Phylogeny of Nearctic Species of the Xylosteana Group of *Archips* Hübner (Lepidoptera: Tortricidae) Based on Combined Analysis of Morphological and Mitochondrial DNA Data Sets

JAMES J. KRUSE[1] AND FELIX A. H. SPERLING[2]

Division of Insect Biology, Department of Environmental Science, Policy and Management, 201 Wellman Hall, University of California, Berkeley, CA 94720

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ABSTRACT The Holarctic *Archips xylosteana* Group consists of at least 18 morphologically similar species in the Nearctic, three of which were synonymized with *A. argyrospila* by Razowski and subsequently returned to species status, two that were described since 1986 but are clearly related to *A. argyrospila*, and an additional Western clade of *A. argyrospila* haplotypes that Razowski had not seen. We examined the morphology of all described Nearctic Xylosteana Group members plus one undescribed species, as well as DNA variation in a 816 bp segment of the mitochondrial COI gene for 17 of these species. We also examined three of five species of *Archips* from the Packardiana Group (=*Archippus* Freeman), and three outgroup genera (*Argyrotaenia* Stephens, *Clepsis* Guenée, and *Choristoneura* Lederer). Parsimony analyses of the combined molecular and morphological data sets gave better resolution and a better supported tree than did analyses of any single data set. All analyses revealed five species groups, rendering paraphyletic the Xylosteana Group as previously defined. An updated systematic list of Nearctic *Archips* is provided. We discuss the possibility that our data could support the resurrection of the genus *Archippus* from synonymy and the recognition of the Cerasivorana Group and the Purpurana Group as new genera. We have elected to leave the genus intact pending future investigations that include the additional Palaearctic members of the group.

KEY WORDS Tortricinae, Archipini, Cytochrome Oxidase Subunit I (COI), total evidence, systematics

APPLICATIONS RANGING FROM the reconstruction of biogeographic scenarios to the implementation of successful biological control programs are founded on the knowledge of systematic relationships. Analyses of relationships based on all available data, including morphology, ecology, and molecular data, are preferred. Several recent studies on a variety of invertebrates, especially insects, have shown that a "total evidence" approach to phylogeny reconstruction gave a tree topology (i.e., phylogeny) that was better resolved and better supported than did analyses of any single data set (Miller et al. 1997, Damgaard et al. 2000, Giribet et al. 2000, Klompen et al. 2000, Normark 2000, Skevington and Yeates 2000). Using such an approach to determine relationships among notable pest species is highly desirable.

Archips Hübner is a widely distributed genus in the Holarctic, especially in the Oriental subregion of the Palaearctic. In the Nearctic it is represented by at least 24 species (Razowski 1977, Powell 1983, Kruse 2000, Kruse and Sperling 2001). These species are distributed largely in the northern and central parts of North America reaching southward as far as Florida, Texas, and southern California (Razowski 1997). Larvae of these moths are commonly known as leafrollers, and several species in the genus are economically important pests of crops, forest trees, and ornamentals (van der Geest and Evenhuis 1991).

The genus was divided into six species groups (Razowski 1977), of which three are represented in the Nearctic: the Packardiana Group, the Asiatica Group, and the Xylosteana Group. The Packardiana Group comprises five closely related species: *A. striana* Fernald, *A. alberta* (McDunnough), *A. dissitana* (Grote), *A. packardiana* (Fernald), and *A. tsugana* (Powell). This group was given generic status (*Archippus*) by Freeman (1958) based largely on the "recurved, slightly invaginated" uncus, the square-shouldered tegumen, and the shape of the valva. Razowski (1977) synonymized this genus with *Archips.* Two of these species, *A. dissitana* and *A. tsugana*, are not included in the current study but are assumed to belong to the Packardiana Group based on work by Freeman (1958).

[1]Current address: University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775–6960.

[2]Current address: Department of Biological Sciences, CW405A Biological Sciences Center, University of Alberta, Edmonton, AB, Canada T6G 2E9.

The Asiatica Group is represented by the introduced *A. oporana* (L.), which was not included in this study, and is herein assumed to be a separate species group as per Razowski (1977). This species is widespread in the Palaearctic where it is a pest of pines (Razowski 1977).

The Xylosteana Group consists of 18 described species. Two species are introduced to North America: *A. rosana* (L.) introduced before 1890 (Chapman and Lienk 1971) and *A. fuscocupreana* (Wlsm.) introduced before 1982 (Maier and Mastro 1998). Sixteen are probably native to North America: *A. argyrospila* (Walker), *A. goyerana* Kruse, *A. nigriplagana* Franclemont, *A. mortuana* Kearfott, *A. eleagnana* (McDunnough), *A. myricana* (McDunnough), *A. semiferana* (Walker), *A. negundana* (Dyar), *A. fervidana* (Clemens), *A. georgiana* (Walker), *A. magnoliana* (Fernald), *A. purpurana* (Clemens), *A. infumatana* (Zeller), *A. grisea* (Robinson), *A. cerasivorana* (Fitch), and *A. rileyana* (Grote). We also have included a potential new species (Kruse and Sperling 2001), a West Coast lineage near *A. argyrospila.* About 16 additional Xylosteana Group species are found almost exclusively in Palaearctic East Asia.

Comprehensive treatments of the genus *Archips* (Freeman 1958, MacKay 1962, Razowski 1977) have proposed species groups but have not attempted to resolve phylogenetic relationships among species in any of these groups. MacKay (1962) called attention to the distinctiveness of *A. cerasivorana, A. rileyana, A. fervidana,* and *A. infumatana* according to larval characters and a tendency for the larvae to aggregate. This group (hereafter referred to as the *Cerasivorana* Group) may be distinguished by the absence of an anal fork in the larvae and aggregation (nest-making) behavior.

Despite wide interest in *Archips* as pests, no phylogenetic studies on the genus or any of its species groups have yet been published, with the exception of the *A. argyrospila* species complex (Kruse and Sperling 2001). Adult morphology alone is not sufficiently diagnostic to construct a definitive phylogeny for the genus, making *Archips* an appropriate group for molecular investigation and a total evidence approach to data analysis. Here, we examine mitochondrial DNA evidence of relationships among *Archips* species found in the Nearctic region and combine these with morphological data to produce a robust phylogeny. This phylogeny is used to construct a systematic list of *Archips* species found in the Nearctic and to make recommendations concerning the taxonomy of the various species groups.

Materials and Methods

Specimens. Institutions are abbreviated throughout the text as follows: Essig Museum of Entomology (EME), University of California, Berkeley, CA, USA; Louisiana State Arthropod Museum (LSAM), Baton Rouge, LA, USA; Mississippi Entomological Museum (MEM), Mississippi State, Mississippi, USA; National Museum of Natural History (NMNH), Washington, DC., USA; University of Minnesota, Saint Paul (UMSP), Saint Paul, MN, USA; Washington State Department of Agriculture (WSDA), Olympia, Washington, USA; Northern Forestry Center (NFC), Edmonton, Alberta, Canada.

The specimens used in this study were provided by collaborators or were collected by the authors (Table 1). We selected 122 *Archips* specimens for study (Table 1), 110 from the Xylosteana Group and 12 from the Packardiana Group. Three outgroups were selected from related archipine genera. Outgroup taxa within *Archips* were *A. packardiana, A. alberta,* and *A. striana.* Outgroup taxa from related genera were *Argyrotaenia coloradana* (Fernald) from Little Spring, Coconino County, AZ., (Landry et al. 1999); *Clepsis peritana* (Clemens) from the Rutherford neighborhood, east of Fairfax City, Fairfax County, VA,; and *Choristoneura rosaceana* Harris from Ste. Agathe, Quebec, Canada (Sperling and Hickey 1994). Outgroups were chosen on the basis of presumed distant yet congeneric relationship (Packardiana Group) and genera within the same tribe (*Argyrotaenia, Clepsis,* and *Choristoneura*). A summary of all ingroup material plus the Packardiana Group species that were examined is provided in Table 1.

We did not sample *A. dissitana* or *A. tsugana* (Packardiana Group) nor *A. oporana* (Asiatica Group). *Archips dissitana* and *A. tsugana* were omitted early in the study, because the Packardiana Group was thought to be sufficiently represented as an outgroup. This omission is assumed to be minor, as Packardiana Group species are thought to be very closely related (Freeman 1958, Razowski 1977) and presumably would have very little, if any, effect on the outcome of this study. For *A. oporana,* insufficient specimens were available. In addition, only the morphology and not mtDNA of *A. eleagnana* and *A. myricana* (Argyrospila Group) were investigated. The mtDNA of these species was not sampled, because recently collected specimens were not available.

