

PHYLOGENETICS OF THE SCOLYTINI (COLEOPTERA: CURCULIONIDAE:
SCOLYTINAE) AND HOST-USE EVOLUTION

By

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ABSTRACT

PHYLOGENETICS OF THE SCOLYTINI (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE) AND HOST-USE EVOLUTION

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The Nearctic bark beetle genus *Scolytus* was revised based in part on a molecular phylogeny. Monophyly of the native species was tested using mitochondrial (COI) and nuclear (28S, CAD, ArgK) genes and 43 morphological characters in parsimony and Bayesian phylogenetic analyses. Parsimony analyses of molecular and combined datasets provided variable results while Bayesian analysis recovered most nodes with posterior probabilities >90%. Native angiosperm and conifer-feeding *Scolytus* spp. were recovered as paraphyletic. Twenty-five species were recognized. Four **new synonyms** were discovered: *Scolytus praeceps* LeConte 1868 (= *S. abietis* Blackman 1934; = *S. opacus* Blackman 1934), *S. reflexus* (= *S. virgatus* Bright 1972; = *S. wickhami* Blackman 1934). Two species were **removed from synonymy**: *Scolytus fiskei* Blackman 1934 and *S. silvaticus* Bright 1972. **Neotypes** were designated for the following species: *Scolytus aztecus* Wood 1967, *S. hermosus* Wood 1968 and *S. mundus* Wood 1968. A key, diagnosis, redescription, distribution, host records and images were provided for each species.

The influence of plants in the diversification of herbivorous insects, specifically those that utilize moribund and dead hosts, is unclear. Scolytini, a diverse tribe of weevils, specialize on many different plant taxa as a source of food. The phylogenetics of the Scolytini were

reconstructed using Bayesian analyses to examine the origin, test the monophyly of Scolytini genera, and illuminate patterns of host-use and feeding habits among the tribe. Analyses were based on COI, 28S, CAD and ArgK. Ancestral host usage was reconstructed using likelihood criteria. Diversification of the Scolytini generally occurred well after host taxa diversified, as a combination of host shifts and lineage tracking. Repeated independent shifts to the same hosts occurred. Diversification occurred on common and widespread hosts, there was a single origination of conifer-feeding from angiosperm-feeding species and evolution of fungus-feeding from phloem-feeding ancestors. Overall, the observed patterns of Scolytini host-use can be explained by a combination of the sequential evolution and host-use oscillation hypotheses.

The Neotropical bark beetle genera *Cnemonyx* Eichhoff 1868 and *Scolytus* Geoffroy 1762 were reviewed as part of ongoing research into the higher-level taxonomy of the Scolytini. *Ceratolepsis* Chapuis 1869 was **removed from synonymy** with *Cnemonyx* and seven **new combinations** are reported: *Ceratolepsis amazonicus* Eggers 1929, *C. boliviae* (Blackman) 1943, *C. hylurgoides* (Schedl) 1948, *C. insignis* (Wood) 1969, *C. jucundus* Chapuis 1869, *C. maculicornis* Blandford 1896 and *C. niger* (Eggers) 1929. One **new species** was described: *Scolytus rabagliatus*. *Cnemonyx setulosus* (Eggers) 1929 was **removed from synonymy** with *C. panamensis* (Blandford) 1896. Four **new synonyms** were discovered: *Ceratolepsis* Chapuis (= *Coptosomus* Schedl 1952), *Cnemonyx setulosus* (Eggers) 1929 (= *Cnemonyx similis* (Eggers) 1929), *Scolytus proximus* Chapuis 1869 (= *Scolytus brevicauda* Wichmann 1915) and *Scolytus thoracicus* Chapuis 1869 (= *Scolytus plaumanni* Wood 2007). One **new distribution record** was reported: *Scolytus multistriatus* in South America (Brazil).

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This work is dedicated to my family who have provided continuous support for all of my academic endeavors and allowed me to pursue my dreams.

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Please note that figures have been edited to conform with the Michigan State University dissertation formatting guidelines. Please refer to resulting publications for the final version of the figures.

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CHAPTER 1

A MONOGRAPH OF THE NEARCTIC *SCOLYTUS* GEOFFROY (COLEOPTERA:
CURCULIONIDAE: SCOLYTINAE)

Abstract

The Nearctic bark beetle genus *Scolytus* was revised based in part on a molecular phylogeny. Monophyly of the native species was tested using mitochondrial (COI) and nuclear (28S, CAD, ArgK) genes and 43 morphological characters in parsimony and Bayesian phylogenetic analyses. Parsimony analyses of molecular and combined datasets provided variable results while Bayesian analysis recovered most nodes with posterior probabilities >90%. Native angiosperm and conifer-feeding *Scolytus* spp. were recovered as paraphyletic. Native Nearctic species were recovered as two lineages with hardwood-feeding species sister to introduced Palearctic hardwood-feeding species rather than native conifer-feeding species. The Nearctic conifer-feeding species were monophyletic. Twenty-five species were recognized. Four **new synonyms** were discovered: *Scolytus praeceps* LeConte 1868 (= *S. abietis* Blackman 1934; = *S. opacus* Blackman 1934), *S. reflexus* (= *S. virgatus* Bright 1972; = *S. wickhami* Blackman 1934). Two species were **removed from synonymy**: *Scolytus fiskei* Blackman 1934 and *S. silvaticus* Bright 1972. **Neotypes** were designated for the following species: *Scolytus aztecus* Wood 1967, *S. hermosus* Wood 1968 and *S. mundus* Wood 1968. A key, diagnosis, redescription, distribution, host records and images were provided for each species.

Introduction

The Scolytinae is comprised of at least 6,000 species in 26 tribes and approximately 225 genera (Wood and Bright 1992; Mandelshtam and Beaver 2003; Oberprieler et al. 2007). These ‘bark beetles’ are ubiquitous in forests worldwide. Many species contribute to the decomposition of dead vegetation while others are capable of causing substantial host mortality. Bark beetle adults and larvae feed on phloem and cambium of living, declining, or dead trees (Wood 1982).

Beetle feeding on phloem hastens the decomposition of trees and the introduction of other xylophagous organisms. Some bark beetle species kill live trees by introducing fungi into otherwise healthy trees as a by-product of phloem feeding and the galleries may girdle the host causing mortality (Wood 1982). At high density these species cause widespread destruction of economically valuable tree species, giving bark beetles their nefarious reputation as ecologically and economically destructive forest pests (Furniss and Carolin 1977), the most destructive of which is the mountain pine beetle, *Dendroctonus ponderosae* Hopkins 1902. This species occurs in Rocky Mountains states and provinces of the US and Canada (Furniss and Carolin 1977). During part of an outbreak that began in the early 1990’s more than four million hectares of pine forest were infested in British Columbia alone (Ebata 2004; Taylor and Carroll 2004). *Ips typographus* (L.) 1758, the European spruce bark beetle, is the most destructive species in Europe and during an outbreak between 1990 and 2001 infested more than 2.8 million hectares of spruce (Grégoire and Evans 2004). *Scolytus* Geoffroy 1762, contains six potential tree killing species that cause significant mortality of both conifers (Cibrián Tovar et al. 1995) and *Carya* spp. (Furniss and Carolin 1977) in the Nearctic region. *Scolytus multistriatus* (Marsham) is a key vector of the fungi associated with lethal Dutch elm disease, a pathogen that has killed millions

of *Ulmus* spp. trees in forest and urban areas across much of the US (Furniss and Carolin 1977). Mortality caused by various *Scolytus* species is often sporadic and short-term, although some outbreaks locally affect thousands of acres a year (Furniss and Carolin 1977). Damage is most severe in times of environmental stress, which is mostly associated with drought and other insect infestations. For example, *Scolytus ventralis* LeConte killed approximately 72,843 hectares of *Abies* spp. in California alone in a year (Furniss and Carolin 1977).

In addition to destruction caused by native North American scolytines, introductions of exotic bark beetle species threaten native forests (Haack 2001, 2006; Brockerhoff et al. 2006; Aukema et al. 2010, 2011; Hulcr and Dunn 2011). Exotic scolytines are among the most frequently intercepted species from shipping dunnage and packing crates (Haack 2001, 2006). The ability to detect and manage both native and exotic species relies on a solid understanding of systematics, phylogenetics, and taxonomy, which has not been achieved for most groups of bark beetles on a worldwide scale (Wood and Bright 1992). Other economically important bark beetle genera such as *Dendroctonus* Erichson 1836 and *Ips* DeGeer 1775 have received considerable attention and therefore have a reasonably solid understanding of the taxonomy (Wood and Bright 1992) but *Scolytus* is also important and notoriously difficult to identify.

Natural History

Scolytus are distributed in the Nearctic, Palearctic and Neotropical regions and some Palearctic *Scolytus* species have been introduced to the Nearctic, South Africa, Australia, New Zealand and temperate South America (Rosel and French 1975; Bain 1990; Wood and Bright 1992; Six et al. 2005; Wood 2007). In the Nearctic region, *Scolytus* species occur from the Atlantic to Pacific Oceans and from the boundary of the Neotropical region to within the Arctic

Circle. In the Nearctic, native angiosperm feeders are generally found from the Atlantic coast to Texas and west to the foothills of the Rocky Mountains. With the exception of *S. piceae* (Swaine), conifer-feeding *Scolytus* are restricted to the occurrence of host trees in western mountain ranges including the Rockies. *Scolytus piceae* has an expansive range from the east and west coasts of North America and from northern California and Colorado north to the Arctic Circle. Introduced *Scolytus* species are found throughout the US, northern Mexico and Southern Canada (*S. mali* (Bechstein) 1805, *S. multistriatus* (Marsham) 1802, *S. rugulosus* (Müller 1802), and *S. schevyrewi* Semenov 1902).

Members of the *Scolytus* conifer-feeding clade feed exclusively on Pinaceae genera, including *Abies* Mill., *Larix* Mill., and *Picea* D.Don. ex Loudon, *Pseudotsuga* Carrière, and *Tsuga* Carrière, but with the notable exception of *Pinus* L. (Wood and Bright 1992) (Table 1.1). Members of the angiosperm feeding clade, *S. muticus* Say, *S. fagi* Walsh, *S. quadrispinosus* Say, feed on the families Cannabaceae (*Celtis* L.), Fagaceae (*Fagus* L., *Quercus* L.) and Juglandaceae (*Carya* Nutt.) respectively (Table 1.2).

All Nearctic *Scolytus* species are monogamous. Females select brood material, begin gallery construction and are subsequently joined by males. Males walk across the host material in search of females. Mating occurs with the female in the gallery and the male on the bark. The female creates an entrance tunnel at a 45-degree angle, boring through the bark to the cambium. From the entrance tunnel, she excavates a nuptial chamber and depending on the species, also one or two egg galleries in either direction of the entrance tunnel. The nuptial chamber and galleries are excavated in the cambium but also etch the sapwood. Females excavate egg niches on both sides of the egg galleries and a single egg is deposited in each niche. Adult males assist in removing frass and generally stay with the female until egg gallery construction is complete. The male then

leaves the gallery and the female dies in the entrance tunnel with her abdomen projecting onto the bark surface. Larval galleries radiate away from the egg tunnels as they feed on phloem, also etching the sapwood. Once larvae mature, the prepupae burrow into the outer sapwood where pupation occurs. The brood overwinters as pupae and adults emerge in the spring (Edson 1967). Upon emergence, species may engage in maturation feeding on twig crotches and/or leaf petioles for *S. mali*, *S. multistriatus*, *S. quadrispinosus*, *S. rugulosus*, *S. schevyrewi* (Hoffman 1942; Baker 1972; Negrón et al. 2005), and within small twigs for *S. fiskei* (as *S. unispinosus* in McMullen and Atkins 1962).

Gallery shape is directly related to the resin system of the host genus. *Larix*, *Picea* and *Pseudotsuga* possess an elaborate system of resin ducts with vertical and radial ducts that are connected to each other (Lieutier 2004). *Scolytus* galleries in these tree genera are consistently parallel to the grain of the wood. The vertical ducts are abundant in these tree genera and when the beetle constructs a vertical egg gallery both ducts are severed. As the gallery is elongated, only vertical canals are severed. This minimizes exposure of *Scolytus* to host resins (Lieutier 2004). *Abies* and *Tsuga* lack resin canals and instead possess resin blisters in these genera galleries are less constrained because there are no resin canals to avoid (Lieutier 2004). Galleries in these genera are quite variable and may be transverse, “V” or epsilon shaped depending on the species.

All conifer-feeding *Scolytus* exhibit primary attraction to host volatiles rather than to pheromones produced by conspecifics (Macías-Sámano et al. 1998a). The attraction of angiosperm-feeding species is not well understood but primary attraction, attraction to the host, seems likely for native *S. quadrispinosus* and the invasive species *S. rugulosus* and *S. schevyrewi* (Goeden and Norris 1964a; Kovach and Gorsuch 1985; Lee et al. 2010). *Scolytus multistriatus*

exhibits secondary attraction, attraction using pheromones, to the pheromones 4-methyl-3-heptanol and multistriatin in combination with alpha-cubene (Lanier et al. 1977). In endemic populations, *Scolytus* will infest over-mature or weakened standing trees, shaded out branches, fresh logging slash, windthrown trees and fallen branches. During outbreaks, vigorous trees may be colonized by more aggressive species such as *S. quadrispinosus*, *S. mundus* and *S. ventralis* (Edson 1967; Furniss and Carolin 1977) and secondary species such as *S. monticolae*, *S. unispinosus* (McMullen and Atkins 1959). While *Scolytus* species are generally common in the forest they are rarely abundant and seldom encountered by collectors. *Scolytus* prefer fresh and moist host material. Sun-baked material is not preferred, but *Scolytus* galleries may be present in cooler, moister areas that receive a lot of shade or on the underside of fallen trees and branches. Infested branches and trees typically still bear green needles (Smith, pers. obs.). The entrance can be identified by peeling off the bark flakes with a knife and searching for white to tan colored boring dust or by close examination of the lateral and ventral sides of trunks and branches of smooth barked hosts. In *Pseudotsuga*, the entrance tunnels of *Pseudohylesinus* Swaine 1917 can be easily confused with those of *Scolytus*, but *Scolytus* entrance tunnels are at a steeper angle and the boring dust is reddish. Some *Scolytus* species, including *S. piceae*, *S. monticolae* and *S. subscaber* typically attack shaded out branches on standing trees. Infested material can be recognized by yellowing needles. *Scolytus* females typically conceal their entrance tunnels under bark flakes (common in *Picea*, *Pseudotsuga*, *Tsuga*) or in rough patches of bark (*Abies*, *Larix*).

Systematics

The Scolytini currently contains 209 species and six genera including *Camptocerus* Dejean 1821, *Ceratolepsis* Chapuis 1869, *Cnemonyx* Eichhoff 1868, *Loganius* Chapuis 1869,

and *Scolytopsis* Blandford 1896 and *Scolytus*. With the exception of *Camptocerus*, the tribe consists of cambium feeding bark beetles. *Scolytus* is unusual among scolytines because it is one of five genera in the subfamily that contain some species that feed exclusively on angiosperms and others that feed exclusively on conifers (Wood 1986). Twenty Nearctic and three Palearctic species feed on conifers. A single apical, unarmed spine-like process that curves toward and extends beyond the process of the inner apical angle of the protibia and a seven-segmented funicle readily distinguishes the tribe. All display a strongly sexually dimorphic head bearing hair-like setae, with the male frons variously excavated and female frons typically flat to convex. The eye is entire and the posterior area of the head is subtruncate. The pronotum is unarmed with a costate lateral margin. In addition, the metapleural suture descends subventrally to the groove, receiving the groove on the costal margin of the elytra, then turns abruptly and parallels the groove near the metacoxal process (Wood 1972, 1978, 1982, 1986). *Scolytus* is perhaps one of the easiest bark beetle genera to recognize with its distinctive ascendant second abdominal sternite, the slightly if at all declivous elytra and by the basal area of the elytra that is depressed around the triangular scutellum (Wood 1982).

Sexual Dimorphism

Scolytus species are sexually dimorphic. Sexually dimorphic structures are typically on the frons and epistoma (Figure 1.9) and the abdominal sternites and vary by clade (see clade discussions in results). Males typically have a flattened, impressed frons when viewed laterally and the female frons is always more strongly convex. The male frons is more strongly and coarsely longitudinally aciculate than the female and covered with longer, more abundant and dense erect setae. The epistomal process (when present) is more strongly developed in the male

and less developed in the female. With the exception of *S. piceae*, the spines, tubercles, denticles, carinae and tumescence on the venter are more pronounced in males.

Taxonomic History

There are currently 125 recognized *Scolytus* species around the world (Wood and Bright 1992; Wood 2007; Knížek 2011). Twenty-three species occur in the Nearctic region, including four invasive Palearctic species. Several Nearctic *Scolytus* species were described as the North American continent was explored. General entomologists including Say (1824), Riley (1867) and Walsh (1867) first described the eastern angiosperm feeders. LeConte (1868, 1876) described the most common California species and species native to the interior mountain ranges. The prominent scolytine taxonomists Swaine (1910, 1917), Blackman (1934), Wood (1962, 1967, 1968) and Bright (1964, 1972) also described several *Scolytus* species. *Scolytus californicus* LeConte (1868) was described from “California” but Blackman (1934) deemed this species a synonym of *S. scolytus* (F.). Blackman also suggested that the specimen given to LeConte might have been incorrectly labeled with the “California” locality. This species has been intercepted within the United States on numerous occasions but has never established a population (Blackman 1934; Wood 1982). *Scolytus scolytus* was therefore excluded from this monograph.

Historically, there has been a great deal of uncertainty regarding the status of several *Scolytus* species, particularly: *S. monticolae* (Swaine) and *S. tsugae* (Swaine), *S. abietis* (Blackman) and *S. opacus* (Blackman), *S. reflexus* Blackman and *S. wickhami* Blackman, and *S. fiskei* Blackman and *S. unispinosus* LeConte. Blackman (1934) and Wood (1982) formally revised the Nearctic *Scolytus*. A third revision by Edson (1967) applied as a M.S. thesis, was never published. Wood (1982) synonymized several species described by Blackman including *S.*

abietis, *S. wickhami* and *S. fiskei*. However, Edson (1967) recognized these species based on morphological, ecological and geographical differences. One of these species, *S. abietis* Blackman, was recently removed from synonymy because of such differences (Equihua-Martinez and Furniss 2009). Within *Scolytus*, species are generally recognized based on differences in male morphology, specifically the shape, concavity or lack thereof, ascending angle and protrusion of the basal margin of the second abdominal sternite, the placement and shape of the spine or lack thereof on the second sternite, presence or absence of a spine on the margin of sternite 2 and 3 and the frons aciculation and vestiture. Differences among species are generally subtle, and substantial knowledge of the intraspecific variation is needed for accurate identifications. Also, diagnostic morphological characters are absent for females; to date diagnostic characters are known only for females of angiosperm feeding species (Smith and Cognato 2010a). Association with a male or comparison to previously identified females is needed to identify female specimens of conifer feeders. Previous keys (LeConte 1876; Swaine 1918; Blackman 1934; Chamberlin 1939, 1958; Edson 1967; Bright and Stark 1973; Bright 1976; Wood 1982; Furniss and Johnson 2002) did not address the above deficiencies in species identification. In addition, previous authors were not explicit about their species concepts, raising doubts about the species boundaries.

Unlike previous investigations (Blackman 1934; Edson 1967; Bright 1976; Wood 1982), this study incorporates molecular and morphological data in phylogenetic analyses, which provides a basis for assessing species boundaries. This is the first modern taxonomic treatment of any group of *Scolytus* species and will serve as the basis from which the rest of the genus will be revised. This regional monograph of the Nearctic *Scolytus* provides a thorough review of taxonomic characters, an assessment of their phylogenetic utility, an evaluation of intraspecific

variation for each species, a key to both sexes and fully illustrates each species and diagnostic characteristics. There are currently 25 Nearctic *Scolytus* species.

A checklist of the Nearctic *Scolytus* species

Scolytus aztecus Wood 1967

Scolytus dentatus Bright 1964

Scolytus fagi Walsh 1867

Scolytus fiskei Blackman 1934 **removed from synonymy**

Scolytus hermosus Wood 1968

Scolytus laricis Blackman 1934

Scolytus mali (Bechstein) 1805 – Introduced

= *Scolytus sulcatus* LeConte 1868

Scolytus monticolae (Swaine) 1917

Scolytus multistriatus (Marsham) 1802 - Introduced

Scolytus mundus Wood 1968

Scolytus muticus Say 1824

Scolytus obelus Wood 1962

Scolytus oregoni Blackman 1934

Scolytus piceae (Swaine) 1910

Scolytus praeceps LeConte 1876

= *Scolytus abietis* Blackman 1934 **syn. n.**

= *Scolytus opacus* Blackman 1934 **syn. n.**

Scolytus quadrispinosus Say 1824

= *Scolytus carya* Riley 1867
 = *Scolytus caryae* Walsh 1867
Scolytus reflexus Blackman 1934
 = *Scolytus virgatus* Bright 1972 **syn. n.**
 = *Scolytus wickhami* Blackman 1934 **syn. n.**
Scolytus robustus Blackman 1934
Scolytus rugulosus (Müller) 1818 - Introduced
Scolytus schevyrewi Semenov 1902 - Introduced
Scolytus silvaticus Bright 1972 **removed from synonymy**
Scolytus subscaber LeConte 1876
Scolytus tsugae (Swaine) 1917
Scolytus unispinosus LeConte 1876
 = *Scolytus sobrinus* Blackman 1934
Scolytus ventralis LeConte 1868

Materials and Methods

Materials

Morphology

This revision is based upon examination of 4,957 adult ingroup specimens and 447 outgroup specimens. Specimens were obtained from field collecting events, reared from host material, or on loan from North American and European collections. The Palearctic species *Scolytus intricatus* (Ratzeburg) 1837, *S. laevis* Chapuis 1869, *S. mali*, *S. multistriatus*, *S. propinquus* Blandford 1896, *S. pygmaeus* (F.) 1787, *S. ratzeburgii* Janson 1856, *S. rugulosus*, *S.*

schevyrewi, *S. scolytus* (F.) 1775, *S. sinopiceus* Tsai 1962, and *S. sulciformis* Rey 1892 were selected as outgroups. *Scolytus propinquus*, a Neotropical species, was selected as the root taxon. The following entomological collection abbreviations (most following Arnett et al. 1993) are referenced in the text. Names of the curators that prepared loans are listed in parentheses.

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania
CASC	California Academy of Sciences, San Francisco, California (David Kavanaugh)
CSCA	California State Collection of Arthropods, Sacramento, California (Andrew Cline and Jacqueline Kishmirian)
CNCI	Canadian National Collection of Insects, Ottawa, Ontario, Canada (Hume Douglas, Patrice Bouchard)
CSUC	C. P. Gillette Museum of Arthropod Biodiversity, Colorado State University, Fort Collins, Colorado (Boris Kondratieff)
CUIC	Cornell University Insect Collection, Cornell University, Ithaca, New York (James Liebherr)
DEBC	Donald E. Bright, Jr. Collection, Fort Collins, Colorado (Donald E. Bright, Jr.), to be housed at the CNCI
EMEC	Essig Museum of Entomology, University of California Berkeley, Berkeley, California (Cheryl Barr)
FMNH	Field Museum of Natural History, Chicago, Illinois (James Boone)
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (Pol Limbourg)
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge,

	Massachusetts (Philip Perkins)
MSUC	Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan (Gary Parsons)
NHMW	Naturhistorisches Museum Wien, Vienna, Austria (Harald Schillhammer)
OSAC	Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon (Christopher Marshall)
RJRC	Robert J. Rabaglia Collection, Annapolis, Maryland (Robert J. Rabaglia)
SBMN	Santa Barbara Museum of Nature, Santa Barbara, California (Michael Caterino)
SMEC	Snow Entomological Museum, Lawrence, Kansas (Zachary Falin)
THAC	Thomas H. Atkinson Collection, Austin, Texas (Thomas Atkinson)
WFBM	William F. Barr Entomological Collection, University of Idaho, Moscow, Idaho (Frank Merickel)
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, Michigan (Mark O'Brien)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC (Including Stephen L. Wood Collection) (Natalia Vandenberg)

Additional distribution records were compiled from the following publications:

Blackman 1922, 1934; Doane et al. 1936; Edson 1967; Bright and Stark 1973; Bright 1976; Furniss and Carolin 1977; Furniss and Johnson 1987; Gast et al. 1989; Wood and Bright 1992; Cibrián Tovar et al. 1995; Furniss and Johnson 2002; Furniss et al. 2002; Lee et al. 2006; Humble et al. 2010; Smith and Cognato 2010a; Furniss and Kegley 2011; Lee et al. 2011). Plant

nomenclature was verified using the Missouri Botanical Garden's Tropicos database (www.tropicos.org) and the International Plant names index (www.ipni.org).

Specimens were examined using either a Leica (Wetzlar, Germany) MZ125 or MZ16 compound microscope and illuminated with a SCHOTT (Mainz, Germany) 150W halogen light source (model ACE®1). Images were taken with a Visionary Digital Passport II system (Palmyra, VA) using a Canon EOS 5D Mark II, 58mm Canon Macro photo lens, Canon Speedlite transmitter ST-E2, two Canon Speedlite 4303X II flashes and a Stack Shot (Cognisys, Inc, Kingsley, MI). Montage images were assembled using Helicon Focus Mac Pro 4.2.8 (Helicon Soft, Kharkov, Ukraine). Measurements were made using an ocular micrometer on the same microscope and with the same light source as above and calibrated with ROK (Shenzhen, China) 150mm digital calipers (model DC-122A) following the protocol of Smith and Cognato (2010b). Measurements were taken from the specimen's dorsal surface. Length was measured from the pronotum apex to the elytral apex. Width was measured at the widest part of the pronotum. Proportions are given as the ratio of length to width. A maximum of 50 specimens were measured for each species and were selected to encompass the known distribution.

If important locality data such as state or county was missing from specimen labels, the information was inserted between square brackets in the material examined. Locality data was obtained through examination of atlases and Google Earth. Holotypes of *Scolytus sulcatus* and *Scolytus californicus* LeConte 1868 were not physically examined. Type images were examined from the MCZ type database (<http://insects.oeb.harvard.edu/mcz/>) and the synonymy of these species was confirmed. *Scolytus californicus* was not included in this revision because it is a synonym of *S. scolytus*, which is not established in the Nearctic.

Taxonomic Characters

External anatomical terminology followed Hopkins (1909) subsequently used by Schedl (1931), Kaston (1936), Edson (1967) and Wood (1982, 1986, 2007). Sculpture terminology followed Torre-Bueno (1989). Several highly informative recently described Scolytini characters were also scored (Smith and Cognato 2010b). Provisional morphological homology was assessed by similarity and relative positions of characters as previously described. Sternites 1 and 2 are internal and are not externally visible (Hopkins 1909) so only visible sternites are referred to in the text. The third and fourth sternites are respectively referred to as the first and second sternites etc., as in Smith and Cognato (2010b).

Characters were scored from both sexes unless otherwise noted. *Scolytus* exhibits strong sexual dimorphism of the frons and abdominal venter; males display a wide array of morphological features, particularly on the venter, whereas females are conserved. As a consequence, characters were predominately male based. Characters and character state numbers correspond to data coded in the morphological data matrix for each taxon. The character matrix (Table 1.3) was constructed and edited using the online database MX (Yoder et al. 2006). Character transformations were evaluated using MacClade 4.0 PPC (Maddison and Maddison 2000) and homology of characters and definitions of characters states were re-examined and modified if necessary.

Ecological characters such as gallery pattern and host were scored. Character states were assigned based on a comprehensive literature review (e.g. von Butovitsch 1929; Chamberlin 1939; Schedl 1948; Balachowsky 1949; Stark 1952; Chamberlin 1958; Edson 1967; Bright and Stark 1973; Michalski 1973; Bright 1976; Furniss and Carolin 1977; Wood 1982; Atkinson and Equihua-Martinez 1986a; Wood and Bright 1992; Pfeffer 1994; Cibrián Tovar et al. 1995; Bright

and Skidmore 1997, 2002; Furniss and Johnson 2002), and with field notes, and label data on pinned museum specimens.

A total of 43 characters were used in this study (19 binary and 24 multistate). Ten characters were coded from the head, two from the thorax, ten from the elytra, one from the metepimeron, 17 from the venter and three ecological characters. Consistency and retention index values (ri and ci respectively) from the morphological phylogeny (Figure 1.1) and generated from MacClade are listed next to each character. Characters, states as follows:

1. *Epistomal emargination* (ci = 0.22; ri = 0.22): (0) weak; (1) moderate; (2) strong.
2. *Male epistomal process* (ci = 0.25; ri = 0.63): (0) absent; (1) present.
3. *Male frons shape* (ci = 0.25; ri = 0.45): (0) convex; (1) flat; (2) impressed.
4. *Male frons vestiture distribution* (ci = 0.33; ri = 0.20): (0) glabrous; (1) uniform; (2) predominately on margins; (3) epistomal region.
5. *Male frons vestiture length* (ci = 0.4; ri = 0.0): (0) less than width of eye; (1) equal to width of eye; (2) greater than width of eye.
6. *Male frons sculpturing* (ci = 0.38; ri = 0.50): (0) coarsely aciculate; (1) weakly aciculate; (2) rugose-reticulate; (3) smooth.
7. *Male frons punctures* (ci = 0.33; ri = 0.71): (0) small, fine; (1) small, coarse; (2) impunctate.
8. *Female frons shape* (ci = 0.67; ri = 0.50): (0) flat; (1) impressed; (2) convex; (3) excavated.
9. *Female frons sculpturing* (ci = 0.29; ri = 0.44): (0) coarsely aciculate; (1) finely aciculate; (2) reticulate.
10. *Female frons punctures* (ci = 0.14; ri = 0.54): (0) small, fine; (1) small, coarse.
11. *Pronotum length to width* (ci = 0.50; ri = 0.50): (0) as long as wide; (1) wider than long.

12. *Metepimeron length* (ci =0.29; ri = 0.50): (0) less than half-length of metepisternum; (1) half length of metepisternum; (2) greater than half-length of metepisternum.
13. *Elytral sides sub-parallel* (Michalski 1973) (ci =0.25; ri = 0.50); (0) on basal half; (1) on apical half.
14. *Interstrial setae* (ci =0.22; ri = 0.56); (0) glabrous; (1) sparse; (2) moderate.
15. *Interstrial impression* (ci =0.13; ri = 0.42): (0) not impressed; (1) faintly impressed.
16. *Interstrial width* (ci =0.29; ri = 0.44): (0) equal to striae; (1) twice width of striae; (2) more than twice the width of striae.
17. *Relative size of interstrial punctures* (ci =0.25; ri = 0.25): (0) equal to striae; (1) smaller than striae.
18. *Strial impression* (ci =0.40; ri = 0.70): (0) not impressed; (1) weakly impressed; (2) moderately impressed
19. *Male elytral apex shape* (ci =0.25; ri = 0.67): (0) rounded; (1) subquadrate.
20. *Elytral apex emargination* (ci =0.38; ri = 0.76): (0) absent; (1) weak; (2) moderate; (3) strong.
21. *Apical margin of elytra serrate* (ci =0.20; ri = 0.33): (0) absent; (1) present.
22. *Punctures on elytral apical margin* (ci =0.20; ri = 0.53): (0) impunctate; (1) small, fine; (2) large, coarse.
23. *Venter appearance* (Blackman 1934) (ci =0.11; ri = 0.50): (0) smooth, shining; (1) shagreened, dull.
24. *Venter setae length* (ci =0.23; ri = 0.50): (0) less than 1 diameter of a puncture; (1) less than width of segment 3; (2) greater than width of segment 3; (3) glabrous.
25. *Female second sternite* (ci =0.60; ri = 0.50): (0) unarmed; (1) apical; (2) basal; (3) medial.

26. *Suture between first and second sternites* (Wood 1982) (ci =0.50; ri = 0.0): (0) clearly visible; (1) obsolete.
27. *Male first sternite apical margin* (ci = 0.42; ri = 0.68): (0) rounded, on vertical face; (1) weakly elevated; (2) lip; (3) weakly produced; (4) strongly produced; (5) flush, not on vertical face.
28. *Male second sternite armature* (ci =0.36; ri = 0.42): (0) unarmed; (1) basal spine; (2) medial spine; (3) apical spine; (4) carina on basal half; (5) carina on apical half.
29. *Male second sternite face* (ci =0.33; ri = 0.67): (0) convex; (1) weakly concave; (2) strongly concave; (3) flat.
30. *Second sternite punctures* (ci =0.25; ri = 0.63): (0) small, fine; (1) small, coarse.
31. *Setal tuft on male second sternite* (ci =1.00; ri = 0.0): (0) absent; (1) present.
32. *Second sternite lateral spines* (ci = 0.50; ri = 0.0): (0) absent; (1) present.
33. *Third sternite lateral spines* (ci = 0.50; ri = 0.0): (0) absent; (1) present.
34. *Fourth sternite lateral spines* (ci = 0.50; ri = 0.0): (0) absent; (1) present.
35. *Male fourth sternite armed medially* (ci = 0.17; ri = 0.29): (0) absent; (1) present.
36. *Male fifth sternite* (ci =0.60; ri = 0.75): (0) unarmed - lacking carina; (1) midpoint of the carina closer to apex; (2) midpoint of the carina closer to base; (3) carina midpoint equidistant from base and apex.
37. *Relative size of male fifth sternite compared to the third and the fourth* (ci =0.15; ri = 0.48): (0) 5 larger; (1) 3+4 larger; (2) equal.
38. *Male fifth sternite setal patch* (ci =0.33; ri = 0.50): (0) absent; (1) present.
39. *Male fifth sternite with a median depression* (ci =0.33; ri = 0.50): (0) absent; (1) present.

40. *Male metatibial setae* (ci = 0.50; ri = 0.0): (0) not conspicuously longer than those of other tibiae; (1) much longer and more abundant than those of other tibiae.
41. *Mating system* (ci = 1.00; ri = 0.0): (0) monogamy; (1) polygamy.
42. *Gallery type* (ci = 0.50; ri = 0.70): (0) vertical; (1) transverse; (2) epsilon; (3) multi-branched.
43. *Host* (ci = 0.73; ri = 0.73): (0) Fabaceae; (1) *Pseudotsuga*; (2) *Abies*; (3) *Picea*; (4) *Larix*; (5) *Tsuga*; (6) Ulmaceae; (7) Rosaceae; (8) Fagaceae; (9) Cannabaceae; (A) Juglandaceae; (B) Betulaceae.

Taxa, DNA sequences and Alignment

I included 83 specimens (Table 1.4) representing 32 *Scolytus* species to reconstruct phylogenies using DNA sequences from mitochondrial and nuclear genes and morphology. The same Palearctic outgroup species used in the morphological analyses were included in the molecular dataset. As many Nearctic species as possible were included in the analysis. I was unable to collect fresh material for *Scolytus dentatus*, *S. hermosus*, *S. mundus*, and *S. silvaticus*, which were therefore excluded from the molecular analyses. Sequences of the following species were obtained from GenBank and included in the analyses: *S. intricatus* (HQ883677, HQ883589, HQ883820, HQ883909) and *S. scolytus* (HQ883678, HQ883590, HQ883821, HQ883910). To assess mitochondrial cytochrome oxidase I (COI) intraspecific variation, I included 88 specimens (Table 1.5) representing 30 *Scolytus* species from as many populations as possible. Specimens were included in the four-gene phylogeny only if molecular characters were available for at least two genes.

DNA was extracted from freshly collected specimens preserved in 200 proof ethanol and from pinned specimens that had been killed in sawdust impregnated with ethyl acetate and then

immediately pinned. Specimens were dissected by removing the head and thorax from the abdomen. DNA extractions were performed on the head and thorax using a Qiagen DNEasy blood and tissue kit (Hilden, Germany) following the manufacturer protocols except for the DNA elution procedure, which consisted of a single elution of 100-200µl of buffer AE depending on the size of the specimen, with specimens measuring less than 5mm in length receiving 100 µl and those greater than 5mm in length receiving 200 µl. After the extraction process was completed, the body parts were rinsed in 70% ethanol, glued onto a mounting board, pinned, labeled and are vouchered in the MSUC. The resulting purified DNA was used to amplify partial gene regions of COI, D2 region of nuclear ribosomal 28S, CAD, and Arginine Kinase (ArgK) using the PCR primers listed in Table 1.6. The COI barcoding primers LCO 1490 and HCO 2198 did not consistently amplify scolytine COI sequences, which necessitated the construction of the degenerate scolytine specific primers, 1495b and rev750. These primers worked best for *Scolytus* specimens and have proven to be effective on a broad array of scolytine taxa (Cognato et al. unpublished). The 1495b and rev750 primers were used to create the *Scolytus* specific F215 and Rev453 primers, respectively for 5-20 years or older pinned specimens. All PCR cocktails consisted of a total volume of 25µl and included 14.25-17.25 µl ddH₂O, 2.5µl 10X PCR buffer (Qiagen), 1.0µl 25mM MgCl₂ (Qiagen), 0.5µl dNTP mix (Qiagen), 2-5µl DNA template, 0.25µl HotStar Taq DNA polymerase (Qiagen). PCR reactions were performed on a thermal cycler (PTC-2000, MJ Research, Waltham, MA or MyCycler Thermocycler, BioRad, Hercules, CA) under the following conditions: one cycle for 15 min at 95°C, 40 cycles for 30 (COI) – 45 (28S, CAD, ArgK) sec at 94°C, 45 sec at 50-58°C (see Table 1.5 for specific annealing temperatures), 1 min at 72°C and a final elongation cycle of 5 min at 72°C. PCR products were cleaned using ExoSAP-IT (USB Corp., Cleveland, OH) and following the manufacturer protocols. Cleaned

PCR products were then prepared for sequencing. Each reaction contained 3.5µl of cleaned PCR product, 1µl 33pM/µl sequencing primers (identical to those used in PCR), and 7.5µl of ddH₂O. Samples were sequenced in the Michigan State University Genomics Core facility using an ABI 3730 Genetic Analyzer (Applied Biosystems, Foster City, CA).

Sequences were received as chromatograms and the sense and antisense strands were compiled using Sequencher (Ann Arbor, MI) to trim sequences, examine for ambiguities and create consensus sequences. Sequences were blasted in GenBank to examine for paralogous copies and other potential problems including contamination and pseudogenes. Sequences for COI, CAD and ArgK were aligned using SE-AL v.2.0a11 Carbon (<http://tree.bio.ed.ac.uk/software/seal/>). Sequence length variation was only observed in 28S. Sequences of 28S were either manually aligned in SE-AL using a scolytine-specific secondary structure model (Jordal et al. 2008). Nexus files are available at <http://www.scolytid.msu.edu>.

Methods

Morphology

Phylogenetic analysis. The phylogeny was reconstructed using the criterion of parsimony implemented in PAUP*4.0 b10 PPC (Swofford 2002). A heuristic search with 1,000 stepwise random additions with tree bisection-reconnection (TBR) for 37 taxa (25 ingroup, 12 outgroup) was performed. Characters were unordered and equally weighted. Bootstrap values were calculated by performing 1,000 pseudoreplicates with simple additions in PAUP*. Bremer support values were calculated by creating a constraint tree in TreeRot v.2 (Sorenson 1999) and analyzed in PAUP* using a heuristic search with 100 addition-sequence replicates.

Molecular

Likelihood Phylogenetic Analyses. I analyzed the molecular and morphological datasets using Bayesian estimation of phylogeny with MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001). There were two Bayesian analyses, one with a molecular dataset (79 taxa) and one with a combined molecular and morphological dataset (83 taxa). Each dataset was divided into partitions, with 4 gene partitions for the molecular dataset and 5 partitions (4 gene and 1 morphological) for the combined dataset. I selected the best model for each data partition using MrModeltest (Nylander 2004). The GTR+I+ Γ (general time reversible with a proportion of invariant sites and a gamma-shaped distribution of rate variation across sites) model selected by Akaike Information Criterion (AIC) was found to have the optimal fit for the gene partitions and Γ (gamma) was chosen for the morphology partition. Taxa that were unable to be sequenced were included in the morphology partition of the combined dataset.

The molecular dataset was analyzed with four Metropolis-Coupled Markov Chain Monte Carlo searches (3 heated, 1 cold) for 2 million generations with sampling every 100th iteration. Approach to stationarity (burn-in) was 0.25. All parameters reached stability at 2 million generations and the split deviation between runs was 0.011074. Bayesian posterior probabilities of clades were calculated by a majority-rule consensus of those trees after the burn-in (15,000 trees).

For the combined analysis, four Metropolis-Coupled Markov Chain Monte Carlo searches (3 heated, 1 cold) were performed for 6.5 million generations with sampling as described for the molecular dataset. *Scolytus dentatus*, *S. hermosus*, *S. mundus*, and *S. silvaticus* were included in this analysis with only morphological characters. All parameters reached stability at 6.5 million generations and the split deviation between runs was 0.024100. Bayesian

posterior probabilities of clades were calculated by a majority-rule consensus of those trees after the burn-in (48,750 trees).

Parsimony Phylogenetic Analysis. Two heuristic searches with 100 stepwise random additions with tree bisection-reconnection (TBR) for 79 taxa (56 ingroup, 23 outgroup) were performed on the molecular dataset. In the first analysis, gaps were treated as missing data and in the second analysis, gaps were treated as a fifth character state. Partition Bremer support (PBS) values were calculated by creating a constraint tree in TreeRot v.2 (Sorenson 1999) and analyzed in PAUP* using a heuristic search with 100 addition-sequence replicates. Intraspecific and interspecific differences were generated by computing pairwise distances for each gene in PAUP*.

A single gene phylogeny was reconstructed using COI using a heuristic search with 100 stepwise random additions with TBR for 89 taxa (59 ingroup, 23 outgroup).

The combined dataset was analyzed using two heuristic searches with 100 stepwise random additions with TBR for 83 taxa (71 ingroup, 12 outgroup) and were analyzed following the protocols listed above.

Species Concept

Species are hypotheses of unique evolutionary entities, which are tested by monophyly (*sensu* Wheeler and Platnick 2000). These monophyletic groups of individuals are named if they are diagnosable by synapomorphies or a unique combination of homoplastic characters. If diagnostic characters are not found, the clade will retain the original species name or will be synonymized with the sister clade. Therefore, based on species level morphological and

molecular phylogenies, species revisions will be based on monophyly of multiple individuals from disjunct populations.

Results

Phylogenetics of Nearctic Scolytus

Morphology

The native Nearctic *Scolytus* were recovered as polyphyletic with native species forming two clades, the native hardwood and conifer clades (Figure 1.1). The parsimony analysis produced 1,016 most parsimonious trees with a length of 262 steps and 41 of 43 parsimony informative characters. There was a moderate amount of homoplasy among the character states (CI = 0.332, RI = 0.539). Overall the phylogeny was weakly supported at the peripheral nodes and poorly supported at deeper nodes with many nodes unresolved.

The morphological phylogeny was poorly resolved and few synapomorphic characters were found (Figure 1.1). This reflects the morphological similarity of many taxa and homoplasy of many characters. The morphological phylogeny recovered two clades of native species, the native hardwood clade and the conifer clade. Two additional clades of Eurasian species were also recovered. The outgroup taxa were poorly resolved except for *S. rugulosus* and *S. sinopiceus*, which were recovered as sister taxa. *Scolytus fiskei* was found to be a distinct lineage separate from *S. unispinosus* in which it was considered a synonym. The relationship among *S. obelus*, *S. praeceps*, *S. abietis* and *S. opacus* was unresolved and *S. reflexus*, *S. virgatus* and *S. wickhami* were strongly supported as monophyletic. The lack of phylogenetically informative characters necessitated the need for further investigation using molecular characters to illuminate species boundaries.

Molecular

Bayesian analysis recovered most nodes with posterior probabilities >90%. The native Nearctic *Scolytus* were recovered as paraphyletic with Palearctic species (Figure 1.2). The Bayesian analysis recovered all taxa found to be monophyletic in the morphological phylogeny as monophyletic and the native species were recovered in two clades: native hardwood (*S. fagi*, *S. muticus* and *S. quadrispinosus*) and a second clade of conifer feeders (*S. aztecus*, *S. fiskei*, *S. laricis*, *S. monticolae*, *S. obelus*, *S. oregoni*, *S. piceae*, *S. praeceps*, *S. reflexus*, *S. robustus*, *S. subscaber*, *S. tsugae*, *S. unispinosus*, and *S. ventralis*) (Figure 1.2). In addition, two species were not monophyletic. *Scolytus reflexus* was polyphyletic with *S. virgatus* and *S. wickhami*, and *S. praeceps* with *S. abietis* and *S. opacus*. *Scolytus unispinosus* and its synonym, *S. fiskei*, were not monophyletic and were recovered as two lineages. *Scolytus rugulosus*, Palearctic hardwood feeder, was sister to the conifer clade. The parsimony analysis of mitochondrial COI produced 2,958 most parsimonious trees with a length of 1,434 steps and 606 of 616 characters were parsimony informative (CI=0.356, RI =0.809) (Figure 1.3).

The parsimony analysis of the molecular dataset with gaps treated as missing data produced 94,002 most parsimonious trees with a length of 2,451 steps and 604 of 2,296 characters were parsimony informative (Figure 1.4). There was strong signal within the phylogeny with the tree exhibiting a relatively low amount of homoplasy (CI=0.479, RI=0.773). The relationships within the phylogeny were strongly supported. Support values for each node were relatively high as compared to when gaps were treated as a fifth character (Table 1.9). Parsimony analysis of the combined dataset with gaps treated as missing data (Figure 1.7) produced a topology that is very similar to that of the molecular dataset except *S. hermosus*, *S.*

dentatus, *S. mundus* and *S. silvaticus* have been placed sister to taxa which they most strongly resemble.

The parsimony analysis of the molecular dataset with gaps treated as a fifth character produced 59,010 most parsimonious trees with a length of 2,647 steps and 636 of 2,296 characters were parsimony informative (Figure 1.5). Treating gaps as a fifth character resulted in an additional 32 characters and slightly reduced the amount of homoplasy within the phylogeny (CI=0.479, RI=0.773). However the topology was mostly unresolved and the overall support for each node and the tree was less than the analysis with gaps as missing data (Table 1.10, Figure 1.4). The native Nearctic *Scolytus* were recovered as polyphyletic and the native species occurred in three clades: conifer-feeding species; *S. fagi* and *S. muticus* sister to a clade consisting of *S. quadrispinosus* and Palearctic species. Parsimony analysis of the combined dataset with gaps treated as a fifth character state (Figure 1.8) produced a topology that is very similar to that of the molecular dataset except the native hardwood clade was monophyletic and *S. dentatus*, *S. hermosus*, *S. mundus* and *S. silvaticus* have been placed sister to taxa which they most strongly resemble.

Combined Analyses

Bayesian analysis of the combined dataset recovered the native Nearctic *Scolytus* as paraphyletic with native species found in two clades: native hardwood and conifer (Figure 1.6). Bayesian analysis of the combined dataset (Figure 1.6) recovered all taxa found to be monophyletic in the morphological phylogeny as monophyletic and the native species were recovered in two clades: native hardwood (*S. fagi*, *S. muticus* and *S. quadrispinosus*) and a second clade of conifer-feeders (*S. aztecus*, *S. dentatus*, *S. fiskei*, *S. hermosus*, *S. laricis*, *S.*

monticolae, *S. mundus*, *S. obelus*, *S. oregoni*, *S. piceae*, *S. praeceps*, *S. reflexus*, *S. robustus*, *S. silvaticus*, *S. subscaber*, *S. tsugae*, *S. unispinosus*, and *S. ventralis*) sister to *S. rugulosus*. The topology is almost identical to the topology of the Bayesian molecular phylogeny except *S. hermosus* (unresolved), *S. dentatus* (unresolved), *S. mundus* (2 synapomorphies) and *S. silvaticus* (2 synapomorphies) have been placed sister to taxa that they most strongly resemble.

Parsimony analysis of the combined dataset with gaps treated as missing data produced 22,003 most parsimonious trees with a length of 2,902 steps and 647 of 2,339 characters were parsimony informative (Figure 1.7). There was a low amount of homoplasy in the phylogeny and the phylogeny was strongly supported but less so than the molecular phylogeny (CI=0.458, RI=0.769) (Table 1.11). The native Nearctic *Scolytus* were recovered as polyphyletic and the native species occurred in three clades: conifer-feeding species; *S. fagi* and *S. muticus* sister to *S. quadrispinosus*; the Palearctic species, as in the molecular analysis. The parsimony analysis of the molecular dataset with gaps treated as missing data (Figure 1.4) had greater support at each node than treating gaps as a fifth character state (Table 1.9, 1.10). The native Nearctic *Scolytus* were recovered as polyphyletic with native species found in three clades, conifer, *S. fagi* and *S. muticus* forming one lineage and *S. quadrispinosus* as sister to a clade of Palearctic species. Three species were recovered polyphyletic. *Scolytus reflexus* was polyphyletic with *S. wickhami* and *S. virgatus*, *S. praeceps* with *S. abietis* and *S. opacus* and *S. fiskei* with *S. laricis*. *Scolytus sinopiceus* was sister to the conifer clade.

Parsimony analysis of the combined dataset with gaps treated as a fifth character state produced 13,003 most parsimonious trees with a length of 3,097 steps and 679 of 2,339 characters were parsimony informative (Figure 1.8). There was a low amount of homoplasy in the phylogeny (CI=0.48, RI=0.771) and the combined analysis was more resolved and more

nodes received support than the molecular analysis, which was almost completely unresolved (Tables 1.10 and 1.12). The native Nearctic *Scolytus* were recovered as paraphyletic with native species found in two clades, native hardwood and conifer. The parsimony analysis of the molecular dataset with gaps treated as a fifth character (Figure 1.5) had much less support than treating gaps as missing data (Table 1.12.). Treating gaps as a fifth character resulted in the placement of *S. rugulosus* as sister to the conifer clade. The hardwood clade was paraphyletic with *S. fagi* and *S. muticus* forming one lineage and *S. quadrispinosus* as sister to a clade of Palearctic species. *Scolytus reflexus* was polyphyletic with *S. virgatus* and *S. wickhami*, as well as *S. praeceps* with *S. abietis* and *S. opacus*. *Scolytus oregoni* was also not recovered as monophyletic. This species is morphologically and biologically distinct. The placement on the phylogeny is likely due to the fact that *S. oregoni* is missing some data for COI. Both *S. oregoni* 5 and 71 were collected from the same branch and directly compared to the holotype.

Discussion

Phylogenetic Analyses

As in other phylogenetic studies, the mitochondrial COI data failed to recover many species as monophyletic (Figure 1.3) (Cognato et al. 2005; Jordal and Hewitt 2005). Many of the relationships found in this phylogeny did not agree with the topologies obtained from different analyses. For example a hardwood-feeder, *S. rugulosus*, was found to be sister to the conifer clade in the Bayesian analysis and the parsimony analyses with gaps treated as a fifth character, while *S. sinopiceus*, a conifer-feeder, was found to be the sister taxa in the parsimony analyses with gaps treated as missing. In addition, the hardwood clade was paraphyletic with *S. fagi* and *S. muticus* forming one lineage and *S. quadrispinosus* as sister to *S. multistriatus*. Saturation of

nucleotide substitutions and a lack of lineage sorting are potential reasons for the discordance among these mitochondrial and nuclear phylogenies (Sota and Vogler 2001; Funk and Ohmland 2003; Lin and Danforth 2004). The mitochondrial phylogeny may suffer from both phenomena because of the observed poor resolution and support for deeper nodes and short-branch lengths among the conifer-feeding species (Figure 1.3). As with other studies, concatenating the COI dataset with multiple genes and morphology remedied its deficiency and elucidated the relationships among the *Scolytus* species (Jordal and Hewitt 2004).

In some other molecular phylogenetic studies, treating gaps as fifth character states help to improve phylogenetic resolution (e.g. Cognato and Vogler 2001; Lee 2001; Ruiz et al. 2009; Dole et al. 2010). Insertion/deletion events presumably represent heritable traits, which are potentially phylogenetically informative (Phillips et al. 2000). It was surprising that treating gaps as fifth character states in a parsimony analysis only slightly affected species relationships (Figures 1.5 and 1.8) and resulted in reduced support (Tables 1.10, 1.12). Treating gaps as fifth character states caused conflict among the molecular data, given that morphology provided the most support (Tables 1.11, 1.12). Suboptimal alignment of length variable regions is a one reason for reduced support and poor tree resolution (Cognato and Vogler 2001; Simmons et al. 2011). However, only 32 gaps were necessary to align our 28S data in reference to a secondary structure model (Jordal et al. 2008) suggesting it is unlikely that the alignment is the cause of the poor results treating gaps as fifth character states. Unraveling the cause of this underlying issue is beyond the scope of this taxonomic revision.

When analyzed together, the genes used in this study (COI, 28S, CAD, ArgK) were useful in resolving the *Scolytus* phylogeny. These genes have demonstrated similar phylogenetic utility in other scolytine studies (Cognato and Sperling 2000; Farrell et al. 2001; Jordal et al.

2002; Jordal and Hewitt 2004; Jordal et al. 2004; Cognato et al. 2005; Cognato and Sun 2007; Jordal et al. 2008; Dole et al. 2010; Cognato et al. 2011; Jordal et al. 2011; Jordal and Cognato 2012). In the four gene parsimony phylogenies, most support for each node derived from the COI dataset followed by CAD, ArgK and 28S (Tables 1.11-1.12). A similar pattern was observed combined analysis with gaps treated as missing data except morphology had the lowest contribution to the phylogeny (Tables 1.9-1.10). Overall, the model-based rates of nucleotide evolution utilized in Bayesian analysis combined with all four genes and morphology allowed us to recover a well-supported and sufficiently resolved phylogeny which enabled the revision of *Scolytus* (Figure 1.6).

Taxonomic Implications

The Nearctic *Scolytus* were not recovered as monophyletic but as two clades (native hardwood and conifer) and a group of introduced Palearctic species (Figure 1.6). Members of the native hardwood clade are sister to the *Scolytus* subgenus *scolytus* of von Butovitsch (1929) rather than the native conifer clade. This is supported by morphological similarities between the native hardwood clade and the *Scolytus* subgenus *scolytus* and the disparate morphology between the conifer clade. The *Scolytus* subgenus *scolytus* clade and the native hardwood feeders share a median impression on male sternite 5 (except *S. laevis* and *S. quadrispinosus*) and a setal patch on sternite 5 (except *S. laevis* and *S. quadrispinosus*). Several species in these groups share the absence of a carina on the male sternite 5 (*S. laevis*, *S. mali*, *S. ratzeburgii*, *S. fagi* and *S. muticus*).

Based on the results of our phylogenetic analyses, 25 valid species occur in the Nearctic. Several species were not recovered monophyletic in any analysis and had less than 1% difference

in COI sequences and were thus placed in synonymy with the oldest described species. The following synonyms were discovered: *S. praeceps* (= *S. abietis*; = *S. opacus*), *S. reflexus* (= *S. virgatus*; = *S. wickhami*). *Scolytus fiskei* was recovered as monophyletic and is removed from synonymy with *S. unispinosus*. Further detail regarding the taxonomic changes are found in the discussion section for each species.

***Scolytus* Geoffroy**

Scolytus Geoffroy 1762; type species: *Bostrichus scolytus* Fabricius 1775.

Ekkoptogaster Herbst 1793; type species: *Bostrichus scolytus* Fabricius 1775.

Coptogaster Illiger 1807; type species: *Bostrichus scolytus* Fabricius 1775.

Eccoptogaster Gyllenhal 1813; type species: *Bostrichus scolytus* Fabricius 1775.

Scolytochelus Reitter 1913; type species: *Ips multistriatus* Marsham 1802.

Ruguloscolytus Butovitsch 1929; type species: *Bostrichus rugulosus* Müller 1818.

Etymology. *Scolytus* is derived from ‘Le Scolyte’, the French common name for ‘bark beetle’ (Geoffroy 1762).

Taxonomic History. For a complete discussion, see Blackman (1934) and China (1962, 1963).

Diagnostic characteristics. *Scolytus* is easily distinguished from all other Nearctic scolytines by the unarmed protibia with a single curved process at the outer apical angle, flattened antennal club with 0-1 septate procurved sutures, seven segmented funicle, the slightly declivous elytra, the depressed scutellar notch and scutellum and by the abruptly ascending abdomen.

Redescription (modified from Wood 1982). Length 1.7 – 6.0mm, 1.7 – 2.9 times as long as wide. Color varies from red brown to black and teneral adults are often light brown.

Frons sexually dimorphic (discussed above and for each species group). Eye elongate, sinuate to shallowly emarginated and finely faceted. Antennal scape shorter than three funicle segments; funicle seven segmented; club large, flattened, oval to obovate, minutely pubescent and with strongly procurved sutures; suture 1 partially to completely septate and with or without a surface groove. Pronotum large, head visible from above, lateral margins marked by a fine raised line. Scutellum large, depressed below level of elytra and triangular. Elytra with a depressed scutellar notch and along the basal fifth to half of elytral suture; striate; slightly declivous apically. Anterior coxae narrowly separated. Abdomen ascending from posterior margin of sternite 1 to meet elytral apex, sternite 2 abruptly ascending (except *S. rugulosus*), often impressed, armed or both; abdomen dimorphic in most species (discussed above).

Taxonomic Treatment

There are some traditionally used terms and characters in *Scolytus* literature that require clarification. The term ‘venter’ is regularly utilized. In general, the term refers to the entire ventral surface of an organism. However in *Scolytus* it only pertains to the abdominal ventral concavity, specifically sternites 2-5. The length of sternite 5 compared to sternite 3 and 4 is another common misleading character in *Scolytus* literature. Rather than measuring the entire length of segment 5, only the distance from the basal margin to the subapical carinate ridge is measured and is compared to the combined lengths of sternites 3 and 4.

Glossary of Terminology

(modified from Hopkins 1909; Torre-Bueno 1937; Edson 1967; Harris 1979)

General

Apical: referring to a point at or close to the apex or tip.

Basal: referring to a point at or closest to the main body.

Impressed: a depression in a surface, typically referring the elytral striae or frons.

Concave: appearing hollowed out.

Convex: appearing rounded.

Vestiture: the surface covering composed of setae, in *Scolytus* the setae are either long or short.

Head (Figure 1.10)

Aciculate: refers to the longitudinal grooves or scratches on the frons that can appear coarse as if made by a knife or fine as if scratched with a needle.

Epistomal process: a raised, sinuate process composed of a median and two lateral sections fringed apically with thick, long bristles that cover the median epistomal area just above the mandibles.

Frons: region of the head from just above the epistoma to a point that is just dorsal to the inner apices of the eyes.

Inner apices of eyes: the innermost mesal margins of the eyes as viewed frontally.

Strigate: having narrow, transverse lines in the cuticle.

Vertex: the top of the head, above the eyes.

Elytra (Figures 1.11 and 1.12)

Apex: end of a structure that is distal to the base.

Disc: the central upper surface of the elytra between the elytral bases and the sloped declivity.

Striae: longitudinal lines or groves extending along the dorsal surface of the elytra, which are often impressed.

Interstriae: longitudinal spaces along the elytra between the striae, which are not impressed and bear smaller punctures.

Corrugated: with alternate ridges and channels, referring to the appearance of the elytral striae and interstriae.

Sutural dehiscence: the central notch at the apical margin of the elytra.

Abdomen (Figure 1.13)

Carina: a ridge-like or keel-shaped projection of the exoskeleton; on the venter.

Cusp: a slight projection or elevation along a margin; refers to the apical margin of sternite 1 in a few species.

Denticle: a small tooth.

Opaque: appearing dull in luster; referring to a surface that reflects little light.

Produced: refers to a part of the exoskeleton that is extended, lengthened, or elevated.

Punctate: set with fine impressed points appearing as pinpricks.

Punctulate: minute punctures.

Rugose: appearing wrinkled.

Shagreened: covered with a closely set roughness and appearing similar to sharkskin.

Shiny: appearing glossy or bright in luster; refers to a surface that appears polished and reflects light well.

Spine: an elongate projection of the exoskeleton that is longer than its basal width.

Sternite: In *Scolytus* there are five visible sternites. They are numbered from anterior to posterior with sternite 1 closest to the head and sternite 5 closest to the elytral apex.

Subapical carinate ridge: a carinate ridge on sternite 5 occurring just before the apical margin.

Tubercle: a small knob-like or rounded protuberance of the exoskeleton.

Tumescence: a swelling of the exoskeleton.

Venter: the undersurface of the abdomen, in *Scolytus* this pertains to sternites 1-5.

Damage Pattern (Figure 1.14)

Adult gallery: the composite tunnel produced by the adult female includes 1-2 egg galleries, the egg niches and the nuptial chamber (if present).

Egg gallery: a single extension of the adult gallery from the nuptial chamber (if present) along which eggs are deposited in niches.

Egg niche: Notches along the sides of the egg gallery excavated by females in which a single egg is deposited.

Larval mine: the excavation tunnel produced by the larva as it feeds.

Nuptial chamber: an enlarged area or short extension from the adult gallery at the base of the entrance tunnel that may be used for mating or as a turning niche.

Pupation chamber: an ovoid or circular excavation at the end of a larval mine in which pupation occurs.

Key to the adults of Nearctic *Scolytus* Geoffroy

This is the first key to Nearctic *Scolytus* adults of both sexes. Unlike previous keys (e.g. Edson 1967; Wood 1982) apriori knowledge of the gender is not required. Only one sex is

necessary to identify the specimen and host or gallery information are not needed. Because the sexual dimorphic characters are not consistent for the Nearctic species (see sexual dimorphism discussion above), the sexes could not be evenly split. In general, males and females of native hardwood-feeding species will key out beginning at couplet 3 and females and males of some *Abies* feeding species beginning at couplet 23. The key lists the gender of the identified specimen. If no gender is designated, the identification applies to both males and females. The length of setae on the frons is measured relative to the midpoint of the eye.

