form a monophyletic group. To test this hypothesis, we used marginal likelihood and Bayes factors to compare the best reconstructed topology against a topology where *C. murinana* was constrained as the sister group of the SBW complex (Appendix S5). This test provided strong evidence in favor of the best topology (difference of marginal likelihood means = 76.25), with the conifer-feeding *Choristoneura* paraphyletic and *C. murinana* unrelated to the SBW complex, a result also found by Dombroskie and Sperling (2013). Aside from the phylogenetic evidence, the main compound of the female pheromone of *C. murinana* differs from that of North American *Choristoneura*: (Z)-9-dodecenyl acetate is unique to the Palearctic species (Priesner et al. 1982, 1988). Consequently, the SBW complex and *C. murinana,* two specialists on Pinaceae, can be considered to have diverged independently from polyphagous angiosperm herbivores, as now seen in *C. rosaceana* and *C. conflictana* (Fig. 3.2).

The synchronicity of the two divergences at about 11 Ma is associated with the formation and expansion of boreal forest or taiga (Fig. 3.2), a biome dominated by Pinaceae. Boreal forest is probably the youngest biome on Earth (Taggard and Cross 2009). Its current area was occupied first by boreotropical forest (Paleogene) and later by temperate mixed mesophytic forest (early Miocene; Pound et al. 2012). Boreal forest was restricted to vegetation belts at high altitude on mountains until the Neogene and migrated to lower elevations when the climate became colder and drier (Taggard and Cross 2009). This migration occurred after the end of the warming period of the middle Miocene (12 Ma, Zachos et al. 2001, 2008), when global cooling transformed the Antarctic in a permanent ice sheet (Lewis et al. 2007, 2008; Pound et al. 2012). Gradual cooling changed the distribution of biomes, pushing boreal forest north of belts of broadleaved deciduous woodland and grassland (Pound et al. 2011, 2012). This biome distribution remained stable during the late Miocene (11.61-7.25 Ma). Thus, the divergence of the Nearctic and Palearctic specialists on Pinaceae, the SBW complex and *C. murinana*, occurred just after boreal forest was established as a major biome in the Holarctic.

Finally, the mitochondrial haplotypes of the SBW complex began to diversify about 4 to 3.5 Ma, during the middle Pliocene (Table 3.3, Fig. 3.2). This was synchronous with the major climatic disruptions of the first two of four massive glaciations that occurred in the Northern Hemisphere during the Pliocene (4.0, 3.6, 3.3, and 2.7 Ma; *sensu* Schepper et al. 2014). These were gradually transformed into the Pleistocene glaciation cycles (Head and Gibbard 2005; Knies et al. 2014; Schepper et al. 2014). Consequently, our results agree with Powell and De Benedictis (1995) who proposed the origin of SBW diversification during the Pliocene. Indeed, the diversification of the five major mitochondrial haplotype lineages may have resulted from early conifer forest isolation events, before the development of the Pleistocene glaciations and classic glacial refugia (Provan and Bennett 2008; Shafer et al. 2010). Since mitogenomes only represent a block of maternally inherited genes, it will be instructive to compare mitochondrial haplotype divergences against similarly calibrated nuclear sequence information (Dupuis et al. 2017).

3.4. Conclusion

Using phylogenetic and dating analyses of mitogenomes, we found synchronous divergence of two *Choristoneura* specialists on Pinaceae, the Palearctic species *C. murinana* and the Nearctic SBW complex, estimated at 11 Ma. The convergent evolution of conifer specialists in a genus of mostly generalist herbivores was associated with the formation and expansion of boreal forest during the late Miocene. In the Pliocene, the diversification of major haplotype lineages of the SBW complex was estimated at 4-3.5 Ma, synchronous with the onset of the first massive glaciations in the Northern Hemisphere. Consequently, mitochondrial haplotype lineage diversification of the SBW complex reflects early divergences before the Pleistocene.

3.5. References

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Table 3.1. Monophyly of tortricid clades based on gene-tree analyses (topologies in Appendix S4). Notation: 1 = monophyly and 0 = paraphyly for ML / Bayesian analysis; COI-658: barcode fragment; COI-470: Sperling & Hickey (1994) fragment; Fagua et al. 2017: monophyly for ML and Bayesian analyses; SBW = spruce budworm species complex; *Adoxo.* = *Adoxophyes*; *Choristo.* = *Choristoneura; Grapho. = Grapholita*; NA = not applicable. *(Table 3.1 continues next page)*.

| | Subfamily | | Tribe | | | Genus | | | | |
Gene (bp length)	Olethreutinae	Tortricinae	Eucosmini	Grapholitini	Archipini	*Grapho.*	*Adoxo.*	*Choristo.*	SBW	Total
ATP6 (681)	0/0	0/1	0/0	1/0	1/0	1/1	1/1	1/1	1/1	7/6
ATP8 (166)	0/0	0/0	0/0	1/1	1/1	1/1	1/1	0/0	0/0	5/5
COI-658 (658)	0/0	0/0	0/0	1/0	0/0	1/1	1/1	1/0	1/1	6/4
COI-470 (470)	1/0	0/0	0/0	0/0	0/0	1/1	1/1	1/1	1/1	6/5
COI (1534)	1/1	1/1	0/0	1/0	0/0	1/1	1/1	1/1	1/1	8/7
CO2 (685)	1/0	1/1	0/0	1/1	0/0	1/1	1/1	1/1	1/1	8/7
CO3 (789)	0/1	1/1	1/1	0/0	1/1	1/1	1/1	1/1	1/1	8/9
CYTB (1159)	0/0	0/0	0/0	0/0	1/1	1/1	1/1	1/1	1/1	6/6
ND1 (952)	0/0	1/1	0/0	1/1	1/0	1/1	1/1	1/1	1/1	8/7
ND2 (1014)	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	10/10
ND3 (357)	0/0	1/1	0/0	1/1	0/0	1/1	1/1	1/1	1/1	7/7
ND4 (1533)	0/0	0/0	1/1	1/1	1/1	1/1	1/1	1/1	1/1	8/8
ND4L (315)	0/0	1/1	0/0	1/0	1/1	0/0	1/1	1/1	0/0	6/5
ND5 (1743)	1/1	0/1	0/0	0/0	1/1	0/0	1/1	1/1	1/1	6/7
ND6 (557)	1/1	1/1	0/0	1/1	1/1	1/0	1/1	1/1	1/1	9/8
12S (838)	1/1	0/0	0/0	0/1	0/0	1/1	0/0	1/1	1/1	5/6

Gene (bp length)	Subfamily		Tribe			Genus				
	Olethreutinae	Tortricinae	Eucosmini	Grapholitini	Archipini	*Grapho.*	*Adoxo.*	*Choristo.*	SBW	Total
16S (1603)	1/1	1/1	0/0	0/0	1/1	1/1	1/1	1/1	1/1	8/8
Total of above	8/7	9/11	3/3	11/8	11/9	15/14	16/16	16/15	15/15	121/115
15 genes (13926)	1/1	1/1	0/0	1/1	1/1	1/1	1/1	1/1	1/1	9/9
Fagua *et al.* 2017	1/1	1/1	1/1	1/1	1/1	NA	NA	NA	NA	NA

Table 3.2. Estimated rates of evolution (substitutions per site per million years) for each protein coding and ribosomal gene of tortricid mitogenomes. Statistics were obtained using *BEAST 1.8.3* with independent molecular clocks (GTR+Γ+I) for each gene, with the analysis performed using a uniform distribution for the tree root prior (80 to 160 Ma) and node calibrations set with uniform distribution for Olethreutinae/Tortricinae (41.2 to 160 Ma) and Tortricidae (80 to 160 Ma). sd = standard deviation. ucld = uncorrelated lognormal distribution. coef. = coefficient.

Gene partition	mean rate	coef. variation	covariance	ucld mean	ucld sd
ATP6	$2.496 \times 10^{-3} \pm 3.34 \times 10^{-4}$	0.1684 ± 0.109	-0.0347 ± 0.152	$2.501 \times 10^{-3} \pm 1.62 \times 10^{-3}$	$1.74 \times 10^{-1} \pm 1.16 \times 10^{-1}$
ATP8	$2.026 \times 10^{-3} \pm 5.08 \times 10^{-4}$	0.2816 ± 0.187	-0.0390 ± 0.157	$1.995 \times 10^{-3} \pm 9.67 \times 10^{-4}$	$2.87 \times 10^{-1} \pm 1.94 \times 10^{-1}$
CO1	$2.469 \times 10^{-3} \pm 3.43 \times 10^{-4}$	0.2392 ± 0.099	-0.0717 ± 0.151	$2.689 \times 10^{-3} \pm 1.36 \times 10^{-3}$	$2.50 \times 10^{-1} \pm 1.20 \times 10^{-1}$
CO2	$3.502 \times 10^{-3} \pm 8.55 \times 10^{-4}$	0.1472 ± 0.108	-0.0481 ± 0.155	$3.596 \times 10^{-3} \pm 1.06 \times 10^{-3}$	$1.52 \times 10^{-1} \pm 1.22 \times 10^{-1}$
CO3	$3.172 \times 10^{-3} \pm 5.00 \times 10^{-4}$	0.1304 ± 0.098	-0.0150 ± 0.151	$3.197 \times 10^{-3} \pm 9.78 \times 10^{-4}$	$1.37 \times 10^{-1} \pm 1.15 \times 10^{-1}$
COB	$3.630 \times 10^{-3} \pm 5.29 \times 10^{-4}$	0.0692 ± 0.071	-0.0280 ± 0.153	$3.674 \times 10^{-3} \pm 1.25 \times 10^{-3}$	$0.73 \times 10^{-1} \pm 0.87 \times 10^{-1}$
ND1	$1.977 \times 10^{-3} \pm 2.35 \times 10^{-4}$	0.2903 ± 0.093	0.0514 ± 0.163	$1.938 \times 10^{-3} \pm 1.24 \times 10^{-3}$	$2.97 \times 10^{-1} \pm 1.12 \times 10^{-1}$
ND2	$2.630 \times 10^{-3} \pm 3.30 \times 10^{-4}$	0.2483 ± 0.079	0.0080 ± 0.163	$2.468 \times 10^{-3} \pm 6.09 \times 10^{-4}$	$2.54 \times 10^{-1} \pm 0.92 \times 10^{-1}$
ND3	$3.305 \times 10^{-3} \pm 6.64 \times 10^{-4}$	0.1339 ± 0.011	-0.0274 ± 0.153	$3.348 \times 10^{-3} \pm 1.39 \times 10^{-3}$	$1.39 \times 10^{-1} \pm 1.20 \times 10^{-1}$
ND4	$1.928 \times 10^{-3} \pm 2.23 \times 10^{-4}$	0.2072 ± 0.101	-0.0035 ± 0.156	$1.973 \times 10^{-3} \pm 8.39 \times 10^{-4}$	$2.14 \times 10^{-1} \pm 1.13 \times 10^{-1}$
ND4L	$2.633 \times 10^{-3} \pm 1.08 \times 10^{-4}$	0.2821 ± 0.154	-0.0468 ± 0.156	$2.492 \times 10^{-3} \pm 1.23 \times 10^{-4}$	$2.84 \times 10^{-1} \pm 1.51 \times 10^{-1}$
ND5	$2.207 \times 10^{-3} \pm 2.67 \times 10^{-4}$	0.5567 ± 0.113	-0.0301 ± 0.126	$2.300 \times 10^{-3} \pm 6.79 \times 10^{-4}$	$6.20 \times 10^{-1} \pm 1.30 \times 10^{-1}$
ND6	$3.437 \times 10^{-3} \pm 5.717 \times 10^{-4}$	0.4546 ± 0.1026	-0.0890 ± 0.133	$3.555 \times 10^{-3} \pm 1.30 \times 10^{-3}$	$4.59 \times 10^{-1} \pm 1.23 \times 10^{-1}$
12S	$9.381 \times 10^{-4} \pm 1.18 \times 10^{-4}$	0.8270 ± 0.198	-0.1265 ± 0.087	$1.212 \times 10^{-3} \pm 6.17 \times 10^{-3}$	$7.82 \times 10^{-1} \pm 1.89 \times 10^{-1}$
16S	$1.532 \times 10^{-3} \pm 1.47 \times 10^{-4}$	0.5448 ± 0.114	0.0843 ± 0.127	$1.645 \times 10^{-3} \pm 5.27 \times 10^{-3}$	$5.71 \times 10^{-1} \pm 1.54 \times 10^{-1}$

Table 3.3. Estimated divergence times of tortricid clades in millions of years (Ma) with 95% confidence intervals. *Fagua* et al. *2017* refers to ages obtained in a tortricid dating analysis on 56 species of 22 tribes using nuclear and mitochondrial genes. *Normal prior* indicates analysis having the tree root prior set with normal distribution (mean 120 Ma, standard deviation [sd] = 20) but the two other node calibrations set with a uniform distribution for Olethreutinae/ Tortricinae (41.2 to 160 Ma) and Tortricidae (80 to 160 Ma). *Uniform prior* represents analysis using a uniform distribution for the tree root prior (80 to 160 Ma) as for the two other calibrations. S*econdary calibration* stands for the analysis in which all node calibrations were set with a normal distribution as follows: Olethreutinae/Tortricinae (mean 72 Ma, sd=10), Tortricidae (mean 120, sd=20), and the tree root (mean 120, sd=20). ESS = Effective Sample Size. An asterisk (*) indicates the selected dated tree.

Clade names	Fagua et al. 2017		Normal prior		*Uniform prior		Secondary calibration	
	Mean age	95% CI	Mean age	95% CI	Mean age	95% CI	Mean age	95% CI
Tortricidae	120.48	99.29 - 140.48	122.65	95.86 - 159.98	126.07	95.86 - 159.98	140.80	115.72 - 168.15
Olethreutinae + Tortricinae	72.42	58.40 - 87.74	62.42	47.71 - 82.17	63.85	47.71 - 82.60	75.02	62.01 - 88.99
Olethreutinae crown	58.95	46.23 - 71.76	53.09	41.30 - 67.93	54.21	41.30 - 70.35	63.99	52.36 - 75.82
Tortricinae crown	65.77	50.75 - 79.51	54.51	41.79 - 70.05	55.83	41.31 - 72.27	65.76	53.97 - 78.12
Eucosmini crown	48.18	37.59 - 58.77	41.48	31.36 - 54.74	42.43	31.76 - 57.07	50.00	39.74 - 60.44
Grapholitini crown	42.18	32.40 - 50.71	40.7	30.64 - 53.73	41.15	30.07 - 55.29	48.96	38.8 - 59.13
Tortricini	46.48	35.75 - 56.73	54.51	41.79 - 70.05	55.83	41.31 - 72.27	65.76	53.97 - 78.12
Archipini crown	38.52	29.71 - 47.68	39.65	29.97 - 51.59	40.57	29.80 - 53.33	47.55	38.04 - 57.03
Choristoneura crown	NA	NA	17.78	13.27 - 23.54	18.19	13.18 - 24.44	21.27	16.62 - 26.13
C. murinana	NA	NA	10.49	7.41 - 14.37	10.66	7.20 - 14.71	12.44	9.26 - 16.10
C. fumiferana complex	NA	NA	10.83	7.83 - 14.53	11.04	7.73 - 14.95	12.86	9.84 - 16.19
C. fumif. complex crown	NA	NA	3.48	2.40 - 4.79	3.53	2.35 - 4.93	4.11	2.97 - 5.39
log-Likelihood (±sd)	NA	NA	-67744.86 ±13.33		-67744.26 ±13.37		-67744.47 ±13.53	
log-Likelihood 95% CI	NA	NA	[-67772.0245, -67719.6923]		[-67770.8451, -67718.535]		[-67772.234, -67719.8585]	
ESS log-Likelihood	NA	NA	1025.75		3294.15		3012.70	
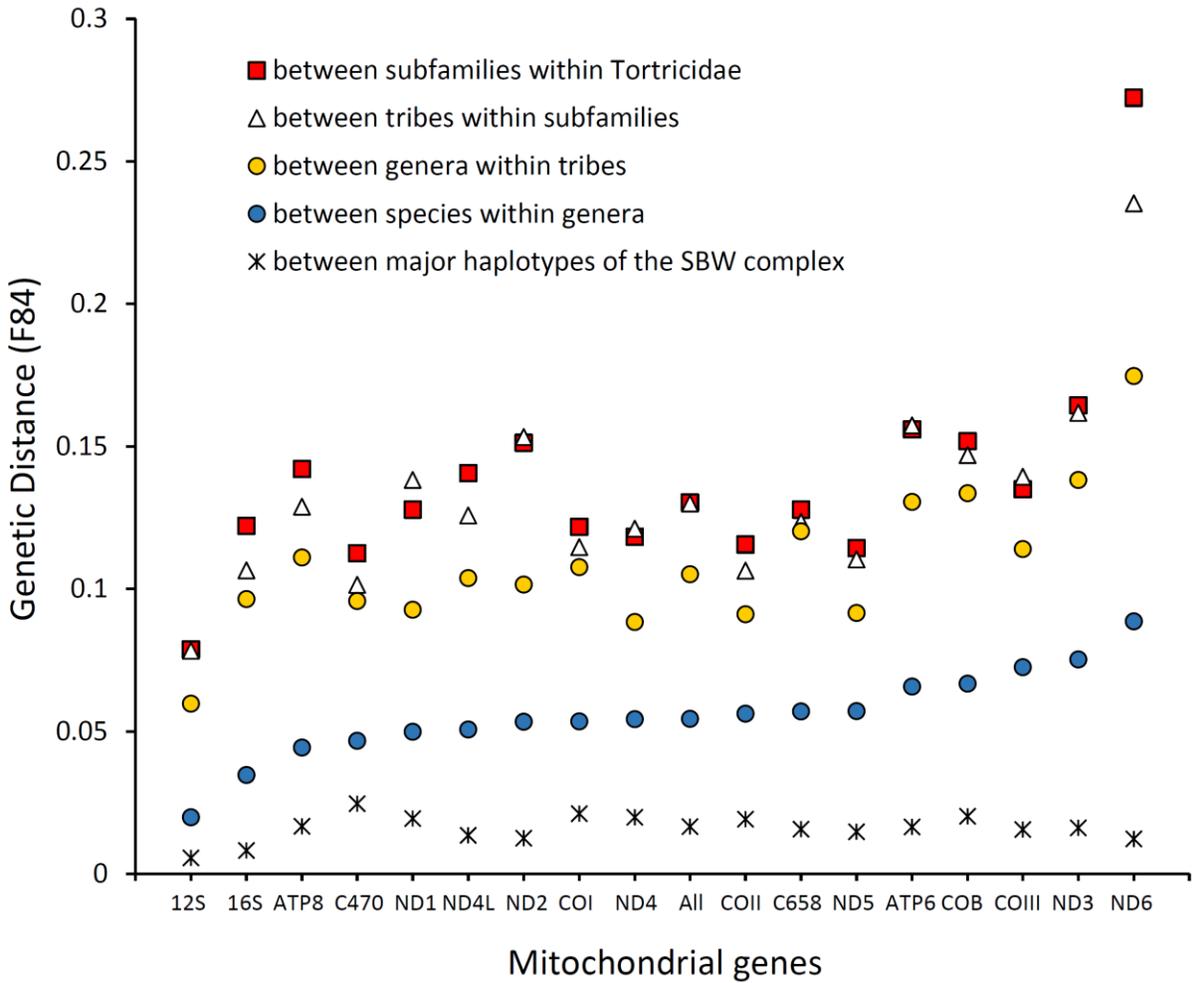
Figure 3.1. Mean mtDNA sequence distance (F84) among Tortricidae at different taxonomic ranks. Values for each mitochondrial gene or all 15 genes combined are arranged in order of increasing distances at the genus level. SBW: spruce budworm species complex. C658: barcode COI fragment. C470: Sperling & Hickey (1994) COI fragment. Values for the genus level and above include only one haplotype of the SBW complex (*C. fumiferana* f), to reduce bias compared to other clades.
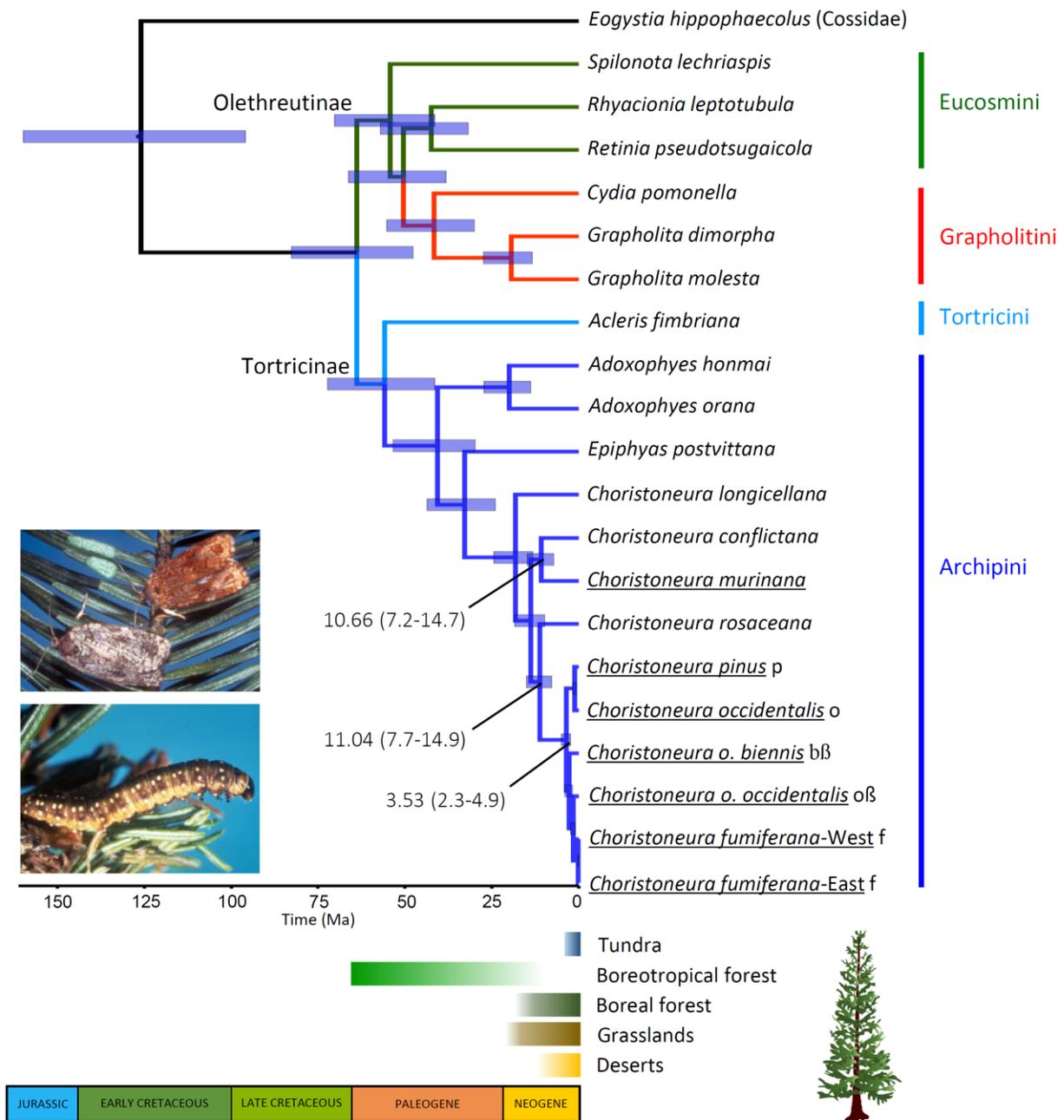
Figure 3.2. Time-calibrated phylogeny of Tortricidae based on mitogenome protein-coding and ribosomal genes using BEAST (1.8.3). Ages in millions of years (Ma) per taxon are detailed in Table 3.3. Dates of divergence of coniferophagous clades and diversification of the spruce budworm complex are given with 95% confidence interval (highest posterior density) in brackets. All branches had PP > 0.98. Node bars show 95% confidence intervals for estimated ages. (*legend Fig. 3.2. continues next page*)

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Underlined species names indicate conifer-feeding *Choristoneura,* with letters after the names corresponding to haplotype lineages (f, p, o, oß, bß) and source of specimen (East = Ontario, West = Alberta). Photos show *C. fumiferana* larva, and adults+eggs (© K.B. Jamieson-Canadian Forest Service, Jerald E. Dewey-USDA Forest Service, Bugwood.org). Color gradients and time scale show origin or extinction of major biomes in the Northern Hemisphere during the Tertiary (redrawn from Nyman et al. 2012).

Chapter 4: Genus delimitation, biogeography and diversification of *Choristoneura* Lederer, 1859 (Lepidoptera: Tortricidae) based on molecular evidence

4.1. Introduction

Lepidoptera, especially moths, are major components of ecosystem dynamics, influencing plant growth and transforming biomass (Miller *et al*. 2006). Leafroller moths (Tortricidae) comprise one of the most species-rich groups of moths and include 22 tribes, of which Archipini is one of the most diverse with more than 1600 species recognized (Horak and Brown 1991; Brown et al. 2008; Gilligan et al. 2014a). Arguably, the best studied of these modulators of forest dynamics are species of *Choristoneura* Lederer, 1859, a genus known for its pest species (Cooke et al. 2007; Nealis 2016).

Choristoneura species include the *C. fumiferana* species complex, also known as the spruce budworm complex (SBW), and *C. murinana*, another conifer-forest defoliator (Volney 1985; Sarýkaya and Avcý 2005), as well as the large aspen tortrix, *C. conflictana*, and *C. rosaceana*, pests of the rose family of plants (Holsten and Hard 1985; Reissig 1978). The genus *Choristoneura* includes 46 recognized species (Gilligan et al. 2014a) restricted principally to the Northern Hemisphere, with 24 species endemic to Asia and Europe (Palearctic), 16 endemic to North America (Nearctic), and five endemic to Africa (African; using Wallace biogeographical regions; Kreft and Jetz 2010). *Choristoneura albaniana* is the only species with a Holarctic distribution (Dang 1992a). Previous studies on the phylogeny of *Choristoneura* include morphological work on species from North America and Eurasia based on male genitalia (Dang 1992b) and various commentary or reviews (Razowski 1987, 1992, 2002, 2008, Jinbo 2000). Molecular phylogenetics has been conducted in the SBW complex (Sperling and Hickey, 1994, 1995; Lumley & Sperling 2010, 2011) and in Archipini (Dombroskie and Sperling 2013), but no molecular study of the genus has yet been published. Despite repeated commentary, delimitation of the genus remains unresolved and a stable phylogeny is lacking due to low taxon sampling of key species (e.g. no phylogeny includes species endemic to Africa) or omission of the type species of the genus, *Choristoneura diversana*.

Building a complete phylogeny for all *Choristoneura* is complicated by the fact that some of the species recently described from Africa or Asia are only known by the holotype or a few pinned specimens, making it difficult to include them in molecular studies (e.g. *Choristoneura africana* Razowski, *C. colyma* Razowski, *C. palladinoi* Razowski & Trematerra, *C. propensa*

Razowski). As a consequence, several taxonomic issues remain. A particularly important one concerns *Archips occidentalis* (Walsingham, 1891), currently treated as a *Choristoneura* species (Gilligan and Brown 2014). The species was originally described as *Cacoecia occidentalis* from specimens collected in Gambia (West Africa), and then placed into *Choristoneura* based on limited morphological evidence (Razowski 2008; Gilligan and Brown 2014). However, this taxonomic change necessitated a name change for *Choristoneura occidentalis* Freeman, 1967, a western North American conifer-feeding species of the SBW complex, because the African name (*Archips occidentalis*) was published earlier (principle of priority, ICZN 1999). This nomenclatural change thus creates confusion about an important western North American forest pest that is an extensively studied forest defoliator (Johns et al. 2016). Our study uses genetic information to test the phylogenetic placement of *Archips occidentalis* Walsingham within Archipini and *Choristoneura*. We reject this transfer because of the ambiguity of Razowski's (2008) study and, to reduce confusion, formally conserve *Archips* as the generic name for *A. occidentalis* Walsingham.

Moreover, the biogeographic origin and diversification history of *Choristoneura* remain unstudied, and it is instructive to examine the evolutionary processes that have acted in the radiation of the clade. Species traditionally assigned to *Choristoneura* are boreal, temperate or Mediterranean in distribution (Razowski 1992; Brown 2005); in contrast, the African *Choristoneura* species, all included or described during the last eight years, are tropical or subtropical (Brown 2005; Gilligan et al. 2014a). The larvae of *Choristoneura* species (Brown et al. 2008) mainly feed on core rosids (Angiospermae) or specialize on conifers, both dominant plant groups in temperate and boreal ecosystems (Willis and McElwain 2014). Several species of *Choristoneura* are polyphagous herbivores, including the type species of the genus, *C. diversana*. Evolutionary study of biogeographic, host association, and diversification patterns requires a well sampled and resolved phylogeny.

Here we aim to reconstruct a well-supported phylogeny for the genus *Choristoneura* using DNA sequence data. We rely on comprehensive sampling of *Choristoneura* species within a large outgroup array of Archipini and Tortricidae species to test hypotheses of the systematic positions of key species, with focus on *Archips occidentalis* and African *Choristoneura* species (Dombroskie and Sperling 2013; Fagua et al. 2014a, b). We use phylogenetic analyses to redefine

the limits of the genus, generate a time-calibrated tree, and examine biogeographic and diversification processes.

4.2. Material and methods

4.2.1. *Samples and DNA extractions*

We sampled 29 specimens of *Choristoneura* on which DNA extractions were performed from entire thoraces using DNeasy Blood & Tissue Kits (Qiagen®), verifying quantity and quality of DNA with the Qubit® dsDNA BR Assay and Nanodrop® (Thermofisher Scientific). Nine of the 29 specimens were sequenced as complete mitogenomes obtained using TruSeq® DNA Library Preparation kit and Nextera® DNA Library Preparation kit (Illumina®; see Fagua et al. 2017b for a detailed description). Other sequences were obtained using combinations of primers for Sanger sequencing (Appendix 4.1: ChorF/K791; ChorF/ChorR; Ron/ChorR; Jerry/Mila; Jerry/Pat; Bryan/Pat; George/Pat; 28SD2F/28SD2R; of which ChorF and ChorR are newly designed for this study). Morphological and DNA voucher specimens are stored at -20° C (Appendix 4.2 contains a complete list with newly sequenced specimens).

4.2.2. *Samples and DNA extractions*

We assemble a molecular dataset for each specimen comprising 1528 base pairs (bp) for the mitochondrial gene cytochrome oxidase subunit I (COI), and 922 bp for the D2 and D3 regions of the 28S rDNA gene (28S). Sampling was extended with 176 specimens retrieved from previous studies: Sperling and Hickey, 1994; Lee et al. 2006; Hulcr et al. 2007; Roe and Sperling 2007; Lumley & Sperling 2010, 2011; Miller et al. 2010; Son and Kim 2011; Zhao et al. 2011, 2016; Zhu et al. 2012; Dombroskie and Sperling 2013; Shi et al. 2013; Wu et al. 2013, 2016; Timmermans et al. 2014; Niu et al. 2016 (see Appendix 4.2 for GenBank accession numbers and specimens). We selected the COI and 28S genes because their DNA could be amplified from old specimens, which expanded our specimen sample substantially.

Since our first objective was to delimit the genus *Choristoneura* and determine the position of *Archips occidentalis* (Walsingham), we used all available sequences of COI and 28S genes from Archipini species to reconstruct the phylogeny. This large outgroup sampling aimed to better define the sister group of *Choristoneura* and to test the monophyly of the genus. Based

on a recent tribal-level time-calibrated tree of tortricids (Fagua et al. 2017a), species of the tribes Tortricini, Schoenotenini, Ceracini, and Epitymbiini were included in the analysis to root and date the phylogeny of Archipini. Limits of the genus were selected to include the type species: *Choristoneura diversana*. In total, our taxon sampling included molecular sequences for 23 species of *Choristoneura* (45 terminals) as the ingroup, plus 82 species of other Tortricidae (87 terminals) as outgroup (Appendix 4.2). The outgroup included species of Olethreutinae (6 species) and Tortricinae (81 species); the latter subfamily included species of Tortricini (1), Schoenotenini (2), Ceracini (1), Epitymbiini (1), and non-*Choristoneura* Archipini (72 including two specimens of *Archips occidentalis*) (Appendix 4.2).

For the DNA dataset, we aligned genes using MUSCLE 3.8 (Edgar, 2004) implemented in the EMBL-EBI server (Lopez et al., 2014). Both alignments were joined in a concatenated molecular dataset comprising 2450 bp (Appendix 4.3). A maximum parsimony (MP) phylogenetic analysis of the alignment was implemented using PAUP* 4.0b (Swofford et al., 2003) with unordered, equal weight characters and settings for heuristic search using parsimony and random addition of sequences (1000 replicates). Maximum parsimony bootstrap (BS) analysis using PAUP* 4.0b was performed using 1000 replicates, and clades were considered supported when the nodal support was BS $\geq$ 75%.

Probabilistic phylogenetic analyses were carried out using the best scheme of molecular partitions as determined by PartitionFinder 1.1.1 (Lanfear et al., 2012) on the entire alignment. With this program, we tested models of nucleotide substitution per codon position in independent runs using the mrbayes and beast models and the Bayesian Information Criterion (BIC) for model selection. Partitions were made using Phylip 3.695 (Felsenstein 1989) and implemented in phylogenetic analyses. A maximum likelihood (ML) analysis was performed with IQ-TREE 1.5.3 (Trifinopoulos et al. 2016) using auto-estimation of substitution models and ultra-fast bootstrap support (UBS) with 1000 replicates. Clades were considered well supported when the UBS node value was $\geq$ 90%. Bayesian inference was performed using MrBayes 3.2.6 (Ronquist et al., 2012) with reversible jump Markov Chain Monte Carlo (MCMC) allowing different substitution models across the entire substitution model space for all partitions (Huelsenbeck et al. 2004) and under different rates of evolution; the parameters governing evolutionary rates were *unlinked*. Bayesian searches were performed using two independent runs of eight chains (one cold and seven hot) to obtain an average standard deviation of split frequencies close to 0.01 and potential

scale reduction factor (PSRF) close to 1.0. Bayesian analyses were performed for the full alignment in a run of 40 million generations sampled every 4000th generation. We discarded the first 25% of samples as burn-in. Convergence and mixing of runs were ensured after checking values of PSRF, values for effective sample size (ESS, above 200) for all parameters, and visual convergence of the analyses using '*Trace Plots*' in Tracer 1.6 (Rambaut et al. 2013). A 50% majority-rule consensus tree was constructed from the remaining trees to estimate posterior probabilities (PP). Clades were considered well supported when the nodes had a posterior probability (PP) $\geq$ 0.95. We estimated the marginal likelihoods of alternative topologies using the stepping-stone sampling running for 100 steps and 10000 generations per step. Marginal likelihood allowed computation of Bayes factors, for which a difference in value above 10 was considered strong evidence in favor of the best model (Kass and Raftery 1995).