We attempted to obtain specimens from a selection of sites across the ranges of ingroup species. Where possible, we sampled at least three specimens of each species to determine the extent of sequence divergence and test species concepts. Specimens were collected using lights (UV, mercury vapor, or incandescent), searching foliage, or rearing from larvae collected in the field. For molecular analyses, live specimens were either frozen at –20°C or –70°C or dropped directly into 95–100% EtOH. Pinned museum specimens were used for the morphological portion of this study and to supplement the fresh specimens in the molecular portion when possible. The oldest successfully amplified samples were collected in 1983 (Table 1).

Specimens were identified initially by phenotype, specifically forewing pattern, before DNA extraction or microdissection for slide preparation. The unused body parts of each specimen were preserved in a gelatin capsule for confirmation of identification, and these vouchers are deposited in the EME. Exceptions

Table 1. Locality data for all *Archips* specimens examined

Species	No. specimens	MtDNA	Slide no.	Specimen label data	Collector and year
A. packardiana	2	X		Saskatchewan: Big River	G. Pohl, 1995
A. packardiana	1		JJK256	MN: Clay Co. Moorhead	J. R. Powers, 1978
A. packardiana	1		JAP3648	MN: Clay Co. Moorhead	J. R. Powers, 1972
A. striana	2	X		Saskatchewan: Big River	G. Pohl, 1995
A. striana	2		JJK259, 260	NM: Sandoval Co. Jemez Mts.	W. Shaupp, 1980
A. alberta	3	X		Alberta: Zama	G. Pohl, 1997
A. alberta	1		JJK246	Saskatchewan: Denare Beach	A. Keddie, 1985
A. rosana	5	X		British Columbia: SE Kelowna	D. Holden, 1998
A. rosana	1		JAP7169	British Columbia: Cultus Lake	J. & S. Shepard, 1990
A. rosana	1		JAP7386	British Columbia: Sproule Creek	J. Shepard, 1987
A. fuscocupreana	2	X	EME3868, 9	WA: Thurston Co. Olympia	E. Lagasa, 1996
A. argyrospila	1	X		CA: Alameda Co. Berkeley	J. A. Powell, 1995
A. argyrospila	1	X		Quebec: LaSarre, Lake Abitibi	B. Landry, 1998
A. argyrospila	1	X		WI: Burnett Co. Grantsburg	M. Sabourin, 1998
A. argyrospila	1	X		CA: Yuba Co. Brushy Creek, nr Marysville	J. J. Kruse, 1999
A. argyrospila	2	X	JJK225, 232	TX: Harris Co. Houston	E. C. Knudson, 1999
A. argyrospila	1		JJK125	AL: DeKalb Co. DeSoto S. P.	Brown & MacGown, 1990
A. argyrospila	1	X	JJK130	CA: San Diego Co. San Clemente Cyn.	N. Bloomfield, 1998
A. argyrospila	1	X	JJK223	IN: Elk Co. (No Further Data)	Unknown, 1998
A. argyrospila	2		JJK226, 230	WI: Burnett Co. Grantsburg	M. Sabourin, 1998
A. argyrospila	1	X	JJK227	Alberta: Demmitt Cpgd., Hythe	F. A. H. Sperling, 1998
A. argyrospila	1		JJK233	Alberta: Edmonton	J. Emond, 1989
A. argyrospila	1		JJK231	Ontario: 17 mi SE Kenora	J. R. Powers, 1965
A. nigriplagana	3	X	JJK234, 235	TN: Wilson Co. Cedars of Lebannon S. F.	Brown & MacGown, 1997
A. goyerana	2	X	JJK222	LA: Assumption Parish, Pierre Part	R. A. Goyer, 1999
A. goyerana	3		JJK210–1, 220	LA: Assumption Parish, Pierre Part	R. A. Goyer, 1999
A. goyerana	2	X		LA: St. Charles Parish, Norco	R. A. Goyer, 1999
A. goyerana	6		JJK212–3, 221 224, 228–229	LA: St. Charles Parish, Norco	R. A. Goyer, 1999
A. mortuana	1	X	JJK116	Quebec: 30 mi N. New Richmond	W. Middlekauff, 1983
A. mortuana	2	X	JJK236, 237	MN: Anoka Co. Blain, Janes Field	M. Sabourin, 1995
A. eleagnana	1		JJK268	Manitoba: Aweme	E. Criddle, 1920
A. myricana	2		JJK267, CAC3	Ontario: Algonquin Park	J. McDunnough, 1922
A. semiferana	2	X		TX: Harris Co. Houston	E. C. Knudson, 1999
A. semiferana	1	X		MS: Winston Co. Tombigbee Natl. Forest	R. L. Brown, 1999
A. semiferana	1	X		NC: New Hanover Co. Peters Point	J. B. Sullivan et al., 1994
A. semiferana	1		JJK240	NC: New Brunswick Co. Bald Head Isl.	J. B. Sullivan et al., 1994
A. semiferana	1		JJK241	PA: Centre Co. Black Moshannon S.P.	Unknown, 1971
A. semiferana	1		JAP295	MI: Missaukee Co. (No Further Data)	R. & K. Dreisbach, 1957
A. negundana	1	X	JJK248	Manitoba: Swan River	Unknown, 1983
A. negundana	1	X	JJK249	Manitoba: Falcon Lake	Unknown, 1985
A. negundana	1	X		MT: Missoula Co. Missoula	S. J. Gast, 1987
A. negundana	1		EME2146	UT: Utah Co. Mt. Timpanogos	J. A. Powell, 1981
A. georgiana	4	X		TX: Harris Co. Houston	E. C. Knudson, 1999
A. georgiana	1	X		LA: Bossier Parish, Barksdale AFB	Brown & Pollock, 1996
A. georgiana	1	X		LA: Bossier Parish, Bodcau W.M.A.	R. L. Brown, 1996
A. georgiana	1		JJK133	OK: Lincoln Co. 1 mi NW Sparks	J. McCarty, 1992
A. georgiana	2		JJK208, 209	AL: Baldwin Co. Bon Seccur NWR	Brown & Pollock, 1994
A. georgiana	1		JAP5222	LA: St. Helena Parish, 4 mi E Greensburg	G. T. Strickland, 1978
A. georgiana	1		JAP5278	MS: Claiborne Co. Rocky Springs	B. Mather, 1970
A. magnoliana	4	X		MS: Winston Co. Tombigbee Natl. Forest	R. L. Brown, 1999
A. magnoliana	2		JJK238–239	NC: Craven Co. Croatan, Rd 147	J. B. Sullivan, 1997
A. magnoliana	1		JJK251	KY: Wolfe Co. Koomer Ridge Camp	C. V. Covell Jr., 1967
A. grisea	3	X		TX: Harris Co. Houston	E. C. Knudson, 1999
A. grisea	1	X		MS: Winston Co. Tombigbee Natl. Forest	R. L. Brown, 1999
A. grisea	1	X	JJK247	LA: Bossier Parish, Bodcau W.M.A.	Brown & Pollock, 1996
A. grisea	1		JJK250	MN: Becker Co. Detroit Lakes	M. Moher, 1981
A. grisea	1		JAP1117	NY: West Point	B. Mather, 1962
A. cerasivorana	1	X		CA: Siskiyou Co. Mt. Shasta	F. A. H. Sperling, 1996
A. cerasivorana	3	X		NY: Tompkins Co. Yellow Barn S. F.	A. E. Hajek, 1998
A. cerasivorana	1	X		British Columbia: Peace Cyn. Rec. Area	F. A. H. Sperling, 1998
A. cerasivorana	2		JJK263, 264	CA: Siskiyou Co. 9 mi. E. McCloud	J. A. Powell, 1974
A. cerasivorana	2		JAP630, 633	CA: Siskiyou Co. 5 mi. E. McCloud	J. A. Powell, 1958
A. fervidana	5	X		WI: Burnett Co. Grantsburg	M. Sabourin, 1998
A. fervidana	1		JJK252	NJ: Montclair	W. D. Kearfott, (No Date)
A. fervidana	1		JJK253	WI: Oneida Co. Lake Katherine	H. M. Bower, 1961
A. infumatana	4	X		MS: Oktibbeha Co. 6 mi. S. Starkville	R. L. Brown, 1999
A. infumatana	2		JJK244, 245	LA: Calcasieu Parish, S. H. Jones S. P.	Brown & Pollock, 1993
A. rileyana	2	X	JJK242, 243	MS: Noxubee Co. Noxube W. R.	R. L. Brown, 1997
A. rileyana	1	X		TX: Harris Co. Houston	E. C. Knudson, 1999
A. purpurana	2	X		IL: Woodland Co.	J. A. Powell, 1998
A. purpurana	1		JJK254	MA: Middlesex Co. West Acton	C. G. Oliver, 1965
A. purpurana	1		JJK255	CT: Greenwich	E. J. Duda, 1957

The collection of mtDNA data is indicated by an X. Slides are deposited in the Essig Museum of Entomology, University of California (EME), except those for *A. myricana* and *A. eleagnana*, which are deposited at the National Museum of Natural History (NMNH), and *A. goyerana* slides 220 and 221 and associated specimens, which are deposited at the Louisiana State Arthropod Museum (LSAM). Remains of specimens used in molecular analyses are deposited in the EME.