1	Elytral apices rounded (Figure 1.15A)	<i>Scolytus rugulosus</i> (Müller)
-	Elytral apices truncate (Figure 1.15B).....	2
2 (1)	Lateral profile of frons clearly flattened and/or impressed (Figure 1.9A).....	3
-	Lateral profile of frons convex (Figure 1.9B)	23
3 (2)	Apical margin of sternite 3 and/or 4 armed with teeth or spines laterally and/ or medially	4
-	Apical margin of sternite 3 and 4 unarmed.....	7
4 (3)	Apical lateral margins of sternites 3 and 4 armed with lateral teeth or spines.....	5
-	Apical lateral margins of sternites 3 and 4 unarmed.....	6
5 (4)	Apical margin of sternite 3 armed by three acute spines (two lateral and one medial); apical margin of sternite 4 armed by one median tooth; sternite 1 apically descending; sternite 2 deeply concave, basal margin produced and bearing a median tubercle.....	<i>Scolytus quadrispinosus</i> Say (male)

- Apical margin of sternite 3 and 4 each armed by two lateral teeth; sternite 1 horizontal; sternite 2 convex and bearing a blunt median tubercle on the basal margin.....
.....*Scolytus multistriatus* (Marsham) (male)
- 6 (4) Apical margin of sternite 4 armed by an acute median denticle; apical margins of sternites 2 and 3 may also each bear a smaller median denticle (variable).....
.....*Scolytus dentatus* Bright (male)
- Apical margin of sternite 4 thickened forming a broad carina with a blunt median tubercle; apical margins of sternites 2 and 3 always unarmed
.....*Scolytus silvaticus* Bright (male)
- 7 (3) Abdominal venter sternites 2-4 covered with abundant erect long hair-like setae.....
.....8
- Abdominal venter sternites 2-4 glabrous or covered with minute ground vestiture or short, sparse recumbent hair-like or scale-like setae10
- 8 (6) Frons with hair-like setae on lateral and dorsal margins thicker, longer, incurved, remaining areas of frons largely devoid of setae; frons strongly longitudinally aciculate
.....*Scolytus muticus* Say
- Frons with equally distributed hair-like setae of uniform length; frons weakly to moderately longitudinally aciculate or weakly aciculate-punctate.....9
- 9 (8) Apical margin of elytra produced between interstriae 1 and 2, deeply emarginated at interstria 3, produced on interstria 4 and deeply emarginated at stria 4; sternite 2 armed with a laterally compressed tubercle that extends from the apical margin of sternite 2 to approximately $\frac{3}{4}$ the length of sternite; frons weakly longitudinally aciculate, strongly punctate; epistoma strongly emarginated.....*Scolytus aztecus* Wood (male)

- Apical margin of elytra slightly emarginated at interstriae 3; apical margin of sternite 2 armed with a median denticle; frons moderately longitudinally aciculate, almost impunctate; epistoma entire to faintly emarginated.....*Scolytus mundus* Wood (male)
- 10 (7) Apical margin of sternite 1 rounded; basal margin of sternite 2 flat or marked by a weak carina; face of sternite 2 convex, often armed with a spine or tubercle.....11
- Apical margin of sternite 1 thickened or produced on the ventral and/or lateral margins, forming a carinate lip along the basal margin of sternite 2, often weakly produced in *S. monticolae* and *S. tsugae*; face of sternite 2 flat to impressed.....19
- 11 (10) Frons impressed above epistoma or medially impressed, strongly longitudinally aciculate12
- Frons flat, weakly to moderately longitudinally aciculate or coarsely punctate15
- 12 (11) Sternite 2 unarmed; elytral surface shining and glabrous.....*Scolytus mali* (Bechstein) (male)
- Sternite 2 armed with a spine; elytral surface dull, sparse setae present (rarely the spine on sternite 2 is absent in *S. schevyrewi*)13
- 13 (12) Base of spine touching apical margin of sternite 2; frons strongly longitudinally aciculate*Scolytus laricis* Blackman (male)
- Base of spine not touching apical margin of sternite 2; frons strigose-punctate.....14
- 14 (13) Spine conical, narrow; elytra always unicolorous; elytral disc shining and glabrous; subapical carina on sternite 5 located 1/2 width of segment from apex.....*Scolytus piceae* (Swaine) (male)

-	Spine broadly conical with blunted apex; elytra often with a banded appearance; subapical carina on sternite 5 located just before end of segment.....	
	 <i>Scolytus schevyrewi</i> Semenov (male)	
15 (11)	Sternite 2 armed with a rounded spine.....	16
-	Sternite 2 unarmed.....	17
16 (15)	Spine on sternite 2 extending from apical margin to three-fourths length of the sternite; sternite 2 surface shining.....	<i>Scolytus fiskei</i> Blackman (male)
-	Spine on sternite 2 extending from apical margin to one half length of the sternite; sternite 2 surface dull	<i>Scolytus unispinosus</i> LeConte (male)
17 (15)	Sternite 5 length at middle longer than or equal to that of sternites 3 and 4 combined; sternite 5 without a transverse carina near base	18
-	Sternite 5 length at middle shorter than that of sternites 3 and 4 combined; sternite 5 with a transverse carinate ridge near base that may or may not be reflexed (variable)	<i>Scolytus reflexus</i> Blackman (male)
18 (17)	Frons either granulate or faintly longitudinally aciculate; frons with setae uniformly distributed, fewer setae on lateral and dorsal margins, shorter, finer; elytra glabrous (except on declivity); sternite 5 unarmed.....	<i>Scolytus fagi</i> Walsh (male)
-	Frons moderately longitudinally aciculate, with long, fine, incurved setae predominately on lateral and dorsal margins, fewer, shorter and finer setae medially; elytra with minute ground vestiture.....	<i>Scolytus quadrispinosus</i> Say (female)
19 (10)	Apical margin of sternite 1 moderately produced and not forming a distinct lip along base of sternite 2.....	20

- Apical margin of sternite 1 distinctly thickened or strongly produced forming a lip along base of sternite 2.....21
- 20 (19) Face of sternite 2 shining but minutely reticulate; elytral striae not impressed; basal margin of sternite 2 more pronounced and produced laterally; elytral stria punctures small, spaced 2-3 diameters of a puncture*Scolytus monticolae* (Swaine) (male)
- Face of sternite 2 opaque; elytral discal striae impressed; basal margin of sternite 2 continuously and evenly elevated; elytral stria punctures large, spaced 1-2 diameters of a puncture.....*Scolytus tsugae* (Swaine) (male)
- 21 (19) Apical margin of sternite 1 distinctly thickened at most slightly produced over base of sternite 222
- Apical margin of sternite 1 strongly acutely produced forming a lip along base of sternite 2, face of sternite 2 appearing concave.....*Scolytus robustus* Blackman (male)
- 22 (21) Base of sternite 2 strongly thickened; face of sternite 2 often weakly medially impressed just above the base; apical margin of sternite 2 unarmed.....
.....*Scolytus oregoni* Blackman (male)
- Base of sternite 2 faintly elevated; face of sternite 2 flat; apical margin of sternite 2 slightly elevated often with a median denticle.....*Scolytus ventralis* LeConte (male)
- 23 (2) Apical margin of elytra produced between interstriae 1 and 2, deeply emarginated at interstria 3, produced on interstria 4 and deeply emarginated at stria 4
.....*Scolytus aztecus* Wood (female)
- Apical margin of elytra entire or slightly emarginated at interstriae three.....24
- 24 (23) Sternite 2 armed either on the face or on apical margin by either a spine or a low median tumescence25

- Sternite 2 unarmed.....	35
25 (24) Sternite 2 face armed with a rounded, keel shaped or broadly acute spine that is at least as long as its basal width	26
- Sternite 2 apical margin armed by a low median tumescence or small denticle	30
26 (25) Base of spine on sternite 2 touches the basal margin of segment; apical margins of sternites 3 and 4 each armed by two lateral teeth	
..... <i>Scolytus multistriatus</i> (Marsham) (female)	
- Base of spine on sternite 2 never touches basal margin of segment; apical margins of sternites 3 and 4 unarmed.....	27
27 (26) Base of spine not touching apical margin of sternite 2.....	28
- Base of spine touching apical margin of sternite 2.....	29
28 (27) Spine conical, narrow; elytra always unicolorous; elytral disc shining and glabrous; subapical carina on sternite 5 located 1/5 width of segment from apex.....	
..... <i>Scolytus piceae</i> (Swaine) (male)	
- Spine broadly conical with blunted apex; elytra often with a banded appearance; subapical carina on sternite 5 located just before end of segment.....	
..... <i>Scolytus schevyrewi</i> Semenov (female)	
29 (27) Sternite 2 armed with a stout and broadly acute spine and extending from the apical margin to one half length of the sternite, never with a longitudinal carina.....	
..... <i>Scolytus fiskei</i> Blackman (female)	
- Sternite 2 armed with a longitudinal carina and a blunt tubercle, appearing keel-shaped, or a low median longitudinal carina.....	<i>Scolytus praeceps</i> LeConte, in part

- 30 (25) Apical margin of sternite 1 produced, forming a carinate lip along the basal margin of sternite 2; sternite 2 appearing impressed..... 31
- Apical margin of sternite 1 rounded; basal margin of sternite 2 flat or marked by a weak carina; face of sternite 2 convex..... 34
- 31 (30) Apical margin of sternite 2 weakly longitudinally tumescent, never pointed.....
.....*Scolytus praeceps* LeConte (male)
- Apical margin of sternite 2 with a small median denticle.....32
- 32 (31) Apical margin of sternite 1 slightly elevated; sternite 2 appearing convex; median denticle on apical margin of sternite 2 broad, broadly pointed.....
.....*Scolytus mundus* Wood (female)
- Apical margin of sternite 1 strongly acutely produced, forming a lip along the base of sternite 2, face of sternite 2 appearing impressed, median denticle on apical margin of sternite 2 narrow, acutely pointed33
- 33 (32) Second sternite punctures abundant, fine and moderately impressed, appearing distinct; second sternite subopaque;.....*Scolytus obelus* Wood
- Second sternite punctures sparse, fine and shallow, almost appearing indistinct; second sternite appearing strongly opaque.....*Scolytus subscaber* LeConte (male)
- 34 (30) Frons finely longitudinally aciculate-punctate; sternite 1 joining base of sternite 2 more obtusely, base of sternite 2 not finely impressed, flush with sternite 1; epistomal process weakly developed, almost indistinct*Scolytus unispinosus* LeConte (female)
- Frons moderately and coarsely longitudinally aciculate-punctate; sternite 1 rounded over onto face of sternite 2, not forming an obtuse angle, base of sternite 2 finely impressed...
.....*Scolytus laricis* Blackman (female)

35 (24) Epistomal process absent.....	36
- Epistomal process present, may be indistinct.....	37
36 (25) Frons weakly longitudinally aciculate, strongly punctate, with uniformly distributed long setae; elytral striae weakly impressed.....	<i>Scolytus fagi</i> Walsh (female)
- Frons finely longitudinally aciculate and glabrous or minutely setose; elytral striae not impressed	<i>Scolytus mali</i> (Bechstein) (female)
37 (35) Setae on frons at least 1.5 times the width of the eye at the middle.....	38
- Setae on frons equal in length to the width of the eye at the middle.....	42
38 (37) Venter sternites 2-5 shining; thorax and apical and lateral margins of elytra covered with long hair-like setae as long as the width of sternites 3 and 4 combined, with pointed apices	39
- Venter sternites 2-5 opaque; thorax covered with setae as long as the width of sternite 3, with quadrate apices	41
39 (38) Epistomal process weakly developed, and faintly emarginated medially.....	
.....	<i>Scolytus hermosus</i> Wood (female)
- Epistomal process strongly developed, and strongly emarginated medially.....	40
40 (39) Apical margin of sternite 1 produced, forming a carinate lip along the basal margin of sternite 2 that is about half as produced as thick; <i>Pseudotsuga menziesii</i>	
.....	<i>Scolytus silvaticus</i> Bright (female)
- Apical margin of sternite 1 produced, forming a carinate lip along the basal margin of sternite 2 that is twice as produced as thick; <i>Abies religiosa</i>	
.....	<i>Scolytus hermosus</i> Wood (male)

41 (38)	Frons distinctly, moderately longitudinally aciculate, weakly punctate; apical margin of sternite 1 weakly produced, forming a weak carinate lip along the basal margin of sternite 2.....	<i>Scolytus subscaber</i> LeConte (female)
-	Frons indistinctly, weakly longitudinally aciculate, strongly punctate; apical margin of sternite 1 flush with basal margin of sternite 2, appearing rounded.....	<i>Scolytus ventralis</i> LeConte (female)
42 (37)	Apical margin of sternite 1 rounded; sternite 2 face rugose, shining, coarsely punctate and convex.....	<i>Scolytus reflexus</i> Blackman (female)
-	Apical margin of sternite 1 with thickened lip or produced, never rounded; sternite 2 face smooth and flat	43
43 (42)	Apical margin of sternite 1 thickened, on face of sternite 2 and nearly flush with the face of sternite 2.....	<i>Scolytus oregoni</i> Blackman (female)
-	Apical margin of sternite 1 not thickened or on the face of sternite 2, often slightly apically produced (unequally carinate in <i>S. monticolae</i>).....	44
44 (43)	Sternite 2 punctulate with small or minute, shallow punctures.....	45
-	Sternite 2 distinctly punctate with large and deep punctures	47
45 (44)	Apical margin of sternite 1 equally and continuously carinate.....	<i>Scolytus praeceps</i> LeConte, in part (female)
-	Apical margin of sternite 1 unequally carinate, more produced laterally forming cusps on each side of sternite 2.....	46
46 (45)	Elytral discal striae not impressed; sternite 2 shining in luster.....	<i>Scolytus monticolae</i> (Swaine) (female)

- Elytral discal striae impressed, giving the elytra a corrugated appearance; sternite 2 dull in luster*Scolytus tsugae* (Swaine) (female)
- 47 (44) Sternite 2 shining.....*Scolytus robustus* Blackman (female)
- Sternite 2 dull, opaque..... 48
- 48 (47) Epistomal process strongly developed, distinct; frons evenly convex.....
.....*Scolytus dentatus* Bright (female)
- Epistomal process weakly developed, almost indistinct; frons flattened or convex with slight medial depression.....*Scolytus praeceps* LeConte, in part

Species Descriptions

Species are redescribed and treated alphabetically by clade or group beginning with the introduced group, native hardwood clade and conifer clade. Common names listed are the official common names of the Entomological Society of America and/or Canada.

Introduced Species Group

The introduced species group (1.9-4.2mm long) (*S. mali*, *S. multistriatus*, *S. rugulosus* and *S. schevyrewi*) is not monophyletic and consists of a morphologically diverse group of Palearctic species that encompasses three formerly recognized species groups/subgenera (von Butovitsch 1929; Balachowsky 1949). This diversity is reflected in the sexual dimorphism exhibited by species in the group. *Scolytus multistriatus* and *S. schevyrewi* exhibit the typical dimorphic pattern of the frons as discussed above. The lateral teeth and spine are identical in both sexes of *S. multistriatus* and the spine on sternite 2 is smaller in the female compared to the male. Sexual dimorphism of *S. mali* and *S. rugulosus* is much more subtle and differentiating the

sexes can be challenging. *Scolytus mali* males have the medial area of the frons and epistomal regions impressed and the lateral margins of the epistoma are lightly covered with more abundant erect setae than the female. *Scolytus rugulosus* males have the medial area of the frons and epistoma slightly more impressed and the frons bearing longer more abundant erect setae.

***Scolytus mali* (Bechstein)**

(Figures 1.16, 1.17)

Bostrichus mali Bechstein 1805: 882. Syntypes (location unknown).

= *Scolytus sulcatus* LeConte 1868: 167. Holotype: male labeled "[pink disc = Middle States (Md., Del., N.Y., N.J., Pa., Conn.?, R.I.?)]; type 969." Synonymy: Brown 1950: 203.

For complete taxonomic history see Wood and Bright (1992).

Diagnosis. Both sexes of *S. mali* are distinguished by having sternite 2 at an oblique angle to sternite 1, the aciculate frons, with most setae found just above the epistoma and on the lateral epistomal margins.

Redescription (male). 3.2 – 4.1 mm long (mean = 3.7 mm; n = 10); 2.1 - 2.5 times as long as wide. Head, pronotum and abdominal venter dark red-brown, legs and antennae light brown, elytra brown to red-brown. Pronotum typically darker than elytra.

Epistoma weakly and broadly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally, moderately transversely impressed above epistoma and longitudinally impressed near median line; surface densely and finely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface sparsely covered by long,

fine, yellow erect hair-like setae, setae as long as the midpoint of the eye and more abundant along the epistoma. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a weakly rounded and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex weakly emarginated at the suture. Disc smooth, shining; interstriae weakly impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, interstitial punctures bearing sparse, long, semi-erect yellow hair-like setae (may have worn off); striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron greater than half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly at an oblique angle to sternite 1; surface smooth, shining, finely punctate with small, fine and shallow punctures; face convex, unarmed; setae erect, short, about half of sternite 3 width in length; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 unarmed; length of sternite 5 equal to the combined lengths of sternites 3 and 4; a setal patch is absent and a median depression is present.

Female. 3.0 – 4.2mm long (mean = 3.7mm; n = 10); 2.0 - 2.5 times as long as wide. Similar to male except epistoma feebly emarginated, frons more strongly convex when viewed laterally, weakly aciculate, setae shorter, less than the width of the eye and less abundant.

Specimens examined. 110.

Type material. Holotype *Scolytus sulcatus* LeConte (MCZC).

Non-type material. **CANADA: ONTARIO:** Hamilton, 14-21.VI.1981, M. Sanborne (CNCI-2), 23.VII.1980, ex. malaise trap (CNCI-1). Owen Sound, 27.V.[19]65, K.E. Stewart, ex. elm [= *Ulmus* sp.] (CNCI-1). Vineland Station, 8.VI.1949, W.L. Putnam, ex. apple [= *Malus* sp.] (CNCI-2). **QUEBEC:** Cantic, 11.VIII.1945, W.J. Brown, ex. apple [= *Malus* sp.] (CNCI-2). Cap-Saint-Ignace, VII.1970 (CNCI-1). Dunham, 2.IX.1998, Vignoble, L'Orpailleur, ECORC/CRDHAg-Cord (DEBC-1). Napierville, 2mi N.E., 13.VIII.1945, W.J. Brown (CNCI-1). Noyan, 0.75mi W., 15.VIII.1945, W.J. Brown (CNCI-1). **UNITED STATES:** **CONNECTICUT:** [Fairfield Co.]: Greenwich, 22.VII.1933, F.J. Dillaway, ex. in plum [= *Prunus* sp.] (USNM-2). *New Haven Co.:* New Haven, 25.VI.1956, C.W. O'Brien (EMEC-1). **MAINE:** [Androscoggin Co.]: Livermore Falls, 5.VIII.1975, ex. plum [= *Prunus* sp.] (USNM-1). **MARYLAND:** *Montgomery Co.:* Ashton, 4mi S.W., 31.V.1986, G.F. & J.F. Hevel, ex. malaise trap (USNM-1). **MASSACHUSETTS:** *Worcester Co.:* 16.II.[19]53, ex. indoors (USNM-2). **MICHIGAN:** *Allegan Co.:* Fennville area, 30.VI.2003, P. McGhee, ex. apple trees [= *Malus* sp.] (MSUC-6). *Genesee Co.:* Richfield County Park, N43°100610, W-83°55810, 16.VI.2008, R. Mech, PI Anthony Cognato (MSUC-1). *Ingham Co.:* Lansing, 2mi N., E. State Rd., N42.7842° W84.5362°, 261m, 2-18.VI.2007, PI Anthony Cognato, ex. Lindgren trap with ipsilure (MSUC-1). *Kalamazoo Co.:* Gourdneck Lake State Game Area, 16.VII.2011, S.M. Smith, A.I. Cognato, ex. *Prunus* sp. (MSUC-2). *Oakland Co.:* Farmington Hills, N42°27.668' W83°25.579',

2.VII.2004, B. Sullivan, ex. Lindgren funnel with multistriatus lure (MSUC-2). *Saginaw Co.*: St. Charles, 25.VI.1968, J.G. Truchan, ex. rotary trap (MSUC-1), 25.VI.1969 (MSUC-1). *Wayne Co.*: 20.VI.1960, G. Steyskai (USNM-2). **NEW JERSEY**: [*Essex Co.*]: Maplewood, 7.VI.[19]34, D. Fivaz, ex. on elm [= *Ulmus* sp.] (USNM-12). [*Morris Co.*]: Chatham, 25.III.[19]34, W.D. Buchanan (USNM-1). **NEW YORK**: *Albany Co.*: Near Rensselaerville, Huyck Preserve, 3-10.VII.1967, R. & J. Matthews, ex. window pane trap (CNCI-1). [*Suffolk Co.*]: Cutchogue, [19]45, Tuthill, ex. in apple [= *Malus* sp.] (USNM-26). [*Tompkins Co.*]: Groton, 24.V.1942, N.M. Downie (FMNH-1), 23.VI.1946 (FMNH-2). [*Westchester Co.*]: Armonk, 5.VI.[19]35, H. Dietrich, ex. apple [= *Malus* sp.] (CNCI-2). **OHIO**: *Medina Co.*: 15.VI.[19]62, C.L. Griswold (DEBC-4). **PENNSYLVANIA**: *Luzerne Co.*: Nanticoke, 20.IX.[19]60, ex. *Malus* sp. (CNCI-1). Nuangola, 12.V-23.VIII.1983, S. & J. Peck, ex. forest intercept (CNCI-1). **WASHINGTON D.C.**: 5.IV.1983, E.R. Hodges, ex. on sweater of collector (USNM-1). **ADDITIONAL SPECIMENS**: *Czech Republic* (MSUC-21) and *Italy* (MSUC-1).

Distribution. CANADA: Ontario, Quebec. UNITED STATES: Connecticut, Maine, Massachusetts, Michigan, New York, Ohio, Pennsylvania, Washington D.C.

Hosts. *Malus* spp. (apple), *Prunus* spp. (cherry), *Ulmus* spp. (elm), *Pyrus* spp. (pear), and *Sorbus* spp. (mountain ash).

Common name. Large shothole borer.

Biology. This species colonizes dying and weakened limbs of its host as well as fresh slash. Typical host material is 15-38cm in diameter but branches as small as 8cm are colonized (Pechuman 1938).

Adult galleries of *S. mali* are somewhat variable and are either parallel with the grain of the wood or at a slight oblique angle. Galleries consist of a nuptial chamber and a single egg

gallery. The adult gallery strongly scores the sapwood and range in size from 3.5-6.0cm in length. Egg niches are constructed along the gallery and score the sapwood. Six to 100 eggs may be laid along the egg galleries with the typical gallery having 40 eggs. Larval mines lightly score the sapwood and radiate perpendicular to the egg gallery. The larval galleries later meander often at an oblique angle to the grain of wood, forming a fan shaped pattern. Pupation occurs within the sapwood and broods can overwinter as larvae. The following year, adults emerge and feed at twig crotches before selecting host material (Pechuman 1938; Balachowsky 1949; Baker 1972; Wood 1982). In New York, *S. mali* has one generation per year although there are two generations per year in temperate Europe (Pechuman 1938).

Collection notes. The author collected this species from an 8cm diameter *Prunus* sp. branch that broke during a recent windstorm. Females constructed gallery entrances beneath large flakes of bark on the sides and bottom surfaces of the branch. Specimens were infesting the same limbs as *Phloeotribus liminaris* (Harris) 1852.

Remarks. This species is native to the Palearctic region and was first detected in New York in 1868 when it was described as *S. sulcatus* LeConte (1868). LeConte (1868) noted in his description that the species most strongly resembled the Palearctic species *S. rugulosus* and did not mention the collection date of the specimens. Interestingly no other specimens of the species were collected until 1933, 65 years after the initial discovery. These specimens were collected from southeastern New York, northern New Jersey and western Connecticut. It is likely that like LeConte's *S. californicus* (= *S. scolytus*), *S. mali* was collected in 1868 but populations never became established. The later collections may be the result of multiple introduction events (Pechuman 1938).

Brown (1950) recognized that LeConte's species was morphologically and behaviorally identical to that of *S. mali* and placed *S. sulcatus* into synonymy. The native range of *S. mali* is Europe (except the Scandinavian Peninsula), Central Asia, Siberia and the Russian Far East (Michalski 1973).

***Scolytus multistriatus* (Marsham)**

(Figures 1.18, 1.19)

Ips multistriatus Marsham 1802: 54. Syntypes (location unknown).

= *Scolytus javanus* Chapuis 1869: 56. Holotype male, labeled "Java, Solier, Dejean"

(ISNB). Synonymy Schedl 1954: 137.

For complete taxonomic history see Wood and Bright (1992).

Diagnosis. Both sexes of the species are distinguished by the presence of lateral teeth on the apical margins of sternites 2-4 and by a median conical spine on the basal margin of sternite 2.

Redescription (male). 2.2 – 3.9mm long (mean = 2.81mm; n = 20); 2.0 - 2.6 times as long as wide. Head, pronotum, and abdominal venter dark red-brown, legs light brown, antennae yellow-brown, elytra usually dark red-brown but may be brown. Color is not uniform and the surface frequently contains patches of red-brown mixed with dark red brown. Pronotum typically darker than elytra.

Epistoma weakly and broadly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape

short, elongate, less than length of the first four funicular segments; club flattened, thinner on apical half, irregularly ovoid, setose with a partial septum and two sharply arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex entire the suture. Disc smooth, shining; interstriae weakly impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, interstitial punctures bearing sparse, long, semi-erect yellow hair-like setae (may have worn off); striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron greater than half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shining, finely punctate with small, coarse punctures; face flattened; basal margin armed with a long, smooth, conical spine with its extending from the basal margin to half the segment; each lateral margin of sternites 2-4 armed with a lateral tooth. Sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.4 – 3.3mm long (mean = 2.95mm; n = 20); 2.2 - 2.7 times as long as wide. Similar to male except epistoma feebly entire, frons strongly convex when viewed laterally, weakly aciculate, setae shorter, less than the width of the eye and less abundant.

Specimens examined. 165.

Type material. Holotype *Scolytus javanus* Chapuis (ISNB).

Non-type material. **CANADA: ALBERTA:** Calgary, 19.VII.[19]94, T. Reichardt, ex. pheromone trap no. EBB XI (CNCI-2). **ONTARIO:** St. Catherines, 22.VI.1961, Kelton, Brumpton (CNCI-1). Toronto, 1970, ex. reared on elm [= *Ulmus* sp.] (CNCI-1). Queenston, 26.VI.[19]50, ex. elm [= *Ulmus* sp.] (CNCI-1). **QUEBEC:** Montreal, 14.VII.1977, E.J. Kiteley (CNCI-1); Ile de Montreal, Ile de Sainte Hélène, 12.VIII.1985, L. Lariviere (CNCI-1). **MEXICO:**

CHIHUAHUA: Ciudad Juarez, II.1987, I.C. Rodriguez (CNCI-2). **UNITED STATES:**

CALIFORNIA: [Alameda Co.]: Berkeley, 23.V.1962, ex. elm [= *Ulmus* sp.] (EMEC-2). *Contra Costa Co.:* Antioch [Dunes] National Wildlife Refuge, 10.X.[19]91, J.A. Powell (EMEC-1).

Fresno Co.: 11.I.1950, N.J. Smith (SBMN-2). *Inyo Co.:* Big Pine, 4000ft, V.1971, D. Guiliani,

ex. black light (CASC-1), VII.1971 (CASC-1). **COLORADO:** *Mesa Co.:* Grand Junction, X.1979, D. Leatherman, ex. European ash [= *Fraxinus* sp.] (CSUC-1). *Weed Co.:* Briggsdale,

1.IX.198, D. Leatherman (CSUC-1). **GEORGIA:** *Clarke Co.:* Whitehall forest, 17-24.IX.1976,

R. Turnbow, ex. window trap F-8 (CNCI-1). **ILLINOIS:** *Alexander Co.:* Horseshoe Lake,

28.IX.1968, T.E. Brooks (CNCI-4). **KENTUCKY:** *Green Co.:* 9.VII.1941, C. Cook (MSUC-1).

MASSACHUSETTS: [Hampshire Co.]: Northampton, 10.VIII.1974, E.J. Kiteley (MSUC-1).

[Suffolk Co.]: Forest Hills [=Boston], 3.VI[?], W.M. Mann (USNM-1). **MICHIGAN:** *Antrim*

Co.: Eastport, ca. 3mi N., N45°08'30" W85°22'50", 3-5.VII.2003, F.W. Stehr, ex. UV light

(MSUC-1). *Cass Co.:* Cassopolis, 2.VI.2007, A.D. Smith (MSUC-3). *Genesee Co.:* Richfield

County Park, N43.100610° W-83.55810°, ex. Lindgren with EtOH (MSUC-1). *Ingham Co.*: Lansing, 2mi N., E. State Rd., N42.7842° W84.5361°, 261m, 16-30.VII.2007, PI A.I. Cognato (MSUC-1); G.L. Parsons, ex. UV light. & white lights (MSUC-1). East Lansing, 1.X.1957, R.C. Fox (MSUC-1), 2.X.1957 (MSUC-5), 3.X.1957 (MSUC-7), 4.X.1957 (MSUC-1), 5.X.1957 (MSUC-3), 6.X.1957 (MSUC-4), 10.X.1957 (MSUC-1), 15.X.1957 (MSUC-5); 25.VI.1981, R. Fischer (MSUC-1); N42°11.320' W84°27.867', 258m, 16.IX.2011, S.M. Smith, A.I. Cognato, I.A. Cognato, ex. *Ulmus* sp. (MSUC-7); Michigan State University campus, 17.VI.2011, D.G. McCullough (MSUC-3). *Kalamazoo Co.*: Gourdneck Lake State Game Area, 19.VI.2011, A.I. Cognato, ex. *Ulmus* sp. (MSUC-21). *Kalkaska Co.*: T27N R7W S18, 28.XII.1986, P. Wacławski, ex. basement wood (MSUC-1), 20.XII.1987 (MSUC-1), 3.I.1987 (MSUC-5). *Lapeer Co.*: Potter Lake, 19.VI.1967, Brivio (MSUC-2). *Macomb Co.*: East of Memphis, 3.V.1964, C. Brivio (MSUC-1), 17.VI.1965 (MSUC-1), 21.VIII.[19]66 (MSUC-2), 23.VIII.1969 (MSUC-1), 30.VIII.1969 (MSUC-1). *Saginaw Co.*: St. Charles, 30.V.1969, J.H. Truchan, ex. rotary trap at 6ft height level (MSUC-2), 11.VI.1969, ex. rotary trap at 12ft height level (MSUC-1), 16.VI.1969 (MSUC-3). *Sanilac Co.*: Port Sanilac, 20.VI.1986, Brivio (MSUC-1). **MONTANA**: *Choteau Co.*: Great Falls, VII-VIII.1977, S. Kohler, ex. caught in flight, sticky trap, multilure bait (CNCI-1). *Gallatin Co.*: Bozeman, VII-VIII.1977, S. Kohler, ex. caught in flight, sticky trap, multilure bait (CNCI-1). **NEW YORK**: [*Westchester Co.*]: Yonkers, VIII.1935, H. Dietrich, ex. elm [= *Ulmus* sp.] (CNCI-3). **OKLAHOMA**: [*Oklahoma Co.*]: Jones, 13.VI.1957, D. Alexander (USNM-1). **TEXAS**: [*El Paso Co.*]: El Paso, 045483, 17.VII.[19]94, lot 94 07975, ex. Mexico – in log of *Prunus* sp. (USNM-10). **WYOMING**: *Carbon Co.*: Medicine Bow National Forest, VI-VIII.1999, ex. *Polyphorus volvatus* [= *Cryptoporus volvatus* (Peck) Shear] (CSUC-1).

ADDITIONAL SPECIMENS: *Czech Republic* (MSUC-2), *Italy* (MSUC-8) and *Russia* (MSUC-22).

Distribution. CANADA: Alberta, Manitoba, Ontario, Quebec. MEXICO: Chihuahua. UNITED STATES: Alabama, Arizona, Arkansas, California, Colorado, Florida, Georgia, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Missouri, Montana, New Jersey, New Mexico, New York, Nevada, Ohio, Oklahoma, Pennsylvania, Rhode Island, South Dakota, Texas, Utah, Virginia, Washington D.C., Wyoming.

Hosts. All native and introduced *Ulmus* spp. including *U. americana* L. (American elm) and *Zelkova serrata* (Thunb.) Makino.

Common names. Smaller European elm bark beetle and the European elm bark beetle.

Biology. *Scolytus multistriatus* colonizes cut, stressed, weakened and diseased elm trees (*Ulmus* spp.) (Wood 1982). It seldom attacks healthy and vigorous trees (Bright 1976). *Scolytus multistriatus* females produce an aggregation pheromone to aggregate conspecifics to host trees. The pheromone bouquet is composed of three components: (-)-4-methyl-3-heptanol, (-)-2,4-dimethyl-5-ethyl-6,8-dioxabicyclo[3.2.1]octane (α)-multistriatin and (-)- α -cubebene (Pearce et al. 1975).

The adult gallery is excavated parallel to the grain of the wood and consists of a single egg gallery without a nuptial chamber. The adult gallery ranges in size from 2.5-5.0cm in length. Egg niches are constructed along the gallery and score the sapwood. Twenty four to 96 eggs may be laid singly along the egg gallery. Larval mines lightly score the sapwood and radiate perpendicular to the egg gallery. The larval galleries later meander often at an oblique angle to the grain of wood, forming a fan shaped pattern. Larvae construct pupal chambers in the bark (Bright 1976).

There are one and one-half generations per year in Canada and three in the southern US (Furniss and Johnson 2002). In Canada, adults emerge in June and July and feed at twig crotches of healthy trees for 7-10 days before selecting host material (Chamberlin 1958; Baker 1972). The brood from these adults either emerges in August or September or overwinters as larvae.

Scolytus multistriatus is the principal vector of the Dutch elm disease fungus *Ceratocystis ulmi* (Buisman) C. Moreau in North America. This beetle vectored disease killed 50-75% of the elms population in northeastern North America prior to the 1930s (Bloomfield 1979). *S. multistriatus* adults become covered in fungal spores upon emergence from brood material. Adults inoculate elms with the Dutch elm disease fungus as they feed in twig crotches. The feeding activity leaves wounds in the bark that allow spores to be transferred from the beetle's cuticle to the tree tissues (Bright 1976).

Collection notes. None.

Remarks. This species is native to the Palearctic region and is primarily distributed throughout Europe but also occurs in Iran and Algeria. *Scolytus multistriatus* was first detected in North America in 1909 from elm trees on the Harvard University campus in Massachusetts (Chapman 1910).

***Scolytus rugulosus* (Müller)**

(Figures 1.20, 1.21)

Bostrichus rugulosus Müller 1818: 247. Syntypes: (IRSNB, ZIFH).

For complete taxonomic history see Wood and Bright (1992).

Diagnosis. Both sexes of *S. rugulosus* are distinguished by the rounded elytral apices, the serrate elytral apex, the deeply emarginated apex and by the face of sternite 2 at an oblique angle to sternite 1.

Redescription (male). 1.9 – 2.6mm long (mean = 2.4mm; n = 10); 2.1 - 2.7 times as long as wide. Color red-brown to dark red brown, antenna yellow-brown. Pronotum typically darker than elytra.

Epistoma weakly and broadly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally, slightly transversely impressed above epistoma; surface moderately and finely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow setae; base weakly bisinuate.

Elytral sides sub-parallel on basal half, narrowing to a strongly rounded and moderately serrate apex; apical margin of elytral apices bearing large, coarse punctures; apex strongly emarginated at the suture. Disc glabrous, smooth, shining; interstriae not impressed and equal in width to striae, interstitial punctures uniseriate, equal in size to those of striae, interstriae bearing

moderately abundant short, semi-erect yellow-brown hair-like setae; striae not impressed.

Declivity bearing sparse, short, erect yellow setae. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 rounded, flush with the base of sternite 2. Sternite 2 nearly at an oblique angle to sternite 1; surface shagreened, dull finely punctate with small, coarse and shallow punctures; face flattened, unarmed; setae abundant, erect, long, greater than width of segment 3 in length; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch is absent median depression is present.

Female. 2.0 – 3.1mm long (mean = 2.5mm; n = 10); 2.1 - 2.8 times as long as wide. Similar to male except frontal setae shorter, less than the width of the eye and less abundant.

Specimens examined. 99.

Type material. None examined.

Non-type material. **CANADA: BRITISH COLUMBIA:** Vancouver, 5.VII.1975, N.M. Downie (FMNH-2). **NOVA SCOTIA:** Middleton, 11.VI.1938 (CNCI-2). **ONTARIO:** Brimley, 17.VII.[19]21 (CNCI-1), 30.VII.[19]22 (CNCI-1). Ottawa, 21.VIII.1999, A.T. Howden, ex. wild grape [= *Vitis* sp.] (CNCI-1). Simcoe, 3.IX.1931, J.A. Hall (CNCI-2). Smith Falls, V.1940, H.S. Fleming (CNCI-1). **UNITED STATES: CALIFORNIA:** [*Los Angeles Co.*]: San Marino, 25.VI.[19]42, G.P. Mackenzie (FMNH-1). [*Orange Co.*]: Santa Ana, 1.IV.1943, L.R. Gillogly, ex. bait traps (USNM-1). [*Placer Co.*]: Penryn, 1.X.1929, A.T. McClay (FMNH-2). **DELAWARE:** [*Kent Co.*]: Camdem, XII.1940, J.M. Amos (FMNH-1). **INDIANA:** *Madison Co.*: 10.VIII.1937, ex. apricot [= *Prunus armeniaca*] (FMNH-2). *Porter Co.*: Jackson Township,

Maple Knoll Farm, 6.IV.[19]60, C.C. Gregg (FMNH-10). *Tippecanoe Co.*: 7.VI.1956, N.M. Downie (FMNH-2), 1.XI.1978 (FMNH-1). **MICHIGAN**: *Allegan Co.*: Fennville area, 30.VI.2003, P. McGhee, ex. on apple trees [= *Malus* sp.], (MSUC-1). [*Cass Co.*]: Edwardsburg, 30.VIII.1928 (MSUC-6). [*Ingham Co.*]: [East Lansing], Agriculture College [= Michigan State University campus], 1.I.1917 (MSUC-3). *Isabella Co.*: 16.IX.[19]55, R.R. Dreisbach (MSUC-1). [*Kent Co.*]: Grand Rapids, 17.X.[19]11 (MSUC-6). [*Lenawee Co.*]: Adrian, 20.VII.1900 (MSUC-7). *Livingston Co.*: Howell, 214 Inverness St, N42.61678° W84.92810°, 23.V-7.VI.2007, R. Mech, ex. Lindgren trap with EtOH + alpha (MSUC-1). *Midland Co.*: 24.VII.[19]46, R.R. Dreisbach (MSUC-1), 14.IX.[19]56 (MSUC-1). *Oakland Co.*: A.W. Andrews (MSUC-1); 28.VI.[19]47, B. Summerville (MSUC-1). [*Washtenaw Co.*]: Manchester, 21.V.1913 (MSUC-4), 31.V.1913 (MSUC-7). **NEW YORK**: *Onodaga Co.*: Syracuse, X.1987, R.J. Rabaglia, ex. mountain ash [= *Sorbus* sp.] (RJRC-1). [*Tompkins Co.*]: Ithaca, ex. peach [= *Prunus* sp.] (CASC-1). [*Ulster Co.*]: Oliveria, 20.VI.[19]18 (USNM-1). *Wayne Co.*: 26.VI.1950, Shumaker (USNM-1), 8.VIII.[19]51 (USNM-1). [*Unspecified County*]: (CASC-2).

PENNSYLVANIA: *Allegheny Co.*: Upper St. Clair Township, 28.VIII.[19]59 (EMEC-1). [*Philadelphia Co.*]: Philadelphia, 20.V.[18]98 (USNM-1). **UTAH**: [*Utah Co.*]: Vineyard, 6.IX.[19]23, T. Spalding (USNM-1). **WASHINGTON**: [*Whitman Co.*]: Steptoe Butte State Park, 9.VII.1971, N.M. Downie (FMNH-1). **WASHINGTON D.C.**: 26.VII.1943, L.J. Bottimer, ex. on *Prunus* sp. (CNCI-2). **ADDITIONAL SPECIMENS**: *Brazil* (MSUC-21), *Czech Republic* (MSUC-1), *Hungary* (MSUC-1), *Morocco* (MSUC-1) and *Italy* (MSUC-2).

Distribution. CANADA: British Columbia, Nova Scotia, Ontario. GREENLAND. MEXICO: Durango. UNITED STATES: Arkansas, California, Colorado, Connecticut, Delaware, Florida, Georgia, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maryland, Massachusetts,

Michigan, Mississippi, Missouri, Montana, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Texas, Utah, Virginia, Washington, Washington D.C, West Virginia, Wisconsin.

Hosts. Stone and pome fruit trees including *Malus* spp. (apple), *Pyrus* spp. (pear), and *Prunus* spp. (cherry) and is less commonly in *Crataegus* (hawthorn), *Sorbus* (mountain ash) and *Ulmus* spp. (elm).

Common name. Shothole borer.

Biology. *Scolytus rugulosus* primarily attacks and kills small twigs and branches but may kill whole trees through the process of excavating adult galleries and larval feeding. Twigs injury is the result of feeding activity at the base of the bud. Attacks can begin near an injury or on a healthy tree (Chamberlin 1939; Bright and Stark 1973).

The *S. rugulosus* adult gallery is parallel with the grain of the wood. The adult gallery solely consists of an egg gallery and lacks a nuptial chamber. The adult gallery strongly scores the cambium, lightly scores the sapwood and ranges in size from 1.0-5.0cm in length (Bright and Stark 1976; Furniss and Johnson 2002). Eggs are laid singly in larval niches on both sides of the egg gallery. Larval mines first radiate perpendicular to the egg gallery against the grain of the wood and later turn parallel with the grain (Bright and Stark 1973). The larval stage typically lasts one month. Pupation occurs in the bark for summer emergence. If the brood is unable to complete development during the warmer months, larvae will burrow 1-2cm deep within the sapwood to overwinter. The following year, adults emerge and feed at twig crotches before selecting host material (Baker 1972). There are one to four generations per year depending on locality with more generations occurring in warmer climates (Chittenden 1898; Baker 1972; Wood 1982).

Remarks. This species is native to the Palearctic region and was first detected in North America in 1877 from New York (Chittenden 1898). The native range of *S. rugulosus* encompasses Europe, North Africa, Asia Minor, middle Asia to Zabaikalye, Russia (Michalski 1973).

***Scolytus schevyrewi* Semenov**

(Figures 1.22, 1.23)

Scolytus schevyrewi Semenov 1902: 265. Holotype, male (location unknown).

For complete taxonomic history see Wood and Bright (1992).

Diagnosis. The *S. schevyrewi* male most strongly resembles that of *S. piceae* because in both species the spine on the second sternite never attains the apical margin. Males are differentiated from those of *S. piceae* by the laterally compressed spine and the banded appearance of the elytra.

The female is differentiated from that of *S. piceae* by the banded pattern of the elytra and by the low median carina (variable and may be absent) that does not touch either margin on the second sternite.

Redescription (male). 2.8 – 3.5mm long (mean = 3.2mm; n = 10); 2.0 – 2.2 times as long as wide. Color red-brown to dark red brown. The elytra of most species appears banded with a characteristic dark brown band on reddish colored elytra, but may also be solely dark brown or red-brown without a band. Antennae yellow-brown. Pronotum typically darker than elytra.

Epistoma weakly and broadly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing impressed when viewed laterally; surface moderately and coarsely reticulate punctate to weakly longitudinally aciculate; punctures dense, small and coarse; surface moderately covered by long, fine, yellow

erect hair-like setae, setae longer than the midpoint of the eye, setae on lateral and dorsal margins longer, thicker and incurved. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, thinner on apical half, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger, coarser, deeper and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on basal half, narrowing to a moderately rounded and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex weakly emarginated at the suture. Scutellar notch densely covered in recumbent white setae (may wear off). Disc glabrous, smooth, shining; interstriae not impressed and equal in width to striae, interstitial punctures uniseriate, equal in size to those of striae, interstriae bearing sparse short, semi-erect yellow hair-like setae; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 flush with the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface shagreened, dull, finely punctate with small, fine and shallow punctures; face convex; densely covered with semi-recumbent, long setae that are as long as the width of sternite 3 or less; face armed with median laterally compressed spine (rarely absent) that has its base close to the basal margin but does not touch it; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of

the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.3 – 3.6mm long (mean = 3.2mm; n = 10); 1.7 – 2.4 times as long as wide. Similar to male except epistoma feebly emarginated, frons flattened when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed above epistoma and longitudinally impressed in median area. Apical margin of sternite 1 weakly elevated above the base of sternite 2. Second sternite armed with a low median carina (variable and may be absent) that does not touch either margin.

Specimens examined. 24.

Type material. None examined.

Non-type material. **UNITED STATES: CALIFORNIA:** Los Angeles Co.: Whittier, Whittier Fertilizer, 7.IX.2006, A. Sanchez, ex. Lindgren funnel + ETOH & alpha pinene (DEBC-1).

COLORADO: Adams Co.: Aurora, wood recycler, N39°807', W104°994', 9.VII.2003, P.

McPherrren, ex. funnel trap with Ips lure (MSUC-11), 15.IV.2003 (MSUC-1), 26.IV.2003

(MSUC-1), 2.V.2003 (MSUC-1), 29.V.2003 (MSUC-1). **MICHIGAN:** Ingham Co.:

N42°11.320' W84°27.867', 258m, 16.IX.2011, S.M. Smith, A.I. Cognato, I.A. Cognato, ex.

Ulmus sp. (MSUC-1). **Wayne Co.:** Trenton-Woodhaven, 26.VII.2004, T. Dutton, ex. Lindgren

funnel alpha-pinene Trap WY4 (MSUC-1). **UTAH:** Weber Co.: Ogden, Ogden Nature Center,

13.VII.2003, ex. funnel trap with alpha pinene & ethanol lure (MSUC-6).

Distribution. CANADA: Alberta, British Columbia, Manitoba, Ontario, Saskatchewan.

UNITED STATES: Arizona, California, Colorado, Connecticut, Delaware, Idaho, Illinois,

Indiana, Kansas, Maryland, Michigan, Minnesota, Missouri, Montana, Nebraska, Nevada, New

Jersey, New Mexico, Ohio, Oklahoma, Oregon, Pennsylvania, South Dakota, Texas, Utah, Virginia, Washington, Wyoming.

Hosts. *Ulmus* spp. including *U. americana* L. (American elm), *U. pumila* L. (Siberian elm), *U. thomasi* Sarg. (rock elm) and *U. procera* Salisb. (English elm).

Common name. Banded elm bark beetle.

Biology. This species prefers to attack drought stressed elms (Negrón et al. 2005). *Scolytus schevyrewi* locate a suitable host via host tree volatiles (Lee et al. 2010).

The adult gallery consists solely of a single egg gallery parallel with grain of the wood (Lee et al. 2006). The adult gallery strongly scores the sapwood. Egg niches are constructed along the gallery and score the sapwood. Twenty to 120 eggs are laid along the egg galleries (Lee et al. 2010). Larval mines lightly score the sapwood and radiate perpendicular to the egg gallery. The larval galleries later meander often at an oblique angle to the grain of wood, forming a fan shaped pattern. Pupation occurs in the outer bark and broods overwinter as mature larvae or pupae (Lee et al. 2006). In California, adult flight occurs from April-September or October. In Nevada, Utah, Wyoming, Colorado, Kansas and Utah, flight occurs from May to September (Lee et al. 2011). There are two to three generations per year (Lee et al. 2011). Development from egg to adult takes 30-45 days (Negrón et al. 2005). Upon emergence, adults feed at twig crotches before selecting host material (Negrón et al. 2005).

Collecting Notes. None.

Remarks. This species is native to the Palearctic region, from western Russia and Uzbekistan and east to China, Mongolia and Korea (Michalski 1973). *Scolytus schevyrewi* was first detected in North America in 2003. The first specimens were collected in Colorado and Utah. By 2005, it was recorded from 21 states suggesting that it had been present for many years before its initial

detection (Negrón et al. 2005; LaBonte 2010). Subsequent review of bark beetle survey collections revealed the earlier occurrence of this species in Denver, Colorado in 1994 and Clovis, New Mexico in 1998 (Lee et al. 2006).

In areas where populations of *S. schevyrewi* and *S. multistriatus* are both present, the abundance of *S. multistriatus* is decreasing to the point where this once common species is difficult to find (Negrón et al. 2005; Lee et al. 2010). This competitive displacement of *S. multistriatus* by *S. schevyrewi* is likely the result of differences in fecundity, generation time, and emergence. *Scolytus schevyrewi* produces larger broods that may overwinter as pupae, have a quicker development period, have an earlier flight, and exhibit rapid, strong aggregation to host kairomones as compared to *S. multistriatus* (Lee et al. 2010).

Scolytus schevyrewi is a highly morphologically variable species. LaBonte (2010) provides an excellent discussion regarding intraspecific variation exhibited within *S. schevyrewi*. There is considerable variation observed in the shape and appearance of spine on the second sternite. The male spine on the second sternite is typically well developed with a blunt apex that is broader than the base and appears triangular when laterally viewed. In females the spine is variously reduced and may even be absent. In most males, the spine is closest to the apical margin of the second sternite. In some males the base of the spine is closer to basal margin. Most individuals exhibit the characteristic dark brown band on reddish colored elytra, which is the derivative of the species' common name. Occasionally individuals have been encountered with unicolorous dark brown or reddish elytra. Additional variation was also observed in the coloration of the pronotum. The pronotum can vary from almost entirely dark brown with reddish coloration along the margins (common form) to the entire dorsal surface being reddish with dark brown margins (uncommon form) (LaBonte 2010).

Native Hardwood Clade

The native hardwood clade (2.2-5.6mm long) (*S. fagi*, *S. muticus*, and *S. quadrispinosus*) is monophyletic. The sexual dimorphism of the native hardwood clade is different from the introduced group and the conifer clade as both the males and females have an impressed frons that is strongly longitudinally aciculate, except *S. fagi* in which the males have a faintly longitudinally aciculate frons and the female frons is granulate punctate. This group arguably has the strongest degree of sexual dimorphism with *S. quadrispinosus* and *S. muticus* each possessing a strongly excavated second sternite numerous spines and teeth or a large setal patch on sternite 5 respectively. The abdominal venter of *S. fagi* is identical in both sexes.

***Scolytus fagi* Walsh**

(Figures 1.24, 1.25)

Scolytus fagi Walsh 1867: 58. Neotype: male, labeled “Galesburg, Illinois, Liebeck Collection”

(MCZC). Neotype designated Smith and Cognato 2010b: 36.

Diagnosis. Both sexes of *S. fagi* are distinguished from *S. mali* and *S. muticus* by the rugose-reticulate frons that is covered by uniformly distributed setae.

Redescription (male). 3.3-5.5mm long (mean = 4.45mm; n = 20); 1.96 - 2.75 times as long as wide. Color dark red-brown to black, antenna light brown. Pronotum typically same color as elytra.

Epistoma weakly and broadly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma and along median line; surface

rugose-reticulate and strongly punctate; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, thinner on apical half, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctulate and punctures moderately abundant, larger, coarse and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a weakly rounded and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex weakly emarginated at the suture. Disc smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, punctures bearing short recumbent yellow setae slightly longer than the size of a puncture (may be broken off); striae moderately impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shining, finely punctate with large, fine and shallow punctures; face flattened; setae semi-recumbent, short, about half the length of segment 3 or less; apical margin unarmed; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 unarmed; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch is absent and a median depression is present.

Female. 3.9 - 5.6mm long (mean = 4.65mm; n = 20); 1.9 - 2.8 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons convex when viewed laterally, weakly longitudinally strigate-punctate, setae shorter, less than the width of the eye and sparse; weakly transversely impressed just above epistoma and between inner apices of eyes.

Second sternite unarmed.

Specimens examined. 74.

Type material. Neotype *Scolytus fagi* Walsh (MCZC).

Non-type material. **CANADA: ONTARIO:** Point Pelee National Park, 27.IX.1989, K. Dunster, ex. *Celtis tenuifolia* (CNCI-9). **UNITED STATES: MISSISSIPPI:** [Sharkey Co.]: Rolling Fork, VIII.1976, J.D. Solomon, ex. Nuttall oak [= *Quercus* sp.] (USNM-1). **PENNSYLVANIA:** *Cumberland Co.:* Roadway Dr @ Schneider Dr, 40.229030°N, 77.111580°W, 26.VI.2009, L.R. Donovall, (MSUC-25), 29.V.2009, ex. Lindgren-alpha pinene/EtOH (MSUC-4), 29.V.2009, ex. Lindgren-EtOH (MSUC-1). *Dauphin Co.:* Wildwood on Industrial Rd., 40.316325°N, 76.888783°W, 6.VIII.2009, S.-E. Spichiger, ex. Lindgren-EtOH (MSUC-2). *Lancaster Co.:* 7031 Elizabethtown Rd., 40.182583°N, 76.498783°W, 23.VII.2009, ex. Lindgren-BEBB/EtOH (MSUC-1). *York Co.:* 400 Mundis Rd., 40.030170°N, 76.705330°W, 10.VI.2009, S. Rebert, ex. Lindgren-alpha/EtOH (MSUC-4). **TEXAS:** [Colorado Co.]: Columbus, [18]88 (MSUC-4, USNM-15). [Unspecified county]: (USNM-3). Fort Worth, 31.VII.[19]12, ex. bred from hackberry [= *Celtis* sp.] (USNM-4).

Distribution. CANADA: Ontario. UNITED STATES: Illinois, Kansas, Mississippi, Ohio, Pennsylvania, Texas.

Hosts. *Celtis occidentalis* L. (common hackberry), *C. tenuifolia* Nutt. (dwarf hackberry), *Celtis laevigata* Willd. var. *texana* Sarg. (Texan sugarberry), *Fagus grandifolia* Ehrh. (American beech), and *Quercus* spp. (oak).

Common name. None.

Biology. The gallery of the species has been reported as very confused and undecipherable. Larvae were reported boring in the wood. In addition, the species did not appear to colonize healthy trees (Packard 1890). Smith and Cognato (2010a) summarized all information known about this species.

Collection notes. None.

Remarks. This species is very rarely encountered. Most museum collections occurred in the early 1900's and most recent collections have been from Lindgren funnel traps. There are many gaps in the known distribution of *S. fagi* but the species likely occurs throughout the eastern US associated with its host trees.

***Scolytus muticus* Say**

(Figures 1.26, 1.27)

Scolytus muticus Say 1824: 182. Holotype: male, Missouri (ANSP, lost).

Diagnosis. *Scolytus muticus* are differentiated from other *Scolytus* species by the presence of long, erect hair-like setae on the elytral interstriae and on the abdominal venter. The male is further distinguished by a pair of strongly elevated areas on the basal two-thirds, each densely covered with abundant fine, long hair-like setae.

Redescription (male). 2.2 – 5.3mm long (mean = 3.65mm; n = 20); 1.75 - 2.6 times as long as wide. Head, pronotum, legs and abdominal venter dark red-brown, antennae yellow-brown, elytra usually dark red-brown but occasionally red-brown. Pronotum typically darker than elytra.

Epistoma moderately and broadly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing strongly flattened when viewed laterally; surface finely and densely longitudinally aciculate; aciculations converging at epistoma; impunctate; setae on lateral and dorsal margins covered by long, thick, incurved, yellow erect hair-like setae, setae longer than the midpoint of the eye, median areas covered with sparse, shorter and thinner setae. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and three very sharply arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger, coarser and dense laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex entire at the suture. Disc reticulate, shining; interstriae faintly impressed and equal to width of striae, interstitial punctures large, uniseriate, equal in size to those of striae, interstitial punctures bearing moderately abundant, long, semi-erect yellow hair-like setae (may have worn off); striae moderately

impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface reticulate, shining, densely and coarsely punctured with large and coarse punctures; face flattened; setae moderately abundant and longer than the width of sternite 3; apical margin unarmed; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 unarmed; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a median depression is absent; a pair of strongly elevated areas on basal two-thirds, each densely covered with abundant fine, long hair-like setae, apical third strongly impressed.

Female. 3.1 – 5.1mm long (mean = 4.0mm; n = 20); 1.96 - 2.45 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons less strongly flattened when viewed laterally, finely and narrowly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between inner apices of eyes and. Second sternite unarmed. Sternite 5 without a pair of strongly elevated areas on basal two-thirds or setal patches.

Specimens examined. 214.

Type material. None examined.

Non-type material. **CANADA: ONTARIO:** Pelee Island, 29.VI.1940, W.J. Brown (CNCI-1). Point Pelee National Park, 23.VI.[19]31, W.J. Brown (CNCI-1); 27.IX.1989, K. Dunster, ex. *Celtis tenuifolia* (CNCI-1), 2.VIII.1990 (CNCI-1). **UNITED STATES: COLORADO:** *Jefferson Co.:* Upper Bear Creek, 11.IX.1980, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1). **ILLINOIS:** *Alexander Co.:* Pleasant Valley, 15.VI.1979, B.C. Weber, ex. Trap 6, Ht. 2 (USNM-1), 22.VI.1979, ex. Trap 14, Ht. 4 (USNM-1). *Champaign Co.:* 28.X.1960, ex.

hackberry [= *Celtis* sp.] (EMEC-4). *Sangamon Co.*: Springfield, 29.V.2003, C. Helm (CUIC-1). *Stephenson Co.*: Freeport, 4.VII.[19]17 (USNM-1). **INDIANA**: *Tippecanoe Co.*: 6.VI.1971, N.M. Downie, ex. *Celtis occidentalis* (USNM-6). **IOWA**: [*Story Co.*]: Ames, 18.VIII.1926, H.H. Harris (DEBC-2), 1.IV.1936 (DEBC-1), 22.V.1939, E. Polderboer (DEBC-1); 22.V.1939, C. Vocom (USNM-2); E. Snead (USNM-1). **KANSAS**: *Douglas Co.*: Lawrence, 5mi N.E., Kansas University Natural History Research Station, 9.VII.1982, D.H. Wahl (CNCI-1). Lawrence, 10.VI.[19]20, M.W. Blackman (USNM-8); 5.IX.1950, S.L. Wood (USNM-4). *Riley Co.*: G.A. Dean (DEBC-1); Popenoe (DEBC-1). [*Unspecified County*]: Manhattan, 1.VI.[19]29, F. Kruger (DEBC-1); 5.VI.[19]29, T.N. Winburn (DEBC-1); 8.V.1968, G. Hevel (USNM-1).

KENTUCKY: *Christian Co.*: 15.VI.1960, J.M. Campbell (CNCI-1). **LOUISIANA**: *Jefferson Parish*: New Orleans, 4.XII.1975, emerged II.1976, S.G. Wellso, ex. *Celtis laevigata* wood (MSUC-13). *Saint Bernard Parish*: J.N. Knull, ex. reared from *Celtis mississippiensis* [= *Celtis tenuifolia*] (USNM-3). **MARYLAND**: [*Cecil Co.*]: Port Deposit, 26.VI.1977, D. Jump (USNM-1), 13.VII.1977 (USNM-1), 9.VI.1979 (USNM-2), 3.VII.1979 (USNM-1). *Montgomery Co.*: Bethesda, 25.V.1981, W.E. Steiner (USNM-1). Plummerville Island, II-III.1912, E.A. Schwarz, ex. branch of *Celtis* sp. (USNM-30). **MICHIGAN**: *Ingham Co.*: East Lansing, Agriculture College [Michigan State University] (MSUC-8); S21 T4N R1W, VII.1970, S.G. Wellso (MSUC-12). East Lansing, IV.1972, D.K. Young (MSUC-4); 15.VI.1970, S.G. Wellso, ex. merged from *Celtis occidentalis* (MSUC-7). Okemos, 12.VIII.1969, S.G. Wellso (MSUC-1), 5.VI.1976 (MSUC-1); 28.V.1970, S.G. Wellso, ex. *Celtis occidentalis* (MSUC-2), 10.VIII.1969 (MSUC-1). *Kalamazoo Co.*: Gourdneck Lake State Game Area, 19.VI.2011, A.I. Cognato, ex. funnel trap with EtOH (MSUC-1). *Wayne Co.*: Grosse Ile, Pke [sic! = Parke] lane, N42.17060° W84.14496°, 23.V-7.VI.2007, R. Mech, ex. Lindgren trap with ipsilure (MSUC-1), ex. Lindgren

trap with EtOH + alpha (MSUC-1), 20.VI-6.VII.2007, ex. Lindgren trap with ipsilure (MSUC-1), 7-20.VI.2007 (MSUC-5). **MISSISSIPPI**: [*Unspecified County*]: 19.V.1920, M.W. Blackman (CNCI-1). **MISSOURI**: [*Boone Co.*]: Columbia, 24.IV.1954, P.J. Spangler (USNM-1). **NEBRASKA**: *Dixon Co.*: Ponca, Ponca State Park, 42.607161°N -96.73223°W, 23.VIII.2007, T.P. Miller, ex. funnel trap with PSB alpha-pinene (MSUC-1). *Knox Co.*: Crofton, Lewis and Clarke Lake, 42.8321983°N -97.575555°W, 5.IX.2007, T.P. Miller, ex. funnel trap with Sirex (MSUC-1). [*Lancaster Co.*]: Lincoln, 29.VIII.[19]53, R. Roselle, ex. elm [= *Ulmus* sp.] (USNM-1). *Sarpy Co.*: Fontenelle Forest, 41.171478°N -95.9068166°W, 30.V.2006, N. Haxton, ex. funnel trap with ethanol lure (MSUC-1), 7.VII.2006 (MSUC-1). **NEW JERSEY**: [*Burlington Co.*]: Riverton, 12.II.1934, Wadley, ex. on Hackberry [= *Celtis* sp.] (USNM-1). [*Essex Co.*]: Newark (USNM-1). [*Somerset Co.*]: North Branch, 9.III.1937, C.H. Hoffman, ex. from gallery made in honey locust [= *Gleditsia triacanthos*] (USNM-1). **NEW YORK**: [*Tompkins Co.*]: Ithaca, 18.VI.[19]59, ex. in *Celtis occidentalis* (CUIC-11). **NORTH CAROLINA**: *Macklenburg Co.*: Charlotte, 15-20.VI.2006, J.F. Cornell, ex. FIT in vacant lot (MSUC-1). **NORTH DAKOTA**: [*Ransom Co.*]: Mcleod, 5mi N.W., 4.VII.1968, H.F. Howden (CNCI-1). **OHIO**: [*Hamilton Co.*]: Cincinnati, 6.VI.[?] (USNM-1), 24.VI.[?] (USNM-1), 9.VII.[?] (USNM-1). [*Unspecified County*]: Columbus (USNM-1); 11.V.[19]14 (DEBC-2). **OKLAHOMA**: *Latimer Co.*: V.1982, K. Stephan (USNM-2). **PENNSYLVANIA**: [*Allegheny Co.*]: Allegheny [=Pittsburgh], 7.VIII.[18]95 (CUIC-12). [*Dauphin Co.*]: Harrisburg, T.H. Hubbell (CUIC-1). Hummelstown, 26.VI.[19]37, J.N. Knull (CUIC-6). **TEXAS**: *Brazos Co.*: College Station, 13.IV.1964, S.G. Wellso (MSUC-1), 26.IV.1964 (MSUC-1). [*Unspecified County*]: Dallas, Hopk. U.S. 9929-X, F.C. Bishop, ex. hackberry [= *Celtis* sp.] (USNM-5). **VIRGINIA**: *Clarke Co.*: Boyne, 2mi S., U[niversity of] Virginia Blandy Experimental Farm, 8-18.VI.1990, D.R. Smith, ex. malaise trap

(USNM-1), 19-30.VI.1990 (USNM-1), 1-12.VII.1990 (USNM-1). *Essex Co.*: Dunnsville, 1mi S.E., 37° 52'N, 76°48'W, 29.V-9.VI.1993, D.R. Smith, ex. malaise trap (USNM-1); 24.VI-9.VII.1992 (USNM-1). *Fairfax Co.*: Mount Vernon, 27.VI.1915, ex. *Cornus stricta* (USNM-1). [*Unspecified County*]: Falls Church, 4.III.1921, E.A. Chapin (USNM-1). **WASHINGTON D.C.**: 21.V.1908 (MSUC-5). **WEST VIRGINIA**: *Morgan Co.*: Near Great Cacapon, 25.V.1985, G.F. & J.F. Hevel (USNM-2). *Wood Co.*: Hopk. U.S. 6675, ex. *Celtis* (USNM-1).

Distribution. UNITED STATES: Colorado, District of Columbia, Florida, Iowa, Illinois, Kansas, Kentucky, Maryland, Michigan, Mississippi, Missouri, New Jersey, North Carolina, North Dakota, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia.

Hosts. *Celtis occidentalis* L. (common hackberry) and *Celtis laevigata* Willd. (sugar hackberry).

Common name. Hackberry engraver.

Biology. *Scolytus muticus* prefers to colonize dead, dying or felled trees and the broken, dead and dying branches of live hackberry (Blackman 1922; Doane et al. 1936; Bright 1976).

The biology of this species is not well known. Adult galleries of *S. muticus* are parallel with the grain of the wood and consist of a single egg gallery without a nuptial chamber. The adult gallery strongly scores the sapwood and range in size from 2.5-5.0cm in length (Blackman 1922). Larval mines first radiate perpendicular to the egg gallery and later meander, giving the galleries a tortuous appearance (Blackman 1922; Bright 1976). Larvae construct pupal chambers in burrows 2-3cm deep within the sapwood (Bright 1976). There are two generations per year in the southeastern US and one generation per year in the northeastern US (Blackman 1922; Baker 1972).

Collection notes. None.

Remarks. The holotype of *Scolytus muticus* has been lost (Wood 1982), however, Say's (1824) description is unambiguous as to the characteristics of this species.

Wood (1982) reports *S. muticus* as having a transverse gallery that is perpendicular to the grain of the wood. Other authors including Blackman (1922), Baker (1972), and Bright (1976) report this species as having a gallery that is parallel to the grain of the wood. After examining the literature and photographs provided by T.H. Atkinson, it is likely that Wood erred in his description and that the gallery is parallel with the grain of the wood.

***Scolytus quadrispinosus* Say**

(Figures 1.28, 1.29)

Scolytus quadrispinosus Say 1824: 182. Holotype: male, Missouri (ANSP, lost).

= *Scolytus carya* Riley 1867: 68. Not located. Synonymy: LeConte 1876: 371.

= *Scolytus caryae* Walsh 1867: 58. Not located. Synonymy: LeConte 1876: 371.

Diagnosis. The *S. quadrispinosus* male is easily distinguished by its autapomorphic features of the abdominal venter which include: the apical margin of sternite 3 armed by three acute spines (two lateral and one medial), the apical margin of sternite 4 armed by one median tooth, sternite 1 apically descending, sternite 2 deeply concave, with the basal margin produced and bearing a median tubercle.

The female is distinguished by the flattened and moderately, finely longitudinally aciculate frons, bearing long, fine, incurved setae on the lateral and dorsal margins.

Redescription (male). 2.8 – 4.8mm long (mean = 4.0mm; n = 20); 1.8 - 2.25 times as long as wide. Color red-brown to dark red-brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process strongly produced and moderately elevated, surface smooth, shining; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing strongly flattened when viewed laterally; surface strongly, densely and coarsely aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye, setae on lateral and dorsal margins longer, thicker and incurved. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect golden setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a weakly rounded and serrate apex; apical margin of elytral apices bearing large, coarse punctures; apex entire at the suture. Disc smooth, shining; interstriae weakly impressed and twice the width of striae, interstitial punctures large, uniseriate, smaller than those of striae, interstitial punctures bearing sparse, long, semi-erect yellow hair-like setae (may have worn off); striae moderately impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 strongly and acutely produced and descending; sternite 2 deeply concave, basal margin produced and bearing a median tubercle. Sternite 2 nearly perpendicular to sternite 1; surface shagreened, dull, finely and obscurely punctate with small, fine and shallow punctures; apical margin armed with a broad median denticle, occasionally

absent. Apical margin of sternite 3 armed by three acute spines (two lateral and one medial); apical margin of sternite 4 armed by one median tooth. Sternite 5 carinate ridge closer to the basal margin than the apical margin of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a median depression is absent, and the apical half of the segment is pubescent.

Female. 2.9 – 5.0mm long (mean = 3.9mm; n = 20); 1.8 - 2.4 times as long as wide. Similar to male except epistoma feebly emarginated, frons less strongly flattened when viewed laterally, moderately and finely aciculate, setae shorter, less than the width of the eye and uniformly distributed. Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 face flattened, nearly perpendicular to sternite 1; setae erect and short, about half the length of segment 3. Venter unarmed.

Specimens examined. 143.

Type material. None examined.

Non-type material. **CANADA: ONTARIO:** Queenston, 15.VII.1938, D.F. Patterson, ex. *Carya ovata* (CNCI-2); Z17 E464 N4820, 20.VII.2004, Seaforth, ex. handpicked from eastern white pine [= *Pinus strobus*], 04-5-0265 (CNCI-1). **UNITED STATES: GEORGIA:** 1.IX.[19]45 (CASC-4). **ILLINOIS:** [*Cook Co.*]: Edgebrook (CNCI-2). [*Unspecified County*]: Willow Springs, 21.VIII.[19]04, (FMNH-1), 13.V.[19]05, A.B Wolcott (FMNH-4). **KANSAS:** [*Shawnee Co.*]: Topeka, 16.VI.[?], Popenoe (USNM-1). **MASSACHUSETTS:** [*Unspecified County*]: (CASC-1). **MICHIGAN:** [*Ingham Co.*]: East Lansing, 15.VII.1932, (MSUC-4). *Wayne Co.*: Detroit, 18.VIII.1902 (MSUC-3). [*Unspecified County*]: Lansing, 9.IX.1929 (MSUC-36). **MISSOURI:** *Dent Co.*: 28.VIII.1973, M.P. Rolling (USNM-1), 31.VIII.1973 (USNM-3). [*Unspecified County*]: (FMNH-1). **MINNESOTA:** [*Sherburne Co.*]: Elk River, 8.VII.1959, E.J.

Kingsley (CNCI-2). **MISSISSIPPI**: [*Madison Co.*]: Canton 16.VI.[19]04 (CUIC-1). [*Oktibbeha Co.*]: [Starkville], Agriculture College of Mississippi [=Mississippi State University], 15.IV.1922, F.M. Hull (CUIC-1). **NEW JERSEY**: [*Middlesex Co.*]: Dunellen (CUIC-1). **NEW YORK**: *Onondaga Co.*: 10.VI.1942, N.M. Downie (FMNH-2), 14.VII.1946 (FMNH-1). Syracuse, C.J. Drake, ex. *Hickoria glabra* [= *Carya glabra*] (USNM-1). [*Orange Co.*]: Highland Falls, 20.VI.1920, F. Schott (CUIC-1). Middletown (CUIC-1). [*Queens Co.*]: Long Island Aqueduct, 14.VII.1912 (MSUC-4). [*Tompkins Co.*]: Groton, 7.VII.1946, N.M. Downie (FMNH-1). Ithaca, 4.VIII.1928, P.P. Babi (CUIC-1). [*Westchester Co.*]: Mount Vernon, VII.1913, ex. from hickory [= *Carya* sp.] (CASC-14). Yonkers, 28.V.1935, P.A. Read, H. Dietrich, ex. taken on air trap (CUIC-1). [*Unspecified County*]: New York City, 15.V.1912, (CNCI-1), 13.V.1912 (CUIC-1). **NORTH CAROLINA**: [*Buncombe Co.*]: Asheville, Bent Creek, 17.VI.[19]29 (FMNH-1). **PENNSYLVANIA**: [*Allegheny Co.*]: Allegheny [=Pittsburgh], (FMNH-3), 24.VI.[18]93 (CUIC-1). *Cumberland Co.*: Roadway Dr @ Schneider Dr, 40.229030°N, - 77.111580°W, 26.VI.2009, L.R. Donovall (MSUC-1). [*Dauphin Co.*]: Harrisburg, 19.IV.1911 (CASC-1), VI.1911 (CASC-3); 1.III.[19]11, emerged 7.IV.[19]11, Champlain (CASC-12); Hopk. U.S. 10935-E, 13-14.VII.[?], W.S. Fisher, ex. *Hicoria* [= *Carya* sp.] (CUIC-1). Hummelstown, 20.VI.[19]15 (CUIC-1). Linglestown, 8.VI.1912, W.S. Fisher (CNCI-1, CUIC-2). [*Philadelphia Co.*]: Angora [=Philadelphia], IX.[19]15, H.A. Kaeber, ex. Hickory bark [= *Carya* sp.] (USNM-7). [*Westmoreland Co.*]: Jeannette, H.G. Klages (CASC-2). [*Unspecified County*]: Ford City, 28.VIII.[19]11 (USNM-1). Tyrone, VII.[19]12, lot 367, ex. *Fraxinus alba* [= *Fraxinus americana*] (CASC-7). **TENNESSEE**: [*Hamilton Co.*]: Chattanooga, 2.VI.[19]19, Leach (FMNH-1).

Distribution. CANADA: Ontario, Quebec. UNITED STATES: Alabama, Connecticut, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Michigan, Minnesota, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia, Washington, D.C., Wisconsin.

Hosts. Primary hosts: *Carya spp.* (hickory). Incidental hosts: *Juglans cinerea* L. (butternut) and *Carya illinoensis* (Wangenh.) K.Koch (pecan).

Common name. Hickory bark beetle.

Biology. *Scolytus quadrispinosus* is one of the most destructive pests of hardwoods in the US and the most important pest of hickory (Doane et al. 1936; Baker 1972). The species generally attacks and kills single trees, or only treetops. However, outbreaks can develop during periods of drought, killing large tracts of hickory. *Scolytus quadrispinosus* kills its host by mass attack in which a multitude of broods develop in the phloem and cambium, effectively girdle the host tree (Blackman 1922).

Adult galleries are parallel with the grain of the wood and deeply score the sapwood. The adult gallery is short (2.5-5.0cm), and consists of a single egg gallery (Blackman 1922). Eggs are deposited singly in niches on each side of the egg gallery with 20-60 niches per gallery (Blackman 1922). After the eggs have been laid, the female constructs a postovipositional feeding tunnel parallel to the egg gallery (Goeden and Norris 1965b). Larval mines are in the cambium. From the egg gallery, the larval mines are first perpendicular to the grain of the wood and then gradually turn and diverge creating a fan shaped appearance. The larvae bore into the inner bark to overwinter. Larvae pupate the following spring and emerge as adults the following summer (Blackman 1922). Upon emergence, adults feed at twig crotches and leaf petioles before

selecting a host (Baker 1972; Goeden and Norris 1964b). There is one generation per year in the north with larvae completing their development in March and April and emergence in May.

There may be two generations per year in the south with the brood overwintering as larvae (Doane et al. 1936). See Goeden and Norris (1964a,b, 1965a,b) for more information regarding the biology of this species.

Collection notes. None.

Remarks. The holotype of *Scolytus quadrispinosus* is lost (Wood 1982), however Say's (1824) description is unambiguous as to the characteristics of this species. The holotype of *S. caryae* Walsh was likely deposited in Walsh's type collection, which was housed in the Chicago Academy of Science Museum. This collection burned in the Great Chicago Fire and the holotypes were lost (Sheppard 2004; J. Colby, pers. comm.).