4.2.3. *Molecular dating analyses*

We estimated a time-calibrated tree using BEAST 1.8.3 (Drummond et al. 2012) and the molecular partitions identified by PartitionFinder. We performed analyses using Yule process for the branching process prior assuming an uncorrelated lognormal distribution clock model (UCLD). We set a uniform prior from 0 to 10 with starting value of 0.1 for the birth rate. We also set an exponential prior with mean one-third of the standard deviation of the UCLD model, and a uniform prior between 0 and 1 for the mean of the UCLD model. The clock was calibrated using fossil (root of the tree) and secondary calibrations (three internal nodes in Tortricinae). The *BEAST* analyses estimated credibility intervals for divergence times using uniform distributions for calibrations based on the most recent common ancestor of Tortricinae, the tree root prior (age of the root), using a fossil selected from the review of Sohn et al. (2012) and original descriptions: †*Spatalistiforma submerga* Skalski 1992 (from the Lutetian, middle Eocene). The upper limits of the uniform distribution for the root prior were defined using the younger boundary of the geological period in which the fossil was found (i.e. 41.3 Ma), while the lower limits were set by the estimated divergence time of 120 Ma for Tortricidae (Fagua *et al.* 2017a). We also used secondary calibrations based on divergence age estimates for tribe Schoenotenini (54.27 Ma), divergence of genus *Adoxophyes* (40.57 Ma), and the crown of genus *Epiphyas* (32.81 Ma) (Fagua et al. 2017a, b). Upper and lower limits of the uniform distribution for each one of these internal nodes were: for Schoenotenini divergence = 40-70 Ma, *Epiphyas* = 10-45

Ma, and *Adoxophyes* crown = 10-42 Ma. The MCMC analysis was performed using two independent runs of 100 million generations sampled every 10,000 generations. The similarity of topologies between the runs was verified and then the corresponding trees and log files were combined using LogCombiner 1.8.3 (Drummond et al. 2012). We reconstructed the maximum clade credibility tree by discarding the first 25% of trees to estimate median ages and associated credibility intervals.

4.2.4. *Ancestral range reconstruction*

We estimated the ancestral area of origin of Archipini and *Choristoneura*, using models of ancestral range reconstruction implemented in the R-package BioGeoBEARS 0.2.1 (BioGeography with maximum likelihood and Bayesian Evolutionary Analysis in R Scripts; Matzke, 2014). We compared three principal models: Dispersal–Extinction–Cladogenesis (DEC; Ree and Smith, 2008), and likelihood implementations of dispersal-vicariance analysis (DIVA-like; Ronquist, 1997) and BayArea (BayArea-like; Landis et al., 2013). Each model may include, or not, founder-event speciation (also known as the jump dispersal parameter, denoted +J), making a suite of six models in total. We built a species distribution matrix (Appendix 4.4) by coding presence/absence of each taxon in the following nine biogeographic regions: AF, Africa (including Madagascar); AU, Australasia; IN, India; NT, Neotropics; EN, East Nearctic; WN, West Nearctic; EP, East Palearctic; WP, West Palearctic; and SA, Southeast Asia. The regions were taken from classical Wallace biogeographic regions (Kreft and Jetz, 2010) but with Nearctic and Palaearctic regions divided into East and West entities.

The time-calibrated tree constructed in BEAST (with Olethreutinae species removed from the tree) was the input for all analyses that were focused on the genus *Choristoneura*; inferences of ancestral ranges for Archipini were not considered well supported since the sample had a bigger proportion of Nearctic species, generating a strong bias for a tribal analysis. We constructed a time-stratified palaeographic model based on the changes in continental plate distribution for the four time intervals defined within geological epochs (Pleistocene, Pliocene, Miocene, Oligocene, and Eocene): 0-5.33, 5.33-23.03, 23.03-33.9, 33.9-56 Mya (geological boundaries *sensu* Cohen et al. 2013). We also built connectivity matrices through time describing when the nine biogeographic regions were (or not) adjacent and connected to each other during the time intervals (Appendix 4.5). The maximum allowable number of areas was set to nine for

all analyses and models. We compared models with two-parameters (without J parameter), taken as null hypotheses, against models with three-parameters (with J parameter), the alternative hypotheses. Model testing selected the best model of the ancestral range reconstruction using the Akaike Information Criterion (AIC), considering the model with the lowest AIC as the best fit (Matzke, 2014).

4.2.5. *Diversification in Tortricidae*

We inferred the temporal pattern of diversification using the same time-calibrated tree in Newick format, with Olethreutinae species removed, as input. Speciation and extinction rates of *Choristoneura* and possible shifts of speciation across clades and through time were inferred using BAMM 2.5 (Bayesian Analysis of Macroevolutionary Mixtures: Rabosky et al. 2013). We performed several runs of BAMM for 5 million generations using default parameters and a burn-in of 25%. Because the prior governing the number of shifts potentially affects the posteriors (Moore et al. 2016; but see Mitchell et al. 2017), we conducted a series of analyses with a gradient of values for this prior (i.e. the *expected number of rate shifts*). This prior was tested from 1.0 (the higher probability of no rate shift) to 0.1 (higher probability of several shifts) with a step of 0.1 plus additional runs for priors of 5 and 10 since the tree had a small number of tips (<500; Rabosky et al. 2013). We checked the convergence and mixing of the MCMC for each BAMM analysis using BAMMtools 2.5 (Rabosky et al. 2014). We also ensured that each independent run provided similar inference of the diversification. We selected the best-fit run based on the highest posterior probability for a given number of shifts and the highest ESS values for the log-likelihood and the number of shifts. Estimates of speciation and extinction rates as well as the best shift configuration were reconstructed using the best-fit analysis.

4.3. Results

4.3.1. *Phylogenetic analyses*

All phylogenetic analyses (MP, ML and Bayesian; Fig. A.4.1-A.4.3) showed similar and well supported topologies, indicating that the genus *Choristoneura* was polyphyletic with only 20 of 23 sampled species forming a well-supported clade in ML and Bayesian analyses (PP $\geq$ 0.95, UBS $\geq$ 90, BS $\geq$ 75; Figs 4.1). This clade of 20 species included *Choristoneura diversana* with

strong support. Some specimens of *C. diversana* were recovered as the sister group of *Choristoneura murinana,* whereas others were basal to *Choristoneura jeozoensis*. This branch was the sister group of a lineage containing two clades: *Choristoneura luticostana* + *Choristoneura hebenstreitella* and *Choristoneura conflictana* + *Choristoneura fractivittana*. The lineage of these seven species, the "type clade", was mostly comprised of Palearctic species. The sister group of the type clade was a Nearctic lineage, the "Nearctic clade", that included 12 species in two divergent branches, one of which was unstable and contained the SBW complex that changed in topology for each analysis, and another stable branch where *C. argentifasciata* + *Cudonigera houstonana* were the sister group of (*C. rosaceana* (*C. parallela* + *C. zapulata*)). *Choristoneura longicellana* was recovered as the sister group of the type + Nearctic clades with strong support in ML and Bayesian analyses (Fig. 4.1) or as part of the sister branch of *Choristoneura* in the MP analysis (Fig. A.4.1), as sister group of *Cacoecimorpha pronubana* + *Choristoneura albaniana*.

On the another hand, our results support the transfer of *C. evanidana* and *C. simonyi* from *Choristoneura*, species closely related to other genera in ML, Bayesian and especially MP analysis. *Archips purpurana* was recovered as the sister group of *C. evanidana* and *Xenotemna pallorana* was the sister group of *C. simonyi*, always with strong support but in a different position for each topology.

The position of *C. albaniana* was ambiguous. This species was well supported as the sister group of *Archips occidentalis* + *Cacoecimorpha pronubana* in ML and Bayesian analyses (Fig. 4.1), but poorly supported as the sister group of *C. longicellana* + *Cacoecimorpha pronubana* in MP (Fig. A.4.1). A third hypothesis was obtained from the time dated tree (Fig. 4.2), where *C. albaniana* was the sister group of other *Choristoneura* but with low support. We compared the estimated marginal likelihoods of the two topologies, Fig. 4.1 vs Fig. 4.2, to test these competing hypotheses, finding stronger evidence in favor of the best model, Fig. 4.2, which had *C. albaniana* as sister group of other *Choristoneura* (absolute differences between Marginal likelihood means = 37.84; differences above 10 are considered very strong evidence in favor of the better model, Fig. 4.2; Appendix 4.6).

Archips occidentalis (Walsingham) was recovered as the sister group of *Cacoecimorpha pronubana* with good support in ML and Bayesian analysis (Fig. 4.1 and 4.2), or as the sister group of *Cryptoptila australana* in MP analysis, with low support (Fig. A.4.1).

4.3.2. *Molecular dating*

The time-calibrated tree (Fig. 4.2) had a similar topology to the Bayesian inference made with MrBayes (Fig. 4.1), but two species showed important differences. The first was *Choristoneura albaniana* recovered as the sister group of other *Choristoneura*, but with weak support. Since the stepping-stone analysis supported this topology (Appendix 4.6), we are accepting it as the best model for upstream analyses. Another difference was the position of the *Choristoneura fumiferana* terminals, recovered as the sister group of other SBW species (Fig. 4.2). This was consistent with the observed high instability in the internal topology of the SBW in other analyses (Fig A.4.1-A.4.3).

The time-calibrated tree shows that Tortricinae diverged from Olethreutinae 52.68 Ma (Table 4.1; Fig. 4.2). Since Archipini was used as outgroups and we included less than 10% of the described species (*ca.* 1623 spp. *sensu* Regier et al. 2012), we focused our results on the most well represented genus: *Choristoneura*. It is nonetheless interesting to note that all divergence times and crown ages of the Archipini genera including more than six species in the analysis occurred generally between 20 to 25 Ma. *Choristoneura*, including *C. albaniana*, diverged in the early Miocene *ca.* 23.31 Ma (see Fig. 4.2 and Table 4.1 for detailed dates and credibility intervals). *Choristoneura + C. longicellana* diverged soon after, at 21.36 Ma, and the crown of the genus diversified by 15.62 Ma. Divergence times for the two major clades within the genus were synchronous, occurring 12.8 Ma. In both clades one of the two main branches diverged sooner, 9 Ma, while the other branch diverged later, 3.42 Ma in the case of the SBW complex (the Nearctic clade), and 1.86 Ma in the case of the type branch (Fig. 4.2; Table 4.1). Most of the sister species diverged during the last 2 million years.

4.3.3. *Ancestral range reconstruction*

BayArea-like+J was selected as the best fit model for *Choristoneura* (Table 4.2, Fig. 4.3). All models including the founder-event speciation (J) were significantly better than models without this parameter (Table 4.2). The inclusion of the founder event reduced the estimates for dispersal (d) and extinction (e) parameters and increased the log-likelihood (Table 4.2). This model recovered a Holarctic origin (Palearctic + Nearctic) for the genus with subsequent separations of internal clades into distinct biogeographic regions: a Nearctic lineage

corresponding to the clade comprising the SBW complex plus other five species, and a mainly Holarctic lineage including the type species. Within the latter clade, a divergence occurred separating a lineage in the Nearctic and another in the Palearctic (Fig. 4.3). It is worth mentioning that the less supported models reconstructed two different biogeographic hypotheses: an East Palearctic origin for the genus when founder-event speciation was included, and a West Nearctic origin when founder-event speciation was not included (Appendix 4.7). Given the low level of sampling for Archipini, we do not discuss the biogeographic estimates for the tribe, although the results are useful for examining the species excluded from *Choristoneura*. First, *Choristoneura simonyi*, an endemic species of Canary Islands, can be considered as a long-distance dispersal from the Holarctic (*C. simonyi* is sister to the Nearctic *Xenotemna*, a monotypic genus). Second, *Choristoneura evanidana* may be the East Palearctic lineage of the Nearctic *Archips purpurana*. Third, *Archips occidentalis* (Walsingham) may be an African lineage that originated from the West Palearctic monotypic genus *Cacoecimorpha* (Fig. 4.3).

4.3.4. *Diversification in Tortricidae and* Choristoneura

The macroevolutionary analyses took the time-calibrated tree of Archipini as support for the background diversification process and as reference for the diversification in *Choristoneura*. All the runs of BAMM analyses inferred a diversification scenario with the highest probability for two shifts in the speciation rate of Archipini (Table 4.3, Fig. 4.4), even when modifying values for the prior governing the number of rate shifts (the *expected number of rate shifts prior*). The run with the prior set at 0.1 was selected as the best since it obtained the highest posterior probability for the number of shifts (PP = 0.88 for two shifts; Table 4.3). BAMM showed a continuous decrease of speciation after the origin of the clade (divergence from Olethreutinae). A first positive shift is recovered at about 34 Ma, and is synchronous with the colonization of the Northern Hemisphere from a Southern Hemisphere (Australian) ancestor (Appendix 4.7). After that shift, we inferred a new slowdown of speciation until the second positive shift occurred about 16 Ma, which corresponds to the crown of *Choristoneura*. Diversification rates within *Choristoneura* increased significantly compared to the rest of Archipini, and they reached the highest value after the Quaternary, *ca.* 2 Ma, when the SBW complex and the clade containing the type species diversified in the Nearctic and Palearctic, respectively (Fig. 4.4).

4.4. Discussion

4.4.1. *Phylogeny and limits of Choristoneura*

Our phylogenetic analyses support delimitation of the genus *Choristoneura* as a clade whose distribution is restricted to the Northern Hemisphere, including *Cudonigera houstonana*. This generic circumscription includes two early divergent species, the Holarctic *Choristoneura albaniana* and the Palearctic *Choristoneura longicellana*, and a main radiation including a mostly Palearctic lineage sister to a Nearctic lineage (Fig. 4.1). Our topology is congruent with Dombroskie & Sperling (2013) for the Nearctic species and with some species groups proposed for Dang (1992b) in his morphological review of the male genitalia of *Choristoneura*. Both genitalia and molecular data supported the close relationship between species of Dang's group 2 corresponding to our (*C. diversana* + *C. murinana*) clade, Dang's groups 5-6 matching our ((*C. luticostana* + *C. hebenstreitella*) (*C. conflictana* + *C. fractivittana*)) clade, and Dang's groups 8-9 corresponding to our (*C. rosaceana* (*C. paralella* + *C. zapulata*)) clade. However, Dang's (1992b) relationships between these groups, his position for *C. longicellana* and *C. albaniana*, and his relationship between the SBW species, C. *diversana* and *C. murinana* were not supported by molecular data. Our data shows synchronous events of speciation between the Nearctic and the mostly Palearctic clades (Fig. 4.2), both experienced early divergence between mainly polyphagous and mainly coniferophagous lineages. Convergent specialization to herbivory on conifers by Palearctic and Nearctic lineages contrasts with Dang's (1992b) hypothesis, which proposed that Palearctic and Nearctic coniferophagous species of *Choristoneura* are sister groups. Our results support evolutionary convergence for coniferophagy, as previously recorded for a phylogenetic analysis of tortricid mitogenomes (Fagua et al. 2017b). This convergent event is also supported by the different composition of female pheromone compounds of *C. murinana* in comparison with species of the Nearctic lineage (Priesner et al. 1982, 1988; Silk and Eveleigh 2016).

The instability of the internal phylogeny within the SBW species complex was expected since previous studies using different data showed the difficulty to recover a stable topology in the complex (e.g. Stock and Castrovillo 1981; Castrovillo 1982; Sperling and Hickey 1994, 1995; Lumley and Sperling 2011; Bird 2013; Dombroskie and Sperling 2013). Although the resolution of internal relationships within the SBW species complex was not a goal of our study, such

phylogenetic instability can be considered to result from recent divergences, incomplete lineage sorting, and hybridization between lineages (Dupuis et al. 2017).

4.4.2. *Proposal of nomenclatural changes*

Transfer of *Cudonigera houstonana* to the crown of *Choristoneura* in the Nearctic clade and as the sister group of *Choristoneura argentifasciata* supports the original proposal of Freeman (1958), who moved the taxon from *Archips* to *Choristoneura* based on the morphology of the uncus, and with the synonymy of Dombroskie & Sperling (2013) based on molecular evidence. *Cudonigera* was described by Powell and Obraztsov (1977) specifically to include *Cudonigera houstonana* due to the distinctive characteristics of its male and female genitalia. However, the robust support for the inclusion of *Cudonigera houstonana* within *Choristoneura* indicates that genitalic characters in these taxa are not well understood, since their morphological differences, especially in the female genitalia of *C. houstonana*, are very evident.

None of the subtropical or tropical taxa analyzed in this work, *Choristoneura simonyi* and *Archips occidentalis*, was included as part of the genus *Choristoneura*. In addition, a Palearctic species, *Choristoneura evanidana*, was excluded too. The three taxa were all transferred by Razowsky (1987, 1992, 2008) from their original placements as *Pandemis simonyi, Cacoecia evanidana* and *Cacoecia occidentalis* based on the genitalia but using limited information. Because of its nomenclatural importance, Gilligan and Brown (2014) detailed the ambiguity concerning *Archips occidentalis* since it affects *Choristoneura occidentalis*, a major forest defoliator in North America (Johnson 2016). Indeed, this change generated nomenclatural and taxonomical consequences for the generic name of *P. simonyi* and *C. evanidana*. Gilligan and Brown (2014) mentioned the ambiguity in the current diagnostic characters that define *Choristoneura* and related genera, a fact noted by Dang (1992). Gilligan and Brown (2014) then proposed a comprehensive phylogenetic analysis of the genus to address this nomenclatural problem (i.e. *Archips* or *Choristoneura occidentalis* Walsingham). Our phylogeny, using a large sample of Archipini, recovered Walsingham's taxon as sister of the monotypic genus *Cacoecimorpha*. As a consequence, we propose the acceptance of the name *Cacoecimorpha occidentalis* (Walsingham, 1891), an African sister of the West Palearctic *Cacoecimorpha pronubana*. In addition, *Choristoneura evanidana* is transferred to the genus *Archips,* and *Choristoneura simonyi* is transferred to the genus *Xenotemna*.

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Choristoneura **Lederer, 1859**

Choristoneura Lederer, 1859, Wien. ent. Monatschr. 3: 426. Type species: *Tortrix diversana* Hübner, [1814-1817].

Choristoneura houstonana **(Grote)**

Choristoneura houstonana (Grote), Freeman, 1958, Can. Ent., 90, suppl. 7: 38. Fig. 164.

Tortrix houstonana Grote, 1873, Bull. Buffalo Soc. Nat.1: 15, Pl. 1, Fig. 5.

Lozotaenia retana Walsingham, 1879, III. Lepid. Het. 4: 13, Plate 63, Fig. 4.

Cacoecia houstonana Grote, Meyrick, 1913, Gen. Insect., Fasc. 149: 25.

Archips houstonana Grote, McDunnough, 1939, Check List Lepid. Can. & U.S.A., Pt. 2, p. 56.

Cudonigera houstonana Grote, Obraztsov and Powell, 1977, J. Lepid. Soc., Figs. 1-5.

Material examined: 1 male: United States, Arizona, Chiricagua Mts, -109.355 W, 32.009 N. 31/07/1996. Collector: J. Powell.

Choristoneura occidentalis **Freeman**

Choristoneura occidentalis Freeman, 1967. Can. Ent., 99: 451

Choristoneura freemani Razowski, 2008. Polskie Pismo Entomol., 77: 246. **syn. nov.**

Material examined: 2 males; 2 females: Canada, Ontario. Collector: Insect Production Services (IPS), Sault Ste. Marie.

Xenotemna **Powell, 1964**

Xenotemna Powell, 1964, Univ. Calif. Publ. Ent. 22: 145. Type species: *Tortrix pallorana* Robinson, 1869.

Xenotemna simonyi **(Rebel, 1892) comb. nov.**

Pandemis simonyi Rebel, 1892, Ann. Nathist. Hofmus., 7: 263, Pl. 17, Figs. 8, 9.

Pandemis permisilana Rebel, 1894, [in:] Rebel & Rogenhofer, Ann. Nathist. Hofmus., 9: 82.

Pandemis mactana Rebel, 1896, Ann. Nathist. Hofmus., 11: 116, Pl. 3, Fig. 4.

Choristoneura simonyi Rebel, Razowski 1979, Nota lepid. 2: 57, Figs. 1-6. **syn. nov.**

Material examined: 1 males, 1 female: Spain, Canary Island, Tenerife, -16.376 W, 28.431 N. 20/06/2013. Collector: M. Baez.

Cacoecimorpha **Obraztsov, 1954**

Cacoecimorpha Obraztsov, 1954, Tijdschr. Ent. 97: 182. Type species: *Tortrix pronubana* Hubner, [1796-1799].

Cacoecimorpha occidentalis **(Walsingham, 1891) comb. nov.**

Cacoecia occidentalis Walsingham, 1891, Trans. Ent. Soc. Lond. 1981: 64. Pl. iii., Fig. 1.

Archips occidentalis Walsingham, Evans, 1968, Kenya Coffee 33: 195.

Archips occidentalis Walsingham, Brown, 2005, World catalogue of insects, 5: 128.

Choristoneura occidentalis Walsingham, Razowski, 2008. Polskie Pismo Entomol., 77: 246. Figs. 1,2. **syn. nov.**

Material examined: 4 males: Tanzania, Morogoro, Udzungwa, 7.848 E, 36.976 S, 19/05/2010. Collector: J & W De Prins. 1 female: Tanzania, Morogoro, Uluguru, 6.987 E, 37.564 S, 14/05/2010. Collector: J & W De Prins.

Archips **Hübner, 1822**

Archips Hübner, 1822, Syst.-alphab. Verz. 58. Type species: *Phalaena (Tortrix) piceana* Linnaeus, 1758.

Archips evanidana **(Kennel, 1901) comb. nov.**

Cacoecia evanidana Kennel, 1901, Dt. ent. Z. Iris, 13(1900): 214.

Choristoneura evanidana Kennel, Razowski, 2008. SHILAP Revta. Lepid., 77: 20. **syn. nov.**

Material examined: 2 males: South Korea, Gangwon, Seokpo-ri, 127.059 E, 36.415 N, 03/06/2012. Collector: B.K. Byun

4.4.3. *Time, biogeography and divergence in* Choristoneura

      The estimates of divergence times obtained for *Choristoneura* using secondary calibrations for external nodes were highly consistent with times obtained in a previous study in Tortricidae (Fagua et al. 2017b; credibility intervals largely overlap between the analyses). The latter was obtained using a dataset of protein-coding and mitochondrial genes but with a smaller sample of *Choristoneura* species. The origin of *Choristoneura* at the beginning of the Neogene was synchronous with other genera in Archipini (Fig. 4.2). At that time, replacement of boreotropical forest by modern biomes occurred due to the global cooling initiated in the Oligocene (Head & Gibbard 2005; Nyman et al. 2012; Pound et al. 2012).

      Biogeographic analyses support a Holarctic origin for *Choristoneura*. The original clade that radiated into the current genus *Choristoneura* could have been composed of species with Holarctic distribution and *C. albaniana*, one of the few microlepidoptera with a natural Holarctic distribution (Dang 1992a, Laundry et al. 2013), may be a remnant of this lineage. Then, speciation in the Palearctic region could be enhanced since 15 species, unfortunately not included in this study, are from central Asia; the divergence of *C. longicellana* is one of these cases (Fig 3). The large gap of cladogenesis between the divergence of *C. albaniana* and *C. longicellana* may be due to extinctions, or may result from the small data set of Palearctic species used in this study. It will be especially interesting to obtain specimens from species distributed across the mountainous regions of Central Asia (e.g. *Choristoneura expansiva* Wang & Yang, *Choristoneura ferrugininotata* Obraztsov, *Choristoneura griseicoma* Meyrick) and from Far Eastern Russia (*Choristoneura improvisana* Kuznetzov, *Choristoneura irina* Dubatolov & Syachina); none of these species are included in any phylogenetic analyses to date.

      Our diversification analyses suggest that an upshift of speciation occurred within *Choristoneura ca.* 16 Ma. This boost of speciation may be attributed to a number of events, like vicariance and/or host-plant shifts. The synchronicity of phylogenetic events between the Nearctic and the mostly Palearctic clades may reflect similar drivers affecting both regions. One is host plants, which are associated with a major divergence of lineages within clades. Nearctic and mostly Palearctic clades experienced divergences almost synchronously between a lineage including polyphagous species (the Nearctic ((*C. argentifasciata* + *Cudonigera houstonana*)(*C. rosaceana* (*C. parallela* + *C. zapulata*))) and the Palearctic ((*Choristoneura luticostana* +

Choristoneura hebenstreitella)(*Choristoneura conflictana + Choristoneura fractivittana*))) and a lineage including coniferophagous species (the Nearctic SBW complex and the Palearctic *C. diversana, C. murinana, C. jezoensis* clade; Fig. 4.3). This divergence event occurred 13 Ma, coincident with the expansion of boreal forest (Taggart and Cross 2009, Pound et al. 2011), a biome mainly composed of Pinaceae, the most common family of host plant in both clades. The stem of coniferophagous lineages did not produce any speciation event for at least 9 million years, and in both cases major diversification occurred 2 Ma, during the early Pleistocene, when speciation may be attributed to the glaciation cycles in the Northern Hemisphere.

The long stem in each of the Palearctic and Nearctic conifer-feeding lineages suggests taxa with high capacity for specialization in response to the availability of plant resources. This may be associated with incomplete lineage sorting and hybridization between lineages reported for the SBW complex (Dupuis et al. 2017). However, there are some differences between clades; all SBW species are specialists on conifers (mostly Pinaceae), with only occasional records on Apiaceae, Balsaminaceae, Fagaceae and Salicaceae for *C. fumiferana* (Brown et al. 2008; Robinson et al. 2010). In contrast, the coniferophagous Palearctic clade includes a broad generalist, *C. diversana*, recorded as feeding on several core eudicots and also on conifers (Brown et al. 2008; Robinson et al. 2010). Allopatric coniferophagous taxa diverged from *C. diversana*: *C. murinana* (continental Palearctic, recorded in Pinaceae and Cupressaceae; Brown et al. 2008) and *C. jezoensis* (Hokkaido Island, Japan; on Pinaceae; Yasuda and Suzuki 1987) (Fig. 4.3). In addition, this coniferophagous Palearctic clade potentially includes at least one more species: *Choristoneura metasequoiacola* Liu, 1983, a specialized herbivorous of a conifer living fossil: *Metasequoia glyptostroboides* (Cupressaceae). Liu (1983) mentioned the "nearest similarity" between the genitalia of *C. diversana* and *C. metasequoiacola*; the morphological differences between these species are similar to those found by Yasuda and Suzuki (1987) between *C. jezoensis* and *C. diversana*. Future studies including this species should test Liu's (1983) hypothesis.

Another quasi-synchronous diversification event occurred 9 Ma in both the Nearctic and the mostly Palearctic polyphagous clades. This time it corresponded to cooling climate and increasing aridity until reaching the Pliocene-Pleistocene glaciations (Pound et al. 2011, 2012; Schepper et al. 2014). Increments in aridity and cooling were parallel with the migration to the south of temperate biomes from northern latitudes until reaching their current area. The current

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position of temperate and boreal vegetation belts is larger than their previous location, pushed against the Arctic ocean by the boreotropical forest (Pound et al. 2011). Some dominant elements of temperate and boreal forest such as *Acer*, *Alnus*, *Betula*, *Populus*, *Salix*, *Quercus*, *Ulmus* (Willis and McElwain 2014), as well as genera of Rosaceae, are recorded as the most frequent host plant of species of these *Choristoneura* polyphagous lineages (Brown et al. 2008) and divergence of polyphagous clades may be related to this expansion in area and separation between boreal and temperate forest.

However, the position of *Choristoneura conflictana* and *Choristoneura fractivittana*, the only two American species within the mostly Palearctic clade, represents a challenge to our scenario. It may be a case of vicariance of an original Holarctic clade or a colonization event after the divergence of an entirely Palearctic clade. Both hypotheses can support our scenario of a vicariant origin of the genus, but we lack information to test the hypotheses.

Biogeographical and diversification analyses offer additional support to the exclusion of *Archips occidentalis* from *Choristoneura*. Its sister species, *Cacoecimorpha pronubana* is a West Palearctic polyphagous species known to feed on several families of angiosperms and conifers (Zhang 1994; Brown et al. 2008; Robinson et al. 2010). Its natural southern limit is the Sahara Desert; consequently, the sub-Saharan *Archips occidentalis* (Walsingham) may be the sister species in a case of vicariance of the clade. However, the long terminal branches of these sister species can be synonymous with more taxa being closely related to this West Palearctic-African lineage. A broader sample of Archipini from African, Indian, Southeast Asia and Palearctic regions will help to clarify the phylogenetic position of this lineage.

4.4. Conclusion

Phylogeny, molecular dating, biogeography and diversification patterns support *Choristoneura* as a genus comprised of species with a Northern Hemisphere distribution. Our study shows that the genus was recovered as paraphyletic because tropical (*Archips occidentalis*) and subtropical taxa (*Choristoneura simonyi*) were excluded from the genus, as well as the Palearctic *Choristoneura evanidana*. Our analyses support previous nomenclatural changes like the inclusion of *Cudonigera houstonana* Grote as a species of *Choristoneura*, and new changes like the transfer of *Archips occidentalis* Walsingham to the genus *Cacoecimorpha*; the transfer of *Choristoneura evanidana* to the genus *Archips*; and the transfer of *Choristoneura simonyi* to

Xenotemna. We found support for a Holarctic origin of the genus with early divergence of Palearctic elements and a major event of divergence that occurred 16 Ma when a Nearctic clade and an initially Palearctic clade diverged. More recent events of divergence in both clades were almost synchronous and related to ecological specializations, resulting in coniferophagous and polyphagous lineages inside each clade; these two convergent events were synchronous with the expansion of boreal forest.

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Table 4.1. Estimated divergence times of *Choristoneura* clades in millions of years (Ma) with 95% confidence intervals. Ages and confidence interval (CI) are presented in Fig. 4.2 for each terminal. *C. = Choristoneura*.

Clade names	Mean age	95% CI
Olethreutinae + Tortricinae	52.68	50.00 - 60.54
Choristoneura + *C. albaniana*	23.31	18.81 - 28.33
Choristoneura + *C. longicellana*	21.36	16.78 - 26.42
Choristoneura longicellana	16.61	12.95 - 20.79
Choristoneura crown	15.62	12.35 - 19.54
Choristoneura Type Clade crown	12.79	9.52 - 16.49
(*C. diversana* + *C. murinana*)(*C. diversana* + *C. jezoensis*) crown	1.86	1.05 - 2.93
Choristoneura murinana	0.64	0.25 - 1.15
Choristoneura jezoensis	0.79	0.40 - 1.35
C. conflictana + *C. fractivittana*	9.03	6.29 - 12.06
C. fractivittana	5.6	3.42 - 8.37
C. luticostana	1.99	0.94 - 3.32
Choristoneura Nearctic Clade crown	12.78	9.83 - 16.25
C. argentifasciata + *Cudonigera houstonana*	9.43	7.07 - 12.29
C. parallela + *C. zapulata*	4.34	2.56 - 6.41
C. parallela	1.62	0.75 - 2.74
C. fumiferana species complex	12.78	0.75 - 2.74
C. fumiferana species complex crown	3.42	9.83 - 16.25
No *C. fumiferana* terminals in *C. fumiferana* species complex	2.44	0.75 - 2.74

Table 4.2. Likelihood scores and model comparison of six biogeographical scenarios estimated using BioGeoBEARS. Chi-square tests between models were performed allowing (*alternative hypothesis: alt*) or not allowing (null hypothesis: null) founder effect (+*J*). Abbreviations: d = dispersal, e = extinction, j = founder effect, lnL = likelihood scores, DF = degrees of freedom, AIC = Akaike information criterion, ΔAIC = Delta Akaike information criterion (difference within AIC values with the best fit score).

Model	Number of parameter	d	e	j	lnL	DF null vs *alt.*	P	AIC	ΔAIC	Akaike weight
DEC null	2	0.0373	0.0327	0.0	-423.91	1	1.7×10^{-50}	851.8	48.7	8.6×10^{-49}
DEC + J alt.	3	*0.0188*	*1×10^{-12}*	*0.0243*	*-312.24*			*630.5*	*0*	*1*
DIVA-like null	2	0.0403	0.0309	0.0	-446.85	1	6.3×10^{-47}	897.7	205	3.1×10^{-45}
DIVA-like + J alt.	3	*0.0212*	*1×10^{-12}*	*0.0188*	*-343.36*			*692.7*	*0*	*1*
BAYAREA-like null	2	0.0366	0.0582	0.0	-388.20	1	1.3×10^{-54}	780.4	237.3	3.0×10^{-52}
*BAYAREA-like + J alt.	3	*1×10^{-7}*	*0.0394*	*0.0028*	**-268.56*			*543.1*	*0*	*1*

*Selected model

Table 4.3. Summary of models compared across a gradient of values for priors governing the number of rate shifts (*expected number of rate shifts prior*) using BAMM 2.5 and BAMMtools 2.1 (Rabosky, 2014). * Selected model according to the highest posterior distribution per number of shifts. Abbreviations: ESS = effective sample size, lnL = likelihood, NA = not applicable.