Table 2. Morphological character matrix

Species	Characters (1–30)																													
	1	2	3	4	5	6	7	8	9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0
Choristoneura spp.	0	0	0	0	0	9	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Argyrotaenia spp.	0	0	1	0	0	9	0	0	0	0	0	1	1	1	2	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0
Clepsis spp.	0	0	1	0	0	9	0	0	1	0	1	0	9	0	2	2	0	0	1	0	0	0	0	0	1	0	0	1	1	1
Archips packardiana	0	0	0	0	1	0	0	1	0	1	1	0	9	1	0	0	2	1	0	0	0	1	0	1	1	1	0	0	0	0
Archips striana	0	0	0	1	1	1	0	1	0	1	1	0	9	1	0	0	2	1	0	0	0	1	0	1	1	1	1	0	0	1
Archips alberta	0	0	0	1	1	0	0	1	0	1	1	0	9	1	0	1	2	1	0	0	0	1	0	1	1	1	0	0	0	0
Archips rosana	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	1	2	1	0	0	0	0	0	2	0	1	1	1	1
Archips fuscocupreana	0	0	9	1	1	0	0	1	1	0	1	1	0	0	1	1	3	2	1	1	0	0	1	1	2	0	1	0	1	1
Archips argyrospila	0	0	1	1	1	1	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	1	1
West Coast *A. argyrospila*	0	0	1	1	1	1	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	1	1
Archips nigriplagana	0	0	9	1	1	1	0	0	0	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	1	1
Archips goyerana	0	0	1	1	1	1	0	0	0	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	1	1
Archips mortuana	0	0	1	1	1	1	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	1	1
Archips semiferana	0	0	9	1	1	0	1	0	1	0	1	1	0	0	0	1	1	2	1	1	0	0	2	0	2	0	0	0	1	1
Archips negundana	0	0	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	2	1	0	0	0	2	0	1	0	0	0	1	1
Archips georgiana	0	0	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	0	1	1
Archips magnoliana	0	0	9	1	1	1	0	0	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0	0	1	0	1	0	1	1
Archips grisea	0	0	9	1	1	0	0	0	1	0	1	1	0	0	1	1	1	2	0	0	0	0	2	0	1	1	0	0	1	1
Archips cerasivorana	1	1	0	1	0	9	0	0	1	0	1	0	9	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	0	1
Archips fervidana	1	1	0	1	0	9	0	1	0	0	1	0	9	1	1	1	1	0	1	1	0	0	1	1	2	1	1	0	0	1
Archips infumatana	1	1	0	1	0	9	0	1	0	0	1	0	9	0	1	1	1	0	1	1	0	0	1	1	2	1	1	0	0	1
Archips rileyana	1	1	0	1	0	9	0	1	0	0	1	0	9	1	1	0	1	0	1	1	0	0	0	0	1	1	0	1	0	1
Archips purpurana	0	0	1	0	0	9	0	1	1	0	1	0	9	1	2	1	0	2	1	0	0	0	1	0	2	1	1	0	0	1

All characters are unordered. Missing data are denoted "9."

to this disposition of specimens are explained in Table 1.

Morphological Techniques. Dissection methodology follows that summarized in Brown and Powell (1991) except that preparations were transferred to 95% isopropyl alcohol (instead of xylene) after the 95% EtOH wash, and all parts were slide-mounted with Euparol mounting medium (Bioquip Products, Gardena, CA) rather than Canada balsam. Characters were chosen according to their utility in phylogenetic study as recommended by Horak (1984), and their prevalence in previously published keys to species (adults: Freeman 1958, larval: MacKay 1962). The morphological character matrix is given in Table 2. Terminology for genitalic structures follows Horak (1984).

We selected 30 characters, one ecological and 29 morphological, of which 23 of the latter were based on genitalia. All characters are unordered and unweighted, and all characters are parsimony-informative. Outgroup genera were examined, and characters were scored in the same manner as ingroup species; however, the most common condition for each character in each genus also was considered for scoring. Morphological or ecological character states for *Choristoneura*, *Argyrotaenia*, and *Clepsis* therefore are assumed to represent the most common condition in their respective genera. Larval ecology and morphological characters are from the literature (MacKay 1962). Characters for female *A. alberta* and *A. eleagnana* are gleaned from the literature (Freeman 1958, Razowski 1977) because of the lack of specimens.

Analysis of Characters. Horak's (1984) analysis of phylogenetically useful characters in Tortricinae included few that are variable below the generic level. We found useful characters to discern the genera and species in question, although they may not be useful in resolving relationships in other archipine genera nor in all species included in the outgroup genera examined here. The following characters were used, taking all available specimens into account. Numbers preceding characters refer to the character state matrix in Table 2.

Larval characters (characters 1–3). Larval characters that were described for all species in MacKay's (1962) treatment are repeated here. There are six species investigated in this study that MacKay did not examine (*A. fuscocupreana*, *A. goyerana*, *A. grisea*, *A. magnoliana*, *A. nigriplagana*, and *A. semiferana*) and for which we have made assumptions about the scoring of larval characters. All assumptions are outlined below.

1. Aggregation behavior. Aggregation behavior in tortricid larvae have been considered unusual and sporadic (MacKay 1962). Character states: larvae (0) nonaggregative or (1) aggregative behavior (MacKay 1962).

2. Anal fork. Because MacKay found an anal fork in all *Archips* species that she examined except the Cerasivorana Group, we assumed that all species in the Rosana and Argyrospila Groups possess an anal fork. Character states: larvae (0) anal fork absent or (1) anal fork present (MacKay 1962).

3. Shape of anal shield. We assumed that West Coast *A. argyrospila* and *A. goyerana* possess a tapered anal shield because of their documented close relationship to *A. argyrospila.* We did not make assumptions about the anal shield character for *A. fuscocupreana*, *A. grisea*, *A. magnoliana* or *A. nigriplagana*, and we scored

it as missing data. Larval anal shield (0) rounded or (1) tapered (MacKay 1962).

4. Costal fold. The costal fold may be modified, reduced, or absent even among closely related species (Horak 1984). The costal fold in *Archips*, when present, was not extensively modified in any species examined, so only presence or absence of this character was scored. Character states: costal fold of forewing (0) absent or (1) present.

5–6. Abdominal dorsal pits. Dorsal pits are found in several tortricid groups. While the function remains obscure, these structures may still be valuable indicators of relationships (Brown and Miller 1999). We scored presence and absence, and the position of individual pits on tergum 2. Character states: 5. Dorsal pits (0) absent or (1) present. 6. Paired dorsal pits are (0) separate or (1) adjoined. If character five was scored "0," then character six was scored "9" in the matrix and treated as missing.

7. Scales for covering ova. At many taxonomic levels within the Tortricidae, females cover their ova with scales derived from modified corethrogyne scaling (Horak 1984). Character states: female (0) without modified corethrogyne scaling or (1) with modified scales.

8–11. Uncus form (Fig. 1 A and B). The length, shape, width of the base, and presence or absence of a subapical fold in the uncus were scored. Character states: 8. Uncus (0) more than four times longer than wide at widest point or (1) about two times longer than wide at widest point. 9. Uncus (0) uniformly wide, very gradually enlarged distally, or subapically widened or (1) apically clubbed. 10. Uncus (0) not folded or (1) folded subapically along a distinct crease. 11. Base of uncus (0) narrower than at its midpoint (1) broader than at its midpoint.

12–13. Socius form. The Xylosteana Group generally possess reduced socii. Character states: 12. Socius (0) absent or (1) present. 13. Socius (0) reduced or (1) large and well formed. If character 12 is scored "0," then character 13 was marked "9" in the matrix and treated as missing.

14. Gnathos form. In all Archipini, the arms of the gnathos are joined distally. Character states: gnathos arms of male (0) joined only at apices or (1) joined along most of a paddle-like distal elongation.

15. Sacculus form. The sacculus was either evenly widened or broadened distally in *Archips* species. Character states: sacculus (0) of equal width throughout, (1) broadened distally, or (2) tapered distally.

16. Transtilla form. The transtilla is weakly sclerotized in *Archips* and often twisted. Twisted transtilla forms were observed in solution and were not an artifact of slide mounting. Character states: transtilla (0) a simple band, (1) twisted, or (2) divided in the middle.