Conifer Clade

The conifer clade (1.7-5.9mm) (*S. aztecus*, *S. dentatus*, *S. fiskei*, *S. hermosus*, *S. laricis*, *S. monticolae*, *S. mundus*, *S. obelus*, *S. oregoni*, *S. piceae*, *S. praeceps*, *S. reflexus*, *S. robustus*, *S. silvaticus*, *S. subscaber*, *S. tsugae*, *S. unispinosus*, and *S. ventralis*) is monophyletic. The sexual dimorphism exhibited by species in the clade follows the general pattern outlined above except for the shape of the frons, which is quite variable. In some species, the frons is convex in both sexes with the female frons more strongly convex than that of the male (*S. hermosus*, *S. obelus*, *S. praeceps*, and *S. subscaber*). *Scolytus laricis* males have a flattened and impressed frons when viewed from a lateral profile and that of the female is convex. In the remaining species, the male frons appears flattened when viewed from a lateral profile.

***Scolytus aztecus* Wood**

(Figures 1.30, 1.31)

Scolytus aztecus Wood 1967: 120. Neotype: male, labeled “Durango, Potreyo del Sauto y Cebadillas, 19.IV.[19]90, J. Tulio Mendez M., 935-A, ex. *Pseudotsuga menziesii*” (USNM). Here designated.

Diagnosis. *Scolytus aztecus* adults of both sexes are distinguished by the characteristics of the elytral apex with the apical margin produced between interstriae 1 and 2, deeply emarginated at interstriae 3, produced on interstriae 4 and deeply emarginated at stria 4.

Description male. 5.0mm long (mean = 5.0mm; n = 2); 2.5 times as long as wide. Body dark red-brown to black, antennae light brown, legs light brown to dark red-brown. Pronotum typically darker than elytra.

Epistoma broadly and deeply emarginated; epistomal process weakly developed and low; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures large, coarse and more dense medially above the epistoma; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, almost subquadrate, setose with a partial septum and two arcuate sutures.

Pronotum as long as wide; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine,

shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical, anterolateral and lateral margins bearing moderately abundant, erect, yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and rounded and serrate apex; apical margin of elytra produced between interstriae 1 and 2, deeply emarginated at interstria 3, produced on interstria 4 and deeply emarginated at stria 4; apical margin of elytral apices bearing large, coarse punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae bearing short, sparse yellow hair-like setae spaced by the length of a setae or less; interstriae weakly impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae moderately impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface rugose, coarsely and deeply punctate; covered with abundant erect setae that are greater than the width of segment 3 in length; face convex; armed medially with a laterally compressed spine with the base extending from the apical margin to $\frac{3}{4}$ of the segment, apex rounded, shining and impunctate; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the apical margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Redescription (female). 4.6 - 5.9mm long (mean = 5.23mm; n = 4); 2.3-2.5 times as long as wide. Similar to male except epistoma feebly and broadly emarginated, epistomal process absent, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and sparse; weakly transversely on lateral margins above epistoma; median line

on frons raised. Apical margin of elytra slightly produced between interstriae 1 and 2, emarginated at interstria 3, slightly produced on interstria 4 and emarginated at stria 4. Second sternite unarmed.

Specimens examined. 7.

Type material. Neotype *Scolytus aztecus* Wood (USNM).

Non-type material. **MEXICO: DURANGO:** Potreyo del Sauto y Cebadillas, 19.IV.[19]90, J.

Tulio Mendez M., 935-A, ex. *Pseudotsuga menziesii* (THAC-3). **NUEVO LEÓN:** Santa Catarina, San Antonio de las Alazanas, 14.XII.2011, Gerardo Cuellar, ex. *Pseudotsuga menziesii* (MSUC-3).

Distribution. MEXICO: Durango, Michoacán, Nuevo León.

Hosts. *Abies religiosa* (Kunth) Schltdl. & Cham. (sacred fir), *A. durangensis* Martínez (Durango fir) and *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir). *Abies* species are likely the preferred host.

Common name. None.

Biology. *Scolytus aztecus* is an uncommon species and little is known regarding its biology.

Scolytus aztecus colonizes both standing trees and felled trees (Wood 1967; Cibrián Tovar et al.

1995). The tops of trees attacked by *S. aztecus* exhibit red foliage. *Scolytus aztecus* has been

collected feeding in the cambium of large *Abies* trees, although it has also been collected from

Pseudotsuga. Because of limited host records, it is unknown whether the primary host is *Abies* or

Pseudotsuga. Phylogenetic placement of the species suggests *Abies* (Figure 1.1) because the

species belongs to a clade of *Abies* feeding taxa. The adult gallery is transverse across the grain

of the wood with a central nuptial chamber, similar in appearance to that of *S. ventralis* (see

Cibrián Tovar et al. 1995, plate 132). Larval mines are in the cambium and do not score the wood. Pupation occurs in the cambium (Wood 1967; Cibrián Tovar et al. 1995).

Collection notes. None.

Remarks. The type series of this species (holotype and 2 paratypes) was lost in transit. A neotype is here designated for this distinctive species.

This is the first description of a male for this species.

***Scolytus dentatus* Bright**

(Figures 1.32, 1.33)

Scolytus dentatus Bright 1964: 167. Holotype: male, labeled “Calif: Monterey Co, Cone Peak, 6-29-63, *Abies bracteata*, C.J. Wray Collector” (CASC).

Diagnosis. The *S. dentatus* male is easily distinguished by the presence of a median denticle on the apical margin of sternite 4, occasionally median denticles may also be present on the apical margins of sternites 2 and 3.

The female is distinguished by its distribution in the Santa Lucia range of California and differentiated from the *S. praeceps* female by the presence of a strongly developed and distinct epistomal process and larger size.

Redescription (male). 3.0-4.0mm long (mean = 3.45mm; n = 15); 1.7 – 2.5 times as long as wide. Head, pronotum and abdominal venter dark red-brown, antennae light brown, legs dark red-brown to light brown, elytra light red-brown. Pronotum darker than elytra.

Epistoma moderately and acutely emarginated; epistomal process strongly produced and elevated; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, not impressed; surface moderately and finely

longitudinally aciculate, coarsely punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctulate and punctures moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on basal half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex not emarginated at the suture. Disc glabrous, smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 strongly produced and elevated above the base of sternite 2, sternite base 2 appearing impressed. Sternite 2 nearly perpendicular to sternite 1; surface glabrous, shagreened, dull, finely, obscurely punctate with small, fine and shallow punctures; face flattened. Apical margins of sternites 2 and 3 may be armed with a median denticle, median denticle always present on apical margin of sternite 4; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 equal to the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 3.4-4.6mm long (mean = 3.7mm; n = 15); 2.2 - 2.5 times as long as wide. Similar to male except epistoma less strongly emarginated, epistomal process less strongly produced and elevated, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly medially impressed between inner apices of eyes and. Sternites unarmed.

Specimens examined. 95.

Type material. Holotype *Scolytus dentatus* Bright (CASC). Allotype, female, *Scolytus dentatus*, identical data as holotype. Paratypes: **UNITED STATES: CALIFORNIA:** Monterey Co., Cone Peak, 29.VI.[19]63, C.J. Wray, ex. *Abies bracteata* (CASC-6, CNCI-20, EMEC-39, USNM-8). Carmel Valley, 15mi S., 22.VII.[19]63, C.J. Wray, ex. *Abies bracteata*, (CASC-4).

Non-type material. **UNITED STATES: CALIFORNIA:** Monterey Co.: Carmel Valley, 15mi S., 23.VII.[19]63, D.E. Bright, ex. *Abies bracteata* (CASC-2); 30.VII.1964 (CASC-2). Cone Peak, 29.VI.[19]63, C.J. Wray, ex. *Abies bracteata* (CASC-1, USNM-12). Williams Canyon, Los Padres National Forest, 24.IV.1992, D.E. Bright, G. Ferrell, ex. *Abies bracteata* limbs (CNCI-1).

Distribution. UNITED STATES: California.

Hosts. *Abies bracteata* (D. Don) Poit. (bristlecone fir, Santa Lucia fir).

Common name. None.

Biology. Little is known regarding the biology of this uncommon and narrowly geographically restricted species. The host, *Abies bracteata*, is narrowly restricted to the Santa Lucia Mountains of California. The tree is distributed in small patches in deep and moist canyon bottoms as well as dry rocky slopes and ledges within Los Padres National Forest in Monterey County, especially near Cone Peak and Church Creek (Griffin and Critchfield 1972; Sullivan 1993). *Scolytus*

dentatus has been collected feeding in the bole of large standing trees (Bright 1964) but is also reported from larger limbs and fresh slash (Edson 1967).

The adult gallery of *S. dentatus* somewhat resembles an expanded 'E'. The gallery is parallel with the grain of the wood and consists of a central nuptial chamber and two egg galleries, one below and one above the nuptial chamber. Each egg gallery ends in a pronounced hook. Galleries strongly score the cambium and lightly score the sapwood. The adult gallery averages 2.5-12.0cm in length (Bright 1964; Edson 1967). Egg niches are closely spaced on both sides of the maternal gallery (Bright and Stark 1973). Larval mines are first perpendicular to the egg gallery and later turn to form a fan shaped pattern before terminating at pupation chambers in the sapwood (Edson 1967).

Collection notes. None.

Remarks. Considerable variation is observed in the presence of median denticles on the apical margins of male sternites 2 and 3. Frequently males only have a median denticle on the apical margin of sternite 4 as those on 2 and 3 may or may not be present in the male. This species is related to *S. robustus* and *S. subscaber* based on morphological characters (Figure 1.1). Both of these species also feed on true firs (*Abies* spp.) and have the apical margin of male sternite 1 strongly apically produced.

***Scolytus fiskei* Blackman, removed from synonymy**

(Figures 1.34, 1.35)

Scolytus fiskei Blackman 1934: 25. Holotype: male, labeled "[Capitan Mountains, N. Mex. 25 April, 1907], Hopk. US 3959, W.F. Fiske Collector, Type No. 43840 USNM" (USNM).
Synonymy: Wood 1977: 388.

Diagnosis. *Scolytus fiskei* is very morphologically similar to *S. laricis* and *S. unispinosus*. Males of *S. fiskei* are distinguished from those of *S. laricis* by the frons flattened when viewed laterally, never deeply impressed, moderately abundant frontal setae (compared to dense) and by the host genus, *Pseudotsuga*. Males are distinguished from those of *S. unispinosus* by the following combination of characters: abdominal venter shiny in luster, the base of the sternite 2 spine extends from the apical margin to three-quarters the length of the segment and geographical distribution east of the Rocky Mountains.

The female is distinguished from that of both species by the shining luster of sternite 2.

Redescription (male). 2.2 – 2.8mm long (mean = 2.4mm; n = 15); 2.1 - 2.8 times as long as wide. Head, antennae, pronotum, and abdominal venter dark red-brown, elytra and legs yellow-brown to light brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process present, moderately developed and low; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally from epistoma to the vertex, slightly transversely impressed above epistoma to inner apices of eyes; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures large, sparse and coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two broadly arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine,

shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae not impressed and twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; punctures bearing short sparse recumbent yellow setae slightly longer than the size of a puncture (may be broken off); striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 rounded, 2 marked by a weak carina. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shining, finely punctate with small, fine and shallow punctures; covered with sparse setae that are less than the width of segment 3 in length; face convex; apical margin armed with a laterally compressed, median spine with the base extending from the apical margin to $\frac{3}{4}$ the length of the segment, apex rounded; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge equidistant between basal and apical margins of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.2 - 3.5mm long (mean = 4.65mm; n = 15); 2.1 - 2.5 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process weakly developed, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between epistoma and inner apices of

eyes. Second sternite apical margin armed with an acute median denticle, with base extending from apical margin to half-length of segment.

Specimens examined. 297.

Type specimens. Holotype *Scolytus fiskei* Blackman (USNM).

Non-type specimens. **CANADA: BRITISH COLUMBIA:** Aspen Grove, 12.VII.1931, H.

Richmond (CNCI-11, FMNH-2). Clinton, 6mi N., 7.VII.1972, D.E. Bright, ex. *Pseudotsuga*

menziesii (CNCI-7). Creston, 8.VI.1958, H. & A. Howden (EMEC-1). Fort Steele, 14.VI.[19]26,

R. Hopping (CASC-1). Indian Meadows, Midday Creek, 13.VII.1920, R. Hopping, ex.

Pseudotsuga taxifolia [= *P. menziesii*] (CASC-2, CNCI-2). Lumby, Creighton Valley,

3.VI.[19]22, R. Hopping (CASC-1). Merritt, Midday Valley, 27.VI.1926, W. Mathers (CASC-2).

Trinity Valley, 24.VI.1928, J.R. Howell, ex. *Pinus monticola* (CASC-1), 10.VII.1928 (CASC-1).

UNITED STATES: ARIZONA: *Pima Co.:* Tucson, Mount Lemmon, 11.VI.1969, S.L. Wood,

ex. *Pseudotsuga menziesii* (MSUC-2). **COLORADO:** *Boulder Co.:* Nederland, 5-7km N.,

5.VIII.2009, D.E. Bright, B.A. Barr, ex. branches of *Pseudotsuga menziesii* (CNCI-4). [*La Plata*

Co.]: Durango, Junction Creek Rd., 10000ft, 12-17.VII.1968, E.C. Becker (CNCI-1). *Larimer*

Co.: Roosevelt National Forest, Big Thompson Canyon, N40°24.456' W105°24.565', 7080ft,

5.V.2010, S.M. Smith, D.E. Bright, B.A. Barr, ex. *Pseudotsuga menziesii* (MSUC-36). **IDAHO:**

[*Adams Co.*]: Tamarack, 10mi S., 3.VII.1967 (WFBM-1). *Boise Co.:* Idaho City, 2.VI.1970

(WFBM-9), 1.I.1971 (WFBM-4). Lowman, Edna Creek, 6.VII.[19]72, A. Vaccares, G. Starr, ex.

Douglas fir stump [= *Pseudotsuga menziesii*] (WFBM-1). *Bonner Co.:* 6.VI.1986, M.M. Furniss,

J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-7). Priest Lake, Indian Creek, 6.VI.1986, M.M.

Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-25). Priest Lake 6.VI.1986, M.M.

Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-1). *Boundary Co.:* Parker Creek,

8.VI.1986, M.M. Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-5). *Clearwater Co.*: Elk River, 12mi S.E., Hopk. U.S. 58536, 9.VII-16.VII.1973, R.D. Oakes (WFBM-1), 30.VII-6.VIII.1973 (WFBM-1); Hopk. U.S. 58771, 25.VI-1.VII.1974, J.M. Wells, ex. in flight (WFBM-1). *Custer Co.*: Herd Lake, Hopk. U.S. 60796-A, 3.IX.1978, M.M. Furniss, ex. *Pseudotsuga menziesii* (WFBM-9). MacKay, 9mi N.E., 19.VII.1985, M.M. Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-3). Summit, W. of Pass Creek, 19.VII.1985, M.M. Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-12). *Latah Co.*: Big Sand Creek, Hopk. U.S. 53545, 11.VI.1969, M.M. Furniss (WFBM-1), 20.VI.1969 (WFBM-1). Moscow, 20.XI.1961, R.E. Stecker, ex. reared from Doug fir [= *Pseudotsuga menziesii*] (WFBM-33). Moscow Mountain, Hopk. U.S. 48869, 18.VII.1967, ex. *Pseudotsuga menziesii* (WFBM-3). Viola, 21.VI.1985, S.J. Gast, M.M. Furniss, ex. *Pseudotsuga menziesii* (WFBM-2). *Nez Perce Co.*: Forest, III.1985, M.M. Furniss, ex. *Pseudotsuga menziesii* (WFBM-6). *Shoshone Co.*: Red Ives Ranger Station, V.1983, M.M. Furniss, ex. *Pseudotsuga menziesii* (WFBM-1). *Valley Co.*: Cascade, 7mi E., 14.VI.1966, R.L. Furniss (WFBM-1). **MONTANA**: *Lake Co.*: Swan Lake, 28.VI.1963, M.M. Furniss, ex. *Pseudotsuga menziesii* (WFBM-1). *Madison Co.*: Alder, 18km S.W., 8.IX.1978, M.M. Furniss, ex. *Pseudotsuga menziesii* (WFBM-6), 12mi S.W. Alder (WFBM-16). *Park Co.*: Livingston, 10mi S.E., 23.VII.1988, M.M. Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-2). **NEW MEXICO**: *Otero Co.*: Cloudcroft, 4.VI.1969, tree 53, S.L. Wood, ex. *Pseudotsuga menziesii* (MSUC-2). *Sierra Co.*: Emory Pass, 24.VII.1974, D.E. Bright, ex. *Pseudotsuga menziesii* (CNCI-1). **WASHINGTON**: [*Whitman Co.*]: Pullman, 23.VI.1951, N.M. Downie (FMNH-1). **WYOMING**: [*Teton Co.*]: Jackson, A.D. Hopkins, ex. *Pseudotsuga menziesii* (USNM-1).

Distribution. CANADA: British Columbia. UNITED STATES: Arizona, Colorado, Idaho, Montana, New Mexico, Washington, Wyoming.

Hosts. *Pseudotsuga menziesii* (Mirb.) Franco (Douglas Fir).

Common name. None.

Biology. *Scolytus fiskei* colonizes suppressed limbs and branches of *Pseudotsuga menziesii* as well as fresh slash (Edson 1967; Smith, pers. obs.). The adult gallery is bayonet shaped and parallel with the grain of wood and consists of two egg galleries, one below and one above the nuptial chamber and a turning niche. The female constructs the adult gallery more in the cambium and lightly scores the sapwood. Larval mines are perpendicular to the egg gallery and turn to form a fan shaped pattern (Edson 1967; Furniss and Johnson 2002; Smith, pers. obs.). The adult gallery measures 3.8-9.0cm in length (Edson 1967). The following year adults emerge and excavate tunnels within twigs of Douglas fir for maturation feeding causing twig flagging (reported as *S. unispinosus* McMullen and Atkins 1962).

Like most *Scolytus* species, there is a very limited amount of information known about *S. fiskei*. For many years it was considered a synonym of *S. unispinosus* and was thus referred to as *S. unispinosus* in publications. Very little was written about this species in the US (see Wood and Bright 1992) other than host preference and gallery descriptions (Keen 1938; Edson 1967; Bright 1976). McMullen and Atkins (1962) reported some notes on the biology of *S. unispinosus* in British Columbia and appear to have reported a combined account of *S. unispinosus* and *S. fiskei*. The authors noted the gallery of the *S. unispinosus* studied in their investigations as “in about 15 per cent of the galleries over 20 days of age were the type described by Chamberlin and Keen [*S. unispinosus*, which has only a single egg gallery]; the majority were of the forked type and were similar to those of *S. tsugae* [referencing a forked or bayonet shaped gallery that is made by *S.*

fiskei”]. McMullen and Atkins (1959) had previously considered *S. monticolae* a synonym of *S. tsugae*. Their description matches the gallery description of *S. fiskei*, which like has two egg galleries as part of a bayonet shaped adult gallery. Because most of the specimens are of *S. fiskei*, this article does offer some information regarding the biology of the species be used with caution because not all of the findings may apply to *S. fiskei*.

Collection notes. None.

Remarks. The holotype of *S. fiskei* does not bear a locality label. Blackman’s (1934) description states the holotype was collected at the Capitan Mountains, New Mexico.

Furniss and Johnson (2002) report *S. unispinosus* from Alberta, Canada. These specimens are likely *S. fiskei* based on the geographic distribution of the species in the Rocky Mountains.

Wood (1977: 388) placed *S. fiskei* in synonymy with *S. unispinosus* after examining both holotypes and 164 specimens from Arizona to British Columbia and concluded that there was too much intraspecific variation to recognize them as separate species. I assessed the intraspecific and interspecific variation (Tables 1.7 and 1.8) for each of the four genes for each species. *Scolytus fiskei* intraspecific variation for COI was low, 0.0-0.0231, and averaged 0.0183 among all sampled populations. *Scolytus unispinosus* intraspecific variation was also low, 0.0016-0.0282 and averaged 0.0121. Interspecific variation between *S. fiskei* and *S. unispinosus* was much higher, 0.0331-0.0521 and averaged 0.043 among populations. Similar differences were also observed with CAD (Table 1.8). The species have separate geographical ranges with *S. fiskei* occurring primarily in the Rocky Mountains and British Columbia while *S. unispinosus* occurs in the Cascade and Sierra mountains from California to British Columbia. Both species are sympatric in the Interior Plateau of British Columbia near Merritt. The species are separated by the characters listed in the diagnosis and by the galleries. The galleries of *S. fiskei* contain two

egg galleries; one above and one below the nuptial chamber. The gallery of *S. unispinosus* only contains a single egg gallery. In addition, the gallery of *S. fiskei* lightly scores the sapwood while that of *S. unispinosus* deeply scores the sapwood. After examining the types, 950 specimens of both species and testing the monophyly of each species using four genes, it is apparent that *S. fiskei* is a distinct lineage and is here removed from synonymy with *S. unispinosus*.

***Scolytus hermosus* Wood**

(Figures 1.36, 1.37)

Scolytus hermosus Wood 1968: 12. Neotype: male, labeled “Tlaxco 11mi. N., 8900ft, 9.VII.1967, S.L. W[ood], ex. *Abies religiosa*” (USNM). Here designated.

Diagnosis. Both sexes of *S. hermosus* resemble the *S. silvaticus* female. The female is distinguished by having a weakly developed epistomal process and the male is distinguished by having the apical margin of sternite 1 produced, forming a carinate lip along the basal margin of sternite 2 that is twice as produced as thick and by the host genus, *Abies*.

Redescription (male). 3.0mm long (mean = 3.0mm; n = 1); 1.5 times as long as wide. Head, antennae, pronotum, and abdominal venter dark red-brown, elytra and legs yellow-brown to light brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process weakly developed and low; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally, slightly transversely impressed above epistoma and between inner apices of eyes; surface moderately and finely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape

short, elongate, less than length of the first four funicular segments; club flattened, elongate, almost subquadrate, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, interstitial punctures bearing sparse, long, erect yellow hair-like setae (may have worn off); striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 produced, forming a carinate lip along the basal margin of sternite 2 that is twice as produced as thick, basal margin of sternite 2 appearing impressed, Sternite 2 nearly perpendicular to sternite 1; surface shagreened, dull, finely punctate with small, fine and shallow punctures; setae moderately abundant, recumbent and short, about four times the length of a puncture; face weakly concave; apical margin armed with a broad median denticle, occasionally absent; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.5 - 3.5mm long (mean = 3.27mm; n = 6); 2.1 - 2.3 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons more strongly convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed above epistoma. Apical margin of sternite 1 weakly elevated above the base of sternite 2. Second sternite unarmed.

Specimens examined. 20.

Type material. Neotype *Scolytus hermosus* Wood (USNM). Paratypes: **MEXICO:** [**PUEBLA**]: Tlaxco, 11mi. N., 8900ft, 9.VII.1967, S.L. W[ood], ex. *Abies religiosa* (USNM-15).

Non-type material. **MEXICO:** **CHIHUAHUA:** La Magdalena, Hopk. U.S. 62081-B, 27.IV.1981, M.M. Furniss, ex. *Abies durangensis* (USNM-1). **NUEVO LEÓN:** Cerro Potosi, Hopk. U.S. 58615-C, 21.III.[19]74, M.M. Furniss, ex. *Abies* sp. (USNM-2, WFBM-1).

Distribution. MEXICO: Chihuahua, Nuevo León, Puebla.

Hosts. *Abies religiosa* (Kunth) Schltdl. & Cham (sacred fir), *Abies durangensis* Martínez (Durango fir) and *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir). *Abies* species are likely the preferred hosts.

Common name. None.

Biology. There is a paucity of information regarding the biology of this uncommon species.

Scolytus hermosus has been collected feeding in the cambium of large *Abies* slash greater than 10cm in diameter (Wood 1967) and weakened and dying large *Pseudotsuga* (Cibrián Tovar et al. 1995). The adult galleries are transverse and perpendicular with the grain of the wood (Wood 1967). This species has been reported to colonize the same material as *S. mundus* (Wood 1968).

Collection notes. None.

Remarks. Part of the type series (holotype, allotype and 4 paratypes) was lost in transit. A neotype is here designated for this species.

Scolytus laricis Blackman

(Figures 1.38, 1.39)

Scolytus laricis Blackman 1934: 24. Holotype: male, labeled “[Cedar Mountain, Moscow, ID] Hopk. US 225d, 8636m [sic!], 6-20-[18]99, Type No. 43839” (USNM).

Diagnosis. *Scolytus laricis* is very morphologically similar to *S. fiskei* and *S. unispinosus*. Males of *S. laricis* are distinguished from those of *S. fiskei* by the dull appearance of abdominal sternite 2 and by the frons densely covered by long setae. Males can be distinguished from those of *S. unispinosus* by the following combination of characters: the base of the sternite 2 spine extends from the apical margin to three-quarters the length of the segment and host.

The female is distinguished from that of *S. fiskei* by the dull luster of sternite 2 and is distinguished from that of *S. unispinosus* by the frons moderately and coarsely aciculate-punctate; sternite 1 rounded over onto face of sternite 2, not forming an obtuse angle, base of sternite 2 finely impressed.

Redescription (male). 2.3 – 4. mm long (mean = 3.1 mm; n = 15); 1.8- 2.5 times as long as wide. Head, pronotum, and abdominal venter dark red-brown to black, elytra and legs light brown, antennae yellow-brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process present, moderately developed and elevated; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally from epistoma to the vertex, moderately transversely impressed above epistoma to vertex; surface strongly and coarsely longitudinally

aciculate-punctate; aciculations converging at epistoma; punctures sparse, large and coarse; surface moderately to densely and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae not impressed and twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, interstitial punctures bearing minute, recumbent setae the length of interstitial punctures (may have worn off); striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 rounded, marked by a weak carina that is on ascendant part of venter. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shining, finely punctate with small, fine and shallow punctures; covered with sparse setae that are less than the width of segment 3 in length; face convex; apical margin armed with a laterally compressed, median spine with the base extending from the apical margin to $\frac{3}{4}$ the length of the segment, apex rounded,

rarely a slightly elevated vertical carina (Oregon: Dixie Pass and Frog Lake) instead of a spine; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge equidistant between basal and apical margins of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.6 – 4.0mm long (mean = 3.2mm; n = 15); 2.1- 2.9 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process weakly developed, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed above epistoma. Second sternite apical margin armed with a blunted median denticle, with base extending from apical margin to a third length of segment. Sternite 5 length greater than the combined lengths of sternites 3 and 4.

Specimens examined. 294.

Type material. Holotype *Scolytus laricis* Blackman (USNM).

Non-type material. **CANADA: BRITISH COLUMBIA:** Canoe, 12.VII.1933, A. Thrupp, ex.

Larix occidentalis (CASC-3). Rossland, 21.IX.[19]61, D.E. Bright, ex. *Larix laricina* (CNCI-2).

UNITED STATES: IDAHO: *Boundary Co.:* [Idaho Panhandle National Forest], Robinson

Creek campground, N48°58.197' W116°13.068', 2748ft, 10.VIII.2010, S.M. Smith, [A.R.

Gillogly], ex. *Larix occidentalis*, emerged II.2011, M.M. Furniss (MSUC-94). *Clearwater Co.:*

Elk River, V.1981, M.M. Furniss, ex. *Larix occidentalis* (WFBM-17), VII.1981 (WFBM-11).

Elk River, 13mi S.W., Hopk. U.S. 60361-A, 23.IV.1975, M.M. Furniss, ex. *Larix occidentalis*

(WFBM-4). *Idaho Co.:* Salmon Mountain, 18.VIII.1985, M.M. Furniss, J.B. Johnson, ex. *Larix*

lyalli (WFBM-29). *Kootenai Co.:* Coeur d'Alene, Hopk. U.S. 16306-B, 2.VIII.1919, J.C.

Evenden, ex. *Larix occidentalis* (WFBM-9), 8.VIII.1919 (MSUC-11). Deception Creek

Experimental Forest, Hopk. U.S. 58889-A, 10.VII.1968, M.M. Furniss (OSAC-4), Hopk. U.S.

53376, 11.VII.1968 (WFBM-2), Hopk. U.S. 60320, 25.VII.1968, (OSAC-2), Hopk. U.S. 50421-B,C, 1.VII.1975 (OSAC-2), Hopk. U.S. 60356, 30.VII.[19]68, M.M. Furniss, ex. *Larix occidentalis* (WFBM-6). *Latah Co.*: Moscow, 2.VIII.1930, 2560ft, P. Rice, ex. trap (WFBM-1). Moscow Mountain, Hopk. U.S. 53632-F, 23.VI.1964, M.M. Furniss, ex. in flight (WFBM-1), Hopk. U.S. 60421-A, 1.VII.1975 (OSAC-1). **MONTANA**: *Missoula Co.*: Missoula, 35mi N.W., 3.XI.[19]65, ex. *Larix occidentalis* (WFBM-2). Nine Mile Creek, Hopk. U.S. 48830, 3.XI.1965, M.M. Furniss, ex. *Larix occidentalis* (WFBM-2, OSAC-1). *Ravalli Co.*: [Bitterroot Mountains], Trapper Peak, 2.X.[19]88, M.M. Furniss, ex. *Larix lyalli* (WFBM-3). [Unspecified County]: Libby, 60mi S.E., 30.VI.[19]72, D.E. Bright, ex. *Larix laricina* (CNCI-7). **OREGON**: *Crook Co.*: Summit Prairie, 12.VI.1940, Schuh, Scott, ex. *Larix occidentalis* (CNCI-3, EMEC-2). [Grant Co.]: Dixie Pass, Malheur National Forest, 23.VI.1961, S.L. Wood, J.B. Karren, D.E. Bright, ex. *Larix occidentalis* (CNCI-6, USNM-6). *Jefferson Co.*: Camp Sherman, T.O. Thatcher, ex. *Larix lyalli* limbs (CSUC-10), 9.VII.[19]66, [L. Edson], ex. *Larix lyalli* (CNCI-2). Suttle Lake, 4mi N., 25.VII.1939, ex. *Larix lyalli* (CSUC-1); 28.VII.1939, F. Grey, J. Schuh, ex. *Larix occidentalis* (CASC-1, FMNH-6, MSUC-1, OSAC-14), W.J. Chamberlin, ex. *Larix lyalli* (EMEC-7, WFBM-3). Suttle Lake, 4mi W., 15.VIII.1939, Schuh, Scott (MSUC-1). [Marion Co.]: Clear Lake, 17.VIII.[19]51, R. Kangur, ex. Larch [=*Larix* sp.] (EMEC-4, WFBM-2). [Umatilla Co.]: Tollgate, 28.X.1948, C. Chastain, ex. *Larix occidentalis* (EMEC-1). [Wasco Co.]: [Mount Hood National Forest] Frog Lake [campground], 4S9 E17, 2.VIII.1951, R. Kangur (CNCI-3). [**WASHINGTON**: *Okanogan Co.*: Disautel, 4.XI.1936, R.L. Furniss, ex. *Larix occidentalis* (OSAC-3). [Pend Oreille Co.]: Metaline Falls, Hopk. U.S. 19905, 20.VII.1930, D. DeLeon, ex. *Larix occidentalis* (OSAC-2, WFBM-1). [Stevens Co.]: Northport, 18.VII.1929, R.

Hopping (OSAC-1). [*Unspecified County*]: Mount Adams, 7000ft, Hopk. U.S. 53359-C, 2.VIII.1968, M.M. Furniss, ex. on snowfield (WFBM-1).

Distribution. CANADA: British Columbia. UNITED STATES: Idaho, Montana, Oregon, Washington.

Hosts. *Larix occidentalis* Nutt. (western larch) and *Larix lyalli* Parl. (subalpine larch).

Common name. None.

Biology. *Scolytus laricis* prefers to colonize suppressed lower limbs of its host and fresh slash.

The adult gallery of *S. laricis* is parallel with the grain of the wood and consists of two egg galleries and a central nuptial chamber. The central nuptial chamber extends at a right angle to the rest of the gallery and opposite the nuptial chamber is a rounded turning niche. This gives the central part of the gallery an ovoid appearance that is different from all other Nearctic *Scolytus*. Egg galleries are extended in parallel to the grain of the wood. The adult gallery scores the sapwood more deeply than the cambium, and range in length from 6.4-11.5cm. The female constructs widely spaced egg niches on both sides of each egg gallery. Larval mines extend against the grain of wood and gradually diverge before terminating at pupation chambers that deeply score the sapwood (Edson 1967; Furniss and Johnson 2002). There is one generation per year and broods overwinter as larvae (Furniss and Johnson 2002).

Collection notes. *Scolytus laricis* was collected four times by the author and each time specimens were collected from fresh broken branches that were less than 5cm in diameter with bright green needles. Specimens were also collected from a fallen *L. occidentalis* of 15cm DBH.

Remarks. Furniss and Johnson (2002) reported that specimens collected from *L. lyalli* create a different gallery structure than those collected from *L. occidentalis* (M.M. Furniss pers. comm.). The galleries on *L. lyalli* are “shorter, less uniform, and with the entrance chamber often

extended a short distance to the sides of the gallery” (Furniss and Johnson 2002). Specimens from *L. lyalli* could not be collected during the course of my investigation. I noticed slight morphological variation among some populations but were unable to determine if the differences represent species limits. Further study is needed to address this question.

The holotype of *S. laricis* does not bear a locality label. Blackman’s (1934) description states A.D. Hopkins collected the holotype on Cedar Mountain near Moscow, Idaho. Numerous collectors listed in the material examined reported this species as collected from *L. lyalli* in Oregon. This host species occurs east of the Cascade Range in the Wenatchee Mountains in Washington and is not known to occur in Oregon (Burns and Honkala 1990). It is probable that the host species for these specimens was *L. occidentalis*.

***Scolytus monticolae* (Swaine)**

(Figures 1.40, 1.41)

Eccoptogaster monticolae Swaine 1917: 32. Lectotype: female, labeled “[Arrowhead, British Columbia], *Pinus monticola*, 2423, J.M. Swaine Coll, female” (CNCI). Lectotype designated Bright 1967: 674.

Diagnosis. *Scolytus monticolae* males are easily confused with males of the *S. reflexus*, especially those exhibiting the wickhami phenotype. They are easily distinguished by the size of male sternite 5. In *S. monticolae*, sternite 5 is equal in length to the width of sternites 3 and 4 combined. In *S. reflexus*, sternite 5 is equal in length to sternite 4. *Scolytus monticolae* lacks an epistomal process while *S. reflexus* typically has a strongly developed epistomal process. Males are distinguished from those of *S. tsugae* by the following combination of characters: face of sternite 2 shining but minutely reticulate; elytral striae not impressed; basal margin of sternite 2

more pronounced and produced laterally; elytral stria punctures small, spaced 2-3 diameters of a puncture.

Females of *S. monticolae* are distinguished from those of *S. reflexus* by having the apical margin of sternite 1 weakly produced, never rounded and the face of sternite 2 smooth and flat, and are separated from those of *S. tsugae* by elytral discal striae not impressed and sternite 2 shining in luster.

Redescription (male). 2.5 – 3.0mm long (mean = 2.9mm; n = 10); 2.0 - 2.5 times as long as wide. Head, pronotum, and abdominal venter dark red-brown, legs light brown, antennae yellow-brown, elytra usually dark red-brown but may be brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process weakly developed; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma; surface weakly aciculate-punctate, medial area appearing shagreened; aciculations converging at epistoma; punctures small, coarse; surface sparsely and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on basal half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex moderately emarginated at the suture. Disc glabrous, smooth, shining; interstriae not impressed and twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, interstitial punctures bearing minute, recumbent setae the length of interstitial punctures (may have worn off); striae not impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2, more pronounced and produced laterally forming two cups. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shining, finely punctate with small, fine and shallow punctures; face flattened, depressed above the basal margin of sternite 2; apical margin unarmed; covered in recumbent setae twice the width of a puncture; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.3 – 3.5mm long (mean = 3.0mm; n = 10); 2.3 - 2.7 times as long as wide. Similar to male except epistoma feebly emarginated, frons convex when viewed laterally, strigate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between inner apices of eyes. Second sternite unarmed. Length of sternite 5 is greater than the combined lengths of sternites 3 and 4.

Specimens examined. 123.

Type material. Lectotype *Eccoctogaster monticolae* Swaine (CNCI).

Non-type material. **CANADA: BRITISH COLUMBIA:** Merritt, Midday Valley, 27.VI.1926, W. Mathers (USNM-2), 4.IX.1926 (USNM-2). Trinity Valley, 4.VII.1954, ex. *Pseudotsuga taxifolia* (USNM-4). **UNITED STATES: COLORADO:** *Custer Co.:* Hillside, 6mi W., Duckett Creek, FR331, Rita Alta Fuelwood area, 23.V.2000, D. Leatherman (CSUC-1). [*Garfield Co.*]: Glenwood Springs (CASC-1). *Jefferson Co.:* Buffalo Creek, 6.VIII.2004, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CASC-2). **IDAHO:** *Benewah Co.:* St. Maries, Hopk. U.S. 618074, 28.VIII.1978, M.M. Furniss, ex. *Pseudotsuga menziesii* (USNM-32). *Boise Co.:* Boise National Forest, Bogus Basin, Bogus Basin Rd., N43°44.347' W116°07.099', 6047ft, 8.VIII.2010, S.M. Smith, A.R. Gillogly, ex. *Pseudotsuga menziesii* (MSUC-8). *Bonner Co.:* Priest River Experimental Forest, Hopk. U.S. 61809-A, 25.X.1978, M.M. Furniss, ex. *Pseudotsuga menziesii* (USNM-26). *Kootenai Co.:* Coeur d'Alene, 30.VIII.1919, J.C. Evenden (MSUC-12); 7.VIII.1919, J.C. Evenden, ex. *Pseudotsuga menziesii* (MSUC-4). *Shoshone Co.:* Coeur d'Alene National Forest, N47°25.708' W115°53.464', 3728ft, 15.VIII.2010, S.M. Smith, A.R. Gillogly, ex. *Pseudotsuga menziesii* (MSUC-19). Prichard, 23.VII.1920, J.C. Evenden, ex. *Abies grandis* (MSUC-2). **MONTANA:** [*Sanders Co.*]: Trout Creek, 1.VIII.1981, J. Dunkel, ex. Douglas fir (USNM-2). **OREGON:** [*Unspecified County*]: Santiam National Forest, 22.VIII.[19]14, W.J. Chamberlin, ex. *Abies amabilis* (EMEC-1). **WASHINGTON:** [*Kittitas Co.*]: Easton (USNM-1). [*Yakima Co.*]: Cliffdell, 7.VII.[19]35, R.H. Beaner (USNM-1). **WYOMING:** [*Park Co.*]: Cody, Hopk. U.S. 34220-F, 10.V.[19]56, H.E. Ostmark, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (CSUC-2).

Distribution. CANADA: British Columbia. UNITED STATES: Colorado, Idaho, Montana, Oregon, Utah, Washington, Wyoming.

Hosts. *Pseudotsuga menziesii* (Mirb.) Franco. (Douglas fir).

Common name. None.

Biology. *Scolytus monticolae* commonly infests the bole, suppressed branches and fresh slash of Douglas fir. *Scolytus monticolae* (as *S. tsugae*, see remarks below) has been reported to kill sapling and pole-sized Douglas fir trees in British Columbia (McMullen and Atkins 1959) and Wyoming (Furniss and Carolin 1977) that had been drought stressed.

Adult galleries of *S. monticolae* strongly resemble those of *S. reflexus*, parallel with the grain of the wood and bayonet shaped. The adult galleries consist of two egg galleries and a central nuptial chamber. From the central nuptial chamber, one egg gallery extends with the grain of the wood and the other egg gallery is slightly transversely extended and then extends parallel with the grain. The nuptial chamber is oblique to the egg galleries. The adult gallery scores the sapwood more than the cambium and averages 5.0-9.0cm in length. Egg niches are generally placed in pairs along the egg galleries and score the sapwood. Larvae extend their mines perpendicular to the egg gallery before diverging in a fan shaped pattern. Pupation may occur under the bark or in the sapwood. In Idaho, *S. monticolae* has one generation per year with flight occurring in July (Furniss and Johnson 2002; Smith, pers. obs.). Broods overwinter as larvae and emerge the following summer (Edson 1967; Furniss and Johnson 2002).

Collection notes. The author found this species to be common in suppressed limbs and slash in Idaho.

Remarks. The lectotype does not bear a locality label. Swaine's (1917) description states the lectotype was collected at Arrowhead, British Columbia.

In their paper describing the biology of *S. tsugae*, McMullen and Atkins (1959) considered *S. monticolae* a synonym of *S. tsugae* based on correspondence with G.R. Hopping (page 417). Wood (1966: 30) formally synonymized *S. monticolae* with *S. tsugae*, and later

removed the species from synonymy (Wood 1982; M.M. Furniss, pers. comm.). However, Wood (1982) did not explicitly state that he was the author that recognized the species. These two species are closely related and have subtle morphological differences. This has led to a confusing account of both species in the literature. The majority of which seems to be applicable to *S. monticolae* rather than *S. tsugae*. The above diagnostic characters and different biologies readily differentiate the species.

***Scolytus mundus* Wood**

(Figures 1.42, 1.43)

Scolytus mundus Wood 1968: 13. Neotype: female, labeled “18 km N Tlaxco, Puebla, Mexico, Wood coll.” (USNM). Here designated.

Diagnosis. This species most strongly resembles *S. aztecus* and *S. ventralis*. Both sexes are differentiated by elytral apices slightly emarginated only at interstria 3, by sternite 3 covered with abundant erect setae that are greater than the width of segment 3 in length. The male can also be differentiated by the apical margin of sternite 2 armed with a broad median denticle; larger size, the geographic distribution.

Redescription (male). 4.0 – 4.5mm long (mean = 4.35mm; n = 4); 2.1 - 2.5 times as long as wide. Color dark brown to black, antennae red brown. Pronotum same color as elytra.

Epistoma weakly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally, moderately transversely impressed above epistoma; surface strongly and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures small, fine; surface densely and uniformly covered by long, fine, yellow erect hair-like setae, setae longer

than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, nearly subquadrate, setose with a partial septum and two arcuate sutures.

Pronotum as long as wide; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical, anterolateral and lateral margins bearing abundant, erect, long dark yellow-brown hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; elytral apices slightly emarginated at interstria 3 and bearing large, coarse punctures; apex weakly emarginated at the suture. Disc smooth, shining; interstriae weakly impressed and more than twice the width of striae, interstitial punctures uniseriate, equal in size to those of striae, interstriae bearing moderately abundant long, erect dark yellow-brown hair-like setae; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shining, finely punctate with small, fine and shallow punctures; covered with abundant erect setae that are greater than the width of segment 3 in length; face flattened; apical margin armed with a broad median denticle; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 3.3 – 4.6mm long (mean = 4.0mm; n = 13); 1.8 – 2.6 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between inner apices of eyes and. Apical margin of second sternite armed by a small broad tumescence.

Specimens examined. 21.

Type material. Neotype *Scolytus mundus* Wood (USNM). Paratypes: **MEXICO:** [**PUEBLA**]: Tlaxco (Tlaxcala), 11mi. N., 8900ft, 9.VII.1967, S.L. W[ood], ex. *Abies religiosa* (USNM-15).

Non-type material. **MEXICO:** [**DISTRITO FEDERAL**]: Desierto de los Leones National Park, III.1951, J.M. Miller, ex. *Abies religiosa* (OSAC-2). **HIDALGO:** El Chico, 31.IX.[19]77, E. Hernandez V., ex. *Abies religiosa* (CNCI-2). **OAXACA:** Valle Nacional, 53mi S., 10000ft, 24.V.[19]71, D.E. Bright, ex. *Abies religiosa* (CNCI-2). **TLAXCALA:** Villarreal Terrenate, 23.II.[19]78, E. Hernandez, ex. *Abies religiosa* (USNM-4, WFBM-5).

Distribution. MEXICO: Distrito Federal, Estado de México, Hidalgo, Michoacán, Morelos, Oaxaca, Puebla, Tlaxcala.

Hosts. *Abies religiosa*. (Kunth) Schltdl. & Cham. (sacred fir).

Common name. None.

Biology. *Scolytus mundus* is a serious pest to *Abies religiosa* in Mexico and its life cycle and habits have been well studied (see Cibrián Tovar et al. 1995). *Scolytus mundus* attacks the tops of mature trees, trunks of recently cut trees and large logging slash greater than 10.0cm in diameter (Wood 1968; Cibrián Tovar et al. 1995). Trees attacked by *S. mundus* exhibit red foliage at the top of the tree. If the population density is high, subsequent generations will colonize the tree from the top down. However, attacks rarely occur at the base and so the host tree typically

survives (Cibrián Tovar et al. 1995). *Scolytus mundus* has been reported to colonize the same material as *S. hermosus* (Wood 1968).

The female initiates the attack by constructing an entrance in bark crevices at branch nodes. The adult galleries are straight and transverse across the grain of the wood, similar to *S. ventralis* and with a central nuptial chamber (see Cibrián Tovar et al. 1995, plates 130-131). Eggs are laid in niches excavated on each side of the central nuptial chamber. The larval mines extend parallel with the grain of wood and are first in the cambium and later penetrate into the sapwood. Pupation occurs in the sapwood and there are two generations per year with the first generation occurring from October to May and the second from June to October (Cibrián Tovar et al. 1995).

Collection notes. None.

Remarks. Part of the type series (holotype, allotype and 4 paratypes) was lost in transit. A neotype is here designated for this species.

***Scolytus obelus* Wood**

(Figures 1.44, 1.45)

Scolytus obelus Wood 1962: 81. Holotype: male, labeled “Payson Canyon, UT, S.L Wood, 14 May 1960, *Abies concolor*, BLNO 001271” (USNM).

Diagnosis. Both sexes of *S. obelus* strongly resemble *S. praeceps* and are distinguished by the presence of a small median denticle on the apical margin of sternite 2.

Redescription (male). 1.8 – 2.9mm long (mean = 2.2mm; n = 20); 2.1 - 2.9 times as long as wide. Color red brown to dark red-brown, antennae brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process weakly developed and low; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally, slightly transversely impressed above epistoma; surface moderately and coarsely aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, ovoid, setose with a partial septum and three arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and weakly serrate apex; apical margin of elytral apices bearing large, coarse punctures; apex weakly emarginated at the suture. Disc glabrous, smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae not impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 strongly, acutely produced forming a lip along the base of sternite 2, basal margin of sternite 2 appearing impressed. Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface, shagreened, dull, finely punctate with small, fine and shallow punctures of varying size, larger

and more abundant near basal margin; face weakly concave; apical margin armed with an acute median denticle; setae short, recumbent, about the length of three times that of a puncture; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 is equal to the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 1.7 – 3.0mm long (mean = 2.3mm; n = 20); 2.0 - 2.7 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons convex when viewed laterally, weakly aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between inner apices of eyes. Apical margin of sternite 1 moderately elevated above the base of sternite 2. Second sternite armed with a median tumescence or a minute denticle.

Specimens examined. 134.

Type material. Holotype, *Scolytus obelus* Wood (USNM). Paratypes *Scolytus obelus* **UNITED STATES: UTAH:** [Beaver Co.]: Beaver, 22.IV.1950, S.L. Wood, ex. *Abies concolor* (USNM-4). *Utah Co.:* Payson Canyon, 14.V.1960, S.L. Wood, ex. *Abies concolor* (USNM-6), 25.VI.1962 (USNM-2).

Non-type material. **UNITED STATES: ARIZONA:** *Coconino Co.:* Coconino National Forest, Arizona Snow Bowl, N35°19.593', W111°42.681', 9230ft, 27.V.2010, S.M. Smith, ex. *Abies lasiocarpa* [var. *arizonica*] (MSUC-62). Jacob Lake, 12mi S., 31.V.1969, W. Harwood, ex. *Abies concolor* branch (USNM-4). *Graham Co.:* Pinaleno Mountains, 15.VII.1968, D.E. Bright, ex. *Pseudotsuga menziesii* (DEBC-3). [Coronado National Forest], [Pinaleno Mountains], Mount Graham, Hospital Flat, 9050ft. 19.VIII.1952, H.B. Leech, J.W. Green (CASC-1), 8950ft, 3.VIII.1965, H.B. Leech (CASC-5). *Yavapai Co.:* Prescott, 1mi S., 3.VIII.1962, S.L. W[ood]

(USNM-1). Prescott, 9mi S., 5 mi E., 7800ft, 5.VI.1969, W. Harwood, ex. *Abies concolor*

(USNM-6). [*Unspecified County*]: Santa Catalina Mountains, elev. 8500ft, 31.V.1969 (DEBC-1).

COLORADO: *Costilla Co.*: Ranch near Fort Garland, Forbes Trinchera, VII-VIII.1976, D. Leatherman, ex. white fir [= *Abies concolor*] (CSUC-4). *Huerfano Co.*: Near Red Wing, 16.VII.1975, D. Leatherman, ex. white fir [= *Abies concolor*] (CSUC-2). **NEVADA:** *Clark Co.*: Mary Jane Falls, 7900ft, 11.VI.1969, Harwood, ex. *Abies concolor* (USNM-7). [*White Pine Co.*]: Baker, S9 T13N R69E, Mount Diablo Meridian, 17.V.1917, T.O. Thatcher, ex. *Abies lasiocarpa*, LCNM 39-12 (CSUC-8, USNM-1, WFBM-1). Mount Wheeler, 19.VIII.1974, S.L. Wood, ex. *Abies concolor* (USNM-9). **NEW MEXICO:** [*Otero Co.*]: Cloudcroft, 14-26.VII.[19]49, W.B.R. Stromberg, ex. fir tree [= *Abies sp.*] (USNM-1). [*Unspecified County*]: Sandia Mountains, 8090ft, 29.V.1969, S.L. W[ood], ex. *Abies concolor* (USNM-3), 30.V.1969 (USNM-9). **UTAH:** *Utah Co.*: Provo, Payson Canyon, VIII.1964, ex. *Abies concolor* (EMEC-4). [*Unspecified County*]: Bryce Canyon National Park, Hopk. U.S. 35-043, 11.VII.1952, R. Washburn, ex. *Abies concolor* (EMEC-2).

Distribution. UNITED STATES: Arizona, Colorado, Nevada, New Mexico, Utah.

Hosts. *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir) and *Abies lasiocarpa* var. *arizonica* (Merriam) Lemmon (corkbark fir).

Common name. None.

Biology. *Scolytus obelus* is an uncommonly encountered species. The species prefers to colonize the limbs, tops and slash of its host. Infested material ranges from 3-10cm in diameter (Wood 1982).

The adult gallery of the *S. obelus* contains two egg galleries that branch from the central nuptial chamber. One egg gallery extends from the nuptial chamber perpendicular to the grain of

wood and the second gallery extends at a 45° angle to the grain. Galleries are frequently initiated near branch crotches and disguised under rough patches of bark. The adult gallery deeply scores the sapwood and lightly scores the cambium. The adult galleries range in size from 1.9-6.5cm in length. Eggs are laid in niches on both sides of each egg gallery and larval mines radiate perpendicular to the egg gallery forming a fan shaped pattern. The larval mines gradually diverge and lightly etch the sapwood. Pupation occurs in the sapwood (Edson 1967).

Collection notes. The author collected specimens from suppressed 2-4cm diameter branches of *A. lasiocarpa* var. *arizonica* that had been girdled at the base by porcupines. Needles of infested branches were pale green to yellow.

Remarks. This species is sister to *S. praeceps* and is very similar both in morphology and gallery architecture. Interspecific divergence in COI nucleotide difference between these two taxa is quite large and averages 0.1036 (Table 1.8).

***Scolytus oregoni* Blackman**

(Figures 1.46, 1.47)

Scolytus oregoni Blackman 1934: 18. Holotype, male, labeled “Ashland Ore., May 20/19, Glendinning, WE Colr, *Pseudotsuga taxifolia*, Hopk. US. 13399a, Type No. 43834 USNM” (USNM).

Diagnosis. *Scolytus oregoni* is a rather distinctive species and both sexes are readily distinguished by having the apical margin of sternite 1 thickened and on the face of sternite 2 and by the unarmed sternite 2.

Redescription (male). 2.6 – 3.6mm long (mean = 3.3mm; n = 20); 2.0 - 2.4 times as long as wide. Color dark red-brown, antennae brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process weakly developed; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures sparse, small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two strongly arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex weakly emarginated at the suture. Disc glabrous, smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 not elevated above the base of sternite 2. Basal margin of sternite 2 strongly thickened, lip-like; sternite 2 nearly perpendicular to sternite 1; surface shagreened, dull, finely punctate with small, fine and shallow punctures; face weakly concave,

weakly to strongly medially impressed just above the base; apical margin unarmed; setae small, less than 1 diameter of a puncture; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 equal to the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.8 – 4.0mm long (mean = 3.23mm; n = 20); 1.6 – 2.7 times as long as wide. Similar to male except epistoma entire, epistomal process absent, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between inner apices of eyes. Second sternite unarmed, basal margin weakly thickened.

Specimens examined. 96.

Type material. Holotype *Scolytus oregoni* Blackman (USNM). Paratypes: **UNITED STATES:**

OREGON: [*Jackson Co.*]: Ashland, Hopk. U.S. 14246-C, 10.III.[19]16, P.D. Sargent, ex.

Pseudotsuga taxifolia (CNCI-2); II.[19]19, W.E Glendinning, Hopk. U.S. 1399-A (USNM-14).

Non-type material. **UNITED STATES: CALIFORNIA:** [*Del Norte Co.*]: [Six Rivers National Forest], Gasquet R.S. [=Ranger Station], Hopk. U.S. 31722-H, 10.VII. R.L. Furniss, ex.

Pseudotsuga taxifolia (OSAC-23). *Lake Co.*: Middletown, 11.XI.1959, G.M. Thomas, ex.

Pseudotsuga menziesii (OSAC-1). *Los Angeles Co.*: Angeles National Forest, Sawmill Mountain, 34.6926°N, 118.5499°W, V.28-VI.14.2007, Caterino, Chatzimanolis, ex. Lindgren trap (SBMN-4). *Marin Co.*: Alpine Lake, V.[19]57 (CASC-4). Mount Tamalpais 14.IX.[19]57, E.L. Smith, ex. *Pseudotsuga menziesii* (OSAC-1). Woodacre Creek, 9.VII.1951, P.S. Bartholomew (CASC-1). *Napa Co.*: Angwin, 2mi N.N.E., N. side of Howell Mountain, 1300ft, 16.VII.1974, H.B. Leech, ex. emerged from log of *Pseudotsuga menziesii* (CASC-1), 21.VII.1974 (CASC-4,

USNM-5), 22.VII.1974 (CASC-1), 25.VII.1974 (CASC-4, USNM-1), 7.VIII.1983 (CASC-1), 12.IX.1983 (CASC-2). Callistoga, 5.X.1947, S.L. Wood, ex. *Pseudotsuga taxifolia* (USNM-2). Mount Saint Helena, Hopk. U.S. 15401-A, F.B. Herbert, ex. *Pseudotsuga taxifolia* (OSAC-1). *Riverside Co.*: Santa Barbara National Forest, Black Mountain Rd., 33.8395°N, 116.7306°W, 1.VII.2005, M. Caterino (SBMN-1). [*Valyermo Co.*]: Fenner Canyon, Hopk. U.S. 33853-A, 15.VIII.[19]51, A.D. Moore, ex. *Pseudotsuga macrocarpa* (EMEC-3, OSAC-8, USNM-4). **OREGON**: *Benton Co.*: Marys Peak, Corvallis Watershed, 9.VIII.1963, ex. rotary traps (EMEC-1). *Jackson Co.*: Ashland, Hopk. U.S. 13363-B, 26.VI.1918, W.E.G, ex. *Pseudotsuga taxifolia*, (OSAC-14). Mistletoe, Hopk. U.S. 15753-A, P.D. Sargent, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (OSAC-3). Rogue River National Forest, Rogue River Gorge viewpoint, N42° 54.540' W122°26.733', 3489ft, 21.VIII.2010, S.M. Smith, ex. *Pseudotsuga menziesii* (MSUC-3). *Linn/Lane Co.*: Blue River, 11mi N.E., H.J. Andrews experimental forest, 5.VIII.1986, Log Decomp Study, Site 2, SE1/4 S15 T15S RSE, Trap 2WA (OSAC-1). [*Tillamok Co.*]: Woods, 18.XI.[19]38 (OSAC-1). *Wasco Co.*: The Dalles, ODA Port/Mill survey, Trap #65-01a, 14.VIII.1997, ex. Lindgren funnel with α -pinene & ethanol lure (MSUC-1).

Distribution. UNITED STATES: California, Oregon, Washington.

Hosts. *Pseudotsuga menziesii* (Mirb.) Franco (= *Pseudotsuga taxifolia* Britton) (Douglas fir) and *Pseudotsuga macrocarpa* (Vasey) Mayr. (big cone Douglas fir).

Common name. None.

Biology. *Scolytus oregoni* colonizes large limbs and tops of its host and also fresh slash (Edson 1967; Smith, pers. obs.).

The *S. oregoni* adult gallery is typically constructed parallel with the grain of the wood and has a central nuptial chamber. The gallery structure is typically bayonet shaped but may also

be longitudinal. Each egg gallery extends in opposite directions with the grain of the wood from the central nuptial chamber. The nuptial chamber is transverse to the egg galleries. The adult gallery deeply scores the sapwood and lightly scores the cambium. The adult gallery averages 6.0-18.0cm in length. Egg niches are closely spaced and deeply score the sapwood. Larvae extend their mines perpendicular to the egg gallery in a fan shaped pattern before terminating in pupation chambers, which are constructed in the sapwood (Edson 1967).

Collection notes. None.

Remarks. Specimens of *S. oregoni* are very rarely collected and the species and is perhaps the least common of the conifer-feeders in the United States. There are many gaps that occur in its distribution range, especially between northern and southern California. Considerable variation is observed in the male sternite 1 and 2 across the geographic range especially between northern California, Oregon and Washington and southern California. Southern California populations colonize *Pseudotsuga macrocarpa* while individuals from the rest of the range colonize *P. menziesii*. In addition, *S. oregoni* males from California and particularly southern California have a greater impression of the second sternite and thicker margin between sternite 1 and 2 compared to Oregon and Washington.

***Scolytus piceae* (Swaine)**

(Figures 1.48, 1.49)

Eccoptogaster piceae Swaine 1910: 34. Lectotype: male, labeled “ St. Anne’s, Que., July 21, 1907” (CUIC). Lectotype designated Bright 1967: 674.

Diagnosis. Both sexes are easily diagnosed by the large conical median spine on the face of the second sternite, of which the spine base never touches any margin, by the lack of lateral denticles on the apical margins of sternites 2-4 and by the unicolorous elytra.

Redescription (male). 2.5 – 3.0mm long (mean = 2.4mm; n = 12); 2.3 - 2.7 times as long as wide. Color red-brown to dark red brown, antennae yellow-brown, legs dark red-brown to yellow brown apically. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process present, moderately developed and low; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally from epistoma to the vertex, slightly transversely impressed above epistoma to inner apices of eyes; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures large, dense and coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex weakly emarginated at the

suture. Disc glabrous, smooth, shining; interstriae weakly impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 rounded, marked by a weak carina on ascendant part of venter, more strongly marked laterally. Sternite 2 nearly perpendicular to sternite 1; surface reticulate, shagreened, dull, finely punctate with small, fine and shallow punctures; covered with sparse setae that are about twice the size of a puncture; face convex; armed with a large conical median spine, apex rounded; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to apical margins of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.3 – 3.0mm long (mean = 2.3mm; n = 12); 2.3 - 2.7 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process weakly developed, frons convex when viewed laterally, weakly longitudinally aciculate, less coarsely punctate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed above epistoma. Second sternite armed with a smaller, rounded, median spine.

Specimens examined. 454.

Type material. Lectotype *Eccoptogaster piceae* Swaine (CUIC). Paralectotype (**here designated**) *Eccoptogaster piceae*, female, **CANADA: QUEBEC:** St. Anne's, 21.VII.1907 (CUIC-1). Paratypes: **CANADA: QUEBEC:** Hudson, 191[sic!] (CUIC-4).

Non-type material. **CANADA: ALBERTA:** Banff (CNCI-2); IX.1916 (CNCI-1); 7.IX.1967, D.E. Bright, ex. *Picea glauca* (CNCI-1). Cypress Hills, 16.VII.[19]32 (CNCI-3). Edmonton, 16.I.1916, Carr (CNCI-1), 27.VIII.1916 (CNCI-1), 28.VIII.1916 (CNCI-1), 5.VII.1924, (CUIC-

1); 6.XII.1916 (CASC-2); 15.VII.[19]24 (CASC-2); 29.VI.[19]16, J.W. Green (CASC-3), 2.IX.[19]16 (CASC-1). [Jasper National Park], Athabasca Falls, 9.VIII.1919, J.M. Swaine (CNCI-5). Medicine Hat, 2.IX.[19]26 (CNCI-2). Seebe, 7.VII.1966, D.F.J. Hilton, ex. *Picea glauca* (CNCI-8). **BRITISH COLUMBIA**: Hixon, 9.VII.1972, D.E. Bright, ex. *Picea* sp. (CNCI-2). Lorna, 6.VII.1924, G. Hopping, ex. *Picea engelmannii* (CASC-1), 10.VIII.1924 (CASC-1), 22.VII.1925 (CASC-1), 14.VII.1926, ex. *Pinus contorta* (CASC-1), 9.VII.1926 (CASC-1); 10.VII.1926, H. Richmond ex. *Picea engelmannii* (CNCI-1), 14.VII.1926 (CNCI-1). Pine Pass, 11.VII.1972, D.E. Bright, ex. *Picea* sp. (CNCI-6). Trinity Valley, 21.VII.[19]30 (CNCI-1), 29.VII.[19]30 (CNCI-1), 13.VII.1928, J.R. Howell, ex. *Pinus monticola* (CASC-1); 23.VII.[19]28, H. Richmond, ex. *Picea engelmannii* (CASC-1). **MANITOBA**: Aweme, 20.IX.[19]06, E. Criddle (CNCI-1); 1.VII.1916, N. Criddle, (CNCI-2) ex. bred from spruce [= *Picea* sp.], 2.VII.1916 (CNCI-4); 10.VII.[19]16 (CNCI-10) ex. spruce [= *Picea* sp.], 27.VII.[19]10 (CNCI-20), 14.VI.1918 (CNCI-2), 15.VI.1918 (CNCI-3); 5.VII.1916 (CNCI-3); 8.VII.1916 (CNCI-6), 9.VII.1916 (CNCI-1); 31.VII.1916 (CNCI-1); 9.VIII.1916 (CNCI-1); 10.IX.1917 (CNCI-10); 11.IX.1917 (CNCI-6); 9.VI.19[18] (CNCI-1). Brandon, 28.V.1940, L. Peterson, ex. *Picea canadensis* (CNCI-2). Gillam, 21.VII.950, W.J. Brown (CNCI-1). Glen Souris, 5.VI.[19]23, N. Criddle (CNCI-1). Grass River Provincial Park, 27.VII.1972, D.E. Bright, ex. *Pinus murrayana* [= *Pinus contorta murrayana*] (CNCI-7). Onah, 11.VII.1924, R.M. White (CNCI-3); N. Criddle, 25.VIII.[19]72 (CNCI-1). Telford, 24.VII.1963, ex. life table plot (CNCI-1), 2.VIII.1963 (CNCI-1). Winnipeg, Hanham (USNM-1). **NEW BRUNSWICK**: Kouchibouguac National Park, VIII.1977, D.E. Bright, Code-6224J (CNCI-1). McGraw Brook, 10mi W., 7.VII.[19]70, D.E. Bright, ex. *Picea glauca* (CNCI-1). **NEWFOUNDLAND**: Deer Lake, 12 mi N.E., 23.VII.[19]70, D.E. Bright, ex. *Picea mariana* (CNCI-11). **NOVA SCOTIA**:

Cape Breton Highlands National Park, MacIntosh Brook, PG703866, 21.VII.1983, D.E. & J.E. Bright, ex. *Picea glauca* (CNCI-7); 29.VII.1983, McKenzie, ex. *Picea* sp. (CNCI-10).

Kejimikujik National Park, 16-17.VII.1967, D.E. Bright, ex. *Picea glauca* (CNCI-14).

ONTARIO: Carp, 5.VIII.[19]66, D.E. Bright, ex. *Picea mariana* (CNCI-2). Lake of the Woods, 1.VIII.1972, D.E. Bright, ex. *Picea* sp. (CNCI-7). Ottawa, 24.VI.1913, J.M. Swaine, ex. crawling on dying *Larix* sp. (CNCI-1). Rainy River District, 3.VIII.[19]24, J.F. Brimley (CNCI-1).

QUEBEC: Aylmer, 12.VII.1924, B.B. Watson, ex. *Picea glauca* (CNCI-1); 30.VII.1924, A.R. Graham (CNCI-1). Hudson, 191[sic!] (CNCI-52). Limbor/Touranine, 27.VI.1974, R. Sexton (CNCI-1). [Gaspésie National Park], Mount Albert, 28.VII.1954, W.J. Brown, ex. north base 650ft (CNCI-1). St. Anne's, 19.VI.[19]19 (CASC-2, CNCI-42). South March, 19.VI.1958, S.D. Hicks (CNCI-1). **SASKATCHEWAN:** Big River, 23.VII.1972, D.E. Bright, ex. *Picea glauca* (CNCI-1). Big River, 40mi N.W., 22.VII.[19]72, D.E. Bright, ex. *Picea glauca* (CNCI-1). Canoe Lake, 21.VII.1972, D.E. Bright, ex. *Picea glauca* (CNCI-2). Christopher Lake, 5.VIII.1959, A. & J. Brooks (CNCI-1). Cypress Hills, 3.IX.1967, D.E. Bright, ex. *Picea glauca* (CNCI-9); 24.IX.1964 (CNCI-2). **YUKON:** Old Crow, 28.VI.[19]81, D.E. Bright (CNCI-5). **UNITED STATES:** **ALASKA:** [North Slope Borough]: Prudhoe Bay Rd., 8 mi N., South Fork Koyukuk River, 150°07'W, 67°13'N, 1000ft [sic!], 8.VII.1978, Smetana, Campbell (CNCI-1). Fairbanks North Star Borough: Fairbanks, 2.VIII.[19]55, W.F. McCambridge, ex. *Picea glauca* (DEBC-7). **CALIFORNIA:** Siskiyou Co: Callahan, 7mi N.W., 16.VI.[19]63, D.E. Bright, ex. *Picea engelmannii* (DEBC-9, EMEC-6). Happy Camp, 18mi N., 31.VII.[19]63, D.E. Bright, ex. *Picea engelmannii* (DEBC-4, EMEC-7). **COLORADO:** Roosevelt National Forest, Chambers Lake, 11.VIII.[19]68, 9200ft, L.A. Kelton (CNCI-1). Denver Co.: Denver, Union Pacific, 14.IX.2000, USDA APHIS, ex. Lindgren funnel APeTOH Lure, (CSUC-1). Larimer Co.: Livermore,

10.IX.2009, K. Smith, USDA APHIS, ex. Lindgren funnel APetOH Lure, (CSUC-1). **MAINE**: [Oxford Co.]: Wilsons Mills, 9.VIII.[19]70, D.E. Bright, ex. *Picea* sp. (CNCI-1).