Poisson rate prior	ESS N shifts	ESS lnL	Posterior distribution per number of shifts							
			1	2	3	4	5	6	7	8
*0.1	2567.574	969.028	0.026	*0.88	0.088	0.0045	0.00013	NA	NA	NA
0.2	3798.314	1384.562	0.0	0.82	0.17	0.016	0.002	NA	NA	NA
0.3	998.1902	384.7506	0.16	0.65	0.16	0.024	0.0016	0.00013	NA	NA
0.4	2734.724	695.401	0.014	0.71	0.23	0.040	0.0048	0.00027	0.00013	NA
0.5	2758.531	1300.218	0.029	0.67	0.24	0.049	0.0064	0.00053	0.00013	NA
0.6	2476.54	736.3104	0.092	0.60	0.25	0.048	0.008	0.0093	0.00013	NA
0.7	2453.584	1814.296	0.016	0.61	0.29	0.070	0.0150	0.0013	0.00027	NA
0.8	2796.338	1967.84	0.0084	0.60	0.30	0.078	0.014	0.0024	0.00013	0.00013
0.9	2413.377	1258.192	0.0023	0.58	0.31	0.084	0.0160	0.0031	0.00027	0.00013
1	2493.838	1440.256	0.0072	0.57	0.31	0.086	0.017	0.0044	0.0004	0.00027
5	2685.102	1272.814	0.0031	0.38	0.36	0.170	0.0620	0.0210	0.0360	0.00053
10	2329.086	967.858	0.0034	0.35	0.34	0.180	0.0730	0.0200	0.0600	0.00019

* Selected model *sensu* highest posterior distribution per number of shifts for the expected number of rate shifts prior.
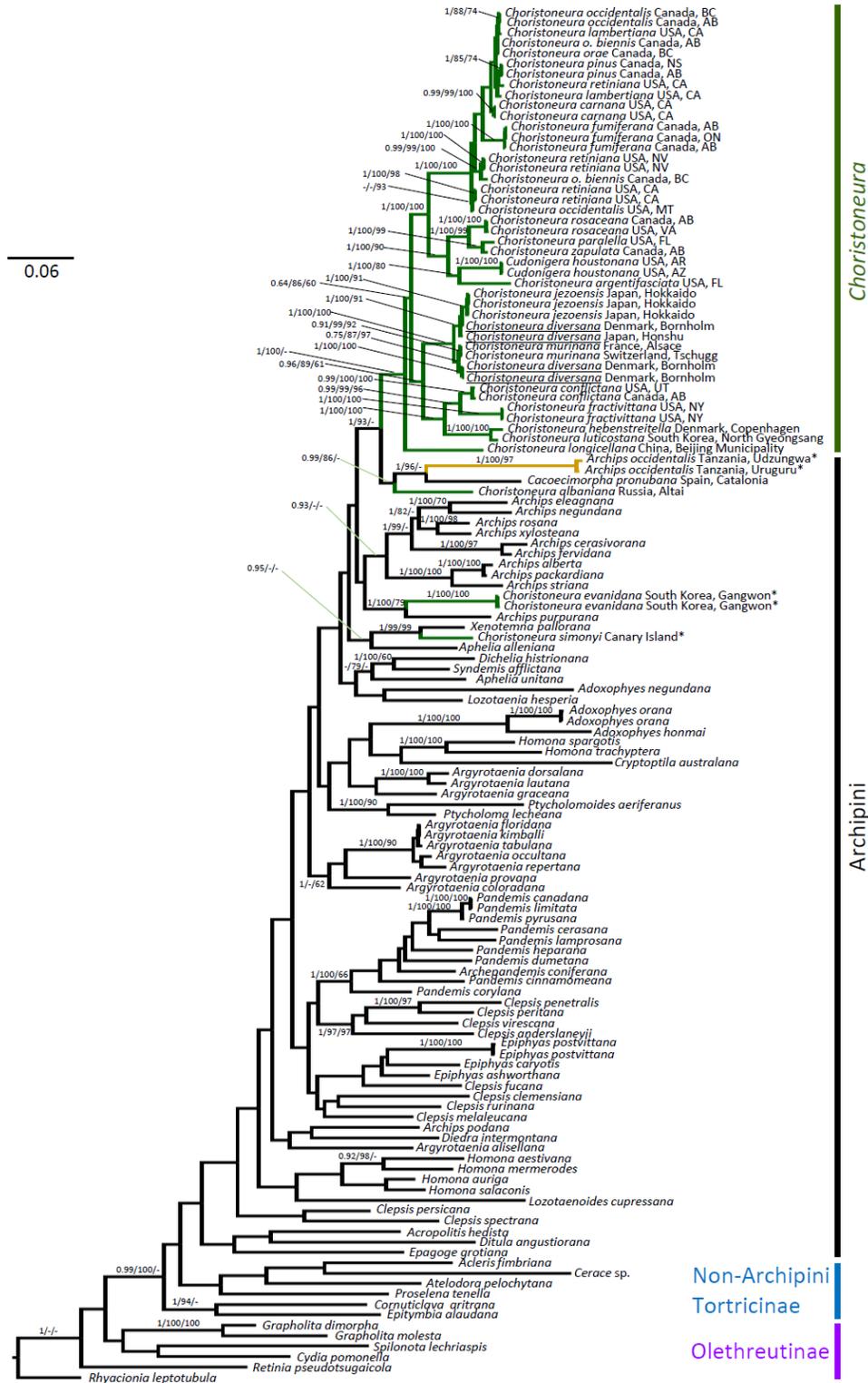
Figure 4.1. Majority-rule consensus tree of the genus *Choristoneura* and Archipini using Bayesian analysis (MrBayes 3.2.6) of 4 partitions (*legend Fig. 4.1. continues next page*)

(the best schema per codon position). Outgroup species represented by black branches, ingroup species represented by green branches. Deep yellow branches represent terminals of *Archips occidentalis* (Walsingham, 1891). Terminals of *Choristoneura diversana*, the type species of the genus, are underlined. Numbers on branches show supports for equivalent nodes in Bayesian, maximum likelihood, and maximum parsimony phylogenetic analyses denoted by: posterior probabilities/ultrafast bootstrap support (%)/bootstrap support (%). Mean of estimated marginal LnL: -30970.22 (run 1 = -30975.90, run 2 = -30969.53); ESS>400 for almost all variables.
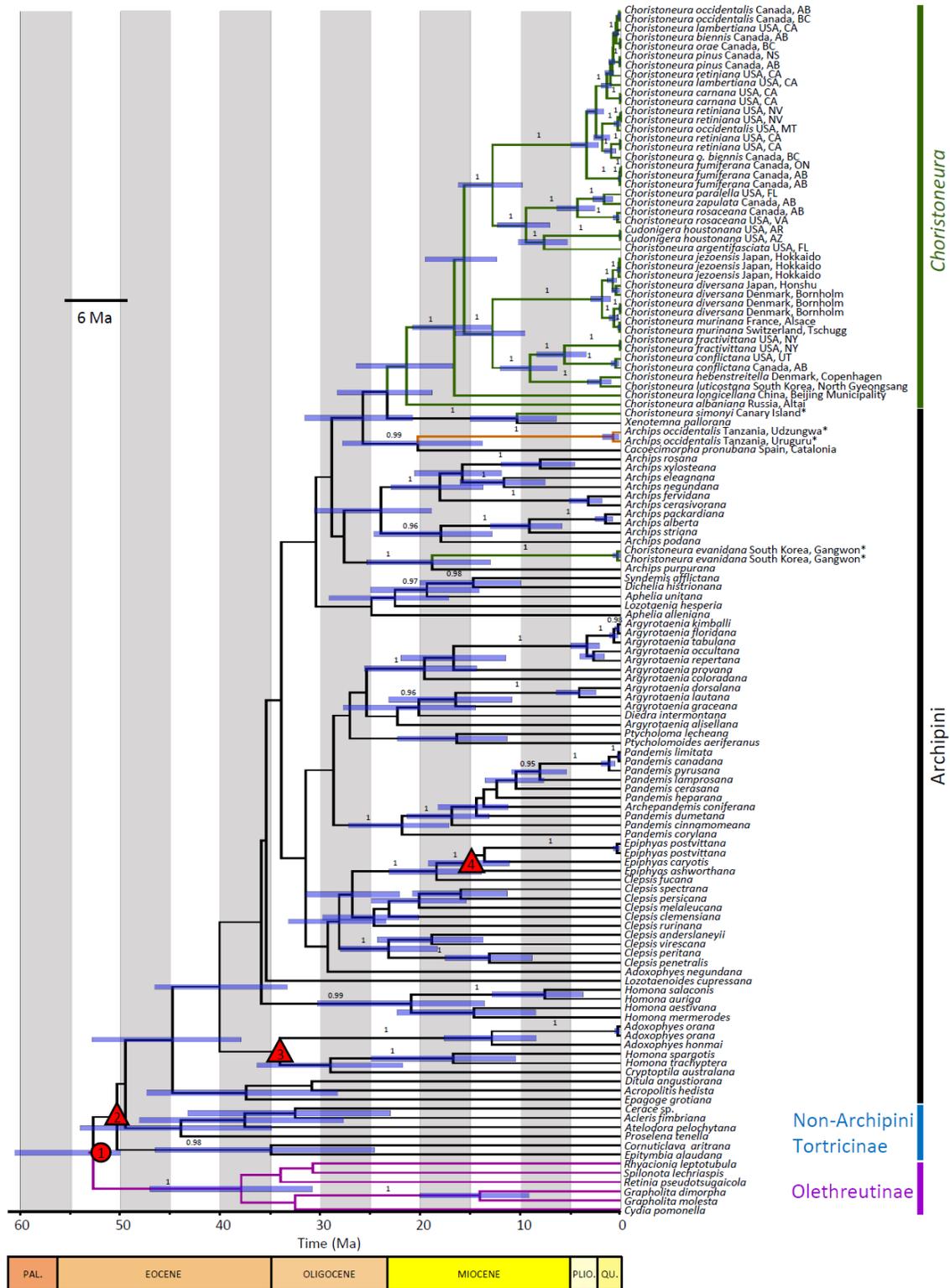
Figure 4.2. Time-calibrated phylogeny of the genus *Choristoneura* and Archipini using BEAST (1.8.3). Time in millions of years (Ma). (*legend Fig. 4.2. continues next page*)

Outgroup species in black branches, ingroup species in green branches; deep yellow branches show *Archips occidentalis* (Walsingham, 1891) terminals. On purple, branches of Olethreutinae species excluded from biogeographical and diversification analyses. Fossils used to calibrate the molecular clock are represented by a red-filled circle (root: 1. †*Spatalistiforma submerge*) and three triangles (nodes: divergence of 2. Schoenotenini; 3. *Adoxophyes*; and crown of 4. *Epiphyas*). Numbers on branches denote their posterior probability; node bars show 95% confidence interval (highest posterior density) for divergence dates. ESS>200 for all variables. PAL. = Paleocene. PLIO. = Pliocene. Qua. = Quaternary.
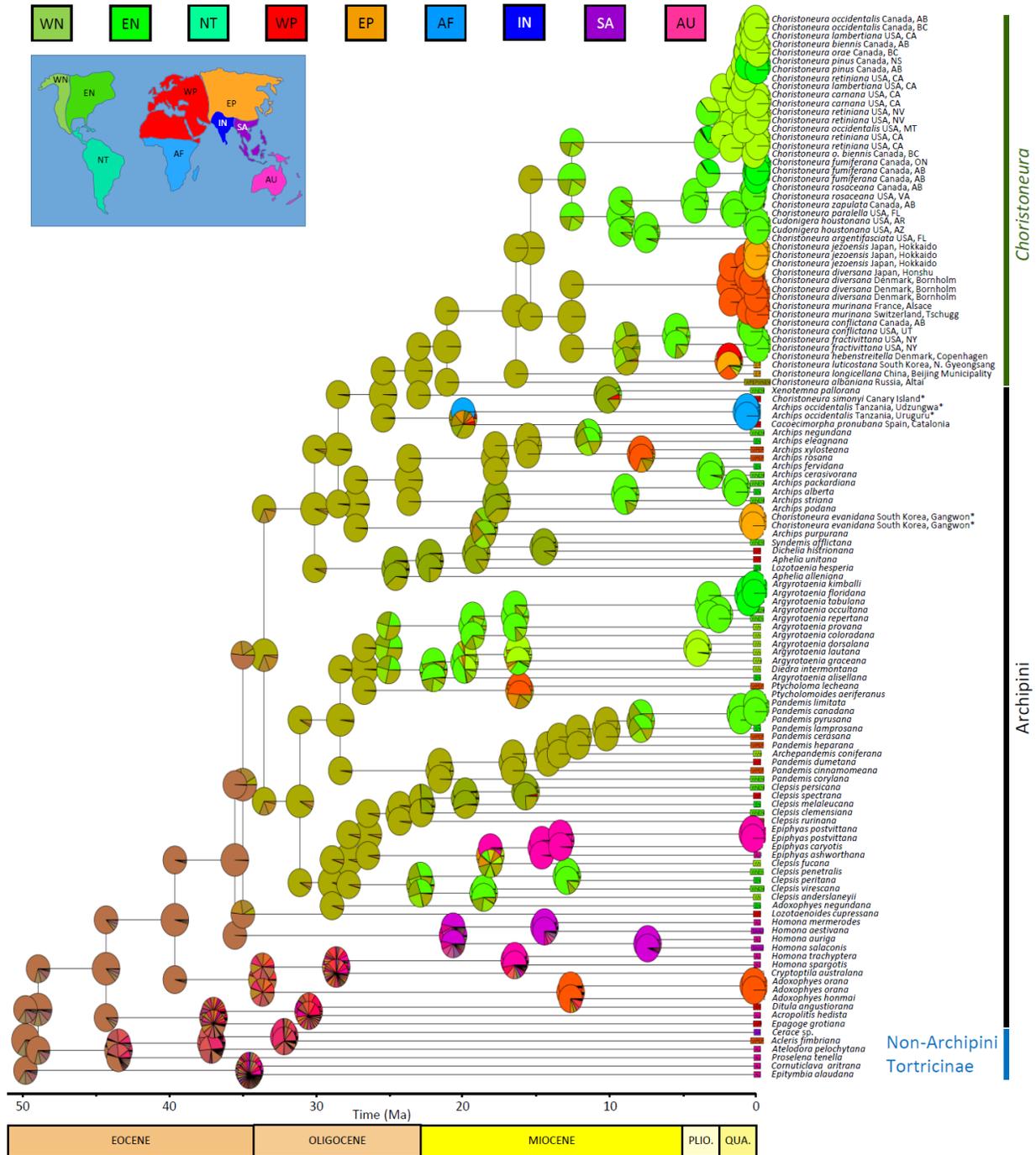
Figure 4.3. Historical biogeography of the genus *Choristoneura* and Archipini using BioGeoBEARS. The best time-stratified palaeographic model with founder effect (Bayarealike+J) is represented. (*legend Fig. 4.3. continues next page*)

Colored boxes identify biogeographical regions: WN = West Nearctic, EN = East Nearctic, NT = Neotropic, WP = West Palearctic, EP = East Palearctic, AF = Africa (including Madagascar), IN = India, SA = Southeast Asia, and AU = Australasia. Pie charts show relative probabilities of ancestral areas. Species distributions with more than one area have combined letters for biogeographical regions and alternate color on boxes and pie charts. PAL. = Paleocene. PLIO. = Pliocene. Qua. = Quaternary.
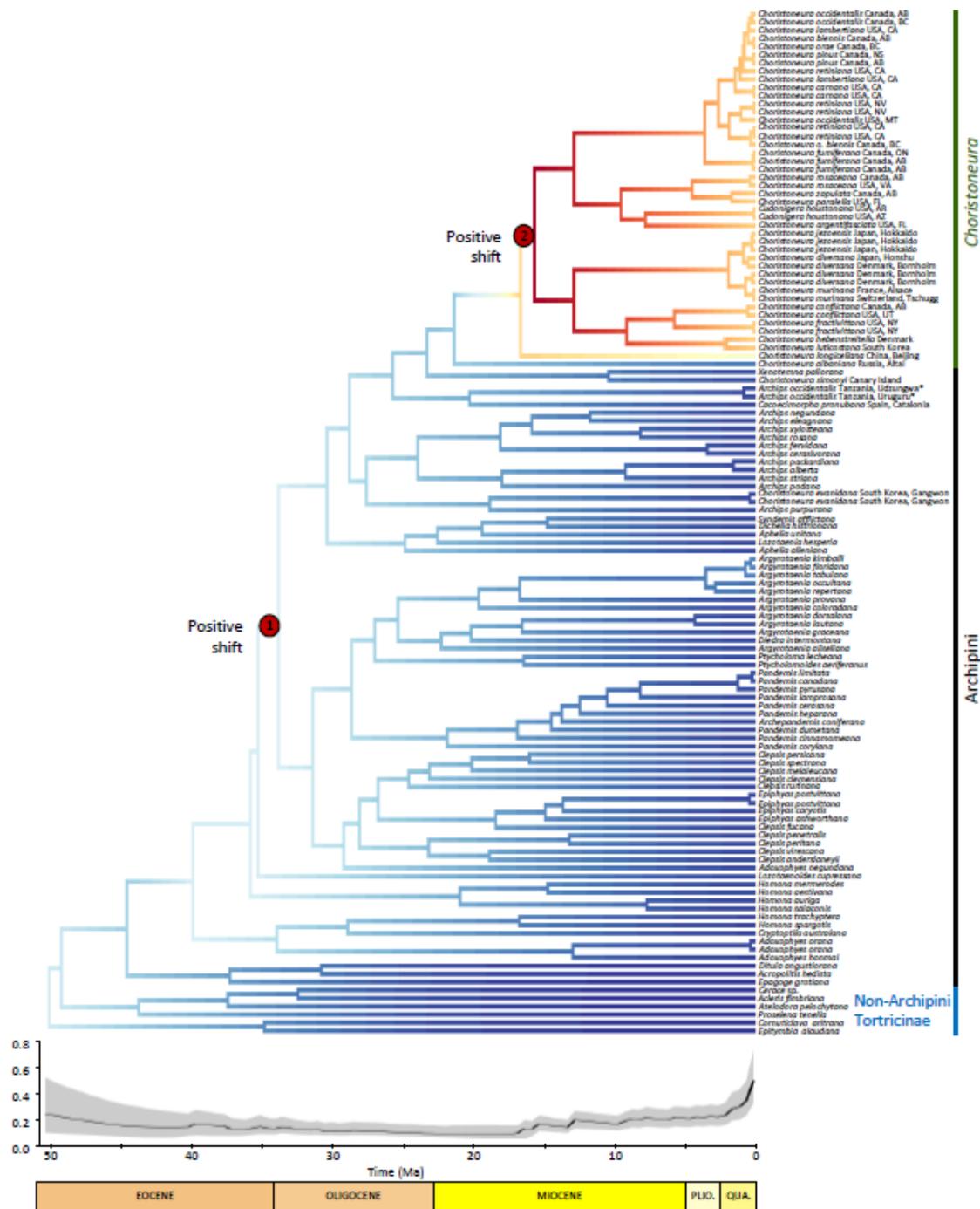
Figure 4.4. Speciation pattern of the genus *Choristoneura* and Archipini inferred with BAMM (2.5). Colors on branches show speciation rates ranging from almost 0 (dark blue) to 0.2.5 (red), based on the best macroevolutionary model. BAMM estimated a significant diversification increase surrounding the base of Archipini (1) and the crown of *Choristoneura* (2) PAL. = Paleocene. PLIO. = Pliocene. Qua. = Quaternary.

Chapter 5: Conclusions and new goals

5.1. *General Conclusions*

Plants and insects include more than 75% of described species on Earth (Grimaldi and Engel 2005). Insects are important biotic regulators of plant dynamics (Crawley 1984), with Lepidoptera being one of the few examples of insect orders that are almost entirely herbivorous (Miller et al. 2006). Cryptic herbivores like tortricid moths (leafroller moths) are usually species-rich taxa and study of their processes of speciation and diversification is important to understanding their ecological dynamics. This kind of knowledge is, in addition, applicable to pest management since several herbivorous species are pests of crops, forestry and garden plants.

Studies on tortricids moths have traditionally focused on pest species because of their economic importance and North America has not been the exception. Here, the most frequent tortricid target has been species of the *Choristoneura fumiferana* species complex, the spruce budworm complex (SBW). In addition to ecological and forestry studies (see Alfaro and Fuentealba 2016 and Nealis 2016 for recent reviews), most molecular studies in the SBW have focused on species definition (Sperling and Hickey 1994, 1995; Lumley and Sperling 2010, 2011a,b; Bird 2013). A major problem with species delimitation in the SBW complex is generated by the practical, but circular, traditional system of species identification, which is based on geographical distribution plus host plant/pheromone lure. Such a system may mask more objective delimitation of species generated by potential ecological speciation or phenotypic specialization events. Recent studies on species delimitation using single nucleotide polymorphisms (SNPs) have shown clear limits between western and eastern species but not among western populations (Brunet et al. 2017; Dupuis et al. 2017; Blackburn et al. 2017 in prep.). However, a common constraint on these analyses is the regional dimension of the studies (except for Dupuis et al. 2017). Comparison with equivalent systems in other regions or the inclusion of outgroup species closer to the SBW complex will help in detecting evolutionary patterns and understanding their processes in the SBW complex and in determining limits among clades. Like the SBW in the Nearctic, species like *Choristoneura murinana* and *Choristoneura jezoensis* cause outbreaks in Palearctic regions (Yasuda and Suzuki 1980; Mills and Kenis 1991; Nealis et al. 2007). One goal of this thesis work has been to complement the analysis of the SBW complex using a more extended sample of *Choristoneura* and Tortricidae species.

A first step toward establishing comparisons is to generate a robust phylogeny for *Choristoneura* and to include species from higher taxonomic ranks and other regions around the world. My work continues the undertaking started with the analysis of the tribe Archipini by Dombroskie and Sperling (2013), extending the study to the family level to generate a broad overview of biogeographic and diversification processes in the evolution of leafrollers. It uses this foundation to analyze the genus *Choristoneura*, complementing these studies to place the SBW complex in the general context of the evolution of Tortricidae and *Choristoneura*.

5.1.1. *Biogeography and diversification analysis applied to the SBW complex*

Leafroller moths are the tenth most species rich family of herbivorous insects (Condamine et al. 2016), providing a very interesting model for work on plant-insect interactions. Furthermore, the SBW complex is one of the most studied herbivorous insects (Alfaro and Fuentealba 2016). This richness in information on SBW gives the opportunity to detect and explore evolutionary processes at the family and generic level that can be corroborated using the information from the SBW complex. Analysis of evolutionary processes at higher taxonomic ranks has revealed four key insights for understanding the origin and diversification of the SBW and matches current information on this species complex.

First, the origin of specialization as conifer feeders by the SBW was geologically recent and was probably related to the availability of abundant new plant resources after the expansion of boreal forest. This biome was dominated by Pinaceae (Taggart and Cross 2009), the principal family of host plant species of the SBW complex (Lumley and Sperling 2011a; Figs 3.2; 4.2).

Second, the SBW complex is the result of speciation in a conifer feeding lineage that diverged 13 million years ago (Ma) from an angiosperm feeding sister clade (Fig. 4.2), but which nonetheless remained a single lineage of generalist herbivores of conifers for almost 10 million years (My), until the mid-Pliocene. After that time, the SBW clade started a series of divergence events, ending the processes associated with the long stem of the SBW (Fig. 4.2).

Third, early divergences within the SBW responded to isolation events caused by glaciations that started before the Pleistocene. Major glaciations in the northern hemisphere that occurred during the Pliocene, 4 and 3.6 Ma (Schepper et al. 2014), were synchronous with isolation processes of lineages in the SBW complex. Diversification was enhanced later during the Pleistocene, when haplotype lineages (Fig. 3.2) and species (Fig. 4.2) diverged. These

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divergences were synchronous with those in other *Choristoneura* clades, such as the divergence of *C. parallela-C. zapulata* or *C. hebenstreitella-C. luticostana*. During the Pliocene the distribution of the boreal forest was located farther north than its current distribution and initial glaciations could have generated a first split between a continuous forest dominated by conifers that ranged from the western mountains to the Arctic ocean. Two isolated groups of conifer forest remnants may have been formed, one in the western mountains and another in remnants of boreal forest in the Midwest and East Nearctic, explaining the existence of current Cordilleran and Boreal groups of SBW species proposed by Dupuis et al. (2017). Time, host plants, perhaps predators or parasites, and new glaciations during the Pleistocene could have promoted phenotypic specialization in the lowland northern populations (the boreal group) where some phenotypes could specialize as *Pinus* eaters and others as *Abies*/*Picea* eaters, a process that may have finally produced the current species *C. pinus* and *C. fumiferana*. These events would have been associated with the early divergence of *C. fumiferana* and *C. pinus* described in Chapters 3 and 4 (Figs 3.2, 4.2) and in the Bayesian clustering of Dupuis et al. (2017). In the mountains, geographical isolation by ice and deserts could have separated populations that used the locally most abundant conifer food resource, but frequent merging of populations may have avoided phenotypic specializations leading to genetic isolation, explaining the low level of genetic differentiation found in western SBW species by Lumley and Sperling (2011a), Bird (2013), Brunet et al. (2017), Dupuis et al. (2017) and this thesis (Chapters 3, 4). However, the results based on mitogenomes in chapter 3 (Fig. 3.2) showed an early divergence of p and o haplotypes (*C. pinus* and *C. o. occidentalis*) indicating that more work is necessary to understand the complex processes of divergence in the SBW complex.

The fourth insight is that speciation events and explanations for the Nearctic SBW are made more plausible by detection of an equivalent process occurring in the Palearctic region. A broadly generalist herbivore that fed on both conifers and angiosperms diverged 13 Ma from a mostly Palearctic clade comprised entirely of angiosperm feeders, with no speciation detected during 10 My just as in the SBW. Then, at 2.5 Ma, the Palearctic lineage diverged into several lineages, in synchrony with the major diversification of the SBW complex (Fig. 4.2). Interestingly, this Palearctic stem of conifer/angiosperm feeders diverged into two branches that included a broad generalist species, *C. diversana*, and two conifer feeders, the trans Palearctic and continental *C. murinana* and an endemic species on Hokkaido Island (Japan), *C. jezoensis*.

Branch lengths and divergence times of this Palearctic clade are similar to the lengths and times of the western species of the SBW complex, a fact that may be associated with *C. diversana-C. murinana-C. jezoensis* remaining a single species. In this case, conifer feeders in the clade are locally specialized phenotypes that are more frequent where conifer forest is dominant and forest was isolated during glaciations, as in Hokkaido Island. This Japanese island is well known for its postglacially depauperate mammal fauna, rich in endemic species (Millien-Parra and Jaeger 1999). The mountainous islands of the Japanese Archipelago, isolated by ocean, are an equivalent analogy to the mountains of western Nearctic where forests on mountains are isolated by desert. An interesting point is that *C. murinana* has not been recorded on any island of Japan, whereas *C. diversana* is recorded in all islands. Four of the five species of *Choristoneura* recorded in Japan, *C. adumbratana*, *C. diversana*, *C. lafauryana*, and *C. longicellana* are polyphagous with only *C. jezoensis* recorded as coniferophagous (Utsugi Jinbo, personal communication). It would be interesting to explore whether *C. diversana* retains some coniferophagous traits outside Hokkaido.

Synchronous divergence of the two *Choristoneura* specialist groups on Pinaceae, the mostly Palearctic clade with *C. diversana-C. murinana-C. jezoensis* and the Nearctic spruce budworm (SBW) complex, was found using independent phylogenetic analysis of tortricid mitogenomes (Chapter 3) and COI and 28S genes from species of the genus *Choristoneura* (Chapter 4), two largely different species samples, and different calibrations. The almost complete overlap of the confidence intervals of both analysis supports the robustness of the time date tree generated. The divergence events in Palearctic and Nearctic *Choristoneura* clades resulted in coniferophagous and polyphagous lineages in each clade during the expansion of boreal forest in the late Miocene (Chapter 3, 4). This finding contrasts with the previous hypothesis of Dang (1992) who considered the Palearctic and Nearctic coniferophagous species of *Choristoneura* to be sister groups, a hypothesis that was generally accepted by morphology-based researchers (Rasowski 1992).

5.1.2. *Origin, biogeography and diversification of* Choristoneura *in Archipini*

Phylogeny, molecular dating, biogeography and diversification patterns all support *Choristoneura* as a genus composed of species with a Northern Hemisphere distribution (Chapter 4, Figs 4.1-4.4). The genus was recovered as polyphyletic, with tropical (*Archips occidentalis*),

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subtropical (*Choristoneura simonyi*), and one Palearctic (*Choristoneura evanidana*) species excluded from the monophyletic core of the genus. The genus *Choristoneura* is defined by the stem and clades of the species (*C. albaniana* (*C. longicellana* (*C. diversana* clade + *C. fumiferana* clade))). The exclusion of tropical and subtropical species contrasts with the recent hypothesis of Razowski (2008), who considered the genus to include tropical species, describing or transferring six more tropical species into the genus during the last two years (*Choristoneura deuteros* Razowski, *C. holovera* Razowski, *C. nowakiana* Razowski, *C. oluduana* Razowski, *C. prostheca* Razowski, and *C. saotome* Razowski & Wojtusiak; Razowski 2014; Razowski and Wojtusiak 2014). However, the Holarctic origin of the genus *Choristoneura*, with early divergence of Palearctic elements, supports an older proposal of Razowski (1987, 1992, 2002), who initially defined *Choristoneura* as a genus with a Holarctic distribution and higher Palearctic diversification. The divergence of the mostly Palearctic and Nearctic clades, estimated at 16 Ma, complements this hypothesis.

An alternative to the proposed nomenclatural changes, which include transfer of *Archips occidentalis* (Walsingham) to *Cacoecimorpha*, *Choristoneura evanidana* to *Archips,* and *Choristoneura simonyi* to *Xenotemna*, would be to describe new genera for each transferred species. This option might be especially useful for *Archips occidentalis* (Walsingham) due to the long internal branches after the node *A. occidentalis-Cacoecimorpha.* These long branches indicate that these species remain as sister groups for 20 My with no speciation events occurring during this time, which seems improbable. On another hand, a new genus may be characterized for mainly Sub-Saharan taxon and could include the new African species of Razowski. My thesis results (Chapter 4) are generally consistent with the phylogeny for Archipini reconstructed by Dombroskie and Sperling (2013), using different outgroups, a lower number of Archipini species and ten more species of *Choristoneura*. It is important to note that my thesis used Archipini only as part of a large outgroup and is not a robust phylogeny of the tribe, especially for underrepresented early diverging taxa. Yet, several results were recovered in both studies, such as the polyphyly of *Homona*, the close relationship of *Diedra* and *Argyrotaenia* and recovery of the *Archips* group as sister of *Choristoneura* and related genera. In both studies *Archips purpurana* was an early diverging taxon at the base of the two groups of genera, but in this thesis the species was the sister group of *C. evanidana* in all phylogenetic analyses with strong support. A notable point is that both studies had a high number of Nearctic species; yet, a

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complete analysis of the tribe indicates that Archipini is cosmopolitan with low diversity in the Neotropics (Dombroskie and Sperling 2012) and the high proportion of Nearctic species may have biased a rigorous analysis of the tribe.

5.1.3. *Patterns in Tortricidae*

At the level of family, the most relevant and unexpected result was the association of the origin and increase in speciation rate of Tortricidae with the rise to dominance of angiosperms, supporting the angiosperm revolution hypothesis. Previous hypotheses of evolution of leafrollers (Horak and Brown 1991) had not supported this relationship at the base of Tortricidae. The Horak and Brown hypothesis establishes a detritivore larva for ancient, early-diverging lineages in Tortricidae. However, interaction with angiosperms appears to have been a dominant factor in tortricid evolution, which is later corroborated by *Choristoneura* host preferences that indicate coniferophagy as a derived character in Tortricidae (Chapters 3, 4). Evolution of Tortricidae is linked with the origin and diversification of angiosperms during the Cretaceous (Chapter 2; Fig. 2.4) as well as with more recent events in the specialization of conifer-feeder lineages in *Choristoneura* (Chapter 4; Fig. 4.2) after the expansion of the boreal forest. Indeed, the effect of plate tectonic dynamics on the diversification of tortricids was expected and the probable Gondwanian origin was previously predicted based on the distributional and morphological work of (Horak 2006) and the molecular study of Regier et al (2012). As a complement, this thesis used probabilistic tools to corroborate this hypothesis.

The time-dated phylogeny constructed using fossil calibrations provided a more accurate estimate of the divergence of Tortricidae from the other Lepidoptera (ca. 120 Ma during the mid-Cretaceous). We also found quantitative support for a Gondwanan center of origin of Tortricidae, as suggested by Regier et al. (2012), and determined a more precise location in the South American plate. Interestingly, the results of two different chapters (2 and 4) both support an Australasian origin of several tribes of Tortricidae, including Archipini as proposed by Horak (1999). The Archipini diversification, after leaving Australasia and colonizing the northern hemisphere (35 Ma), was supported by two data sets (chapters 2 and 4; Figs 2.2, 4.3), a result obtained through combined biogeographic and diversification analysis. The biogeographical analyses had the advantage of including founder-event speciation, which indicated the most parsimonious reconstructions of ancestral areas and facilitated tests of hypotheses. The relevance

of this approach for biogeographical analysis of flying insects like Tortricidae has been demonstrated in other studies (Cardé 2008; McCulloch et al. 2016; Rota et al. 2016) and is now frequently used in plant biogeography. Our analysis found that worldwide colonization of tortricids occurred between the late Cretaceous and the early Paleogene, mainly through dispersal-vicariance and founder events. These results may be useful in pest control since they explain how pest species might colonize new areas, such as by using wind currents. In the case of Tortricidae in an outbreak phase, we must be careful about potential infestations by wind transportation even at very long distances.

5.1.4. *Mitochondrial protein-coding and ribosomal genes as molecular markers in phylogeny*

An important contribution of this work for future studies is the identification of the most efficient mitochondrial genes in tortricids for reconstruction of phylogenies (COI, COII, ND1, ND2, ND4, and ND6; Chapter 3). This result validates the use of COI and COII markers in previous studies in the SBW complex (Sperling and Hickey 1994, 1995; Lumley and Sperling 2010, 2011a,b; Dombroskie and Sperling 2013) based on non-comparative knowledge of their accuracy. The confirmation of COI as an efficient marker in phylogenetic analysis involving species belonging to closely related genera supports its use for the delimitation of the genus *Choristoneura,* together with an rDNA gene (28S, Chapter 4). However, the results showing that fragments shorter than 700 bp fail to recover clades that have been recovered as being well supported by nuclear genes or the entire data set of mitochondrial protein coding and ribosomal genes challenges the use of the barcode fragment or the 470 bp fragment (Sperling and Hickey 1994) in phylogenetic analysis. Based on the results of this thesis (Chapter 3), the utility of short fragments is restricted principally to population studies and species differentiation. The exception was ND6, which was a very interesting gene with one of the fastest rates of evolution and good differentiation at any taxonomic level (Fig. 3.1). ND6 is used with some frequency in Lepidoptera (369 accessions for Lepidoptera; 62 accessions for Tortricidae in GenBank; accessed June 2017; Clark *et al.* 2016); however, these results contrast with those of the most efficient mitochondrial gene, which was ND2 (1 accession for Lepidoptera and Tortricidae in GenBank; accessed June 2017; Clark *et al.* 2016).

In addition, estimation of rates of evolution for 20 genes of Tortricidae (Chapter 2 and 3, Tables 2.3, 3.3) provides a useful tool for estimating time-calibrated trees for Tortricidae taxa

without the use of fossil calibrations. Yet, it is important to note that analysis of genetic distances against time of divergence estimated using fossil calibrations indicates that substitution rates are faster in recent times. This result does not support the use of regression to estimate times of divergence because times of recent divergences of species can be overestimated by this bias.