17. Valva form (Fig. 1C). The general shape of the valva was characterized. Character states: valva (0) elongated and triangular or rectangular and very broad basally; (1) subtriangular; (2) subtriangular with a basal lobe; or (3) subtriangular with a deep basal lobe.

18. Tegumen form (Fig. 1D). The shape of the tegumen at the attachment site of the gnathos arms was scored. Character states: tegumen (0) rounded at attachment site of gnathos arms, (1) angular, or (2) distinctly squared (Fig. 1D from left to right).

19–25. Aedeagus form and processes (Fig. 1E). As seen in other other archipines such as *Argyrotaenia* and *Diedra* (Rubinoff and Powell 1999), the aedeagus can be a structure rich in discrete characters. Size, general shape, number of cornuti, and variable apical, subapical, or median armature of the aedeagus were scored. Character states: 19. Aedeagus beyond attachment to juxta (0) equal in length to phallobase or (1) longer than phallobase. 20. Aedeagus (0) straight or (1) curved. 21. Aedeagus (0) possessing a straight tip or (1) a strongly curved tip. 22. Aedeagus (0) without apical armature or (1) with an apical tooth. 23. Aedeagus (0) without subapical armature, (1) with subapical tooth, or (2) with subapical dent(s). 24. Aedeagus (0) without median armature or (1) with median dentate crest ventrally. 25. Cornuti (0) numerous, generally >10, (1) with two cornuti, or (2) with three or four cornuti.

26–30. Female genitalia (Fig. 1 F). The sterigma, ostium, and cestum are all important characters throughout the Tortricidae (Horak 1984). Character states: 26. Sterigma (0) a narrow band or (1) widened to at least one-third of the widest lateral measurement. 27. Cup part of sterigma above antrum (0) a shallow bowl or (1) a deep cup (see Fig. 1 F). 28. Antrum (0) robust, about twice as long as wide and heavily sclerotized or (1) short and narrow, about three times as long as wide, poorly developed. 29. Ostium (0) about twice as wide as width of ductus bursae or (1) only slightly wider than width of ductus bursae. 30. Cestum (0) very weak or absent or (1) well formed.

Molecular Techniques. Total genomic DNA was extracted using a QIAamp DNA Mini Kit # 51306 (QIAGEN, Valencia, CA.). Most amplified fragments were ≈400–500 bp long. Amplifications were performed on an Ericomp TwinBlock EasyCycler using a hot start: *Taq* was added at the end of an initial denaturation at 94°C, followed by 35 cycles of 30 s at 94°C, 30 s at 45°C, 1 min at 72°C, and a subsequent 10 min final extension at 72°C. For many of the older museum specimens, amplifications were performed on an MJ Research PTC200 using a hot start: *Taq* was added at the end of an initial denaturation at 94°C, followed by 10 repetitions of 30 s at 94°C, 30 s at 40°C and 40 s at 72°C, 10 repetitions of 30 s at 94°C, 30 s at 45°C and 40 s at 72°C, and 15 repetitions of 30 s at 94°C, 30 s at 50°C and 40 s at 72°C, and a subsequent 3 min final extension.

Polymerase chain reaction (PCR) products were cleaned using a QIAquick PCR Purification Kit #28106 (QIAGEN). The PCR product was cycle sequenced with a Perkin-Elmer/ABI Dye Terminator Cycle Sequencing Kit with AmpliTaq FS (Perkin-Elmer/Applied Biosystems, Foster City, CA) on an MJ Research PTC200 according to Perkin-Elmer's suggested thermal profile. The sequenced product was filtered through Sephadex-packed columns and dried. This

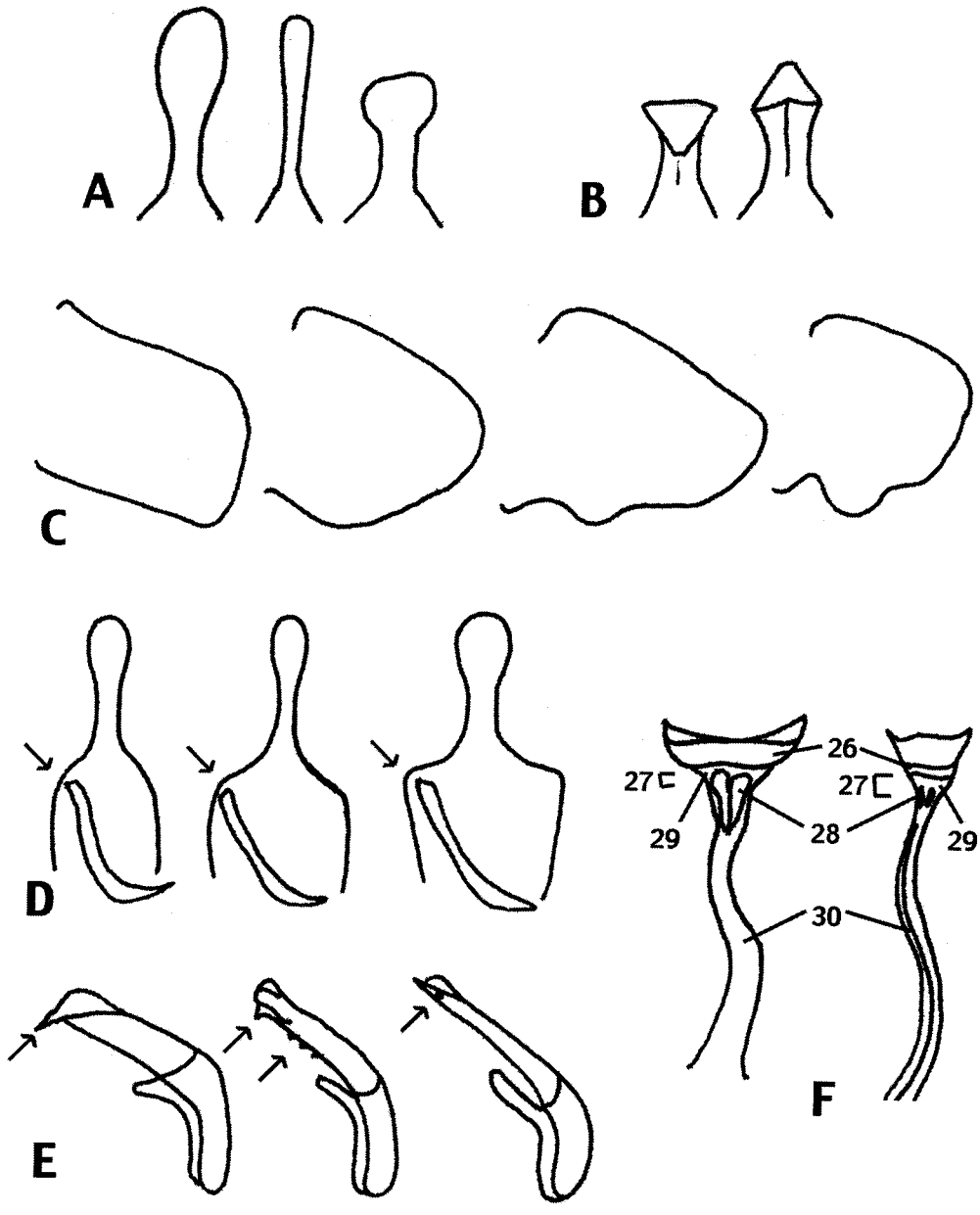

Fig. 1. Detail drawings for eight male (A-E) and five (F) female genitalic characters. All character states described read from left to right:(A) Characters 8–9, uncus form: uncus long (character 8, state 0), clubbed (character 9, state 1), as in *A. negundana;* uncus long, and narrow (character 9, state 0), as in *A. rosana;* uncus short (character 8, state 1), clubbed, as in *A. purpurana. (*B) Character 10, state 0: uncus folded over a distinct crease, as in *A. alberta;* same structure drawn from uncus mounted so that the fold is held open. (C) Character 17, valva form: state 0, as in *C. rosaceana;* state 1, as in *A. semiferana;* state 2, as in *A. striana;* state 3, as in *A. fuscocupreana. (*D) Character 18, tegumen form: state 0, as in *A. cerasivorana;* state 1, as in *A. argyrospila;* state 2, as in *A. fuscocupreana. (*E) Characters 22–24, processes of the aedeagus: with apical tooth (character 22, state 1) and without subapical armature (character 23, state 0), as in *A. striana;* with subapical tooth (character 23, state 1) and with a median dentate crest ventrally (character 24, state 1), as in *A. fuscocupreana;* with a subapical dent (character 23, state 2) and without apical armature (character 22, state 0), as in *A. semiferana. (*F) Characters 26–30, female genitalic characters, *A. alberta,* left, *A. rosana,* right: 26, sterigma anterior-posteriorly widened, or narrow; 27, cup part of sterigma a shallow bowl, or a deep cup; 28, antrum long and heavily sclerotized, or short and poorly developed; 29, ostium broadly opened, or narrowly opened; 30, cestum absent, or well formed in ductus bursae.

product was resuspended and electrophoresed on an Applied Biosystems International 377 automated sequencer. All fragments were sequenced in both directions. Sequences were aligned manually to the sequence of *Drosophila yakuba* Burla (Clary and Wolstenhome 1985).