MASSACHUSETTS: [Norfolk Co.]: Dover, 8.VII.1933, C.W. Collins, ex. reared from blue spruce [= *Picea pungens*] (USNM-11). **MINNESOTA**: Cook Co.: Superior National Forest, Hwy 12 nr. Seagull Guard Station, 48°6'29"N, 90°50'12"W, 23.VI-9.VII.2003, K.J.K. Gandhi, ex. Lindgren funnel trap in *Pinus banksiana*, wind-disturbed-salvaged-logged, site D (CASC-1). Mille Lacs Co.: 2.VII.[19]36, H.R. Dodge, ex. under bark of tamarack tree [= *Larix* sp.] (CASC-2). **MONTANA**: Glacier National Park, 15.VII.[19]29 (CUIC-1). **NORTH DAKOTA**: Bottineau Co.: S30 T162 R75, Hopk. U.S. 56561-A, 27.V.1973, A.D. Tagestad, ex. collected from *Picea glauca densata* (USNM-3). Rolette Co.: S15 T162 R69, Hopk. U.S. 56446, 19.V.[19]72, A.D. Tagestad, ex. collected from *Picea pungens* (USNM-2). **OREGON**: [Jefferson Co.]: Suttle Lake, 4mi W., 3.IX.[19]39, Schuh, Gray, ex. *Picea engelmannii* (FMNH-3). [Unspecified County]: Blue Mountains, 13.VII.[19]14, W.J. Chamberlain, ex. *Picea engelmannii* (CNCI-2). **SOUTH DAKOTA**: Lawrence Co.: Near Leads, Brownsville Rd., N44.2922°, W103.7828°, 5650ft, 27.VII.2004, K.P. Dole, ex. *Picea glauca* (MSUC-14). [Unspecified County]: Black Hills, 7.VII.[19]75, D.E. Bright, ex. *Picea glauca* (CNCI-5). **UTAH**: [Daggett Co.]: McKee Draw, Ashley National Forest, 16.VI.1960, ex. *Picea pungens* (USNM-1). [Unspecified County]: Logan Canyon, S27 T13 NR4, 6.VII.1948, S.L. Wood, ex. *Picea engelmannii* (USNM-8). **WYOMING**: Carbon Co.: [Medicine Bow National Forest], Mirror Lake, 4mi W., 6.IX.2010, D.E. Bright, B.A. Barr, ex. *Picea engelmannii* branches (DEBC-1); [Medicine Bow National Forest] Snowy Mountains, WY130, Lake Marie, N41°19.965', W106°19.516', 3208m, 26.VII.2011, S.M. Smith, D.E. Bright, B.A. Barr, ex. emerged 1-5.IX.2011, ex. *Picea engelmannii* (MSUC-36). Johnson Co.: Buffalo, 16km SW, 20.VI.1968, S.L. Wood, ex. *Picea engelmannii* (USNM-1).

Distribution. CANADA: Alberta, British Columbia, Manitoba, Nova Scotia, Northwest Territories, New Brunswick, Newfoundland, Ontario, Prince Edward island, Quebec, Saskatchewan, Yukon. UNITED STATES: Alaska, California, Colorado, Idaho, Maine, Massachusetts, Michigan, Montana, New York, North Dakota, Oregon, South Dakota, Utah, Washington, Wisconsin, Wyoming.

Hosts. Most spruce species including: *Picea breweriana* S. Watson (Brewer spruce), *Picea engelmannii* Parry ex Engelm. (Engelmann spruce), *Picea glauca* (Moench) Voss (white spruce), *Picea mariana* (Mill.) B.S.P. (black spruce), *Picea pungens* Engelm. (blue spruce), and *Picea rubens* Sarg. (red spruce). This species rarely attacks *Larix* spp. (larch) and *Abies balsamea* (L.) Mill (balsam fir).

Common name. None.

Biology. *Scolytus piceae* infests dead and dying limbs (Chamberlin 1939; Bright and Stark 1973) and is commonly found in branches of fallen spruce trees and suppressed limbs of standing hosts (Smith, pers. obs.).

The adult gallery is parallel with the grain of the wood and bayonet shaped. From the central nuptial chamber, one egg gallery extends with the grain of the wood and the other egg gallery is slightly transversely extended and then extends parallel with the grain. The nuptial chamber is oblique to the egg galleries. The adult gallery equally scores the sapwood and cambium but in some instances may only lightly score the sapwood. Adult galleries average 5.0-8.0cm in length. Ten to 30 egg niches are widely spaced and deeply score the sapwood. Larvae extend their mines perpendicular to the egg gallery before diverging in a fan shaped pattern. Pupation may occur under the bark or in the sapwood (Edson 1967; Bright and Stark 1973). There is likely one generation per year (Bright and Stark 1973; Furniss and Johnson 2002).

Collection notes. None.

Remarks. The female paralectotype has been returned to CUIC from the CNCI following the repositories listed in Swaine (1910).

***Scolytus praeceps* LeConte**

(Figures 1.50-1.53)

Scolytus praeceps LeConte 1876: 373. Lectotype: female, labeled “Cali. [California, Calaveras, Crotch Coll], Type 967” (MCZC). Lectotype designated Wood 1982: 439.

= *Scolytus abietis* Blackman 1934: 21. Holotype: male, labeled “8637iss [Sandpoint, Idaho], 6-20-[18]99, [A.D. Hopkins], Hopk. US 224, Type No. 43837” (USNM). **New synonymy.**

= *Scolytus opacus* Blackman 1934: 20. Holotype: male, labeled “Ouray, Colo[rado], 7,500-8,000 ft., July 1-15, [18]97, HF Wickham, Type No. 43836” (USNM). **New synonymy.**

Diagnosis. *Scolytus praeceps* is a morphologically variable species across its range. Both sexes most closely resemble *S. obelus* and is differentiated by a median tubercle on the apical margin of sternite 2 in both sexes. The female is differentiated from that of *S. dentatus* by the presence of a weakly developed and almost indistinct epistomal process and smaller size.

Redescription (male). 1.8 – 3.2mm long (mean = 2.5mm; n = 20); 2.0 - 2.9 times as long as wide. Color dark red-brown to black, antennae yellow-brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed

laterally, slightly transversely impressed above epistoma and along the median line to upper level of eyes (may not be impressed in some specimens); surface moderately and coarsely aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex weakly emarginated at the suture. Disc glabrous, smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae not impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 strongly, acutely produced forming a lip along the base of sternite 2, basal margin of sternite 2 appearing impressed. Sternite 2 nearly perpendicular to sternite 1; surface glabrous, shagreened, finely punctate (obscurely punctate in some specimens) with small, fine and shallow punctures; face weakly concave; apical margin unarmed or armed with a longitudinal carina and a blunt tubercle, appearing keel-shaped or a low median longitudinal carina; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate

ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 equal to the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 1.7 – 3.5mm long (mean = 2.69mm; n = 20); 2.0 – 3.0 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons more strongly convex when viewed laterally, weakly aciculate, setae shorter, less than the width of the eye and less abundant; entirely convex to weakly transversely impressed above epistoma. Apical margin of sternite 1 weakly elevated above the base of sternite 2. Apical margin of sternite 2 unarmed or weakly longitudinally tumescent.

Specimens examined. 627.

Type material. Holotype *Scolytus praeceps* LeConte (MCZC). Holotype *Scolytus abietis* Blackman (USNM). Holotype *Scolytus opacus* Blackman (USNM).

Non-type material. **CANADA: BRITISH COLUMBIA:** [Big Creek Provincial Park], Lorna [Lake], 5.VIII.1926, H. Richmond, ex. *Abies lasiocarpa* (CASC-2). Duncan, Genoa Bay, 16.VIII.1928, W.G. Mathers, ex. *Abies grandis* (CNCI-10), 17.VIII.1928 (CASC-3). **UNITED STATES: CALIFORNIA:** *Alpine Co.:* Humboldt-Toiyabe National Forest, Hwy 88, N38°45.824' W119°51.498', 6262ft, 24.VII.2010, S.M. Smith, ex. *Abies concolor* (MSUC-3). *El Dorado Co.:* Georgetown, 10mi E., University of California Blodgett [Experimental] Forest, VI.[19]62, R.W. Stark, ex. *Abies concolor* (DEBC-3, EMEC-8); 30.V.1986, K. Hobson (EMEC-2), 1-2.VI.1986 (EMEC-2), 21-24.VI.1986 (EMEC-2), 1-7.VII.1986 (EMEC-9), 9-16.VII.1986 (EMEC-3); 2.VI.2003, K. Apigian (EMEC-2), 5.VI.2003 (EMEC-1). Ice House Reservoir, 25.V.2007, A.I. Cognato (MSUC-5). [Lake Tahoe], Fallen Leaf Lake, 6300ft, 5.VII.1940, H.T. Reynolds (EMEC-2). Pacific House, 0.7mi E., 2.VII.1989, F.G. Andrews, ex. flume (CSCA-1). Pacific House, 1mi E., 1.V.1994, C.B. Barr, ex. seining El Dorado ditch (EMEC-1). South Lake

Tahoe, 16.VI.1988, D. Adams, ex. reared from *Abies concolor* (CSCA-1). [Fresno Co.]:
Huntington Lake, 23.VII.[19]19, F.C. Clark (CASC-52). Shaver, 14.IX.[19]08, Miller, ex. *Abies concolor* (CNCI-3). [Madera Co.]: Northfork, 22.VI.1935, R.P. Allen (EMEC-1). Marin Co.:
Inverness, 8.VIII.[19]62, C.A. Toschi (EMEC-1). Mariposa Co.: Yosemite Valley, 7.VII.1921
(CASC-21). Mendocino Co.: Noyo River, VI.1896 (CASC-2). Modoc Co.: Alturas, Knox
Mountain, 8.VII.1964, D.L. Dahlsten (EMEC-1). Warner Mountains, 4.VII.1919, G. Hopping,
ex. *Abies concolor* (CASC-4, USNM-2). Monterey Co.: 30.VII.1964, D.E. Bright, ex. *Abies bracteata*
(CASC-8). Carmel Valley, 15mi S., 22.VI.1963, C.J. Wray, ex. *Abies bracteata*
(CNCI-7, DEBC-1, EMEC-5). Williams Canyon, Los Padres National Forest, 24.IV.1992, D.E.
Bright, G. Ferrell, ex. *Abies bracteata* limbs (CNCI-22). Nevada Co.: Donner Memorial State
Park, 10.IX.[19]87, S. Seybold, ex. collected on *Abies concolor* (CNCI-2, EMEC-1),
11.IX.[19]87 (CNCI-1, EMEC-1), 29.X.1987 (CNCI-2, EMEC-2). Nevada City, 28.V.1939, R.P.
Allen (CNCI-5). Riverside Co.: Mount San Jacinto State Park, 33.807°N, 116.654°W,
15.VII.2003, M. Caterino (SBMN-1). Santa Rosa Mountain, 15.IX.[19]56, D.E. Bright, D.N.
King, ex. *Abies concolor* (EMEC-4). San Bernardino Co.: San Bernardino National Forest, E. of
Arrowbear Lake, 34.2076°N, 117.0584°W, 29.V.2004, M. Caterino (SBMN-2); S. Fork Trail,
34.1297°N, 117.8426°W, 28.V.2004, M. Caterino (SBMN-1). San Bernardino Mountains, Dollar
Lake trail, 10.VII.1956, R.W. Bushing (EMEC-2), 11.VII.1956 (DEBC-1, EMEC-10). Sierra
Co.: Calpine, 2.3mi N.W., 5200ft, 27.VIII.1961, H.B. Leech, ex. under bark of *Abies* sp. (CASC-
9). Siskiyou Co.: McCloud, 14.VI.1961, S.L. Wood, J.B. Kerren, D.E. Bright, ex. *Abies concolor*
(DEBC-5). Mount Shasta, 28.VII.1980, A.J. Gilbert (CASC-1). Trinity Co.: Klamath National
Forest, FR 41N16, 0.2mi E. FR 93, N41°14.822' W122°53.562', 5081ft, 28.VII.2010, S.M.
Smith, ex. *Abies concolor* (MSUC-2). Tuolumne Co.: Cow Creek, 5mi N. Strawberry,

18.VII.1964, C.W. O'Brien, ex. *Abies* sp. (CASC-102, DEBC-11). Pinecrest, IX.1966, emerged
28.III.1967, G.T. Ferrell, ex. *Abies concolor* (EMEC-4). Sierra Village, 10.VII.1966, B.A.
Tolden (EMEC-1). [*Unspecified County*]: Pinecrest, Hopk. U.S. 19192-A, 29.VII.1930, G.R.
Struble, ex. *Abies concolor* (DEBC-3). Shasta [-Trinity] National Forest, Hopk. U.S. 21078,
10.V.1934, K.A. Salmon (DEBC-4). **COLORADO**: Clear Creek Co.: Idaho Springs, 12mi S.,
12.VII.2007, D.E. Bright, B.A. Barr, ex. bole *Abies lasiocarpa* (CSUC-2, DEBC-4). Eagle Co.:
Basalt Mountain, 20.VI.1996, D. Leatherman (CSUC-1). **IDAHO**: [Bonner Co.]: Sandpoint,
2.VII.1964, N.M. Downie (FMNH-1). Clearwater Co.: Angel Butte thinning, T37N R3E, sec 3,
ex. *Abies grandis* #86 (USNM-10). Kootenai Co.: Coeur d'Alene, 28.IV.1922, H.J. Rust, ex.
Abies grandis (MSUC-3); 15.V.1951, 2157ft, W.F. Barr, ex. *Abies grandis* (EMEC-3). Latah
Co.: Flat Creek, N48°58.385' W116°13.351', 2713ft, 10.VIII.2010, S.M. Smith, [A.R. Gillogly],
M.M. Furniss, ex. *Abies lasiocarpa*, emerged II.2011, M.M. Furniss (MSUC-72). Lewis Co.:
Nezperce, 3mi N., 3.VII.[19]69, R.C. Biggum (EMEC-1). **OREGON**: Deschutes Co.: Deschutes
National Forest, Black Butte Rd., Black Butte, N44°24.924' W121°38.323', 4212ft,
31.VIII.2010, S.M. Smith, ex. *Abies grandis* (MSUC- 91). Paulina Lake, 2mi W., 12.VI.1940,
Schuh, Scott, ex. *Abies concolor* (EMEC-2). Douglas Co.: Diamond Lake, 9.VII.[19]64, D.E.
Bright, ex. *Abies* sp. (EMEC-7). Jackson Co.: Copper, 2mi N., 3.IX.1970, W.G. Harwood, ex.
Abies lasiocarpa, emerged 21.X.1970 (MSUC-7). [Klamath Co.]: Keno, 16.VII.[19]29, J.A.
Beal, ex. *Abies concolor* (CSUC-2). Linn/Lane Co.: Blue River, 11mi N.E., H.J. Andrews
Experimental Forest, 5.VIII.1988, log decomp study, site 2, SE1/4 S15 T15S RSE, trap 2WA
(OSAC-1). [Umatilla Co.]: Tollgate, 6.VI.[19]49, C. Chastain, ex. *Abies grandis* (CSUC-3,
EMEC-2, FMNH-1). **UTAH**: Utah Co.: Hobbie Creek Canyon, 14.VI.[19]60, D.E. Bright, ex.
Abies concolor (DEBC-2). [*Unspecified County*]: (CNCI-1). 1952, T.O. Thatcher (CSUC-10).

WYOMING: *Albany Co.:* Snowy Mountains, [Medicine Bow National Forest], Spruce campground, 6.IX.2010, D.E. Bright, B.A. Barr coll., ex. *Abies concolor* branches (DEBC-2).

[*Carbon Co.*]: Saratoga, Hopk. U.S. 31518-E, 1.IX.[19]38, ex. *Abies lasiocarpa* (CSUC-1).

Distribution. CANADA: Alberta, British Columbia. UNITED STATES: California, Idaho, Montana, Oregon, Utah, Washington, Wyoming.

Hosts. *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir), *Abies bracteata* (D. Don) Poit. (bristlecone fir) and *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir).

Common name. None.

Biology. *Scolytus praeceps* prefers to colonize fresh slash but is also found in small limbs and tops of small standing trees (Edson 1967; Bright and Stark 1973).

The adult gallery of the *S. praeceps* contains two egg galleries that branch from the central nuptial chamber. Typically, one egg gallery extends from the nuptial chamber perpendicular to the grain of wood and the second egg gallery extends at a 45° angle to the grain. Occasionally both egg galleries are extended obliquely to the grain, at a 45° angle to the grain or perpendicular to the grain (Edson 1967). Galleries are frequently initiated near branch crotches and disguised under rough patches of bark. The adult gallery equally scores the sapwood and cambium. The adult galleries range in size from 2.5-6.4cm in length. Eggs are laid in niches on both sides of each egg gallery and larval mines radiate perpendicular to the egg gallery. The larval mines gradually diverge forming a fan shaped pattern and lightly etch the sapwood. Pupation occurs in the sapwood (Edson 1967). There is one generation per year and broods overwinter as larvae (Furniss and Johnson 2002).

Collection notes. None.

Remarks. There has been a great deal of historical uncertainty regarding the placement of *S. abietis* and *S. opacus* since they were described. The species are extremely morphologically similar and thus difficult to differentiate. This similarity led several authors to treat *S. abietis* as either a synonym of *S. opacus* (Wood 1982) or as a subspecies (Bright 1976). Equihua-Martinez and Furniss (2009) removed *S. abietis* from synonymy with *S. opacus* based on differences in host use, submentum shape, and striations on the underside of the head and characters of the second sternite including setae, punctures and spine shape.

The species *S. abietis*, *S. opacus* and *S. praeceps* were not recovered as monophyletic in any of my analyses (Figures 1.1-1.8). I observed very low intraspecific COI and ArgK nucleotide differences among populations (COI: 0-0.0049; mean= 0.0032), (ArgK: 0-0.0044; mean= 0.0024) and no differences in 28S or CAD (Table 1.7). Considerable variation was also observed in the shape of the spine on the male second sternite, especially within *S. praeceps*. *Scolytus abietis* and *S. opacus* are here placed in synonymy with *S. praeceps* because they were recovered as polyphyletic (Figures 1.1-1.8), there are minute molecular difference among populations sampled from California, Oregon, Idaho and Wyoming (Tables 1.4, 1.5, 1.7), the species have identical galleries (Edson 1967, Wood 1982) and variability of the spine on male sternite 2.

The lectotype of *S. praeceps* bears a partial locality label. LeConte's (1868) description states that the lectotype was collected at Calaveras, California by Mr. Crotch.

***Scolytus reflexus* Blackman**

(Figures 1.54, 1.55)

Scolytus reflexus Blackman 1934: 13. Holotype: male, labeled “Sta Catalina Mts, Ariz., Chrisman, M. Coll, *Pseudotsuga taxifolia*, Hopk. U.S. 12210, Reared June 1-14 H.B. Kirk, Type No. 43831 USNM” (USNM).

= *Scolytus virgatus* Bright 1972: 1490. Holotype: male, labeled “MEX., N.L., Cerro Potosi, V.2.71, 8500’, D.E. Bright, *Pseudotsuga menziesii*, CNC No. 12604” (CNCI).

New Synonymy.

= *Scolytus wickhami* Blackman 1934: 13. Holotype: male, labeled “ Buena Vista, Col. H.F. Wickham July 1-6 ’96, 7,900-8,000 ft, Type No. 43832 USNM” (USNM). **New Synonymy.**

Diagnosis. *Scolytus reflexus* Males exhibiting the reflexus phenotype are readily distinguished by the presence of a strong recurved subapical carinate ridge on sternite 5 that is medially produced to form a slightly recurved and subrostriform ridge that appears “reflexed”. Males of this species exhibiting the wickhami phenotype are easily confused with males of *S. monticolae*. They are easily distinguished by the size of male sternite 5. In *S. reflexus*, sternite 5 is equal in length to sternite 4. In *S. monticolae*, sternite 5 is equal in length to the width of sternites 3 and 4 combined. *Scolytus monticolae* lacks an epistomal process while *S. reflexus* typically has a strongly developed epistomal process.

Scolytus reflexus females are distinguished from those of *S. monticolae* by having the apical margin of sternite 1 rounded and by the sternite 2 face rugose, shining, coarsely punctate and convex.

Redescription (male). 2.4 – 3.8mm long (mean = 3.2mm; n = 20); 1.8 – 2.5 times as long as wide. Color dark red-brown to black, antenna brown. Pronotum typically darker than elytra.

Epistoma weakly to acutely and deeply emarginated; epistomal process weakly to strongly developed and elevated; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma; surface moderately longitudinally aciculate and deeply and coarsely punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and three sharply arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical, anterolateral and lateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae weakly impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, interstriae bearing minute, recumbent setae less than length of a puncture; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 rounded, marked by a weak carina on vertical face of segment. Sternite 2 nearly perpendicular to sternite 1; surface rugose, shagreened, finely punctate with small, coarse and shallow punctures; face convex; setae moderately abundant, long, erect

and longer than the width of sternite 3, lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 typically armed with strong recurved subapical carinate ridge but may instead be modified and medially produced to form a slightly recurved and subrostriform ridge that appears “reflexed” (Chiricahua Mountains and Chihuahua, Mexico populations). Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.5 – 4.0mm long (mean = 3.2mm; n = 20); 1.87 – 2.5 times as long as wide. Similar to male except epistoma entire, epistomal process absent, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed just above epistoma and between inner apices of eyes. Second sternite unarmed, setae sparse, recumbent erect and the size of three diameters of a puncture. Length of sternite 5 greater than the combined lengths of sternites 3 and 4, armed with an apical strong recurved subapical carinate ridge.

Specimens examined. 357.

Type material. Holotype *Scolytus reflexus* Blackman (USNM). Holotype *Scolytus virgatus* Bright (CNCI). Holotype *Scolytus wickhami* Blackman (USNM). Paratypes *Scolytus reflexus* **UNITED STATES: ARIZONA:** [*Cochise Co.*]: Chiricahua Mountains, 18.VI.[?], Hubbard, Schwarz (EMEC-1). *Pima/ Pinal Co.*: Santa Catalina Mountains, M. Chrisman, reared 25.VI.[19]14, H.B. Kirk, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (EMEC-1). Paratypes *Scolytus wickhami* **UNITED STATES: ARIZONA:** [*Cochise Co.*]: Chiricahua Mountains, Hopk. U.S. 5558-A, 5.VIII.[19]07, J.L. Webb, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (CNCI-1). **NEW MEXICO:** [*Lincoln Co.*]: Capitan Mountains, Hopk. U.S. 5674, J.L. Webb, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (CNCI-1). Paratypes *Scolytus virgatus* **MEXICO:**

NUEVO LEON: Cerro Potosi, 8500ft, 2.V.[19]71, D.E. Bright, ex. *Pseudotsuga menziesii* (CNCI-4).

Non-type material. **MEXICO:** **CHIHUAHUA:** San Juanito, 16km N.E., 50m, 19.VII.1960, S.L. Wood, ex. *Pseudotsuga menziesii* (MSUC-3, USNM-7). San Juanito, Hopk. U.S. 58592, 16.III.1974, M.M. Furniss, ex. *Pinus* sp. (USNM-1, WFBM-5). **DURANGO:** Hopk. U.S. 58685, 24.III.1974, M.M. Furniss, ex. *Pseudotsuga menziesii* (USNM-14). **UNITED STATES:** **ARIZONA:** *Cochise Co.:* Chiricahua Mountains, 21.VII.1916, C.R. Bruck, (DEBC-2), 29.IX.[19]47, D.J. & J.N. Knull (DEBC-4). Coronado National Forest, Chiricahua Mountains, N31°54.915' W109°16.040', 8196ft, 20.V.2010, S.M. Smith, ex. *Pseudotsuga menziesii* (MSUC-7). Huachuca Mountains, Upper Carr Canyon, 7500ft, 6-10.VIII.[19]52, H.B. Leech, J.W. Green (CASC-1). [*Coconino Co.*]: Jacob Lake, Kaibab National Forest, 19.VI.[19]66, [L. Edson], ex. *Pseudotsuga menziesii* (EMEC-3). *Greenlee Co.:* Hannagan [Meadows] campground, 12.VII.1968, D.E. Bright, ex. *Pseudotsuga menziesii* (CNCI-5). *Pima Co.:* Tucson, Mount Lemmon, 11.VI.1969, S.L. Wood, ex. *Pseudotsuga menziesii* (MSUC-1). *Pima/Pinal Co.:* Santa Catalina Mountains, 9000ft, 6.VI.1926, R.B. Streets (CASC-1); 5.VIII.1968, D.E. Bright, ex. *Pseudotsuga menziesii* (CNCI-1); Bear Wallow, 7800ft, 11.VI.1969, S.L. Wood (USNM-5). *Santa Cruz Co.:* Carr Canyon, 8.VIII.1962, S.L. Wood, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (USNM-12). *Yavapai Co.:* Prescott National Forest, Mount Union Lake, [L. Edson], ex. *Pseudotsuga menziesii* (EMEC-1). **COLORADO:** [*Boulder Co.*]: Boulder, Hopk. U.S. 17700-Y, 21.IV.[19]37, J.A. Beal, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (CSUC-3, USNM-5). *Chaffee Co.:* N. of Poncha Pass, 25.VII.1997, D. Leatherman, ex. ponderosa pine [= *Pinus ponderosa*] (CSUC-1). *Clear Creek Co.:* Idaho Springs, 7.5mi S., 12.VII.2007, D. Bright, B.A. Barr, ex. bole *Pseudotsuga menziesii* (DEBC-3). Lawson, 26.VII.1994, D.

Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-4). Near Lawson, 26.VII.1994, S. Kelley, ex. *Pseudotsuga menziesii* (CNCI-2). [Garfield Co.]: Glenwood Springs, VII.[?] (CASC-1). Jefferson Co.: 1-15.VII.2010, Colorado Dept of Agriculture, ex. Lindgren funnel UHR EtOH & Ω -pinene conifer (CSUC-3). Buffalo Creek, 6.VIII.2004, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1). Larimer Co.: Estes Park, 19.VI.[19]35, ex. *Pseudotsuga taxifolia* [= *Pseudotsuga menziesii*] (USNM-3); 28-VI-13.VII.2010, Colorado Dept of Agriculture, ex. Lindgren funnel UHR EtOH & Ω -pinene conifer (CSUC-3). Fort Collins, 29.VI.[19]35, (USNM-2). Mount Margaret trailhead, 4.VIII.1994, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1). Pingree Park, 30.VIII.1995, D. Leatherman (CSUC-1). Poudre Canyon, 27.V.1975, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1). Rist Canyon, 28.X.[19]56, D.E. Bright, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (DEBC-1); S28 T8 NR70W, 3.III.1957, T.O. Thatcher, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (DEBC-7). Rist Canyon Picnic Area, 26.VI.2008, D. Leatherman, ex. fallen Douglas fir [= *Pseudotsuga menziesii*] (CSUC-3). Roosevelt National Forest, Big Thompson Canyon, N40°24.456' W105°24.565', 7080ft, 5.V.2010, S.M. Smith, D.E. Bright, B.A Barr, ex. *Pseudotsuga menziesii* (MSUC-2). Red Feather Lakes, 12.III.2003, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1), VI.2000 (CSUC-3). CR 63E, 2mi S. off Hwy 14, 4.VII.2007, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-11). Mineral Co.: Wolf Creek Pass off US 160, Sheep Mountain, 25.VII.2005, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1). Prowers Co.: Red Feather Lakes, VI.2000, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1). Pueblo Co.: SR 165, 5mi S.E. San Isabel Millset trailhead, 23.VI.2000, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-3). Teller Co.: Ridgewood Subdivision, 5.VIII.2004, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*]

(CSUC-1). *Weld Co.*: Red Feather Lakes, VI.2000, D. Leatherman, ex. Douglas fir [= *Pseudotsuga menziesii*] (CSUC-1). **NEVADA**: [*Lander Co.*]: Austin, 12.VIII.[19]40, D.E. Hardy (USNM-1). **NEW MEXICO**: *Otero Co.*: Cloudcroft, 4.VI.1969, tree 53, S.L. Wood, ex. *Pseudotsuga menziesii* (MSUC-14); 11-13.VII.[19]74, D.E. Bright, ex. *Pseudotsuga menziesii* (CNCI-4). Lincoln National Forest, Apache Point Observatory, N32°47.046' W105°48.841', 9116ft, 15.V.2010, S.M. Smith, ex. *Pseudotsuga menziesii* (MSUC-145). [*Sandoval Co.*]: Jemez Springs, Hopk. U.S. 37218-F, ex. *Pseudotsuga menziesii* (USNM-4); Hopk. U.S. 37214-D, 1.IX.[19]57, F.M. Yasinski, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (USNM-15). **TEXAS**: *Culberson Co.*: Guadalupe Mountains National Park, The Bowl, 17.VII.1974, Bright, ex. *Pseudotsuga menziesii* (CNCI-6). **UTAH**: [*Utah Co.*]: Wasatch National Forest, Mount Timpanogos, 13.VII.1957, D.E. Bright, ex. *Abies concolor*. [*Unspecified County*]: Logan Canyon, 5000ft, 31.XII.1945, S.L. Wood, ex. Douglas fir [= *Pseudotsuga menziesii*] (USNM-3), 28.IV.1946 (USNM-2), 16.VI.,1946 (USNM-4), 3.VII.1946 (USNM-4).

Distribution. MEXICO: Chihuahua, Durango, Nuevo Leon. UNITED STATES: Arizona, Colorado, Nevada, New Mexico, Texas, Utah.

Hosts. *Pseudotsuga menziesii* (Mirb.) Franco (= *Pseudotsuga taxifolia* Britton) (Douglas fir).

Common name. None.

Biology. *Scolytus reflexus* is relatively common throughout its range and is found in fresh slash and branches of Douglas fir (Edson 1967).

The adult gallery consists of two egg galleries and a central nuptial chamber. The adult gallery is parallel with the grain of the wood and bayonet shaped. From the central nuptial chamber, one egg gallery extends parallel with the grain of the wood and the other egg gallery is slightly transversely extended and then extends parallel with the grain. The nuptial chamber is

oblique to the egg galleries. The adult gallery equally scores the sapwood and cambium and averages 3.9-7.6cm in length. Egg niches are closely spaced and score the sapwood. Larvae extend their mines perpendicular to the egg gallery before diverging in a fan shaped pattern. Pupation may occur under the bark or in the sapwood (Edson 1967).

Collection notes. The author has collected *S. reflexus* in the Chiricahua Mountains, Arizona and Apache Point Observatory, New Mexico killing small (less than 10cm DBH) Douglas fir trees. This species was also reported killing Douglas fir in the Sacramento Mountains and Santa Fe National Forest of New Mexico, and was tentatively and incorrectly identified as *S. monticolae* (USFS 2004). *Scolytus monticolae* strongly resembles *S. reflexus* (see diagnosis) but does not occur in New Mexico.

Remarks. Wood (1977: 388) placed *S. reflexus* and *S. wickhami* in synonymy with *S. tsugae*. Wood (1982) removed *S. reflexus* from synonymy with *S. tsugae*. In this publication he also listed *S. wickhami* as a synonym of *S. reflexus* and cited Wood (1977) for the synonymy. Wood and Bright (1992: 364) also cite Wood (1977) for the synonymy. However, *S. wickhami* was never removed from synonymy with *S. tsugae* and designated as a synonym of *S. reflexus*.

In his description of *S. virgatus*, Bright (1972) posited that the species was closely related to *S. wickhami* or either a subspecies or variety. Wood (1982) considered *S. wickhami* a synonym of *S. reflexus*, but as discussed above, never formally placed it in synonymy. All three species are here treated as one slightly morphologically variable species. I assessed intraspecific variation within these three species for four genes (Table 1.7). It was found to be small for each gene with the average COI divergence of 0.0130 among sampled populations (Table 1.7). There are two main characteristics found that vary among the populations; the male fifth sternite carina and the male epistomal process. There are two main phenotypes observed in populations;

reflexus and wickhami. The reflexus phenotype includes individuals that were previously considered to be *S. reflexus* with the male sternite 5 armed with a strong recurved subapical carinate ridge that at its crest is closer to the basal than the apical margin of the segment. This character is only found in the Chiricahua Mountains, Arizona and in Chihuahua, Mexico. The wickhami phenotype includes individuals that were formerly considered *S. wickhami* and *S. virgatus*. In the wickhami phenotype the process on the male fifth sternite is reduced in the wickhami phenotype and but still forms strong recurved subapical carinate ridge. However it is important to note that both the reflexus and wickhami phenotypes are sympatric in the Chiricahua Mountains. The male epistomal process also varies from a strongly developed and elevated ridge above the epistoma to weakly developed and elevated ridge. In general, the ridge is more strongly developed in the reflexus phenotype but considerable variation is observed especially in the wickhami phenotype. Additional variation is observed in the density of punctures on the male second sternite and the coarseness of the male frons aciculations. In addition, the gallery structure of *S. reflexus* and *S. wickhami* are identical; the gallery of *S. virgatus* is has not been noted. *Scolytus wickhami* and *S. virgatus* are here designated as synonyms of *S. reflexus*.

***Scolytus robustus* Blackman**

(Figures 1.56, 1.57)

Scolytus robustus Blackman 1934: 19. Holotype: male, labeled "Prescott N.F. Ariz., VII-24-[19]30, M.W. Blackman Collector, *Abies concolor*, Hopk. US 20410E, Type No. 43835 USNM" (USNM).

Diagnosis. The *S. robustus* male is quite distinctive with its strongly flattened frons, apical margin of sternite 1 strongly, acutely produced forming a lip along the base of sternite 2, basal margin of sternite 2 appearing impressed and by the unarmed apical margin of sternite 2.

The *S. robustus* female is morphologically similar to that of *S. ventralis*. The *S. robustus* female is distinguished by having the apical margin of sternite 1 forming a carinate lip along the basal margin of sternite 2.

Redescription (male). 2.5 – 4.0mm long (mean = 3.2mm; n = 20); 1.8 – 2.7 times as long as wide. Head, pronotum and abdominal venter dark red-brown, antennae light brown, legs dark red-brown to light brown, elytra red-brown. Pronotum typically darker than elytra.

Epistoma moderately emarginated; epistomal process strongly developed and elevated; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two sharply arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and weakly serrate apex; apical margin of elytral apices bearing large, coarse punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae, interstriae bearing minute, recumbent setae less than length of a puncture; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 strongly, acutely produced forming a lip along the base of sternite 2, basal margin of sternite 2 appearing impressed. Sternite 2 nearly perpendicular to sternite 1; surface glabrous, shining, rugose, finely punctate with small, fine and shallow punctures; face flattened, unarmed or with a weak median tumescence on apical margin; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 equal to the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.2 – 4.1mm long (mean = 3.2mm; n = 20); 1.9- 2.5 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process less strongly developed and elevated, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between inner apices of eyes and. Second sternite unarmed.

Specimens examined. 143.

Type material. Holotype *Scolytus robustus* Blackman (USNM).

Non-type material. **UNITED STATES: ARIZONA:** [*Coconino Co.*]: Grand Canyon North Rim, Kaibab National Forest, VI.[19]66, [L. Edson] (EMEC-4). [*Graham Co.*]: Pinaleno Mountains, Swift Trail, 3mi, Lady Bug Saddle, 11.IX.1964, C.W. O'Brien, ex. *Abies* sp. (CASC-1, CNCI-4,

EMEC-2); Coronado National Forest, SR 366, N32°37.702' W109°49.472', 7896ft, S.M. Smith, ex. *Abies concolor* (MSUC-2). **COLORADO:** *Costilla Co.:* Near Fort Garland, Forbes Trinchera Ranch, VII-VIII.1976, D. Leatherman ex. white fir [= *Abies concolor*] (CSUC-1). *Huerfano Co.:* Near Red Wing, 16.VII.1975, D. Leatherman, ex. white fir [= *Abies concolor*] (CSUC-4). Pass Creek, 20.VIII.1975, D. Leatherman, ex. white fir [= *Abies concolor*] (CSUC-2). *La Plata Co.:* Columbine Lake, 11.VIII.2004, D. Leatherman, ex. subalpine fir [= *Abies lasiocarpa*] (CSUC-1). **NEVADA:** *Clark Co.:* 19.VII.[19]29, C.C. Searl (DEBC-1, EMEC-4). Cathedral Rock, emerged 7-9.V.2002, R. Turnbow, ex. *Abies* sp. (WFBM-2). *White Pine Co.:* Baker, 17.V.1939, T.O. Thatcher (CNCI-2). **NEW MEXICO:** *Bernalillo Co.:* Cibola National Forest, Sandia Peak, 9.VII.[19]68, D.E. Bright (CNCI-1); NM536, N35°12.853' W106°24.743', 8753ft, 10.V.2010, S.M. Smith, A.I. Cognato, ex. *Abies concolor* (MSUC-15), N35°11.655' W106°24.075', 8317ft (MSUC-30). [*Santa Fe Co.:*] Santa Fe, Little Teseque Canyon, 14.VI.[19]35, Van Dyke (CASC-3). [*Unspecified County*]: Sandia Mountains, tree 9, 29.V.1969, S.L. Wood, ex. *Abies concolor* (MSUC-13), tree 18, 30.V.1969 (MSUC-19). **TEXAS:** [*Unspecified county*]: San Antonio, Hopk. U.S. 3938, W.F. Fiske, ex. bred 15.VI.[19]07 (USNM-3). **UTAH:** *Cache Co.:* Logan (CNCI-1). [*San Juan Co.:*] Mount Navajo, 8500ft, 10.VI.[19]36, McAbee (CASC-4). *Utah Co.:* Payson Canyon, 14.V.1960, D.E. Bright, ex. *Abies concolor* (CNCI-3); 20.V.1961, S.L. Wood, ex. *Abies concolor* (USNM-9). [*Unspecified County*]: Bryce Canyon National Park, 10.V.1981, M.M. Furniss, ex. *Abies concolor* (WFBM-10). **UNSPECIFIED STATE:** (CASC-1).

Distribution. UNITED STATES: Arizona, Colorado, Nevada, New Mexico, Texas, Utah.

Hosts. Principle host: *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr (white fir). Incidental host: *Abies lasiocarpa* (Hook.) Nutt (subalpine fir).

Common name. None.

Biology. *Scolytus robustus* is found in the limbs and tops of its host and fresh slash. Galleries are often initiated near limb bases (Edson 1967).

The adult gallery of *S. robustus* contains two egg galleries that branch from the central nuptial chamber. Gallery shape is quite variable and ranges from ‘S’ shaped at an oblique angle to the grain to nearly perpendicular against the grain. Typically one egg gallery obliquely extends from the central nuptial chamber against the grain of wood for a short distance before becoming apically recurved. The second egg gallery is identical to the first but runs in the opposite direction. However galleries may extend perpendicular to the grain of the wood or may not be apically recurved. The adult gallery deeply scores the sapwood and range in size from 2.5-7.0cm in length. Egg niches are distinct, score the sapwood and are closely spaced along the egg galleries. Larval mines rapidly diverge perpendicular to the adult gallery and are parallel with the grain of the wood. Larval mines terminate in pupation chambers that score the sapwood (Edson 1967).

Collection notes. The author collected this species from 10cm diameter slash with thick (5mm) bark.

Remarks. There was a relatively large amount of intraspecific variation (0.0537) observed in mitochondrial COI sequences from specimens collected from Arizona and New Mexico and low variation observed between the two Arizona populations (Tables 1.5 and 1.7). *Scolytus robustus* only occurs on *Abies*. In southeastern Arizona, *Abies* spp. and *S. robustus* are confined to high elevation sites on the sky islands. These Arizona populations are isolated from the New Mexico populations by large areas that are unsuitable for *Abies*. No specific geographic morphological differences were observed among the examined specimens.

***Scolytus silvaticus* Bright, removed from synonymy**

(Figures 1.58, 1.59)

Scolytus silvaticus Bright 1972: 1489. Holotype: male, labeled “MEX., N.L., Cerro Potosi, V.3.71, 1100’, D.E. Bright, *Pseudotsuga menziesii*, CNC No. 12603” (CNCI).

Diagnosis. The *S. silvaticus* male is distinguished from other species by having the apical margin of sternite 4 thickened, forming a broad carina with a blunt median tubercle.

The female is distinguished from the morphologically similar male of *S. hermosus* by having the apical margin of sternite 1 produced, forming a carinate lip along the basal margin of sternite 2 that is about half as produced as thick and by the host and is distinguished from the *S. hermosus* female by having a strongly developed epistomal process.

Redescription (male). 3.0mm long (mean = 3.0mm; n = 1); 2.0 – 2.1 times as long as wide.

Color dark red-brown to black. Pronotum same color as elytra.

Epistoma moderately and broadly emarginated; epistomal process weakly developed; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma; surface moderately and coarsely aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow-brown erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, almost subquadrate, setose with a partial septum and two broadly arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine,

shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect dark yellow-brown setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; interstitial punctures bearing sparse, recumbent, long dark yellow-brown setae; striae weakly impressed. Declivity bearing abundant, long, erect dark yellow-brown hair-like setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 moderately elevated above the base of sternite 2, sternite 2 appearing impressed. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shining, finely punctate with small, fine and shallow punctures; setae small, about two diameters of a puncture in length; face flattened; lateral margins of sternites 2-4 unarmed. Apical margin of sternite 4 thickened forming a broad carina with a blunt median tubercle. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 3.3 – 3.6mm long (mean = 3.4mm; n = 3); 2.2 – 2.8 times as long as wide. Similar to male except epistomal process more strongly developed, frons convex when viewed laterally, weakly aciculate, setae shorter, less than the width of the eye and sparse; weakly transversely impressed between inner apices of eye. Second sternite unarmed.

Specimens examined. 4.

Type material. Holotype *Scolytus silvaticus* Bright (CNCI). Allotype, female, identical data as holotype. Paratypes, identical data as holotype (CNCI-2).

Non-type material. None examined.

Distribution. MEXICO: Nuevo Leon.

Hosts. *Pseudotsuga menziesii* (Mirb.) Franco. (Douglas fir).

Common name. None.

Biology. *Scolytus silvaticus* is only known from a single collecting event from broken branches of *Pseudotsuga menziesii* (Bright 1972). The gallery and biology of this species are unknown but the gallery structure is presumably similar to that of other *Pseudotsuga* feeding *Scolytus*, parallel with the grain of the wood.

Collection notes. None.

Remarks. Wood (1975: 22) placed *S. silvaticus* in synonymy with *S. hermosus*, which occurs on the same mountain as *S. silvaticus*. Wood reasoned that only one *Scolytus* species could occur in the same location and that the observed morphological variation was due to intraspecific differences. In addition, he stated that Bright's image of the *S. silvaticus* male was a normal male of *S. hermosus*. I here remove *S. silvaticus* from synonymy with *S. hermosus* because of the many distinct morphological and host differences originally noted by Bright (1972). In the male of *S. silvaticus*, the apical margin of sternite 1 is moderately thickened and weakly produced, the posterior margin of sternite 3 is slightly medially thickened and the posterior margin of sternite 4 is strongly produced and thickened medially, forming a broad carina with a blunt median tubercle. In the male of *S. hermosus* sternite 1 apical margin is thickened and strongly produced and sternites 3-4 are flat and *S. hermosus* colonizes *Abies* species rather than *Pseudotsuga*. It is also not uncommon for multiple *Scolytus* species to have overlapping distributions.

Scolytus subscaber LeConte

(Figures 1.60, 1.61)

Scolytus subscaber LeConte 1876: 373. Lectotype: female, Vanc. [Vancouver, B.C.], Type 968”

(MCZC). Lectotype designated Wood 1982: 443.

Diagnosis. The *S. subscaber* male most closely resembles those of *S. obelus* and *S. praeceps*. It is distinguished from that of *S. obelus* by the sparse, obscure, fine and shallow punctures of sternite 2, the dull luster of sternite 2 and by the geographic distribution. The male can be distinguished from that of *S. praeceps* by the presence of a median denticle on the apical margin of sternite 2.

Scolytus subscaber females closely resemble those of *S. ventralis* and are distinguished by the distinctly, moderately longitudinally aciculate and weakly punctate frons, the weakly produced apical margin of sternite 1 that forms a weak carinate lip along the basal margin of sternite 2.

Redescription (male). 2.0 – 4.3mm long (mean = 3.5mm; n = 20); 1.8 – 2.3 times as long as wide. Head, pronotum and abdominal venter dark red-brown, antennae light brown, legs dark red-brown to light brown, elytra red brown. Pronotum typically darker than elytra.

Epistoma moderately and very broadly emarginated; epistomal process moderately developed and elevated; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally, slightly transversely impressed above epistoma; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures minute, fine; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, ovoid, setose with a partial septum and three arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; punctures bearing short sparse recumbent yellow setae slightly longer than the size of a puncture (may be broken off); striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 strongly, acutely produced forming a lip along the base of sternite 2, basal margin of sternite 2 appearing impressed. Sternite 2 nearly perpendicular to sternite 1; surface glabrous, shagreened, dull, finely and obscurely punctate with small, fine and shallow punctures; face weakly concave; apical margin armed with a broad median denticle; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 3.1 – 5.0mm long (mean = 3.85mm; n = 20); 1.9 – 2.6 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons more strongly convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the

eye and less abundant. Apical margin of sternite 1 weakly elevated above the base of sternite 2.

Second sternite unarmed, face weakly rugose, punctures larger, deeper

Specimens examined. 111.

Type material. Lectotype *Scolytus subscaber* LeConte (MCZC).

Non-type material. **UNITED STATES: CALIFORNIA:** *Alpine Co.:* Stanislaus National Forest, Hermit Valley, Hopk. U.S. 19193-A, J.M. Miller, ex. *Abies concolor* (EMEC-1, OSAC-4). Humboldt-Toiyabe National Forest, Hwy 89, 6.6mi E. NF 4188, N38°39.906' W119°38.540', 8011ft, 24.VII.2010, S.M. Smith, ex. *Abies magnifica* (MSUC-3). *El Dorado Co.:* Echo Lake, Hopk. U.S. 18381-A, 27.V.[19]31, J.M. Miller, ex. *Abies magnifica* (CSUC-1, EMEC-17, OSAC-20, USNM-3). Lake Tahoe, Fallen Leaf Lake, 22.VII.1930, A.C. Browne (CASC-1). Uncle Tom's, 0.1 road mile W., 28.VII-12.VIII.1978, J.A. Benedictis, ex. from pheromone trap baited with E-11 tetradecenyl acetate (EMEC-1). [*Madera Co.*]: Bass Lake, Hopk. U.S. 19376-A, 2.VII.[19]32, G.R. Struble, ex. *Abies concolor* (EMEC-2, OSAC-3). Sugar Pine [community], 12.VIII.1920, E. Schiffel (CASC-1). *Placer Co.:* Lake Tahoe, 1mi N., 3.VIII.[19]67, G.T. Ferrell (EMEC-3). *Plumas Co.:* LaPort, Hopk. U.S. 17933-A, J.M. Miller, ex. *Abies magnifica* (EMEC-2, OSAC-2). [*Unspecified County*]: Stanislaus National Forest, Hopk. U.S. 19818, J.M. Miller, ex. *Abies concolor* (OSAC-1). **IDAHO:** *Clearwater Co.:* Pierce, 4mi W.N.W., 18.VII.1973, H.L. Osborne, ex. flight trap (USNM-1). *Latah Co.:* 1992, M.M. Furniss, ex. *Abies grandis* (WFBM-1). Flat Creek, 11.II.1995, M.M. Furniss, ex. *Abies grandis* (WFBM-4). Harvard, 3.5mi N.N.E., 6.VIII.1973, H.L. Osborne, ex. flight trap (USNM-1). Moscow, 20.VII.[19]73, LC-1 (USNM-1), 24.VII.[19]73, LC-1 (USNM-2). Potlatch, 4mi N.E., 3.VIII.1973, H.L. Osbourne, ex. flight trap (USNM-1). **OREGON:** [*Benton Co.*]: [Corvallis], Kiger Island, IX.1922, W.J. Chamberlain (USNM-1). [*Klamath Co.*]: Crater Lake [National Park], 11.VI.[19]33, Hopk. U.S. 18966-A,

W.J. Buckhorn, ex. *Abies concolor* (EMEC-4), 14.XII.[19]33 (EMEC-3, OSAC-20, WFBM-1).

WASHINGTON: [*Chelan Co.*]: Lake Wenatchee [State Park], VII.[19]69 (EMEC-1). [*King*

Co.]: Seattle, 9.VI.[19]12 (OSAC-2). [*Thurston Co.*]: Olympia, 25.IV.[18]94 (OSAC-2).

Distribution. CANADA: British Columbia. UNITED STATES: California, Idaho, Montana, Oregon, Washington.

Hosts. Principal host: *Abies grandis* (Dougl. Ex D. Don) Lindl. (grand fir), Incidental hosts:

Abies lasiocarpa (Hook.) Nutt. (subalpine fir), *Abies magnifica* A. Murr. (red fir).

Common name. None.

Biology. Furniss and Kegley (2011) provide detailed and thorough account of the biology of *S. subscaber*. Adults infest suppressed branches in the crowns of mature trees and are rarely found in slash (Edson 1967; Furniss and Kegley 2011). *Scolytus subscaber* is also associated with a staining fungus, *Spicaria anomale* (Corda) Harz. that kills the host cambium (Wright 1938).

The adult galleries of *S. subscaber* are distinct from other *Scolytus* species. Adult galleries are epsilon (“ε”) shaped and are deeply excavated in the sapwood. The gallery consists of a central nuptial chamber and two egg galleries that are recurved around the nuptial chamber (Edson 1967). The adult gallery 2-5cm in length and varies by branch size, with larger branches having larger galleries (Furniss and Kegley 2011). Egg niches lightly score the sapwood. In Oregon 12-30 eggs are laid per gallery and in Idaho the upper limit appears to be 12 (Furniss and Kegley 2011). Larval mines radiate from the egg gallery in all directions, often crossing each other. The larval mines are located in the phloem and cambium for about the first centimeter of their length. After the first centimeter, larval mines lightly score the sapwood. Pupation chambers are formed in the cambium or outer bark. There is one generation per year and the

brood overwinters as larvae. In Idaho, flight occurs in July and adults leave the gallery once eggs have been laid (Furniss and Kegley 2011).

Collection notes. Old galleries of this species were observed by the author while hiking along the Tuolumne Grove Trail in Yosemite National Park on 23.VII.2010.

Remarks. The lectotype bears a partial locality label. LeConte's (1868) description states the lectotype was collected at Vancouver Island.

***Scolytus tsugae* (Swaine)**

(Figures 1.62, 1.63)

Eccoptogaster tsugae Swaine 1917: 32. Lectotype: female, labeled "Entomological Branch, Ottawa, Canada No. 2251, female, J.M. Swaine Coll., Lectotype CNCNo. 9239" (CNCI).

Lectotype designated Bright 1967: 674.

Diagnosis. *Scolytus tsugae* most strongly resembles *S. monticolae* and the two species are easily and often confused. Both sexes are distinguished from those of *S. monticolae* by the impressed elytral discal striae, giving the elytra a corrugated appearance, by the dull luster of sternite 2 and the host genus *Tsuga*.

Redescription (male). 2.8 - 3.4mm long (mean = 3.1mm; n = 16); 2.1-2.5 times as long as wide.

Body dark red-brown and antennae light brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally, slightly transversely impressed above epistoma; surface weakly longitudinally aciculate and moderately punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than

the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect dark yellow-brown hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on basal half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing large, coarse punctures; apex moderately emarginated at the suture. Disc glabrous, smooth, shining; interstriae weakly impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae weakly impressed, elytra with a corrugated appearance. Declivity bearing sparse, short, erect yellow setae. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 weakly and continuously elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface glabrous, shagreened, dull, finely punctate with small, fine and shallow punctures; face flattened; apical margin unarmed; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 greater than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.3 - 3.5mm long (mean = 3.0mm; n = 16); 1.9-2.8 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process present, moderately developed, low,

frons convex when viewed laterally, weakly strigate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between inner apices of eyes.

Specimens examined. 369.

Type material. Lectotype *Eccoptogaster tsugae* Swaine (CNCI). Paralectotypes *Eccoptogaster tsugae* (CNCI), [Unspecified locality]: 2251 (CNCI-12, CUIC-2, EMEC-1), 2327 (CNCI-2).

Non-type material. **CANADA: BRITISH COLUMBIA:** Adams Lake, 8.V.[19]22, R. Hopping, ex. *Tsuga mertensiana* (CASC-1). Bowman Creek, 10.VIII.1928, R. Hopping, ex. *Tsuga heterophylla* (CASC-2). Garibaldi, 7.VII.1988, R.J. Rabaglia (RJRC-1). Merritt, Midday Valley, 5.VI.1926, Wm. Mathers, 17134, lot 94, ex. *Pinus ponderosa* (CASC-1), 11.VI.1926, 17190, lot 23 (CNCI-1). North Vancouver, Lynn Canyon, 1.VI.[19]23, N.L. Cutler, L. 17003, ex. *Abies amabilis* (CASC-12, CNCI-2). Pender Harbor, 17189, lot 1, 11.V.[19]26, G.R. Hopping, ex. *Tsuga heterophylla* (CNCI-9); lot 2, 12.V.[19]26 (CASC-1, CNCI-8), lot 4, 29.V.[19]26 (CASC-1, CNCI-6), lot 5, 1926 (CNCI-1), 13.VI.1928 (CASC-4). Terrace, Mrs. W.W. Hippisley (CNCI-1). Trinity Valley, 16.VIII.1927, J.R. Howell (CASC-2), 1722, lot 46, 10.VII.1928, (CASC-1), lot 50, 24.VII.1928 (CASC-1), 17339, lot 12, 19.VI.[19]30, (CASC-2); 16.VI.1927, 17213, lot 27, E.A. Rendell (CASC-1). Vancouver, 11.VI.1935, A. Graham, ex. *Tsuga mertensiana* (CASC-2); 27.V.1939, W.G. Mathers, ex. *Tsuga heterophylla* (CASC-2), 31.V.1939 (CASC-5), 5.VI.1939 (CASC-3), 12.VI.1939 (CASC-3), 27.VI.1939 (CASC-5), 4.VII.1939 (CASC-1), 10.VII.1939 (CASC-2). **UNITED STATES: CALIFORNIA:** Yosemite National Park, Hopk. U.S. 15727-A, 2.VII.1918, J.E. Patterson, ex. *Tsuga mertensiana* (OSAC-4). *Alpine Co.:* Ebbetts Pass, 8730ft, 13.VIII.[19]63, D.E. Bright, ex. *Tsuga mertensiana* (CNCI-8, EMEC-9). *Eldorado Co.:* [Georgetown, 10mi E.], Blodgett [Experimental] Forest, 2.VI.2003, K. Apigian (EMEC-1), 30.V.1986, K. Hobson (EMEC-1). Pollock Pines, 22.VI.[19]48, A. Bartel (EMEC-1). *Lassen*

Co.: Grassy Lake, 27.IX.[19]14, lot 142, ex. *Tsuga mertensiana* (CASC-2). **Nevada Co.:** 39.4149°N, 120.3109°W, Tahoe National Forest, Sagehen Basin, Carpenter Ridge, 15.VII.2003, M. Caterino (SBMN-1). **IDAHO:** **Bonner Co.:** Priest River Experimental Forest, Hopk. U.S. 61810, 28.X.1978, M.M. Furniss, ex. *Tsuga heterophylla* (USNM-8). Priest Lake, Reader Bay, 6.VIII.1985, M.M. Furniss, J.B. Johnson, ex. *Tsuga heterophylla* (WFBM-54). **Boundary Co.:** Idaho Panhandle National Forest, Roman Nose, N48°40.911' W116°34.345', 4353ft, S.M. Smith, A.R. Gillogly, ex. *Tsuga heterophylla* (MSUC-7). **Kootenai Co.:** Deception Creek Experimental Forest, Hopk. U.S. 58885-B, 10.VII.1968, M.M. Furniss, ex. *Tsuga heterophylla* (OSAC-1), 16.VII.1968 (OSAC-1), 24.VII.1968 (OSAC-4), 30.VII.1968 (OSAC-2), 8.VIII.1968 (OSAC-1). Magee, VII.[19]29, R.L. Furniss, ex. hemlock [= *Tsuga* sp.] (OSAC-4). **MONTANA:** [*Unspecified County*]: Glacier [National] Park, 8.VII.[19]49, D. Giuliani (CASC-1). **OREGON:** [*Douglas Co.*]: Diamond Lake, Hopk. U.S. 20959-A, VII.[19]31, R.L. Furniss, ex. *Tsuga mertensiana* (OSAC-18). **Hood River Co.:** Mount Hood National Forest, Hwy 35, Sherwood Forest campground, N45°19.278' W121°37.104', 4293ft, 2.VIII.2010, S.M. Smith, ex. *Tsuga heterophylla* (MSUC-5). **Klamath Co.:** Crescent Lake, 6.VII.[19]60, [L. Edson], ex. *Tsuga mertensiana* (CASC-4). Crater Lake [National Park], Hopk. U.S. 18.916-A, 22.V.[19]30, W.J. Buckhorn, ex. *Tsuga mertensiana* (OSAC-30), Hopk. U.S. 18,950-A, 16.VI.[19]31, (OSAC-44); Hopk. U.S. 18851-A, 14.VI.[19]31, J.A. Beal, ex. *Tsuga mertensiana* (OSAC-6, USNM-2); Hopk. U.S. 20537-A, 17.VI.[19]33, F.P. Keen, ex. *Tsuga mertensiana* (OSAC-19); 24.VIII.[19]62, D.E. Bright, ex. *Tsuga mertensiana* (CNCI-1); 12.VIII.1984, M.M. Furniss, ex. *Tsuga mertensiana* (WFBM-16); Hopk. U.S. 20807-A, R.L. Furniss, ex. *Tsuga heterophylla* (OSAC-2). **Linn Co.:** Santiam Pass 7.VII.[19]64 (EMEC-1). [*Yamhill Co.*]: McMinnville, 27.XI.1937, K.M. & D.M. Fender (OSAC-1). **WASHINGTON:** **King Co.:** Montlake Terrace,

20.VIII.[19]62, D.E. Bright, ex. *Tsuga heterophylla* (CNCI-4). Seattle, 27.V.[19]07 (OSAC-1), 10.IV.[19]12 (OSAC-2), 12.IV.[19]12 (OSAC-1). **UNSPECIFIED LOCALITY**: Hopk. U.S. 13247-A, ex. *Tsuga mertensiana* (OSAC-2). Summit Viola Trail, 9.IX.1910, J.M. Miller, ex. *Tsuga mertensiana* (OSAC-1).

Distribution. CANADA: Alberta, British Columbia. UNITED STATES: California, Idaho, Montana, Oregon, Washington.

Hosts. *Tsuga heterophylla* Sarg. (western hemlock) and *Tsuga mertensiana* (Bong.) Carrière (mountain hemlock).

Common name. Hemlock engraver.

Biology. *Scolytus tsugae* attacks fresh slash, the main bole and large branches of hemlock (Edson 1967).

Scolytus tsugae is an uncommon and poorly studied species. The adult galleries of *S. tsugae* are typically perpendicular to the grain of the wood and 4-10cm in length (Edson 1967; Furniss and Johnson 2002). Adult galleries score the cambium slightly more than the sapwood. However, Edson (1967) reported that specimens from a series in northern California produced an adult gallery that was oriented obliquely to the grain of the wood. Galleries consist of a central nuptial chamber and two egg galleries. Each egg gallery is extended perpendicular to the grain of the wood from the central nuptial chamber. Egg niches are irregularly spaced and faintly score the sapwood. Larval tunnels are extended parallel with the grain of the wood, etching the sapwood lightly at first and deeply near the pupation chamber. There is one generation per year and broods overwinter as larvae (Furniss and Johnson 2002).

Collection notes. The author collected this species from fresh logging slash limbs that were 6-10cm in diameter in Idaho and Oregon.

Remarks. The lectotype does not bear a locality label. Swaine's (1917) description states the type series was collected at "Cherry Creek valley, Vernon District, British Columbia, Glacier, B.C., Jasper Park, Alta." from both *Tsuga mertensiana* and *Pseudotsuga mucronata* [= *P. menziesii*]. In Bright's (1967) lectotype designation he lists the locality of the lectotype as "Glacier, BC, XI-26-15, *Tsuga mertensiana*".

For many years *S. monticolae* was considered a synonym of *S. tsugae* (see *S. monticolae* remarks). In their paper describing the biology of *Scolytus tsugae*, McMullen and Atkins (1959) actually described the biology of *S. monticolae*. In their investigation the species studied was from *Pseudotsuga menziesii* rather than *Tsuga* spp. and created vertical instead of transverse galleries.

***Scolytus unispinosus* LeConte**

(Figures 1.64, 1.65)

Scolytus unispinosus LeConte 1876: 372. Lectotype: male, labeled "Or. [Oregon], Type 965"

(MCZC). Lectotype designated: Wood 1982: 432.

= *Scolytus sobrinus* Blackman 1934: 23. Holotype: male, labeled "Burke Colr, Kent, WA, *Pseudotsuga taxifolia* [= *P. menziesii*], Hopk. US 41900, Type No. 43838"

(USNM). Synonymy: Wood 1966: 30.

Diagnosis. *Scolytus unispinosus* is very morphologically similar to *S. fiskei* and *S. laricis*. Males of *S. unispinosus* are distinguished from those of *S. laricis* by the frons flattened when viewed laterally, never deeply impressed, less moderately abundant frontal setae (compared to dense) and by the host genus, *Pseudotsuga*. Males are distinguished from those of *S. fiskei* by the following combination of characters: abdominal venter dull in luster, the base of the sternite 2

spine extending from the apical margin to half the length of the segment and by the geographical distribution.

The female is distinguished from that of *S. fiskei* by the dull luster of sternite 2 and is distinguished from that of *S. laricis* by the frons finely aciculate-punctate; sternite 1 joining base of sternite 2 more obtusely, base of sternite 2 not finely impressed, flush with sternite 1; epistomal process weakly developed, almost indistinct.

Redescription (male). 2.2 – 3.2mm long (mean = 2.7mm; n = 15); 2.3 - 2.7 times as long as wide. Head, antennae, pronotum, and abdominal venter dark red-brown. Elytra and legs yellow-brown to light brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process present, weakly developed and low; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing flattened when viewed laterally from epistoma to the vertex, slightly transversely impressed above epistoma to inner apices of eyes; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures sparse, small and fine; surface sparsely and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and two arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction;

apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex moderately emarginated at the suture. Disc smooth, shining; interstriae not impressed and twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; punctures bearing short sparse recumbent yellow setae slightly longer than the size of a puncture (may be broken off); striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 rounded, marked by a weak carina. Sternite 2 nearly perpendicular to sternite 1; surface shagreened, dull, finely punctate with small, fine and shallow punctures, that are nearly obscure; covered with sparse setae that are less than the width of segment 3 in length; face convex; apical margin armed with a laterally compressed, median spine with the base extending from the apical margin to half the length of the segment, apex rounded; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to apical margin of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.2 – 3.0mm long (mean = 2.7mm; n = 15); 2.3 - 2.7 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process feebly developed, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between epistoma and inner apices of eyes. Second sternite apical margin armed with an acute median denticle, with base extending from apical margin to half-length of segment.

Specimens examined. 655.

Type material. Lectotype *Scolytus unispinosus* LeConte (MCZC). Holotype *Scolytus sobrinus* Blackman (USNM). Paratypes *Scolytus sobrinus* Blackman **UNITED STATES: OREGON:** [Jackson Co.]: Little Applegate River, Hopk. U.S. 14238-B, J.E. Patterson (EMEC-6). Ashland, Hopk. U.S. 14264-T, F.P. Keen (EMEC-3). **WASHINGTON:** [King Co.]: Kent, Hopk. U.S. 4190-A, [H.E.] Burke, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-5).

Non-type material. **CANADA: BRITISH COLUMBIA:** Cloverdale, 28.XII.[19]22, N.L. Cutler, ex. *Tsuga heterophylla* (CASC-32, CNCI-11). Duncan, Genoa Bay, 10.VII.1928, W.G. Mathers, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (CNCI-1). Indian Meadows, Midday Creek, 13.VII.1920, R. Hopping, ex. *Pinus ponderosa* (CNCI-1). Merritt, Midday Valley, 31.V.1926, W. Mathers (CNCI-1), 2.VII.1926 (CNCI-2); 7.VII.1926, R. Hopping (CNCI-1), 3.VIII.1923 (CNCI-1), 15.VIII.19[23] (CNCI-1). Nanaimo, [Pacific] Biological Station, 23.VI.1920 (CASC-1). Nelson Island, West Lake, 1701, 23.VI.1922, R. Hopping, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (CNCI-12). Oliver, 25mi N.W., 15.VI.1958, H. & A. Howden (EMEC-3). Pender Harbor, 30.VI.1928, G. Hopping, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (CASC-2). Squamish, Diamond Head trail, 3200ft, 9.VIII.1953, G.J. Spencer (CNCI-1). Shuswap, 24.IV.[19]13, T. Wilson, ex. Douglas fir [=*Pseudotsuga menziesii*] (CNCI-1). Vancouver, 7.VI.1934, W. Mathers ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (CASC-1), 11.VI.1934 (CASC-2). Vanguard, 23.VI.[19]32, R. Hopping, ex. *Pseudotsuga mucronata* [=*P. menziesii*] (CASC-2, CNCI-2). Vernon, 27.V.1932, R. Hopping (CASC-1). **UNITED STATES: CALIFORNIA:** Del Norte Co.: 3.VII.[19]24, E.B. Leach (EMEC-1). El Dorado Co.: [Georgetown, 10mi E.], Blodgett Experimental Forest, 4000ft, 26.V.1986, Hobson, Atkinson, ex. Lindgren trap, ponderosa pine resin, H&L B.P. fractions, burned over area (EMEC-3); 27.V.1986, Hobson,

Irving, ex. Lindgren trap, ponderosa pine resin, untreated Oleo, burned over area (EMEC-2); 30.V.1986, Hobson, Atkinson, ex. Lindgren trap, unbaited, logged area (EMEC-1); 30.V.1986, Hobson, Atkinson, ex. Lindgren trap, unbaited, burned over area (EMEC-2). Placerville, Hopk. U.S. 33961-A, 26.III.[19]54, M.M. Furniss, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-16). Pollack Pines, 22.VI.[19]48, R.C. Bynum (EMEC-6). *Humboldt Co.*: Blocksburg, 13.V.[19]34, B.P. Biven (CASC-2). Orleans, 15mi N.W., 13.VI.[19]64, D.E. Bright, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-7). Orick, 11mi S., 11.VI.[19]62, D.E. Bright, B.A. Barr, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (DEBC-4, EMEC-3). *Lake Co.*: Whispering Pines, 14.IV.1964, ex. Douglas fir [=*Pseudotsuga menziesii*] (CASC-1). *Los Angeles Co.*: Coquillett (EMEC-2). *Madera Co.*: 1.VII.[19]38 (EMEC-1). *Marin Co.*: Inverness, 11.X.[19]61, D.E. Bright, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (DEBC-3, EMEC-2). [*Mariposa Co.*]: [Yosemite National Park], Yosemite Valley, Hopk. U.S. 2810, Hopkins (EMEC-4). *Mendocino Co.*: (CASC-7). 14.VII.[19]22, E.R. Leach (CASC-4). Bransomb, CDF#870697, 11.VII.[20]01, M. Garvin, ex. Lindgren funnel trap with ISP (CSCA-1), 25.VII.[20]01 (CSCA-3). Flynn Creek between Comptche and Navarro, 17.VIII.1953, P.S. Bartholomew (CASC-1). Mill Creek, 20.III.[19]59, R.E. Stevens, ex. Douglas fir [=*Pseudotsuga menziesii*] (EMEC-13). Noyo River, VI.1896 (CASC-14). *Napa Co.*: Angwin, 2mi N.N.E., North side of Howell Mountain, 1300ft, 24.V.1974, H.B. Leech, ex. emerged from log of *Pseudotsuga menziesii* (CASC-3, USNM-6), 20.VII.1974 (CASC-16), 21.VII.1974 (CASC-11), 22.VII.1974 (CASC-4), 23.VII.1974 (CASC-8), 25.VII.1974 (CASC-15), 26.VII.1974 (CASC-2, USNM-3), 27.VII.1974 (CASC-1), 28.VII.1974 (CASC-6, USNM-3), 1.VIII.1974 (CASC-3), 3.VIII.1974 (CASC-3), 7.VII.1974 (CASC-3). Callistoga, 26.V.[19]57 (CASC-4); 4.X.1947, T.O. Thatcher, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-3); 1.V.[19]63, D.E. Bright, ex. *Pseudotsuga*

menziesii (EMEC-3). Nevada Co.: Grass Valley, 17.I.1961, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (CASC-2). Middleton [labeled as Lake Co.], Hopk. U.S. 37588-A, R.W. Bushing, ex. *Pseudotsuga menziesii* (EMEC-3), G.M. Thomas (EMEC-3). [Placer Co.]: Colfax, 1mi E., Hopk. U.S. 34068-A, 31.I.[19]37, ex. *Pseudotsuga menziesii* (EMEC-4). Towle, 11.XI.1932 (EMEC-1). Plumas Co.: Walker Mine, 15.VII.[19]30 (EMEC-3). [San Francisco Co.]: San Francisco, Hopk. U.S. 8557, 11.V.[18]99, ex. on pine [=Pinus sp.] (EMEC-1), 15.V.[18]99 (EMEC-1). Santa Cruz Co.: 16.IV.[19]59, J.E. Henry (WFBM-16). Aptos, New Brighton Beach State Park, 13.IX.1986, D. Adams, ex. *Pinus radiata* (EMEC-54). Shasta Co.: Hat Creek, 17.VI.[19]62, D.E. Bright, B.A. Barr, ex. *Abies concolor* (EMEC-2). Siskiyou Co.: Grass Valley, 16.X.[19]60, R.W. Bushing, emerged XI.1960, ex. *Pseudotsuga menziesii* (EMEC-6). Sonoma Co.: (CNCI-1). Fort Ross, 2mi E., 2.XI.1947, T.O. Thatcher, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-3). Mount Saint Helena, 3.VI.[19]31, E.C. Zimmermann, ex. digger pine [=Pinus sabiniana] (EMEC-1); Hopk. U.S. 21,125-F, 3.IV.1934, R.L. Furniss, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-4). Sebastopol, Hopk. U.S. 32638-A, 20.I.1940, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (DEBC-4, EMEC-5). Stillwater Cove, 12.V.1951, H.R. Moffitt (EMEC-1). Trinity Co.: 14.V.[19]23, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (CASC-4). [Unspecified County]: (CUIC-7). Yosemite National Park, Hopk. U.S. 20953-B, 19.VI.1932, J.M. Miller, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-8). **IDAHO**: Bonner Co.: Sandpoint, 13.VI.931, N.M. Downie (FMNH-1), 9.VII.1977 (FMNH-1); 9.VII.1977 (FMNH-1). **OREGON**: [Benton Co.]: Corvallis, 17.IV.[19]16, W.J. Chamberlin, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-3); 8.VII.1946, K.R. Hobbs (EMEC-1). Coos Co.: Myrtle Point, 18.VI.[19]64, D.E. Bright, ex. *Pseudotsuga menziesii* (EMEC-10). Curry Co.: Agness, 6mi S.W., 10.VII.1990, M.M. Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-6). Brookings,

12mi E.N.E., 12.VIII.1990, M.M. Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-4).
 Illahe, 4mi N., 9.VIII.[19]90, M.M. Furniss, J.B. Johnson, ex. *Pseudotsuga menziesii* (WFBM-2). *Custer Co.*: Herd Lake, 3.IX.1978, M.M. Furniss, ex. *Pseudotsuga menziesii* (WFBM-1).
Deschutes Co.: Deschutes National Forest, Black Butte Rd., Black Butte, N44°24.924' W121°38.323', 4212ft, 31.VIII.2010, S.M. Smith, ex. *Pseudotsuga menziesii* (MSUC- 44).
Douglas Co.: Roseburg, W.J. Chamberlin, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (DEBC-2, EMEC-6, WFBM-2). [*Grant Co.*]: Dixie Pass, Malheur National Forest, 23.VI.1961, S.L. Wood, J.B. Karren, D.E. Bright, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (DEBC-5). *Jackson Co.*: Dead Indian Spring, 17.V.1962, J. Schuh (CNCI-1). Mistletoe, Hopk. U.S. 15753-A, P.D. Sargent, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-3), Hopk. U.S. 15753-B, 21.VIII.1918, P.D. Sargent (DEBC-5, EMEC-10). Pinehurst, 2mi E., 18.VII.[19]64, D.E. Bright, ex. *Pseudotsuga menziesii* (CNCI-5, EMEC-6). Prospect, 10.VII.[19]64, D.E. Bright, ex. *Pseudotsuga menziesii* (CNCI-11, EMEC-14). [*Klamath Co.*]: Klamath Falls, 17.VI.[19]64, D.E. Bright, ex. *Pseudotsuga menziesii* (EMEC-2). [*Lane Co.*]: McCredie Springs, 19.VI.1961, D.E. Bright, ex. *Tsuga heterophylla* (CNCI-2). Vaughn, J. Pierce, ex. Douglas fir limbs [=*Pseudotsuga menziesii*] (WFBM-4); 21.VI.1955, J.A. Rudinsky, J.R. Pierce, ex. Doug fir branches [=*Pseudotsuga menziesii*] (WFBM-3). *Linn Co.*: Santiam Pass, 19.VI.1951, S.L. Wood, J.B. Karren, D.E. Bright, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (DEBC-1). [*Malheur Co.*]: Monument Peak, 25.IX.[19]53, ex. *Pseudotsuga taxifolia* [=*P. menziesii*] (EMEC-3). [*Marion Co.*]: Clear Lake, 17.VIII.[19]51, R. Kangur, ex. Larch [=*Larix* sp.] (WFBM-2). [*Multnomah Co.*]: Portland, Hubbard, Schwarz (EMEC-2). [*Umatilla Co.*]: Tollgate, 30.VI.1950, E.S. McClurskey, ex. on aluminum roof (CNCI-1), 1.IX.1950 (CNCI-1). [*Unspecified County*]: Clear Lake, 17.VIII.[19]51, R. Kangur (EMEC-4). Detroit, 25mi E., 17.VII.1939, Schuh, Scott, ex.