5.2. *New goals*

Several questions remain to be resolved in future research after this thesis study. A larger sample of leafroller species from the Paleotropics, especially from Africa and Indochina, and the Palearctic, especially from the Far East Palearctic, will be needed for a rigorous test of the hypothesis that the South American plate was the center of origin of Tortricidae. In addition, it will be desirable to obtain specimens from species of *Choristoneura* in the mountainous regions of Central Asia and Far East Asia, since several of these species are not included in any phylogenetic analyses to date. Another task is the identification of morphological characters that, including the derived *Choristoneura houstonana*, allow clear differentiation of *Choristoneura* from *Archips, Homona, and Meridemis*. Objectively, the uncus form and position are not sufficiently strong synapomorphies for *Choristoneura*, especially because the genitalia of *C. houstonana* appears to be highly derived in comparison with other *Choristoneura.*

Convergent herbivore specialization on conifers by Palearctic and Nearctic lineages could be associated with different composition of the female pheromone. The primary compound of *Choristoneura murinana* is (Z)-9-dodecenyl acetate (Priesner et al. 1982, 1988; El Sayed 2016), which is unique to the Palearctic species and differs from (E/Z)-11-Tetradecenal, (E/Z)-11-Tetradecen-1-ol, and (E/Z)-11-Tetradecenyl acetate, reported for Nearctic *Choristoneura* (El Sayed 2016; Silk and Eveleigh 2016). Analysis of other Palearctic species will reveal whether this is a frequent component in the Palearctic lineage. However, it is important to note that *Choristoneura lafauryana* Ragonot (Z-11-Tetradecen-1-ol; Castellari 1985; El Sayed 2016) and *Choristoneura hebenstreitella* Müller (Z/E-11-Tetradecen-1-ol; Z-11-Tetradecenal; Frerot 1979; Booij1985; El Sayed 2016) are the only other European species for which a pheromone component is recorded. Further, these reports are based on screening experiments using synthetic lures made for Nearctic species. No other studies of the composition of female pheromone in European species have been performed.

The synchronous diversification that occurred in the Nearctic and Palearctic lineages of *Choristoneura* (Chapter 4) is another potential starting point for further research. Conditioning

factors that might have affected cladogenesis in both continental land masses appear be similar. One of these is their host plant association; however, this factor cannot explain all of the parallel process of divergence. More detailed analyses are required. Ice sheets during glaciations pushed the forest against mountains in the Palearctic as in the Nearctic. However, mountains such as the Alps and Himalayas and deserts made the Palearctic a more stringent environment for life.

A final research goal is the reconstruction of phylogenies using more nuclear genes and SNPs in *Choristoneura*, ideally also using more fossils to corroborate the results observed. This is because the presented analyses are supported mainly by maternal inheritance and only three, two or one fossil calibrations. Under this scenario, it is probable that only small differences can be observed in the estimated times if the same group of fossils is used, which is highly likely because of the low number of fossils with specimens sufficiently well preserved for identification. However, topologies may change with the inclusion of nuclear genes and SNPs.

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6. Appendices and supplementary tables and figures

Appendix 2.1. List of terminal taxa and corresponding GenBank accession numbers used in this study.

Substitute species of the same genus for the barcode fragment (COI) are underlined. Abbreviations: CAD = carbamoyl-phosphate synthetase II, DDC = Dopa decarboxylase, Eno = Enolase, PER = Period, WG = wingless, COI = 658 bp barcode fragment of Cytochrome Oxidase subunit I.

	Superfamily	Tortricoidea							
	Family	Tortricidae			**Gene**		regions		
	Subfamily	**Tribe**	**Species**	**CAD**	**DDC**	**Eno**	**PER**	**WG**	**COI**
1.	Chlidanotinae	Chlidanotini	*Auratonota dispersa* Brown, 1990	JQ784335	JQ785698	JQ789357		JQ786691	KF491575
2.	Chlidanotinae	Chlidanotini	*Heppnerographa tricesimana* (Zeller, 1877)	JQ784590	JQ785933	JQ789574	JQ785446		KF491783
3.	Chlidanotinae	Hilarographini	*Hilarographa* sp.		JQ785916	JQ789561	JQ785433		KF491792
4.	Chlidanotinae	Polyorthini	*Histura* sp.	JQ784574	JQ785917	JQ789562	JQ785434	JQ786852	
			Histura perseavora Brown, 2010						JQ540881
5.	Chlidanotinae	Polyorthini	*Pseudatteria volcanica* (Butler, 1872)	JQ784788	JQ786108	JQ789741		JQ787010	JQ536815
6.	Olethreutinae	Bactrini	*Bactra furfurana* (Haworth, 1811)	JQ784350	JQ785712	JQ789369	JQ785302		KF492265
7.	Olethreutinae	Bactrini	*Bactra maiorina* Heinrich, 1923	JQ784354	JQ785716	JQ789372	JQ785304		KF492266
8.	Olethreutinae	Enarmoniini	*Ancylis sparulana* (Staudinger, 1859)	JQ784313	JQ785679	JQ789335	JQ785282		KF491535
9.	Olethreutinae	Enarmoniini	*Episimus tyrius* Heinrich, 1923	JQ784518	JQ785862	JQ789516	JQ785399	JQ786807	KF491711
10.	Olethreutinae	Endotheniini	*Endothenia hebesana* Walker, 1863	JQ784488	JQ785837	JQ789492		JQ786787	KF491703
11.	Olethreutinae	Eucosmini	*Epiblema abruptana* (Walsingham, 1879)	GQ283515	GQ283602	GQ283679	GQ283761	GQ283831	KC430476
12.	Olethreutinae	Eucosmini	*Epiblema foenella* (L.)	JQ784485	JQ785834	JQ789490	JQ785384	JQ786784	KC430475
13.	Olethreutinae	Eucosmini	*Epinotia* sp.	JQ784501	JQ785850	JQ789503	JQ785393		
			Epinotia nisella (Clerck, 1759)						JQ775253
14.	Olethreutinae	Eucosmini	*Eucosma picrodelta* Meyrick, 1932	JQ784520	JQ785864	JQ789517	JQ785400		

	Family	Tortricidae				**Gene**	**regions**		
	Subfamily	**Tribe**	**Species**	**CAD**	**DDC**	**Eno**	**PER**	**WG**	**COI**
15.	Olethreutinae	Eucosmini	*Pelochrista zomonana* (Kearfott, 1907)	GQ283540	GQ283624	GQ283702	GQ283781	GQ283854	
			<u>*Pelochrista caecimaculana* (Hubner, 1799)</u>						KM573580
16.	Olethreutinae	Eucosmini	*Spilonota eremitana* Moriuti, 1972	JQ784817	JQ786134	JQ789765	JQ785586		KF523836
17.	Olethreutinae	Grapholitini	*Cydia pomonella* (L.)	GQ283522	EU032801	GQ283686	EU032972	GQ283838	KM572180
18.	Olethreutinae	Grapholitini	*Cryptophlebia ombrodelta* (Lower, 1898)	JQ784418	JQ785775	JQ789433	JQ785345		KF403816
19.	Olethreutinae	Grapholitini	*Multiquaestia purana* Aarv. & Karis., 2009	JQ784432	JQ785788	JQ789445	JQ785352	JQ786747	
20.	Olethreutinae	Grapholitini	*Dichrorampha cancellatana* Kennel, 1901	JQ784457			JQ785368	JQ786763	KF491686
21.	Olethreutinae	Grapholitini	*Grapholita delineana* Walker, 1863	JQ784541	JQ785884	JQ789536	JQ785412	JQ786826	KF491772
22.	Olethreutinae	Grapholitini	*Grapholita packardi* Zeller, 1875	JQ784632	JQ785971	JQ789614	JQ785478		KF491773
23.	Olethreutinae	Microcorsini	*Cryptaspasma querula* (Meyrick, 1912)	JQ784421	JQ785777	JQ789436		JQ786740	KF491658
24.	Olethreutinae	Microcorsini	*Cryptaspasma* sp.	JQ784715	JQ786044	JQ789686	JQ785528	JQ786959	
			<u>*C. brachyptycha* (Meyrick, 1911)</u>						GU695639
25.	Olethreutinae	Olethreutini	*Afroploce karsholti* Aarvik, 2004	JQ784303	JQ785670	JQ789326	JQ785274		
			<u>*Afroplace* sp.</u>						KJ592266
26.	Olethreutinae	Olethreutini	*Hedya dimidiana* (Clerck, 1759)	JQ784563	JQ785906	JQ789554	JQ785427		
			<u>*Hedya pruniana* (Hubner, [1796-1799])</u>						KM573180
27.	Olethreutinae	Olethreutini	*Lobesia aeolopa* Meyrick, 1907	JQ784612	JQ785954	JQ789596	JQ785463	JQ786882	KF523800
28.	Olethreutinae	Olethreutini	*Olethreutes fasciatana* (Clemens, 1860)	JQ784701	JQ786033	JQ789673	JQ785517		GU090055
29.	Olethreutinae	Olethreutini	*Oxysemaphora* sp.	JQ784710		JQ789682	JQ785523		KF522631
30.	Olethreutinae	Gatesclarkeanini	*Gatesclarkeana tenebrosa* (Turner, 1916)						KF401335
31.	Tortricinae	Archipini	*Argyrotaenia alisellana* (Robinson, 1869)	GQ283512	GQ283599	GQ283676	GQ283759	GQ283828	KF491561
32.	Tortricinae	Archipini	*Atelodora* sp.	JQ784330	JQ785694	JQ789352	JQ785293		
			<u>*Atelodora pelochytana* Meyrick, 1881</u>						KF401595
33.	Tortricinae	Archipini	*Pandemis limitata* (Robinson, 1869)	GQ283520	GQ283607	GQ283684	GQ283765	GQ283836	KF491975

	Family	Tortricidae		Gene	regions			
	Subfamily	**Tribe**	**Species**	**CAD**	**DDC**	**Eno**	**PER**	**WG**	**COI**
34.	Tortricinae	Archipini	*Choristoneura rosaceana* (Harris, 1841)	JQ784424	JQ785780	JQ789438	JQ785346	JQ786743	GU438808
35.	Tortricinae	Archipini	*Clepsis melaleucana* (Walker, 1863)	GQ283523	GQ283609	GQ283687	GQ283767	GQ283839	KF491638
36.	Tortricinae	Archipini	*Dichelia cosmopis* Lower, 1894	JQ784450	JQ785804	JQ789463	JQ785364		KF397152
37.	Tortricinae	Ceracini	*Cerace* sp.		JQ785746	JQ789401	JQ785322		
			<u>*Cerace diehli* Buchsbaum & Miller, 2002</u>						AJ416577
38.	Tortricinae	Schoenotenini	*Cornuticlava aritrana* Common, 1965	KC315487					KF398054
39.	Tortricinae	Schoenotenini	*Proselena tenella* (Meyrick, 1910)	KC315497					KC315457
40.	Tortricinae	Atteriini	*Anacrusis nephrodes* (Walsingham, 1914)	GQ283511	GQ283598	GQ283675	GQ283758	GQ283827	JQ538605
41.	Tortricinae	Cnephasiini	*Cnephasia alfacarana* Razowski, 1958	JQ784372	JQ785734	JQ789389			
			<u>*Cnephasia stephensiana* (Doub., 1850)</u>						KM573292
42.	Tortricinae	Cnephasiini	*Decodes asapheus* Powell, 1980	JQ784445		JQ789458			KF491677
43.	Tortricinae	Cochylini	*Aethes promptana* (Robinson, 1869)	GQ283507	GQ283594	GQ283671	GQ283754		KF491515
44.	Tortricinae	Cochylini	*Carolella sartana* (Hubner, 1823)	JQ784430	JQ785786	JQ789444	JQ785350		
45.	Tortricinae	Cochylini	*Eugnosta busckana* (Comstock, 1939)	JQ784515	JQ785860	JQ789513	JQ785398		
			<u>*Eugnosta percnoptila* (Meyrick, 1933)</u>						KJ592394
46.	Tortricinae	Euliini	*Bonagota* sp.	JQ784356	JQ785718	JQ789374	JQ785305		
47.	Tortricinae	Euliini	*Eulia ministrana* (L.)	JQ784525	JQ785868	JQ789520		JQ786812	KM573628
48.	Tortricinae	Euliini	*Netechma* sp.	JQ784690	JQ786022	JQ789662	JQ785511		KF491916
49.	Tortricinae	Euliini	*Pseudomeritastis* sp.	JQ784813	JQ786130	JQ789761	JQ785582		KF492055
50.	Tortricinae	Phricanthini	*Phricanthes asperana* Meyrick, 1881	JQ784716	JQ786045	JQ789687			KF396664
51.	Tortricinae	Sparganothini	*Amorbia humerosana* Clemens, 1860	JQ784299				JQ786667	KF492227
52.	Tortricinae	Sparganothini	*Platynota idaeusalis* Walker, 1859	GQ283566	GQ283645	GQ283727	GQ283802	GQ283880	GU089177
53.	Tortricinae	Sparganothini	*Sparganothis reticulatana* (Clemens, 1860)	JQ784828	JQ786145	JQ789775	JQ785594	JQ787037	KF492132
54.	Tortricinae	Tortricini	*Acleris affinatana* (Snellen, 1883)	JQ784278	JQ785649	JQ789303	JQ785257		KF491489

	Family	Tortricidae				Gene	regions		
	Subfamily	**Tribe**	**Species**	**CAD**	**DDC**	**Eno**	**PER**	**WG**	**COI**
55.	Tortricinae	Tortricini	*Acleris semipurpurana* (Kearfott, 1905)	JQ784396	JQ785756	JQ789412	JQ785329	JQ786722	KF491491
56.	Tortricinae	Epitymbiini	*Epitymbia alaudana* Meyrick, 1881	KC315494					KF395451
	Superfamily	Tortricoidea							
	Family	Heliocosmidae							
57.			*Heliocosma melanotypa* Turner, 1925	JQ784578	JQ785921	JQ789565	JQ785437	JQ786856	
			Heliocosma argyroleuca Lower, 1916						KF522580
	Family	Galacticidae							
58.			*Homadaula anisocentra* Meyrick, 1922	JQ784556	JQ785899	JQ789548	JQ785421	JQ786838	KF491795
	Superfamily	Zygaenoidea							
	Family	Lacturidae							
59.			Lacturidae sp.	GQ283546	GQ283629	GQ283708	GQ283787	GQ283860	
			Lactura subfervens (Walker, 1854)						JQ570326
	Family	Limacodidae							
60.			*Pantoctenia prasina* (Butler 1896)	JQ784755	JQ786078		JQ785552	JQ786988	KF491981
	Superfamily	Cossoidea							
	Family	Cossoidae							
61.			*Archaeoses pentasema* (Lower, 1915)	JQ784298	JQ785666	JQ789322	JQ785271	JQ786666	KF522536
	Superfamily	**Sesioidea**							
	Family	**Sesiidae**							
62.			*Vitacea polistiformis* (Harris, 1854)	JQ784885	JQ786197	JQ789824		JQ787080	GU090234

Appendix 2.2. General alignment of all sequences for each taxon included in the study (digital file).

Appendix 2.3. Tortricidae species included in Chapter 2 and their biogeographical distribution by presence (1) or absence (0). Areas of distribution: WP = West Palearctic, EP = East Palearctic, WN = West Nearctic, EN = East Nearctic, NT = Neotropics, AF = Africa+Madagascar, IN = India, SA = Southeast Asia, AU = Australasia. Distributions are from Brown (2005), Gilligan et al. (2014) and Schmidt et al. (2010).

Subfamily	Tribe	Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Chlidanotinae	Chlidanotini	*Auratonota dispersa*	0	0	0	0	1	0	0	0	0
Chlidanotinae	Chlidanotini	*Heppnerographa tricesimana*	0	0	0	0	1	0	0	0	0
Chlidanotinae	Hilarographini	*Hilarographa* sp.	0	0	0	0	1	0	0	0	0
Chlidanotinae	Polyorthini	*Histura* sp.	0	0	0	0	1	0	0	0	0
Chlidanotinae	Polyorthini	*Pseudatteria volcanica*	0	0	0	0	1	0	0	0	0
Olethreutinae	Bactrini	*Bactra furfurana*	1	1	1	1	0	0	0	0	0
Olethreutinae	Bactrini	*Bactra maiorina*	0	0	1	1	0	0	0	0	0
Olethreutinae	Enarmoniini	*Ancylis sparulana*	1	0	0	0	0	0	0	0	0
Olethreutinae	Enarmoniini	*Episimus tyrius*	0	0	0	1	0	0	0	0	0
Olethreutinae	Endotheniini	*Endothenia hebesana*	0	0	1	1	0	0	0	0	0
Olethreutinae	Eucosmini	*Epiblema abruptana*	0	0	0	1	0	0	0	0	0
Olethreutinae	Eucosmini	*Epiblema foenella*	1	1	0	0	0	0	0	0	0
Olethreutinae	Eucosmini	*Epinotia* sp.	1	1	1	1	0	0	0	0	0

Subfamily	Tribe	Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Olethreutinae	Eucosmini	*Eucosma picrodelta*	0	0	0	0	0	1	0	0	0
Olethreutinae	Eucosmini	*Pelochrista zomonana*	0	0	1	1	0	0	0	0	0
Olethreutinae	Eucosmini	*Spilonota eremitana*	0	1	0	0	0	0	0	0	0
Olethreutinae	Grapholitini	*Cydia pomonella*	1	0	0	0	0	0	0	0	0
Olethreutinae	Grapholitini	*Cryptophlebia ombrodelta*	0	0	0	0	0	0	1	1	1
Olethreutinae	Grapholitini	*Multiquaestia purana*	0	0	0	0	0	1	0	0	0
Olethreutinae	Grapholitini	*Dichrorampha cancellatana*	0	1	0	0	0	0	0	0	0
Olethreutinae	Grapholitini	*Grapholita delineana*	0	1	0	0	0	0	0	1	0
Olethreutinae	Grapholitini	*Grapholita packardi*	0	0	0	1	0	0	0	0	0
Olethreutinae	Microcorsini	*Cryptaspasma querula*	0	0	0	0	0	0	0	0	1
Olethreutinae	Microcorsini	*Cryptaspasma* sp.	0	0	0	0	0	0	1	0	0
Olethreutinae	Olethreutini	*Afroploce karsholti*	0	0	0	0	0	1	0	0	0
Olethreutinae	Olethreutini	*Hedya dimidiana*	1	1	0	0	0	0	0	1	0
Olethreutinae	Olethreutini	*Lobesia aeolopa*	0	1	0	0	0	0	1	1	0
Olethreutinae	Olethreutini	*Olethreutes fasciatana*	0	0	0	1	0	0	0	0	0
Olethreutinae	Olethreutini	*Oxysemaphora* sp.	0	0	0	0	0	0	0	0	1
Olethreutinae	Gatesclarkeanini	*Gatesclarkeana tenebrosa*	0	0	0	0	0	0	0	0	1
Tortricinae	Archipini	*Argyrotaenia alisellana*	0	0	0	1	0	0	0	0	0
Tortricinae	Archipini	*Atelodora* sp.	0	0	0	0	0	0	0	0	1
Tortricinae	Archipini	*Pandemis limitata*	0	0	1	1	0	0	0	0	0

Subfamily	Tribe	Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Tortricinae	Archipini	*Choristoneura rosaceana*	0	0	1	1	0	0	0	0	0
Tortricinae	Archipini	*Clepsis melaleucana*	0	0	0	1	0	0	0	0	0
Tortricinae	Archipini	*Dichelia cosmopis*	0	0	0	0	0	0	0	0	1
Tortricinae	Ceracini	*Cerace* sp.	0	0	0	0	0	0	0	1	0
Tortricinae	Schoenotenini	*Cornuticlava aritrana*	0	0	0	0	0	0	0	0	1
Tortricinae	Schoenotenini	*Proselena tenella*	0	0	0	0	0	0	0	0	1
Tortricinae	Atteriini	*Anacrusis nephrodes*	0	0	0	0	1	0	0	0	0
Tortricinae	Cnephasiini	*Cnephasia alfacarana*	1	0	0	0	0	0	0	0	0
Tortricinae	Cnephasiini	*Decodes asapheus*	0	0	1	0	0	0	0	0	0
Tortricinae	Cochylini	*Aethes promptana*	0	0	1	1	0	0	0	0	0
Tortricinae	Cochylini	*Carolella sartana*	0	0	0	1	0	0	0	0	0
Tortricinae	Cochylini	*Eugnosta busckana*	0	0	1	0	0	0	0	0	0
Tortricinae	Euliini	*Bonagota* sp.	0	0	0	0	1	0	0	0	0
Tortricinae	Euliini	*Eulia ministrana*	1	1	1	1	0	0	0	0	0
Tortricinae	Euliini	*Netechma* sp.	0	0	0	0	1	0	0	0	0
Tortricinae	Euliini	*Pseudomeritastis* sp.	0	0	0	0	1	0	0	0	0
Tortricinae	Phricanthini	*Phricanthes asperana*	0	0	0	0	0	0	0	0	1
Tortricinae	Sparganothini	*Amorbia humerosana*	0	0	0	1	0	0	0	0	0
Tortricinae	Sparganothini	*Platynota idaeusalis*	0	0	1	1	0	0	0	0	0
Tortricinae	Sparganothini	*Sparganothis reticulatana*	0	0	0	1	0	0	0	0	0

Subfamily	Tribe	Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Tortricinae	Tortricini	*Acleris affinatana*	0	1	0	0	0	0	0	0	0
Tortricinae	Tortricini	*Acleris semipurpurana*	0	0	0	1	0	0	0	0	0
Tortricinae	Epitymbiini	*Epitymbia alaudana*	0	0	0	0	0	0	0	0	1

Appendix 2.4. Connectivity matrices through time.

Column headings identify biogeographical regions: WP = West Palearctic, EP = East Palearctic, WN = West Nearctic, EN = East Nearctic, NT = Neotropics, AF = Africa+Madagascar, IN = India, SA = Southeast Asia, and AU = Australasia. Rows are arranged in the same order. Number 1 indicates connectivity. The first time period is an artifact to permit initiation of runs in the time stratified analysis.

```
0-0.25 Ma
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1
1    1    1    1    1    1    1    1    1

0.25-5.33 Ma
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    1    0    0    0    1    0    0    0
1    1    1    0    0    0    1    1    0
0    1    1    1    0    0    0    0    0
0    0    1    1    0    0    0    0    0
0    0    0    0    1    0    0    0    0
1    0    0    0    0    1    0    0    0
0    1    0    0    0    0    1    1    0
0    1    0    0    0    0    1    1    1
0    0    0    0    0    0    0    1    1

5.33-23.03 Ma
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    1    0    0    0    1    0    0    0
1    1    1    0    0    0    1    1    0
0    1    1    1    0    0    0    0    0
0    0    1    1    0    0    0    0    0
0    0    0    0    1    0    0    0    0
1    0    0    0    0    1    1    0    0
0    1    0    0    0    1    1    1    0
0    1    0    0    0    0    1    1    0
0    0    0    0    0    0    0    0    1
```

```
23.03-33.9 Ma
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    1    0    0    0    1    0    0    0
1    1    1    0    0    0    1    1    0
0    1    1    1    0    0    0    0    0
0    0    1    1    0    0    0    0    0
0    0    0    0    1    0    0    0    0
1    0    0    0    0    1    0    0    0
0    1    0    0    0    0    1    1    0
0    1    0    0    0    0    1    1    0
0    0    0    0    0    0    0    0    1

33.9-56 Ma
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    0    0    1    0    0    0    0    0
0    1    1    0    0    0    1    1    0
0    1    1    1    0    0    0    0    0
1    0    1    1    0    0    0    0    0
0    0    0    0    1    0    0    0    1
0    0    0    0    0    1    0    0    0
0    1    0    0    0    0    1    1    0
0    1    0    0    0    0    1    1    0
0    0    0    0    1    0    0    0    1

56-66 Ma
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    0    0    1    0    0    0    0    0
0    1    1    0    0    0    0    1    0
0    1    1    1    0    0    0    0    0
1    0    1    1    0    0    0    0    0
0    0    0    0    1    0    0    0    1
0    0    0    0    0    1    0    0    0
0    0    0    0    0    0    1    0    0
0    1    0    0    0    0    0    1    0
0    0    0    0    1    0    0    0    1

66-100.5 Ma
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    0    0    1    0    0    0    0    0
0    1    1    0    0    0    0    1    0
0    1    1    0    0    0    0    0    0
1    0    0    1    0    0    0    0    0
0    0    0    0    1    0    0    0    1
0    0    0    0    0    1    0    0    0
0    0    0    0    0    0    1    0    0
0    1    0    0    0    0    0    1    0
0    0    0    0    1    0    0    0    1
```

Appendix 2.5. Detailed results and discussion of phylogenetic analyses.

Results

MP analysis found a single most parsimonious tree (Length = 34477, CI = 0.221, RI = 0.396; 3503 parsimony-informative characters, 13 Tree-island profiles, Appendix 2.6). For this tree, numerous clades showed strong support, including 28 of 61 nodes with BS ≥ 75 (46% of total nodes, including out-groups), 24 of these with BS ≥ 90 (39%). The best ML tree recovered strong nodal support for most clades using the scheme with 13 partitions (Appendix 2.7); 54 of 61 nodes had HS/UFBS ≥ 75 (88 % of total) and 50 of these had HS/UFBS ≥ 90 (81%). Similarly, the Bayesian consensus tree recovered strong nodal support for most clades using the 13 partitions (Appendix 2.8) as well as with the scheme with five gene partitions (Appendix 2.9): 48 of 61 nodes with PP ≥ 0.95 (80% of total nodes), 38 of these with PP = 1 (62%). The MP and ML/Bayesian topologies differed in the position of *Phricanthes* and *Oxysemaphora*, clades comprising *Pandemis*, *Argyrotaenia*, *Choristoneura*, *Dichelia*, *Epitymbia* and *Cerace*, and relationships between *Phricanthes, Cornuticlava* and *Proselena* (Appendices 2.6-2.9); all of which showed low nodal support (i.e. BS and HS/UFBS < 75; PP < 0.9). The 13-partition analysis was selected as the best scheme for dating, diversification and biogeography analyses since it received the highest LnL values in Bayesian analysis (13 partitions LnL = -134,848.17 vs. 5 partitions LnL = -138,840.49) and recovered strong support for the majority of clades (Appendix 2.8).

The overall topology of the trees indicated monophyly of Tortricidae, but only with strong support in the ML and Bayesian analyses (Appendices 2.6-2.9; node 7: BS < 50, HS/UFBS = 100, PP = 1, 1). Subfamily Chlidanotinae was recovered as paraphyletic in all analyses (MP, ML, and Bayesian), with Polyorthini as sister to all other Tortricidae, and Hilarographini+Chlidanotini as sister group of Olethreutinae+Tortricinae. Olethreutinae and Tortricinae were moderately or well supported clades in ML and Bayesian analyses (Appendices 2.7-2.9; node 13: BS = 100; PP = 1, 1; node 37: HS/UFBS = 71; PP = 0.73, 1) but Tortricinae was paraphyletic in the MP analysis (Appendix 2.6).

Within Olethreutinae, Microcorsini is the sister group of the remaining Olethreutinae (Appendices 2.6-2.9), and Enarmoniini is either the sister group of other Olethreutinae (Appendix 2.6) or the sister group of Olethreutini (Appendices 2.7-2.9). Olethreutini was recovered as a

clade in all analyses (node 19 Appendices 2.6, 2.7; node 18 Appendices 2.8, 2.9; BS < 50, HS/UFBS = 98, PP = 0.99, 1) that includes Bactrini, Endotheniini and Gatesclarkeanini and excludes *Oxysemaphora*. Eucosmini and Grapholitini are sister groups and well-differentiated tribes and form a well supported clade (nodes 27 Appendix 2.6, node 26 Appendices 2.7-2.9; BS = 87, HS/UFBS = 100, PP = 1,1).

For the Tortricinae, Phricanthini was the sister group of Tortricinae+Olethreutinae in MP (Appendix 2.6), but in ML and Bayesian analyses Phricanthini was inside Tortricinae, grouped with Schoenotenini as part of the sister group to all other Tortricinae (Appendices 2.7-2.9). Within Tortricinae three clades are well supported independently, but relationships between them are not well supported; the first shows Ceracini as the sister group of Archipini plus Epytimbiini (Appendices 2.7-2.9) or inside Schoenoteninii (Appendix 2.6), the second shows Atteriini as sister group of Sparganothini (Appendices 2.6-2.9), and the third presents Cnephasiini and Tortricini as sister groups (Appendices 2.6-2.9).

Discussion

Our results support the topology of Regier et al. (2012, 2013), including the monophyly of Tortricidae and the paraphyly of Chlidanotinae (all analyses; Appendices 2.6-2.9). The addition of three more tribes and the COI barcode fragment does not alter the general topology. Chlidanotinae was never recovered as a monophyletic group, and the tribe Polyorthini and the clade Chlidanotini+Hilarographini may be considered as subfamilies. The monophyly of Chlidanotini+Hilarographini with Tortricinae+Olethreutinae was recovered with high support values for ML and Bayesian but not MP analyses (BS < 50, HS/UFBS ≥ 86; PP = 1,1; Appendices 2.6-2.9). This molecular evidence, combined with diversification and biogeographical analysis (see main text), supports the Regier et al. (2012) hypothesis that a diagnostic character of Chlidanotinae, the dorso-longitudinal invagination containing a hair pencil arising from the eighth segment (Horak, 1999), may be a homology of Tortricidae, lost early in the divergence of clade Tortricinae+Olethreutinae (node 12; Appendix 2.6-S9).

The phylogenetic position of Phricanthini remains ambiguous, although the addition of two Schoenotenini to our analyses now generally shows a basal position for these two tribes within Torticidae, supporting the phylogenetic results of Regier et al. (2012) which included only Phricanthini. However, the MP analysis recovered Phricanthini as sister group of

Tortricinae+Olethreutinae with weak support (node 12, BS 53; Appendix 2.6), contrasting with ML and Bayesian analyses that recovered Phricanthini close to or within Schoenoteninii, also with low support (nodes 38, 39; Appendices 2.7-2.9). The position of Phricanthini in the MP topology may be a case of long branch attraction affecting node support for Tortricinae (BS < 50%) and Olethreutinae (54%) in the MP tree. Both subfamilies were better supported in ML and Bayesian analyses (Appendices 2.7-2.9). Nevertheless, early divergence of Phricanthini, before the differentiation of Tortricinae+Olethreutinae, was originally hypothesized by Diakonoff (1981) when he described the tribe. Horak (1999) noted several distinctive characteristics of the tribe as being the position of the vein M1 in FW, the particular egg shape, and its exclusive host association with Dilleniaceae, an angiosperm (Powell et al., 1999). We cannot currently resolve the topology; further studies should include more species of Phricanthini and Schoenoteninii to potentially reduce long branch attraction in MP and increase support in ML and Bayesian analyses. It is notable that the Bayesian time-calibrated tree (BEAST) recovered the early divergence of only Phricanthini, not Schoenotenini, as sister group of other Tortricinae (Fig. 3.1) with low support (PP= 0.7), the same position recovered by Regier et al. (2012).

Tortricinae and Olethreutinae were recovered as monophyletic in all analyses but with strong support only in the ML and Bayesian analyses (nodes 13, 37; Appendices 2.7-2.9). Phylogenetic relationships between tribes supported the topology of Regier et al. (2012) in all analyses: Bactrini and Endotheniini are part of Olethreutini (nodes 19, 18; Appendices 2.6-2.9) and Cochylini is part of Euliini (node 56; Appendices 2.6-2.9). Thus, molecular evidence does not support the tribal status of Bactrini, Endotheniini (Olethreutinae) and Cochylini (Tortricinae). Nonetheless, these results are interesting in light of the biogeographical analysis (Fig. 3.3 of the main text) and will be discussed of the main text. Other tribes were strongly supported in all analyses (Appendices 2.6-2.9), within Olethreutinae: Microcorsini (nodes 15, 14), Enarmoniini (nodes 17, 18), Grapholitini (nodes 28, 27) and Eucosmini (nodes 32, 33) have strong node supports, and within Tortricinae: Atterini (nodes 53, 49), Sparganothini (nodes 54, 50), Tortricini and Cnephasiini (nodes 39, 53) and Euliini (Node 56) have also high nodal support. On the contrary, Ceracini was recovered with low BS support as a clade with Schoenoteninii in the MP tree (node 51 Appendix 2.6); however, Ceracini was recovered as sister group of Archipini with strong support in both ML and Bayesian analyses (node 42; Appendices 2.7-2.9), supporting Ceracini as a valid tribe.

The phylogenetic positions of the three tribes that were not included in the study by Regier et al. (2012), Gatesclarkeanini, Schoenotenini and Epitymbiini, are detailed in the main text Discussion, and above in the context of Phricanthini for Schoenotenini.

Appendix 2.6. Single most parsimonious tree for Tortricidae obtained using MP analysis (PAUP 4.0b).