We chose an 816-bp segment in the COI gene to compare 107 specimens from 16 species in the Xylosteana Group, 15 specimens of three species in the Packardiana Group, and one specimen of each of the three outgroup species (Table 1). This fragment corresponds to the second half of COI between basepair numbers 2184 and 3000. Sequence was obtained by PCR amplification using the end primers CI-J-2183: 5′ CAA CAT TTA TTT TGA TTT TTT GG 3′, CI-N-2659: 5′ GCT AAT CCA GTG AAT AAT GG 3′ and TL2-N-3014: 5′ TCC AAT GCA CTA ATC TGC CAT ATT A 3′. *Archips purpurana* and *Clepsis peritana* required a different version of CI-N-2659: 5′ GAT AAT CCT GTA AAT AAA GG 3. *Choristoneura rosaceana* and *Argyrotaenia coloradana* sequences are from other studies (Sperling and Hickey 1994, Landry et al. 1999).

Phylogenetic Analyses. Analyses using parsimony and maximum likelihood were carried out using PAUP 4.0b4 (Swofford 1999). Sequence alignments were done manually, and no indels were found relative to *D. yakuba.* Variable nucleotide positions and morphological characters were treated as unordered characters with one state for each nucleotide or character. We used heuristic searches with 1,000 random taxon addition sequence replicates. Identical mtDNA COI haplotypes were removed for the searches.

To assess branch support, the sequence data set and the morphological data set were bootstrapped 500 times each using a heuristic parsimony search. Decay indices were assessed by successively relaxing parsimony one step at a time until the phylogeny collapsed into a polytomy. Sequences and morphological characters from *Choristoneura rosaceana* (Sperling and Hickey 1994), *Argyrotaenia niscana* (Landry et al. 1999), and *Clepsis peritana* (J.J.K., unpublished data) (all Archipini) were used to root respective trees. Genbank accession numbers may be found at the conclusion of this paper.

For the maximum likelihood analysis we used the Hasegawa-Kishino-Yano (Hasegawa et al. 1985) model of sequence evolution with the transition/transversion ratio set to two (estimated by PAUP from the parsimony tree). All sites were assumed to evolve at the same rate. Starting branch lengths were obtained using the Rogers-Swofford approximation method (Rogers and Swofford 1998).

Combined mtDNA and morphological analyses were carried out after a partition homogeneity test of parsimony informative molecular and morphological characters in PAUP statistically demonstrated insignificant differences between the data sets ($P = 0.44$). We used heuristic searches under parsimony with 1,000 random taxon addition sequence replicates involving all 179 (149 molecular and 30 morphological) parsimony-informative characters of the 20 species where both molecular and morphological characters were available.

Results

Morphological Phylogeny. A heuristic parsimony search involving 30 parsimony-informative morphological characters of 21 recognized *Archips* species and three outgroup genera in PAUP resulted in four most parsimonious trees of 90 steps (CI = 0.411; RI = 0.702; RC = 0.289). A representative phylogram is shown in Fig. 2A. The exceptions to complete correspondence among phylograms include varied placements of *A. magnoliana* and *A. georgiana; A. cerasivorana* and *A. rileyana;* and internally within the *A. argyrospila* complex. A strict consensus tree of the four most parsimonious trees is shown in Fig. 1B, and corresponds to the bootstrap consensus tree. Bootstrap values are given for comparisons with molecular data.

Five clades were derived in all analyses in PAUP (Fig. 2 A and B; *Appendix 1: Systematic List*). The first clade, which contained the Rosana Group plus *A. georgiana,* was derived consistently but poorly supported. Only the species pair of *A. negundana* plus *A. semiferana* was supported by bootstrap values >50%. Most of the species in this group possess separated abdominal dorsal pits, a twisted transtilla, a straight-tipped aedeagus, a narrow sterigma, and a heavily sclerotized antrum. However, none of these characters is autapomorphic to any group.

The second clade, which contained the Argyrospila Group minus *A. georgiana,* was strongly supported by bootstrap (84%). However, resolution among species of this closely related group was very poor. The Argyrospila Group was characterized by the presence of adjoined abdominal dorsal pits, an aedeagus with a strongly curved tip (minus *A. georgiana*), and a poorly developed antrum.

The third clade, containing the Cerasivorana Group, was supported by a bootstrap value of 56%. Aggregation tendencies of larvae, the absence of an anal fork in the larvae, absence of abdominal dorsal pits and socii, and a rounded tegumen helped to diagnose this group. The clear differences in larval characters described by MacKay (1962) were the major reason that this clade was strongly supported in all morphological analyses.

The fourth clade contained the closely related outgroup species belonging to the Packardiana Group. These species were the most robustly supported (bootstrap of 96% and decay index of 3). They were characterized by a folded uncus, lack of socii, lobed subtriangular valvae, an apically toothed aedeagus, and broadly joined apices of the gnathos.

The fifth clade consisted of the Purpurana Group, containing only *A. purpurana.* The Purpurana Group was basal to the rest of the *Archips* species examined. This group shared a number of characters with outgroup taxa, such as a tapering sacculus (character 15, state 2) and valva form (character 17, state 0).

Sequence Variation. We were able to obtain 816 bp of mtDNA sequence for 74 ingroup specimens (Table

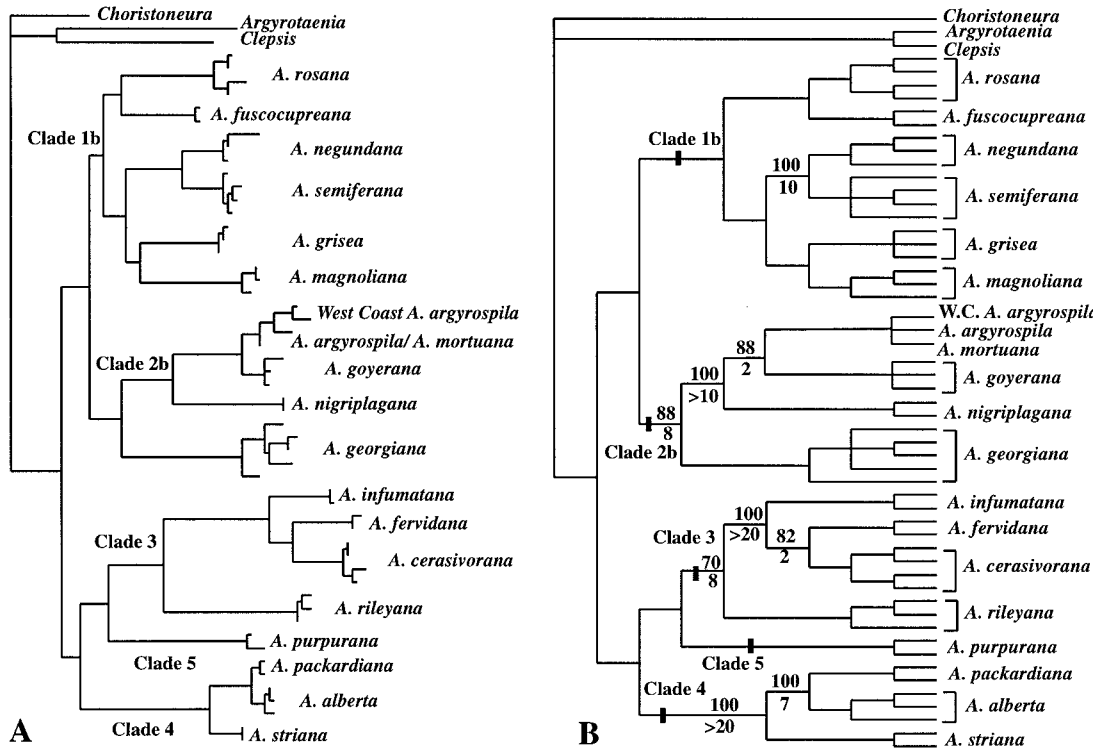

Fig. 2. Trees derived from four most parsimonious unrooted trees of 30 morphological characters representing 21 *Archips* species and three outgroup genera (90 steps, CI = 0.411; RI = 0.702; RC = 0.289). West Coast *A. argyrospila* is synonymous with *A. argyrospila* in morphological analyses. Clades representing species groups as described in the text are indicated by vertical bars. The species composition of clades marked with a letter differ from other analyses. (A.) Representative phylogram. (B) Strict consensus. Numbers above branches indicate bootstrap values, and below branches indicate decay index. Only bootstrap values >50% are shown.