Tsuga mertensiana (FMNH-6). Middle Sister Mountain, 8000ft, Hopk. U.S. 53349-G, 4.VIII.1968, M.M. Furniss, ex. on snowfield (WFBM-2). Portland, Wickham (CNCI-1). Tillamook burn, 18.VII.1941, R. Kangur (EMEC-1). Warm Springs Indian Reservation, 15.VIII.[19]51, R. Kangur, ex. Douglas fir [= *Pseudotsuga menziesii*] (EMEC-4).

WASHINGTON: [*Clallam Co.*]: Port Angeles, Hopk. U.S. 130, A.D. Hopkins, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (EMEC-1). Port Williams [Marlyn Nelson County Park at Port Williams], Hopk. U.S. 168-F, A.D. Hopkins, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (EMEC-1). *Cowlitz Co.*: Castle Rocks, 10mi E., 27.VI.[19]64, D.E. Bright, ex. *Pseudotsuga menziesii* (DEBC-18, EMEC-9). [*Grays Harbor Co.*]: Humptulips, 28.V.1914, E.C. VanDyke (CASC-3). [*Kittitas Co.*]: Easton (CASC-6, EMEC-2). *Okanogan Co.*: Disautel, 4.XI.1936, R.L. Furniss, ex. *Pseudotsuga menziesii* (OSAC-17, WFBM-7). [*Pend Oreille Co.*]: Metaline Falls, Hopk. U.S. 21340, 17.VII.1931, W.D. Bedard, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (WFBM-15). *Skamania Co.*: Mineral Springs, 27.VI.[19]64, D.E. Bright, ex. *Pseudotsuga menziesii* (EMEC-9). [*Snohomish Co.*]: [labeled King Co.] Mountlake Terrace, 20.VIII.[19]62, ex. *Pseudotsuga menziesii* (CNCI-3). *Thurston Co.*: Olympia, 7-30.V.1996, E. LaGasa, ex. Washington Department of Agriculture port trapping survey (WFBM-1). *Yakima Co.*: Naches, 14mi W., Dry Creek Ridge, Snoqualamie National Forest, 3.VII.1965, R.B. Hutt (DEBC-2). [*Unspecified County*]: Mount Adams, Bird Creek, 6000-7000ft, 2.VII.1925 (CASC-1). Mount Rainier National Park, 21.VIII.[19]62, ex. *Pseudotsuga taxifolia* [= *P. menziesii*] (CNCI-6).

Distribution. CANADA: British Columbia. UNITED STATES: California, Idaho, Oregon, Washington.

Hosts. *Pseudotsuga menziesii* (Mirb.) Franco. (Douglas fir) but also likely occurs in *P. macrocarpa* (Vasey) Mayr (Big cone Douglas fir) in Southern California.

Common name. Douglas-fir engraver.

Biology. *Scolytus unispinosus* is very common (Chamberlin 1939; Smith pers. obs.) and attacks the boles and branches of weakened, injured, dying and recently killed Douglas fir. Populations of this species can build up in windfalls, slash and during drought when the species becomes capable of killing young trees (Keen 1938; Chamberlin 1939; Wood et al. 2003). Outbreaks are sporadic and are of short duration (Keen 1938; Wood et al 2003).

The adult gallery of this species consists of a single egg gallery that extends with the grain of the wood. The nuptial chamber includes a short extension at a 45° angle from the egg gallery and is located at one end on the egg gallery. The gallery deeply scores the sapwood and lightly scores the cambium (Chamberlin 1958). The female deposits 40-100 eggs in egg niches on both sides of the egg gallery 0.5-1.0mm apart (Doane et al. 1936). Larvae extend their mines at a right angle to the egg gallery forming a fan shaped pattern (Chamberlin 1939). There are two generations per year in California and the broods overwinter as either eggs or larvae (Keen 1938; Wood et al. 2003). Adults emerge from late April through July (Keen 1958). In Oregon one generation per year has been observed at high elevations in and two at lower elevations (Chamberlin 1939).

McMullen and Atkins (1962) reported some notes on the biology of *S. unispinosus* in British Columbia and appear to have reported a combined account of *S. unispinosus* and *S. fiskei* (see *S. fiskei* biology for more information). This paper was the main source of information regarding the biology of *S. unispinosus* and served as the basis for describing the biology of the species in numerous publications (including Bright 1976; Furniss and Carolin 1977; Furniss and Johnson 2002; Wood et al. 2003). Chamberlin (1939, 1958) provides the most reliable source of information regarding the biology of the species.

Collection notes. None.

Remarks. There are 25 *S. sobrinus* specimens bearing paratype labels found in the EMEC. These specimens are not designated as such by Blackman (1934) and have been labeled “not Paratype” by the authors. These specimens bear the following Hopkins numbers: 4205-A (EMEC-2), 4272-A (EMEC-4), 1968-D1 (EMEC-1), 1968-D3 (EMEC-1), 4273-B (EMEC-1), 4204 (EMEC-2), 4220-A (EMEC-3), 4226-D (EMEC-1), 4201-A (EMEC-2), 13232-C (EMEC-1), 17 (EMEC-1), 18 (EMEC-1), 19 (EMEC-2) and Sonoma, California (EMEC-3).

This species occurs along the western coastal states of the United States and British Columbia, Canada. The range of *S. unispinosus* does not overlap with that of *S. fiskei* except in south central British Columbia where species are sympatric in the Interior Plateau near Merritt.

***Scolytus ventralis* LeConte**

(Figures 1.66, 1.67)

Scolytus ventralis LeConte 1868: 167. Lectotype: male, labeled “[Washington Territory] Type 970” (MCZC). Lectotype designated: Wood 1982: 441.

Diagnosis. *Scolytus ventralis* males are distinguished from those of other species by having the base of sternite 2 faintly elevated and the face of sternite 2 flat, the apical margin of sternite 2 is slightly elevated and often bears a median denticles, the second sternite is glabrous.

Females most closely resemble those of *S. robustus* and *S. subscaber*. Females are distinguished from those of both species by the indistinctly and weakly aciculate and strongly punctate frons and by the apical margin of sternite 1 flush with basal margin of sternite 2, appearing rounded.

Redescription (male). 3.0 - 4.0mm long (mean = 3.65mm; n = 20); 2.1-2.7 times as long as wide. Head, pronotum and abdominal venter dark red-brown, antennae light brown, elytra and legs yellow-brown to light brown. Pronotum typically darker than elytra.

Epistoma weakly emarginated; epistomal process weakly elevated; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally, slightly transversely impressed above epistoma; surface moderately and coarsely longitudinally aciculate-punctate; aciculations converging at epistoma; punctures small, coarse; surface moderately and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, irregularly ovoid, setose with a partial septum and three arcuate sutures.

Pronotum wider than long; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex, and forming a weak transverse impression near apical margin; surface smooth, shining, punctures on disc fine, shallow and moderately abundant, larger and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral sides sub-parallel on apical half, narrowing to a subquadrate and smooth apex; apical margin of elytral apices bearing small, fine punctures; apex moderately emarginated at the suture. Disc glabrous, smooth, shining; interstriae not impressed and more than twice the width of striae, interstitial punctures uniseriate, smaller than those of striae; striae weakly impressed. Declivity bearing sparse, short, erect yellow setae. Metepimeron half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface glabrous, shagreened, dull, finely punctate with small, fine and shallow punctures; face flattened; apical margin armed with a broad median denticle, occasionally absent; lateral margins of sternites 2-4 and sternite 4 unarmed. Sternite 5 carinate ridge closer to the apical margin than the basal margin of the segment; length of sternite 5 less than the combined lengths of sternites 3 and 4; a setal patch or median depression is absent.

Female. 2.2 – 4.6mm long (mean = 3.56mm; n = 20); 2.1-2.7 times as long as wide. Similar to male except epistoma feebly emarginated, epistomal process absent, frons convex when viewed laterally, weakly longitudinally aciculate, setae shorter, less than the width of the eye and less abundant; weakly transversely impressed between epistoma and inner apices of eyes. Second sternite unarmed.

Specimens examined. 324.

Type material. Lectotype *Scolytus ventralis* LeConte (MCZC).

Non-type material. **CANADA: BRITISH COLUMBIA:** Duncan, Genoa Bay, 30.VI.1928, W.G. Mathers, ex. *Abies grandis* (CNCI-4), 21.VI.1928 (CNCI-1), 23.VI.1928 (CASC-1), 24.VI.1928 (CASC-1), 16.VII.1928 (CASC-1), 13.VIII.1936 (CASC-1). Steelhead, 6.VII.1933, H.B. Leech, ex. *Abies amabilis* (CNCI-1), 27.VII.1933 (CASC-1), 24.VII.1933 (CNCI-1), 26.VII.1933 (CNCI-1). Trail, 22km S.E., 24.V.1991, J.E. Macias, ex. *Abies grandis* (CNCI-1). Vancouver, 10.VI.1935, K. Graham, ex. *Abies grandis* (CASC-12). **MEXICO: BAJA CALIFORNIA:** San Pedro Mártir, Hopk. U.S. 32716-A, 5.VI.1944, F.P. Keen, ex. *Abies concolor* (EMEC-1). **UNITED STATES: ARIZONA:** Cochise Co.: Coronado National Forest, Chiricahua Mountains, 14.VII.2009, J. Hulcr, ex. *Pseudotsuga menziesii* (MSUC-3). **CALIFORNIA:** [Amador Co.]: Jackson, 31.III.[19]55, ex. *Abies concolor* (EMEC-1). Calaveras Co.: Big Trees [State Park],

VII.1930, F.E. Blaisdell (CASC-1). *El Dorado Co.*: Bijou at south end of Lake Tahoe, H.B. Leech, ex. Douglas fir log [= *Pseudotsuga menziesii*], emerged San Francisco, 18-20.V.1965, W.E. Kuhl (CASC-8). [Georgetown, 10mi E.], Blodgett [Experimental] Forest, 30.V.1986, K. Hobson (EMEC-1), 11.VI.1986 (EMEC-1), 21-24.VI.1986 (EMEC-6), 25-27.VI.1986 (EMEC-1), 1-7.VII.1986 (EMEC-2), 9-16.VII.1986 (EMEC-4); 30.V.1986, Hobson, Atkinson, ex. Lindgren trap, unbaited over burned area (EMEC-3), ex. Lindgren trap, turpentine bait, logged area (EMEC-1); 27.V.1986, Hobson, Irving, ex. Lindgren trap, ponderosa pine resin H&L B.P. fractions, logged area (EMEC-1), ex. Lindgren trap, ponderosa pine resin, untreated oleo, burned over area (EMEC-1). Ice House Reservoir, 23.VI.[19]90, J.B. Johnson (EMEC-1). Pacific, 8.VII.[19]62, R.L. McDonald (CASC-1). *Fresno Co.*: Huntington Lake, 16.VII.[19]19, F.E. Blaisdell (CASC-5). *Lassen Co.*: Lassen National Forest, 20-25.VII.1994, S1/2 S35 T34N R7E, A.I. Cognato (MSUC-20, SBMN-4); Black Mountain Experimental Forest, VII.1995, A.I. Cognato (MSUC-1). Near Loon Lake campground, 6300ft, 28.VII-12.VIII.1978, J.A. De Benedictis (EMEC-1). Norval Flats, 5500ft, 18.VII.[19]20, J.O. Martin, ex. *Abies concolor* (CASC-47). Uncle Tom's, 0.1 road mile W., 28.VII-12.VIII.1978, J.A. De Benedictis (EMEC-1). *Marin Co.*: VI-VIII.[19]56, D. Giuliani (CASC-1). *Mariposa Co.*: Miami Ranger Station, 2mi S., 19.VII.1946, H.P. Chandler (DEBC-3). Miami Lodge, 17.VII.1946, G.R. Struble, ex. *Abies concolor* (CSUC-1). *Mendocino Co.*: Noyo River, VI.1896 (CASC-22). *Modoc Co.*: Modoc National Forest, Hwy 299, 5.3mi W. Cedarville at creek near exit from ski area, 41°32.9'N 120°14'W, 9.IX.1995, J. Schweikert, ex. swept creek side plants (CASC-1). Davis Creek, 4mi N.E., Sugar Hill, 6300ft, 9.VI.1970, W. Middlekauff (EMEC-1). *Nevada Co.*: Sagehen Creek Field Station, 39.4298°N, 120.2429°W, 12-18.VIII.2003, M. Caterino, ex. FIT (SBNM-1). Near Sagehen campground, 39.4344°N, 120.2808°W, 15.VIII.2003, M. Caterino (SBNM-1). Sagehen

Creek, 20.VII.1966, W.J. Turner (EMEC-1). [*Placer Co.*]: Cisco (USNM-1). *Plumas Co.*: Bartle, 9mi N., 12-15.VI.1974, L. Green, (EMEC-1). Chester, 8mi N.W., Warner Creek, 5000ft, 21.VI.1989, E.E. Lundquist (CNCI-2). Jamesville, 15-21.VIII.[19]50, M. Wasbauer, ex. *Abies concolor* (EMEC-1). *Riverside Co.*: Mount San Jacinto State Park, 33.800°N, 116.673°W, 15.VII.2003, M. Caterino (SBMN-1). Santa Rosa Mountains, 10.IV.[19]63, D.E. Bright, ex. *Abies concolor* (EMEC-1). [*San Bernardino Co.*]: San Bernardino Mountains, Dollar Lake trail, 10.VII.1956, H.W. Michalk (CSCA-1). *Siskiyou Co.*: Happy Camp, 18mi N., 31.VII.[19]63, C.J. Wray, ex. *Picea breweriana* (DEBC-2, EMEC-1). Klamath National Forest, gooseneast adaptive management area, 41.5°N, 121.9°W, 26.VII.2000, ex. pitfall 3-840 (SBNM-1). McCloud, 22.VI.1914 (CASC-23), 14.VI.1962, D.E. Bright, B.A. Barr, C. Hector (CASC-1). *Tehama Co.*: Mineral, 11.VIII.[19]35 (CASC-1). *Trinity Co.*: Carville, 30.VI.1913, ex. dug out of *Abies concolor* (CASC-1), 2400-2500ft, 23.V.1934 (CASC-1). Nash Mine, 12.VI.1913 (CASC-1). *Tulare Co.*: Giant Forest, 6500ft, VII.1908, Hopping (CASC-3). Kaweah, 100ft, Hopping (CASC-1). Sequoia National Park, Redwood Canyon, 20.IX.1980, S.F. Muzzio (CASC-2). [*Unspecified county*]: Pinecrest, 24.VII.1930, G.R. Struble, ex. *Abies magnifica* (EMEC-1).

COLORADO: *Costilla Co.*: Pass Creek, 17.VI.1976, D. Leatherman, ex. white fir [= *Abies concolor*] (CSUC-4). *Huerfano Co.*: Near Red Wing, 16.VI.1975, D. Leatherman, ex. white fir [= *Abies concolor*] (CSUC-1). *Las Animas Co.*: Monument Lake, 6.VII.1994, S. Kelley, ex. white fir [= *Abies concolor*] (DEBC-2). *Pueblo Co.*: SR 165, 5mi S.E. San Isabel Millset trailhead, D. Leatherman, ex. burned white fir [= *Abies concolor*] (CSUC- 6). **IDAHO:** *Benewah Co.*: Plummer, 4mi S., 14.VIII.1956, W.F. Barr, E.C. Clark, ex. *Abies grandis* (FMNH-1). *Boundary Co.*: Idaho Panhandle National Forest, Hwy 95, Robinson Lake campground, N48°58.200' W116°13.067', 2696ft, 13.VIII.2010, S.M. Smith, A.R. Gillogly, ex. *Abies grandis* (MSUC-6).

Kootenai Co.: Coeur d'Alene, 5.IX.1919, J.C. Evenden, ex. *Abies grandis* (MSUC-3).

MONTANA: [*Unspecified county*]: Glacier [National] Park, 15.VII.[19]31 (CUIC-1). **NEW**

MEXICO: *Bernalillo Co.*: Cibola National Forest Sandia Peak, NM536, N35°11.655' W106°24.075', 8317ft, 10.V.2010, S.M. Smith, A.I. Cognato, ex. *Abies concolor* (MSUC-1).

[*Otero Co.*]: Cloudcroft, 900ft, W. Knaus (CNCI-1). *Santa Fe Co.*: Little Tesuque Canyon, 14.VI.[19]35 (CASC-1). *Socorro Co.*: VII[?], Wickham (CASC-1). **OREGON**: *Benton Co.*: Corvallis, VIII.1919, W.J. Chamberlin, ex. *Pseudotsuga taxifolia* [= *Pseudotsuga menziesii*] (EMEC-1), Kiger Island, VII.[19]22, W.J. Chamberlin (EMEC-2). Mary's Peak, 14mi W Corvallis. XII.1958 (EMEC-2). [*Deschutes Co.*]: Bend, Hopk. U.S. 33,531-B, 8.VII.[19]58, W.J. Buckhorn, P.W. Orr, ex. *Abies grandis* (OSAC-8). [*Klamath Co.*]: Klamath Falls, Geary Ranch, 4.X.1962, J. Schuh, ex. *Abies concolor* (CNCI-2, FMNH-4, MSUC-7). [*Linn Co.*]: McMinnville, 7.VIII.1951, R. Kangur (WFBM-2). [*Wallowa Co.*]: Wallowa Lake, 19.VII.[19]51, Quintus, ex. *Abies concolor* (WFBM-1). **UTAH**: *Juab Co.*: Mount Nebo, 20.VII.1958, D.E. Bright, ex. *Abies concolor* (CNCI-2). *Utah Co.*: Payson Canyon, 20.V.1961, S.L. Wood, ex. *Abies concolor* (USNM-18). **WASHINGTON**: [*Jefferson Co.*]: Quilcene, Hopk. U.S. 65564, 30.IX.1946 (OSAC-6). [*Pend Oreille Co.*]: Metaline Falls, Hopk. U.S. 21405, 17.VII.[19]31, W.D. Bedard, ex. flying (USNM-4). [*Stevens Co.*]: Northport, 1.IX.1930, R. Hopping (CASC-3). [*Walla Walla Co.*]: Walla Walla, VIII.1933, M.C. Lume (USNM-11). [*Yakima Co.*]: [Mount Baker], Snoqualmie National Forest, Dry Creek Ridge, 14mi W. of Naches, 3.VII.1965, R.B. Hutt (DEBC-1).

Distribution. CANADA: British Columbia. MEXICO: Baja California. UNITED STATES: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, Washington, Wyoming.

Hosts. Principle hosts: *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir), *Abies grandis* (Douglas ex D. Don) Lindl. (grand fir), and *Abies magnifica* A. Murray (red fir).

Incidental hosts: *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir).

Common name. Fir engraver.

Biology. *Scolytus ventralis* can cause significant fir mortality and is the most destructive conifer-feeding *Scolytus* species in the Nearctic (Keen 1938; Bright and Stark 1973). During a period from 1924-1936, *S. ventralis* killed 15% and damaged an additional 25% of the merchantable fir in California. It has also been reported to be quite destructive in Oregon (Keen 1938). *Scolytus ventralis* is associated with a symbiotic stain fungus, *Trichasporium symbioticum* Wright, which the adult beetle introduces when it excavates the adult gallery. The fungus spreads in all directions around the gallery system (Bright and Stark 1973). Due to the potential of *S. ventralis* to kill fir trees, this species is the most well studied native *Scolytus* in North America. Attacks usually occur on the boles of weakened and stressed standing trees from a few feet above the base to the top of the tree, but can also occur in large slash and fresh and fallen trees (Chamberlin 1958; Edson 1967; Furniss and Johnson 2002). Attacks at the top of the tree are more common on overmature standing trees during drought and healthy, vigorous trees are not preferred (Chamberlin 1958; Raffa and Berryman 1987). Trees can also become successively attacked over a period of years and slowly die. Healthy trees may survive the attacks but can develop rots and defects that reduce timber value (Struble 1937). Unlike most tree-killing or primary bark beetles, *S. ventralis* does not have pheromone to aggregate conspecifics to host trees. The beetles locate suitable hosts via primary attraction to host volatiles (Macías-Sámano et al 1998a,b).

Adult galleries of *S. ventralis* are perpendicular to the grain of the wood. Adult galleries deeply score the sapwood, lightly score the cambium and consist of two egg galleries with a

central nuptial chamber (Edson 1967). The nuptial chamber is typically short and at a right angle to the egg galleries but may also extend at an oblique angle. When this occurs, one of the egg galleries is briefly extended at an oblique angle against the grain before becoming perpendicular to the grain (Edson 1967). Eggs are deposited singly in triangular niches spaced 1-1.5mm apart on each side of the egg gallery with 80-300 niches per gallery. Galleries range in size from 8-30cm in length (Chamberlin 1958; Edson 1967; Bright and Stark 1973; Furniss and Johnson 2002). Larval mines are perpendicular to the egg gallery and parallel with the grain of the wood. Larval mines are also parallel to each other both above and below the egg gallery, giving the gallery a diamond shaped appearance (Keen 1938; Edson 1967). Larval mines lightly score the sapwood and deeply score the cambium. Larvae construct pupation chambers in the phloem or outer bark (Edson 1967). Broods overwinter as larvae or adults (Bright and Stark 1973). The number of generations per year varies both geographically and with elevation. Development time can range from as little as 41 days at low latitudes and elevations to as many as 380 days at high latitudes and elevations (Bright and Stark 1973). There is typically one generation per year (Bright and Stark 1973). In Idaho, pupation occurs from June to July and peak flight occurs in July (Furniss and Johnson 2002).

Collection notes. None.

Remarks. The lectotype does not bear a locality label. LeConte's (1868) description states that George Gibbs collected the lectotype in the Washington Territory.

CHAPTER 2

PHYLOGENETICS AND EVOLUTION OF HOST-USE AMONG THE SCOLYTINI (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE)

Abstract

The influence of plants in the diversification of herbivorous insects, specifically those that utilize moribund and dead hosts, is unclear. Scolytini, a diverse tribe of weevils, specialize on many different plant taxa as a source of food. The phylogenetics of the Scolytini were reconstructed using Bayesian analyses to examine the origin, test the monophyly of Scolytini genera, and illuminate patterns of host-use and feeding habits among the tribe. Analyses were based on rDNA nucleotides from the D2-D3 segment of 28S, and nucleotides from encoding gene fragments of CAD, ArgK and mitochondrial COI. Ancestral host usage was reconstructed using likelihood criteria. Results support monophyletic Scolytini, *Ceratolepsis*, *Loganius*, and *Scolytus* and paraphyletic *Camptocerus* and *Cnemonyx*. Diversification of the Scolytini generally occurred well after host taxa diversified, as a combination of host shifts and lineage tracking. Repeated independent shifts to the same hosts occurred. Diversification occurred on common and widespread hosts, there was a single origination of conifer-feeding from angiosperm-feeding species and evolution of fungus-feeding from phloem-feeding ancestors. Overall, the observed patterns of Scolytini host-use can be explained by a combination of the sequential evolution and host-use oscillation hypotheses, a pattern that has been found for other insect taxa that colonize living host plants.

Introduction

The bark and ambrosia beetles are a diverse weevil subfamily (Coleoptera: Curculionidae: Scolytinae) with at least 6,000 recognized species and representing roughly 10% of weevil diversity (Wood and Bright 1992; Oberprieler et al. 2007). Scolytines utilize a wide array of plant taxa including ferns, conifers, monocots and dicots and species exhibit a multitude of ecological feeding habits (Browne 1961; Gray 1970; Wood 1982). Despite the diversity of feeding habits, scolytines are primarily composed of two distinct groups: true bark beetles and ambrosia beetles. True bark beetles are phloeophagous and feed exclusively on phloem and cambium of living, moribund, or dead host trees (Wood 1982). Ambrosia beetles, which are xylomycetophagous, bore into the xylem of a moribund or dead host tree and cultivate a symbiotic fungal, bacterial and yeast garden. This ambrosial feeding habit has evolved at least ten times within the Scolytinae (Farrell et al. 2001; Jordal and Cognato 2012).

Boring under bark and into xylem hastens decomposition of woody debris via the introduction of other xylophagous organisms (Stokland 2012). Scolytines are ubiquitous in global forest ecosystems and primarily contribute to the decomposition of dead vegetation. However, a small number of bark beetle species kill live trees (Wood 1982). While the majority of scolytine species are not ambrosia beetles, they passively introduce fungi into otherwise healthy trees as a by-product of phloem-feeding. At high densities, bark beetle species cause widespread mortality of economically valuable tree species, giving bark beetles their nefarious reputation as ecologically and economically destructive forest pests (Browne 1961; Furniss and Carolin 1977).

Bark beetles are intrinsically interesting organisms. Variation in mating systems and host-plant use provides the intellectual fodder for investigation of general evolutionary hypotheses (e.g., Kelley and Farrell 1998; Farrell et al. 2001; Jordal et al. 2004; Hulcr and Cognato 2010; Jordal et al. 2011; Jordal and Cognato 2012). The study of evolution of bark beetles and host trees has been of particular interest and underlies diversification of beetle species (Farrell and Mitter 1993; Becerra 1997; Farrell 1998; Mitter et al. 1988; McKenna et al. 2009). Once structural and/or chemical barriers that deter or prevent beetle feeding on a particular host taxon are overcome through natural selection, subsequent generations tend to feed only on that plant taxon (Erhlich and Raven 1964). However, species-rich beetle lineages often feed on phylogenetically unrelated plants, suggesting changes in host plant use are a driving force in beetle evolution. Similarities in secondary compounds of unrelated hosts likely facilitate host shifts and promote beetle diversity (Erhlich and Raven 1964; Jaenike 1990). Broad patterns of the evolution of host-plant use by weevils include ancestral weevil feeding on old lineages of conifers (such as Cycadaceae), a shift of some groups (including Scolytinae) to angiosperms and subsequent shifts to younger conifers (such as Pinaceae) (McKenna et al. 2009). Although there are few examples of lineage diversification of bark beetles and their hosts, shifts to novel hosts with similar secondary compounds (Kelley et al. 1999; Kerdelhué et al. 2002; Jordal et al. 2004) and geographic isolation (Kelley et al. 1999; Cognato et al. 2005; Ruiz et al. 2009) are important factors in species diversification. Our understanding of evolutionary processes that form the patterns of host-plant use is not complete because knowledge of Curculionoidea phylogeny is at best preliminary (Oberprieler et al. 2007). Thus, detailed knowledge of host-plant preferences and species-level phylogenies will provide a foundation for testing hypotheses related to evolution of host and host preference (Farrell et al. 2001).

Most research addressing evolution of host-use has focused on herbivorous insects that feed on live, healthy plants (Farrell and Mitter 1990; Farrell 1998) rather than on insects in dying and dead plants (Jordal et al. 2004). I aim to augment the knowledge of evolution of host-use among phloem-feeding insects of dying and dead trees via a study of host tree use among tropical and temperate species in a tribe of scolytine weevils. Data from this research will add to the growing number of studies addressing the central paradigm of herbivorous insect evolution and host-plant association (Erhlich and Raven 1964; Jermy 1976; Janz and Nylin 2008). These results will further increase our understanding of the evolution of insect species and their potential to invade novel host plants.

Study Group

Scolytini offers an opportunity to examine the evolution of host-use within a monophyletic group of species that feed on a wide variety of plants. In particular, six genera *Camptocerus* Dejean 1821, *Ceratolepsis* Chapuis 1869, *Cnemonyx* Eichhoff 1868, *Loganius* Chapuis 1869, *Scolytus*, and *Scolytopsis* Blandford 1896, of this tribe show a diversity of host-use and diet in the Neotropic and the Holarctic regions (Wood 1982). All genera except the ambrosia feeding *Camptocerus* are phloeophagous and all genera exclusively use angiosperm hosts, except *Scolytus*, which includes 22 species that feed exclusively on conifers in the Holarctic (Table 2.1) (Smith, Chapter 1; Michalski 1973). *Scolytus* is unusual in this regard because it is one of five scolytine genera that possess this broad host-use pattern (Wood 1986). Nearly all Neotropical *Scolytus* species feed exclusively on woody species of the diverse and ubiquitous (Boom 1986) angiosperm family Fabaceae. In contrast, nearly all native Nearctic species feed on Pinaceae, including the genera *Abies* Mill., *Larix* Mill., *Picea* D.Don. ex Loudon,

Pseudotsuga Carrière, and *Tsuga* Carrière (Smith, Chapter 1; Wood and Bright 1992). To date, patterns of Scolytini and host tree coevolution have not been examined in a phylogenetic context.

Reconstruction of a Scolytini phylogeny allows hypotheses related to the evolution of scolytines in relation to their hosts to be tested. Specifically, this study is designed to examine (1) the evolution of conifer-feeding from an ancestral angiosperm-feeding lineage, (2) patterns of host plant-use among the Scolytini, (3) the independent evolution of fungus-feeding in *Camptocerus* from phloem-feeding ancestors, (4) the monophyly of Scolytini genera and the age of Scolytini genera. This study also addresses broader evolutionary hypotheses of beetle/host evolution including the phylogenetic conservation of host-plant use such that related beetle species feed on related plant species.

Materials and Methods

Taxa, DNA sequences and Alignment

I sequenced up to four genes for 131 specimens (Table 2.2) representing 65 Scolytini species including representatives of *Camptocerus* (13 spp.), *Ceratolepsis* (2 spp.), *Cnemonyx* (5 spp.), *Loganius* (3 spp.) and *Scolytus* (42 spp.). *Coptonotus cyclopus* Chapuis 1869 was selected as an outgroup species based on the result of a previous phylogenetic study (Jordal et al. 2011). Specimens of *Scolytopsis* could not be sampled for this study due to unavailability. Sequences of the following species were obtained from GenBank and included in the analyses: *S. ecksteini* 166 (JX416906.1), *S. ecksteini* 167 (JX416909.1), *S. rugulosus* 165 (JX089344.1), *S. intricatus* (HQ883677, HQ883589, HQ883820, HQ883909) and *S. scolytus* (HQ883678, HQ883590, HQ883821, HQ883910). Specimens were included in the dataset only if molecular data were

available for at least two of the four genes. DNA extraction, amplification and sequencing protocols were identical to those used by Smith (Chapter 1). Purified DNA was used to amplify partial gene regions of mitochondrial cytochrome oxidase 1 (COI), D2 region of nuclear ribosomal 28S, CAD, and Arginine Kinase (ArgK) using the PCR primers listed in Table 1.6. Nexus files are available at <http://www.scolytid.msu.edu>.

Bayesian Analyses

I analyzed the dataset using Bayesian estimation of phylogeny with MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001) and selected the best model for each data partition using MrModeltest (Nylander 2004) and implemented in PAUP*4.0 b10 PPC (Swofford 2002). The models selected by the AIC was found to have the optimal fit (Table 2.3). However MrBayes is limited in the models of nucleotide evolution that it can accommodate and so the closest model was implemented, GTR+I+ Γ (general time reversible with a proportion of invariant sites and a gamma-shaped distribution of rate variation across sites) (Bennett and O'Grady 2012). The dataset was divided into partitions by either genome (mitochondrial vs. nuclear) and by nucleotide position. Run 1 consisted of all data under a single partition, run 2 consisted of 4 (COI, 28S, CAD and ArgK) and run 3 consisted of 3 partitions (COI, 28S, CAD+ArgK). Parsimony analyses were not performed because they were previously found to recover several of the species included in the analysis as para- and polyphyletic despite many discrete morphological, ecological, behavioral and distributional similarities (see Smith, Chapter 1).

The molecular datasets were each analyzed with four Metropolis-Coupled Markov Chain Monte Carlo searches (3 heated, 1 cold) (Huelsenbeck and Ronquist 2001) for 2-2.5 million generations with sampling every 100th iteration. Approach to stationarity (burn-in) was 0.25.

Burn-in discards the first 25% of trees sampled to minimize the effect of the initial posterior distribution. All parameters reached stability and the split deviation between runs was below 0.05 indicating that the four changes had converged on a topology. Bayesian posterior probabilities of clades were calculated by a majority-rule consensus of those trees after the burn-in. Nexus files are available at <http://www.scolytid.msu.edu>.

Hosts

Species included in the analyses and the known hosts are shown in Table 2.4-2.6. Host records and feeding habit were obtained from a comprehensive literature review (von Butovitsch 1929; Chamberlin 1939; Schedl 1948; Balachowsky 1949; Stark 1952; Chamberlin 1958; Edson 1967; Beaver 1972; Bright and Stark 1973; Michalski 1973; Nobuchi 1973; Bright 1976; Furniss and Carolin 1977; Wood 1982; Yin et al. 1984; Atkinson and Equihua-Martinez 1986a; Wood and Bright 1992; Pfeffer 1994; Cibrián Tovar et al. 1995; Bright and Skidmore 1997, 2002; Furniss and Johnson 2002; Wood 2007; Smith and Cognato 2010b), field notes, discussions with other scolytine experts (T.H. Atkinson, D.E. Bright, M.M. Furniss, A.V. Petrov) and label data on museum specimens.

Host plant nomenclature was verified by querying the International Plant Name Index (www.ipni.org) or Tropicos (www.tropicos.org) databases. Angiosperm classification follows that of the Angiosperm Phylogeny Group (APG) III (Angiosperm Phylogeny Group 2009).

Ancestral State Reconstruction

Feeding habit and host associations were scored and entered into a nexus file in Mesquite v. 2.75 (Maddison and Maddison 2011). The number of origins of wood-boring behavior and

patterns of host plant-use were then traced in Mesquite using the likelihood criterion onto each tree obtained from the above Bayesian analyses. The Markov k-1 (mk-1) model was used which allows for equal rates of change between character states. Taxa were coded as follows:

Feeding habit:

0, phloem-feeding

1, wood boring, including ambrosia fungus feeding and xylophagy

Most frequently observed host plant family:

0, Pinaceae

1, Burseraceae

2, Ulmaceae

3, Rosaceae

4, Fabaceae

5, Juglandaceae

6, Cannabaceae

7, Betulaceae

8, Fagaceae

9, Myristicaceae

A, Clusiaceae

B, Euphorbiaceae

C, Malvaceae

Genera of coniferous hosts:

0, *Picea*

1, *Abies*

2, *Larix*

3, *Tsuga*

4, *Pseudotsuga*

Total diet breadth for each species could not be tested using the likelihood criterion because current methods are unable to process polymorphic characters (Bollback 2006; Maddison and Maddison 2011). Nexus files are available at <http://www.scolytid.msu.edu>.

Conservation of Host-Use

Permutation tail probability (PTP) tests were used to determine conservation of host-use among the tribe. PTP tests measure the proportion of datasets producing a tree shorter or equal in length to the actual tree (Faith and Cranston 1991). Performing a PTP test serves as the basis to test the null hypothesis that there is no structure in the tree and that the observed pattern is due to random chance. Under a PTP test, a constraint tree is loaded and characters are randomly permuted across the topology, then the resulting length is measured (Maddison and Slatkin 1991; Faith and Cranston 1991).

PTP tests were performed in PAUP* b10 (Swofford 2002) for both the most common utilized plant family and conifer host genus (Kelley and Farrell 1998). The host character was randomized 10,000 times over a constraint tree. Since the phylogeny of the group is known, host character states were randomized over a constraint tree to test the frequency of each character state (Maddison and Slatkin 1991; Faith and Cranston 1991).

Estimating Divergence Times

I estimated lineage divergence times using the BEAST v1.7.5 software package (Drummond et al. 2012). Input xml files were generated in BEAUti v1.7.5 (part of the BEAST package) using a user-specified start tree and topology from my run 2 Bayesian analysis. The consensus tree was pruned to remove polytomies. A Yule prior process model was selected as the tree prior, which assumed a constant speciation rate for each lineage (Gernhard 2008). The topology was unconstrained and allowed a separate GTR+I+ Γ with 6 gamma categories for each gene as selected by MrModeltest. An uncorrelated lognormal relaxed molecular clock allowing for rate variation among lineages because different lineages evolve at different rates (Drummond et al. 2006). Two separate analyses were performed, for minimum and maximum clade ages. Each analysis was performed with four independent chains of 60,000,000 generations with trees sampled every 1,000 generations. The tree files were combined in TreeAnnotator v1.7.5 (part of the BEAST package) with the burn-in set to 20,001 trees (33% burn-in). A large burn-in was used due to limited computational resources. The remaining 40,000 trees were used to create a maximum clade credibility (MCC) tree with mean node heights. XML files are available at <http://www.scolytid.msu.edu>.

Five priors based on the fossil record were used to calibrate the phylogeny and the minimum age for each node. *Calibration 1, Scolytini*: 100 mya *Microborus* (Hexacolini) from Burmese amber (Cognato and Grimaldi 2009). Numerous phylogenetic studies have recovered the Scolytini at the base of the Scolytinae and basal to the Hexacolini, indicating a minimum age of the Scolytini of 100 mya (Jordal et al. 2011; Jordal and Cognato 2012). *Calibration 2, South American Scolytus*: *Scolytus poinari* Bright, Dominican amber 20-17 mya (Bright and Poinar 1994). This species is morphologically aberrant from extant *Scolytus* in the shape of the antennal club. It most closely resembles species from southern Brazil in the shape of the frons, abdominal

spine placement and setal length and distribution and thus was used to date the clade of *S. excavatus* and *S. proximus*. *Calibration 3*, *Tubuloscolytus* species group: *Scolytus duplicatus* compression fossil from the Upper Miocene and Lower Turolian ~9-5.3 mya in France (Petrov and Zherikhin 2000). The species is very morphologically similar to *S. koenigi*, an extant member of the *Tubuloscolytus* species group and indicates a minimum clade age of 5.3 mya. *Calibration 4*, *Cnemonyx*: *Cnemonyx priscus* Bright and Poinar, fossil in Dominican amber, 20-17 mya (Bright and Poinar 1994). This species is easily associated with extant *Cnemonyx* and is morphologically similar to *C. vismiacolens* Wood and *C. rugulosus* (Eggers) and thus was used to calibrate *Cnemonyx*. *Calibration 5*, *Cylindrobrotus*: *Cylindrobrotus pectinatus* Kirejtshuk, Azar, Beaver, Mandelshtam and Nel, fossil in Cretaceous Lebanese amber was thus used to calibrate the maximum age of the Scolytini at 120 mya (Kirejtshuk et al. 2009).

Two BEAST analyses were performed: one with a maximum clade age at 100 mya (calibration 1) and the most recent dates for each fossil calibration (analysis A) and one analysis with a maximum age at 120 mya (calibration 5) and the most distant dates for each fossil calibration (analysis B).

Results

Phylogenetic Results

Overall, the three Bayesian analyses produced trees with strikingly similar topology (Figures 2.1-2.3) and the majority of genera were recovered as monophyletic with the exception of *Camptocerus s.l.* and *Cnemonyx*. Most differences were observed in the run 1 tree (Figure 2.1) in which *S. oregoni* 5 and 71 were not recovered as monophyletic, the placement of *S. quadrispinosus* was unresolved with regards to Western European or Nearctic taxa and *S.*

orientalis was recovered as sister to *S. ecksteini* rather than unresolved with *S. multistriatus* and *S. ecksteini*. The run-3 tree (Figure 2.3) did not resolve the relationships between *S. cristatus*, and the Central American taxa and the South American taxa.

Ancestral State Reconstruction of Feeding Habit and Host-Use

The Bayesian tree topologies uniformly displayed a loss of wood-boring in the most recent common ancestor (tmrca) of the Scolytini and two separate originations of wood-boring within the Scolytini from phloeophagous ancestors. The character was mapped onto the run-2 topology (Figure 2.4). Xylomycetophagy was the result of one shift in the tmrca of *Camptocerus s.s.* and once in the tmrca of *Camptocerus s.l.*

The tree topologies reported identical patterns of host-plant family usage throughout the tribe. Host-use was largely conserved among closely related taxa but several shifts to different plant families were also observed (Figure 2.5). The tmrca of *Scolytus* most likely fed on Ulmaceae or Fabaceae. All Neotropical *Scolytus* feed upon Fabaceae and the tmrca of the Holarctic species fed on Ulmaceae. Several shifts away from Ulmaceae to families such as Rosaceae, Betulaceae, Ulmaceae, Fagaceae, Juglandaceae and Cannabaceae are observed with no reversals to Ulmaceae. There is also a shift from Pinaceae to Rosaceae. Two separate shifts to Fagaceae, Rosaceae and Pinaceae were also observed. The tmrca of *Loganius* likely fed on Euphorbiaceae, *Ceratolepsis* on Myristicaceae and that of *Camptocerus* and *Cnemonyx* on Burseraceae.

The three Bayesian topologies are congruent for conifer host-use among *Scolytus* (Figure 2.6). Patterns of conifer host-use shows conservatism among closely related taxa. The analysis showed two separate shifts to conifers from angiosperm feeding ancestors, once to *Picea* in the

Palearctic and once to *Abies* in the Nearctic. From *Abies* there was a shift to *Pseudotsuga* and shifts from *Pseudotsuga* to *Larix*, *Picea* and *Tsuga*.

Conservation of Host-Use

The PTP test failed to reject the null hypothesis that host use is uncorrelated with phylogeny ($p=1.0$) for both most common host plant family ($p=1.0$) and for conifer host genus ($P=1.0$). For most common host plant family, the length was 16 steps (CI= 0.75, RI =0.927); however, randomization was able to generate trees with a length of 12 steps, indicating that the pattern of host-use could have been more parsimonious. There were seven steps in the conifer-host genus (CI= 0.714, RI =0.957) and randomization produced trees with a length of five steps.

Estimating Divergence Times

The maximum clade credibility trees for analysis A (Figures 2.7) and analysis B (Figures 2.8) produced a topology similar to that of the single partition dataset, Bayesian analysis 1 (Figure 2.1). Estimates of clade ages were derived from FigTree v1.7.5 (part of the BEAST package) (Table 2.7). Scolytini was found to have a stem age of 113-94 mya, *Scolytus* 59-50 mya, *Camptocerus s.s.* 43-34 mya, and Nearctic conifer-feeding *Scolytus* 20-16 mya.

Discussion

Taxonomic Implications

Camptocerus was recovered as paraphyletic with members of the genus forming two clades, *Camptocerus sensu stricto* (*s.s.*) and *Camptocerus sensu lato* (*s.l.*). *Camptocerus s.s.* was comprised of species from the aeneipennis, latipillis and costatus clades (*sensu* Smith and

Cognato 2010b) and was strongly supported (pp > 95). Each clade was also monophyletic and the relationships among clades was identical to those obtained through parsimony analysis of morphological characters (Smith and Cognato 2010b). *Camptocerus s.l.* was composed of species in the auricomus and opacicollis clades (*sensu* Smith and Cognato 2010b) and several *Cnemonyx* species that superficially resemble *Camptocerus* (pp > 95). The monophyly of these two *Camptocerus* clades previously found by Smith and Cognato (2010b) was not recovered, suggesting that the generic limits between *Camptocerus* and *Cnemonyx* need to be clarified.

Loganius (pp > 95) and *Ceratolepsis* (pp > 95) were both recovered as monophyletic lineages. *Ceratolepsis* has been removed from synonymy with *Cnemonyx* and *Loganius* should be given new status (Smith, Chapter 3). *Cnemonyx* was not recovered as monophyletic and species formed two clades, one that rendered *Camptocerus* paraphyletic and one clade consisting of *C. panamaensis* (Blandford) and *C. setulosus* (Eggers). *Cnemonyx s.s.* were not included in this study however these species are morphologically dissimilar from the *Cnemonyx* included in this study. *Cnemonyx s.s.* all possess crenulations along the elytral base while *Cnemonyx s.l.* do not. *Cnemonyx* has had a very confused taxonomic history (e.g. Schedl 1962; Wood 1972; Smith, Chapter 3), with ambiguous generic limits and is clearly in need of revision. *Ceratolepsis amazonicus* from two localities in Loreto, Peru and Orellana, Ecuador were not recovered as monophyletic. Each specimen was obtained from large series and directly compared to the holotype. No observable morphological differences were observed. It is possible that one of the specimens represents a cryptic species.

Scolytus was recovered as monophyletic and formed two main clades, the first of which was composed of Neotropical species and the second of Holarctic species. In the Neotropical clade, there was a distinct split between the Central American and the South American species,

except in run 2. *Scolytus cristatus* Wood is distributed in both Central and South America (Petrov and Mandelshtam 2010; Wood 1982) and was found at the base of the Central American clade, thus suggesting a colonization of Central America by South American species (Figures 2.1, 2.2). All of the Neotropical species have been collected from Fabaceae (except *S. mozolevskae* Petrov and Mandelshtam 2010 for which the host was reported as an unknown vine). Holarctic *Scolytus* formed several clades that corresponded to species groups initially proposed by von Butovitsch (1929), which had been subsequently modified or dismissed by later authors (e.g. Schedl 1948; Balachowsky 1949; Stark 1952; Michalski 1973). Subsequent authors based their classification systems on the occurrence, shape and placement of spines on the abdominal venter. von Butovitsch's classification system was based on the structure of the aedeagus and proventriculus rather than external characters that often show a large amount of intraspecific variation (e.g. LaBonte 2010; Smith, Chapter 1). von Butovitsch's system divided the genus into two sub genera: *Scolytus* s.s. and *ruguloscolytus*. *Scolytus* s.s. was composed of five species groups: *archaeoscolytus*, *pygmaeoscolytus*, *Scolytus* s.s., *spinuloscolytus* and *tubuloscolytus*. *Ruguloscolytus* was composed of two species groups: *pinetoscolytus* and *ruguloscolytus*. One of von Butovitsch's two subgenera, *ruguloscolytus*, and six species groups were recovered as monophyletic with $pp \geq 90$ (Figure 2.2). Species belonging to the *archaeoscolytus* species group could not be sampled. von Butovitsch's classification system was almost identical to what my analyses recovered in regards to both his placement of species groups and the monophyly of these groups, with two exceptions: *S. quadrispinosus* Say and *S. japonicus* Chapuis, which von Butovitsch tentatively placed in the *tubuloscolytus* and *ruguloscolytus* species groups, respectively, and noted uncertainty regarding this placement. *Scolytus quadrispinosus* was recovered in the *Scolytus* s.s. species group and *S. japonicus* formed

a clade with *S. scheyvyrewi* Semenov. The Nearctic *Scolytus* species were recovered in two clades, the *Scolytus s.s.* and the ruguloscolytus clade, indicating two separate colonizations of North America, once on angiosperm hosts in the Eastern North America from a clade of western European species and once on coniferous hosts in Western North America from East Asian species (Figure 2.2).

Evolution of Host-Plant Use by Insects

The ‘escape and radiate’ coevolutionary model proposed by Erhlich and Raven (1964) states that diversification of plants is tied to the evolution of novel secondary compounds which release plants from herbivore pressure. Corresponding evolution of a trait in herbivores that allows circumvention of these secondary compounds leads to diversification in phytophagous insects. This model implies reciprocal evolution in which episodes of plant radiation alternate with radiation of herbivorous species (Thompson 1994). Several studies have supported the ‘escape and radiate’ model of coevolution but it has often been found to be extremely asymmetrical. Escape from herbivores through the evolution of novel secondary compounds generally has little impact on plant diversification but instead creates a new adaptive zone that allows bursts of herbivore diversification (Farrell and Mitter 1993; Farrell 1998; Fordyce 2010). Most research addressing this model has focused on insects that feed on living leaf tissues or within seeds rather than on insects that consume phloem and xylem of dead and dying host-plants, such as scolytines (Jordal et al. 2004).

The alternative model is the sequential evolution model proposed by Jermy (1984) which states that coevolutionary interactions between phytophagous insects and plants are asymmetric. Phytophagous insects can apply diversifying selection on plant defensive traits but have an

insignificant effect on the evolution of the host. However, diversification of host plants can lead to increased resource heterogeneity, particularly among the diversity of biochemical and structural traits. This diversifies plant selection pressures and increases the possibility of evolutionary radiation among insects, especially those that consume phloem and xylem tissues of dead and dying host-plants (Jermy 1984; Nyman 2010). The extensive radiation of angiosperms into lineages with very different secondary compounds provided the substrate necessary for radiations of herbivorous insects. Several studies have found that insect-plant associations are predominately the result of continuous host-plant shifts among pre-existing host plant taxa (Morse and Farrell 2005; Janz and Nylin 2008; Kato et al. 2010; Nyman 2010; Nyman et al. 2010; Kergoat et al. 2011; Bennett and O'Grady 2012; Leppänen et al. 2012). The sequential evolution model is also supported based on data from recent investigations that showed the diversification of most insect groups followed their host taxa (Gómez-Zurita et al. 2007; McKenna et al. 2009; Nyman 2010).

Thompson (1994) identified several characteristics for host specialization in phytophagous insects that complete their life on a single host individual: 1, the host species should be readily available throughout the year; 2, the host should be predictably available over time; 3, the insect should have the genetic ability to circumvent host defenses and be able to digest the host with specialized foraging techniques, morphology or physiology; 4, hosts should be sessile in nature and relatively easy to locate the host. Bark beetles meet these criteria and are predisposed to host specialization for the following reasons: 1. the occurrences of tree species are predictable through space and time because bark beetle species occur in abundant and common host taxa and thus an individual of a common host tree is more likely to be dead or dying at any point of time compared to rare host taxa; 2, they complete their development in a single host tree

and, then mate and reproduce on another host tree; 3, the beetles have the ability to circumvent host defenses; 4, Scolytini utilize host-tree volatiles to locate suitable material for colonization (Macías-Sámano et al. 1998).

Host-use is also driven by relative host abundance along with host characteristics including secondary compounds and anatomical defensive features such as resin canals (Browne 1961; Atkinson and Equihua-Martinez 1986a). Bark beetles are commonly found in hosts possessing resins or latex (Browne 1961; Wood 1982; Equihua-Martinez et al. 1984; Atkinson and Equihua-Martinez 1986a,b) and these types of trees are reportedly very common in Neotropical and Holarctic forests (Boom 1986; Prance et al. 1976; Mori and Boom 1987; Taggart and Cross 2009). Phloem-feeders consume living or moribund host tissues and are exposed to latex and resins. In dead and moribund trees, however, secondary compounds are degraded over time and phloem-feeders are exposed to less toxic compounds (Jordal et al. 2004). Hence, the beetles have capitalized on the volatility of these compounds and use them as cues to locate suitable trees, while avoiding the brunt of toxicity. This behavior has likely contributed to the maintenance of host specificity among the Scolytini (Atkinson and Equihua-Martinez 1986a) given that closely related bark beetles typically show a preference for only congeneric tree species (Browne 1961; Deyrup and Atkinson 1987; Noguera-Martinez and Atkinson 1990). These tree genera are generally found in very common host families with large geographic ranges (Wood 1982; Stevens 1986). Widespread tree species tend to be more locally abundant and have more herbivores than rare and isolated species (Lawton and Strong 1981; Lawton 1993; Kelly and Southwood 1999; Lewinsohn et al. 2005). A host can be considered an island in an archipelago of resource space, where abundant hosts represent larger islands on which species are less likely to become extinct (Nyman 2010). Such hosts are a predictable food resource for

bark beetles because it is likely that within a local area, individuals of these trees may be killed or damaged. Thus, it appears that bark beetles meet the criteria for becoming specialized to feed on a single genus or family of tree.

Numerous phylogenetic studies have shown that insect host-use evolution is conservative with respect to host taxon (Farrell and Mitter 1990, 1993; Becerra 1997; Janz and Nylin 1998; Kelly and Farrell 1998; Farrell et al. 2001; Jordal et al. 2004; Ødegaard et al. 2005; Winkler and Mitter 2008; Fordyce 2010; Leppänen et al. 2012). Frequently host shifts within an insect genus involve host plants that are already colonized by congeneric species, suggesting a constraint to host range expansion and behavioral or physiological preadaptations to colonize such taxa (Futuyma et al. 1993, 1994, 1995; Janz et al. 2001; Nosil 2002; Morse and Farrell 2005; Weingartner et al. 2006; Nyman et al. 2006). Shifts occur more often among closely related plants (Nyman 2010) and rarely among more distantly related taxa such as angiosperms and conifers (Nyman 2010) or monocots and dicots (Ødegaard et al. 2005).

Browne (1961) postulated that specialist bark beetles are derived from generalists. This hypothesis was supported in the phloem-feeding genus *Dendroctonus* Erichson (Kelley and Farrell 1998) but was disputed in an investigation of the genus *Coccotrypes* Eichhoff (Jordal et al. 2002). Unlike diplodiploid *Dendroctonus*, *Coccotrypes* is haplodiploid and exhibits feeding habits that encompass fruits and seeds, leafstalks, phloem and pith. Within *Coccotrypes*, it was found that generalists are derived from specialists (Jordal and Hewitt 2004). This lends support to the idea that specialization does not always evolve from generalized feeding habits but that all types of phylogenetic scenarios involving specialist and generalist species can occur and that specialization is not a dead end but a dynamic process (Thompson 1994; Nosil 2002). The degree of host specificity is directly related to feeding habit, with ambrosia beetles exhibiting low host

specificity and phloem-feeders high host specificity (Beaver 1979). Specialization is normally at the family level, uncommon at the genus and rare at the species level (Browne 1961). Species of Nearctic *Scolytus* are restricted to feeding on hosts in a single genus of Pinaceae. *Scolytus* are rarely collected from other non-host genera, but these events could be attributed to host misidentification, forced alternative host (Kelly and Farrell 1998) or potentially local adaptation (Slove and Janz 2011).

The oscillation hypothesis of host-plant range and speciation proposed by Janz and Nylin (2008) posits that specialist species undergo a host range expansion, and become oligophagous or polyphagous. This increase in host range causes a geographical range expansion as two hosts rarely occupy exactly the same spatial distribution. These oscillations in host specificity and range provide the foundation for speciation. As the polyphagous species spread across the host plants' geographic ranges, the subpopulations emerge with more restricted geographic distributions and potentially host distributions as they undergo local adaptation. Adaptations not only include climate, but habitat availability, host abundance, resource competitors and predators (Janz and Nylin 2008; Slove and Janz 2011). These oscillations are maintained by the inheritance of the ability to use ancestral hosts and allows for recurrence of this ability throughout the phylogeny. The accumulation of hosts during periods of increased resource use drives diversification and explains why species rich lineages frequently show shifts among host plants, as observed within *Scolytus* species with regard to Ulmaceae, Betulaceae, Fagaceae and Pinaceae (Janz and Nylin 2006, 2008; Janz 2011).

The oscillation hypothesis also helps to explain why various studies have reached a multitude of conclusions regarding the derivation of specialization from generalization and vice-versa. It also explains why species with large geographic ranges tend to be polyphagous

(Päivinen et al. 2005; Slove and Janz 2011). Indeed this pattern of broad geographic ranges and diet diversity is exhibited in several Palearctic *Scolytus* species (Table 2.6) who occupy ranges that span large areas of Eurasia including *S. ratzeburgii*, *S. rugulosus*, *S. multistriatus*, *S. schevyrewi*, *S. carpini*, *S. intricatus* and *S. scolytus* (Wood and Bright 1992; Pfeffer 1994). *Scolytus cristatus* occurs in Central and South America and is distributed from Jalisco, Mexico to Peru and southern Brazil.

Scolytus exhibits two large host shifts from angiosperms to conifers and from conifers to angiosperms (Figure 2.5). These large shifts can be explained by the oscillation hypothesis as well. *Polygraphus grandiclava* (Thompson) is a Palearctic scolytine species that has populations that occur only on pine (*Pinus*), only on cherry (*Prunus*) and on both pine and cherry in Central Europe. The sister species is not known but all other Holarctic *Polygraphus* utilize conifer hosts (Wood 1982; Yin et al. 1984; Pfeffer 1994). An investigation into the phylogenetic history of the *P. grandiclava* showed that the genetic diversity within the species was not the result of host-use, but of geography (Avtzis et al. 2008). This suggests that in the past, the species went through a host-range expansion and subsequently a geographic range expansion that led to local adaptation and may eventually lead to speciation (Janz and Nylin 2008; Nylin and Janz 2009). *Polygraphus grandiclava* also serves as a model as to how such a shift occurred in *Scolytus rugulosus*. *Scolytus rugulosus* also utilizes *Prunus* hosts (Michalski 1973; Wood and Bright 1992; Smith, Chapter 1) and was likely derived from a Pinaceae feeding ancestor.

Correlation with Host-Use Oscillation Hypothesis

The host-use oscillation hypothesis cannot be tested on the Scolytini at this time. Because the hypothesis is based on the placement of specialist and generalist species in the phylogeny, the

hypothesis is dependent on sampling. False conclusions are possible if clades are not adequately sampled. Research examining the patterns of host-use among Nymphalid butterflies (Nylín and Wahlberg 2008) and Nematine sawflies (Leppänen et al. 2012), have supported this hypothesis and these groups have well-known phylogenies and host associations.

Conservation of Host-Use

The null hypothesis of random host-use among Scolytini and conifer-feeding *Scolytus* species was not rejected, but this does not imply that the patterns observed among the Scolytini was truly the result of random processes. Rather, the data do not reveal cladistic structure. A better interpretation of this result is that several independent host shifts to families have occurred throughout their history (Faith and Cranston 1991). The lack of conservatism of plant-use within the Scolytini rejects the predictions of Erhlich and Raven (1964) in that radiations of plant taxa are not responsible for the diversification of the tribe. This also suggests that shifts between existing host plant families are the primary drivers of diversity within the Scolytini, thus supporting the host use oscillation hypothesis. Frequent host shifts may have occurred because the Scolytini utilize dead and degraded hosts. Beetles experience fewer dietary constraints due to degraded secondary compounds and thus increased likelihood for host shifts (Jordal et al. 2004).

Ancestral State Reconstruction of Feeding Habit and Host-Use

The Bayesian tree topologies were congruent in the patterns of ancestral host-feeding among all Scolytini genera (Figure 2.5). The ancestral host for Holarctic *Scolytus* species was Ulmaceae and several shifts away from Ulmaceae are present in each of the *Scolytus s.s.* species

groups. *Spinuloscolytus* was found at the base of the Holarctic *Scolytus* clade and contains species that exclusively occur on Ulmaceae. The clade of *S. japonicus* with *S. schevyrewi* and *pygmaeoscolytus* also primarily occur on Ulmaceae. The *pygmaeoscolytus* and *tubuloscolytus* clades were recovered as sister. The *tubuloscolytus* clade exhibits two host-shifts away from Ulmaceae (Rosales) once to *Carpinus* (Betulaceae) and once to *Quercus* (Fagaceae), both in the Fagales. The *Scolytus s.s.* species group primarily occur on Ulmaceae. Within this group, there have been with two shifts to the Fagales, including once to Betulaceae, and once to Juglandaceae and subsequently Fagaceae. In addition, there were two shifts to other Rosales, including Cannabaceae and Rosaceae, once from Ulmaceae to Rosaceae and once from Fagaceae/Juglandaceae to Cannabaceae.

The *ruguloscolytus* subgenus *sensu* Butovitsch was also recovered as monophyletic and includes two separate shifts to conifers, once in the Palearctic and once in the Nearctic. The tmrca of the *ruguloscolytus* clade was likely a conifer-feeder and there was a subsequent shift to Rosaceae in the tmrca of *S. rugulosus* and its sister taxa, *S. amygdali* (not sampled). The Nearctic conifer-feeders show distinct patterns in their host-use with basal clades found on *Abies* and subsequent shifts to *Pseudotsuga* and from *Pseudotsuga* to *Larix* and *Tsuga* (Figure 2.6).

It is interesting to note that *Scolytus* colonize most Pinaceae genera but do not colonize *Pinus* species. This may reflect both interspecific competition for pine, as well as differential tolerance to host resins. A multitude of genera including *Dendroctonus* Erichson, *Ips* DeGeer, *Hylastes* Erichson, *Hylurgops* LeConte, *Orthotomicus* Ferrari, *Pityogenes* Bedel, *Pityophthorus* Eichhoff, and *Pseudohylesinus* Swaine are feed on pine tissue, from root to twig. In contrast, genera colonized by Nearctic *Scolytus* are utilized by relatively few bark beetle species compared to *Pinus* spp. (Wood and Bright 1992; Pfeffer 1994). *Scolytus* tend to colonize taxa

that host only a few other bark beetle species (Wood and Bright 1992; Pfeffer 1994), many of which previously colonized pines in North America prior to the arrival of the conifer-feeding *Scolytus*. Studies have also suggested that *Scolytus* are relatively intolerant of host resins. To colonize pine, *Scolytus* species must be able to tolerate high levels of preformed monoterpenes present in resin canals in bark and foliage. *Scolytus* species exposed to monoterpene resins, however, have higher mortality rates compared to species that occur on *Pinus* (Raffa and Berryman 1987).

Surprisingly the two mk-1 ancestral state reconstructions resulted in different conclusions regarding the origination of conifer hosts among *Scolytus*. Mapping the most common host family onto the topology resulted in a scenario in which there was a single shift to conifers (Figure 2.5) and mapping conifer host genus onto the phylogeny resulted in a scenario in which there were two separate colonizations of conifers, once to *Picea* and once to *Abies* (Figure 2.6). Host shifts from angiosperms to conifers are relatively rare and are reportedly very difficult from an evolutionary standpoint (Nyman 2010). It seems likely that because of the way that characters were scored in the conifer-host genus ancestral state reconstruction, information was lost by lumping all angiosperm-feeding taxa under a single character state. Because all previous taxa were coded the same, the mk-1 model found two-shifts to be more probable than a single event because of a lack of information. The most common host family ancestral state reconstruction (Figure 2.5) should be considered a more reliable inference because of the greater information found in more character states, which increases the amount of detailed information in the phylogeny.

The tmrca of the clade of non-*Scolytus* genera likely fed on Euphorbiaceae, as the basal genus, *Loganius*, is only reported to feed on Euphorbiaceae. The tmrca of *Ceratolepsis* was

likely Myristicaceae. Host records are available for most species of *Ceratolepsis* and all have been from *Virola* (Myristicaceae). Unfortunately, the host record for *C. amazonicus* has not been reported. If other species had been included in the analysis, the likelihood of a Myristicaceae specific tmrca would be greater. The tmrca of *Cnemonyx* and *Camptocerus* shifted from Myristicaceae to Burseraceae as both genera show a strong pattern of using Burseraceae hosts. However, *Cnemonyx s.l.* have a more diverse host range including Burseraceae in the taxa that most strongly resemble *Camptocerus*, and others that occur on both Burseraceae and Meliaceae or Myrtaceae and one species that occurs on Clusiaceae, *C. vismiacovens* Wood. There is a paucity of host records for *Cnemonyx s.s.* but specimens of the type species, *C. galeritus* Eichhoff, have been collected from Euphorbiaceae. The phylogenetic placement of *Cnemonyx s.s.* is unknown. *Scolytopsis* was not included in this analysis and host records indicate that species occur on Combretaceae (Myrtales) hosts.

Estimating Divergence Times

My fossil calibrations produced clade ages that were consistent with the results of Jordal and Cognato (2012), the only other BEAST phylogeny for scolytines that included ages for the Scolytini (Jordal and Cognato 2012). Jordal and Cognato (2012) used BEAST to determine when ambrosia feeding habits evolved within the subfamily using a broad taxon sample representing half the scolytine genera and more than 200 species. Jordal and Cognato estimated the clade age of *Camptocerus* to be between 40-33 mya. My analysis estimated the age of this group to be 43-34 mya.

Scolytini lineage diversification occurred after that of the host plant family with three exceptions: *Camptocerus s.s.*, *Camptocerus s.l.* and *Ceratolepsis*. *Camptocerus s.s.* (43-34 mya)

and *Camptocerus s.l.* (39-30 mya) have divergence times that correspond to that of the host genus, *Protium*, at 40 mya (Becerra et al. 2012). *Ceratolepsis* (26-21 mya) may have diversified with its host family, Myristacaceae, which is 21-15 my old (Magallón and Castillo 2009). The similar divergence times of bark and ambrosia beetles and their hosts is characteristic of lineage tracking. Divergence estimates for all other Scolytini lineages occurred millions of years after the host family. All *Loganius* which diverged 32-26 mya use Euphorbiaceae hosts which have been dated to 102 mya (van Ee et al. 2008). Neotropical *Scolytus* diverged 22-21 mya. All Neotropical *Scolytus* are specific to Fabaceae, and diverged 22-21 mya. The Fabales, the plant order that contains Fabaceae has been estimated to originate 101.1 mya (Magallón and Castillo 2009) and Fabaceae 79-74 mya (Wikström et al. 2001). Holarctic *Scolytus* diverged 38-32 mya and primarily utilize Fagaceae (90 mya), Betulaceae (88-83 mya), Juglandaceae (98-83 mya), Ulmaceae (at least 50 mya), and Rosaceae (at least 55 mya) (Crepet et al. 2004; Wang et al. 2010; Li et al. 2011). Conifer-feeding Nearctic *Scolytus* diverged 20-16 mya. This clade colonizes several lineages that are specialized to Pinaceae genera, including *Abies* (106-55 mya and 73 mya in the Nearctic), *Larix* (87-70 mya), *Pseudotsuga* (87-70 mya), *Picea* (142 mya), and *Tsuga* (78-38 mya) (Gernandt et al. 2008; Aguirre-Planter et al. 2012). The above divergence times for the Scolytini derived from the BEAST analyses indicate that most Scolytini diverged after their hosts, lending support to the sequential evolution and more specifically, the host-use oscillation hypotheses.