Length 34377, CI = 0.221, RI = 0.396. Characters are unordered with equal weight, 3976 non informative characters excluded, 3503 parsimony-informative characters included. Tree-island profile of 13. Bootstrap support from 1000 replicates is on branches if >50%. Species from the same tribe are represented by branches of the same color (outgroups in red). Selected node numbers are in blue-filled squares. Asterisk indicates a taxon that includes sequence for the barcode fragment (COI) for a substitute species of the same genus (see Appendix 2.1).
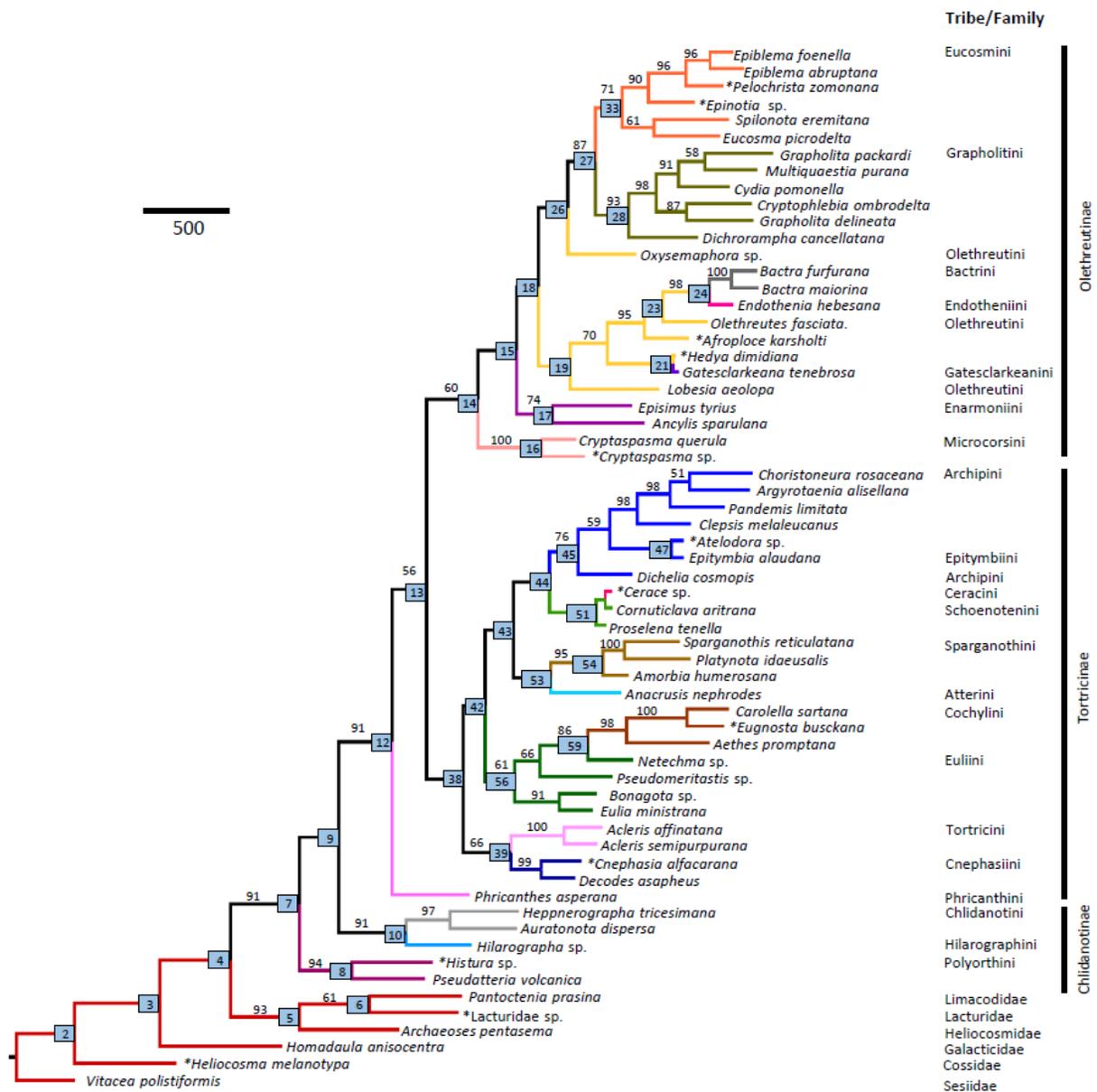
Appendix 2.7. Best tree for Tortricidae using ML analysis (IQ-Tree 1.3.11.1) of 13 partitions (best schema per codon position).

Tree lnL= -138,213.839. Support values on branches from 1000 replicates are SH-aLRT support (%) / ultrafast bootstrap support (%). Species from the same tribe are represented by branches of the same color (outgroups in red). Selected node numbers are in blue-filled squares. Asterisk indicates a taxon that includes sequence for the barcode fragment (COI) for a substitute species of the same genus (see Appendix 2.1).

169
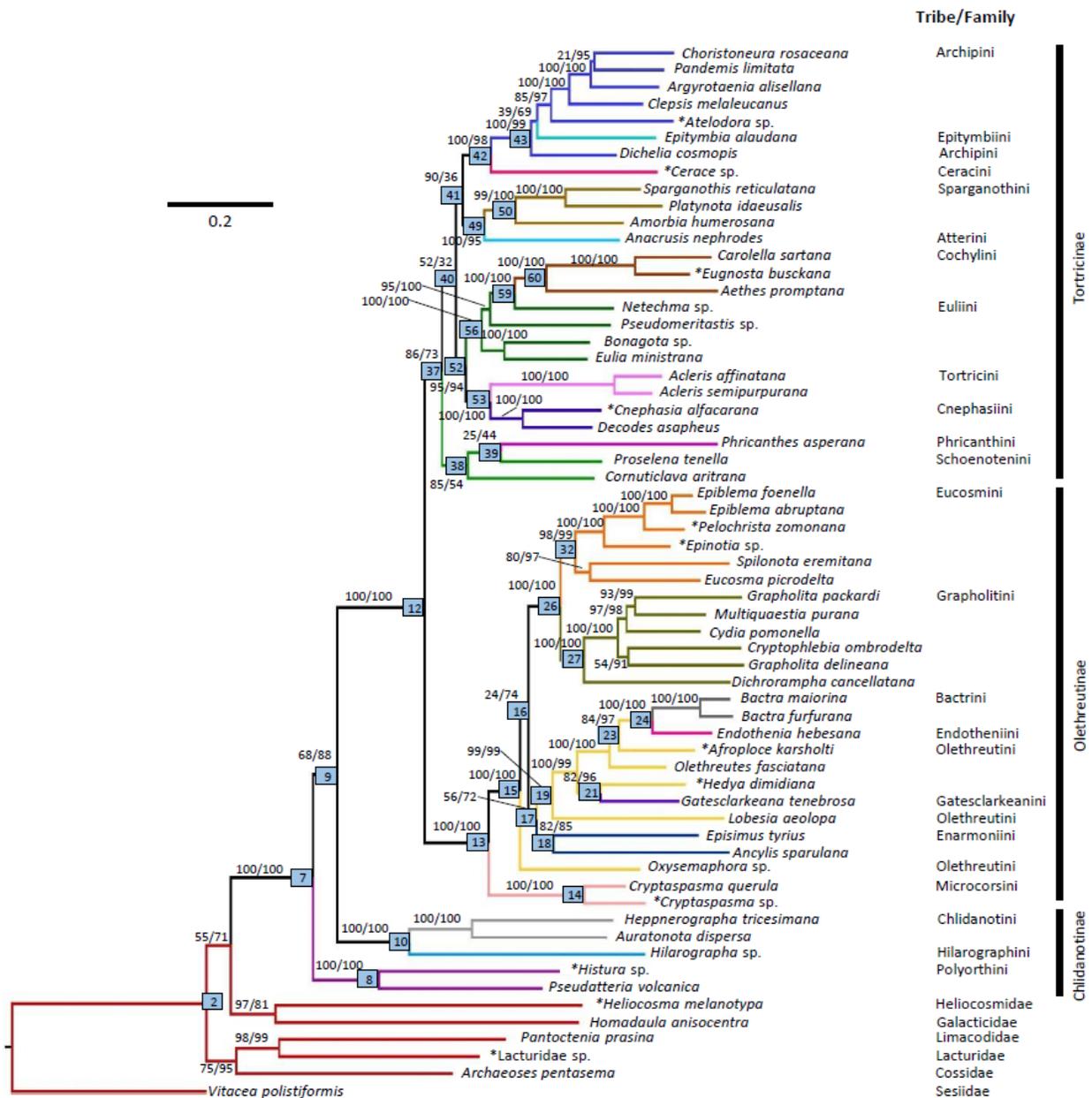
Appendix 2.8. Majority-rule consensus tree of Tortricidae using Bayesian analysis (MrBayes 3.2.6) of 13 partitions (the best schema per codon position).

Two runs used 8 chains for 20 million generations. Species from the same tribe are represented by branches of the same color (outgroups in red). Numbers on branches denote posterior probabilities. Selected node numbers are in blue-filled squares. Mean LnL run 1 = -134,846.92, run 2 = -134,849.42. ESS>400 for all variables. Asterisk indicates a taxon that includes sequence for the barcode fragment (COI) for a substitute species of the same genus (see Appendix 2.1).
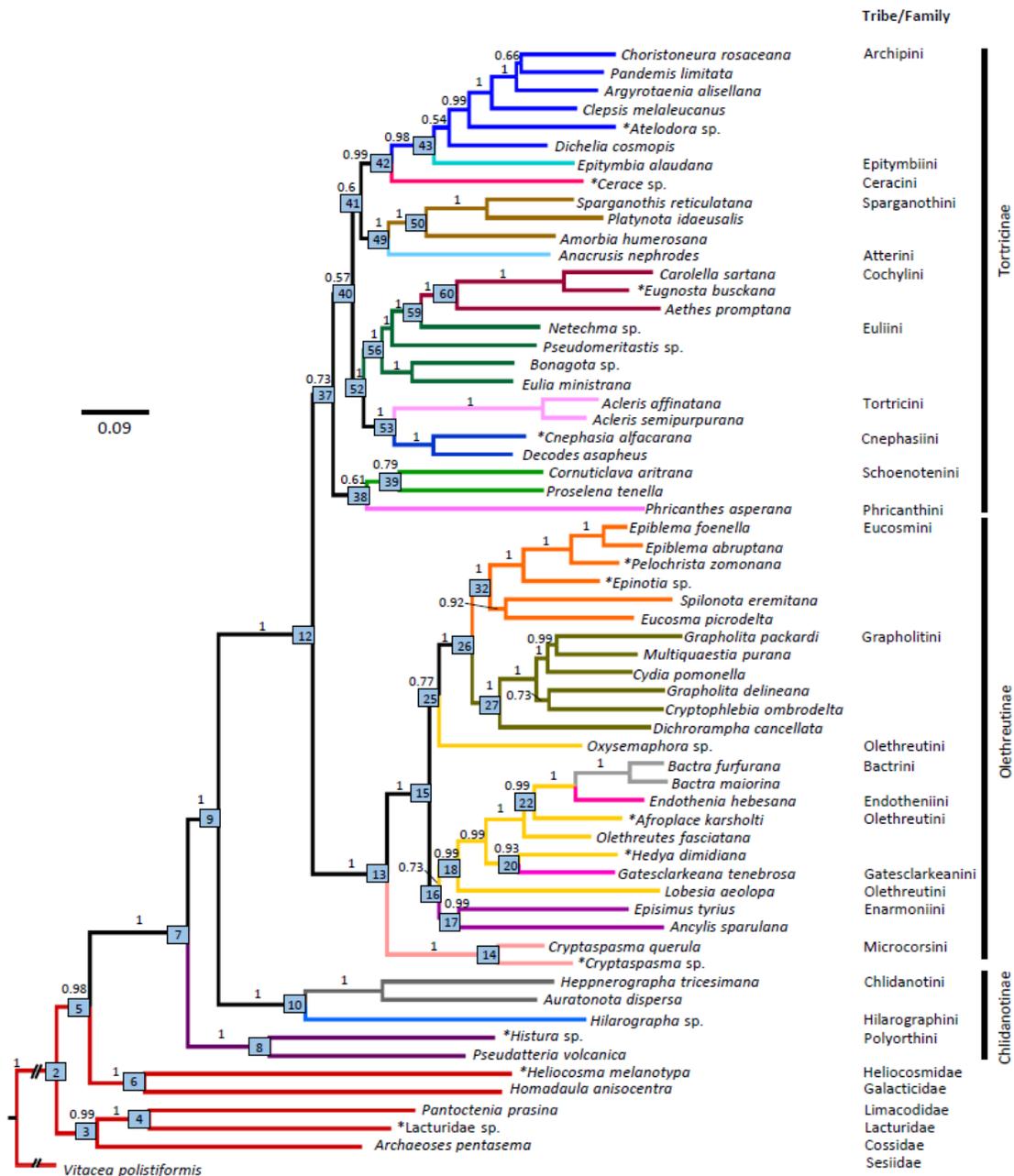
Appendix 2.9. Majority-rule consensus tree of Tortricidae using Bayesian analysis (MrBayes 3.2.6) of five gene partitions (Table 2.2).

Selected node numbers are in blue-filled squares. Two runs used 8 chains for 20 million generations. Numbers on branches denote posterior probabilities. Mean LnL run 1 = -138,840.32, run 2 = 138,840.65. ESS > 400 for all variables. Asterisk indicates a taxon including a sequence for the barcode fragment (COI) for a substitute species of the same genus (see Appendix 2.1).
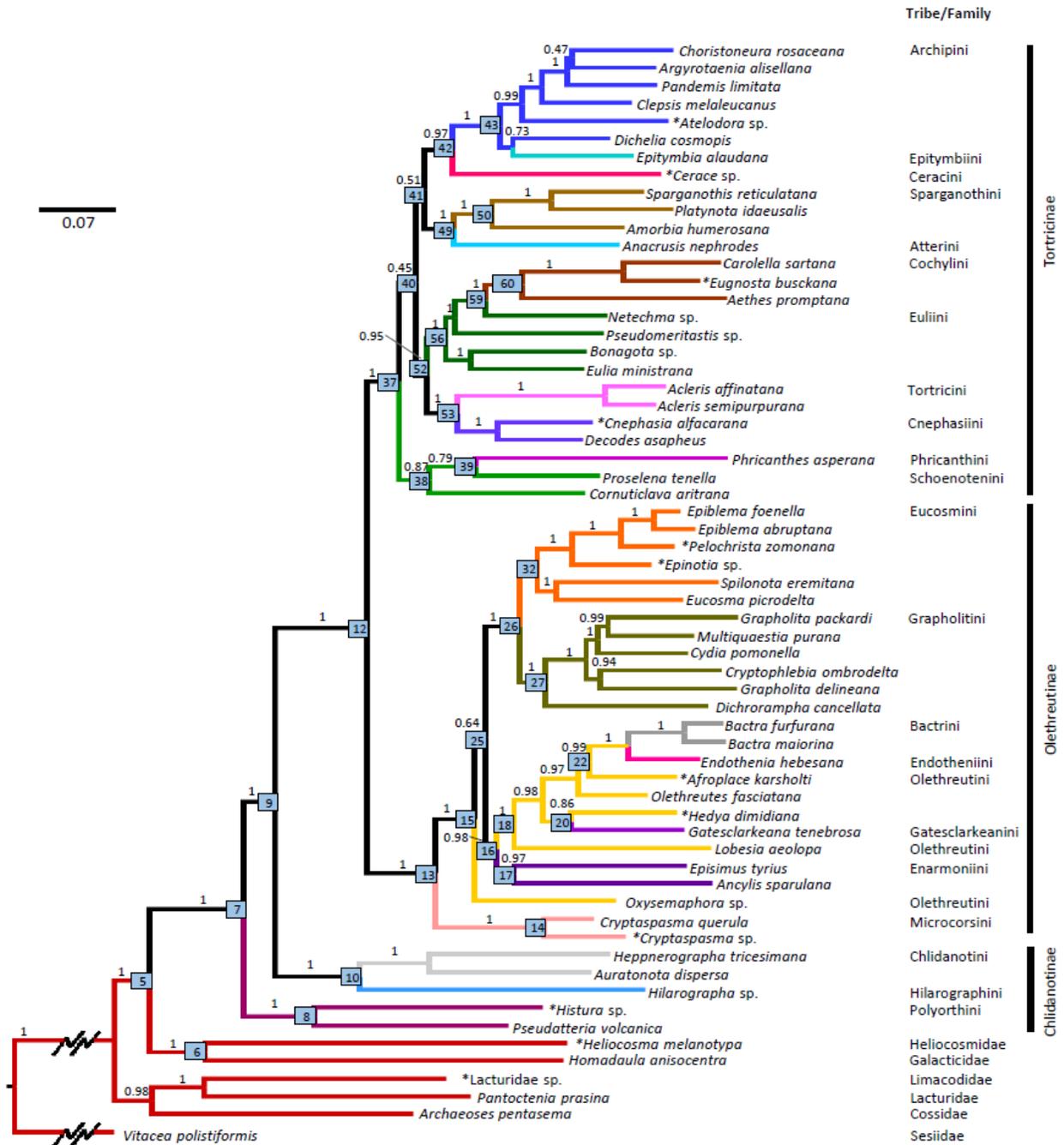
Appendix 2.10. Putative ancestral areas tested using six models for 56 species of Tortricidae using BioGeoBEARS 0.2.1.

Ancestral states = global optimum. Areas maximum = 9. Pie charts show relative probabilities of ancestral areas. Species distributions with more than one area have combined letters for biogeographical regions and alternate color boxes. Colored boxes identify biogeographical regions: WP = West Palearctic, EP = East Palearctic, WN = West Nearctic, EN = East Nearctic, NT = Neotropics, AF = Africa+Madagascar, IN = India, SA = Southeast Asia, and AU = Australasia. Species distributions with more than one area have combined letters for biogeographical regions and alternate color boxes.

BioGeoBEARS DEC+J on 56spstrat M1_stratified
ancstates: global optim, 9 areas max. d=0.0096; e=0; j=0.0667; LnL=−181.97

BioGeoBEARS DEC on 56genustrat M1_stratified
ancstates: global optim, 9 areas max. d=0.0486; e=0.0439; j=0; LnL=−360.74

WN *Eugnosta busckana
EN Carolella sartana
WN EN Aethes promptana
NT Netechma sp.
NT Pseudomeritastis sp.
WPEPWNEN Eulia ministrana
NT Bonagota sp.
WP *Cnephasia alfacarana
WN Decodes asapheus
EN Acleris semipurpurana
EP Acleris affinatana
EN Sparganothis reticulatana
WN EN Platynota idaeusalis
EN Amorbia humerosana
NT Anacrusis nephrodes
WN EN Choristoneura rosaceana
WN EN Pandemis limitata
EN Argyrotaenia alisellana
EN Clepsis melaleucanus
AU *Atelodora sp.
AU Epitymbia alaudana
AU Dichelia cosmopis
SA *Cerace sp.
AU Proselena tenella
AU Cornuticlava aritrana
AU Phricanthes asperana
WPEP Epiblema foenella
EN Epiblema abruptana
WN EN *Pelochrista zomonana
WPEPWNEN *Epinotia sp.
AF Eucosma picrodelta
EP Spilonota eremitana
EN Grapholita packardi
AF Multiquaestia purana
WP Cydia pomonella
EPSA Grapholita delineana
INSAAU Cryptophlebia ombrodelta
EP Dichrorampha cancellatana
AU Oxysemaphora sp.
WN EN Bactra maiorina
WPEPWNEN Bactra furfurana
WN EN Endothenia hebesana
AF *Afroploce karsholti
EN Olethreutes fasciatana
AU Gatesclarkeana tenebrosa
WPEPSA *Hedya dimidiana
EPINSA Lobesia aeolopa
EN Episimus tyrius
WP Ancylis sparulana
AU *Cryptaspasma sp.
IN Cryptaspasma querula
NT Auratonota dispersa
NT Heppnerographa tricesimana
NT Hilarographa sp.
NT *Histura sp.
NT Pseudatteria volcanica

Time (Mya)

173

BioGeoBEARS DIVALIKE+J on 56sp M1_stratified
ancstates: global optim, 9 areas max. d=0.0099; e=0; j=0.0643; LnL=−182.46

Taxon	Area
*Eugnosta busckana	WN
Carolella sartana	EN
Aethes promptana	WN EN
Netechma sp.	NT
Pseudomeritastis sp.	NT
Eulia ministrana	WPEPWNEN
Bonagota sp.	NT
*Cnephasia alfacarana	WP
Decodes asapheus	WN
Acleris semipurpurana	EN
Acleris affinatana	EP
Sparganothis reticulatana	EN
Platynota idaeusalis	WN EN
Amorbia humerosana	EN
Anacrusis nephrodes	NT
Choristoneura rosaceana	WN EN
Pandemis limitata	WN EN
Argyrotaenia alisellana	EN
Clepsis melaleucanus	EN
*Atelodora sp.	AU
Epitymbia alaudana	AU
Dichelia cosmopis	AU
*Cerace sp.	SA
Proselena tenella	AU
Cornuticlava aritrana	AU
Phricanthes asperana	AU
Epiblema foenella	WPEP
Epiblema abruptana	EN
*Pelochrista zomonana	WN EN
*Epinotia sp.	WPEPWNEN
Eucosma picrodelta	AF
Spilonota eremitana	EP
Grapholita packardi	EN
Multiquaestia purana	AF
Cydia pomonella	WP
Grapholita delineana	EPSA
Cryptophlebia ombrodelta	INSAAU
Dichrorampha cancellatana	EP
Oxysemaphora sp.	AU
Bactra maiorina	WN EN
Bactra furfurana	WPEPWNEN
Endothenia hebesana	WN EN
*Afroploce karsholti	AF
Olethreutes fasciatana	EN
Gatesclarkeana tenebrosa	AU
*Hedya dimidiana	WPEPSA
Lobesia aeolopa	EPINSA
Episimus tyrius	EN
Ancylis sparulana	WP
*Cryptaspasma sp.	AU
Cryptaspasma querula	IN
Auratonota dispersa	NT
Heppnerographa tricesimana	NT
Hilarographa sp.	NT
*Histura sp.	NT
Pseudatteria volcanica	NT

Time (Mya)
100   80   60   40   20   0

BioGeoBEARS DIVALIKE on 56sp M1_stratified
ancstates: global optim, 9 areas max. d=0.0459; e=0.0396; j=0; LnL=−360.33

WN	*Eugnosta busckana
EN	Carolella sartana
WN EN	Aethes promptana
NT	Netechma sp.
NT	Pseudomeritastis sp.
WPEPWNEN	Eulia ministrana
NT	Bonagota sp.
WP	*Cnephasia alfacarana
WN	Decodes asapheus
EN	Acleris semipurpurana
EP	Acleris affinatana
EN	Sparganothis reticulatana
WN EN	Platynota idaeusalis
EN	Amorbia humerosana
NT	Anacrusis nephrodes
WN EN	Choristoneura rosaceana
WN EN	Pandemis limitata
EN	Argyrotaenia alisellana
EN	Clepsis melaleucanus
AU	*Atelodora sp.
AU	Epitymbia alaudana
AU	Dichelia cosmopis
SA	*Cerace sp.
AU	Proselena tenella
AU	Cornuticlava aritrana
AU	Phricanthes asperana
WPEP	Epiblema foenella
EN	Epiblema abruptana
WN EN	*Pelochrista zomonana
WPEPWNEN	*Epinotia sp.
AF	Eucosma picrodelta
EP	Spilonota eremitana
EN	Grapholita packardi
AF	Multiquaestia purana
WP	Cydia pomonella
EPSA	Grapholita delineana
INSAAU	Cryptophlebia ombrodelta
EP	Dichrorampha cancellatana
AU	Oxysemaphora sp.
WN EN	Bactra maiorina
WPEPWNEN	Bactra furfurana
WN EN	Endothenia hebesana
AF	*Afroploce karsholti
EN	Olethreutes fasciatana
AU	Gatesclarkeana tenebrosa
WPEPSA	*Hedya dimidiana
EPINSA	Lobesia aeolopa
EN	Episimus tyrius
WP	Ancylis sparulana
AU	*Cryptaspasma sp.
IN	Cryptaspasma querula
NT	Auratonota dispersa
NT	Heppnerographa tricesimana
NT	Hilarographa sp.
NT	*Histura sp.
NT	Pseudatteria volcanica

Time (Mya)
100   80   60   40   20   0

175

BioGeoBEARS BAYAREALIKE+J on 56genus M1_stratified
ancstates: global optim, 9 areas max. d=8e−04; e=0.0259; j=0.0062; LnL=−213.09

*Eugnosta busckana
Carolella sartana
Aethes promptana
Netechma sp.
Pseudomeritastis sp.
Eulia ministrana
Bonagota sp.
*Cnephasia alfacarana
Decodes asapheus
Acleris semipurpurana
Acleris affinatana
Sparganothis reticulatana
Platynota idaeusalis
Amorbia humerosana
Anacrusis nephrodes
Choristoneura rosaceana
Pandemis limitata
Argyrotaenia alisellana
Clepsis melaleucanus
*Atelodora sp.
Epitymbia alaudana
Dichelia cosmopis
*Cerace sp.
Proselena tenella
Cornuticlava aritrana
Phricanthes asperana
Epiblema foenella
Epiblema abruptana
*Pelochrista zomonana
*Epinotia sp.
Eucosma picrodelta
Spilonota eremitana
Grapholita packardi
Multiquaestia purana
Cydia pomonella
Grapholita delineana
Cryptophlebia ombrodelta
Dichrorampha cancellatana
Oxysemaphora sp.
Bactra maiorina
Bactra furfurana
Endothenia hebesana
*Afroploce karsholti
Olethreutes fasciatana
Gatesclarkeana tenebrosa
*Hedya dimidiana
Lobesia aeolopa
Episimus tyrius
Ancylis sparulana
*Cryptaspasma sp.
Cryptaspasma querula
Auratonota dispersa
Heppnerographa tricesimana
Hilarographa sp.
*Histura sp.
Pseudatteria volcanica

Time (Mya)

176

BioGeoBEARS BAYAREALIKE on 56genus M1_stratified
ancstates: global optim, 9 areas max. d=0.0623; e=0.0675; j=0; LnL=−359.69

*Eugnosta busckana
Carolella sartana
Aethes promptana
Netechma sp.
Pseudomeritastis sp.
Eulia ministrana
Bonagota sp.
*Cnephasia alfacarana
Decodes asapheus
Acleris semipurpurana
Acleris affinatana
Sparganothis reticulatana
Platynota idaeusalis
Amorbia humerosana
Anacrusis nephrodes
Choristoneura rosaceana
Pandemis limitata
Argyrotaenia alisellana
Clepsis melaleucanus
*Atelodora sp.
Epitymbia alaudana
Dichelia cosmopis
*Cerace sp.
Proselena tenella
Cornuticlava aritrana
Phricanthes asperana
Epiblema foenella
Epiblema abruptana
*Pelochrista zomonana
*Epinotia sp.
Eucosma picrodelta
Spilonota eremitana
Grapholita packardi
Multiquaestia purana
Cydia pomonella
Grapholita delineana
Cryptophlebia ombrodelta
Dichrorampha cancellatana
Oxysemaphora sp.
Bactra maiorina
Bactra furfurana
Endothenia hebesana
*Afroploce karsholti
Olethreutes fasciatana
Gatesclarkeana tenebrosa
*Hedya dimidiana
Lobesia aeolopa
Episimus tyrius
Ancylis sparulana
*Cryptaspasma sp.
Cryptaspasma querula
Auratonota dispersa
Heppnerographa tricesimana
Hilarographa sp.
*Histura sp.
Pseudatteria volcanica

Time (Mya)

Appendix 2.11. Congruence of angiosperm revolution and continental colonization with rates of speciation through time in BAMM analysis for Tortricidae. Grey areas around speciation rate represent the 95% HPD interval.
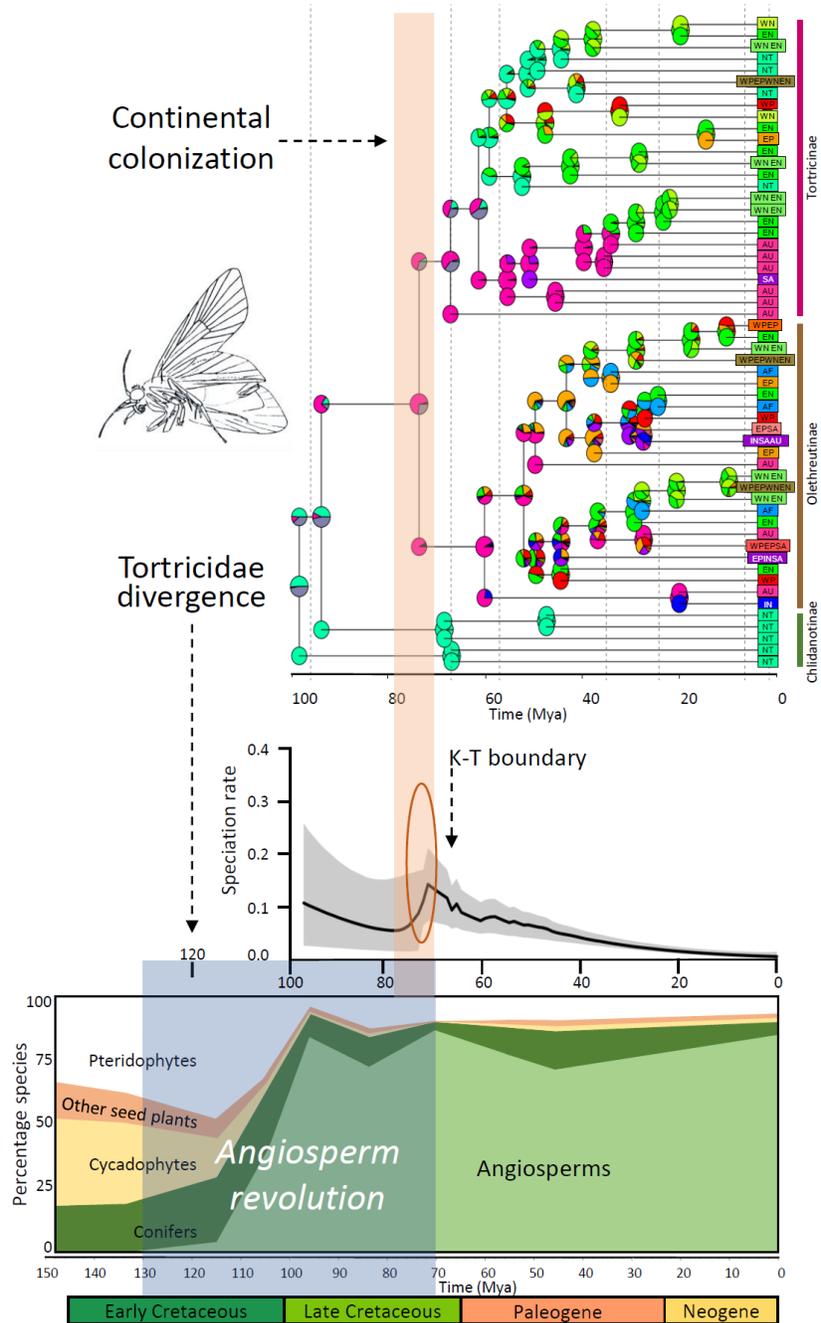
Appendix 3.1. Specimens and taxa used in Chapter 3, including previously published sequences from GenBank and newly sequenced specimens.

NA: Not applicable. [New mitogenome sequences will be deposited on GenBank after acceptation of manuscript.]

		NCBI GenBank accesion				
	Family	**Cossidae**				
	Subfamily	**Tribe**	**Species and mitochondrial lineage**	**GenBank #**	**Reference**	**Location and collector**
1	Cossinae	Zeuzerocossini	*Eogystia hippophaecolus* (Hua, Chou, Fang & Chen, 1990)	NC_023936	Gong *et al.* 2014	China, no more data reported
	Family	**Tortricidae**				
	Subfamily	**Tribe**	**Species and mitochondrial lineage**	**GenBank #**	**Reference**	**Location and collector**
2	Olethreutinae	Eucosmini	*Spilonota lechriaspis* Meyrick, 1932	NC_014294	Zhao *et al.* 2011	China, Beijing Municipality, Beijing
3	Olethreutinae	Eucosmini	*Rhyacionia leptotubula* Liu & Bai, 1984	NC_019619	Zhu *et al.* 2012	China, Yunnan
4	Olethreutinae	Eucosmini	*Retinia pseudotsugaicola* Liu & Wu, 2001	NC_022865	Wu *et al.* 2013 Unpublished	China, Yunnan, Anning county. Collector: Y. Pan.
5	Olethreutinae	Grapholitini	*Cydia pomonella* (L.)	NC_020003	Shi *et al.* 2013	China, no more data reported
6	Olethreutinae	Grapholitini	*Grapholita dimorpha* Komai, 1979	NC_024582	Niu *et al.* 2016	China, Sichuan, Chengdu
7	Olethreutinae	Grapholitini	*Grapholita molesta* (Busck, 1916)	NC_014806	Son and Kim 2011	South Korea, North Gyeongsang, Andong
8	Tortricinae	Tortricini	*Acleris fimbriana* (Thunberg & Becklin, 1791)	NC_018754	Zhao *et al.* 2016	China, Beijing Municipality, Changping. Collector: J. Zhao
9	Tortricinae	Archipini	*Adoxophyes honmai* Yasuda, 1998	NC_008141	Lee *et al.* 2006	South Korea, Chonnam, Naju; 35° 00' 55" N; 126° 42' 37" W; altitude 39 m
10	Tortricinae	Archipini	*Adoxophyes orana* (Fischer von Röslerstamm, 1834)	NC_021396	Wu *et al.* 2013	China, no more data reported.
11	Tortricinae	Archipini	*Epiphyas postvittana* (Walker, 1863)	- KJ508051	Timmermans *et al.* 2014	United Kingdom, no more data reported.
12	Tortricinae	Archipini	*Choristoneura longicellana* (Walsingham, 1900)	NC_019996	Wu *et al.* 2016	China, Beijing Municipality, Beijing.

| | Subfamily | Tribe | Newly sequenced specimens | | | |
			Species and mitochondrial lineage	Sperling lab extraction number	Collection date	Location and collector
13	Tortricinae	Archipini	*Choristoneura conflictana* (Walker, 1863)	10987	18/07/2014	USA, Utah, Park City, Summit Co.; 40° 39' 56" N; 111° 30' 29" W; 2090 m. Collector: J. Dupuis
14	Tortricinae	Archipini	*Choristoneura murinana* (Hübner, 1799)	10146	01/05/1996	France; Alsace; Guebwiller; 47° 54' 37" N; 07° 12' 32" E; 274 m
15	Tortricinae	Archipini	*Choristoneura rosaceana* (Harris, 1841)	10081	20/07/2013	Canada, Alberta, Red Lodge Provincial Park; 51° 56' 51" N; 114° 14' 42" W; 950 m. Collector: G. Fagua
16	Tortricinae	Archipini	*Choristoneura pinus* (Harris, 1841), p lineage	NA	01/08/2010	Canada, Nova Scotia, Fourth Lake, Digby Co.; 44° 20' 46" N; 65° 38' 01" W; 150 m. Collector: Nova Scotia Department of Natural Resources
17	Tortricinae	Archipini	*Choristoneura occidentalis* Freeman 1963, o lineage	NA	2009	Canada, British Columbia, probably Nicola Valley near Merritt. Collector: V. Nealis and R. Turnquist
18	Tortricinae	Archipini	*Choristoneura occidentalis biennis* (Freeman, 1967), bß lineage	bibi10	1999	Canada, British Columbia, probably Fort Saint James or Ospika. Collector: V. Nealis
19	Tortricinae	Archipini	*Choristoneura occidentalis* Freeman 1963, oß lineage	3634	04/07/2007	USA, Montana, Bitterroot, Beaverland Co.; 45° 39' 09" N; 113° 42' 32" W; 1910 m. Collector: L. Lumley
20	Tortricinae	Archipini	*Choristoneura fumiferana* (Clemens, 1865) - West, f lineage	399	20/06/1991	Canada, Alberta, Hawk Hills; 57° 09' 18" N; 117° 33' 46" W; 464 m. Collector: FIDS (Forest Insect and Disease Survey).
21	Tortricinae	Archipini	*Choristoneura fumiferana* (Clemens, 1865) - East, f lineage	NA		No more data available. Collector: Insect Production Services (IPS), Sault Ste. Marie

Appendix 3.2. Gene Alignment of 13 protein coding and two ribosomal genes of tortricid mitogenomes. General alignment of all sequences for each taxon included in the study (digital file).