1). All pinned specimens that were collected before 1982 failed to amplify; however, there were some pinned specimens collected as recently as 1997 that failed to amplify. No specimens preserved by freezing at −70°C or −20°C, placed alive into 95–100% EtOH, or recently field-pinned failed to amplify.

Among the 74 ingroup sequences obtained, there were 51 unique haplotypes, with parsimony-informative nucleotide variation at 149 nucleotide sites (Table 3), and parsimony-uninformative variation at 73 nucleotide sites. Sequence variation among the 149 parsimony-informative characters resulted in 25 first codon position changes, 6 second position changes, and 118 third position changes. These codon changes resulted in 25 inferred amino acid replacements, 18 replacements from first position changes, six from second position, and one from a third position change. Sequence variation among the 73 parsimony uninformative characters resulted in 24 first position changes, 5 second position changes, and 44 third position changes. These codon changes resulted in 21 amino acid replacements, 15 resulting from first position changes, five from second position, and one from a third position change.

MtDNA Phylogeny. A heuristic parsimony search of the 51 haplotypes of 20 species of *Archips* and outgroup genera resulted in 16 trees of 633 steps. A randomly selected representative phylogram is shown in Fig. 3A. The exceptions to complete correspondence among phylograms include various placements of individual specimens within species (*A. semiferana*, *A. grisea*, *A. goyerana* and *A. georgiana*) and within clade placements of *A. argyrospila*, West Coast *A. argyrospila*, and *A. mortuana.* A strict consensus tree of the 16 most parsimonious trees is shown in Fig. 3B which corresponds to the bootstrap consensus tree.

Most species examined in this study were distinctly monophyletic in molecular analyses. The mtDNA of specimens that were identified as *A. mortuana* did not show a pattern of relationships that supported separation of this taxon as a distinct species. *Archips mortuana* comprised two haplotypes that were exact matches of two *A. argyrospila* haplotypes (see also Kruse and Sperling 2001). For purposes of this article, specimens initially identified as *A. mortuana* are grouped with those of nominate *A. argyrospila* populations in further discussions.

Five clades of the topology (Fig. 3 A and B; *Appendix 1: Systematic List*) were consistently derived in all parsimony analyses in PAUP. The Rosana Group was consistently derived but poorly supported. Within it, only *A. negundana* and *A. semiferana* were supported

Table 3. Parsimony-informative nucleotide variation in 20 species of *Archips*

A. Base pair numbers

Species	2222222222222222222222222222222222222222222222222222222222222222222222222222222 1111222222222222333333333333333333344444444444444444445555555555555555555 8899122334567788111222345556778889900111334445567778889011223445666677788994709439254624803014258402587092581469258390681491287890557096470025814769250
purpurana	TCTTARTTTATGACTAATCTAAATAAATATTTTTATAATACAGTATTTGCAAAGATGAAAATTTGTATTTTAACT
packardiana	..W..A...TG.TTA..CTC.TCC....TC.C.C...TATT........T.G..T....T.CCC..T.C...T..
striana	..A..AC..TA.TTA..CTC.TCC....TC.C.....TACT........T....T....T..C...T.....T..
alberta	.AA..A...TG.TTAG.CTC.TCC....TC.C.C...TATT........T.G..T....T..CC..T.C...T..
rosana	.T.CGT.C.TARGTAG..T..TT.G...Y.C..AT...ATT........TT.......R.............TC
fuscocupreana	.T..GT...CA.......T..TT.....T..A.AT...ATT.......ATC....C..G.............TT.
argyrospila	ATC..T..CTAA......T.R.T..TG......ATA..ATT.A..C...TT.....A.R.G...A.T..C...Y.
WC argyrospila	AYC..T..CTAA......T...T..TG......ATAR.ATT.A..C..STT.....A.R.G...A.T..C...T.
nigriplagana	AT...T...CA.....T.T...C..T.......AT...ATT.A...C..TT.G...A...G..............
goyerana	ATC..T..CT.A......T.G.T..T.......ATAG.ATT.A..Y.C.TT.....A...G...A.T........
mortuana	ATC..T..CTAA......T.R.T..TG......ATA..ATT.A..C...TT.....A.G.G...A.T..C.....
semiferana	.Y...A.C.C...........TT..T.CTC.CAAT.TCATTG........TT.......G..............T.
negundana	.T...A.C.T.AR........TT..C..TC.CGAT.TTATT........TT.......RG.....C.......T.
georgiana	YT...T.C.YA..TR...T..RT.....T.C..AT...A.T..A...C.TT.......R.GC...R.....T...
magnoliana	.T...T..C....TA..CT..TT..R..T....AT...ATTR.....CATC.......G....C........T.C
grisea	AT...T...T...YA...T..TT.....T...CAT..TATT........TC.......R....C.C.......T.
cerasivorana	.TY.GTC..TAA......T..TT.....C....AT...A.T..CT...ATT.GC..........A..C....TT.
fervidana	W...GTC..TA...A...T..TT.....C....AT...A.T..CT....TT.GC......GC..A..C..C.TT.
infumatana	...C.TC..TAA.TA...T..CT.....C....AT...A....CT..CATT.GC....G.....A.......TT.
rileyana	..C..Y...TAA.TA.T.T..TT.....T....AT...A.T..CT.C..TC..C...T.............T.C

B. Base pair numbers

Species	2222222222222222222222222222222222222222222222222222222222222222222222222222222 6666666666666666677777777777777777778888888888888888888899999999999999999 0111123455666778911123334456678999900111222333455578999000012355666678880369249281270751234734958739287036948012469258401677356146892429147892590
purpurana	CTTAACTATTTTTATTTCACATTATTTTTTTTTATTTATTATTAATCTTTTGTTATAGATTTTTCAAGATCT
packardiana	TA...A....ACCCA..T..TC..C..A.A.C..C.C.CC.GCC..ATG.....AG......CCCT...T.TC
striana	TA..GA....ACCCA..T..T......A.A....C.C.CC.ACC..ATG.....AG......C.CT..AT.TC
alberta	TA...A....ACCCA..T..TC..C..G.A....C.C.CC.GCC..ATG.....AG......CCCTG..T.TH
rosana	..A.G........TG.CT..T.C...CAC....CC.C.CC.....G.T.C....A.....CC.YCTR..YWT.
fuscocupreana	.......T.Y...TG..T..T...C.CA......C.C.CT.....G.T.....A........CCT...T.T.
argyrospila	..AGGT.TC.A..T.C.T..T..TC.CA.AYY...AC.CT.......T.....AA......C.CCT...T...
WC *argyrospila*	..AGGT.TC.A..T.C....T..TC.CA.A.Y...GC.CT.......T.....AA......C.CCT...T...
nigriplagana	.......T..A..TAC....TC.TC.CA.....C..T.CT..C.....C....AA.....CC.......T...
goyerana	..A...T.C.A..T.C.T..T..TC.CA.ACC...AC.CT.......T.....AA......C.CCT...T.T.
mortuana	..AGGT.TC.A..T.C.T..T..TC.CA.ACC...AC.CT.......T.....AA......C.CCT...T...
semiferana	..A....T.....TG..T..T.....CR......YCC.CC.......T......A..R.......ACM.T.TC
negundana	..AG...T.....TG..T..T......A..C...CCC.CC.......T......A..G.......AT..T.TC
georgiana	..YR...T.YA..T...T......C.CA..C...C.C.CC.GA....T.....AA..R...C.Y..R..Y.T.
magnoliana	.......T....CTA.....T...C.CA....T..CC.CY.......T......A........C.AC..TCT.
grisea	.......TC.AC.TGC....T....CCGA.C...C.C.C...C.T..T......A......C...AC..C.T.
cerasivorana	.C.......C.......TGTT.A...CA.A......C..TAT...R.TA.C.A.....AG.C..CT..ATCTW
fervidana	.CY.....Y...TA.CTG.T.A...CA.A.....AC..CAT..G..TA.CCA...C.AGC....T....TT.
infumatana	.C..........TA..TGTTCA...CA.A.....AC..TA....G.TA.C.A...C.AGCC..CTT.AT.T.
rileyana	....G....CCC.TA.CT..T.A.C..A..CC..C.CC..A.....T...C.........CC..T.T.C.T.