Conclusions

This investigation represents the first molecular phylogeny of the Scolytini and results support a monophyletic Scolytini, *Ceratolepsis*, *Loganius*, and *Scolytus* and paraphyletic

Camptocerus and *Cnemonyx*. The currently recognized Holarctic *Scolytus* species groups were found to be artificial and based on convenience of diagnosis rather than shared ancestry. Holarctic *Scolytus* formed several clades that correspond to species groups proposed by von Butovitsch (1929). These species should be revised in the context of von Butovitsch's character system to provide a reliable classification system. The generic limits of *Cnemonyx* and *Camptocerus* require additional examination and taxonomic changes should be made to create monophyletic lineages.

Scolytini diversity is the result of a combination of processes including host-shifts and independent shifts to the same hosts, lineage tracking, and diversification on widespread and common hosts, with shifts that occurred well after the diversification of the host family. Changes in feeding habit, from phloem to fungus-feeding were also important in the diversification of *Camptocerus s.s* and *s.l.*, with two independent shifts to fungus-feeding. In addition, the pattern of host-use among the Scolytini was not conservative to plant taxa. Overall, the observed patterns of Scolytini host-use can be explained by a combination of the sequential evolution and host-use oscillation hypotheses as well as lineage tracking, a pattern that has been found for other insects that colonize living host plants (Morse and Farrell 2005; Gómez-Zurita et al. 2007; Janz and Nylin 2008; McKenna et al. 2009; Nyman 2010; Kato et al. 2010; Nyman 2010; Kergoat et al. 2011; Bennett and O'Grady 2012; Leppänen et al. 2012). This suggests that these same processes drive host-use among taxa that colonize dead and dying hosts.

Future Directions

In the coming months, I plan to reanalyze the dataset in both MrBayes and BEAST using sequences from additional Scolytini taxa. Additional taxa include several *Cnemonyx s.l.*, *Scolytus*

carpini from Sweden and most importantly, *Scolytopsis*. In May, I will also participate in a collecting expedition to the Brazilian Atlantic forest where I could potentially acquire additional Neotropical taxa. These additional taxa will potentially help resolve the phylogeny and elucidate the taxonomic confusion among *Camptocerus s.l.* and *Cnemonyx s.l.* In July, I will travel to the University of Bergen, Norway where my colleague Dr. Bjarte Jordal will provide instruction on BEAST and how to confidently set fossil priors to minimize error and obtain a more reliable estimate for clade ages. While I incorporated a large degree of uncertainty in my fossil calibrations here, the calibrations will likely become more exact when I fine-tune the priors.

CHAPTER 3

PROGRESS TOWARD A REVISION OF THE SCOLYTINI I (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE)

Abstract

The Neotropical bark beetle genera *Cnemonyx* Eichhoff 1868 and *Scolytus* Geoffroy 1762 were reviewed as part of ongoing research into the higher-level taxonomy of the Scolytini. *Ceratolepsis* Chapuis 1869 was **removed from synonymy** with *Cnemonyx* and seven **new combinations** are reported: *Ceratolepsis amazonicus* Eggers 1929, *C. boliviae* (Blackman) 1943, *C. hylurgoides* (Schedl) 1948, *C. insignis* (Wood) 1969, *C. jucundus* Chapuis 1869, *C. maculicornis* Blandford 1896 and *C. niger* (Eggers) 1929. One **new species** was described: *Scolytus rabagliatus*. *Cnemonyx setulosus* (Eggers) 1929 was **removed from synonymy** with *C. panamensis* (Blandford) 1896. Four **new synonyms** were discovered: *Ceratolepsis* Chapuis (= *Coptosomus* Schedl 1952), *Cnemonyx setulosus* (Eggers) 1929 (= *Cnemonyx similis* (Eggers) 1929), *Scolytus proximus* Chapuis 1869 (= *Scolytus brevicauda* Wichmann 1915) and *Scolytus thoracicus* Chapuis 1869 (= *Scolytus plaumanni* Wood 2007). One **new distribution record** was reported: *Scolytus multistriatus* in South America (Brazil).

Introduction

The Scolytini includes ambrosia and phloem-feeding Scolytinae among its five genera and approximately 221 recognized species, of which 136 occur in the Neotropical and 85 in the Holarctic regions. Most species, 133, belong to *Scolytus* Geoffroy, which contains species distributed in the Holarctic and Neotropical regions. The remaining four genera strictly occur in the Neotropics.

Wood (2007) reviewed the South American fauna in his monumental monograph, which was intended to serve as a starting point for future investigations. However, this monograph is problematic. Several species were described that were morphologically identical to previously described species and several questionable synonyms were created (e.g., Mandelsham 2009, Smith and Cognato 2010b). This publication is the second step toward a revision of the Neotropical Scolytini and aims to clarify the genera *Ceratolepsis*, *Cnemonyx* and *Scolytus*. The genus *Camptocerus* has recently been revised (Smith and Cognato 2010b).

To revise the Nearctic *Scolytus* and assemble a robust taxon sample for a phylogenetic analysis of the Scolytini (Smith, Chapters 1 and 2), I individually examined approximately ~10,000 specimens representing almost the entire diversity of the tribe except for some Palearctic taxa. These specimens were identified by direct comparison to the holotype, lectotype or paratypes.

Taxonomic History of the Scolytini

Before the last tribal revision (Wood 1972), the Scolytini consisted of two clearly defined genera (*Scolytus* Geoffroy 1762 and *Scolytopsis* Blandford 1896) and six morphologically similar genera (*Camptocerus* Dejean 1821, *Ceratolepsis* Chapuis 1869, *Cnemonyx* Eichhoff

1868, *Coptosomus* Schedl 1952 and *Loganius* Chapuis 1869). *Minulus* Eggers 1912 had previously been placed in synonymy with *Cnemonyx galeritus* Eichhoff 1868 (Eggers 1923), the type species of *Cnemonyx*. *Camptocerus*, *Ceratolepsis*, and *Coptosomus* possess meso- and metathoracic tibiae that are identical to the prothoracic tibiae, in which the apical margin is straight, sharp, and smooth on anterior edge to the base of the outer apical spine. In *Cnemonyx* and *Loganius*, the surface of the tibial anterior edge from the apical margin to the base of the outer apical spine bears one or more denticles. Species with these denticles also have two to three sutures on the antennal club marked with setae. Species without denticles lack externally marked sutures, but at least part of suture 1 is marked internally by a septum. Schedl (1962) noted the characters used to distinguish these genera were inconsistent and formed a spectrum of morphological variation and placed *Ceratolepsis* in synonymy with *Camptocerus*. However, Wood (1972) determined the genus *Camptocerus* was a distinct group without any synonymies. In addition, Wood found that the characters used to identify *Ceratolepsis* (scales on antennal club), *Cnemonyx* (crenulations of elytral base), and *Coptosomus* (oddly placed antennal suture) were insufficient to clearly define species groups and transferred them to the oldest described genus, *Cnemonyx*. *Loganius* species were split between *Cnemonyx* and *Camptocerus*. Currently there is a broad spectrum of morphological variation within *Cnemonyx* that can be partitioned into discrete groups. Recent phylogenetic analyses have shown that *Ceratolepsis* is a monophyletic and morphologically distinct lineage (Smith and Cognato 2010b; Smith, Chapter 2). Further investigation is necessary to determine whether *Loganius* and *Minulus* represent monophyletic lineages.

Materials and Methods

The following entomological collection abbreviations are referenced in the text. Names of the curators that prepared loans are listed in parentheses.

CNCI	Canadian National Collection of Insects (Hume Douglas, Patrice Bouchard)
DEBC	Donald E. Bright, Jr. Collection, Fort Collins, Colorado (Donald E. Bright, Jr.), to be housed at the CNCI
MSUC	Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan (Gary Parsons)
RJRC	Robert J. Rabaglia collection, Annapolis, Maryland, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC (Natalia Vandenberg)

Specimens were examined using either a Leica (Wetzlar, Germany) MZ125 or MZ16 compound microscope and illuminated with a SCHOTT (Mainz, Germany) 150W halogen light source (model ACE®1). Images were taken with a Visionary Digital Passport II system (Palmyra, VA) using a Canon EOS 5D Mark II, 58mm Canon Macro photo lens, Canon Speedlite transmitter ST-E2, two Canon Speedlite 4303X II flashes and a Stack Shot (Cognisys, Inc, Kingsley, MI). Montage images were assembled using Helicon Focus Mac Pro 4.2.8 (Helicon Soft, Kharkov, Ukraine). Measurements were made using an ocular micrometer on the same microscope and with the same light source as above and calibrated with ROK (Shenzhen, China) 150mm digital calipers (model DC-122A) following the protocol of Smith and Cognato (2010b). Measurements were taken from the specimen's dorsal surface. Length was measured

from the pronotum apex to the elytral apex. Width was measured at the widest part of the pronotum. Proportions are given as the ratio of length to width. A maximum of 20 specimens were measured for each species and were selected to encompass the known distribution.

Results and Discussion

Ceratolepsis Chapuis 1869 **status restored**

= *Coptosomus* Schedl 1952 **new synonymy**

Chapuis 1869: 52. Type species, *Ceratolepsis jucundus* Chapuis 1869 by monotypy.

(Figures 3.1-3.2)

Diagnosis. *Ceratolepsis* is readily distinguished from the other Scolytini genera by unique features of the antennal club which include: strong asymmetry, a covering of short palmate setae and a partial septum. The sutures are never marked by rows of setae. The funicle also lacks a setal tuft on each funicular segment and bears two to four setae on the ventral and dorsal margins (Figure 3.1 A).

Ceratolepsis is further distinguished from *Scolytus* and *Scolytopsis* by the scutellum, which is flush with the elytra, the unimpressed scutellar area of elytral interstriae 1 (Figure 3.2B), the gradually ascending profile of the abdominal venter, and the costal margin of the elytra above the metepisternum unarmed by a carina (Figure 3.2 A).

Ceratolepsis is closely related to *Cnemonyx* and *Camptocerus* and is distinguished by the lack of supplemental denticles on the apical margin of the meso- and metathoracic tibiae (Figure 3.1 B), the strongly bilobed tarsal segment 3, the lack of a carina on the base of the tenth interstria (Smith and Cognato 2010b; Figure 3.2 A), absence of crenulations along the elytral

base (Figure 3.2A), mesosternum shape (type G, Smith and Cognato 2010b; Figure 3.1 C) and the elongated and distally narrowly rounded scape in both sexes (Figure 3.1 A).

Redescription. Head never sexually dimorphic. Epistoma never emarginated, often armed with a carina. Frons concave from epistoma to the inner apices of the eyes, moderately covered with long erect setae. Eye elongate, ovoid, entire and finely faceted. Antennal scape elongate and narrowly rounded distally, funicle shorter than or equal in length to the scape. Each scape segment bears 2-4 setae on the ventral and dorsal margins. Antennal club flattened, strongly asymmetrical, covered in short palmate setae, with a short partial septum that is not marked externally by rows of setae.

Pronotum large, head visible from above, lateral margins marked by a fine raised line. Pronotal disc finely punctate, punctures larger, coarser toward the margins, surface appearing smooth to strigate; median line impunctate. Pronotal base bisinuate. Meso- and metathoracic tibia unarmed by supplemental denticles on apical margin.

Scutellum smooth, flush with the level of elytra. Elytra without a scutellar notch; striate. Discal striae weakly impressed. Declivital striae moderately to strongly impressed, interstriae often carinate. Elytral apex weakly serrate. Abdominal profile gradually ascending to meet the elytra. Mesosternum shape type G (Smith and Cognato 2010b)

Distribution. *Ceratolepsis* is restricted to the Neotropical region from Costa Rica to Bolivia.

Biology. *Ceratolepsis* species have only been reported as occurring on *Virola* Aubl. species (Myristicaceae) (Wood 2007, Smith pers. obs.).

Comments. Chapuis' Latin description of the genus was somewhat vague, "antennarum articuli 2-7 in faemina simplices, clava solida. Tarsorum articulus 1 duobus sequentibus, 3 bilobatus" which translates as "antennal articles 2-7 in the female simple, club solid. Tarsal joint 1

following 2, 3 bilobed” (S.M. Smith translated). The description of the club could be applicable to *Camptocerus* species and the tarsal description is characteristic of the Scolytini. However, the type species, *C. jucundus*, is morphologically distinct from *Camptocerus* and *Cnemonyx*.

The holotype of the type species of *Coptosomus*, *C. hylurgoides* Schedl, has been lost except for a slide mount of an antenna (Wood 2007). *Coptosomus* is placed in synonymy with *Ceratolepsis* because of the lack of supplemental denticles on the meso- and metathoracic tibiae and by the characteristics of the antennal club.

Very little sexual dimorphism in external characters is exhibited in this genus. Examination of the shape of abdominal tergites 7 and 8 or dissection is required to determine the sex of specimens.

Included Species

Ceratolepsis amazonicus (Eggers) **new combination**

- = *Loganius amazonicus* Eggers 1929: 60.
- = *Cnemonyx amazonicus* (Eggers 1929). Schedl 1962: 486.
- = *Ceratolepsis amazonicus* Schedl 1952: 349. Schedl 1962: 486.

Ceratolepsis boliviae (Blackman) **new combination**

- = *Camptocerus boliviae* Blackman 1943: 378.
- = *Cnemonyx boliviae* (Blackman). Wood 1972: 244.

Ceratolepsis hylurgoides (Schedl) **new combination**

- = *Coptodryas hylurgoides* Schedl 1948: 262
- = *Coptosomus hylurgoides* (Schedl 1948). Schedl 1952: 363.
- = *Cnemonyx hylurgoides* (Schedl 1948). Wood 1972: 244.

Ceratolepsis insignis (Wood) **new combination**

= *Cnemonyx insignis* Wood 1969: 9.

Ceratolepsis jucundus Chapuis **status restored**

= *Ceratolepsis jucundus* Chapuis 1869: 52.

= *Cnemonyx jucundus* (Chapuis 1869). Schedl 1962: 486.

Ceratolepsis maculicornis Blandford **status restored**

= *Ceratolepsis maculicornis* Blandford 1896: 127.

= *Loganius maculicornis* (Blandford 1896). Schedl 1962: 486.

= *Cnemonyx maculicornis* (Blandford 1896). Wood 1972: 244.

Ceratolepsis niger (Eggers) **new combination**

= *Loganius niger* Eggers 1929: 60.

= *Cnemonyx niger* (Schedl 1962: 485). Wood 1972: 244.

= *Camptocerus nigricans* Schedl 1962: 486 (see Wood and Bright 1992 for a complete discussion).

Cnemonyx Eichhoff 1868

Taxonomic Changes

Cnemonyx setulosus (Eggers) 1929 **removed from synonymy**

= *Cnemonyx similis* (Eggers) 1929 **new synonymy**

Wood (2007) considered *Cnemonyx setulosus* to be a synonym of *C. panamensis* (Blandford) 1896, which are closely related (Smith, Chapter 2) and superficially resemble each other, but they are morphologically distinct. In *C. setulosus*, the male epistoma is weakly excavated and is typically weakly carinate along the basal epistomal margin, the frons is moderately excavated from the epistoma to the anterodorsal margin of the eyes and almost

borders the ocular margin. In *C. panamensis*, the epistoma and frons are flattened and there is a short median weakly elevated carina along the basal epistomal margin. In *C. setulosus*, the dorsal half of the frons is covered by two thick bands of long, yellow setae, those clearly divided between the median line while in *C. panamensis* the dorsal half of the frons is covered by long, yellow setae which are contiguous across the median line. In addition, the declivital interstriae of *C. setulosus* each bear 3-5 rows of pale, yellow setae while those of *C. panamensis* only bear 1-3 rows. The pronotum of *C. setulosus* appears rugose with dense, abundant setae on the anterior half and lateral margins and that of *C. panamensis* appears longitudinally strigate with sparse setae on the anterolateral areas.

With the inclusion of *C. similis* and *C. setulosus* as synonyms, Wood created a very broad concept for *C. panamensis* Blandford 1896 that included a great amount of morphological variation (Wood 2007: 191). The distribution range for his concept of *C. panamensis* was quite large, spanning Costa Rica to Bolivia. With *C. setulosus* removed from synonymy, the range of these species is more discrete; *C. panamensis* occurs in Costa Rica and Panama and *C. setulosus* occurs in Bolivia, Peru and Venezuela.

Cnemonyx similis is placed in synonymy with *C. setulosus* because the holotypes of both species are identical except for the development of the carina on the basal margin of the male epistoma. In *C. similis*, the carina is moderately developed and in *C. setulosus* it is weakly developed to absent within a brood. Similar variation in the basal epistoma carina was also demonstrated in *Camptocerus niger* (F.) 1801 and its synonym *C. tectus* Eggers 1943 (Smith and Cognato 2010b). *Cnemonyx similis* and *C. setulosus* were described in the same publication. I have chosen the name *C. setulosus* because the name has page priority and this name best

describes the species, which is abundantly covered in long recumbent setae on the pronotum and the elytral interstriae.

Scolytus Geoffroy 1762

New Distribution Record

Scolytus multistriatus (Marsham) 1802. BRAZIL: *Mato Grosso*: Sinop, X.1975, M. Alvarenga (DEBC-1, male). **New Continent Record.**

Wood (2007) reports this species as occurring in Argentina and Chile, but was never given specimens to examine and confirm the identification. Bright (*in press*) also expressed doubt regarding these records and considered them anecdotal. This specimen is the first positively identified specimen collected from South America.

Taxonomic Changes

Scolytus proximus Chapuis 1869

=*Scolytus brevicauda* Wichmann 1915 **new synonymy**

Scolytus brevicauda had previously been considered a synonym of *S. thoracicus* Chapuis (Schedl 1937: 161). Upon examination of the holotype of *S. brevicauda*, *S. thoracicus* and large series of *S. proximus*, it is apparent that *S. brevicauda* is a synonym of *S. proximus*. In *S. brevicauda* and *S. proximus* the shape of the spine on male sternite 2 is long and narrow and has a hooked apex unlike that of *S. thoracicus* which is long and narrow with the apex blunted and bifurcated appearing as though it is composed of two ‘steps’. The male frons of *S. brevicauda* and *S. proximus* is flattened on the dorsal half and weakly transversely impressed on apical third, and the median line is slightly elevated and bearing a median callous-like tumescence. In

contrast, in *S. thoracicus* the frons is flattened on the dorsal half and strongly, transversely impressed on the lower third, and the median area is laterally subcarinate and bears a strongly dorsoventrally compressed tubercle. The male epistoma is broadly and weakly emarginated in *S. proximus* and narrowly and deeply emarginated in *S. thoracicus*.

Scolytus thoracicus Chapuis 1869

= *Scolytus plaumanni* Wood 2007 **new synonymy**

After examining the holotype of *S. thoracicus*, the female paratype of *S. plaumanni*, as well as large series of *S. thoracicus* from Santa Catarina, Brazil, it is evident that *S. plaumanni* is *S. thoracicus* as the two species are morphologically identical.

Species Description

Scolytus rabagliatus Smith and Cognato, **new species**

(Figures 3.3-3.7)

Type Material. Holotype, female, VENEZUELA: *Táchira*: 42km SE San Cristobal, 700m, 19.V.1974, H. & A. Howden (DEBC). Paratypes: VENEZUELA: Intercepted at Detroit, MI, 30.VI.1983, W. Waisanen, Detroit MI 003178, ex. in dunnage (MSUC-2, RJRC-2, USNM-14).

Diagnosis. *Scolytus rabagliatus* has distinctive morphology: Both sexes are easily distinguished from other Neotropical *Scolytus* by the presence of lateral teeth on the apical margins of sternites 2-4, the absence of a callus or bulla on sternite 5, the convex and reticulate frons that is impressed just above the epistoma, a strongly laterally compressed and falx-shaped median spine on sternite 2 with the base just reaching the apical margin of the segment, by the minutely and obscurely punctured sternites 3-5 and by the dull and shagreened appearance of sternites 3-5.

Description (male). 3.0-3.2 mm long (mean = 3.12 mm; n=4); 2.13-2.46 times as long as wide. Head, pronotum, elytra and abdominal venter dark red-brown; legs and antennae yellow-brown. Pronotum typically darker than the elytra.

Epistoma entire; epistomal process absent; median area above mandibles bearing a dense patch of long yellow hair-like setae. Frons appearing convex when viewed laterally; apical third of frons transversely impressed above epistoma; surface moderately and coarsely longitudinally rugose-reticulate and punctate to just dorsal of inner apices of eyes; reticulations converging at epistoma; punctures small, coarse; surface slightly and uniformly covered by long, fine, yellow erect hair-like setae, setae longer than the midpoint of the eye. Antennal scape short, elongate, less than length of the first four funicular segments; club flattened, oblong, about twice as long as wide, densely setose; sutures not evident.

Pronotum about as long as wide; apical margin broadly rounded, area between the eyes lined with scales; sides distinctly arcuate, strongly constricted near apex; basal half of pronotal surface smooth, shining, punctures on disc fine; apical half weakly strigose, punctures shallow and moderately abundant, larger, coarser and more abundant laterally and on apical constriction; apical and anterolateral margins bearing sparse, erect yellow hair-like setae; base weakly bisinuate.

Elytral bases weakly elevated from interstriae 1-6. Elytral sides sub-parallel on apical half, narrowing to a quadrate and smooth apex; apical margin of elytral apices smooth, shining; apex entire. Disc smooth, shining; interstrial punctures weakly impressed, interstriae more than twice the width of striae, interstrial punctures uniseriate, equal in size to those of striae; striae punctures weakly impressed, punctures bearing sparse, long, semi-erect pale yellow hair-like setae from base to apex. Metepimeron less than half-length of metepisternum.

Apical margin of sternite 1 weakly elevated above the base of sternite 2. Sternite 2 nearly perpendicular to sternite 1; surface smooth, shagreened, finely punctate with small, coarse punctures; face flattened; apical margin armed with a long, latitudinally flattened and wide spine with the base extending from the basal margin to at least $\frac{3}{4}$ the length of the segment, the spine is variable but always long, flattened and apically hooked towards the elytra, resembling a falx or a shark caudal fin; each lateral margin of sternites 2-4 armed with a lateral tooth, lateral teeth are progressively smaller from sternites 2-4. Sternite 5 carinate ridge runs along the apical margin of the segment. Venter covered in moderately abundant, long erect pale yellow setae.

Female. 2.0-3.0 mm long (mean = 2.9 mm; n=15); 2.1-2.5 times as long as wide. Similar to male except, setae more abundant on frons, spine on segment 2 smaller, shorter, narrower and less strongly flattened with its base extending from the apical margin to $\frac{1}{2}$ the length of segment, spine uniformly falx-shaped.

Specimens Examined. 19.

Distribution. Venezuela (Táchira).

Host. Unknown.

Biology. Unknown. This species was intercepted in transit to Detroit, Michigan, United States of America on 30 June 1983.

Etymology. This species name, *rabagliatus* honors Robert Rabaglia's (USDA Forest Service) contribution to the knowledge of adventive bark beetles. We deviate from the accepted Latin ending (-*anus*) to create a more euphonic name. It is a noun in apposition.

Notes. There was a large amount of variation observed in shape of the median spine on male sternite 2. Of the four individuals examined, one had a median longitudinal carina instead of a

spine and the size of the falx-shaped spine was variable but was always larger than those of the female.

Conclusions

An accurate classification is critical to accurate species identification. The taxonomic changes presented in this paper are an important step towards a more accurate classification system for the Scolytini. However, further work is necessary to clarify the generic limits of the tribe, especially within *Cnemonyx*. Results shown in Smith (Chapter 2) provide strong support that *Loganius* is a distinct genus and should be removed from synonymy with *Cnemonyx*.

Loganius was not treated here because of a lack of specimens in my collection at MSU. Upon graduation, I will travel to the USNM where representatives of all *Loganius* species are housed in the S.L. Wood collection. Each species will be examined and taxonomic changes will be made if the taxa display the unique combination of characters that define *Loganius*. Correct taxonomic placement of species provides valuable insight into their biology and behaviors as closely related species often have similar biologies.

APPENDICES

APPENDIX A:
Tables and Figures for Chapter 1

Table 1.1. Host genus for conifer-feeding (Pinaceae) Nearctic *Scolytus* species.

Species	<i>Abies</i>	<i>Larix</i>	<i>Picea</i>	<i>Pseudotsuga</i>	<i>Tsuga</i>
<i>Scolytus aztecus</i>					
<i>Scolytus dentatus</i>					
<i>Scolytus fiskei</i>					
<i>Scolytus hermosus</i>					
<i>Scolytus laricis</i>					
<i>Scolytus monticolae</i>					
<i>Scolytus mundus</i>					
<i>Scolytus obelus</i>					
<i>Scolytus oregoni</i>					
<i>Scolytus piceae</i>					
<i>Scolytus praeceps</i>					
<i>Scolytus reflexus</i>					
<i>Scolytus robustus</i>					
<i>Scolytus silvaticus</i>					
<i>Scolytus subscaber</i>					
<i>Scolytus tsugae</i>					
<i>Scolytus unispinosus</i>					
<i>Scolytus ventralis</i>					

Table 1.2. Hosts plant families for all *Scolytus* species occurring in the Nearctic.

Species	<i>Cannabaceae</i>	<i>Fagaceae</i>	<i>Juglandaceae</i>	<i>Pinaceae</i>	<i>Roseaceae</i>	<i>Ulmaceae</i>
<i>Scolytus aztecus</i>						
<i>Scolytus dentatus</i>						
<i>Scolytus fagi</i>						
<i>Scolytus fiskei</i>						
<i>Scolytus hermosus</i>						
<i>Scolytus laricis</i>						
<i>Scolytus mali</i>						
<i>Scolytus monticolae</i>						
<i>Scolytus multistriatus</i>						
<i>Scolytus mundus</i>						
<i>Scolytus muticus</i>						
<i>Scolytus obelus</i>						
<i>Scolytus oregoni</i>						
<i>Scolytus piceae</i>						
<i>Scolytus praeceps</i>						
<i>Scolytus quadrispinosus</i>						
<i>Scolytus reflexus</i>						
<i>Scolytus robustus</i>						
<i>Scolytus rugulosus</i>						
<i>Scolytus schevyrewi</i>						
<i>Scolytus silvaticus</i>						
<i>Scolytus subscaber</i>						
<i>Scolytus tsugae</i>						
<i>Scolytus unispinosus</i>						
<i>Scolytus ventralis</i>						

Table 1.3. Morphological character matrix of 43 characters for 37 species. Characters and states are described in Materials and Methods.

Species	Characters																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Scolytus abietis</i>	0	0	0	1	2	1	1	2	1	1	1	1	1	0	0	2	1	0	1	1	0	2	1	0
<i>Scolytus aztecus</i>	2	1	1	1	2	1	1	2	1	0	0	1	1	2	1	2	1	2	1	2	1	2	1	2
<i>Scolytus dentatus</i>	1	1	1	1	2	1	1	2	1	1	1	1	0	0	0	2	1	1	1	0	0	2	1	0
<i>Scolytus fagi</i>	0	0	1	1	2	2	1	2	1	0	1	1	1	1	0	2	1	2	0	0	0	1	0	0
<i>Scolytus fiskei</i>	0	1	1	1	2	1	1	2	1	1	1	0	1	1	0	1	1	1	1	2	0	1	0	1
<i>Scolytus hermosus</i>	0	0	0	1	2	1	1	2	1	0	1	1	1	0	0	2	1	1	1	2	0	2	1	1
<i>Scolytus laricis</i>	0	0	1	1	2	0	1	2	1	1	1	0	1	1	0	1	1	1	1	2	0	2	0	1
<i>Scolytus mali</i>	0	0	0	3	1	1	0	2	1	0	1	2	1	0	1	2	1	1	0	1	0	1	0	1
<i>Scolytus monticolae</i>	0	0	1	1	2	1	1	2	1	1	1	0	0	0	0	1	1	0	1	2	0	2	0	1
<i>Scolytus multistriatus</i>	0	0	1	1	2	0	1	2	0	0	1	2	1	1	1	2	1	1	1	0	0	1	1	1
<i>Scolytus mundus</i>	0	0	1	1	2	0	0	2	1	1	0	1	1	2	1	2	0	1	1	1	0	2	0	2
<i>Scolytus muticus</i>	1	0	1	2	2	0	2	0	0	0	1	1	1	2	1	0	0	2	1	0	0	1	0	2
<i>Scolytus obelus</i>	0	0	0	1	0	0	1	2	0	0	1	1	1	0	0	2	1	0	1	1	1	2	1	0
<i>Scolytus opacus</i>	0	0	0	1	2	1	1	2	1	1	1	1	1	0	0	2	1	0	1	1	0	2	1	0
<i>Scolytus oregoni</i>	0	0	1	1	2	0	1	2	1	1	1	0	1	0	0	2	1	1	1	1	0	2	1	0
<i>Scolytus piceae</i>	0	0	1	1	2	1	1	2	1	1	1	1	1	0	1	2	1	1	1	1	0	2	1	1
<i>Scolytus praeceps</i>	0	0	0	1	2	1	1	2	1	1	1	1	1	0	0	2	1	0	1	1	0	2	1	0
<i>Scolytus quadrispinosus</i>	0	1	2	2	2	0	2	0	0	0	1	1	1	1	1	1	1	2	0	0	1	2	1	0
<i>Scolytus reflexus</i>	1	1	1	1	2	1	1	2	1	0	1	1	1	0	1	2	1	1	1	2	0	1	0	2
<i>Scolytus robustus</i>	1	1	1	1	2	1	1	2	0	0	1	1	1	0	0	2	1	1	1	2	1	2	0	3
<i>Scolytus rugulosus</i>	0	0	0	1	2	1	0	2	0	0	1	0	0	2	0	0	0	0	0	3	1	2	1	2
<i>Scolytus schevyrewi</i>	0	0	2	2	2	1	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	1	1
<i>Scolytus silvaticus</i>	1	0	1	1	2	0	0	2	1	1	0	1	1	2	0	2	1	1	1	1	1	2	0	1
<i>Scolytus subscaber</i>	1	1	1	1	2	1	1	2	1	1	1	1	1	1	0	2	1	1	1	2	0	1	1	3
<i>Scolytus tsugae</i>	0	0	0	1	2	1	1	2	1	0	1	0	0	0	0	2	1	1	1	2	0	2	1	1
<i>Scolytus unispinosus</i>	0	0	1	1	2	1	0	2	1	0	1	0	1	1	0	1	1	1	1	2	0	1	1	1

Table 1.3 (cont'd).

Species	Characters																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Scolytus ventralis</i>	0	0	0	1	2	1	1	2	1	1	1	1	1	0	0	2	1	1	1	2	0	1	1	3
<i>Scolytus virgatus</i>	0	1	1	1	2	1	1	2	1	0	1	1	1	0	1	2	1	1	1	2	0	1	0	2
<i>Scolytus wickhami</i>	0	1	1	1	2	1	1	2	1	0	1	1	1	0	1	2	1	1	1	2	0	1	0	2
<i>Scolytus intricatus</i>	1	0	1	1	1	1	0	2	0	0	1	1	0	2	0	1	0	0	0	0	0	2	1	1
<i>Scolytus laevis</i>	0	0	1	3	2	1	0	2	1	0	1	1	1	1	0	1	1	1	0	0	0	1	0	3
<i>Scolytus propinquus</i>	1	0	1	2	2	3	0	1	1	0	1	2	1	1	1	2	1	1	1	0	0	1	1	1
<i>Scolytus pygmaeus</i>	0	0	1	1	2	1	0	2	0	0	1	1	1	1	1	2	1	1	1	0	0	1	0	2
<i>Scolytus ratzeburgii</i>	1	0	1	1	2	0	0	2	1	0	1	1	1	0	0	2	1	1	0	1	0	0	0	1
<i>Scolytus scolytus</i>	0	0	1	1	0	2	0	2	2	1	1	1	1	0	0	2	1	1	0	0	0	0	1	2
<i>Scolytus sinopiceus</i>	2	0	2	2	2	1	0	2	1	0	1	0	0	2	0	1	1	0	0	3	1	0	0	2
<i>Scolytus sulcifrons</i>	0	0	0	?	1	2	0	2	2	?	1	0	1	0	1	2	1	1	1	0	0	1	0	3

Table 1.3 (cont'd).

Species	Characters																			
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	
<i>Scolytus abietis</i>	0	0	3	5	1	0	0	0	0	0	0	1	2	0	0	0	0	1	2	
<i>Scolytus aztecus</i>	0	0	1	5	0	1	0	0	0	0	0	1	0	0	0	0	0	1	2	
<i>Scolytus dentatus</i>	0	0	4	0	1	0	0	0	0	0	1	1	2	0	0	0	0	0	2	
<i>Scolytus fagi</i>	0	0	1	0	3	0	0	0	0	0	0	0	0	1	1	0	0	?	8	
<i>Scolytus fiskei</i>	1	0	0	3	0	0	0	0	0	0	0	3	1	0	0	0	0	0	1	
<i>Scolytus hermosus</i>	0	0	3	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	2	
<i>Scolytus laricis</i>	1	0	0	3	0	0	0	0	0	0	0	3	1	0	0	0	0	0	4	
<i>Scolytus mali</i>	0	0	5	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	7	
<i>Scolytus monticolae</i>	0	0	1	0	3	0	0	0	0	0	0	1	2	0	0	0	0	0	1	
<i>Scolytus multistriatus</i>	2	0	5	1	3	1	0	1	1	1	0	1	0	0	0	0	0	0	6	
<i>Scolytus mundus</i>	1	0	1	3	3	0	0	0	0	0	0	1	0	0	0	0	0	0	2	
<i>Scolytus muticus</i>	0	0	5	0	3	0	0	0	0	0	0	0	0	1	1	1	0	1	9	
<i>Scolytus obelus</i>	0	0	3	3	1	0	0	0	0	0	0	1	2	0	0	0	0	1	2	
<i>Scolytus opacus</i>	0	0	3	5	1	0	0	0	0	0	0	1	2	0	0	0	0	1	2	
<i>Scolytus oregoni</i>	0	0	2	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	1	
<i>Scolytus piceae</i>	3	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	3	
<i>Scolytus praeceps</i>	0	0	3	3	1	0	0	0	0	0	0	1	2	0	0	0	0	1	2	
<i>Scolytus quadrispinosus</i>	0	0	4	5	2	0	0	1	1	1	1	2	1	0	0	0	0	0	A	
<i>Scolytus reflexus</i>	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	1	
<i>Scolytus robustus</i>	0	0	4	0	3	1	0	0	0	0	0	1	2	0	0	0	0	1	2	
<i>Scolytus rugulosus</i>	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	7	
<i>Scolytus schevyrewi</i>	2	0	5	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	6	
<i>Scolytus silvaticus</i>	0	0	3	0	3	0	0	0	0	0	1	1	2	0	0	0	0	?	1	
<i>Scolytus subscaber</i>	0	0	4	3	1	0	0	0	0	0	0	1	0	0	0	0	0	2	2	
<i>Scolytus tsugae</i>	0	0	1	0	3	0	0	0	0	0	0	1	0	0	0	0	0	1	5	
<i>Scolytus unispinosus</i>	1	0	0	3	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	

Table 1.3 (cont'd).

Species	Characters																		
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
<i>Scolytus ventralis</i>	0	0	1	3	3	0	0	0	0	0	0	1	1	0	0	0	0	1	2
<i>Scolytus virgatus</i>	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	?	1
<i>Scolytus wickhami</i>	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	1
<i>Scolytus intricatus</i>	0	0	5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	8
<i>Scolytus laevis</i>	0	1	5	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	6
<i>Scolytus propinquus</i>	0	1	1	1	3	1	1	0	0	0	0	1	0	0	0	1	1	3	0
<i>Scolytus pygmaeus</i>	0	0	5	0	3	0	0	0	0	0	1	1	0	0	0	0	0	0	6
<i>Scolytus ratzeburgii</i>	0	0	5	0	3	0	0	0	0	0	1	0	2	1	1	0	0	0	B
<i>Scolytus scolytus</i>	0	0	5	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	6
<i>Scolytus sinopiceus</i>	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	0	0	0	3
<i>Scolytus sulcifrons</i>	0	0	5	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	6

Table 1.4. Table of Nearctic specimens sequenced, the collection locality, collector and host.

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus abietis</i>	USA: California: Siskiyou Co.: Klamath National Forest, FR 41N16, N41°14.822' W122°53.562', 5081ft, 28.VII.2010, S.M. Smith coll. Ex. <i>Abies concolor</i>	Sco abi 14	SMS 14
<i>Scolytus abietis</i>	USA: Idaho: Bonner Co.: Kaniksu National Forest, FR 232, N48°20.609' W116°20.507', 2717ft, S.M. Smith, A.R. Gillogly coll. Ex. <i>Abies grandis</i>	Sco abi 16	SMS 16
<i>Scolytus aztecus</i>	Mexico: Nuevo Leon: San Antonio de las Alazanas: Santa Catarina, G. Cuellar coll., Ex. <i>Pseudotsuga menziesii</i>	Sco aze 161	SMS 161
<i>Scolytus fagi</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco fagi 1	Sco fagi 1
<i>Scolytus fagi</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco fagi 2	Sco fagi 2
<i>Scolytus fiskei</i>	USA: Colorado: Mesa Co.: Grand Mesa overlook, 8.VIII.2008, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i> branches	Sco uni 1	Sco uni 1
<i>Scolytus fiskei</i>	USA: Colorado: Eastern Slope Rocky Mountains, 6.V.2010, D.E. Bright, B.A Barr, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 36	SMS 36
<i>Scolytus fiskei</i>	USA: Colorado: Larimer Co.: Roosevelt National Forest, 9 km E Estes Park, Hwy 34, Big Thompson Canyon, N40°24.456' W105°24.565', 2143m, 5.V.2010, S.M. Smith, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 37	SMS 37
<i>Scolytus fiskei</i>	USA: Idaho: Boise Co.: Boise Natioanl Forest, Bogus Basin, NF275, N43°44.347' W116°07.099', 6042ft, 8.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 38	SMS 38

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus fiskei</i>	USA: Idaho: Latah Co.: Univeristy of Idaho experimental forest, N46°51.764' W116°43.786', 2855ft, 10.VIII.2010, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 41	SMS 41
<i>Scolytus intricatus</i>	Sweden: Smaaland: Karlsburg, 15.VII.2005, B.H. Jordal coll., Ex. <i>Quercus</i> sp.	Sco int 64	SMS 64
<i>Scolytus intricatus</i>	Sweden: Smaaland: Oskarshamn [GenBank]	Sco int BJ	
<i>Scolytus laevis</i>	Denmark, Rødby Havn, 24.VIII.2005, J. Pedersen leg.	Sco laevis	
<i>Scolytus laricis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.197' W116°13.068', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Larix occidentalis</i>	Sco lar 12	SMS 12
<i>Scolytus laricis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Larix occidentalis</i>	Sco lar 2	SMS 2
<i>Scolytus mali</i>	USA: Pennsylvania: Lebanon Co.: Mt. Gretna, N40.242501 W76.462406, IV-VIII.2009, S.E. Spichiger coll., Ex. Lindgren funnel trap	Sco mal 1	Sco mal 1
<i>Scolytus mali</i>	Czech Republic: South Bohemia: Jindřichov Hradec env. #im\$!; 23.VII.2011, M.Knížek lgt., Ex. <i>Prunus</i> sp.	Sco mal 78	SMS 78
<i>Scolytus mali</i>	USA: Michigan: Kalamazoo Co.: Gourdneck Lake State Game Area, 6.VIII.2011, S.M. Smith, A.I. Cognato coll., Ex. <i>Prunus</i> sp.	Sco mal 81	SMS 81
<i>Scolytus monticolae</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 33	SMS 33

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus monticolae</i>	USA: Idaho: Soshone Co.: Coeur D'Alene National Forest, Placer Creek Rd N47°25.746' W115°53.601', 3547ft, 15.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 34	SMS 34
<i>Scolytus monticolae</i>	USA: Idaho: Boise Co.: Boise National Forest, Bogus Basin, NF275, N43°44.347' W116°07.099', 6042ft, 8.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 35	SMS 35
<i>Scolytus multistriatus</i>	Denmark: Storstrøm: Rødbyhavn, 24.VIII.2005, J. Pedersen coll.	Sco mul 65	SMS 65
<i>Scolytus multistriatus</i>	USA: Michigan: Kalamazoo Co.: Gourdneck Lake State Game Area, 19.VI.2011, A.I. Cognato coll., Ex. <i>Ulmus</i> sp.	Sco mul 82	SMS 82
<i>Scolytus multistriatus</i>	Russia: Moscow Oblast: Dolgoprudny, N55°58.266', E37°30.191' 570m, 28.VII.2011, A.V. Petrov coll., Ex. <i>Ulmus laevis</i>	Sco mul 147	SMS 147
<i>Scolytus muticus</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco mut 1	Sco mut 1
<i>Scolytus muticus</i>	USA: Michigan: Wayne Co.: Grosse Ile, N42.17060 W83.14496, 7-20.VI.2007, R. Mech coll., Ex. Lindgren funnel trap	Sco mut 2	Sco mut 2
<i>Scolytus muticus</i>	USA: South Carolina: Columbia, 26.X.2011, W. Jones coll., Ex. <i>Celtis</i> sp.	Sco mut 169	SMS 169
<i>Scolytus obelus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°55.987' W109°16.331', 7022ft, 22.V.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco obe 18	SMS 18
<i>Scolytus obelus</i>	USA: New Mexico: Torrance Co.: Cibola National Forest, W. Manzano, N34°37.226' W106°24.752', 7999ft, 11.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco obe 44	SMS 44

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus opacus</i>	USA: Idaho: Latah Co.: Univeristy of Idaho experimental forest, N46°51.372' W116°44.038', 2857ft, 10.VIII.2010, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Abies lasiocarpa</i>	Sco opa 21	SMS 21
<i>Scolytus opacus</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.200' W116°13.067', 2696ft 13.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies lasiocarpa</i>	Sco opa 68	SMS 68
<i>Scolytus oregoni</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, Rogue River gorge viewpoint, Hwy 62 1/4 mi N Union Creek Rd, N42°54.540' W122°26.733', 3489ft, 21.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ore 5	SMS 5
<i>Scolytus oregoni</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, Rogue River gorge viewpoint, Hwy 62 1/4 mi N Union Creek Rd, N42°54.540' W122°26.733', 3489ft, 21.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ore 71	SMS 71
<i>Scolytus piceae</i>	USA: Montana: Jefferson Co.: highway 15 N. of Butte, N46.2075 W112.3360, 6013ft, 24.VII.2004, K.P. Dole coll., Ex. <i>Picea sp.</i>	Sco pic	Sco pic 1
<i>Scolytus piceae</i>	USA: Michigan: Livingston Co.: Howell, 431 Bishop Rd, N42.5076 W83.85698, 25.VI.2009, R. Mech coll., Ex. Lindgren funnel trap	Sco pic 1	Sco mul 1
<i>Scolytus piceae</i>	USA: Idaho: Latah Co: University of Idaho Experimental Forest, N46°51.164' W116°44.838', 2939ft, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Picea engelmanni</i>	Sco pic 7	SMS 7
<i>Scolytus piceae</i>	USA: South Dakota: Lawrence Co.: Brownsville Rd near Leads, N44.2922 W103.7828, 27.VII.2004, 5650ft, K.P. Dole coll., Ex. <i>Picea glauca</i>	Sco pic 73	SMS 73

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus piceae</i>	USA: Wyoming: Carbon Co.: Medicine Bow National Forest, Snowy Mountains, WY130, Lake Marie, N41°19.965' W106°19.516' 3208m, 26.VII.2011, S.M. Smith, D.E. Bright, B.A Barr coll., Emerged 1-5.IX.2011, Ex. <i>Picea engelmannii</i> branches	Sco pic 83	SMS 83
<i>Scolytus praeceps</i>	USA: California: El Dorado Co.: El Dorado National Forest, nr. Ice House Reservoir N38°50.002' W120°21.160', 5413ft, 25.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco pra 29	SMS 29
<i>Scolytus praeceps</i>	USA: California: Siskiyou Co: Shasta Trinity National Forest, Mt. Shasta, N41°20.844' W122°16.691', 4892ft, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco pra 30	SMS 30
<i>Scolytus praeceps</i>	USA: Wyoming: Albany Co.: Snowy Mountains, Medicine Bow National Forest, Spruce campground, 6.IX.2010, D.E. Bright, B.A. Barr coll., Ex. <i>Abies concolor</i>	Sco pra 91	SMS 91
<i>Scolytus propinquus</i>	Mexico: Oaxaca: Huatulco, 15.76234, -96.12885, 41m, 23.VI.2009, T.H. Atkinson coll., THA 874, Ex. legume tree	Sco pro 1	Sco pro 1
<i>Scolytus propinquus</i>	Mexico: Oaxaca: Huatulco, 15.76234, -96.12885, 41m, 23.VI.2009, T.H. Atkinson coll., THA 874, Ex. legume tree	Sco pro 2	Sco pro 2
<i>Scolytus pygmaeus</i>	Czech Republic: Moravia: B!eclav Kamci obora, 2004, K. Novakova coll.	Sco pyg 62	SMS 62
<i>Scolytus pygmaeus</i>	Denmark: Storstrøm: Rødbyhavn, 24.VIII.2005, J. Pedersen coll.	Sco pyg 67	SMS 67
<i>Scolytus quadrisphosus</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 24.VII.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco qua 1	Sco qua 1
<i>Scolytus quadrisphosus</i>	USA: Maryland: Ann Aruridel Co.: Annapolis, 26.V.2012, R.J. Rabaglia coll., Ex. Lindgren funnel trap	Sco qua 170	SMS 170

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus ratzeburgii</i>	Russia: Primorsky: Anisimovka, 12.VII.2008, B.H. Jordal coll.	Sco ratz 60	SMS 60
<i>Scolytus reflexus</i>	USA: Arizona: Pima Co.: Coronado National Forest, Santa Catalina Mountains, N32°24.529' W110°42.678', 7869ft, 22.V.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ref 26	SMS 26
<i>Scolytus reflexus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°54.915' W109°16.040', 8196ft, 20.V.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ref 27	SMS 27
<i>Scolytus reflexus</i>	USA: Colorado: Larimer Co.: Roosevelt National Forest, 9 km E Estes Park, Hwy 34, Big Thompson Canyon, N40°24.456' W105°24.565', 2143m, 5.V.2010, S.M. Smith, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ref 32	SMS 32
<i>Scolytus reflexus</i>	USA: Colorado: Boulder Co.: Roosevelt National Forest, St. Vrain canyon, N40°10.072' W105°23.623', 2127m, 24.VII.2011, S.M. Smith, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ref 85	SMS 85
<i>Scolytus robustus</i>	USA: Arizona: Graham Co.: Coronado National Forest, Pinaleno Mountains, N32°37.702' W109°49.472', 7896ft, 23.V.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco rob 3	SMS 3
<i>Scolytus robustus</i>	USA: New Mexico: Taos Co.: Carson National Forest, Agua Piedra campground, Hwy 75, N36°07.960' W105°31.828' 8477 ft, 13.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco rob 43	SMS 43
<i>Scolytus robustus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°54.665' W109°16.336', 2445m, 5.VIII.2012, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco rob 178	SMS 178

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus rugulosus</i>	Morocco: 30 km S. Asni, Tizi'n'Test, 18.IV.2002, B.H. Jordal coll., Ex. <i>Prunus dulcis</i>	Sco rug 72	SMS 72
<i>Scolytus rugulosus</i>	Hungary: Győr-Ménfőcsanak-Sopron: Sopron, 2003, F. Lakatos coll.	Sco rug 66	SMS 66
<i>Scolytus rugulosus</i>	Czech Republic: South Bohemia: Jindřichův Hradec env. Štěpánov, 23.VII.2011, M. Kníže Igt., Ex. <i>Prunus</i> sp.	Sco rug 79	SMS 79
<i>Scolytus rugulosus</i>	Iran: Guilan: Khoshkestalkh, N37°27'01" E49°42'06", 17.VII.2011, S. Amini coll., Ex. <i>Malus</i> sp.	Sco rug 165	SMS 165
<i>Scolytus schevyrewi</i>	USA: Missouri: Saint Louis Co.: Maryland Heights, 22.V.2008, Ex. Lindgren funnel trap	Sco sch 2	Sco sch 2
<i>Scolytus scolytus</i>	Denmark: NEJ, Tofte Skov [GenBank]	Sco sco BJ	
<i>Scolytus sinopiceus</i>	China: Qinghai: MaiXiu Forest Preserve, N35°16.288' E101°55.904', 2927m, 21.V.2008, A.I. Cognato coll., Ex. Lindgren funnel trap	Sco sin 1	Sco sin 1
<i>Scolytus sinopiceus</i>	China: Sichuan: Highway 213 near Zhangla, 9.VII.2004, A.I. Cognato coll., Ex. <i>Picea purpurea</i>	Sco sin 70	SMS 70
<i>Scolytus subscaber</i>	USA: California: Alpine Co.: Toiyabe National Forest, 11.6 miles E of Markleeville, N38°39.906' W119°38.540', 24.VII.2010, S.M. Smith coll., Ex. <i>Abies magnifica</i>	Sco sub 6	SMS 6
<i>Scolytus subscaber</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.197' W116°13.068', 2748ft 13.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies lasiocarpa</i>	Sco sub 51	SMS 51
<i>Scolytus sulcifrons</i>	Russia: Moscow Oblast: Dolgoprudny, N55°58.266', E37°30.191' 570m, 28.VII.2011, A.V. Petrov coll., Ex. <i>Ulmus laevis</i>	Sco sul 146	SMS 146

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus tsugae</i>	USA: Idaho: Soshone Co.: St. Joe National Forest, N47°00.790' W116°12.359', 3192 ft, 15.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Tsuga occidentalis</i>	Sco tsu 10	SMS 10
<i>Scolytus tsugae</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, N48°40.911' W116°34.345', 4353ft, 12.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Tsuga heterophylla</i>	Sco tsu 11	SMS 11
<i>Scolytus unispinosus</i>	USA: Oregon: Deschutes Co.: Deschutes National Forest, Black Butte Rd, Black Butte, N40°24.924' W121°38.323', 4212ft, 1.VIII.2010 S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 1	SMS 1
<i>Scolytus unispinosus</i>	USA: Oregon: Hood River Co.: Mount Hood National Forest, Sherwood Campground, Hwy 35, N45°19.278' W121°37.104', 4293ft, 2.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 39	SMS 39
<i>Scolytus unispinosus</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, NF 60, N42°53.926' W122°19.177', 4547ft, 30.VII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 40	SMS 40
<i>Scolytus unispinosus</i>	USA: Oregon: Klamath Co.: Deschutes National Forest, NF 4672, N43°30.474' W121°52.147', 4923ft, 31.VII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 42	SMS 42
<i>Scolytus unispinosus</i>	USA: Oregon: Marion Co.: Williamette National Forest, Breitenbush Rd, N44°47.200' W121°56.557', 2645ft, 1.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 151	SMS 151
<i>Scolytus ventralis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies lasiocarpa</i>	Sco ven 22	SMS 22

Table 1.4 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus ventralis</i>	USA: Idaho: Adams Co.: Payette National Forest, N45°00.225' W116°09.651', 6025ft, 17.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies grandis</i>	Sco ven 45	SMS 45
<i>Scolytus ventralis</i>	USA: Idaho: Benewah Co.: McCroskey State Park, N47°04.801' W116°54.960', 3744ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies grandis</i>	Sco ven 46	SMS 46
<i>Scolytus ventralis</i>	USA: New Mexico: Torrance Co.: Cibola National Forest, W. Manzano, N34°37.325' W106°24.642', 8026ft, 11.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco ven 48	SMS 48
<i>Scolytus ventralis</i>	USA: California: El Dorado Co.: El Dorado National Forest, nr. Ice House Reservoir N38°50.002' W120°21.160', 5413ft, 25.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco ven 49	SMS 49
<i>Scolytus ventralis</i>	USA: Arizona: Coconino Co.: Arizona Snowbowl, N36°24.381' W112°05.619', 8923ft, 30.V.2010 S.M. Smith, K. Bush coll., Ex. <i>Abies lasiocarpa</i>	Sco ven 50	SMS 50
<i>Scolytus virgatus</i>	Mexico: Nuevo Leon: San Antonio de las Alazanas: Santa Catarina, G. Cuellar coll., Ex. <i>Pseudotsuga menziesii</i>	Sco vir 162	SMS 162
<i>Scolytus wickhami</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°55.360' W109°15.702', 7882ft, 20.V.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco wick 24	SMS 24
<i>Scolytus wickhami</i>	USA: New Mexico: Otero Co.: Lincoln National Forest, Apache Point observatory, N32°47.046' W105°48.841', 9116ft, 16.V.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco wick 25	SMS 25
<i>Scolytus wickhami</i>	USA: New Mexico: Colfax Co.: Highway 64 near Ute Park, N36°33'9.26" W105°07'6.74", 2242m, 24.VI.2004, A.I. Cognato, S.A. Stephens coll., Ex. <i>Pinus ponderosa</i>	Sco wick 74	SMS 74

Table 1.5. Table of Nearctic specimens sequenced to assess intraspecific variation, the collection locality, collector and host.

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus abietis</i>	USA: California: Siskiyou Co.: Klamath National Forest, FR 41N16, N41°14.822' W122°53.562', 5081ft, 28.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco abi 14	SMS 14
<i>Scolytus abietis</i>	USA: Idaho: Latah Co.: St. Joe National Forest, Moscow Mountain, N46°48.252' W116°49.811', 3834ft, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Abies grandis</i>	Sco abi 15	SMS 15
<i>Scolytus abietis</i>	USA: Idaho: Bonner Co.: Kaniksu National Forest, FR 232, N48°20.609' W116°20.507', 2717ft, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies grandis</i>	Sco abi 16	SMS 16
<i>Scolytus abietis</i>	USA: Oregon: Deschutes Co.: Deschutes National Forest, Black Butte Rd, Black Butte, N40°24.924' W121°38.323', 4212ft, 1.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco abi 17	SMS 17
<i>Scolytus fagi</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco fagi 1	Sco fagi 1
<i>Scolytus fagi</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco fagi 2	Sco fagi 2
<i>Scolytus fiskei</i>	USA: Colorado: Mesa Co.: Grand Mesa overlook, 8.VIII.2008, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i> branches	Sco uni 1	Sco uni 1
<i>Scolytus fiskei</i>	USA: Colorado: Eastern Slope Rocky Mountains, 6.V.2010, D.E. Bright, B.A. Barr, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 36	SMS 36
<i>Scolytus fiskei</i>	USA: Colorado: Larimer Co.: Roosevelt National Forest, 9 km E Estes Park, Hwy 34, Big Thompson Canyon, N40°24.456' W105°24.565', 2143m, 5.V.2010, S.M. Smith, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 37	SMS 37
<i>Scolytus fiskei</i>	USA: Idaho: Boise Co.: Boise National Forest, Bogus Basin, NF275, N43°44.347' W116°07.099', 6042ft, 8.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fisi 38	SMS 38
<i>Scolytus fiskei</i>	USA: Idaho: Latah Co.: Univeristy of Idaho experimental forest, N46°51.764' W116°43.786', 2855ft, 10.VIII.2010, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 41	SMS 41

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus intricatus</i>	Sweden: Smaaland: Karlsburg, 15.VII.2005, B.H. Jordal coll., Ex. <i>Quercus</i> sp.	Sco int 64	SMS 64
<i>Scolytus laricis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Larix occidentalis</i>	Sco lar 2	SMS 2
<i>Scolytus laricis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.197' W116°13.068', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Larix occidentalis</i>	Sco lar 12	SMS 12
<i>Scolytus laricis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, N48°39.185' W116°32.662', 5311ft, 12.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Larix occidentalis</i>	Sco lar 13	SMS 13
<i>Scolytus mali</i>	Czech Republic: South Bohemia: Jindřichov Hradec env. #1m\$!; 23.VII.2011, M.Knížek lgt., Ex. <i>Prunus</i> sp.	Sco mal 78	SMS 78
<i>Scolytus mali</i>	USA: Michigan: Kalamazoo Co.: Gourdneck Lake State Game Area, 6.VIII.2011, S.M. Smith, A.I. Cognato coll., Ex. <i>Prunus</i> sp.	Sco mal 81	SMS 81
<i>Scolytus monticolae</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 33	SMS 33
<i>Scolytus monticolae</i>	USA: Idaho: Soshone Co.: Coeur D'Alene National Forest, Placer Creek Rd N47°25.746' W115°53.601', 3547ft, 15.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 34	SMS 34
<i>Scolytus monticolae</i>	USA: Idaho: Boise Co.: Boise National Forest, Bogus Basin, NF275, N43°44.347' W116°07.099', 6042ft, 8.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 35	SMS 35

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus multistriatus</i>	Denmark: Storstrøm: Rødbyhavn, 24.VIII.2005, J. Pedersen coll.	Sco mul 65	SMS 65
<i>Scolytus multistriatus</i>	USA: Michigan: Kalamazoo Co.: Gourdneck Lake State Game Area, 19.VI.2011, A.I. Cognato coll., Ex. <i>Ulmus</i> sp.	Sco mul 82	SMS 82
<i>Scolytus multistriatus</i>	Russia: Moscow Oblast: Dolgoprudny, N55°58.266', E37°30.191' 570m, 28.VII.2011, A.V. Petrov, Ex. <i>Ulmus laevis</i>	Sco mul 147	SMS 147
<i>Scolytus muticus</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco mut 1	Sco mut 1
<i>Scolytus muticus</i>	USA: Michigan: Wayne Co.: Grosse Ile, N42.17060 W83.14496, 7-20.VI.2007, R. Mech coll., Ex. Lindgren funnel trap	Sco mut 2	Sco mut 2
<i>Scolytus muticus</i>	USA: Pennsylvania: Dauphin Co.: Harrisburg, N40.316325 W76.888783, IV-VIII.2009, S.E. Spichiger coll., Ex. Lindgren Funnel trap	Sco mut 4	Sco mut 4
<i>Scolytus muticus</i>	USA: South Carolina: Columbia, 26.X.2011, W. Jones coll., Ex. <i>Celtis</i> sp.	Sco mut 169	SMS 169
<i>Scolytus obelus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°55.987' W109°16.331', 7022ft, 22.V.2010, S.M. Smith coll. Ex. <i>Abies concolor</i>	Sco obe 18	SMS 18
<i>Scolytus obelus</i>	USA: Arizona: Graham Co.: Coronado National Forest, Pinaleno Mountains, N32°37.702' W109°49.472', 7896ft, 23.V.2010, S.M. Smith coll. Ex. <i>Abies concolor</i>	Sco obe 19	SMS 19
<i>Scolytus obelus</i>	USA: Arizona: Coconino Co.: Arizona Snowbowl, N35°19.593' W111°42.681', 9032ft, 27.V.2010 S.M. Smith coll., Ex. <i>Abies lasiocarpa</i>	Sco obe 20	SMS 20
<i>Scolytus obelus</i>	USA: New Mexico: Torrance Co.: Cibola National Forest, W. Manzano, N34°37.226' W106°24.752', 7999ft, 11.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco obe 44	SMS 44

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus opacus</i>	USA: Idaho: Latah Co.: Univeristy of Idaho experimental forest, N46°51.372' W116°44.038', 2857ft, 10.VIII.2010, S.M. Smith, A.R. Gillogly, M.M. Furniss, Ex. <i>Abies lasiocarpa</i>	Sco opa 21	SMS 21
<i>Scolytus opacus</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.200' W116°13.067', 2696ft 13.VIII.2010, S.M. Smith, A.R. Gillogly, Ex. <i>Abies lasiocarpa</i>	Sco opa 68	SMS 68
<i>Scolytus oregoni</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, Rogue River gorge viewpoint, Hwy 62 1/4 mi N Union Creek Rd, N42°54.540' W122°26.733', 3489ft, 21.VIII.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco ore 71	SMS 71
<i>Scolytus piceae</i>	USA: Michigan: Livingston Co.: Howell, 431 Bishop Rd, N42.5076 W83.85698, 25.VI.2009, R. Mech coll., Ex. Lindgren funnel trap	Sco pic 1	Sco mul 1
<i>Scolytus piceae</i>	USA: Montana: Jefferson Co.: highway 15 N. of Butte, N46.2075 W112.3360, 6013ft, 24.VII.2004, K.P. Dole coll., Ex. <i>Picea sp.</i>	Sco pic	Sco pic
<i>Scolytus piceae</i>	USA: Idaho: Latah Co.: University of Idaho Experimental Forest, N46°51.164' W116°44.838', 2939ft, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Picea engelmannii</i>	Sco pic 7	SMS 7
<i>Scolytus piceae</i>	USA: Idaho: Valley Co.: Boise National Forest, Hwy 55, S. of Donnelly, N44°20.117' W116°02.698', 4816ft, 17.VIII.2010, S.M. Smith, A.R. Gillogly, Ex. <i>Picea engelmannii</i>	Sco pic 8	SMS 8
<i>Scolytus piceae</i>	USA: South Dakota: Lawrence Co.: Brownsville Rd near Leads, N44.2922 W103.7828, 27.VII.2004, 5650ft, K.P. Dole coll., Ex. <i>Picea glauca</i>	Sco pic 73	SMS 73
<i>Scolytus piceae</i>	USA: Wyoming: Carbon Co.: Medicine Bow National Forest, Snowy Mountains, WY130, Lake Marie, N41°19.965' W106°19.516' 3208m, 26.VII.2011, S.M. Smith, D.E. Bright, B.A Barr coll., Emerged 1-5.IX.2011, Ex. <i>Picea engelmannii</i> branches	Sco pic 83	SMS 83
<i>Scolytus praeceps</i>	USA: California: El Dorado Co.: El Dorado National Forest, Ise house resevoir, N38.50 W 120.22, 1653m, 17.VI.2003, A.I. Cognato coll., Ex. <i>Abies sp.</i>	Sco pra	Sco pra

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus praeceps</i>	USA: California: Alpine Co.: Toiyabe National Forest, 11.6 miles E of Markleeville, N38°39.906' W119°38.540', 24.VII.2010, S.M. Smith coll., Ex. <i>Abies magnifica</i>	Sco pra 28	SMS 28
<i>Scolytus praeceps</i>	USA: California: El Dorado Co.: El Dorado National Forest, nr. Ice House Reservoir N38°50.002' W120°21.160', 5413ft, 25.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco pra 29	SMS 29
<i>Scolytus praeceps</i>	USA: California: Siskiyou Co.: Shasta Trinity National Forest, Mt. Shasta, N41°20.844' W122°16.691', 4892ft, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco pra 30	SMS 30
<i>Scolytus praeceps</i>	USA: California: Siskiyou Co.: Klamath National Forest, FR 41N16, N41°14.822' W122°53.562', 5081ft, 28.VII.2010, S.M. Smith coll. Ex. <i>Abies concolor</i>	Sco pra 31	SMS 31
<i>Scolytus praeceps</i>	USA: Wyoming: Albany Co.: Snowy Mountains, Medicine Bow National Forest, Spruce campground, 6.IX.2010, D.E. Bright, B.A. Barr coll., Ex. <i>Abies concolor</i>	Sco pra 91	SMS 91
<i>Scolytus propinquus</i>	Mexico: Oaxaca: Huatulco, 15.76234, -96.12885, 41m, 23.VI.2009, T.H. Atkinson coll., THA 874, Ex. legume tree	Sco pro 1	Sco pro 1
<i>Scolytus pygmaeus</i>	Czech Republic: Moravia: B!eclav Kamci obora, 2004, K. Novakova coll.	Sco pyg 62	SMS 62
<i>Scolytus pygmaeus</i>	Denmark: Storstrøm: Rødbyhavn, 24.VIII.2005, J. Pedersen coll.	Sco pyg 67	SMS 67
<i>Scolytus quadrisphosus</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 24.VII.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco qua 1	Sco qua 1
<i>Scolytus quadrisphosus</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 24.VII.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco qua 2	Sco qua 2
<i>Scolytus quadrisphosus</i>	USA: Pennsylvania: Lebanon Co.: Mt. Gretna, N40.242501 W76.462406, IV-VIII.2009, S.E. Spichiger coll., Ex. Lindgren funnel trap	Sco qua 3	Sco qua 3
<i>Scolytus quadrisphosus</i>	USA: Maryland: Ann Aruridel Co.: Annapolis, 26.V.2012, R.J. Rabaglia coll., Ex. Lindgren funnel trap	Sco qua 170	SMS 170

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus ratzeburgii</i>	Russia: Primorsky: Anisimovka, 12.VII.2008, B.H. Jordal coll.	Sco ratz 60	SMS 60
<i>Scolytus reflexus</i>	USA: Arizona: Pima Co.: Coronado National Forest, Santa Catalina Mountains, N32°24.529' W110°42.678', 7869ft, 22.V.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco ref 26	SMS 26
<i>Scolytus reflexus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°54.915' W109°16.040', 8196ft, 20.V.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco ref 27	SMS 27
<i>Scolytus reflexus</i>	USA: Colorado: Larimer Co.: Roosevelt National Forest, 9 km E Estes Park, Hwy 34, Big Thompson Canyon, N40°24.456' W105°24.565', 2143m, 5.V.2010, S.M. Smith, D.E. Bright, B.A. Barr coll. Ex. <i>Pseudotsuga menziesii</i>	Sco ref 32	SMS 32
<i>Scolytus reflexus</i>	USA: Colorado: Boulder Co.: Roosevelt National Forest, St. Vrain canyon, N40°10.072' W105°23.623', 2127m, 24.VII.2011, S.M. Smith, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ref 85	SMS 85
<i>Scolytus robustus</i>	USA: Arizona: Graham Co.: Coronado National Forest, Pinaleno Mountains, N32°37.702' W109°49.472', 7896ft, 23.V.2010, S.M. Smith coll. Ex. <i>Abies concolor</i>	Sco rob 3	SMS 3
<i>Scolytus robustus</i>	USA: New Mexico: Taos Co.: Carson National Forest, Agua Piedra campground, Hwy 75, N36°07.960' W105°31.828' 8477 ft, 13.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco rob 43	SMS 43
<i>Scolytus robustus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°54.665' W109°16.336', 2445m, 5.VIII.2012, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco rob 178	SMS 178
<i>Scolytus rugulosus</i>	Czech Republic: South Bohemia, Jindřich v Hradec env. #im\$!; 23.VII.2011, M.Knížek coll., Ex. <i>Prunus</i> sp.	Sco rug 79	SMS 79

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus scolytus</i>	Denmark: NEJ, Tofte Skov [GenBank]	Sco sco BJ	
<i>Scolytus sinopiceus</i>	China: Qinghai: Mai Xiu Forest Preserve, N35°16.288' E101°55.904', 2927m, 21.V.2008, A.I. Cognato coll., Ex. Lindgren funnel trap	Sco sin 1	Sco sin 1
<i>Scolytus sinopiceus</i>	China: Sichuan: Highway 213 near Zhangla, 9.VII.2004, A.I. Cognato coll., Ex. <i>Picea purpurea</i>	Sco sin 70	SMS 70
<i>Scolytus subscaber</i>	USA: California: Alpine Co.: Toiyabe National Forest, 11.6 miles E of Markleeville, N38°39.906' W119°38.540', 24.VII.2010, S.M. Smith coll., Ex. <i>Abies magnifica</i>	Sco sub 6	SMS 6
<i>Scolytus subscaber</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.197' W116°13.068', 2748ft 13.VIII.2010, S.M. Smith, A.R. Gillogly, Ex. <i>Abies lasiocarpa</i>	Sco sub 51	SMS 51
<i>Scolytus sulcifrons</i>	Russia: Moscow Oblast: Dolgoprudny, N55°58.266', E37°30.191' 570m, 28.VII.2011, A.V. Petrov coll., Ex. <i>Ulmus laevis</i>	Sco sul 146	SMS 146
<i>Scolytus tsugae</i>	USA: Oregon: Hood River Co.: Mount Hood National Forest, Sherwood Campground, Hwy 35, N45°19.278' W121°37.104', 4293ft, 2.VIII.2010, S.M. Smith coll., Ex. <i>Tsuga heterophylla</i>	Sco tsu 9	SMS 9
<i>Scolytus tsugae</i>	USA: Idaho: Soshone Co.: St. Joe National Forest, N47°00.790' W116°12.359', 3192 ft, 15.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Tsuga occidentalis</i>	Sco tsu 10	SMS 10
<i>Scolytus tsugae</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, N48°40.911' W116°34.345', 4353ft, 12.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Tsuga heterophylla</i>	Sco tsu 11	SMS 11

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus unispinosus</i>	USA: Oregon: Deschutes Co.: Deschutes National Forest, Black Butte Rd, Black Butte, N40°24.924' W121°38.323', 4212ft, 1.VIII.2010 S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 1	SMS 1
<i>Scolytus unispinosus</i>	USA: Oregon: Hood River Co.: Mount Hood National Forest, Sherwood Campground, Hwy 35, N45°19.278' W121°37.104', 4293ft, 2.VIII.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco uni 39	SMS 39
<i>Scolytus unispinosus</i>	USA: Oregon: Klamath Co.: Deschutes National Forest, NF 4672, N43°30.474' W121°52.147', 4923ft, 31.VII.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco uni 42	SMS 42
<i>Scolytus unispinosus</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, NF 60, N42°53.926' W122°19.177', 4547ft, 30.VII.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco uni 40	SMS 40
<i>Scolytus unispinosus</i>	USA: Oregon: Marion Co.: Willamette National Forest, Breitenbush Rd, N44°47.200' W121°56.557', 2645ft, 1.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 151	SMS 151
<i>Scolytus ventralis</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, 14.VII.2009, J. Hulcr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ven 1	Sco sp 1
<i>Scolytus ventralis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll. Ex. <i>Abies lasiocarpa</i>	Sco ven 22	SMS 22
<i>Scolytus ventralis</i>	USA: Idaho: Adams Co.: Payette National Forest N45°00.225' W116°09.651', 6025ft, 17.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies grandis</i>	Sco ven 45	SMS 45

Table 1.5 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus ventralis</i>	USA: Idaho: Benewah Co.: McCroskey State Park, N47°04.801' W116°54.960', 3744ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies grandis</i>	Sco ven 46	SMS 46
<i>Scolytus ventralis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.200' W116°13.067', 2696ft 13.VIII.2010, S.M. Smith, A.R. Gillogly, Ex. <i>Abies grandis</i>	Sco ven 47	SMS 47
<i>Scolytus ventralis</i>	USA: New Mexico: Torrance Co.: Cibola National Forest, W. Manzano, N34°37.325' W106°24.642', 8026ft, 11.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco ven 48	SMS 48
<i>Scolytus ventralis</i>	USA: California: El Dorado Co.: El Dorado National Forest, nr. Ice House Reservoir N38°50.002' W120°21.160', 5413ft, 25.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco ven 49	SMS 49
<i>Scolytus ventralis</i>	USA: Arizona: Coconino Co.: Arizona Snowbowl, N36°24.381' W112°05.619', 8923ft, 30.V.2010 S.M. Smith, K. Bush coll., Ex. <i>Abies lasiocarpa</i>	Sco ven 50	SMS 50
<i>Scolytus wickhami</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°55.360' W109°15.702', 7882ft, 20.V.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco wick 24	SMS 24
<i>Scolytus wickhami</i>	USA: New Mexico: Otero Co.: Lincoln National Forest, Apache Point observatory, N32°47.046' W105°48.841', 9116ft, 16.V.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco wick 25	SMS 25
<i>Scolytus wickhami</i>	USA: New Mexico: Colfax Co.: Highway 64 near Ute Park, N36°33'9.26" W105°07'6.74", 2242m, 24.VI.2004, A.I. Cognato, S.A. Stephens coll., Ex. <i>Pinus ponderosa</i>	Sco wick 74	SMS 74

Table 1.6. Table of PCR primers and the annealing temperatures used for the amplification of gene sequences.