Appendix 3.3. Topologies recovered using 13 protein coding and 2 ribosomal genes.

Page 1: Best scheme partition for codon position using models = beast (PartitionFinder 1.1.1). Page 2: Consensus tree using BEAST 1.8.3 compared with the topology of reference (Fagua et al. 2017). Page 3: Maximum likelihood consensus tree (IQ-TREE 1.3.11.1). Page 4: Bayesian consensus tree (MrBayes 3.2.6).

Best scheme partition for codon position using *models = beast* (*PartitionFinder* 1.1.1)

Subset | Best Model | Subset Partitions

1 | TrN+G | ATP8_p1, ATP8_p2, ND2_p1, ND3_p1, ND4L_p3, ND6_p1, ND6_p2

2 | HKY+I+G | ATP6_p2, CO1_p2, CO2_p2, CO3_p2, CYTB_p2, ND2_p2, ND3_p2

3 | GTR+I+G | ATP6_p3, ATP8_p3, CO1_p3, CO2_p3, CO3_p3, CYT0B_p3, ND2_p3, ND1_p2, ND3_p3, ND4L_p1

4 | TrN+G | CO1_p1

5 | GTR+I+G | ATP6_p1, CO2_p1, CO3_p1, CYTB_p1

6 | GTR+I+G | ND1_p1, ND1_p3, ND4L_p2, ND4_p2, ND4_p3, ND5_p1, ND5_p3

7 | HKY+G | ND4_p1, ND5_p2, ND6_p3

8 | GTR+I+G | 12S_p1, 12S_p2, 12S_p3, 16S_p1, 16S_p2, 16S_p3

Page 2 shows the consensus using *BEAST 1.8.3* compared with the topology of reference (Fagua *et al*. 2017).

Page 3 shows ML consensus tree (*IQ-TREE* 1.3.11.1). Ultra Fast Bootstrap support (UFBS) after 1000 replicates on branches.

Page 4 shows the Bayesian consensus tree (*MrBayes* 3.2.6). Posterior probability (PP) is on nodes. Replicates run for 20 million generations.
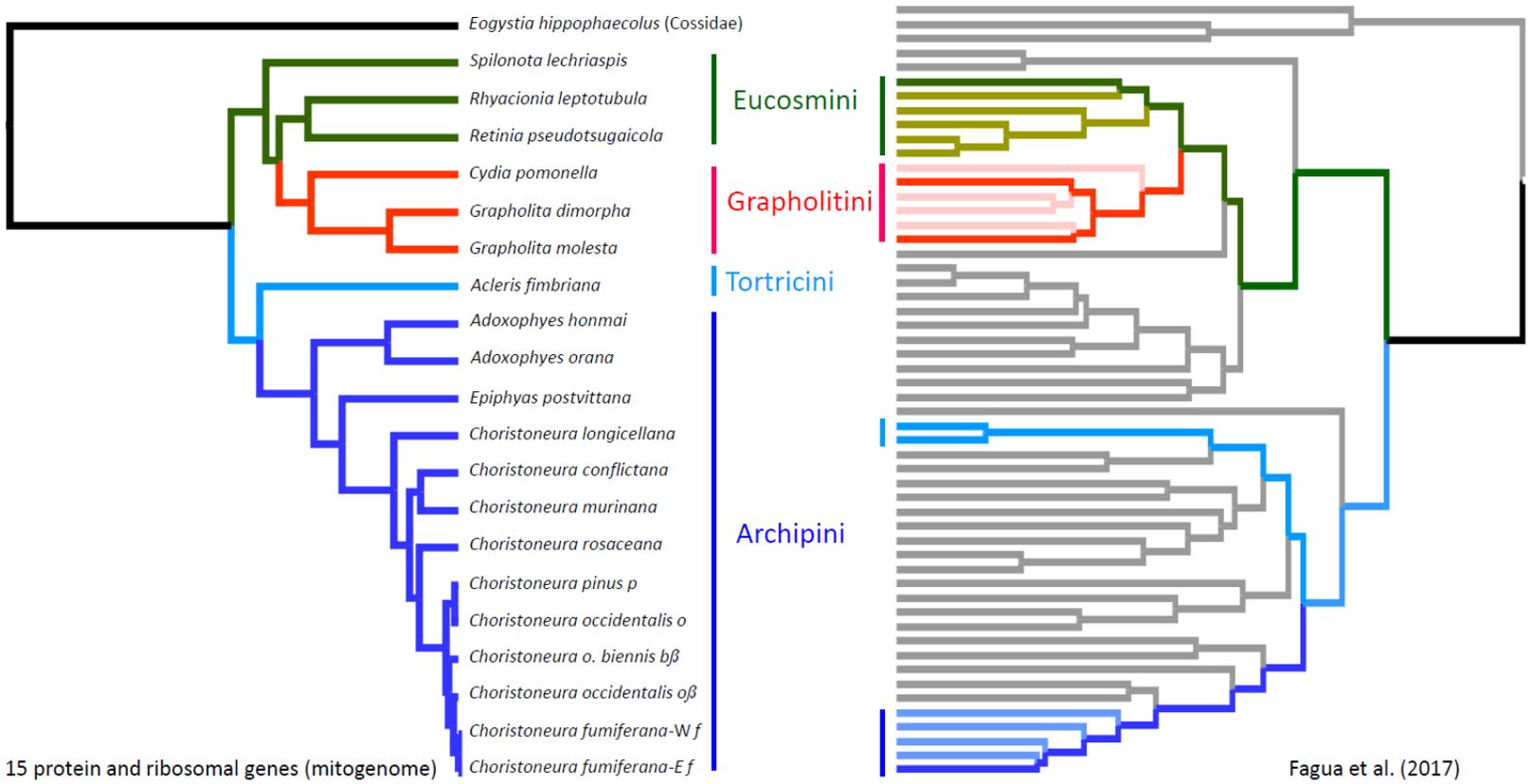
Comparison of the topologies obtained using BEAST (1.8.3) of mitochondrial protein and ribosomal genes vs the topology recovered by Fagua et al. (2017) using a complete set of the Tortricidae tribes (22 tribes). Species from the same tribe used in both studies are represented by branches of the same color. Deep colors indicate use of species from the same genus.
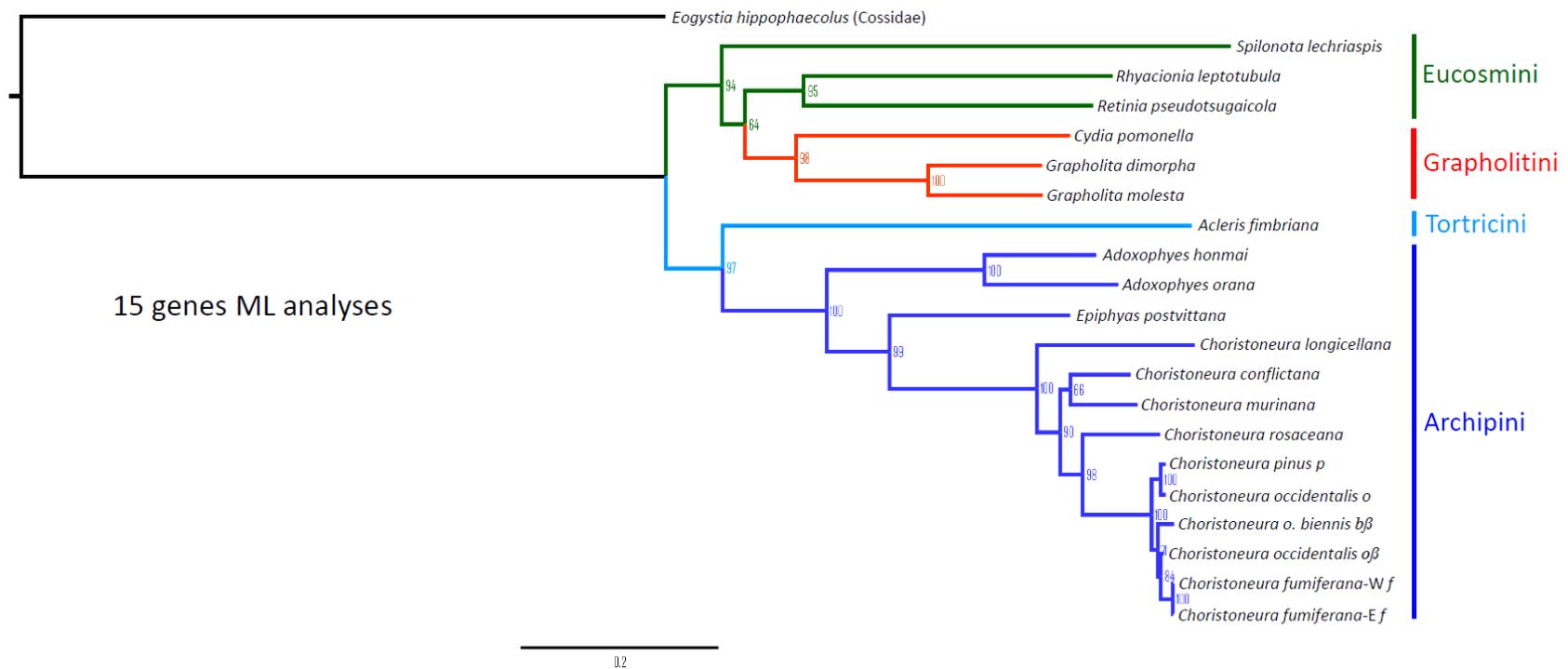
Consensus tree (lnL= -66694.44) for Tortricidae using ML analysis (*IQ-Tree 1.3.11.1*) of 8 partitions (best schema for codon position using *models = mrbayes*). Support values on branches from 1000 replicates ultrafast bootstrap support (%). Species from the same tribe are represented by branches of the same color.
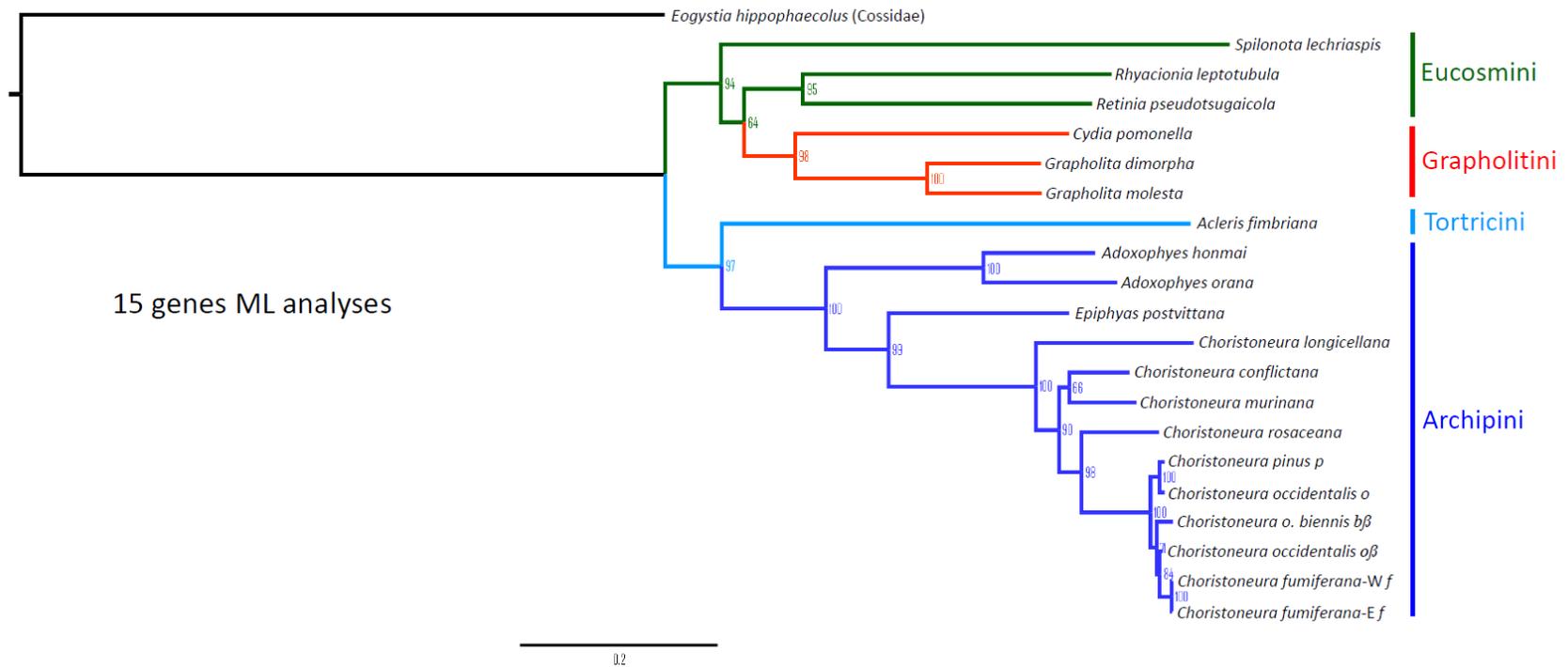
Majority-rule consensus tree of Tortricidae using Bayesian analysis (MrBayes 3.2.6) of 8 partitions (the best schema for codon position using *models = mrbayes*). Two runs used 8 chains for 20 million generations. Species from the same tribe are represented by branches of the same color (outgroup in red). Numbers on nodes denote posterior probabilities. Mean LnL of run 1 = -65930.22, and of run 2: = - 65933.03. ESS>1000 for most variables.

Appendix 3.4. Topologies recovered for each mitochondrial gene using Maximum Likelihood (ML) and Bayesian analysis.

Page 1: Best scheme partition per gene using models = mrbayes (*PartitionFinder 1.1.1*). Pages 2-5: consensus tree for each gene obtained using ML (*IQ-TREE 1.3.11.1*). Pages 7-10: Bayesian consensus tree for each gene (*MrBayes 3.2.6*). Pages 6 and 11: Bayesian and ML consensus tree for fragments of COI gene.

Best scheme partition per gene using *models = mrbayes* (*PartitionFinder* 1.1.1)

Subset	Best Model	Subset Partitions
1	GTR+I+G	ATP6, ATP8, NAD2, NAD3, NAD6
2	GTR+I+G	COI, CO II, COIII, COB
3	GTR+I+G	NAD1, NAD4, NAD4L, NAD5
4	GTR+I+G	12S, 16S

Pages 3 to 6 show ML consensus tree for each gene obtained using ML (*IQ-TREE* 1.3.11.1). Ultra Fast Bootstrap support (UFBS) after 1000 replicates on branches. Pages 8 to 11 show the Bayesian consensus tree for each gene (*MrBayes* 3.2.6). Posterior probability (PP) is on nodes. Replicates run for 5 million generations.Pages 7 and 12 show ML and Bayesian consensus tree for fragments of COI gene.

Abbreviations:
Eogystia: *Eogystia hippophaecolus*
Spilonota: *Spilonota lechriaspis*
Rhyacionia: *Rhyacionia leptotubula*
Retinia: *Retinia pseudotsugaicola*
Cydia: *Cydia pomonella*
G. dimorpha: *Grapholita dimorpha*
G. molesta: *Grapholita molesta*
Acleris: *Acleris fimbriana*
A. honmai: *Adoxophyes honmai*
A. orana : *Adoxophyes orana*
Epiphyas : *Epiphyas postvittana*

C. rosaceana: *Choristoneura rosaceana*
C. conflictana: *Choristoneura conflictana*
C. murinana: *Choristoneura murinana*
C. pinus p: *Choristoneura pinus* haplotype *p*
C. occidentalis o: *Choristoneura occidentalis* haplotype *o*
C. fumiferana West-*f*: *Choristoneura fumiferana* haplotype *f* West
C. fumiferana East-*f* : *Choristoneura fumiferana* haplotype *f* East
C. o. biennis bß: *Choristoneura o. biennis* haplotype *bß*
C. occidentalis oß: *Choristoneura occidentalis* haplotype *oß*

C. longicellana: *Choristoneura longicellana*

ATP6

ATP8

ND2

ND3

ND6

2

COB

COI

COII

COIII

0.06

0.03

0.04

0.05

3

188

ND1

ND4

ND4L

ND5

4

16S

Eogystia
Retinia
Spilonota
Cydia
Rhyacionia
G. dimorpha
G. molesta
Acleris
A. honmai
A. orana
Epiphyas
C. longicellana
C. murinana
C. conflictana
C. rosaceana
C. pinus p
C. occidentalis o
C. o. biennis bβ
C. o. occidentalis oβ
C. fumiferana-West f
C. fumiferana-East f

0.04

12S

Eogystia
A. orana
Acleris
Rhyacionia
Cydia
Spilonota
Retinia
G. dimorpha
G. molesta
A. honmai
Epiphyas
C. longicellana
C. rosaceana
C. conflictana
C. murinana
C. pinus p
C. occidentalis o
C. o. biennis bβ
C. o. occidentalis oβ
C. fumiferana-West f
C. fumiferana-East f

0.03

5

190

COI-658

COI-470

ATP6

ATP8

ND2

ND3

ND6

7

ND1

ND4

ND4L

ND5

9

194

16S

12S

10

COI-658

COI-470

11

Appendix 3.5. Comparison using Bayes factors on the relationship of Nearctic and Palearctic coniferophagous taxa of *Choristoneura*.

Comparison using Bayes factors on the relationship of Nearctic and Palearctic coniferophagous taxa of *Choristoneura*: the SBW complex and *Choristoneura murinana*. Model 1: analysis performed without constraints. Model 2: analysis constraining *C. murinana* as the sister group of the SBW complex.

```
Comparison using Bayes factors on the relationship of Nearctic and
Palearctic coniferophagous taxa of Choristoneura: the SBW complex and
Choristoneura murinana.
Model 1: analysis performed without constraints.
Model 2: analysis constraining C. murinana as the sister group
of the SBW complex.

Absolute differences between Harmonic means of Model 1 - Model 2
66184.86 - 66264.27: **79.41
Absolute differences between Marginal likelihood means estimated using
stepping-stone sampling of Model 1 - Model 2
66270.01 - 66346.26: **76.25
**Difference above 10 are considered very strong evidence in favor of
the better model (higest likelihood value: M1)

Model 1
Estimated marginal likelihoods for runs sampled in No-Constrained files
(Model 1)
     Run    Arithmetic mean    Harmonic mean
     ------------------------------------------
      1       -66127.98          -66182.55
      2       -66127.16          -66185.50
     ------------------------------------------
     TOTAL   -66127.49          -66184.86
     ------------------------------------------

Marginal likelihood (in natural log units) estimated using stepping-
stone sampling based on 100 steps with 1000 generations (1 samples)
within each stepin No-Constrained files (Model 1).

     Run    Marginal likelihood (ln)
     ----------------------------------
      1       -66429.33
      2       -66269.31
     ----------------------------------
     Mean:   -66270.01
```

Model 2
Estimated marginal likelihoods for runs sampled in Constrained files
(Model 2).

```
     Run    Arithmetic mean    Harmonic mean
     ----------------------------------------
      1       -66201.19          -66264.97
      2       -66200.86          -66257.05
     ----------------------------------------
     TOTAL   -66201.01          -66264.27
     ----------------------------------------
```

Marginal likelihood (in natural log units) estimated using stepping-
stone sampling based on 100 steps with 1000 generations (1 samples)
within each step in Constrained files (Model 2).

```
     Run    Marginal likelihood (ln)
     ----------------------------------
      1      -66502.64
      2      -66345.57
     ----------------------------------
     Mean:  -66346.26
```

Appendix 4.1. Primers used in Chapter 4.

Primers used in this study. Letters and numbers after the name indicate the oligonucleotide starting position (5'- 3') defined against the mitogenome of *Drosophila yakuba* using the nomenclature of Simon et al. 1994. (Tm) melting temperature.

Primer name and position	Oligo sequence	Tm	Fragment length
	New primers		
COI			
TY-J-1421 Chor F	5- CAA TTT ATC GCT TAA TTC TCA GC-3	50.4 °C	796
CI-N-2263 Chor R	5- TTC CTA AAC ATC AAA AAG TTT CTT -3	51.1 °C	
COI	**Published primers**	**Reference**	
C-J-1751 Ron V F	5- GGA GCT CCA GAT ATA GCT TTC CC-3	Simon et al. 1994	
CI-N-1840 K791 R	5- TGG GGG GTA TAC TGT TCA T/ACC -3	Bromilow and Sperling 2011	
C-J-2183 Jerry F	5- CAA CAT TTA TTT TGA TTT TTT GG -3	Simon et al. 1994	
C-J-2495 Brian F	5- CTT CTA TAC TTT GAA GAT TAG G -3	Wahlberg 2010	
C-N-2659 Mila R	5- GCT AAT CCA GTG AAT AAT GG-3	Sperling and Hickey 1994	
C-J-2792 George V F	5- ATA CCT CGA CGA TAT TCC GA -3	Wells and Sperling 1999	
TL2-N-3013 Pat2 R	5- TCC ATT ACA TAT AAT CTG CCA TAT TAG -3	Sperling et al. 1994	
28S			
28SD2fwtort	5- ACGYGC ACG CGTTCWTAC -3	Dombroskie & Sperling 2013	
28SD2rctort	5- GACTCC TTG GTC CGT TC -3	Dombroskie & Sperling 2013	

Appendix 4.2. Terminal taxa used in Chapter 4, including previously published sequences from GenBank and newly sequenced specimens.

NA: Not applicable. [DAA: deposited after acceptance. New mitogenome sequences will be deposited on GenBank after accepted for publication.] SBW: Choristoneura fumiferana species complex

| | | NCBI GenBank accesion | | | | | | | | | |
| | | | | Outgroup | | | | | | | |
	Species and mitochondrial lineage	COI #	28 #	Reference	Country	Province/State	Collection Location	Longitude	Latitude	Collector
	Family Tortricidae									
	Subfamily Olethreutinae									
	Tribe Eucosmini									
1	*Retinia pseudotsugaicola* Liu & Wu, 2001	NC_022865	-	Wu *et al.* 2013 Unpublished	China	Yunnan	Anning county	-	-	Y. Pan
2	*Rhyacionia leptotubula* Liu & Bai, 1984	NC_019619	-	Zhu *et al.* 2012	China	Yunnan	not reported	-	-	-
3	*Spilonota lechriaspis* Meyrick, 1932 Grapholitini	NC_014294	-	Zhao *et al.* 2011	China	Beijing Municipality	Beijing	-	-	-
4	*Cydia pomonella* (L.)	NC_020003	-	Shi *et al.* 2013	China	not reported	not reported	-	-	-
5	*Grapholita dimorpha* Komai, 1979	NC_024582	-	Niu *et al.* 2016	China	Sichuan	Chengdu	-	-	-
6	*Grapholita molesta* (Busck, 1916)	NC_014806	-	Son and Kim 2011	South Korea	North Gyeongsang	Andong	-	-	-
	Subfamily Tortricinae									
	Tribe Tortricini									
7	*Acleris fimbriana* (Thunberg & Becklin, 1791)	NC_018754	-	Zhao *et al.* 2016	China	Beijing Municipality	Changping	-	-	J. Zhao
	Tribe Schoenotenini									
8	*Cornuticlava aritrana* Common, 1965	KC315444	-	Fagua et al. 2017	Australia	not reported	not reported	-	-	-
9	*Proselena tenella* (Meyrick, 1910)	KC315457	-	Fagua et al. 2017	Australia	not reported	not reported	-	-	-
	Tribe Ceracini									
10	*Cerace* sp.	JF703049	JF702961	Dombroskie & Sperling 2013	Taiwan	Yilan Co.	Fu-Shan Res. Sta.	121.595	24.765	L. C. Shih

	Species and mitochondrial lineage	COI #	28 #	Reference	Country	Province/State	Collection Location	Longitude	Latitude	Collector
	Tribe Epitymbiini									
11	*Epitymbia alaudana* Meyrick, 1881	KC315453	-	Fagua et al. 2017	Australia	not reported	not reported	-	-	-
	Tribe Archipini									
12	*Acropolitis hedista* (Turner, 1916)	KC315441	-	Zwick et al. 2012. Unpublished.	Australia	not reported	not reported	-	-	-
13	*Adoxophyes negundana* (McDunnough, 1923)	JF703014	JF702925	Dombroskie & Sperling 2013	Canada	Alberta	Lethbridge	-112.827	49.689	M. Vankosky
14	*Adoxophyes orana* (Fischer von Röslerstamm, 1834)	NC_021396	-	Wu *et al.* 2013	China	not reported	not reported	-	-	-
15	*Adoxophyes orana*	JF703015	JF702926	Dombroskie & Sperling 2013	Românía	Constanta	Canarau Feteii	27.645	44.068	J.J. Dombroskie, A. Sandor
16	*Adoxophyes honmai* Yasuda, 1998	NC_008141	-	Lee *et al.* 2006	South Korea	Chonnam	Naju	126.713	35.015	-
17	*Aphelia alleniana* (Fernald, 1882)	JF703016	JF702927	Dombroskie & Sperling 2013	Canada	Alberta	Porcupine Hills	-114.087	49.972	J.J. Dombroskie et al.
18	*Aphelia unitana* (Hubner, [1796-1799])	JF703018	JF702929	Dombroskie & Sperling 2013	Românía	Brașov	Stațiunea Sâmbăta	24.791	45.674	J.J. Dombroskie et al.
19	*Archips alberta* (McDunnough, 1923)	JF703019	JF702930	Dombroskie & Sperling 2013	Canada	Alberta	Kootenay Plains Ecol. Res.	-116.496	51.999	J.J. Dombroskie, B. C. Schmidt
20	*Archips cerasivorana* (Fitch, 1856)	JF703020	JF702931	Dombroskie & Sperling 2013	Canada	Alberta	Waterton Lakes	-113.915	49.056	J.J. Dombroskie et al.
21	*Archips eleagnana* (McDunnough, 1923)	JF703022	JF702933	Dombroskie & Sperling 2013	Canada	Alberta	Kootenay Plains Ecol. Res.	-116.465	52.003	J.J. Dombroskie, B. C. Schmidt
22	*Archips fervidana* (Clemens, 1860)	JF703023	JF702934	Dombroskie & Sperling 2013	United States	Arizona	Crawford Co., Ozark-St. Francis Nat. For.	-94.296	35.702	J.J. Dombroskie, D. Lawrie
23	*Archips negundana* (Dyar, 1902)	JF703024	JF702935	Dombroskie & Sperling 2013	Canada	Alberta	Edmonton	-113.492	53.525	J.J. Dombroskie, A. Rose
24	*Archips packardiana* (Fernald, 1886)	JF703025	JF702936	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., Jasper Lake	-118.003	53.097	B. C. Schmidt, G. Anweiler
25	*Archips podana* (Scopoli, 1763)	JF703026	JF702937	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
26	*Archips purpurana* (Clemens, 1865)	JF703027	JF702938	Dombroskie & Sperling 2013	Canada	Alberta	Bindloss	-110.294	50.901	J.J. Dombroskie, B. Proshek

	Species and mitochondrial lineage	COI #	28 #	Reference	Country	Province/State	Collection Location	Longitude	Latitude	Collector
27	*Archips rosana* (Linnaeus, 1758)	JF703028	JF702939	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
28	*Archips striana* Fernald, 1905	JF703029	JF702940	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., The Palisades	-118.058	52.963	B. C. Schmidt, G. Anweiler
29	*Archips xylosteana* (Linnaeus, 1758)	JF703030	JF702941	Dombroskie & Sperling 2013	Canada	NF and Labrador	St. John's	-52.738	47.575	B. C. Schmidt
30	*Archepandemis coniferana* Mutuura, 1978	JF703021	JF702932	Dombroskie & Sperling 2013	Canada	Alberta	Clear Hills Upland	-118.33	56.751	E. Kamunya
31	*Argyrotaenia alisellana* (Robinson, 1869)	JF703031	JF702942	Dombroskie & Sperling 2013	United States	Virginia	Fairfax Co.; Fairfax City	-77.295	38.847	J. W. Brown
32	*Argyrotaenia coloradana* (Fernald, 1882)	JF703032	JF702943	Dombroskie & Sperling 2013	United States	Utah	Cache Nat. For., Logan Canyon	-111.139	41.78	J.J. Dombroskie et al.
33	*Argyrotaenia dorsalana* (Dyar, 1903)	JF703033	JF702944	Dombroskie & Sperling 2013	Canada	British Columbia	Tranquille Ecol. Res.	-120.589	50.755	J.J. Dombroskie
34	*Argyrotaenia floridana* Obraztsov, 1961	JF703034	JF702945	Dombroskie & Sperling 2013	United States	Florida	Marion Co., Ocala Nat. For., Delancey Lake	-81.789	29.427	J.J. Dombroskie et al.
35	*Argyrotaenia graceana* Powell, 1960	JF703035	JF702947	Dombroskie & Sperling 2013	United States	California	Ventura Co., Los Padres Nat. For., Mt. Pinos	-119.099	34.812	J.J. Dombroskie et al.
36	*Argyrotaenia kimballi* Obraztsov, 1961	JF703036	JF702948	Dombroskie & Sperling 2013	United States	Florida	Baker Co., Osceola Nat. For.	-82.331	30.384	J.J. Dombroskie et al.
37	*Argyrotaenia lautana* Powell, 1960	JF703037	JF702949	Dombroskie & Sperling 2013	United States	California	Ventura Co., Los Padres Nat. For., Mt. Pinos	-119.099	34.812	J.J. Dombroskie et al.
38	*Argyrotaenia occultana* Freeman, 1942	JF703040	JF702952	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., Jasper Lake	-118.003	53.097	B. C. Schmidt, G. Anweiler
39	*Argyrotaenia provana* (Kearfott, 1907)	JF703041	JF702953	Dombroskie & Sperling 2013	United States	Oregon	Wasco Co., Mt. Hood Nat. For.	-121.627	45.232	J.J. Dombroskie et al.
40	*Argyrotaenia repertana* Freeman, 1944	JF703044	JF702956	Dombroskie & Sperling 2013	Canada	Alberta	Wagner Bog	-113.832	53.565	J.J. Dombroskie et al.
41	*Argyrotaenia tabulana* Freeman, 1944	JF703045	JF702957	Dombroskie & Sperling 2013	United States	Arizona	Pulaski Co., Little Rock	-92.459	34.826	J.J. Dombroskie et al.
42	*Atelodora pelochytana* Meyrick, 1881	KF401595	-	Hebert et al. 2013. Unpublished.	Australia	New South Wales	8km SE of Wauchope	152.78	31.52 S	I.F.B.Common
43	*Cacoecimorpha pronubana* (Hübner, 1799)	JF703047	JF702959	Dombroskie & Sperling 2013	Spain	Catalonia	Sant Fost de Campsentelles	2.235	41.515	T. Gilligan & V. Santo Monteys
44	*Clepsis anderslaneyii* Dombroskie & Brown, 2009	JF703057	JF702976	Dombroskie & Sperling 2013	United States	Arizona	Cochise Co., SW Res. Sta., Chiricahua Mtns.	-109.207	31.881	J. W. Brown

	Species and mitochondrial lineage	COI #	28 #	Reference	Country	Province/State	Collection Location	Longitude	Latitude	Collector
45	*Clepsis clemensiana* (Fernald, 1879)	JF703058	JF702977	Dombroskie & Sperling 2013	Canada	Alberta	Edmonton	-113.492	53.525	J.J. Dombroskie, A. Rose
46	*Clepsis fucana* (Walsingham, 1879)	JF703060	JF702979	Dombroskie & Sperling 2013	United States	California	Alameda Co., Berkeley	-122.273	37.872	J. Powell
47	*Clepsis melaleucana* (Walker, 1863)	JF703061	JF702980	Dombroskie & Sperling 2013	Canada	Alberta	Edmonton	-113.434	53.545	G. Anweiler
48	*Clepsis penetralis* Razowski, 1979	JF703062	JF702981	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., The Palisades	-118.058	52.963	B. C. Schmidt, G. Anweiler
49	*Clepsis peritana* (Clemens, 1860)	JF703063	JF702982	Dombroskie & Sperling 2013	United States	Virginia	Fairfax Co., Fairfax City	-77.295	38.847	J. W. Brown
50	*Clepsis persicana* (Fitch, 1856)	JF703064	JF702983	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., The Palisades	-118.058	52.963	B. C. Schmidt, G. Anweiler
51	*Clepsis rurinana* (Linnaeus, 1758)	JF703065	JF702984	Dombroskie & Sperling 2013	Italia	Lombardia	Samarate	8.798	45.621	J.J. Dombroskie, D. Lawrie
52	*Clepsis spectrana* (Treitschke, 1830)	JF703067	JF702986	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
53	*Clepsis virescana* (Clemens, 1865)	JF703068	JF702987	Dombroskie & Sperling 2013	Canada	Alberta	Waterton Lakes Nat. Pk., Belleview Hill	-113.905	49.099	J.J. Dombroskie et al.
54	*Cryptoptila australana* (Lewin, 1805)	KC315447	-	Zwick et al. 2012. Unpublished.	Australia	not reported	not reported	-	-	-
55	*Cudonigera houstonana* (Grote, 1873)	JF703069	JF702988	Dombroskie & Sperling 2013	United States	Arizona	Logan Co., Ozark-St. Francis Nat. For.	-93.645	35.193	J.J. Dombroskie et al.
56	*Dichelia histrionana* (Frolich, 1828)	JF703070	JF702989	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
57	*Diedra intermontana* Rubinoff & Powell, 1999	JF703071	JF702990	Dombroskie & Sperling 2013	United States	Utah	Lander Co., Toiyabe Nat. For.	-117.139	39.225	J.J. Dombroskie et al.
58	*Ditula angustiorana* (Haworth, [1811])	JF703072	JF702991	Dombroskie & Sperling 2013	United States	California	Alameda Co., Berkeley	-122.273	37.872	FAHS
59	*Epagoge grotiana* (Fabricius, 1781)	JF703074	JF702993	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
60	*Epiphyas ashworthana* (Newman, 1856)	JF703075	JF702994	Dombroskie & Sperling 2013	Australia	not reported	not reported	-		T. Gilligan
61	*Epiphyas postvittana* (Walker, 1863)	KJ508051	-	Timmermans *et al.* 2014	United Kingdom	not reported	not reported	-	-	-
62	*Epiphyas postvittana*	JF703077	JF702996	Dombroskie & Sperling 2013	United States	California	Alameda Co., Berkeley	-122.273	37.872	J. Powell
63	*Epiphyas caryotis* (Meyrick, 1910)	JF703076	JF702995	Dombroskie & Sperling 2013	Australia	not reported	not reported	-	-	T. Gilligan
64	*Homona aestivana* (Walker, 1866)	EF070743	-	Hulcr et al. 2007	Papua New Guinea	Madang	Madang	141.08	4.62 S	-
65	*Homona auriga* (Durrant, 1915)	EF070825	-	Hulcr et al. 2007	Papua New Guinea	Madang	Madang	145.78	5.183 S	-