One of the 179 parsimony-informative base pairs (2695) was omitted because it was relevant only to non-*Archips* outgroups. Base pair numbering corresponds to homologous sequence in *D. yakuba* (Clary & Wolstenholme 1985). IUPAC code symbols denote nucleotide variation within species: R = A or G, Y = C or T, M = A or C, S = C or G, W = A or T, and H = A, C, or T. All haplotypes of *A. mortuana* are identical to other *A. argyrospila* haplotypes. Haplotype variation in *A. argyrospila, A.* near *argyrospila,* and *A. mortuana* is documented in Kruse & Sperling (2001).

by bootstrap values >50% and more than one decay index. *Archips georgiana* was not included in this clade in mtDNA analyses as it was in morphological analyses (Fig. 2).

The Argyrospila Group was strongly supported by bootstrap (88%) and decay indices (parsimony relaxed over eight steps). The species arrangement in this second clade differs from that found in morphological analyses (Fig. 2). Without *A. georgiana,* the group was supported by a bootstrap value of 100% and a decay index >10.

The Cerasivorana Group, first identified by MacKay (1962), was supported by a bootstrap value of 70% and a decay index of 8. The Packardiana Group was robustly supported (bootstrap of 100% and decay index >20). At the base of the Cerasivorana Group, without support, was the Purpurana Group consisting of *A. purpurana.* This placement of the Purpurana Group is

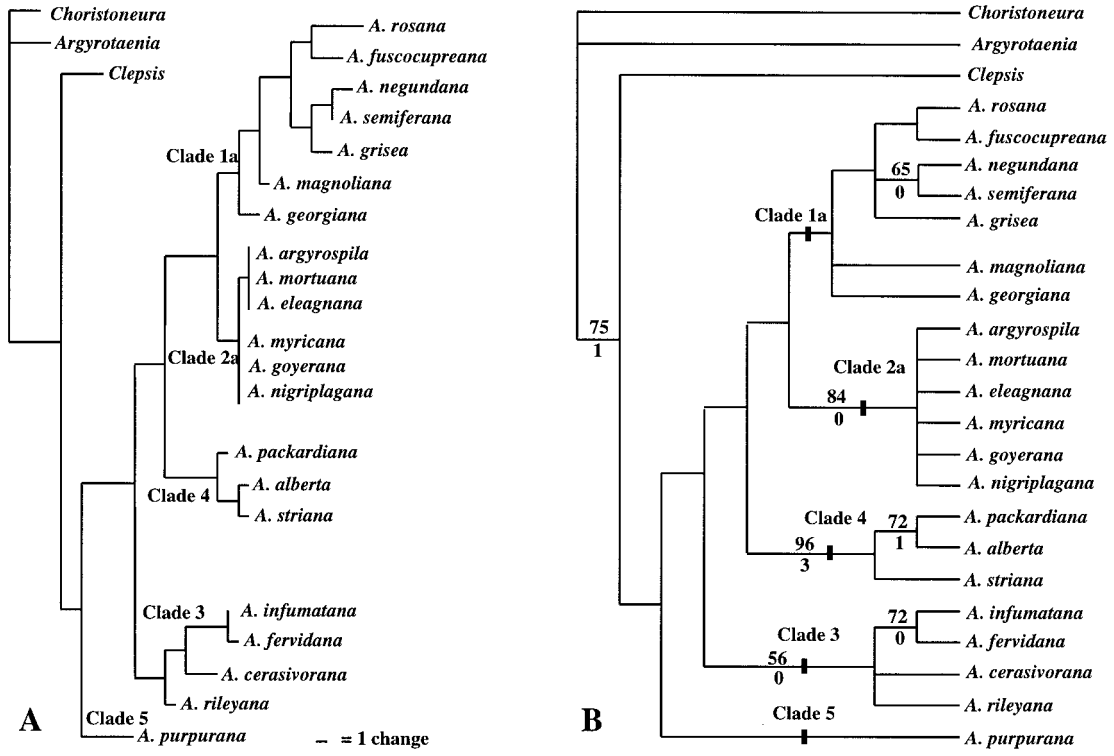

Fig. 3. Trees derived from 16 most parsimonious unrooted trees of 51 ingroup mtDNA COI haplotypes representing 20 *Archips* species and three outgroup genera (633 steps, CI = 0.548; RI = 0.841; RC = 0.461). West Coast *A. argyrospila* is labeled as a separate taxon. Sequences for *A. eleagnana* and *A. myricana* were unavailable, and these taxa are excluded. *Archips mortuana* mtDNA COI sequence was not distinguishable from that of *A. argyrospila.* Clades representing species groups as described in the text are indicated by vertical bars. The species composition of clades marked with a letter differ from other analyses. (A) Representative phylogram. (B) Strict consensus. Numbers above branches indicate bootstrap values, and below branches indicate decay index. Only bootstrap values >50% between species are shown. With the exceptions of *A. argyrospila*, *A. mortuana* and *A. goyerana*, bootstrap values within species exceeded 95% but are not shown.

different than that obtained in the morphological analyses (Fig. 2) or maximum likelihood analyses.

The maximum likelihood phylogram is shown in Fig. 4. The five species groups are identical and similar in position to those found in the parsimony trees. A minor exception is that the Cerasivorana and the Packardiana Groups are successively basal to the other groups rather than sister to them. The Purpurana Group is basal to all *Archips* in this analysis as it was in the morphological analyses (Fig. 2), rather than in a position basal to the Cerasivorana Group as in the heuristic parsimony results using the same mtDNA data.

Combined Analyses. A heuristic parsimony search, involving all 179 parsimony-informative characters of 20 species of *Archips* where both molecular and morphological characters were available, resulted in three most parsimonious trees of 553 steps (CI = 0.443; RI = 0.594; RC = 0.263). The only exception to complete correspondence among trees is the *A. argyrospila*/*A. mortuana*/West Coast *A. argyrospila* polytomy. A representative phylogram is shown in Fig. 5. This tree corresponds to the bootstrap consensus tree and to the consensus of the three phylograms.

As with separate molecular and morphological analyses, combined analysis revealed five clades (Fig. 5). These clades agreed in species composition with the molecular topology, and in species group arrangement as a composite of both morphological and molecular topologies (Figs. 2–5). The Rosana Group, containing *A. rosana*, *A. fuscocupreana*, *A. negundana*, *A. semiferana*, *A. grisea*, and *A. magnoliana*, was consistently derived but poorly supported, closely following separate molecular analysis results. Only the species pair of *A. negundana* and *A. semiferana* was supported by bootstrap values and decay indices (99% and nine, respectively). The Argyrospila Group, containing *A. argyrospila*, *A. mortuana*, West Coast *A. argyrospila*, *A. goyerana*, *A. nigriplagana*, and *A. georgiana*, was supported by a bootstrap value of 53% and a decay index of 2. Without *A. georgiana*, the group was supported by a bootstrap value of 100% and a high decay index (8), a result similar to the molecular analysis alone.

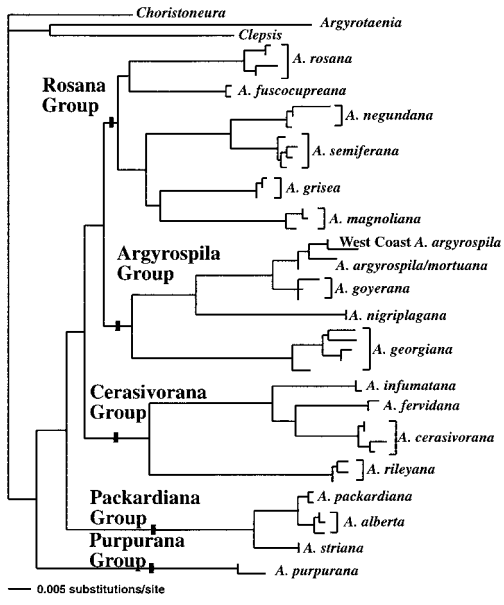

Fig. 4. Maximum likelihood hypothesis of relationships. Model: HKY85 with transition/transvertion ratio set to two (estimated by PAUP from the parsimony tree in Fig. 3A). All sites were assumed to evolve at the same rate. Starting branch lengths were obtained using the Rogers-Swofford approximation method (Rogers and Swofford 1998). Species groups as described in the text are indicated by vertical bars.