Gene	Primer	Primer sequence	Annealing Temp °C	BP analyzed	First Cited
COI	LCO 1490	5'-GGTCAACAAATCATAAAGATATTGG-3'	50	615	Hebert et al. 2003
	HCO 2198	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	50	615	Hebert et al. 2003
	1495b	5'-AACAAATCATAAAGATATTGGRAC-3'	50	615	This study
	rev 750	5'-GAAATTATNCCAATTCCTGG-3'	50	615	This study
	ScoCOI F215	5'-CCCCCGACATAGCTTTCCC-3'	50	271	This study
	ScoCOI Rev453	5'-TATTTGATCGAACTTTATTCC-3'	50	271	This study
28S	3665	5'-AGACAGAGTTCAAGAGTACGTG-3'	55	402-496	Belshaw and Quicke 1997
	4068	5'-TTGGTCCGTGTTTCAAGACGGG-3'	55	402-496	Belshaw and Quicke 1997
CAD	apCADforB2	5'-TGGAARGARGTBGARTACGARGTGGYCG-3'	56 or 58	690	Dole et al. 2010
	apCADfor4	5'-TGGAARGARGTBGARTACGARGTGGTYCG-3'	56 or 58	472	Danforth et al. 2006
	apCADrev1mod	5'-GCCATYRCTCBCCTACRCTYTTCAT-3'	56 or 58	472 or 690	Danforth et al. 2006
ArgK	ArgKforB2	5'-GAYTCCGGWATYGGWATCTAYGCTCC-3'	56 or 58	692	Dole et al. 2010
	ArgKrevB2	5'-GTATGYTCMCCRCGRGTACCACG-3'	56 or 58	692	Dole et al. 2010

Table 1.7. Intraspecific differences among COI, 28S, CAD and ArgK expressed as the proportion of sites differing between sequences. N/A applies to taxa for which sequence data was not available.

Species	Gene							
	COI		28S		CAD		ArgK	
	Range	Average	Range	Average	Range	Average	Range	Average
<i>Scolytus aztecus</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Scolytus fagi</i>	0	0	0	0	N/A	N/A	N/A	N/A
<i>Scolytus fiskei</i>	0-0.0231	0.0183	0	0	0	0	0-0.0058	0.0034
<i>Scolytus intricatus</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Scolytus laricis</i>	0-0.0043	0.0020	0	0	0	0	0.0043	0.0043
<i>Scolytus mali</i>	0.0433	0.0433	0	0	0	0	0-0.0030	0.0020
<i>Scolytus monticolae</i>	0-0.0017	0.0011	0	0	N/A	N/A	N/A	N/A
<i>Scolytus multistriatus</i>	0-0.0016	0.0033	0-0.0027	0.0009	0-0.0127	0.0078	N/A	N/A
<i>Scolytus muticus</i>	0.0034-0.0105	0.0079	0-0.0074	0.0049	0	0	0	0
<i>Scolytus obelus</i>	0.0081-0.0195	0.0135	0	0	0.0021	0.0021	0.0014	0.0014
<i>Scolytus oregoni</i>	N/A	N/A	0	0	0.0085	0.0085	0	0
<i>Scolytus piceae</i>	0-0.0163	0.0100	0-0.0025	0.0008	0-0.00850	0.0050	0	0
<i>Scolytus praeceps</i>	0-0.0148	0.0077	0	0	0	0	0-0.0044	0.0024
<i>Scolytus propinquus</i>	0	0	N/A	N/A	0	0	0.0063	0.0063
<i>Scolytus pygmaeus</i>	0	0	0	0.0000	0	0	0	0
<i>Scolytus quadrisphosus</i>	0.0016-0.0049	0.0032	0	0.0000	0	0	0.0014	0.0014
<i>Scolytus ratzeburgii</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Scolytus reflexus</i>	0-0.0130	0.0070	0-0.0049	0.0012	0-0.0023	0.0003	0-0.0043	0.0029
<i>Scolytus robustus</i>	0.0033-0.0537	0.0358	0-0.0025	0.0017	0-0.0043	0.0029	0.0015-0.0260	0.0153
<i>Scolytus rugulosus</i>	N/A	N/A	0-0.0074	0.0050	0.0065-0.0192	0.0128	0-0.0274	0.0150
<i>Scolytus schevyrewi</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Scolytus scolytus</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Scolytus sinopiceus</i>	0.0157	0.0157	0.0123	0.0123	0	0	0	0
<i>Scolytus subscaber</i>	0.0158	0.0158	0.0049	0.0049	N/A	N/A	0.0101	0.0101
<i>Scolytus sulcifrons</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Scolytus tsugae</i>	0.0016-0.0147	0.0103	0	0	0	0	N/A	N/A
<i>Scolytus unispinosus</i>	0.0016-0.0282	0.0121	0	0	0-0.0023	0.0015	0-0.0029	0.0007
<i>Scolytus ventralis</i>	0-0.0181	0.0089	0-0.0025	0.0010	0-0.0043	0.0022	0-0.0043	0.0022

Table 1.8. Interspecific differences among COI, 28S, CAD and ArgK expressed as the proportion of sites differing between sequences among sister taxa. N/A applies to taxa for which sequence data was not available.

Species	Gene			
	COI		28S	
	Range	Average	Range	Average
<i>S. aztecus</i> vs. <i>S. ventralis</i>	N/A	N/A	0-0.0025	0.0020
<i>S. fagus</i> vs. <i>S. muticus</i>	0.1317-0.1382	0.1361	0.0176-0.0251	0.0201
<i>S. fagus</i> vs. <i>S. quadrispinosus</i>	0.1789-0.1821	0.1801	0.0528	0.0528
<i>S. fiskei</i> vs. <i>S. laricis</i>	0-0.0297	0.0143	0	0
<i>S. fiskei</i> vs. <i>S. piceae</i>	0-0.0.028	0.0109	0.0025-0.0049	0.0031
<i>S. fiskei</i> vs. <i>S. unispinosus</i>	0.0331-0.0520	0.043	0	0
<i>S. laricis</i> vs. <i>S. piceae</i>	0-0.0179	0.0151	0.0025-0.0052	0.0032
<i>S. laricis</i> vs. <i>S. unispinosus</i>	0.0397-0.0520	0.046	0	0
<i>S. monticolae</i> vs. <i>S. oregoni</i>	0.0390-0.0396	0.0393	0.0025	0.0025
<i>S. monticolae</i> vs. <i>S. reflexus</i>	0.0765-0.0846	0.0798	0.0025-0.0049	0.0031
<i>S. monticolae</i> vs. <i>S. tsugae</i>	0.0380-0.0413	0.0398	0.0025	0.0025
<i>S. muticus</i> vs. <i>S. quadrispinosus</i>	0.1626-0.1691	0.1659	0.0500-0.0575	0.0525
<i>S. obelus</i> vs. <i>S. praeceps</i>	0.0934-0.1089	0.1036	0.0025	0.0025
<i>S. oregonis</i> vs. <i>S. tsugae</i>	0.0098-0.0179	0.0131	0.0000	0.0000
<i>S. robustus</i> vs. <i>S. subscaber</i>	0.0791-0.1041	0.0902	0.0025-0.0099	0.0066
<i>S. rugulosus</i> vs. <i>S. sinopiceus</i>	0.1260-0.1366	0.1320	0.0099-0.0149	0.0120

Table 1.8 (cont'd).

Species	Gene			
	CAD		ArgK	
	Range	Average	Range	Average
<i>S. aztecus</i> vs. <i>S. ventralis</i>	0.0047-0.0088	0.0067	0.0119-0.0133	0.0128
<i>S. fagus</i> vs. <i>S. muticus</i>	0.0171-0.208	0.0190	0.0267	0.0267
<i>S. fagus</i> vs. <i>S. quadrispinosus</i>	0.0531-0.0533	0.0532	0.0533-0.0549	0.0541
<i>S. fiskei</i> vs. <i>S. laricis</i>	0-0.0128	0.0051	0.0029-0.0072	0.0051
<i>S. fiskei</i> vs. <i>S. piceae</i>	0.0065-0.0234	0.0096	0.0130-0.0159	0.0145
<i>S. fiskei</i> vs. <i>S. unispinosus</i>	0-0.0149	0.0074	0-0.0072	0.0043
<i>S. laricis</i> vs. <i>S. piceae</i>	0.0043-0.0149	0.0138	0.013-0.0145	0.01375
<i>S. laricis</i> vs. <i>S. unispinosus</i>	0.0043-0.0093	0.007	0-0.0043	0.0024
<i>S. monticolae</i> vs. <i>S. oregoni</i>	N/A	N/A	0.0043-0.0046	0.0045
<i>S. monticolae</i> vs. <i>S. reflexus</i>	N/A	N/A	0.0072-0.0087	0.0077
<i>S. monticolae</i> vs. <i>S. tsugae</i>	N/A	N/A	0.0185	0.0185
<i>S. muticus</i> vs. <i>S. quadrispinosus</i>	0.0488-0.0532	0.0510	0.0522-0.0552	0.0537
<i>S. obelus</i> vs. <i>S. praeceps</i>	0.0021	0.0021	0.0052-0.0103	0.0089
<i>S. oregonis</i> vs. <i>S. tsugae</i>	0.0064-0.0142	0.0103	0.0155-0.0169	0.0162
<i>S. robustus</i> vs. <i>S. subscaber</i>	0.0150-0.0194	0.0172	0.0089-0.0321	0.0173
<i>S. rugulosus</i> vs. <i>S. sinopiceus</i>	0.0336-0.0414	0.0370	0.0135-0.0245	0.0204

Table 1.9. Partition Bremer support values for the four gene parsimony phylogeny with gaps treated as missing data. Nodes refer to Figure 1.4.

Node	Gene Partition				Total
	COI	28S	CAD	ArgK	
1	41.8	4.2	-2.0	-2.0	42.0
2	24.7	2.1	0.2	0.1	27.1
3	12.7	10.2	2.4	2.7	28.0
4	0.1	3.1	6.9	8.9	19.0
5	0.0	3.0	1.0	3.1	7.1
6	0.5	1.5	1.4	3.7	7.1
7	0.3	5.0	20.8	12.9	39.0
8	-7.0	9.0	3.7	6.3	12.0
9	29.1	15.1	9.5	7.3	61.0
10	-10.5	7.7	6.6	-0.8	3.0
11	1.7	-0.4	-0.6	0.3	1.0
12	29.8	7.1	12.8	13.3	63.0
13	30.6	5.9	12.4	0.2	49.1
14	1.3	4.5	0.9	0.2	6.9
15	-12.8	9.2	82.3	53.2	131.9
16	-5.6	4.1	1.9	1.6	2.0
17	28.7	1.1	9.0	16.3	55.1
18	-4.6	4.5	4.2	-1.0	3.1
19	2.6	0.6	-1.6	-1.6	0.0
20	-1.0	2.3	10.8	2.9	15.0
21	-0.4	-0.9	0.1	3.2	2.0
22	-0.3	0.0	0.1	4.2	4.0
23	2.6	0.6	-1.6	-1.6	0.0
24	11.9	-0.6	2.4	4.3	18.0
25	-0.5	3.9	2.3	5.3	11.0
26	2.7	-0.1	-0.6	0.9	2.9
27	3.7	-0.2	0.2	-0.7	3.0
28	0.3	-0.2	0.9	1.9	2.9
29	-0.2	0.6	-0.6	0.2	0.0
30	0.1	-0.3	0.3	-0.1	0.0
31	-0.5	0.9	6.1	3.5	10.0
32	0.0	-0.1	0.1	0.1	0.1
33	0.4	0.0	-0.3	-0.1	0.0
34	0.0	-0.4	0.1	2.3	2.0
35	8.7	0.9	0.2	0.2	10.0
36	-0.9	-0.1	0.8	0.2	0.0
37	6.1	0.1	-1.5	-1.8	2.9
38	3.0	-0.1	0.1	-1.0	2.0
39	0.1	0.0	1.9	0.0	2.0
40	-0.1	-0.1	4.0	0.2	4.0

Table 1.9 (cont'd).

Node	Gene Partition				Total
	COI	28S	CAD	ArgK	
41	0.3	0.0	3.9	-0.3	3.9
42	2.6	0.6	-1.5	-1.7	0.0
43	-0.4	0.6	8.5	7.3	16.0
44	8.1	2.1	1.0	-0.3	10.9
45	10.0	0.7	-0.7	0.0	10.0
46	-0.2	1.6	2.3	5.3	9.0
47	-0.4	0.5	0.5	1.4	2.0
48	-0.3	-0.4	1.4	-0.7	0.0
49	-0.6	0.6	1.7	3.3	5.0
50	-0.3	-0.4	1.4	0.3	1.0
51	3.0	-0.1	0.0	0.1	3.0
Total	220.9	109.5	216.1	163.5	710.0

Table 1.10. Partition Bremer support values for the four gene parsimony phylogeny with gaps treated as a fifth character state. Nodes refer to Figure 1.5.

Node	Gene Partition				Total
	COI	28S	CAD	ArgK	
1	0.6	-0.1	-0.2	-0.2	0.1
2	0.0	0.2	-0.2	0.0	0.0
3	-0.2	-0.2	0.4	0.0	0.0
4	0.5	0.0	-0.1	-0.4	0.0
5	0.8	0.1	-0.4	-0.4	0.1
6	0.7	0.0	-0.2	-0.5	0.0
7	0.5	0.2	-0.5	-0.2	0.0
8	0.0	0.0	-0.1	0.1	0.0
9	0.2	0.0	-0.2	0.1	0.1
10	0.0	-0.3	0.3	0.0	0.0
11	0.6	-0.2	0.1	-0.5	0.0
12	0.0	-0.2	0.0	0.2	0.0
13	-0.1	-0.2	0.2	0.1	0.0
14	-0.3	0.1	0.1	0.1	0.0
15	0.4	0.0	-0.2	-0.2	0.0
16	1.0	0.0	-0.6	-0.4	0.0
17	0.2	0.0	-0.1	-0.1	0.0
18	0.2	0.1	-0.3	0.0	0.0
19	-0.1	0.0	0.0	0.1	0.0
20	-0.1	0.0	0.0	0.1	0.0
21	0.1	-0.1	0.0	0.0	0.0
22	-0.2	-0.3	0.3	0.2	0.0
23	-0.1	0.1	0.0	0.0	0.0
24	0.2	-0.1	-0.1	0.0	0.0
25	0.1	-0.3	0.2	0.1	0.1
26	-0.2	-0.2	0.3	0.1	0.0
27	0.2	0.2	-0.5	0.2	0.1
28	-0.1	-0.1	0.2	0.0	0.0
29	1.1	-0.2	-0.4	-0.5	0.0
30	0.5	0.3	-0.5	-0.3	0.0
31	0.7	0.0	-0.3	-0.4	0.0
32	-0.1	-0.2	0.2	0.1	0.0
33	0.3	0.0	-0.3	0.0	0.0
34	0.1	-0.1	0.0	0.0	0.0
35	0.1	-0.1	0.1	0.0	0.1
36	0.1	-0.3	0.4	-0.2	0.0
37	0.0	-0.2	0.2	0.0	0.0
38	-0.3	-0.1	0.4	0.0	0.0
39	0.5	-0.1	-0.2	-0.2	0.0
40	0.9	-0.1	-0.2	-0.6	0.0

Table 1.10 (cont'd).

Node	Gene Partition				Total
	COI	28S	CAD	ArgK	
41	0.2	-0.2	0.0	0.0	0.0
42	0.2	0.1	-0.2	0.0	0.1
43	0.2	0.0	0.0	-0.2	0.0
44	0.0	-0.2	0.1	0.1	0.0
45	-0.3	-0.2	0.3	0.2	0.0
46	0.8	0.0	-0.6	-0.2	0.0
47	0.3	-0.6	0.3	0.0	0.0
48	0.6	0.0	-0.2	-0.4	0.0
49	-0.1	0.0	0.0	0.2	0.1
50	0.3	-0.2	0.1	-0.2	0.0
51	0.0	-0.6	1.0	-0.4	0.0
Total	11.0	-4.3	-1.4	-4.5	0.8

Table 1.11. Partition Bremer support values for the combined phylogeny with gaps treated as missing data. Nodes refer to Figure 1.7.

Node	Partition					Total
	COI	28S	CAD	ArgK	Morphology	
1	13.3	2.0	-2.3	-4.0	1.9	10.9
2	1.3	0.0	-0.2	0.0	-0.2	0.9
3	28.2	5.3	-1.6	-1.7	3.8	34.0
4	0.9	0.0	-0.5	0.0	5.5	5.9
5	-0.7	7.0	3.3	1.0	0.3	10.9
6	-0.6	7.0	3.3	1.0	-5.7	5.0
7	0.2	0.0	-0.1	0.0	3.9	4.0
8	13.6	2.0	-2.8	-4.0	-1.8	7.0
9	-1.6	9.0	4.8	7.0	-9.2	10.0
10	31.2	16.0	10.9	13.0	1.9	73.0
11	0.2	7.0	2.9	1.0	-10.1	1.0
12	0.5	7.0	2.7	1.0	-10.3	0.9
13	-0.6	7.0	3.3	1.0	0.3	11.0
14	-0.9	0.0	2.0	0.0	0.0	1.1
15	15.1	2.0	-2.7	-4.0	3.6	14.0
16	0.2	7.0	2.9	1.0	-10.1	1.0
17	51.9	0.0	61.1	34.0	9.1	156.1
18	-7.3	5.7	3.9	1.4	-1.7	2.0
19	29.5	1.0	8.7	16.0	1.7	56.9
20	-10.5	8.7	7.4	0.0	-3.6	2.0
21	0.5	3.0	1.1	-0.3	-3.2	1.1
22	-0.1	0.0	0.0	0.0	3.0	2.9
23	0.2	-1.0	-0.1	3.0	-0.1	2.0
24	-0.7	7.0	4.9	2.0	-8.1	5.1
25	6.8	1.5	-1.0	-1.7	-3.6	2.0
26	-0.1	0.0	0.0	0.0	12.0	11.9
27	1.5	-0.3	-0.5	-0.2	2.5	3.0
28	6.1	0.8	-1.4	-1.7	-1.8	2.0
29	0.2	0.0	-0.1	0.0	0.9	1.0
30	3.2	0.0	-0.8	0.7	-0.1	3.0
31	3.4	-0.4	-0.1	0.1	0.0	3.0
32	-0.7	0.0	0.3	0.0	5.3	4.9
33	0.4	0.0	-0.2	0.0	0.8	1.0
34	0.2	0.0	-0.1	0.0	5.9	6.0
35	-0.2	0.0	0.1	0.0	6.1	6.0
36	-0.2	0.0	0.1	0.0	1.1	1.0
37	-0.1	0.0	0.1	0.0	4.0	4.0
38	0.3	0.0	-0.1	0.0	1.9	2.1
39	2.2	0.0	0.9	0.0	-0.1	3.0
40	0.0	0.0	1.0	0.0	0.0	1.0

Table 1.11 (cont'd).

Node	Partition					Total
	COI	28S	CAD	ArgK	Morphology	
41	0.2	0.0	-0.1	0.0	5.9	6.0
42	1.5	0.0	-0.7	0.3	1.8	2.9
43	1.6	0.0	-0.6	0.2	-0.2	1.0
44	-1.4	0.0	-0.1	2.7	-0.1	1.1
45	-1.9	0.0	0.0	2.0	1.0	1.1
46	1.0	0.0	-0.5	0.0	4.5	5.0
47	1.1	0	-0.1	0	-0.1	0.9
48	1	0	0	0	0	1
49	-5.1	0	0	4	5.1	4
50	-0.5	0	0.3	0	2.3	2.1
51	0.2	0	-0.1	0	3.9	4
52	-5.7	0	0.9	2	4.9	2.1
53	1	0	-0.5	0	2.5	3
54	4.1	0.5	-0.9	-1.1	0.4	3
55	0.2	0	-0.1	0	0.9	1
56	0.3	0	-0.2	0	7.8	7.9
57	0.2	0	-0.1	0	1.9	2
58	0.2	0	-0.1	0	1.9	2
59	0.2	0	-0.1	0	0.9	1
60	0.2	0	-0.1	0	2.9	3
61	0.5	0	-0.3	0	6.7	6.9
62	-0.6	0	0.3	0	4.3	4
63	3.1	0	-0.1	0	-0.1	2.9
64	1.2	0	0.4	0	-0.6	1
65	0.8	0	0.1	0	0.1	1
Total	190.2	104.8	108.4	75.7	64.4	543.5

Table 1.12. Partition Bremer support values for the combined phylogeny with gaps treated as a fifth character. Nodes refer to Figure 1.8.

Node	Partition					Total
	COI	28S	CAD	ArgK	Morphology	
1	-6.2	5.4	3.4	-0.7	7.1	9.0
2	-1.3	-1.3	-0.7	3.5	-0.2	0.0
3	25.9	2.4	-3.0	0.0	6.8	32.1
4	-1.2	-1.3	-1.0	1.8	7.6	5.9
5	29.3	18.6	11.9	8.3	9.9	78.0
6	-0.5	-1.3	-0.9	1.0	1.7	0.0
7	6.0	-1.1	-2.0	-0.9	-2.0	0.0
8	2.0	15.7	2.1	2.5	-9.3	13.0
9	6.4	-2.3	-1.7	-1.5	9.0	9.9
10	42.5	6.7	6.8	0.1	5.8	61.9
11	-2.0	-1.3	1.1	2.5	-0.3	0.0
12	12.2	-1.3	-3.5	-2.5	-2.9	2.0
13	-2.0	-1.3	1.1	5.5	-0.3	3.0
14	14.8	0.7	12.8	8.5	1.1	37.9
15	0.6	-2.0	-1.0	0.7	5.8	4.1
16	-1.2	-1.4	-0.5	1.0	12.1	10.0
17	1.0	0.8	0.0	0.6	2.8	5.2
18	3.7	-0.8	-0.4	-1.5	12.1	13.1
19	4.4	-2.2	-2.0	-0.1	-0.1	0.0
20	2.1	0.0	-0.5	-0.4	-1.2	0.0
21	-4.7	4.7	3.0	-1.0	-2.0	0.0
22	9.4	-1.0	-2.7	-1.7	-2.0	2.0
23	-0.4	-1.5	-0.6	0.6	14.0	12.1
24	4.0	-0.2	-1.2	-0.6	-2.0	0.0
25	-4.8	1.2	1.6	4.9	4.1	7.0
26	-1.0	-2.3	-0.9	4.5	1.7	2.0
27	4.6	-1.8	-1.8	-0.2	1.1	1.9
28	7.8	-1.0	-2.0	-1.2	-3.6	0.0
29	-2.3	-1.3	-0.7	2.5	1.8	0.0
30	-2.2	-1.3	-0.8	2.5	5.8	4.0
31	0.5	-1.3	-1.4	3.2	-0.1	0.9
32	1.1	-1.6	-0.8	2.5	-0.2	1.0
33	-1.7	-1.3	-1.0	2.5	1.5	0.0
34	-2.3	-1.3	-0.7	2.5	1.8	0.0
35	-2.3	-1.3	-0.7	2.5	1.8	0.0
36	-2.4	-1.3	-0.8	2.8	1.7	0.0
37	-2.1	-1.3	-0.9	2.5	7.7	5.9
38	-2.1	-1.3	-0.9	2.5	1.8	0.0
39	-0.6	-1.0	-0.6	0.9	4.3	3.0
40	-8.3	-1.2	0.2	4.5	4.8	0.0

Table 1.12 (cont'd).

Node	Partition					Total
	COI	28S	CAD	ArgK	Morphology	
41	6.3	-1.0	-2.2	-0.6	-1.6	0.9
42	-2.2	-1.3	-0.8	2.5	3.8	2.0
43	-2.8	-1.3	-0.5	2.5	2.1	0.0
44	-6.8	-1.3	-1.0	6.4	4.6	1.9
45	-1.3	-2.3	-0.7	2.5	-0.2	-2.0
46	-1.4	-1.3	0.7	2.5	0.2	0.7
47	6.4	-0.8	-1.8	1.8	-0.6	5.0
48	-1.5	-1.3	-1.1	2.5	5.4	4.0
49	0	-1.3	0.1	2.5	-0.4	0.9
50	-1	-1.3	0.1	2.5	-0.3	0.0
51	-3.4	-1.3	-1.2	4.5	1.4	0.0
52	-1.4	-1.3	-1	3.5	0.2	0.0
53	-1.6	-1.3	-1.2	3.2	1.9	1.0
54	-4.7	-1.3	-0.4	5.2	1.2	0.0
55	-1.9	-1.3	-1	2.5	1.7	0.0
56	-2.3	-1.3	-0.7	2.5	3.8	2.0
57	-1.8	-1.3	-0.5	2.5	1.1	0.0
58	-2.5	-1.3	-0.6	2.5	5.9	4.0
59	-1.7	-1.3	-1	2.5	5.5	4.0
60	2.6	-0.6	-0.6	-0.4	1.9	2.9
61	-2.3	-1.3	-0.7	2.5	6.8	5.0
62	-2.9	-1.3	-0.4	2.5	4.1	2.0
63	0.2	-1.3	-0.5	2.5	0.1	1.0
64	-1	-1.3	-0.4	2.5	-0.8	-1.0
65	-1.8	-1.3	-0.5	2.5	1.1	0.0
66	-1	-1.3	-1.4	2.5	1.2	0.0
Total	94.9	-18.0	-11.0	133.7	159.6	359.2

Figure 1.1. Morphological phylogeny of Nearctic *Scolytus*. Phylogram of one of 1016 most parsimonious trees (262 steps; consistency index 0.332; retention index = 0.539) generated for 37 taxa with 43 characters from a heuristic search of 1000 stepwise random additions with TBR in PAUP*. Numbers above the node indicate bootstrap values (>50) based on 1000 pseudoreplicates. Bremer support values are listed below the node and were generated from a heuristic search of 100 random addition sequence replicates. The Nearctic hardwood and conifer clades are indicated in blue and green respectively. Non-monophyletic species are indicated in brown. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis (or dissertation).

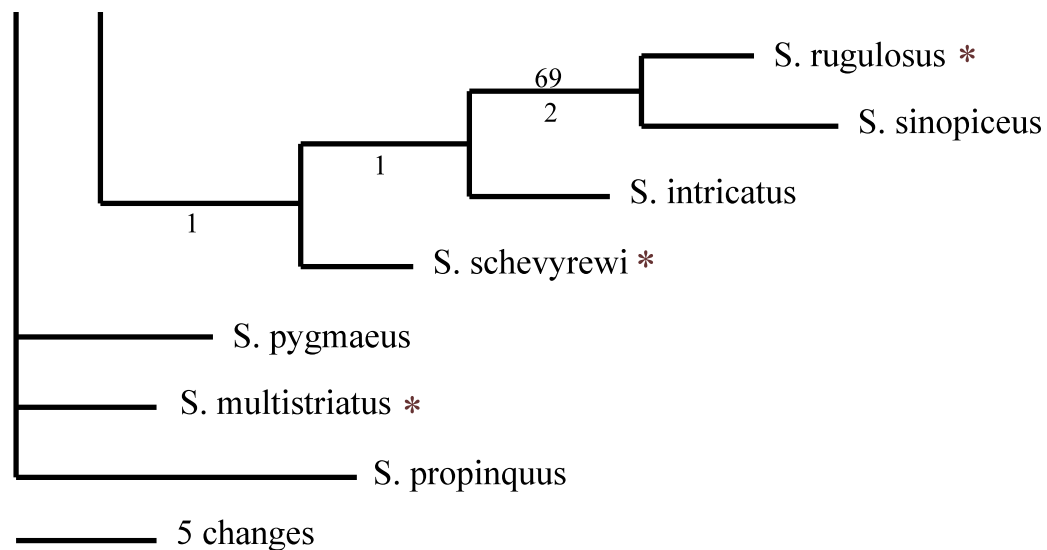


Figure 1.1 (cont'd).

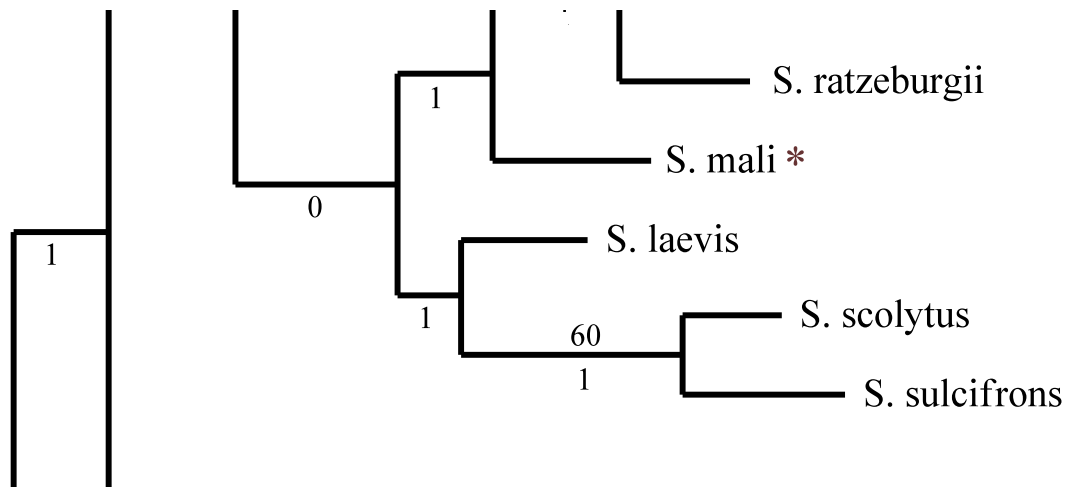


Figure 1.1 (cont'd).

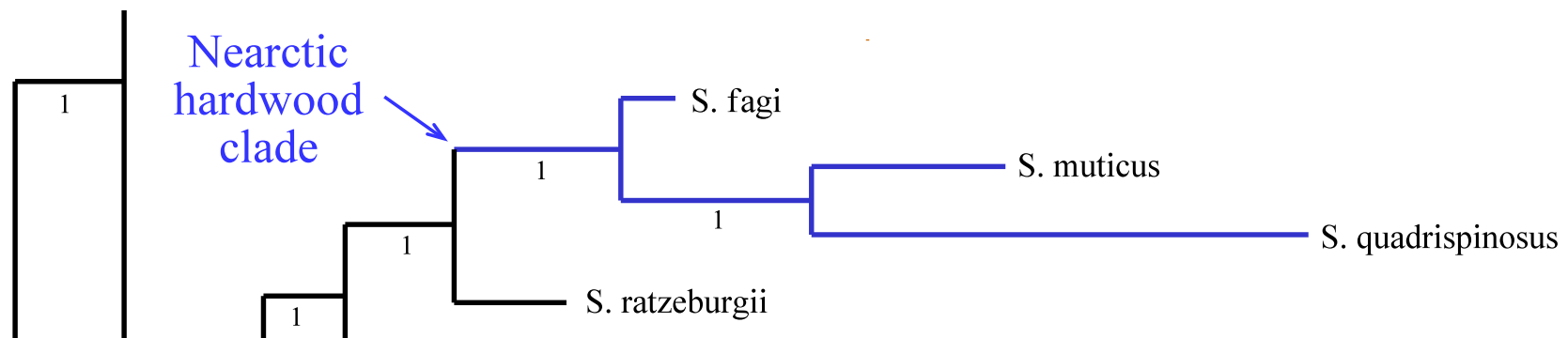


Figure 1.1 (cont'd).

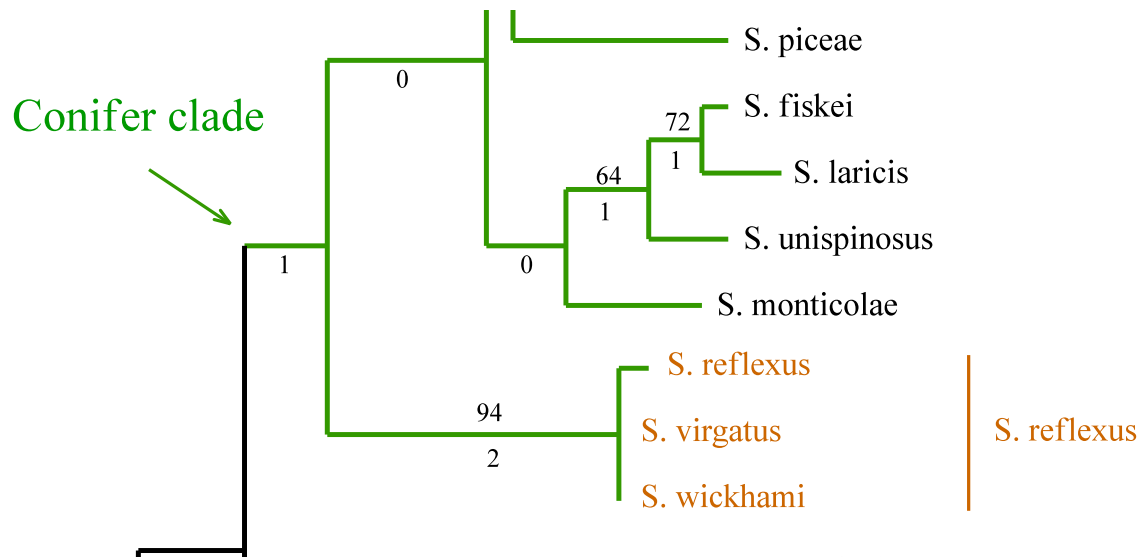


Figure 1.1 (cont'd).

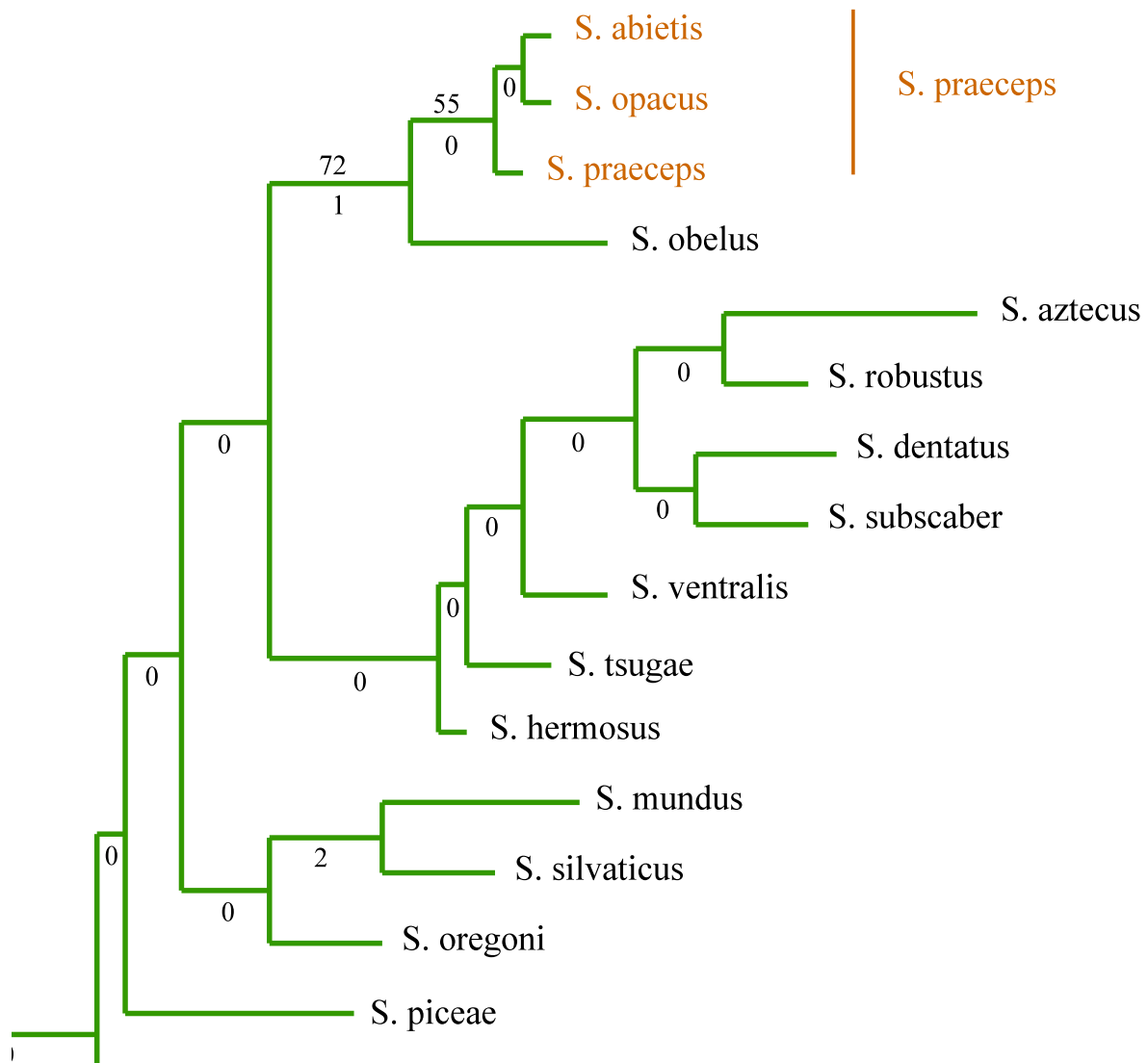


Figure 1.2. Bayesian tree found by analysis of data using the molecular dataset. Numbers above the nodes are Bayesian posterior probabilities. Taxa in brown were not recovered as monophyletic. *Scolytus fiskei* is listed in purple and is considered a synonym of *S. unispinosus*.

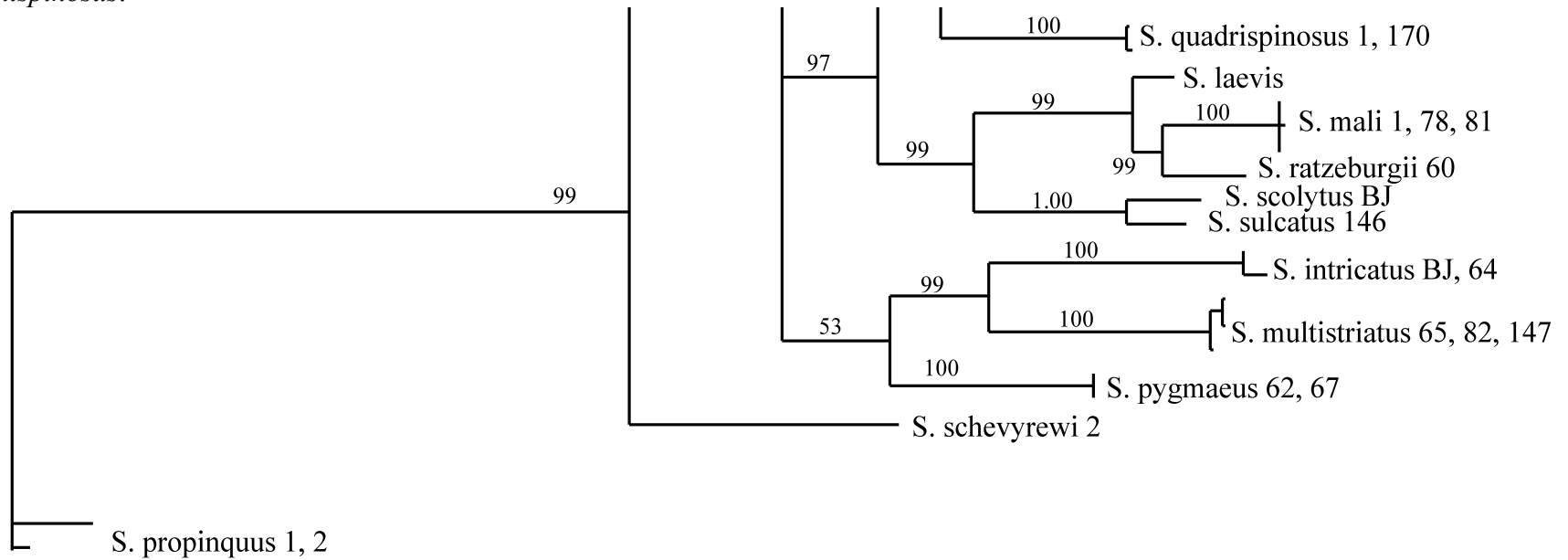


Figure 1.2 (cont'd).

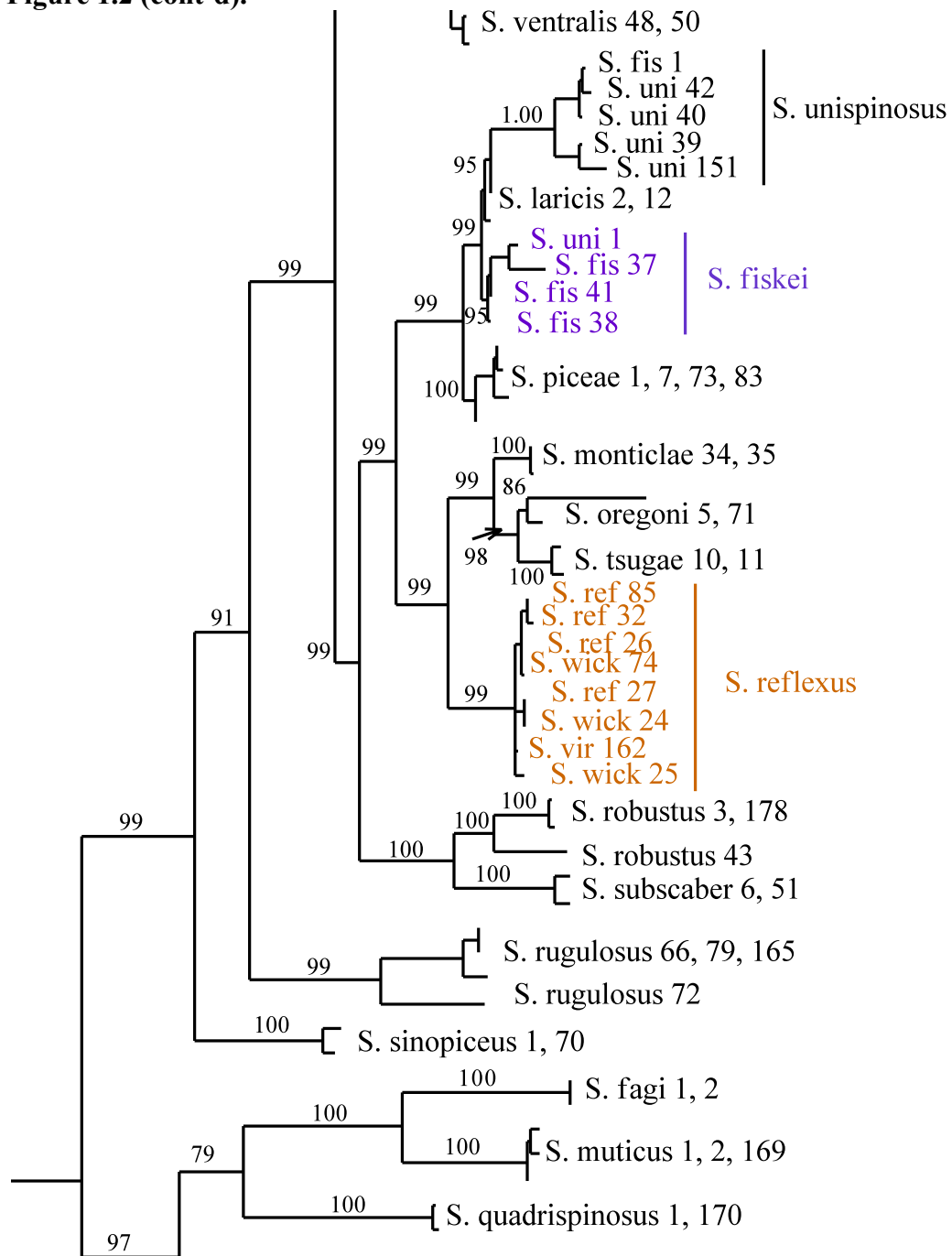


Figure 1.2 (cont'd).

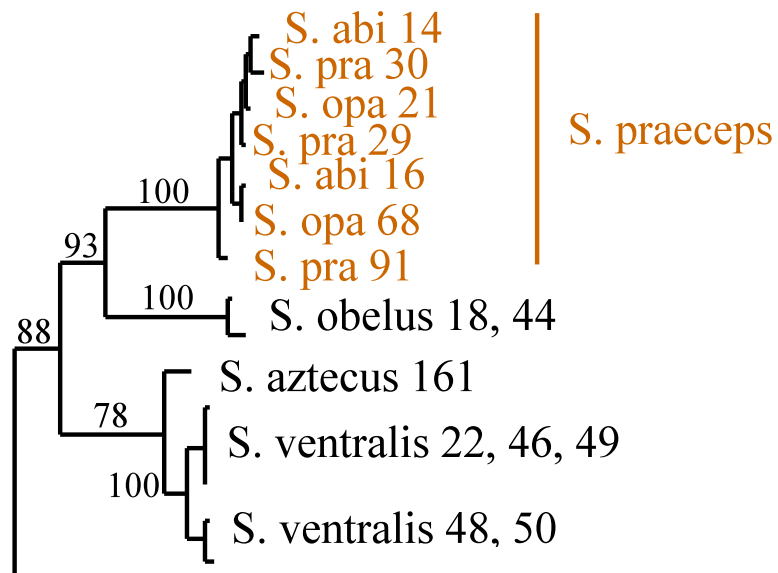


Figure 1.3. Mitochondrial COI phylogeny of Nearctic *Scolytus*. Phylogram of one of 2958 most parsimonious trees (1434 steps, consistency index 0.356; retention index 0.809) generated from a heuristic search of 1000 stepwise random additions with TBR in PAUP*. Numbers above the node indicate bootstrap values (>50) based on 1000 pseudoreplicates. Bremer support values are listed below the node and were generated from a heuristic search of 100 random addition sequence replicates. Mean intraspecific nucleotide differences (listed next to each taxon) and mean interspecific interspecific nucleotide differences (right of solid lines) are given. Taxa highlighted in red were not recovered as monophyletic.

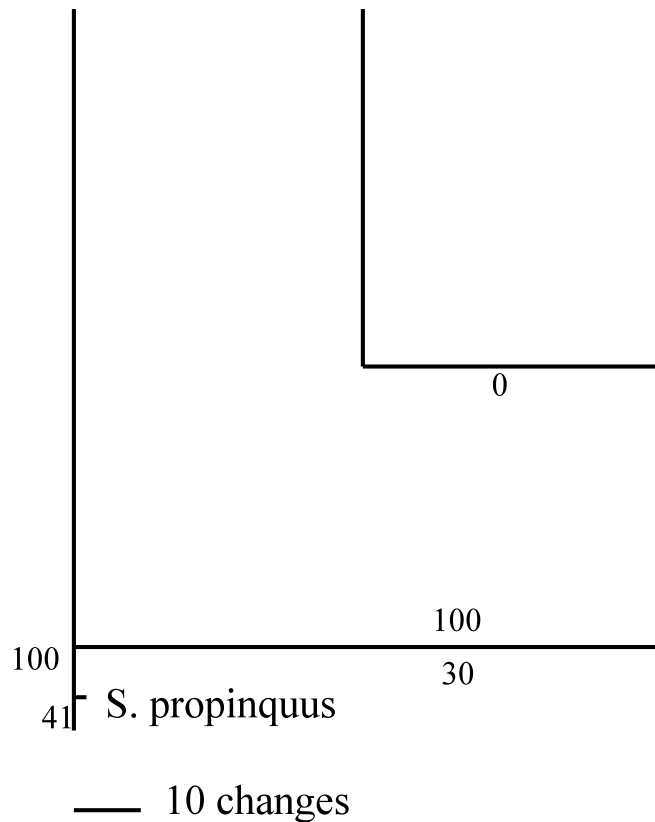


Figure 1.3 (cont'd).

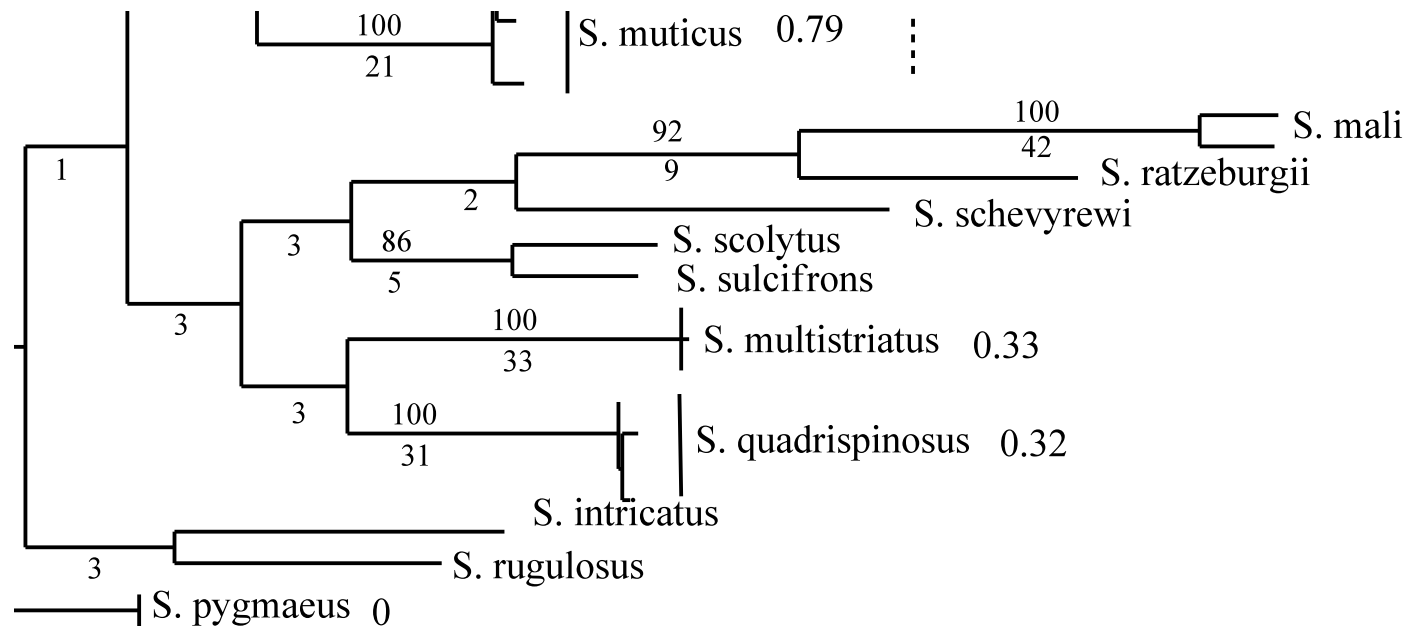


Figure 1.3 (cont'd).

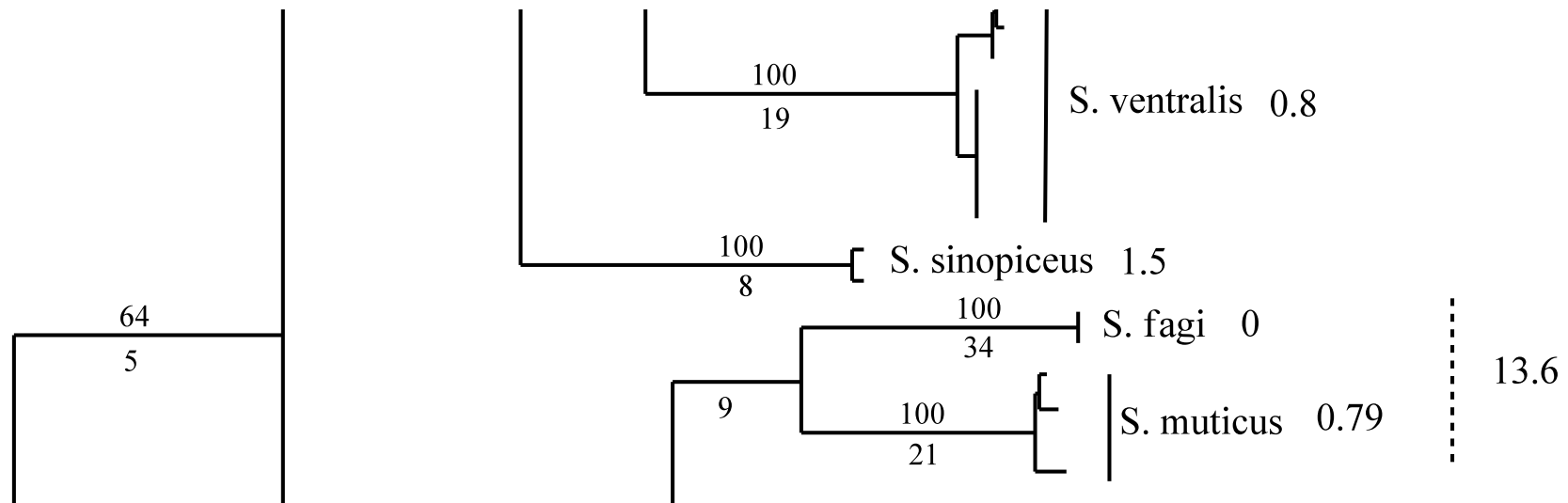


Figure 1.3 (cont'd).

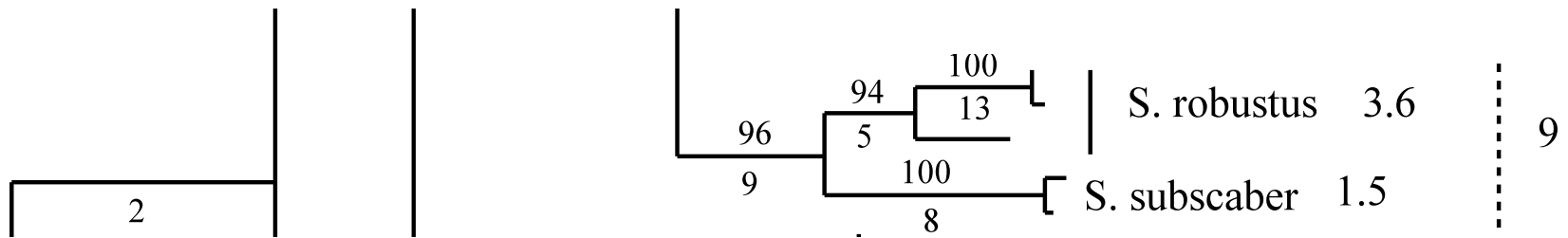


Figure 1.3 (cont'd).

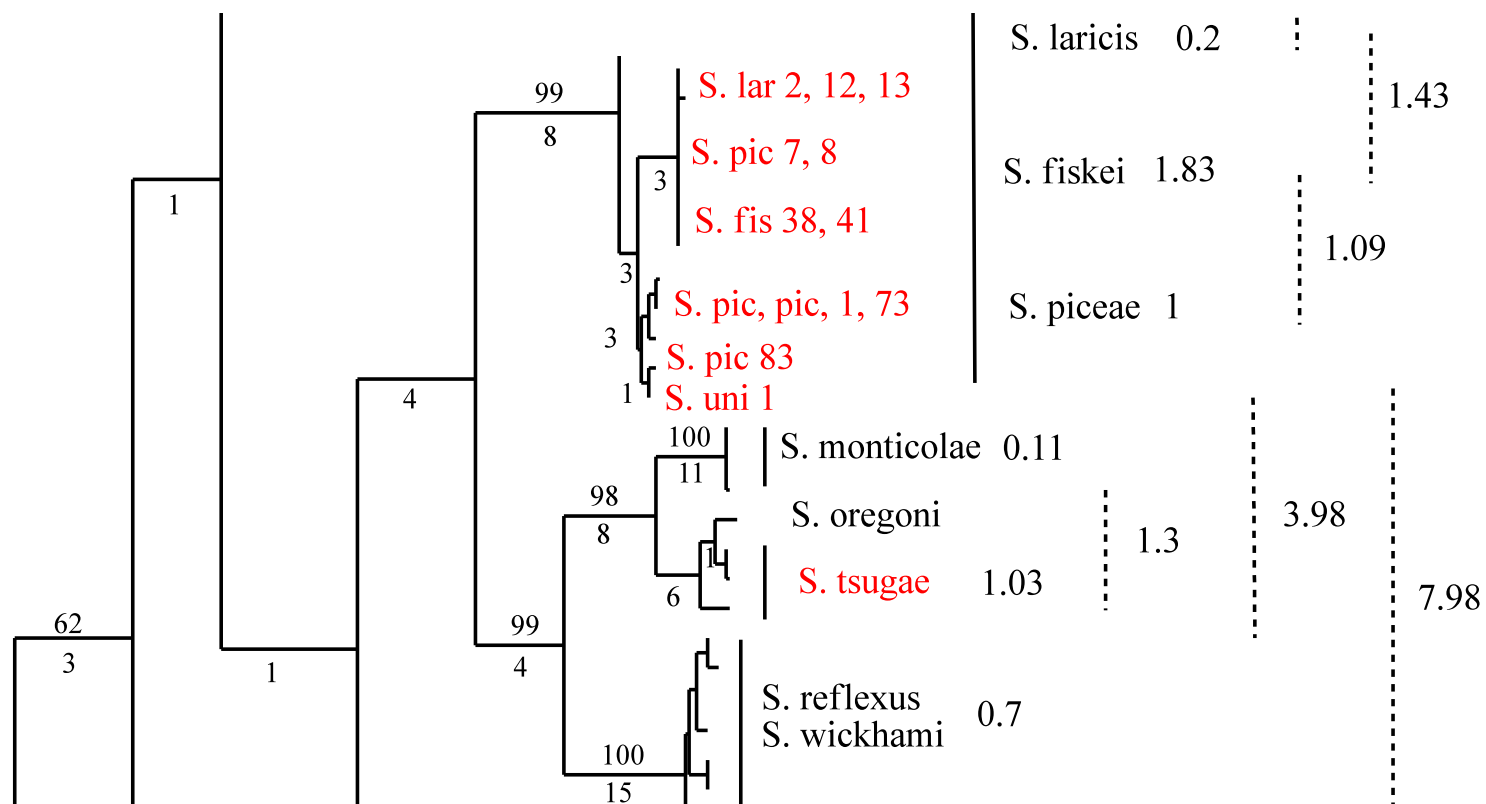


Figure 1.3 (cont'd).

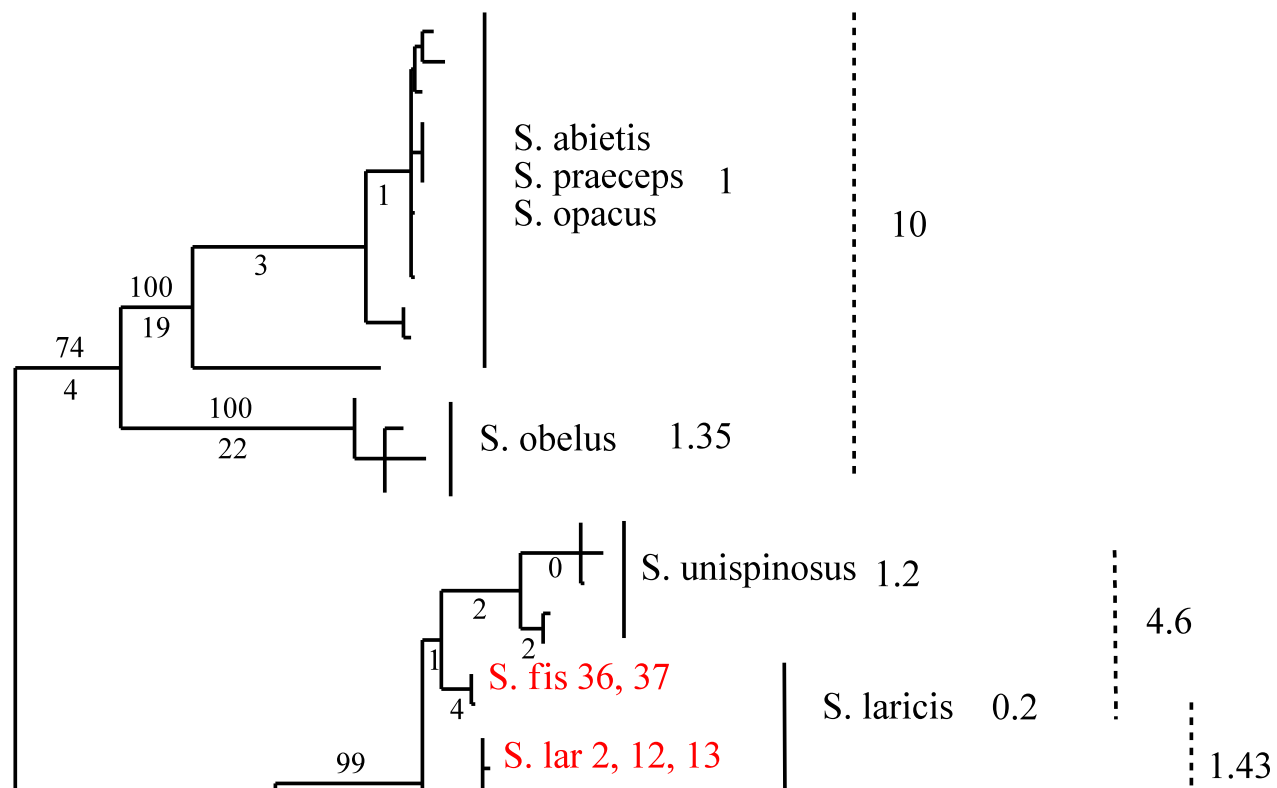


Figure 1.4. Phylogram of one of 94, 002 most parsimonious trees found by parsimony analysis of the four gene dataset with gaps treated as missing data (2,451 steps, consistency index 0.479; retention index 0.773) generated from a heuristic search of 1000 stepwise random additions with TBR in PAUP*. Numbers above the node indicate bootstrap values (>50) based on 1000 pseudoreplicates. Node numbers are given below the node and refer to PBS values in Table 1.9. Taxa in brown, blue and green were not recovered as monophyletic. *Scolytus fiskei* is listed in purple and is considered a synonym of *S. unispinosus*. *Scolytus laricis* is listed in green and was not recovered as monophyletic. *Scolytus oregoni* (blue) is a distinct species but was not monophyletic in this analysis. * denotes species that are recognized as valid.

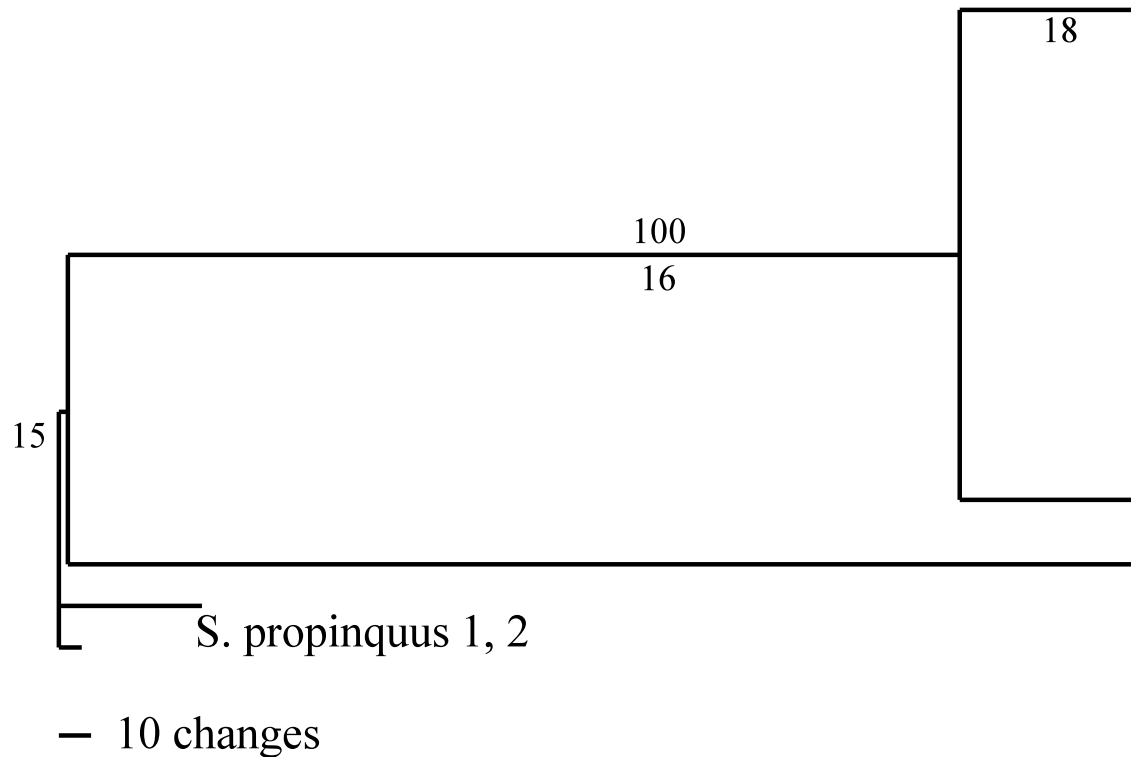


Figure 1.4 (cont'd).