	Species and mitochondrial lineage	COI #	28 #	Reference	Country	Province/State	Collection Location	Longitude	Latitude	Collector
66	*Homona mermerodes* Meyrick, 1910	EF070749	-	Hulcr et al. 2007	Papua New Guinea	Madang	Madang	-	-	-
67	*Homona salaconis* (Meyrick, 1912)	GU440205	-	Miller, *et al.* 2010	Philippines	Laguna	Luzon, Mt. Makiling	121.22	14.13	W. Mey, K. Ebert
68	*Homona spargotis* Meyrick, 1910	EF070839	-	Hulcr et al. 2007	Papua New Guinea	Madang	Madang	145.78	5.18 S	-
69	*Homona trachyptera* Diakonoff, 1941	EF070863	-	Hulcr et al. 2007	Papua New Guinea	Morobe	Morobe	-	-	Y. Basset
70	*Lozotaenia hesperia* Powell, 1962	JF703079	JF702998	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., Jasper Lake	-118.003	53.097	B. C. Schmidt, G. Anweiler
71	*Lozotaeniodes cupressana* (Duponchel, 1836)	JF703078	JF702997	Dombroskie & Sperling 2013	Spain	Valencian	Pobla de Benifassa,	-0.212	40.669	T. M. Gilligan, *et al.*
72	*Pandemis canadana* Kearfott, 1905	JF703080	JF702999	Dombroskie & Sperling 2013	Canada	Alberta	Edmonton	-113.434	53.545	G. Anweiler
73	*Pandemis cerasana* (Hübner, 1786)	JF703081	JF703000	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
74	*Pandemis cinnamomeana* (Treitschke, 1830)	JF703082	JF703001	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
75	*Pandemis corylana* (Fabricius, 1794)	JF703083	JF703002	Dombroskie & Sperling 2013	Italia	Lombardia	Italia, LOM, Samarate	8.798	45.621	J.J. Dombroskie, D. Lawrie
76	*Pandemis dumetana* (Treitschke, 1835)	JF703084	JF703003	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
77	*Pandemis heparana* ([Denis & Schiffermuller], 1775)	JF703085	JF703004	Dombroskie & Sperling 2013	România	Gorj	România, GJ, Cheile Sohodolului	23.139	45.139	J.J. Dombroskie, D. Lawrie
78	*Pandemis lamprosana* (Robinson, 1869)	JF703086	JF703005	Dombroskie & Sperling 2013	United States	Maryland	Prince George's Co., Patuxeut W. R.	-76.798	39.027	J. Powell
79	*Pandemis limitata* (Robinson, 1869)	JF703087	JF703006	Dombroskie & Sperling 2013	United States	Virginia	Fairfax Co., Fairfax City	-77.295	38.847	J. W. Brown
80	*Pandemis pyrusana* Kearfott, 1907	JF703088	JF703007	Dombroskie & Sperling 2013	United States	California	Modoc Co., Modoc Nat. For.	-120.233	41.519	J.J. Dombroskie et al.
81	*Ptycholomoides aeriferana* (Herrich-Schäffer, 1851)	JF703089	JF703008	Dombroskie & Sperling 2013	Denmark	Zealand	Mandemarke	12.491	54.967	O. Karsholt
82	*Ptycholoma lecheana* (Linnaeus, 1758)	JF703090	JF703009	Dombroskie & Sperling 2013	Denmark	Copenhagen	Copenhagen	12.568	55.676	O. Karsholt
83	*Syndemis afflictana* (Walker, 1863)	JF703092	JF703011	Dombroskie & Sperling 2013	Canada	Alberta	Dunvegan Prov. Pk.	-118.594	55.926	J.J. Dombroskie et al.
84	*Xenotemna pallorana* (Robinson, 1869)	JF703093	JF703012	Dombroskie & Sperling 2013	Canada	Alberta	Pakowki Dunes	-110.875	49.397	J.J. Dombroskie, A. Rose

	Species and mitochondrial lineage	COI #	28 #	NCBI GenBank accesion Ingroup Reference	Country	Province/State	Location	Longitude	Latitude	Collector
	Archipini									
85	*Choristoneura albaniana* (Walker, 1863)	JF703050	JF702962	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., Jasper Lake	-118.003	53.097	B. C. Schmidt, G. Anweiler
86	*Choristoneura argentifasciata* Heppner, 1989	JF703051	JF702963	Dombroskie & Sperling 2013	United States	Florida	Baker Co., Osceola Nat. For.	-82.331	30.384	J.J. Dombroskie et al.
87	*Choristoneura conflictana* (Walker, 1863)	JF703052	JF702965	Dombroskie & Sperling 2013	Canada	Alberta	Jasper Nat. Pk., The Palisades	-118.058	52.963	B. C. Schmidt, G. Anweiler
88	*Choristoneura hebenstreitella* (Muller, 1764)	JF703053	JF702968	Dombroskie & Sperling 2013	Denmark	Copenhagen	Copenhagen	12.568	55.676	O. Karsholt
89	*Choristoneura longicellana* (Walsingham, 1900)	NC_019996	-	Wu *et al.* 2016	China	Beijing Municipality	Beijing	-	-	-
90	*Choristoneura parallela* (Robinson, 1869)	JF703054	JF702971	Dombroskie & Sperling 2013	United States	Florida	Baker Co., Osceola Nat. For.	-82.331	30.384	J.J. Dombroskie et al.
91	*Choristoneura rosaceana* (Harris, 1841)	JF703055	JF702974	Dombroskie & Sperling 2013	United States	Virginia	Fairfax Co., George Washington Mem. Pkwy	-77.228	38.817	J. W. Brown
	SBW									
92	*Choristoneura zapulata* (Robinson, 1869)	JF703056	JF702975	Dombroskie & Sperling 2013	Canada	Alberta	Pakowki Dunes	-110.875	49.397	J.J. Dombroskie et al.
93	*Choristoneura biennis* Freeman, 1967	DQ792587	JF702964	Lumley & Sperling 2010; Dombroskie & Sperling 2013	Canada	Alberta	Peter Lougheed Prov. Pk.	-115.122	50.618	L. M. Lumley, A. Roe
94	*Choristoneura fumiferana* (Clemens, 1865)	GQ890278	JF702967	Sperling & Hickey 1994; Dombroskie & Sperling 2013	Canada	Alberta	Ft McMurray	-111.354	56.686	L. M. Lumley
95	*Choristoneura occidentalis* Freeman, 1967	L19094	JF702966	Roe & Sperling 2007; Dombroskie & Sperling 2013	Canada	Alberta	Porcupine Hills, Beaver Creek CG	-113.948	49.804	L. M. Lumley
96	*Choristoneura orae* Freeman, 1967	DQ792586	JF702970	Roe & Sperling 2007; Dombroskie & Sperling 2013	Canada	British Columbia	Kincolith	-129.839	55.005	L. M. Lumley, *et al.*
97	*Choristoneura pinus* Freeman, 1953	L19095	JF702972	Sperling & Hickey 1994; Dombroskie & Sperling 2013	Canada	Alberta	Redwater Nat. Area	-112.952	53.937	L. M. Lumley
98	*Choristoneura retiniana* (Walsingham, 1879)	DQ792588	-	Roe & Sperling 2007	United States	California	Sierraville	-120.366	39.588	J. Powell

	Species and mitochondrial lineage	COI #	28 #	Reference	Country	Province/State	Collection Location	Longitude	Latitude	Collector
99	*Choristoneura retiniana* (Walsingham, 1879)	DQ792589	-	Roe & Sperling 2007	United States	Nevada	Mt. Charleston	-115.601	36.266	J. Powell & F. Sperling
100	*Choristoneura retiniana* (Walsingham, 1879)	DQ792590	-	Roe & Sperling 2007	United States	California	Tehachapi	-118.518	35.082	J. Powell & F. Sperling
101	*Choristoneura retiniana* (Walsingham, 1879)	HM223217	-	Lumley & Sperling 2011	United States	Nevada	Mt. Charleston	-115.601	36.266	J. Powell & F. Sperling
102	*Choristoneura retiniana* (Walsingham, 1879)	HM223218	-	Lumley & Sperling 2011	United States	California	Sierraville	-120.366	39.588	J. Powell

Newly sequenced specimens

Outgroup

	Species and mitochondrial lineage	COI #	28 #	Extraction #	Country	Province/State	Collection Location	Longitude	Latitude	Collector	Collection date

Tribe Archipini

	Species and mitochondrial lineage	COI #	28 #	Extraction #	Country	Province/State	Collection Location	Longitude	Latitude	Collector	Collection date
103	*Cudonigera houstonana* Grote, 1873	DAA	-	Sperling lab #10142	United States	Arizona	Chiricagua Mts	-109.355	32.009	J. Powell	31/07/1996
104	*Archips occidentalis* (Walsingham, 1891)	DAA	-	Sperling lab #10113	Tanzania	Morogoro	Udzungwa	7.848	36.976 S	J & W De Prins	19/05/2010
105	*Archips occidentalis* (Walsingham, 1891)	DAA	-	Sperling lab #11303	Tanzania	Morogoro	Uluguru	6.987	37.564 S	J & W De Prins	14/05/2010

Ingroup

Tribe Archipini

	Species and mitochondrial lineage	COI #	28 #	Extraction #	Country	Province/State	Collection Location	Longitude	Latitude	Collector	Collection date
108	*Choristoneura conflictana* (Walker, 1863)	DAA	DAA	Sperling lab #10987	United States	Utah	Park City, Summit Co.	-111.508	40.665	J. Dupuis	18/07/2014
109	*Choristoneura diversana* (Hubner, [1814-1817])	DAA	-	Sperling lab #10191	Denmark	Bornholm Island	Rutsker Højlyng	14.851	55.199	P. Falk	01/08/2015
110	*Choristoneura diversana* (Hubner, [1814-1817])	DAA	-	Sperling lab #10195	Denmark	Bornholm Island	Rutsker Højlyng	14.851	55.199	P. Falk	01/08/2015
111	*Choristoneura diversana* (Hubner, [1814-1817])	DAA	-	Sperling lab #10196	Denmark	Bornholm Island	Rutsker Højlyng	14.851	55.199	P. Falk	01/08/2015
112	*Choristoneura diversana* (Hubner, [1814-1817])	DAA	-	Sperling lab #11301	Japan	Honshu Island	Morioka	141.149	39.767	S. Suzuki	05/06/1981
113	*Choristoneura evanidana* (Kennel, 1901)	DAA	-	Sperling lab #10109	South Korea	Gangwon	Seokpo-ri	127.059	36.415	B.K. Byun	03/06/2012
114	*Choristoneura evanidana* (Kennel, 1901)	DAA	-	Sperling lab #10110	South Korea	Gangwon	Seokpo-ri	127.059	36.415	B.K. Byun	03/06/2012
115	*Choristoneura fractivittana* (Clemens, 1865)	DAA	-	Sperling lab #7469	United States	New York	Forest Home, Tompkins Co. Ithaca	-76.468	42.452	JJ. Dombroskie	02/06/2013
116	*Choristoneura fractivittana* (Clemens, 1865)	DAA	-	Sperling lab #7470	United States	New York	Forest Home, Tompkins Co. Ithaca	-76.468	42.452	JJ. Dombroskie	31/05/2013

	Species and mitochondrial lineage	GenBank COI #	GenBank 28S #	Extraction #	Country	Province/State	Collection Location	Longitude	Latitude	Collector	Collection date
119	*Choristoneura jezoensis* Yatsuda & Suzuki, 1980	DAA	-	Sperling lab #10992	Japan	Hokkaido Island	Bibai, Koshunai	141.857	43.282	H. Hara	31/05/2016
120	*Choristoneura jezoensis* Yatsuda & Suzuki, 1980	DAA	-	Sperling lab #10993	Japan	Hokkaido Island	Bibai, Koshunai	141.857	43.282	H. Hara	31/05/2016
121	*Choristoneura jezoensis* Yatsuda & Suzuki, 1980	DAA	-	Sperling lab #10995	Japan	Hokkaido Island	Bibai, Koshunai	141.857	43.282	H. Hara	31/05/2016
124	*Choristoneura luticostana* (Christoph, 1888)	DAA	-	Sperling lab #10108	South Korea	North Gyeongsang	Mt. Munsu, Bonghwa-gun	128.782	37.006	B.K. Byun	31/05/2012
125	*Choristoneura murinana* (Hübner, 1799)	DAA	DAA	Sperling lab #10188	Switzerland	Bern Canton.	Forêt de Tschugg	7.088	47.023	Rudolf Bryner	17/06/2015
126	*Choristoneura murinana* (Hübner, 1799)	DAA	DAA	Sperling lab #10146	France	Alsace	Guebwiller	7.208	47.91	Unavailable	01/05/1996
131	*Choristoneura rosaceana* (Harris, 1841)	DAA	DAA	Sperling lab #10081	Canada	Alberta	Red Lodge Provincial Park	-114.244	51.947	G. Fagua	20/07/2013
132	*Choristoneura simonyi* (Rebel, 1892)	DAA	-	Sperling lab #7479	Spain	Canary Island	Tenerife	-16.376	28.431	M. Baez	20/06/2013
106	*Choristoneura carnana* (Barnes & Busck, 1920)	DAA	-	Sperling lab #7486a	United States	California	Mokelumne River	-120.714	38.316	D. Rubinoff	26/07/1996
107	*Choristoneura carnana* (Barnes & Busck, 1920)	DAA	-	Sperling lab #7486b	United States	California	Mokelumne River	-120.714	38.316	D. Rubinoff	26/07/1996
	SBW										
117	*Choristoneura fumiferana* (Clemens, 1865)	DAA	-	NA	Canada	Ontario	-	-	-	-	-
118	*Choristoneura fumiferana* (Clemens, 1865)	DAA	DAA	Sperling lab #399	Canada	Alberta	Hawk Hills	-117.562	57.155	FIDS (Forest Insect and Disease Survey)	20/06/1991
122	*Choristoneura lambertiana* (Busck, 1915)	DAA	-	Sperling lab #7472	United States	Nevada	Sagehen Crk, Nevada Co.	-120.24	39.431	D. Rubinoff & F. Sperling	26/07/2013
123	*Choristoneura lambertiana* (Busck, 1915)	DAA	-	Sperling lab #7473	United States	Nevada	Sagehen Crk, Nevada Co.	-120.24	39.431	D. Rubinoff & F. Sperling	26/07/2013
127	*Choristoneura occidentalis biennis* (Freeman, 1967)	DAA	DAA	Nealis family # bibi10	Canada	British Columbia	Probably Fort Saint James or Ospika	-	-	V. Nealis	-
128	*Choristoneura occidentalis* Freeman 1963	DAA	DAA	NA	Canada	British Columbia	Probably Nicola Valley near Merritt	-	-	V. Nealis and R. Turnquist	1999
129	*Choristoneura occidentalis* Freeman 1963	DAA	DAA	Sperling lab #3634	United Sates	Montana	Bitterroot, Beaverland Co.	-113.708	45.652	L. Lumley	04/07/2007
130	*Choristoneura pinus* (Harris, 1841)	DAA	DAA	NA	Canada	Nova Scotia	Fourth Lake, Digby Co.	-65.641	44.346	Nova Scotia Dpt. of Natural Resources	NA

Appendix 4.3. General alignment of sequences for each taxon included in Chapter 4 (Digital file).

Appendix 4.4. Tortricinae species included in Chapter 4 and their biogeographical distribution by presence (1) or absence (0).

Areas of distribution: WP = West Palearctic, EP = East Palearctic, WN = West Nearctic, EN = East Nearctic, NT = Neotropics, AF = Africa+Madagascar, IN = India, SA = Southeast Asia, AU = Australasia. Distributions are from Brown (2005), Gilligan et al. (2014) and Schmidt et al. (2010).

Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Acleris fimbriana	1	1	0	0	0	0	0	0	0
Acropolitis hedista	0	0	0	0	0	0	0	0	1
Adoxophyes negundana	0	0	0	1	0	0	0	0	0
Adoxophyes orana	1	1	0	0	0	0	0	0	0
Adoxophyes honmai	0	1	0	0	0	0	0	0	0
Adoxophyes orana	1	1	0	0	0	0	0	0	0
Aphelia alleniana	0	0	0	1	0	0	0	0	0
Aphelia unitana	1	0	0	0	0	0	0	0	0
Archips alberta	0	0	0	1	0	0	0	0	0
Archips cerasivorana	0	0	1	1	0	0	0	0	0
Archips eleagnana	0	0	0	1	0	0	0	0	0
Archips fervidana	0	0	0	1	0	0	0	0	0
Archips negundana	0	0	1	1	0	0	0	0	0
Archips packardiana	0	0	1	1	0	0	0	0	0
Archips podana	1	0	0	0	0	0	0	0	0
Archips purpurana	0	0	0	1	0	0	0	0	0
Archips rosana	1	1	0	0	0	0	0	0	0
Archips striana	0	0	1	1	0	0	0	0	0
Archips xylosteana	1	1	0	0	0	0	0	0	0
Archepandemis coniferana	0	0	1	0	0	0	0	0	0
Argyrotaenia alisellana	0	0	0	1	0	0	0	0	0

Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Argyrotaenia coloradana	0	0	1	0	0	0	0	0	0
Argyrotaenia dorsalana	0	0	1	0	0	0	0	0	0
Argyrotaenia floridana	0	0	0	1	0	0	0	0	0
Argyrotaenia graceana	0	0	1	0	0	0	0	0	0
Argyrotaenia kimballi	0	0	0	1	0	0	0	0	0
Argyrotaenia lautana	0	0	1	0	0	0	0	0	0
Argyrotaenia occultana	0	0	1	1	0	0	0	0	0
Argyrotaenia provana	0	0	1	0	0	0	0	0	0
Argyrotaenia repertana	0	0	1	1	0	0	0	0	0
Argyrotaenia tabulana	0	0	0	1	0	0	0	0	0
Atelodora pelochytana	0	0	0	0	0	0	0	0	1
Choristoneura occidentalis	0	0	1	0	0	0	0	0	0
Cacoecimorpha pronubana	1	0	0	0	0	0	0	0	0
Choristoneura carnana	0	0	1	0	0	0	0	0	0
Cerace sp.	0	0	0	0	0	0	0	1	0
Choristoneura albaniana	1	1	1	1	0	0	0	0	0
Choristoneura argentifasciata	0	0	0	1	0	0	0	0	0
Choristoneura o. biennis	0	0	1	0	0	0	0	0	0
Choristoneura o. biennis	0	0	1	0	0	0	0	0	0
Choristoneura carnana	0	0	1	0	0	0	0	0	0
Choristoneura conflictana	0	0	1	1	0	0	0	0	0
Choristoneura conflictana	0	0	1	1	0	0	0	0	0
Choristoneura evanidana	0	1	0	0	0	0	0	0	0
Choristoneura evanidana	0	1	0	0	0	0	0	0	0
Choristoneura fumiferana	0	0	0	1	0	0	0	0	0
Choristoneura fractivittana	0	0	1	1	0	0	0	0	0
Choristoneura fractivittana	0	0	1	1	0	0	0	0	0
Choristoneura fumiferana	0	0	0	1	0	0	0	0	0
Choristoneura fumiferana	0	0	0	1	0	0	0	0	0
Choristoneura hebenstreitella	1	0	0	0	0	0	0	0	0

Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Choristoneura longicellana	0	1	0	0	0	0	0	0	0
Choristoneura luticostana	0	1	0	0	0	0	0	0	0
Choristoneura murinana	1	1	0	0	0	0	0	0	0
Choristoneura occidentalis	0	0	1	0	0	0	0	0	0
Choristoneura occidentalis	0	0	1	0	0	0	0	0	0
Choristoneura orae	0	0	1	0	0	0	0	0	0
Choristoneura parallela	0	0	1	1	0	0	0	0	0
Choristoneura pinus	0	0	0	1	0	0	0	0	0
Choristoneura pinus	0	0	0	1	0	0	0	0	0
Choristoneura rosaceana	0	0	1	1	0	0	0	0	0
Choristoneura rosaceana	0	0	1	1	0	0	0	0	0
Choristoneura simonyi	1	0	0	0	0	0	0	0	0
Choristoneura zapulata	0	0	1	1	0	0	0	0	0
Clepsis anderslaneyii	0	0	1	0	0	0	0	0	0
Clepsis clemensiana	0	0	1	1	0	0	0	0	0
Clepsis fucana	0	0	1	0	0	0	0	0	0
Clepsis melaleucana	0	0	0	1	0	0	0	0	0
Clepsis penetralis	0	0	1	1	0	0	0	0	0
Clepsis peritana	0	0	0	1	0	0	0	0	0
Clepsis persicana	0	0	1	1	0	0	0	0	0
Clepsis rurinana	1	1	0	0	0	0	0	0	0
Clepsis spectrana	1	0	0	0	0	0	0	0	0
Clepsis virescana	0	0	1	1	0	0	0	0	0
Choristoneura murinana	1	1	0	0	0	0	0	0	0
Cornuticlava aritrana	0	0	0	0	0	0	0	0	1
Cryptoptila australana	0	0	0	0	0	0	0	0	1
Cudonigera houstonana	0	0	1	1	0	0	0	0	0
Cudonigera houstonana	0	0	1	1	0	0	0	0	0
Dichelia histrionana	1	0	0	0	0	0	0	0	0
Diedra intermontana	0	0	1	0	0	0	0	0	0

Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Ditula angustiorana	1	0	0	0	0	0	0	0	0
Choristoneura diversana	1	1	0	0	0	0	0	0	0
Choristoneura diversana	1	1	0	0	0	0	0	0	0
Choristoneura diversana	1	1	0	0	0	0	0	0	0
Choristoneura diversana	1	1	0	0	0	0	0	0	0
Epagoge grotiana	1	0	0	0	0	0	0	0	0
Epiphyas ashworthana	0	0	0	0	0	0	0	0	1
Epiphyas postvittana	0	0	0	0	0	0	0	0	1
Epiphyas caryotis	0	0	0	0	0	0	0	0	1
Epiphyas postvittana	0	0	0	0	0	0	0	0	1
Epitymbia alaudana	0	0	0	0	0	0	0	0	1
Homona aestivana	0	0	0	0	0	0	0	1	1
Homona auriga	0	0	0	0	0	0	0	0	1
Homona mermerodes	0	0	0	0	0	0	0	0	1
Homona salaconis	0	0	0	0	0	0	0	1	1
Homona spargotis	0	0	0	0	0	0	0	0	1
Homona trachyptera	0	0	0	0	0	0	0	0	1
Choristoneura jezoensis	0	1	0	0	0	0	0	0	0
Choristoneura jezoensis	0	1	0	0	0	0	0	0	0
Choristoneura jezoensis	0	1	0	0	0	0	0	0	0
Choristoneura lambertiana	0	0	1	0	0	0	0	0	0
Choristoneura lambertiana	0	0	1	0	0	0	0	0	0
Lozotaenia hesperia	0	0	0	1	0	0	0	0	0
Lozotaeniodes cupressana	1	0	0	0	0	0	0	0	0
Pandemis canadana	0	0	0	1	0	0	0	0	0
Pandemis cerasana	1	1	0	0	0	0	0	0	0
Pandemis cinnamomeana	1	1	0	0	0	0	0	0	0
Pandemis corylana	0	0	1	1	0	0	0	0	0
Pandemis dumetana	1	0	0	0	0	0	0	0	0
Pandemis heparana	1	1	0	0	0	0	0	0	0

Species	WP	EP	WN	EN	NT	AF	IN	SA	AU
Pandemis lamprosana	0	0	0	1	0	0	0	0	0
Pandemis limitata	0	0	1	1	0	0	0	0	0
Pandemis pyrusana	0	0	1	0	0	0	0	0	0
Proselena tenella	0	0	0	0	0	0	0	0	1
Ptycholomoides aeriferana	0	1	0	0	0	0	0	0	0
Ptycholoma lecheana	1	1	0	0	0	0	0	0	0
Choristoneura retiniana	0	0	1	0	0	0	0	0	0
Choristoneura retiniana	0	0	1	0	0	0	0	0	0
Choristoneura retiniana	0	0	1	0	0	0	0	0	0
Choristoneura retiniana	0	0	1	0	0	0	0	0	0
Choristoneura retiniana	0	0	1	0	0	0	0	0	0
Syndemis afflictana	0	0	1	1	0	0	0	0	0
Archips occidentalis	0	0	0	0	0	1	0	0	0
Archips occidentalis	0	0	0	0	0	1	0	0	0
Xenotemna pallorana	0	0	1	1	0	0	0	0	0

Appendix 4.5. Connectivity matrices through time in Chapter 4.

Column headings identify biogeographical regions: WP = West Palearctic, EP = East Palearctic, WN = West Nearctic, EN = East Nearctic, NT = Neotropics, AF = Africa+Madagascar, IN = India, SA = Southeast Asia, and AU = Australasia. Rows are arranged in the same order. Number 1 indicates connectivity. The first time period is an artifact to permit initiation of runs in the time stratified analysis.

```
0-0.25 Mya
WP      EP      WN      EN      NT      AF      IN      SA      AU
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1
1       1       1       1       1       1       1       1       1

0.25-5.33 Mya
WP      EP      WN      EN      NT      AF      IN      SA      AU
1       1       0       0       0       1       0       0       0
1       1       1       0       0       0       1       1       0
0       1       1       1       0       0       0       0       0
0       0       1       1       0       0       0       0       0
0       0       0       0       1       0       0       0       0
1       0       0       0       0       1       0       0       0
0       1       0       0       0       0       1       1       0
0       1       0       0       0       0       1       1       1
0       0       0       0       0       0       0       1       1

5.33-23.03 Mya
WP      EP      WN      EN      NT      AF      IN      SA      AU
1       1       0       0       0       1       0       0       0
1       1       1       0       0       0       1       1       0
0       1       1       1       0       0       0       0       0
0       0       1       1       0       0       0       0       0
0       0       0       0       1       0       0       0       0
1       0       0       0       0       1       1       0       0
0       1       0       0       0       1       1       1       0
0       1       0       0       0       0       1       1       0
0       0       0       0       0       0       0       0       1
```

```
23.03-33.9 Mya
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    1    0    0    0    1    0    0    0
1    1    1    0    0    0    1    1    0
0    1    1    1    0    0    0    0    0
0    0    1    1    0    0    0    0    0
0    0    0    0    1    0    0    0    0
1    0    0    0    0    1    0    0    0
0    1    0    0    0    0    1    1    0
0    1    0    0    0    0    1    1    0
0    0    0    0    0    0    0    0    1

33.9-56 Mya
WP   EP   WN   EN   NT   AF   IN   SA   AU
1    0    0    1    0    0    0    0    0
0    1    1    0    0    0    1    1    0
0    1    1    1    0    0    0    0    0
1    0    1    1    0    0    0    0    0
0    0    0    0    1    0    0    0    1
0    0    0    0    0    1    0    0    0
0    1    0    0    0    0    1    1    0
0    1    0    0    0    0    1    1    0
0    0    0    0    1    0    0    0    1
```

Appendix 4.6. Comparison using Bayes factors on the relationships of competing topologies of phylogenetic relationships of *Choristoneura*.

Topologies presented in Fig. 4.1 vs Fig. 4.2 in the main text.

```
Model 1: analysis of performed without constraints (Fig. 4.1).
Model 2: analysis constraining C. albaniana as the sister group
of Choristoneura (Fig. 4.2).


Absolute differences between Harmonic means of Model 1 - Model 2
31079.33 - 31065.46: **13.87



Absolute differences between Marginal likelihood means estimated
using stepping-stone sampling of Model 1 - Model 2
31615.85 - 31578.01: **37.84

**Difference above 10 are considered very strong evidence
in favor of the better model (higest likelihood value: Model 2)
We accepted the model including C. albaniana as the sister group
of Choristoneura (Fig. 4.2)


Model 1 (Fig. 4.1)

Estimated marginal likelihoods for runs sampled in files

      Run    Arithmetic mean    Harmonic mean
      --------------------------------------
       1       -30975.28          -31065.03
       2       -30971.43          -31080.03
      --------------------------------------
      TOTAL   -30972.11          -31079.33
      --------------------------------------


Marginal likelihood (in natural log units) estimated using stepping-
stone sampling based on
   100 steps with 1000 generations (1 samples) within each step.

      Run    Marginal likelihood (ln)
      ----------------------------
       1     -31838.94
       2     -31615.16
      ----------------------------
      Mean:  -31615.85
```

Model 2 (Fig. 4.2)

Estimated marginal likelihoods for runs sampled in files

```
     Run    Arithmetic mean    Harmonic mean
     ---------------------------------------
      1       -30972.88          -31066.16
      2       -30969.70          -31055.71
     ---------------------------------------
     TOTAL   -30970.35          -31065.46
     ---------------------------------------
```

Marginal likelihood (in natural log units) estimated using stepping-stone sampling based on
   100 steps with 1000 generations (1 samples) within each step.

```
     Run    Marginal likelihood (ln)
     ----------------------------
      1      -31798.70
      2      -31577.32
     ----------------------------
     Mean:  -31578.01
```

Appendix 4.7. Putative ancestral areas tested using six models for Archipini and *Choristoneura* using BioGeoBEARS 0.2.5.

Ancestral states = global optimum. Areas maximum = 9. Colored boxes identify biogeographical regions: WP = West Palearctic, EP = East Palearctic, WN = West Nearctic, EN = East Nearctic, NT = Neotropics, AF = Africa+Madagascar, IN = India, SA = Southeast Asia, and AU = Australasia. Species distributions with more than one area have combined letters for biogeographical regions and alternate color boxes.