The third clade, containing the Cerasivorana Group, was supported by a bootstrap value of 91% and a decay index of 8. This support was greater than molecular or morphological data alone. The Packardiana Group, comprising the fourth group, was robustly supported (bootstrap of 100% and decay index >20) and was sister to the Cerasivorana Group. This result corresponds to the molecular parsimony trees but does not agree exactly with the maximum likelihood tree. Together, the Packardiana Group and the Cerasivorana Group are sister to the rest of the *Archips* represented here. The position of the Purpurana Group follows that of the morphological data set and the maximum likelihood tree, basal to all other species of *Archips.*

Discussion

The utility of mitochondrial DNA sequence analyses in systematic studies at the species level has been demonstrated in recent studies involving the family Tortricidae (Sperling and Hickey 1994, Newcomb and Gleeson 1998, Landry et al. 1999). Mitochondrial genes provide a wealth of variation that may be particularly useful in generating phylogenies in taxa where morphological differences are subtle (Sperling and Hickey 1994, Cognato et al. 1999, Kruse and Sperling 2001). Combined data sets that involve molecular, morphological, and/or ecological data in insects have led to better and more resolved trees than have analyses of any single data set alone (Miller et al. 1997, Damgaard et al. 2000, Normark 2000, Skevington and Yeates 2000). Combined morphology and molecular data sets for lepidopterans have produced excellent templates for testing evolutionary hypotheses about other phenotypic characters (Brown et al. 1994).

Differences between rates of evolution in morphological and molecular characters may allow morphological evidence to provide substantial support for internal nodes that are supported by few molecular synapomorphies (Brown et al. 1994, Sperling et al. 1997). *Archips* species provide an example in which molecular genetic variation and morphology combine to produce a more robust phylogeny than when analyzed independently. Key basal nodes unsupported by bootstrap or decay indices in separate analyses were better supported when data sets were combined (Figs. 2 and 3, 5). For example, the clade containing the Rosana Group and the Argyrospila Group was supported by a bootstrap value of 62% and a decay index of 4 in the combined tree. *Archips* other than the Purpurana Group was supported by a bootstrap value of 57% and a decay index of 1, and all 20 *Archips* species represented in the combined analysis were supported by a bootstrap value of 50% and a decay index of 1. These nodes received less support in both of the separate analyses.

There were three conflicts between the hypotheses of the two separate data sets: the position of *A. georgiana*, the position of the Cerasivorana and Packardiana Groups relative to each other and the rest of *Archips*, and the position of the Purpurana Group. The basal position of *A. georgiana* to the Argyrospila Group was strongly indicated by mtDNA phylogeny using parsimony and maximum likelihood (Figs. 3 and 4). Overall morphological similarity caused *A. georgiana* to be affiliated with the Rosana Group in morphological analyses. In combined analyses, the molecular topology was dominant but had reduced support when compared with the molecular topology alone (Figs. 3 and 5).

Razowski (1977) placed *A. purpurana* within the Xylosteana Group, noting several autapomorphies. The position of *A. purpurana* within the Xylosteana Group could not be supported in this study by molecular or morphological analyses. In combined analyses, there was substantive support for a placement of the Purpurana Group as basal within *Archips.* The addition of Palaearctic Xylosteana Group species and other species groups in future analyses will be vital to any further decisions about the placement of the Purpurana Group.

The integrity of the Cerasivorana and Packardiana Groups was strongly supported in all analyses (Figs. 2–5). In this study, support was found in combined analyses to place the groups together as a sister clade to the rest of *Archips* exclusive of the Purpurana Group (Fig 5). The Packardiana Group has been proposed as a separate genus, *Archippus* (Freeman 1958) and as a group that is primitive and basal to the rest of *Archips* (Razowski 1977). We were unable to diagnose the "recurved, slightly invaginated" uncus character de-

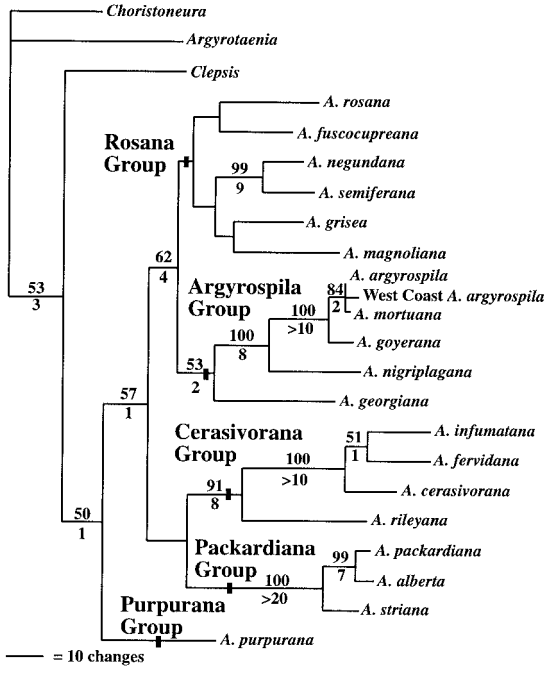

Fig. 5. Representative phylogram from three most parsimonious unrooted trees resulting from heuristic search of 179 combined molecular and morphological parsimony-informative characters. Molecular portion comprised 149 parsimony-informative characters from 51 ingroup mtDNA COI haplotypes, combined with 30 parsimony-informative morphological characters representing 20 *Archips* species where both data sets were available (553 steps, CI = 0.443; RI = 0.594; RC = 0.263). Major clades as described in the text are indicated by vertical bars. Numbers at branch nodes indicate bootstrap-decay index values. Only bootstrap values >50% are shown.

scribed by Freeman (1958) for *Archippus;* however, we found other autapomorphic characters for the group (Table 2).

Our molecular data are the first robust evidence uniting the Cerasivorana Group using other than larval characters as described by MacKay (1962) and the first evidence separating the Cerasivorana Group from the Xylosteana Group of Razowski (1977). The Cerasivorana Group was basal to the Packardiana outgroup in morphological analyses with the strong influence of MacKay's (1962) larval data (Fig. 2). In the combined analyses, the morphological and molecular data strongly supported monophyly of the group.

According to our data, the Cerasivorana and Purpurana Groups are considered species groups on the same level as Razowski's (1977) original six and Freeman's (1958) concept of *Archippus.* We confirm the synonymy of *Archippus* is correct if the Cerasivorana and Purpurana Groups remain in the genus *Archips.* If *Archippus* is considered a genus, so must also the Cerasivorana and Purpurana Groups to keep *Archips* monophyletic (which seems prudent in this case). We do not recommend the elevation of these three groups to genera at this time. Future research should involve the addition of species to these analyses that represent additional Palaearctic members of the Xylosteana Group, other species groups within *Archips,* and further investigations of the systematic position of the Purpurana Group.

Sequence Availability. Sequences for *Archips* species are available from GenBank (accession numbers): *Clepsis peritana* (AF309512), *Argyrotaenia coloradana* (AF44166), *Archips argyrospila* West Coast (AF308931), *A. mortuana*/*A. argyrospila* (AF44167), *A. goyerana* (AF309509), *A. nigriplagana* (AF309510), *A. purpurana* (AF309511), *A. packardiana* (AF44168), *A. striana* (AF44169), *A. alberta* (AF44170), *A. rosana* (AF44171), *A. fuscocupreana* (AF44172), *A. semiferana* (AF44173), *A. negundana* (AF44174), *A. georgiana* (AF44175), *A. magnoliana* (AF44176), *A. grisea* (AF44177), *A. cerasivorana* (AF44178), *A. fervidana* (AF44179), *A. infumatana* (AF44180), *A. rileyana* (AF44181), and *Choristoneura rosaceana* (L19099).

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Appendix 1: Systematic List of Nearctic *Archips*

***Archips* Hübner, 1822**

See Razowski (1977) for a complete synonymy of the genus and species. We followed Powell (1983), who resurrected *A. eleagnana, A. myricana,* and *A. mortuana* from synonymy where Razowski (1977) had placed them under *A. argyrospila.*

I. Packardiana Group
1. *packardiana* (Fernald 1886)
2. *striana* Fernald 1905
3. *alberta* (McDunnough 1923)
4. *dissitana* (Grote 1879)*
5. *tsugana* (Powell 1962)*

II. Asiatica Group
6. *oporana* (L. 1758)*

III. Xylosteana Group
7. *rosana* (L. 1758)
8. *fuscocupreana* (Walsingham 1900)
9. *argyrospila* (Walker 1863)
10. *nigriplagana* Franclemont 1986
11. *goyerana* Kruse 2000
12. *mortuana* Kearfott 1907**

13. *eleagnana* (McDunnough 1923)
14. *myricana* (McDunnough 1923)
15. *semiferana* (Walker 1863)
16. *negundana* (Dyar 1902)
17. *georgiana* (Walker 1863)
18. *magnoliana* (Fernald 1892)
19. *grisea* (Robinson 1869)

IV. Cerasivorana Group
20. *cerasivorana* (Fitch 1856)
21. *fervidana* (Clemens 1860)
22. *infumatana* (Zeller 1875)
23. *rileyana* (Grote 1868)

V. Purpurana Group
24. *purpurana* (Clemens 1865)

* Species not examined in this study. We default them here to previous assignments (Razowski 1977).

** We have stopped short of synonymizing *A. mortuana* in this work. See Kruse and Sperling (2001) for a more thorough discussion.