BioGeoBEARS DEC+J on 126spp_strat M1_stratified
ancstates: global optim, 9 areas max. d=0.0158; e=0; j=0.0243; LnL=-312.23

Choristoneura occidentalis Canada, AB
Choristoneura occidentalis Canada, BC
Choristoneura lambertiana USA, CA
Choristoneura biennis Canada, AB
Choristoneura orae Canada, BC
Choristoneura pinus Canada, NS
Choristoneura pinus Canada, AB
Choristoneura retiniana USA, CA
Choristoneura lambertiana USA, CA
Choristoneura carnana USA, CA
Choristoneura carnana USA, CA
Choristoneura retiniana USA, NV
Choristoneura retiniana USA, NV
Choristoneura occidentalis USA, MT
Choristoneura retiniana USA, CA
Choristoneura retiniana USA, CA
Choristoneura o. biennis Canada, BC
Choristoneura fumiferana Canada, ON
Choristoneura fumiferana Canada, AB
Choristoneura fumiferana Canada, AB
Choristoneura rosaceana Canada, AB
Choristoneura rosaceana USA, VA
Choristoneura zapulata Canada, AB
Choristoneura paralella USA, FL
Cudonigera houstonana USA, AR
Cudonigera houstonana USA, AZ
Choristoneura argentifasciata USA, FL
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
Choristoneura diversana Japan, Honshu
Choristoneura diversana Denmark, Bornholm
Choristoneura diversana Denmark, Bornholm
Choristoneura diversana Denmark, Bornholm
Choristoneura murinana France, Alsace
Choristoneura murinana Switzerland, Tschugg
Choristoneura conflictana Canada, AB
Choristoneura conflictana USA, UT
Choristoneura fractivittana USA, NY
Choristoneura fractivittana USA, NY
Choristoneura hebenstreitella Denmark, Copenhagen
Choristoneura luticostana South Korea, N. Gyeongsang
Choristoneura longicellana China, Beijing Municipality
Choristoneura albaniana Russia, Altai
Xenotemna pallorana
Choristoneura simonyi Canary Island*
Archips occidentalis Tanzania, Udzungwa*
Archips occidentalis Tanzania, Uruguru*
Cacoecimorpha pronubana Spain, Catalonia
Archips negundana
Archips eleagnana
Archips xylosteana
Archips rosana
Archips fervidana
Archips cerasivorana
Archips packardiana
Archips alberta
Archips striana
Archips podana
Choristoneura evanidana South Korea, Gangwon*
Choristoneura evanidana South Korea, Gangwon*
Archips purpurana
Syndemis afflictana
Dichelia histrionana
Aphelia unitana
Lozotaenia hesperia
Aphelia alleniana
Argyrotaenia kimballi
Argyrotaenia floridana
Argyrotaenia tabulana
Argyrotaenia occultana
Argyrotaenia repertana
Argyrotaenia provana
Argyrotaenia coloradana
Argyrotaenia dorsalana
Argyrotaenia lautana
Argyrotaenia graceana
Diedra intermontana
Argyrotaenia alisellana
Ptycholoma lecheana
Ptycholomoides aeriferanus
Pandemis limitata
Pandemis canadana
Pandemis pyrusana
Pandemis lamprosana
Pandemis cerasana
Pandemis heparana
Archepandemis coniferana
Pandemis dumetana
Pandemis cinnamomeana
Pandemis corylana
Clepsis persicana
Clepsis spectrana
Clepsis melaleucana
Clepsis clemensiana
Clepsis rurinana
Epiphyas postvittana
Epiphyas postvittana
Epiphyas caryotis
Epiphyas ashworthana
Clepsis fucana
Clepsis penetralis
Clepsis peritana
Clepsis virescana
Clepsis anderslaneyii
Adoxophyes negundana
Lozotaenoides cupressana
Homona mermerodes
Homona aestivana
Homona auriga
Homona salaconis
Homona trachyptera
Homona spargotis
Cryptoptila australana
Adoxophyes orana
Adoxophyes orana
Adoxophyes honmai
Ditula angustiorana
Acropolitis hedista
Epagoge grotiana
Cerace sp.
Acleris fimbriana
Atelodora pelochytana
Proselena tenella
Cornuticlava aritrana
Epitymbia alaudana

Choristoneura

Time (Ma)

| 50 | 40 | 30 | 20 | 10 | 0 |

| EOCENE | OLIGOCENE | MIOCENE | PLIO. | QUA. |

WN   EN   NT   WP   EP   AF   IN   SA   AU

BioGeoBEARS BAYAREALIKE on 126_species M1_stratified
ancstates: global optim, 9 areas max, d=0.0367; e=0.0582; j=0; LnL=-388.20

Choristoneura occidentalis Canada, AB
Choristoneura occidentalis Canada, BC
Choristoneura lambertiana USA, CA
Choristoneura biennis Canada, AB
Choristoneura orae Canada, BC
Choristoneura pinus Canada, NS
Choristoneura pinus Canada, AB
Choristoneura retiniana USA, CA
Choristoneura lambertiana USA, CA
Choristoneura carnana USA, CA
Choristoneura carnana USA, CA
Choristoneura retiniana USA, NV
Choristoneura retiniana USA, NV
Choristoneura occidentalis USA, MT
Choristoneura retiniana USA, CA
Choristoneura retiniana USA, CA
Choristoneura o. biennis USA, BC
Choristoneura fumiferana Canada, ON
Choristoneura fumiferana Canada, AB
Choristoneura fumiferana Canada, AB
Choristoneura rosaceana Canada, AB
Choristoneura rosaceana USA, VA
Choristoneura zapulata Canada, AB
Choristoneura paralella USA, FL
Cudonigera houstonana USA, AR
Cudonigera houstonana USA, AZ
Choristoneura argentifasciata USA, FL
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
Choristoneura diversana Japan, Honshu
Choristoneura diversana Denmark, Bornholm
Choristoneura diversana Denmark, Bornholm
Choristoneura diversana Denmark, Bornholm
Choristoneura murinana France, Alsace
Choristoneura murinana Switzerland, Tschugg
Choristoneura conflictana Canada, AB
Choristoneura conflictana USA, UT
Choristoneura fractivittana USA, NY
Choristoneura fractivittana USA, NY
Choristoneura hebenstreitella Denmark, Copenhagen
Choristoneura luticostana South Korea, N. Gyeongsang
Choristoneura longicellana China, Beijing Municipality
Choristoneura albaniana Russia, Altai
Xenotemna pallorana
Choristoneura simonyi Canary Island*
Archips occidentalis Tanzania, Udzungwa*
Archips occidentalis Tanzania, Uruguru*
Cacoecimorpha pronubana Spain, Catalonia
Archips negundana
Archips eleagnana
Archips xylosteana
Archips rosana
Archips fervidana
Archips cerasivorana
Archips packardiana
Archips alberta
Archips striana
Archips podana
Choristoneura evanidana South Korea, Gangwon*
Choristoneura evanidana South Korea, Gangwon*
Archips purpurana
Syndemis afflictana
Dichelia histrionana
Aphelia unitana
Lozotaenia hesperia
Aphelia alleniana
Argyrotaenia kimballi
Argyrotaenia floridana
Argyrotaenia tabulana
Argyrotaenia occultana
Argyrotaenia repertana
Argyrotaenia provana
Argyrotaenia coloradana
Argyrotaenia dorsalana
Argyrotaenia lautana
Argyrotaenia graceana
Diedra intermontana
Argyrotaenia alisellana
Ptycholoma lecheana
Ptycholomoides aeriferanus
Pandemis limitata
Pandemis canadana
Pandemis pyrusana
Pandemis lamprosana
Pandemis cerasana
Pandemis heparana
Archepandemis coniferana
Pandemis dumetana
Pandemis cinnamomeana
Pandemis corylana
Clepsis persicana
Clepsis spectrana
Clepsis melaleucana
Clepsis clemensiana
Clepsis rurinana
Epiphyas postvittana
Epiphyas postvittana
Epiphyas caryotis
Epiphyas ashworthana
Clepsis fucana
Clepsis penetralis
Clepsis peritana
Clepsis virescana
Clepsis anderslaneyii
Adoxophyes negundana
Lozotaenoides cupressana
Homona mermerodes
Homona aestivana
Homona auriga
Homona salaconis
Homona trachyptera
Homona spargotis
Cryptoptila australana
Adoxophyes orana
Adoxophyes orana
Adoxophyes honmai
Ditula angustiorana
Acropolitis hedista
Epagoge grotiana
Cerace sp.
Acleris fimbriana
Atelodora pelochytana
Proselena tenella
Cornuticlava aritrana
Epitymbia alaudana

Choristoneura

Time (Ma)

50   40   30   20   10   0

| EOCENE | OLIGOCENE | MIOCENE | PLIO. | QUA. |

| WN | EN | NT | WP | EP | AF | IN | SA | AU |

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BioGeoBEARS DIVALIKE on 126sp M1_stratified
ancstates: global optim, 9 areas max. d=0.0403; e=0.0309; j=0; LnL=-446.85

Choristoneura occidentalis Canada, AB
Choristoneura occidentalis Canada, BC
Choristoneura lambertiana USA, CA
Choristoneura biennis Canada, AB
Choristoneura orae Canada, BC
Choristoneura pinus Canada, NS
Choristoneura pinus Canada, AB
Choristoneura retiniana USA, CA
Choristoneura lambertiana USA, CA
Choristoneura carnana USA, CA
Choristoneura carnana USA, CA
Choristoneura retiniana USA, NV
Choristoneura retiniana USA, NV
Choristoneura occidentalis USA, MT
Choristoneura retiniana USA, CA
Choristoneura retiniana USA, CA
Choristoneura o. biennis Canada, BC
Choristoneura fumiferana Canada, ON
Choristoneura fumiferana Canada, AB
Choristoneura fumiferana Canada, AB
Choristoneura rosaceana Canada, AB
Choristoneura rosaceana USA, VA
Choristoneura zapulata Canada, AB
Choristoneura paraliella USA, FL
Cudonigera houstonana USA, AR
Cudonigera houstonana USA, AZ
Choristoneura argentifasciata USA, FL
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
Choristoneura diversana Japan, Honshu
Choristoneura diversana Denmark, Bornholm
Choristoneura diversana Denmark, Bornholm
Choristoneura murinana France, Alsace
Choristoneura murinana Switzerland, Tschugg
Choristoneura conflictana Canada, AB
Choristoneura conflictana USA, UT
Choristoneura fractivittana USA, NY
Choristoneura fractivittana USA, NY
Choristoneura hebenstreitella Denmark, Copenhagen
Choristoneura luticostana South Korea, N. Gyeongsang
Choristoneura longicellana China, Beijing Municipality
Choristoneura albaniana Russia, Altai
Xenotemna pallorana
Choristoneura simonyi Canary Island*
Archips occidentalis Tanzania, Udzungwa*
Archips occidentalis Tanzania, Uruguru*
Cacoecimorpha pronubana Spain, Catalonia
Archips negundana
Archips eleagnana
Archips xylosteana
Archips rosana
Archips fervidana
Archips cerasivorana
Archips packardiana
Archips alberta
Archips striana
Archips podana
Choristoneura evanidana South Korea, Gangwon*
Choristoneura evanidana South Korea, Gangwon*
Archips purpurana
Syndemis afflictana
Dichelia histrionana
Aphelia unitana
Lozotaenia hesperia
Aphelia alleniana
Argyrotaenia kimballi
Argyrotaenia floridana
Argyrotaenia tabulana
Argyrotaenia occultana
Argyrotaenia repertana
Argyrotaenia provana
Argyrotaenia coloradana
Argyrotaenia dorsalana
Argyrotaenia lautana
Argyrotaenia graceana
Diedra intermontana
Argyrotaenia alisellana
Ptycholoma lecheana
Ptycholomoides aeriferanus
Pandemis limitata
Pandemis canadana
Pandemis pyrusana
Pandemis lamprosana
Pandemis cerasana
Pandemis heparana
Archepandemis coniferana
Pandemis dumetana
Pandemis cinnamomeana
Pandemis corylana
Clepsis persicana
Clepsis spectrana
Clepsis melaleucana
Clepsis clemensiana
Clepsis rurinana
Epiphyas postvittana
Epiphyas postvittana
Epiphyas caryotis
Epiphyas ashworthana
Clepsis fucana
Clepsis penetralis
Clepsis peritana
Clepsis virescana
Clepsis anderslaneyii
Adoxophyes negundana
Lozotaenoides cupressana
Homona mermerodes
Homona aestivana
Homona auriga
Homona salaconis
Homona trachyptera
Homona spargotis
Cryptoptila australana
Adoxophyes orana
Adoxophyes orana
Adoxophyes honmai
Ditula angustiorana
Acropolitis hedista
Epagoge grotiana
Cerace sp.
Acleris fimbriana
Atelodora pelochytana
Proselena tenella
Cornuticlava aritrana
Epitymbia alaudana

Choristoneura

Time (Ma)

| EOCENE | OLIGOCENE | MIOCENE | PLIO. | QUA. |

WN EN NT WP EP AF IN SA AU

BioGeoBEARS DEC on 56genustrat M1_stratified
ancstates: global optim, 9 areas max. d=0.0373; e=0.0327; j=0; LnL=-423.91

Choristoneura occidentalis Canada, AB
Choristoneura occidentalis Canada, BC
Choristoneura lambertiana USA, CA
Choristoneura biennis Canada, AB
Choristoneura orae Canada, BC
Choristoneura pinus Canada, NS
Choristoneura pinus Canada, AB
Choristoneura retiniana USA, CA
Choristoneura lambertiana USA, CA
Choristoneura carnana USA, CA
Choristoneura carnana USA, CA
Choristoneura retiniana USA, NV
Choristoneura retiniana USA, NV
Choristoneura occidentalis USA, MT
Choristoneura retiniana USA, CA
Choristoneura retiniana USA, CA
Choristoneura o. biennis Canada, BC
Choristoneura fumiferana Canada, ON
Choristoneura fumiferana Canada, AB
Choristoneura fumiferana Canada, AB
Choristoneura fumiferana Canada, AB
Choristoneura rosaceana Canada, AB
Choristoneura rosaceana USA, VA
Choristoneura zapulata Canada, AB
Cudonigera houstonana USA, AR
Cudonigera houstonana USA, AZ
Choristoneura paralella USA, FL
Choristoneura argentifasciata USA, FL
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
Choristoneura jezoensis Japan, Hokkaido
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Choristoneura diversana Denmark, Bornholm
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Choristoneura diversana Denmark, Bornholm
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Choristoneura fractivittana USA, NY
Choristoneura hebenstreitella Denmark, Copenhagen
Choristoneura luticostana South Korea, N. Gyeongsang
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Archips occidentalis Tanzania, Uruguru*
Cacoecimorpha pronubana Spain, Catalonia
Archips negundana
Archips eleagnana
Archips xylosteana
Archips rosana
Archips fervidana
Archips cerasivorana
Archips packardiana
Archips alberta
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Archips podana
Choristoneura evanidana South Korea, Gangwon*
Choristoneura evanidana South Korea, Gangwon*
Archips purpurana
Syndemis afflictana
Dichelia histrionana
Aphelia unitana
Lozotaenia hesperia
Aphelia alleniana
Argyrotaenia kimballi
Argyrotaenia floridana
Argyrotaenia tabulana
Argyrotaenia occultana
Argyrotaenia repertana
Argyrotaenia provana
Argyrotaenia coloradana
Argyrotaenia dorsalana
Argyrotaenia lautana
Argyrotaenia graceana
Diedra intermontana
Argyrotaenia alisellana
Ptycholoma lecheana
Ptycholomoides aeriferanus
Pandemis limitata
Pandemis canadana
Pandemis pyrusana
Pandemis lamprosana
Pandemis cerasana
Pandemis heparana
Archepandemis coniferana
Pandemis dumetana
Pandemis cinnamomeana
Pandemis corylana
Clepsis persicana
Clepsis spectrana
Clepsis melaleucana
Clepsis clemensiana
Clepsis rurinana
Epiphyas postvittana
Epiphyas postvittana
Epiphyas caryotis
Epiphyas ashworthana
Clepsis fucana
Clepsis penetralis
Clepsis peritana
Clepsis virescana
Clepsis anderslaneyii
Adoxophyes negundana
Lozotaenoides cupressana
Homona mermerodes
Homona aestivana
Homona auriga
Homona salaconis
Homona trachyptera
Homona spargotis
Cryptoptila australana
Adoxophyes orana
Adoxophyes orana
Adoxophyes honmai
Ditula angustiorana
Acropolitis hedista
Epagoge grotiana
Cerace sp.
Acleris fimbriana
Atelodora pelochytana
Proselena tenella
Cornuticlava aritrana
Epitymbia alaudana

Choristoneura

Time (Ma)

| 50 | 40 | 30 | 20 | 10 | 0 |

| EOCENE | OLIGOCENE | MIOCENE | PLIO. | QUA. |

| WN | EN | NT | WP | EP | AF | IN | SA | AU |

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Supplementary material.

Table A.3.1. Primers designed to verify mitogenome sequences in Chapter 3. Numbers after the acronym (TortMtg) identify the starting position of each couple of oligonucleotides (5'-3'), defined against the mitogenome of *Choristoneura longicellana* (HQ452340, Wu et al. 2016). (Tm) melting temperature.

	Primer name and position	Oligo sequence	Tm	Fragment length
1	TortMtg-652F	5- CCC ATA ATT TTAYTG TCA TA -3	43.5 °C	591
	TortMtg-652R	5- AAG GTT CTA RTA ATT ATT CC -3	42.9 °C	
2	TortMtg-1193F	5- TTT TTATCT CTA GGA GGAY -3	44.7 °C	524
	TortMtg-1193R	5- GTT CCA ATATCC TTATGA TT -3	44.6 °C	
3	TortMtg-3920F	5- TAC CAATTG TAATTG AAA GA -3	44.3 °C	557
	TortMtg-3920R	5- ATT TGT TCC TARTAA GGTTT -3	45.3 °C	
4	TortMtg-6950R	5- AAATTATTG CTT TAT CAA CA -3	43 °C	600
	TortMtg-6950F	5- CCY ATT AAT ATT CCT AAA ATT C -3	43.4 °C	
5	TortMtg-8057F	5- GAT ACT AAY CCY AAA CCATC -3	47.4 °C	593
	TortMtg-8057R	5- AYT CYC AAC ATG GWA AAT AT -3	46.5 °C	
6	TortMtg-10183F	5- ATA AAC CAT CCT TTATCA AT -3	43.9 °C	588
	TortMtg-10183R	5- TTC ATC AAGTRG AAATAT TA -3	42.3 °C	
7	TortMtg-12310F	5- CCT GAA ACT AAT TCT CTT TC -3	45.8 °C	597
	TortMtg-12310R	5- TAG GRGTTT TAATTG GRGTT -3	48.7 °C	
8	TortMtg-13152F	5- ATATTT GAT CCT TTC GTA CT -3	46 °C	595
	TortMtg-13152R	5- TAATTG GTG ACT TGT ATG AA -3	46.4 °C	
9	TortMtg-13570F	5- TCA TAC AAGTCA CCA ATT AA -3	46.4 °C	571
	TortMtg-13570R	5- AAA AAT TTA CTG TAG CAA AA -3	43.4 °C	
10	TortMtg-14090F	5- ATT AAA GCT TAT CCCTTA AY -3	44.2 °C	551
	TortMtg-14090R	5- TGA AAT AAGTCG TAA CAA AG -3	45.5 °C	
11	TortdMtg-14913F	5- GGC ACA AAATTT GTT ATT -3	43.5 °C	811
	TortdMtg-14913R	5- TAY CCT ATC AGA ATA ATC CT -3	45.3 °C	
12	TortdMtg-14914AF	5- GCA CAA AAT TTG TTATTA AT -3	42.5 °C	502
	TortdMtg-14914AR	5- AGC AAATGT AAT TTT CAATA -3	43 °C	
13	TortdMtg-15561BF	5- TGA AAATTA CAT TTG CTATT -3	43 °C	600
	TortdMtg-15561BR	5- GGG ATA AAA CTC AAT AAATT -3	43 °C	

Figure A.3.1. Secondary structure of the large ribosomal RNA (16S) of *Choristoneura fumiferana* and *Choristoneura longicellana* obtained using MITOS.

16S *Choristoneura fumiferana* <u>East f</u>

16S *Choristoneura longicellana*
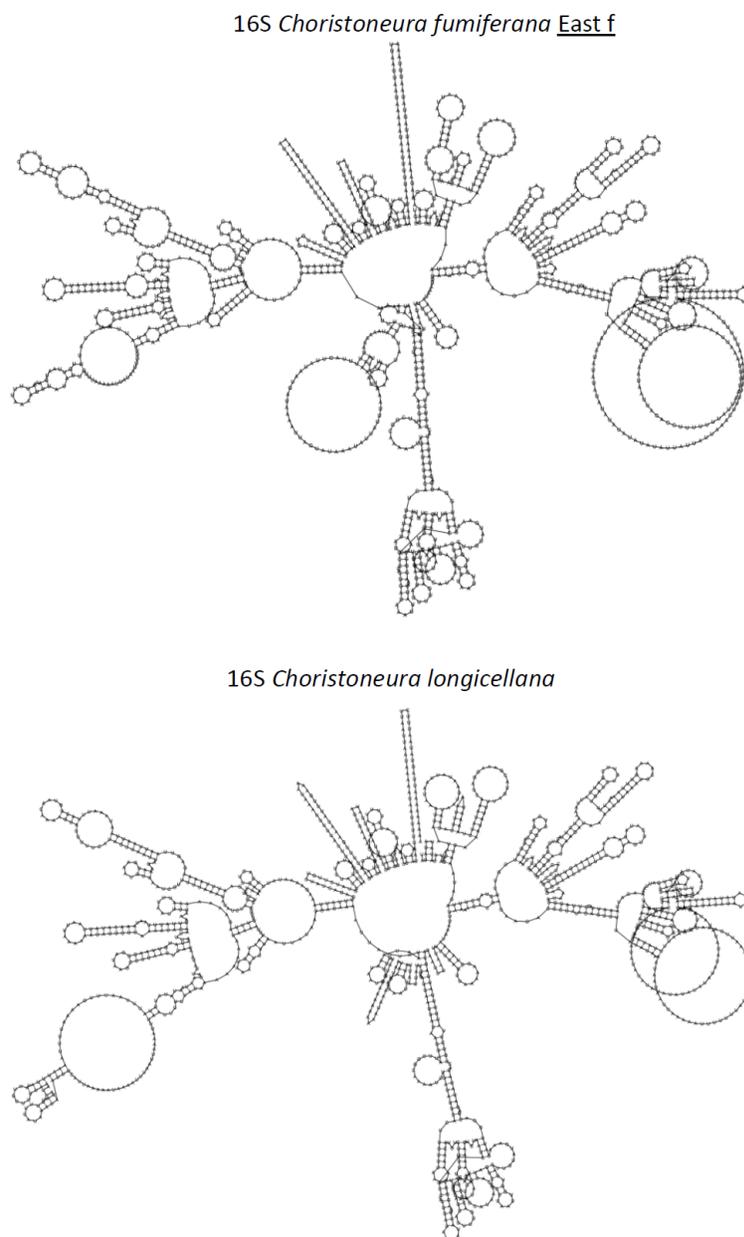
Figure A.3.1. Secondary structure of the large ribosomal RNA (16S) of *Choristoneura fumiferana* and *Choristoneura longicellana* obtained using MITOS WebServer (Bertn et al. 2013).

Figure A.4.1. Selected topology of 24 equally parsimonious trees of the genus *Choristoneura* and Archipini using maximum parsimony analysis (PAUP 4.0b).
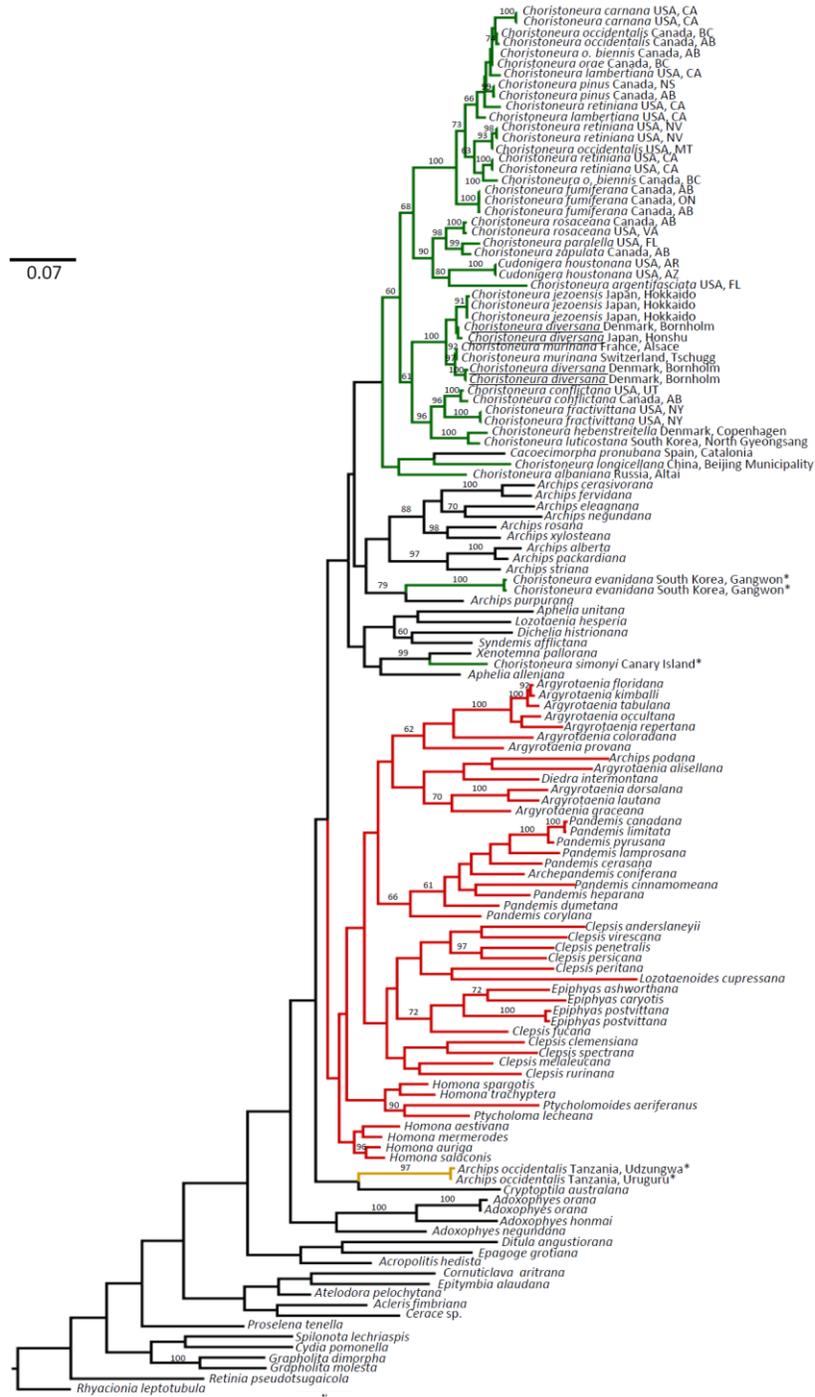
Figure A.4.1. Selected topology of 24 equally parsimonious trees of the genus *Choristoneura* and Archipini using maximum parsimony analysis (PAUP 4.0b). Changes between the 24 topologies were circumscribed to the red branches. (*legend Fig. A.4.1. continues next page*)

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Length = 6293, CI = 0.203, RI = 0.513. Characters unordered with equal weight, 1607 constant, 196 uninformative and 647 parsimony-informative. Tree-island profile of 544. Bootstrap support from 1000 replicates is on branches if >59%. Outgroup species in black/red branches; ingroup species in green branches. Deep yellow branches represent terminals of *Archips occidentalis* (Walsingham, 1891). Terminals of *Choristoneura diversana*, the type species of the genus, are underlined.

Figure A.4.2. Consensus tree of the genus *Choristoneura* and Archipini using Maximum Likelihood analysis (IQ-Tree 1.3.11.1) of 4 partitions.
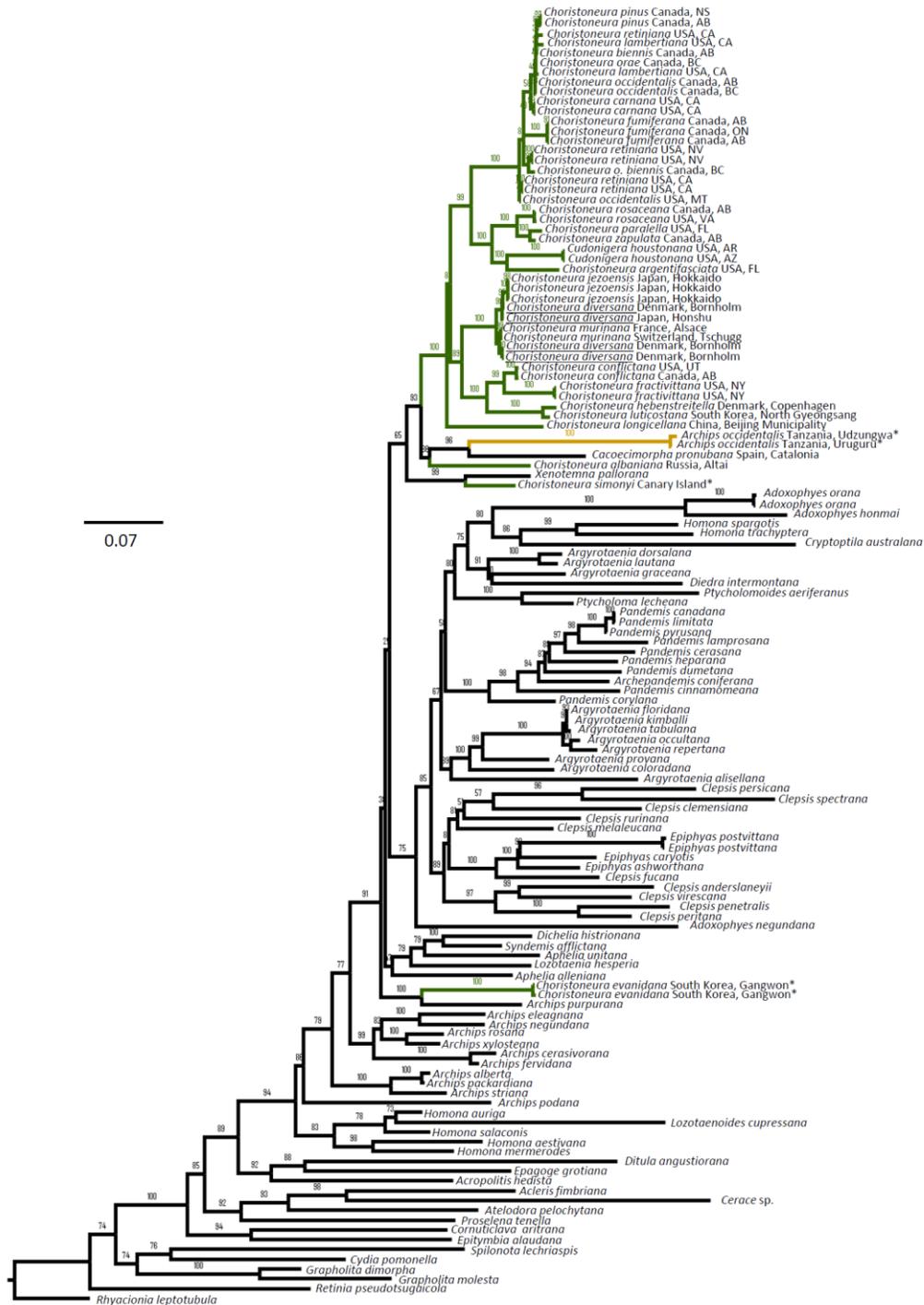
Figure A.4.2. Consensus tree of the genus *Choristoneura* and Archipini using Maximum Likelihood analysis (IQ-Tree 1.3.11.1) of 4 partitions (best schema per codon position). lnL= -32853.538791. (*legend Fig. A.4.2. continues next page*)

Support values on branches from 1000 replicates of ultrafast bootstrap support (%). Outgroup species in black branches; ingroup species in green branches. Deep yellow branches represent terminals of *Archips occidentalis* (Walsingham, 1891). Terminals of *Choristoneura diversana*, the type species of the genus, are underlined.

Figure A.4.3. Majority-rule consensus tree of the genus *Choristoneura* and Archipini using Bayesian analysis (MrBayes 3.2.6) of 4 partitions (the best schema per codon position).
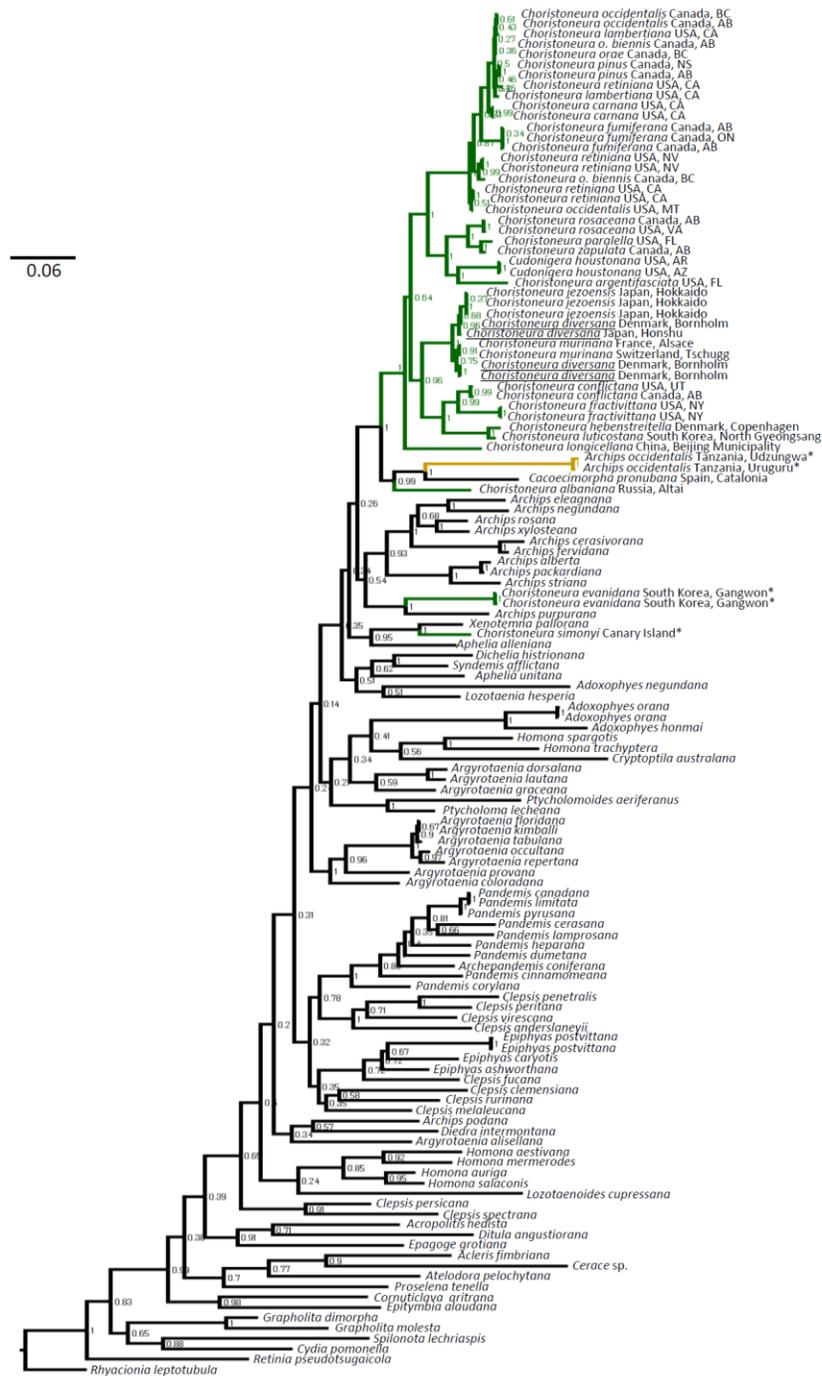
Figure A.4.3. Majority-rule consensus tree of the genus *Choristoneura* and Archipini using Bayesian analysis (MrBayes 3.2.6) of 4 partitions (the best schema per codon position). (*legend Fig. A.4.1. continues next page*)

Outgroup species represented by black branches, ingroup species represented by green branches. Deep yellow branches represent terminals of *Archips occidentalis* (Walsingham, 1891). Terminals of *Choristoneura diversana*, the type species of the genus, are underlined. Numbers on branches show supports denoted by posterior probabilities. Mean of estimated marginal LnL: -30970.22 (run 1 = -30975.90, run 2 = -30969.53); ESS>400 for almost all variables.

Biography

I was born on May 11, 1968, in Bogotá, Colombia. I was the first of three children of my parents, Jose María Fagua and Blanca Beatriz González, migrant peasants who arrived in the city looking for opportunities. I had always dreamed of being a naturalist. The most pristine memory of my childhood occurred when I was three-four years old, observing an ant nest with my mom. I was asking about ants; my mom says that I asked about everything. And she answered me, and answered, and answered. She only finished her third year of basic education, the regular level of education for a peasant woman at this time, but I have always marvelled about her general knowledge. She read about everything! I am an urban guy with a fascination for nature mostly because of my mom.

I was lucky to grow up in front of a park with a lake; something very different from the usual "green-free" landscape of my city. Consequently, the study of Nature was an early goal of my childhood. Then school, jobs, and money arrived, and confusion too. When I was ready to enter university in 1986, I had no idea about my future life. Yet I remembered my first experience and the happiness associated with that and I decided. I finished my Bachelor (1993) and Master (1997) degrees in Biology at the National University of Colombia, in Bogotá. There I had to decide again between a lot of possibilities for specialization and again my memories of childhood decided for me. I will work with insects as a biological model to answer questions. I was linked early with Socolen, the Colombian Society of Entomology; I helped to organize conferences, cycles of talks and several other things with the Society as a student and later as a professor and researcher. With five other guys, I formed a student "research" group on insects during my Bachelor's (1994); we made field trips to Macarena National Park and the region of the Carare-Opón with the support of the National University. Then the reality of my country appeared. We faced guerrillas and paramilitary groups in these travels; they and the war are part of some rural landscapes of my Nation. Fortunately, this conflict has been decreasing.

National University is more than an institution but rather is an amplified state of the reality of my country. The weaknesses and strengths of my people merge there, and the sense of homeland can be strengthened or ruined depending on your experience. Then, the week after my Master graduation in 1997, I was lucky to get a job at Javeriana University, the biggest private university in Colombia, the antithesis of the public National University. I am currently an

Associate Professor at Javeriana University (on study leave). During 15 years at Javeriana, I rebuilt the Laboratory of Entomology and the Javerian Museum of Natural History, with the help of several other professors and dozens of very enthusiastic undergraduate and graduate students. Several of them are now doing research around the world.

Then I took time to continue my studies, together with my wife, by enrolling in a doctoral program here at the University of Alberta (2012). I was lucky to experience the two opposite sides of high-level education in my country and I had a sense of academic pride too. I always remember my dad's answer when I told him about the academic world: "I never, never thought that people with education made this kind of things". My father, a migrant peasant and urban laborer, firmly believed that education must improve you as thinker but most importantly as person, as a man of integrity. I believe the same.