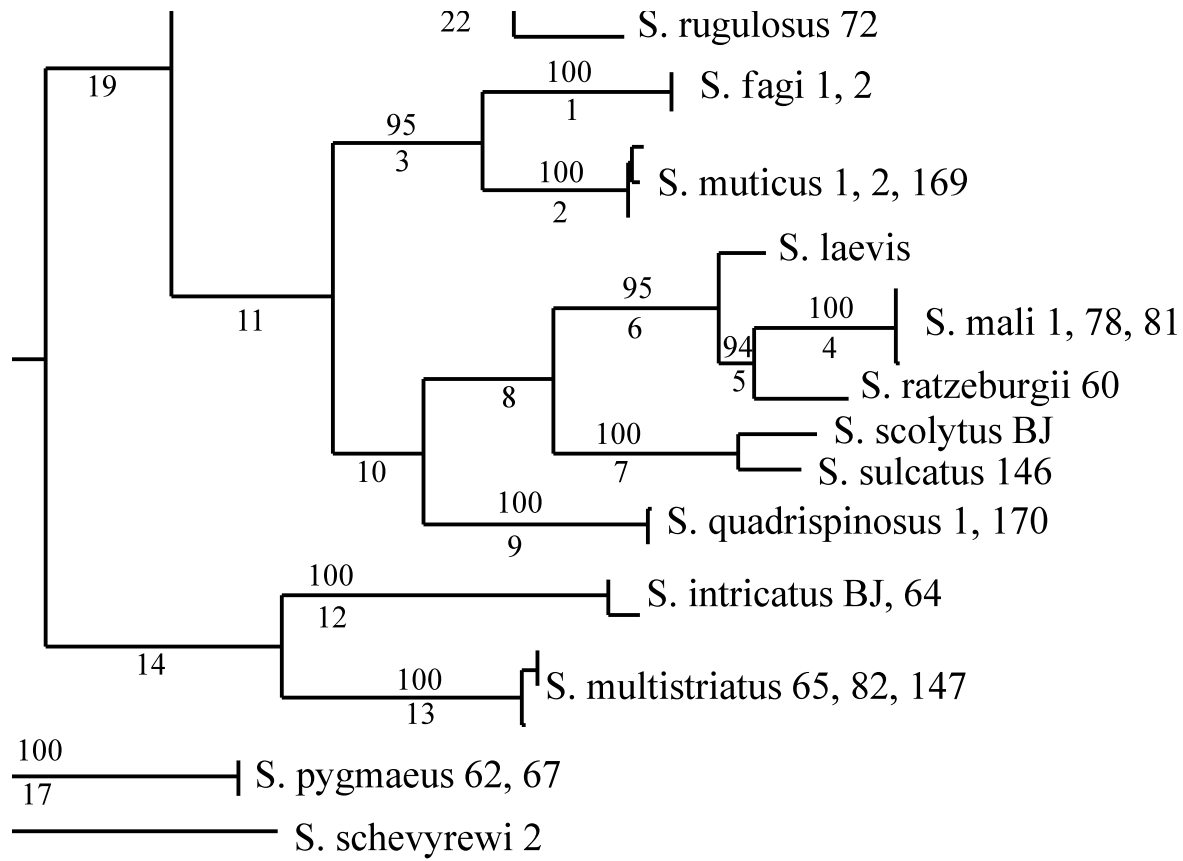


Figure 1.4 (cont'd).

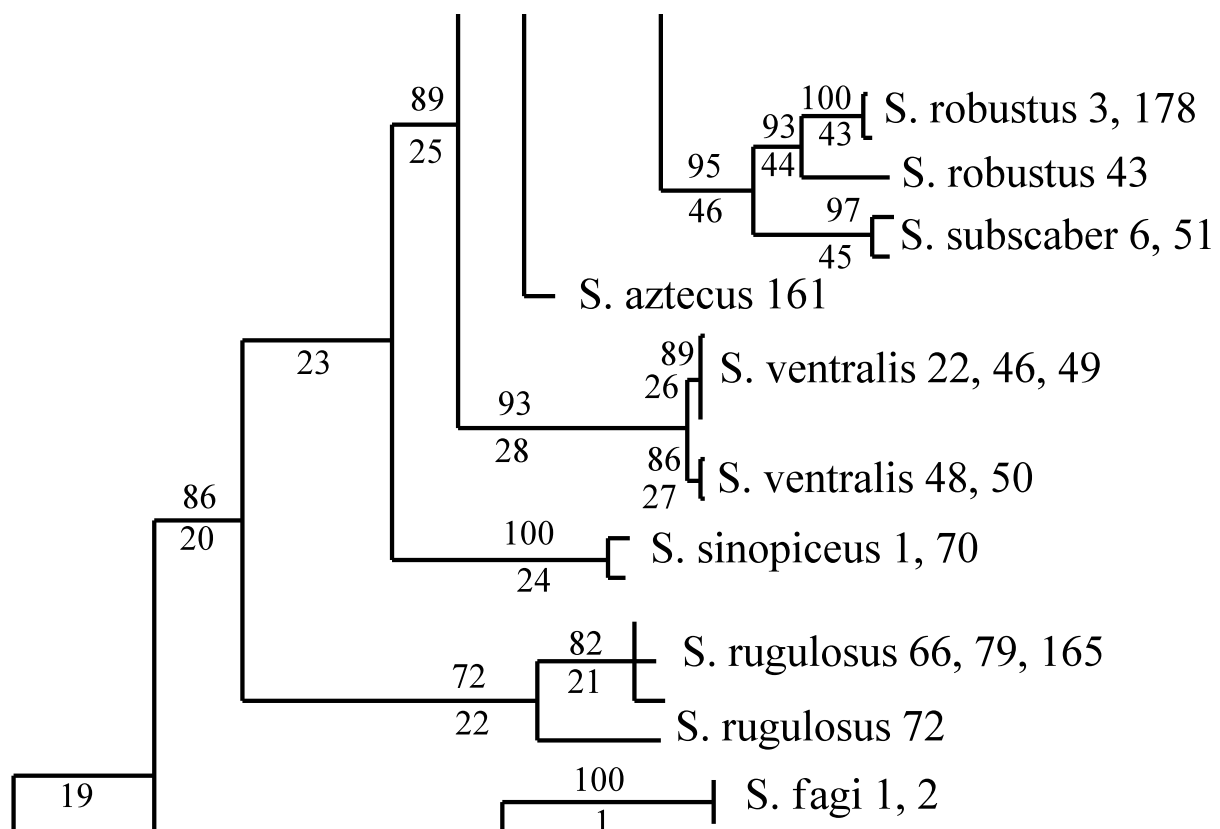


Figure 1.4 (cont'd).

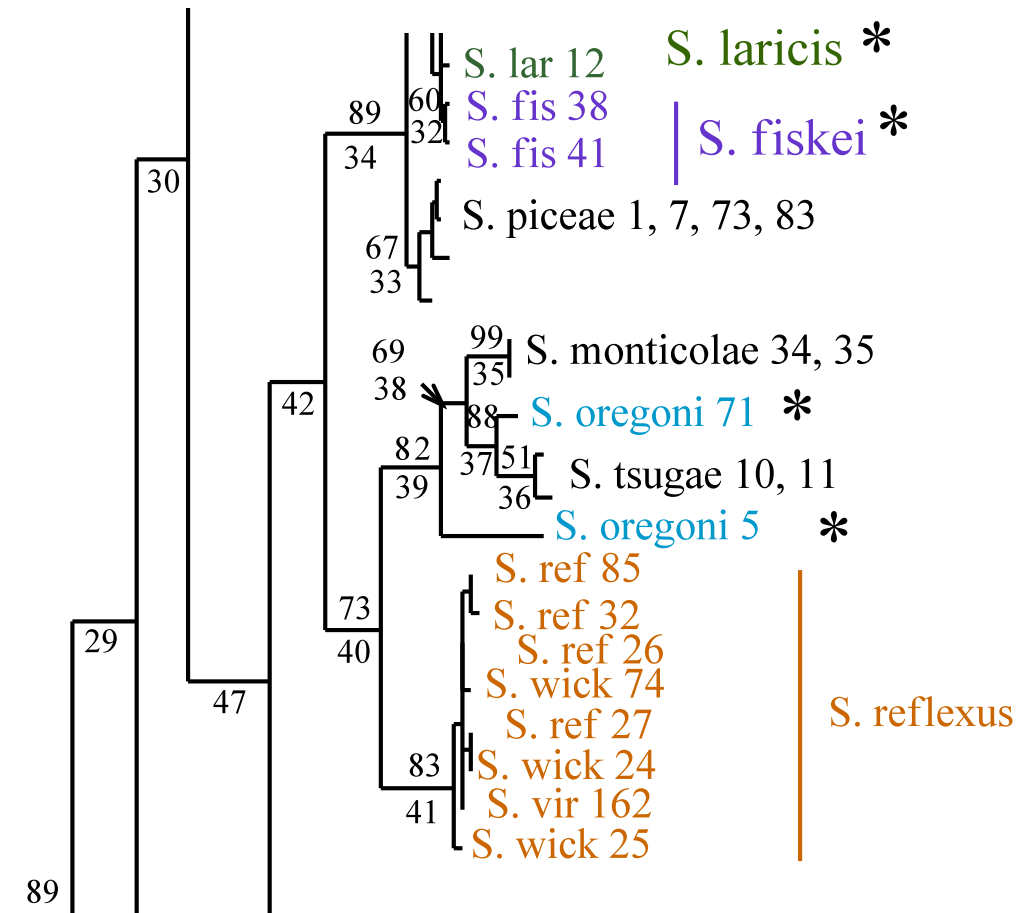


Figure 1.4 (cont'd).

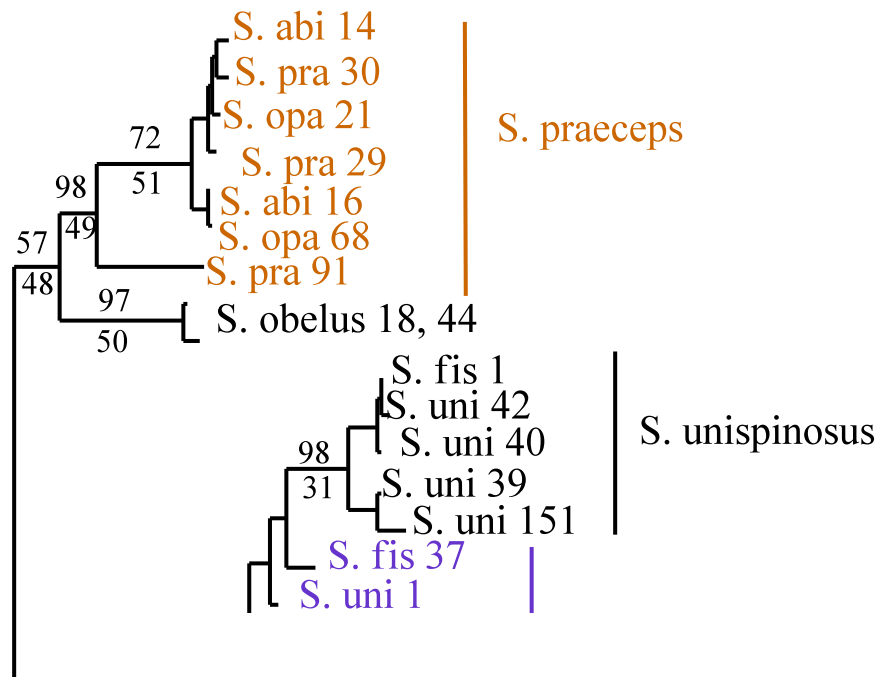


Figure 1.5. Phylogram of one of 59,010 most parsimonious trees found by parsimony analysis of the combined molecular dataset with gaps as a fifth character (2,647 steps, consistency index 0.479; retention index 0.773) generated from a heuristic search of 1000 stepwise random additions with TBR in PAUP*. Numbers above the node indicate bootstrap values (>50) based on 1000 pseudoreplicates. Node numbers are given below the node. Node numbers refer to PBS values in Table 1.10. Taxa in brown, blue and green were not recovered as monophyletic. *Scolytus fiskei* is listed in purple and is considered a synonym of *S. unispinosus*. *Scolytus laricis* is listed in green and was not recovered as monophyletic. *Scolytus oregoni* (blue) is a distinct species but was not monophyletic in this analysis. * denotes species that are recognized as valid.

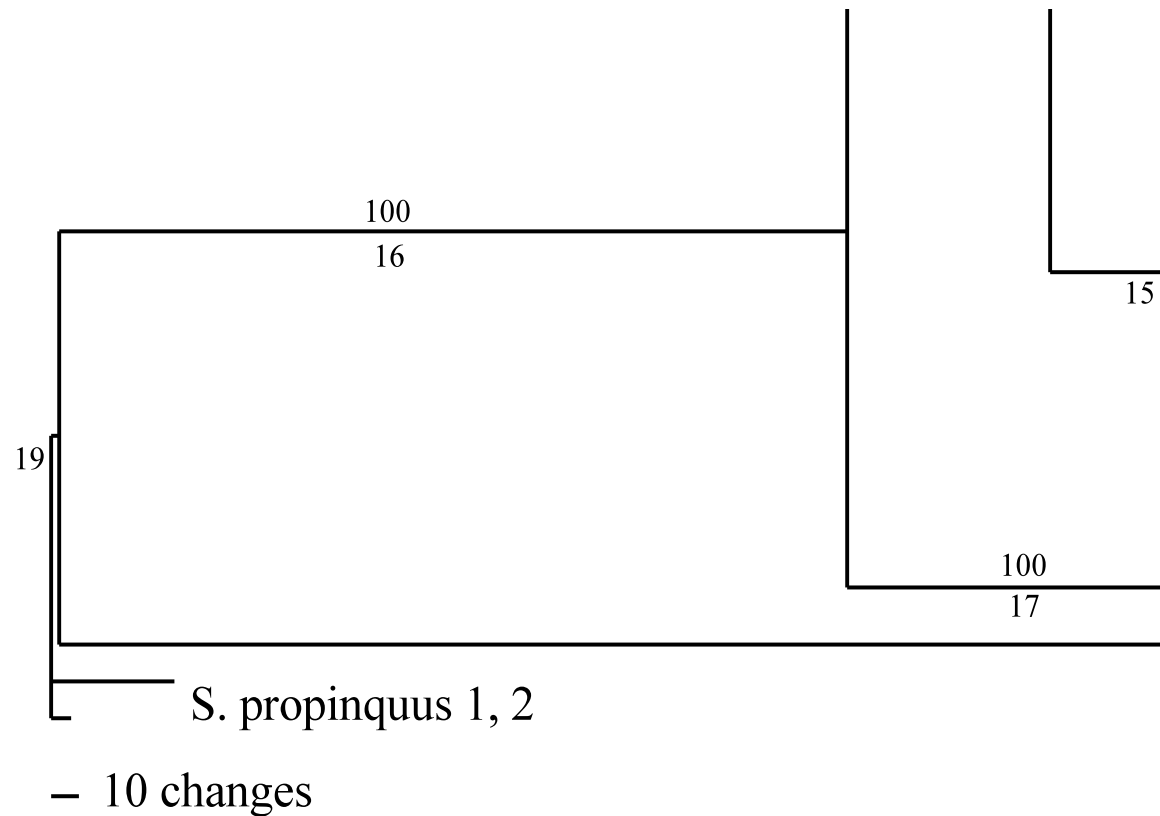


Figure 1.5 (cont'd).

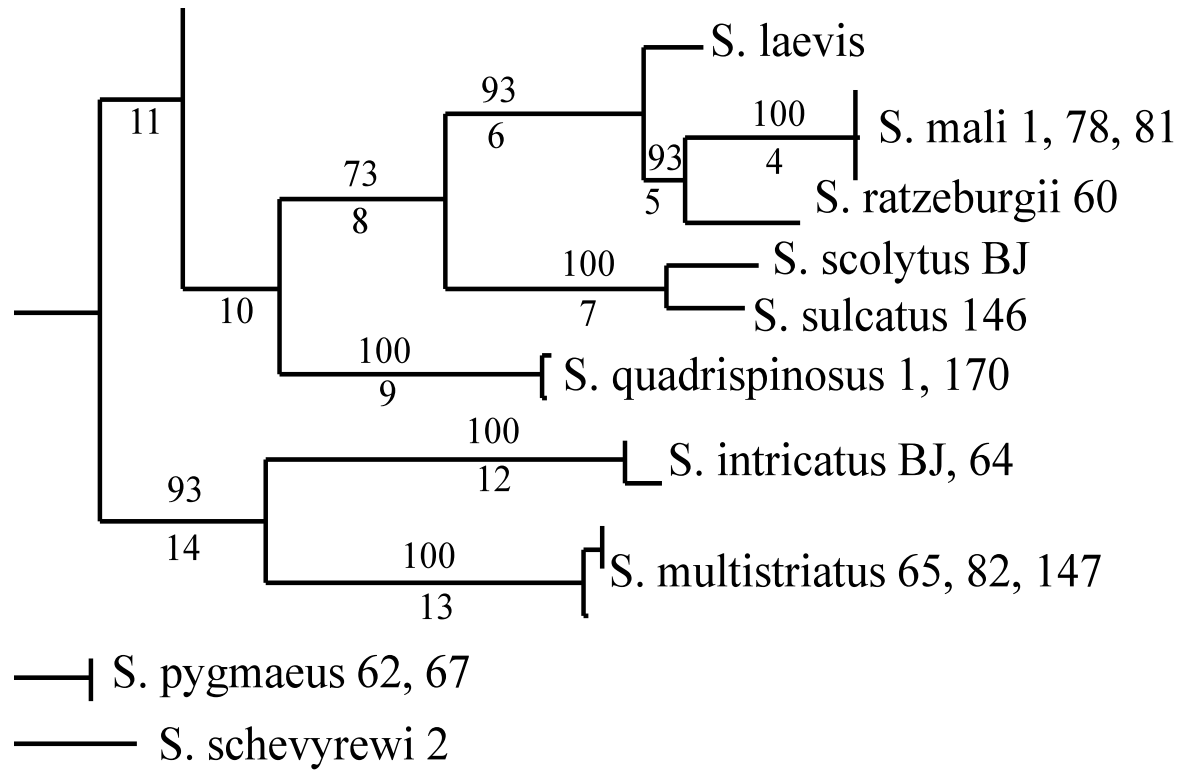


Figure 1.5 (cont'd).

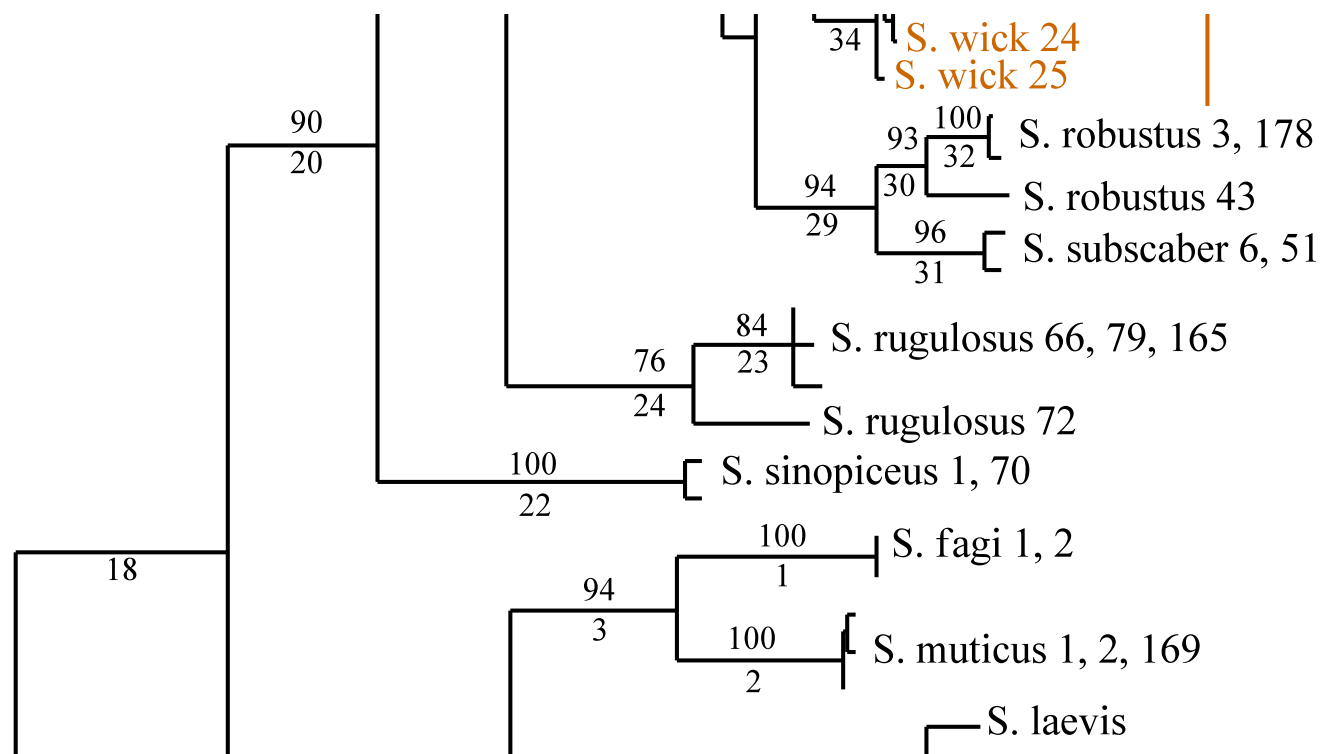


Figure 1.5 (cont'd).

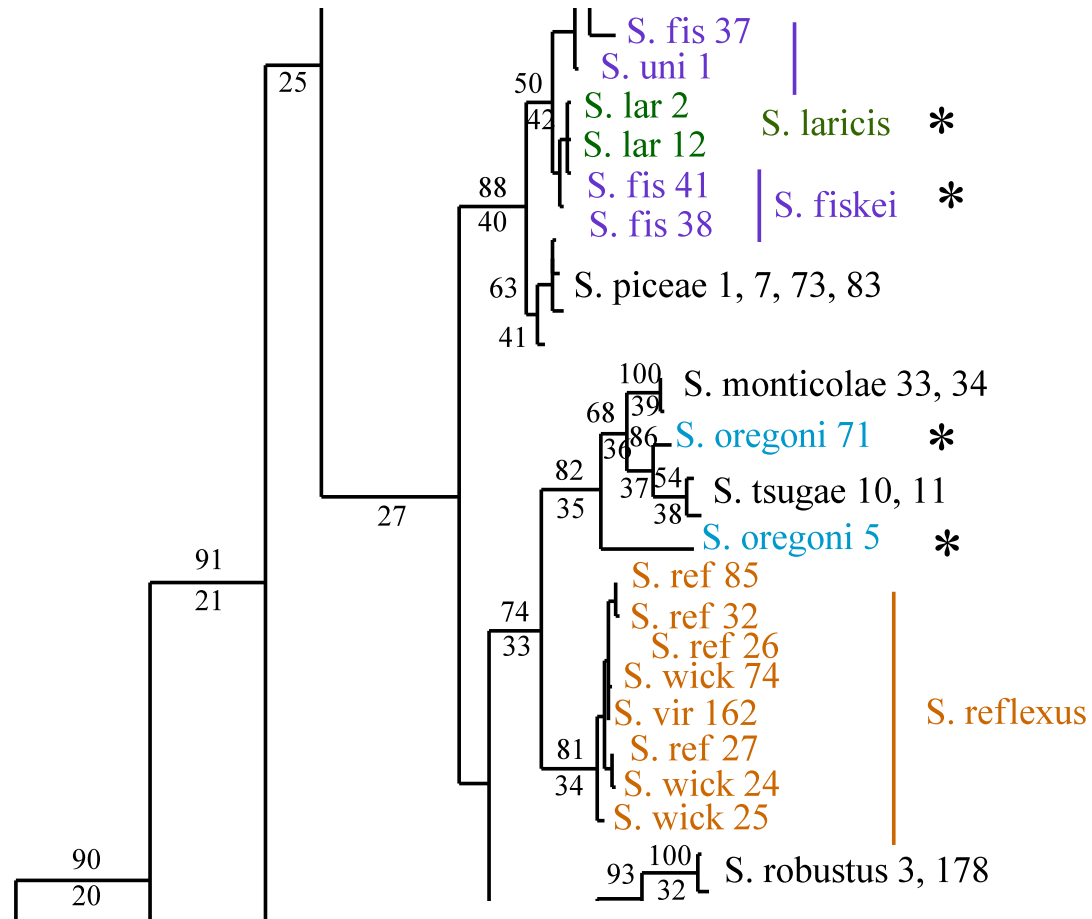


Figure 1.5 (cont'd).

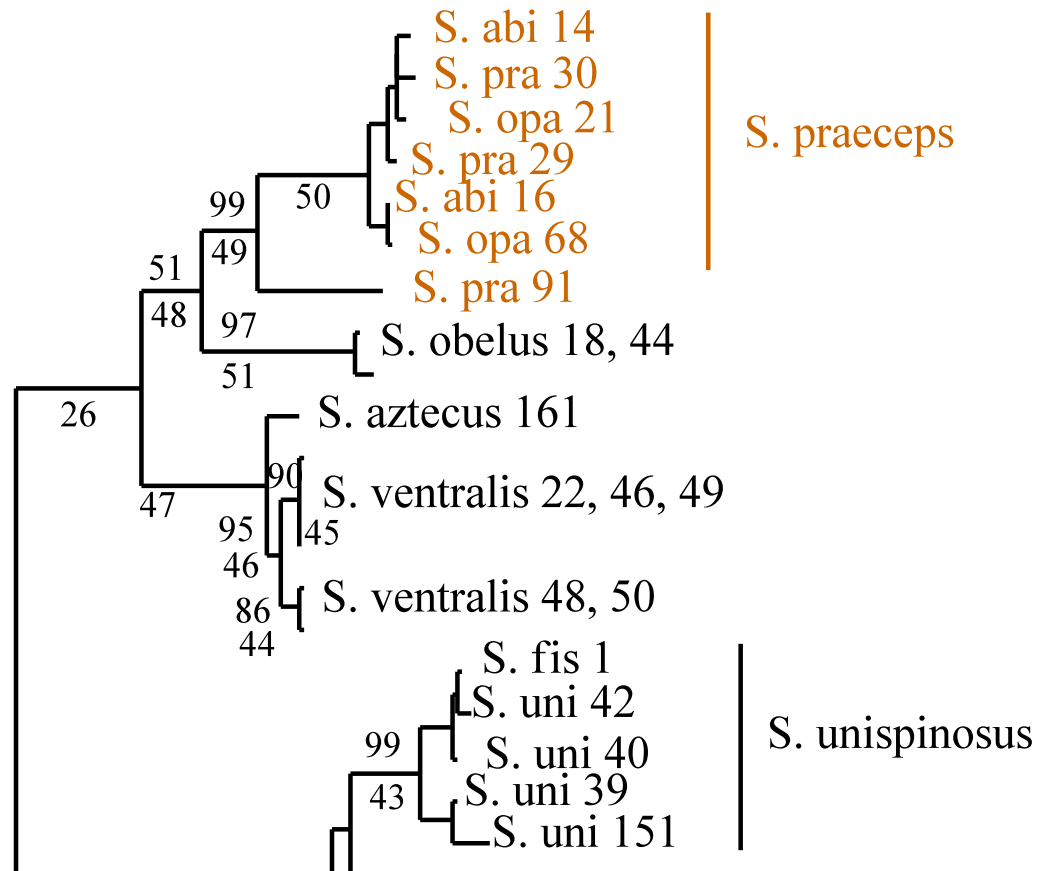


Figure 1.6 (cont'd).

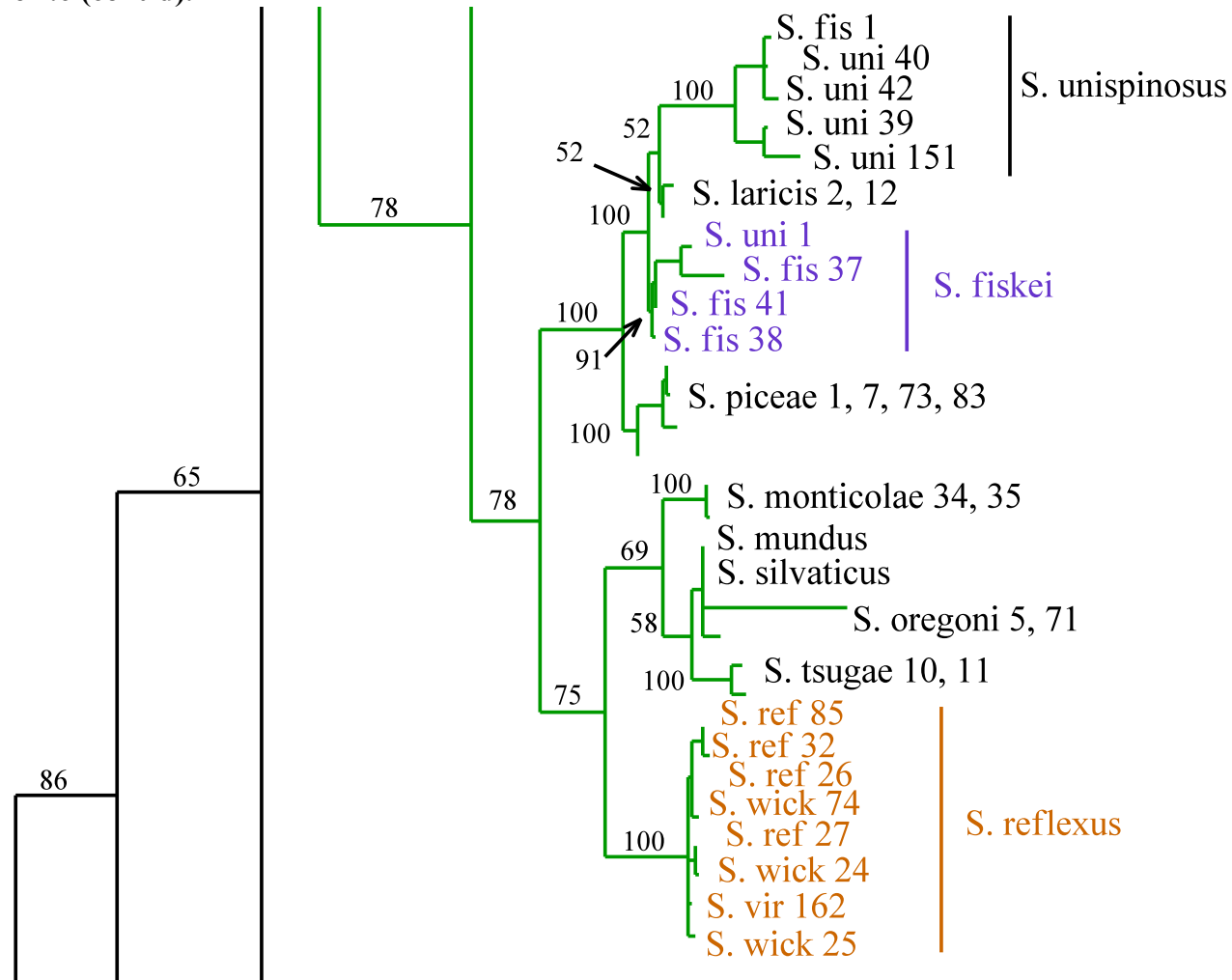


Figure 1.6 (cont'd).

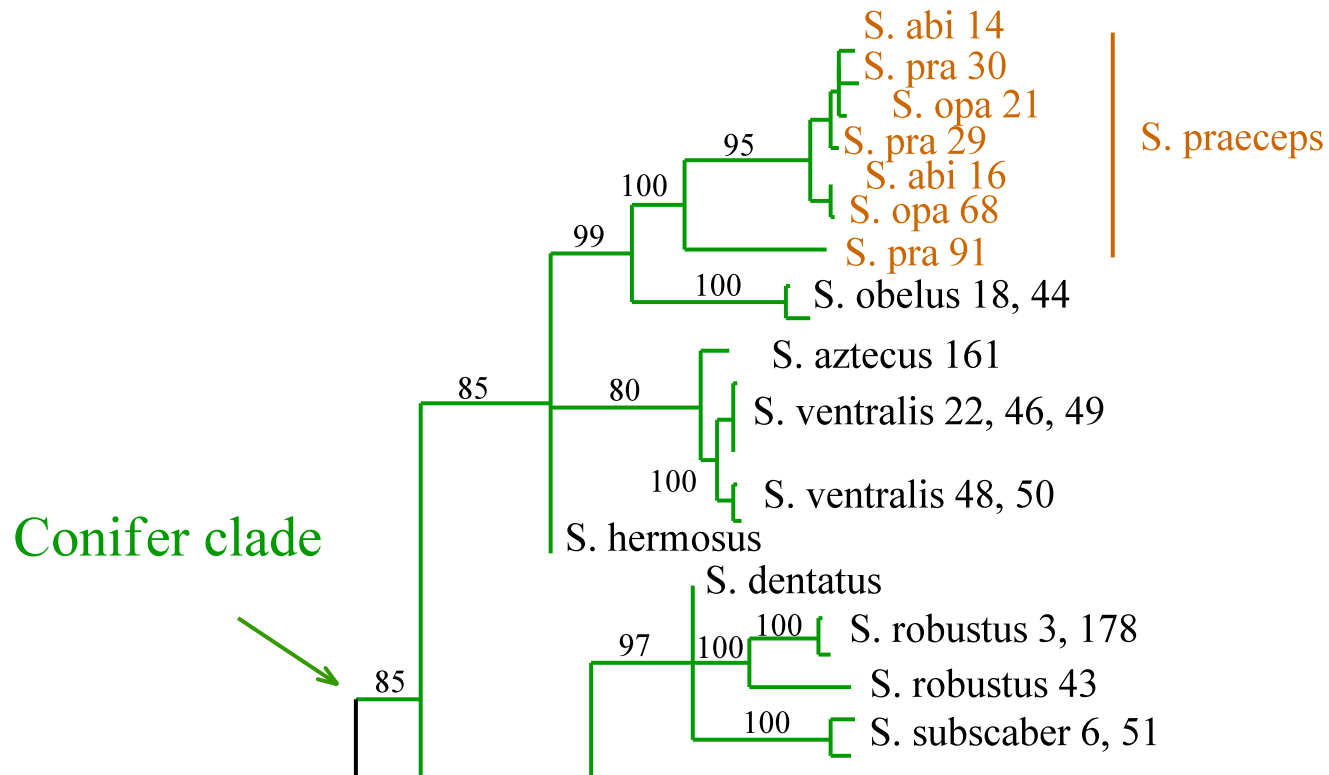


Figure 1.7. Strict consensus tree of 22,003 most parsimonious trees found by parsimony analysis of the combined molecular and morphological dataset with gaps treated as missing data (2,902 steps. consistency index 0.458; retention index 0.769) generated from a heuristic search of 100 stepwise random additions with TBR in PAUP*. Numbers above the node indicate bootstrap values (>50) based on 1000 pseudoreplicates. Node numbers are given below the node and refer to PBS values in Table 1.11. Taxa in brown were not recovered as monophyletic. *Scolytus fiskei* is listed in purple and is considered a synonym of *S. unispinosus*. * denotes species that are recognized as valid.

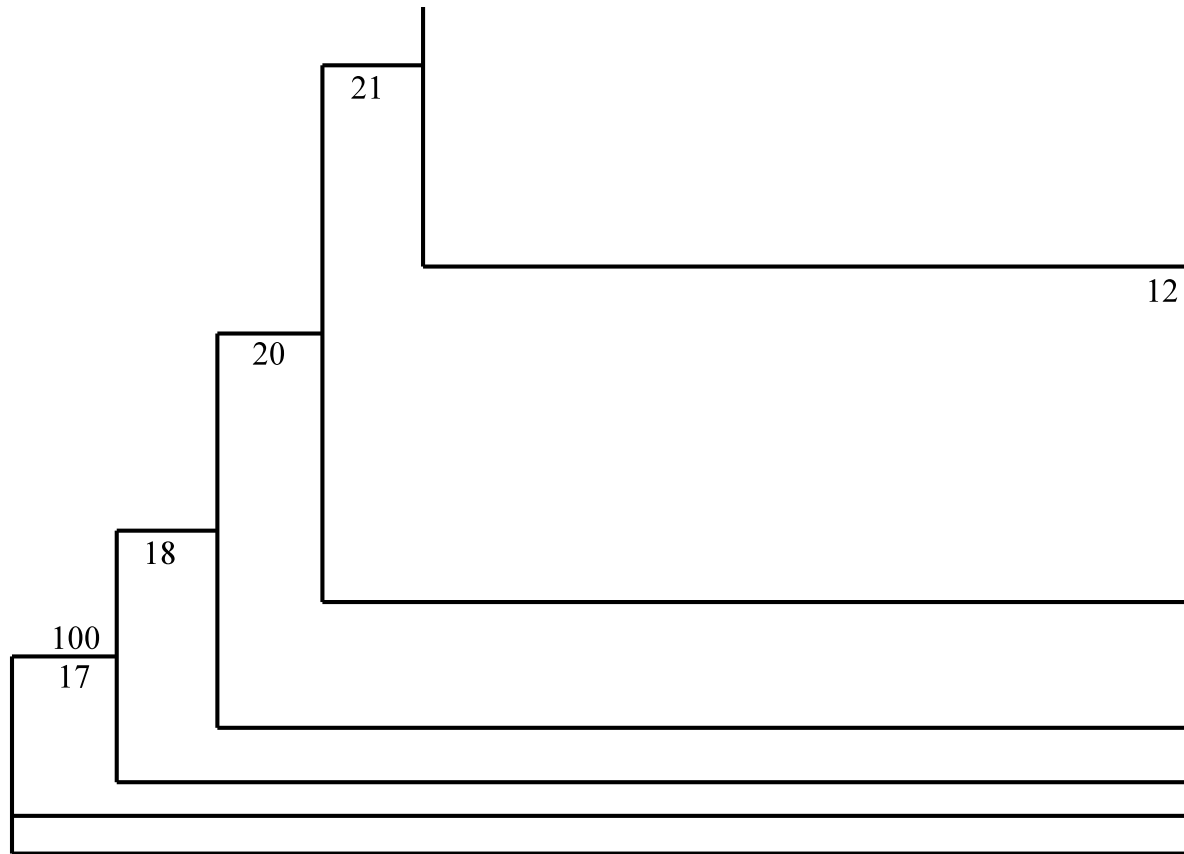


Figure 1.7 (cont'd).

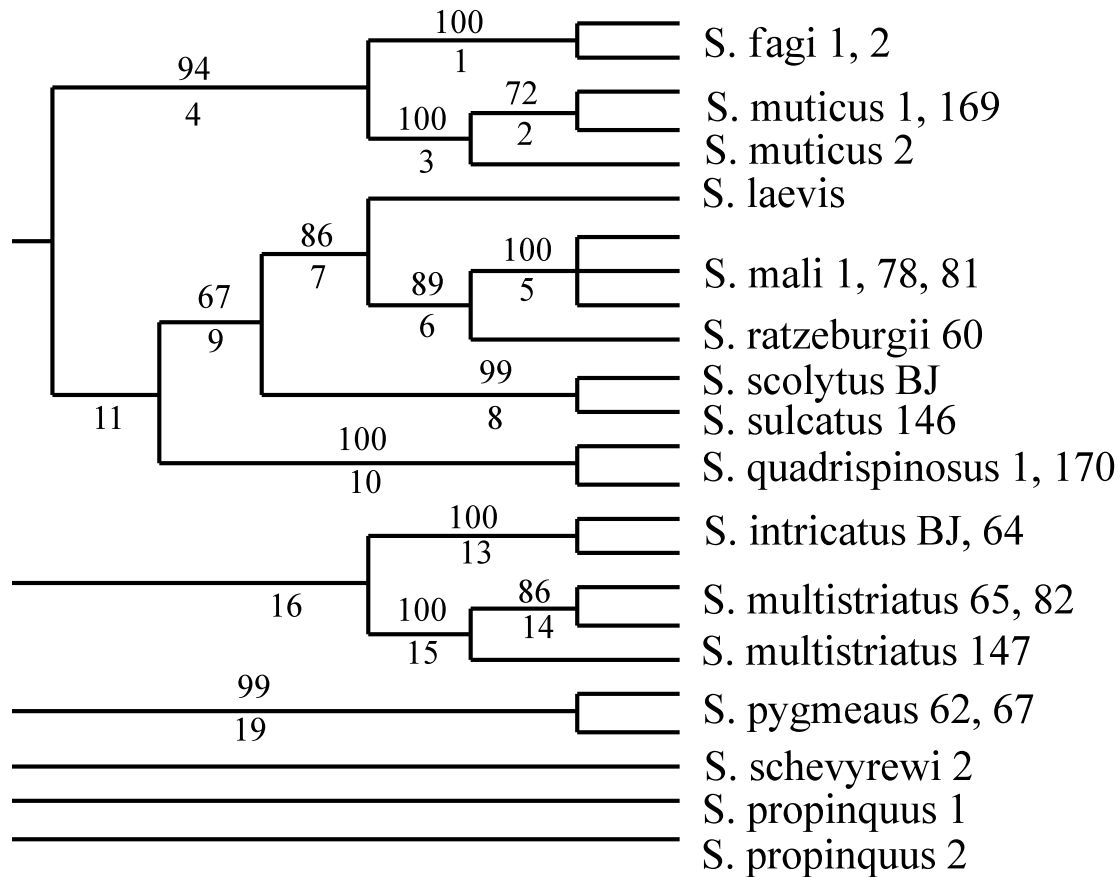


Figure 1.7 (cont'd).

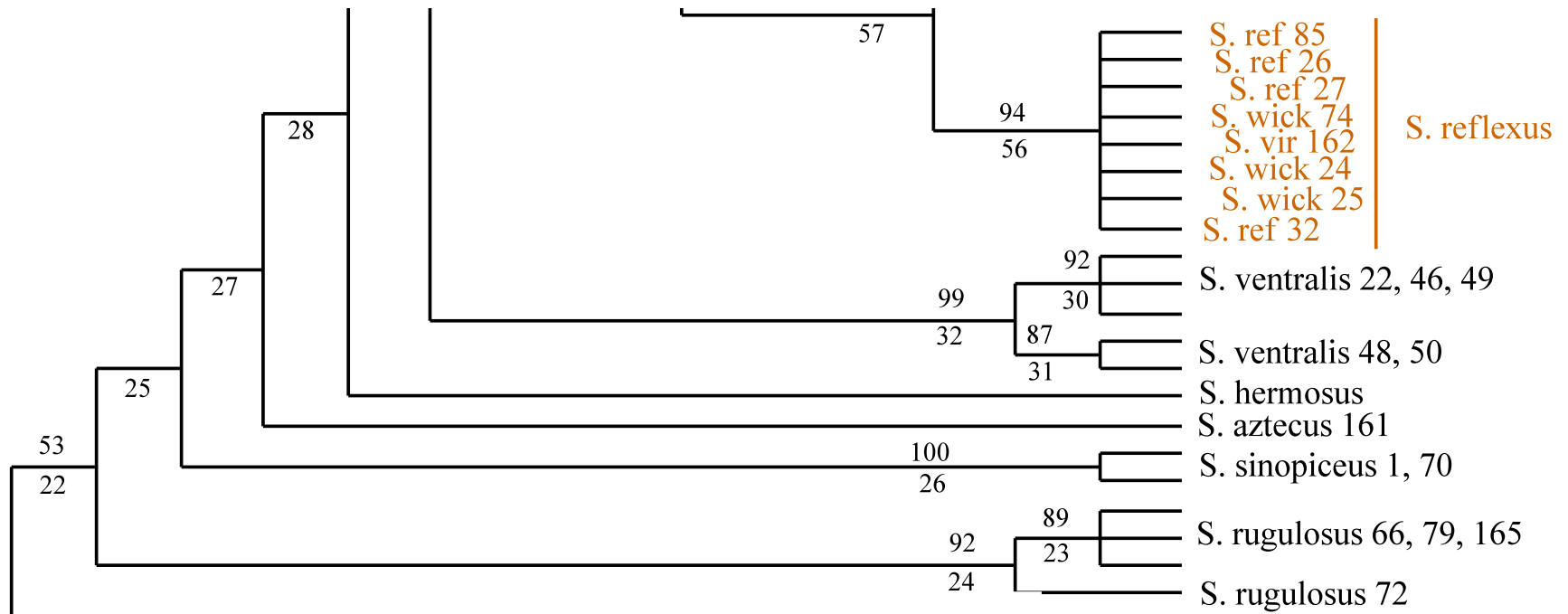


Figure 1.7 (cont'd).

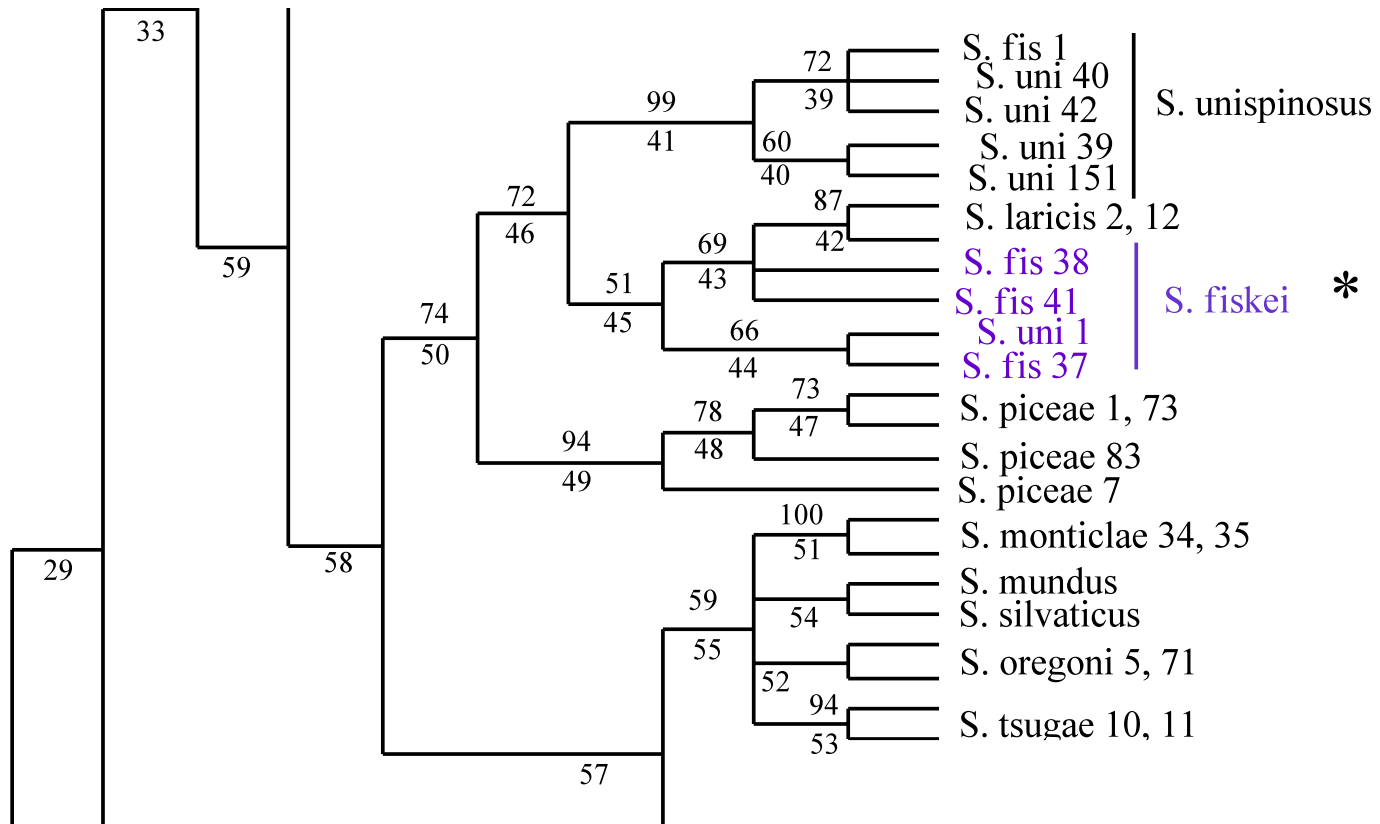


Figure 1.7 (cont'd).

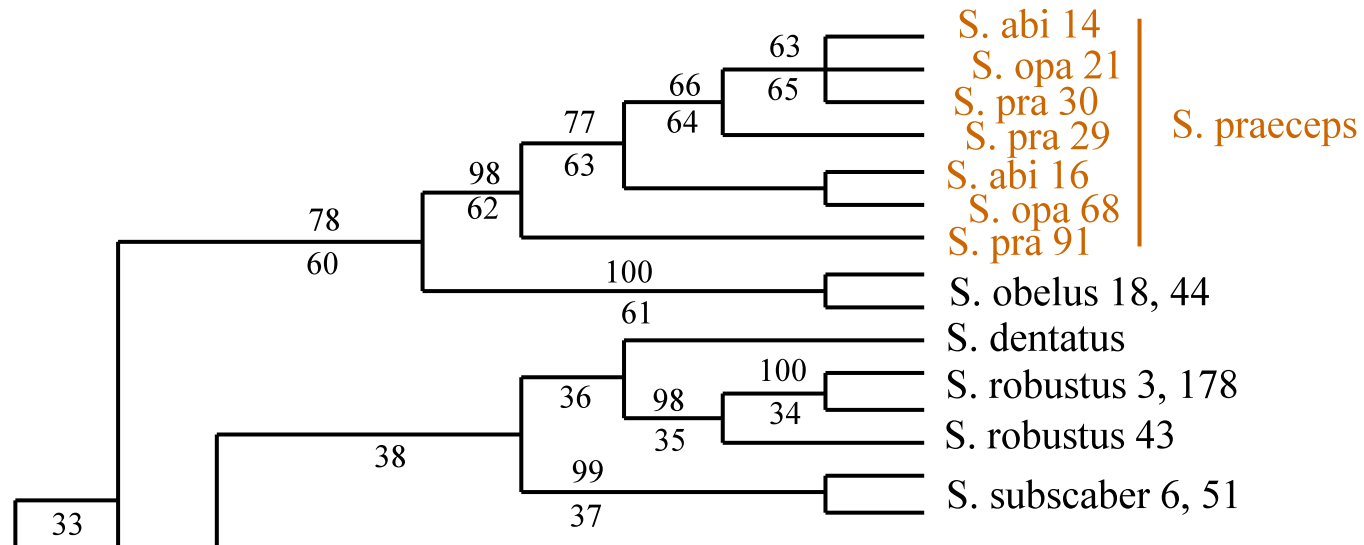


Figure 1.8. Strict consensus tree of 13,003 most parsimonious trees found by parsimony analysis of the combined molecular and morphological dataset with gaps as a fifth character (3,097 steps. consistency index 0.48; retention index 0.771) generated from a heuristic search of 1000 stepwise random additions with TBR in PAUP*. Numbers above the node indicate bootstrap values (>50) based on 1000 pseudoreplicates. Node numbers are given below the node and refer to PBS values in Table 1.12. Taxa in brown were not recovered as monophyletic. *Scolytus fiskei* is listed in purple and is considered a synonym of *S. unispinosus*. * denotes species that are recognized as valid.

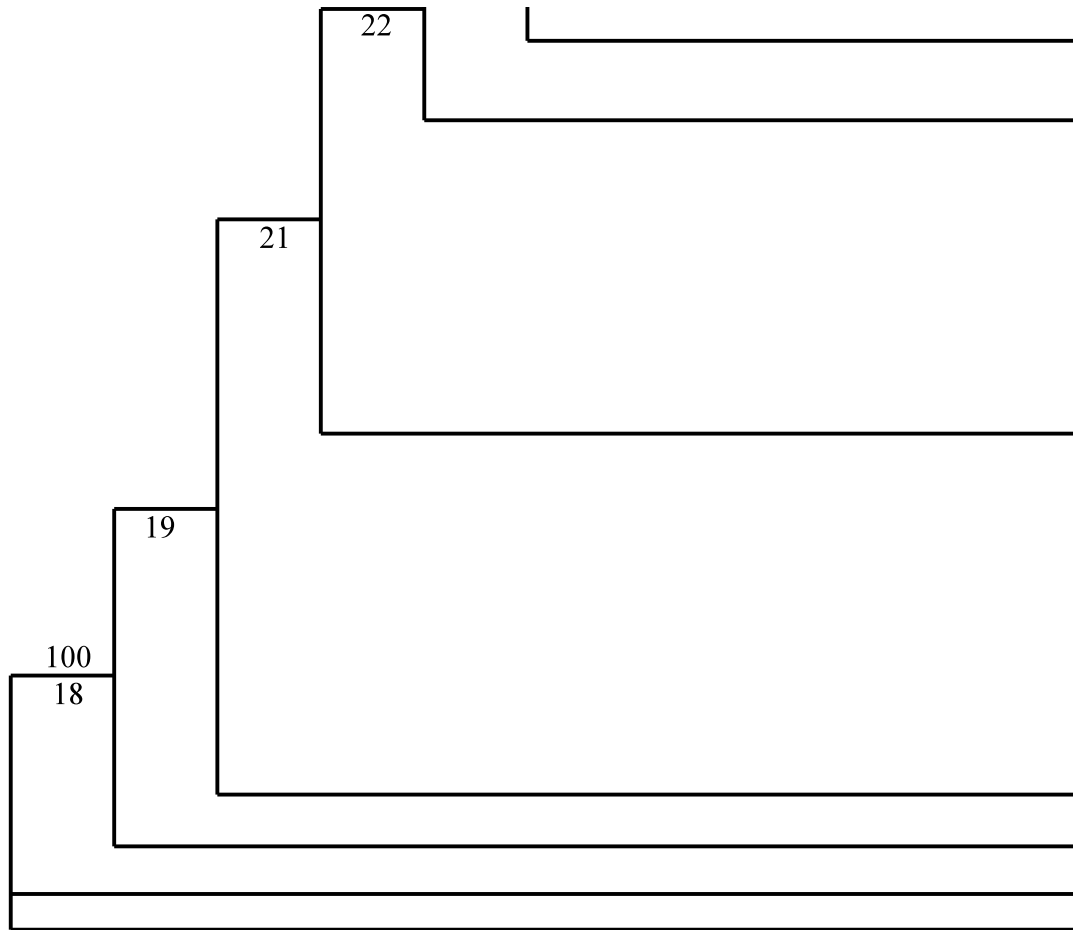


Figure 1.8 (cont'd).

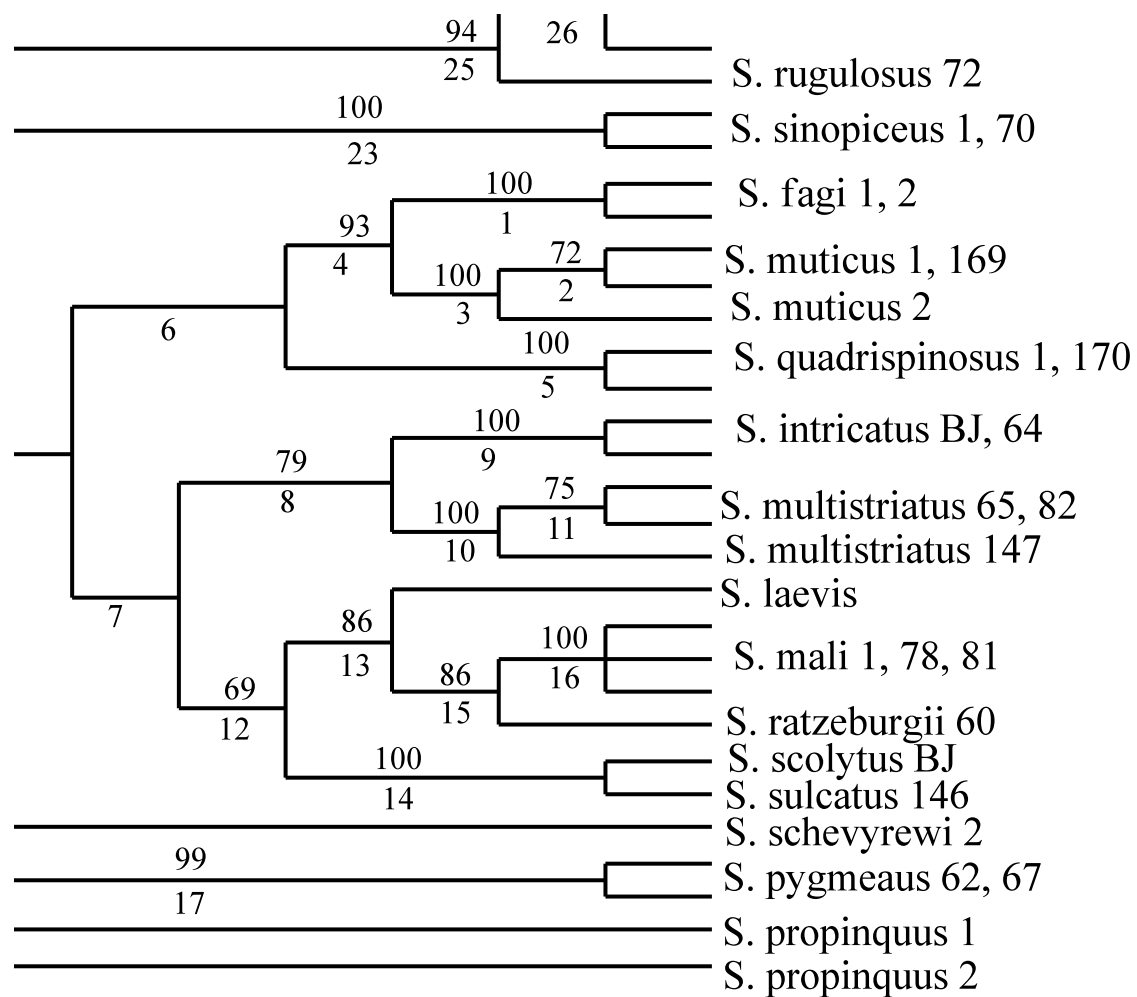


Figure 1.8 (cont'd).

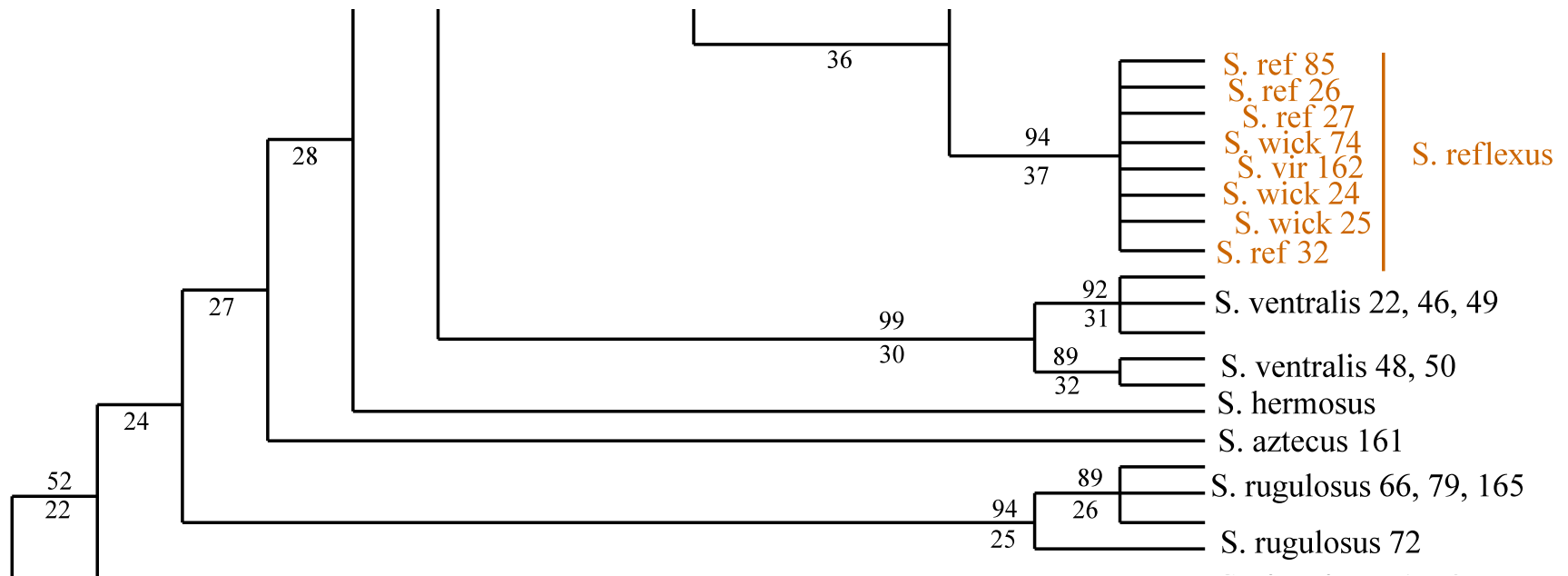


Figure 1.8 (cont'd).

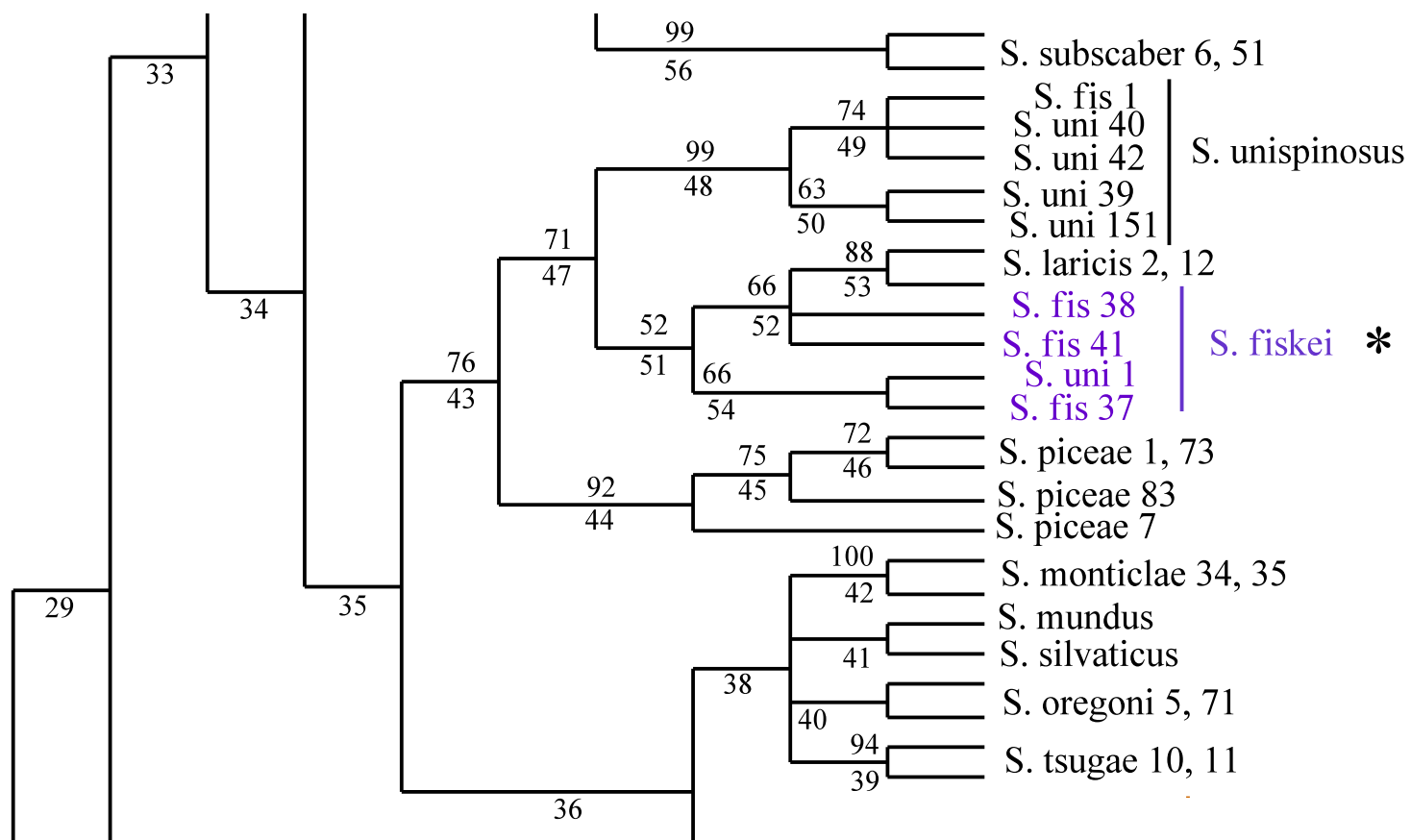


Figure 1.8 (cont'd).

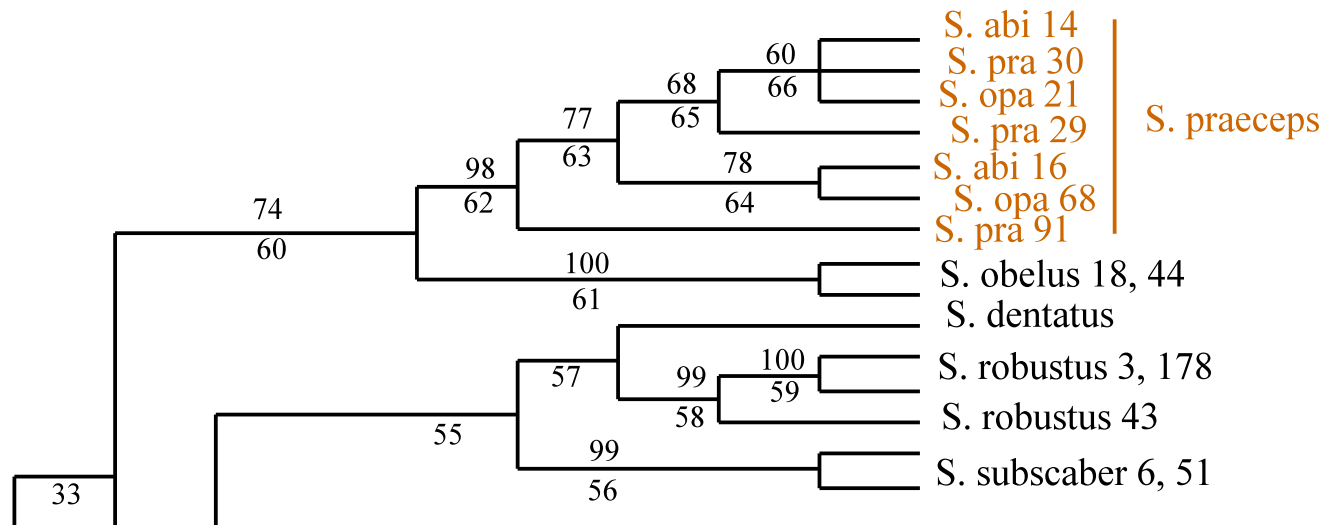


Figure 1.9. Sexual dimorphism of the head (*Scolytus reflexus*) lateral profiles of male (A) and female (B), anterior view of male (C) and female (D).

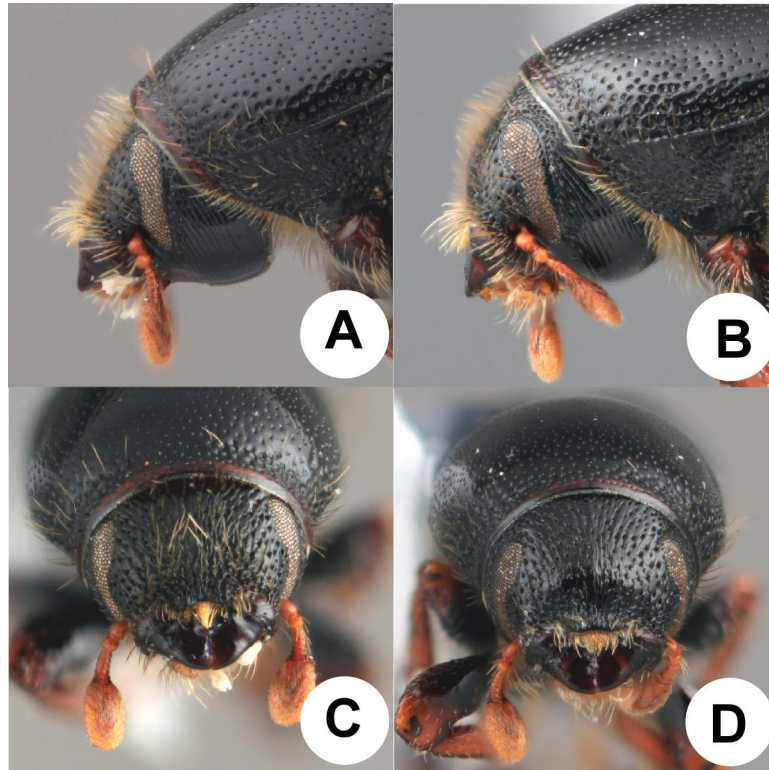


Figure 1.10. Terminology of the head. Terms are defined in the glossary section (*Scolytus reflexus* male).

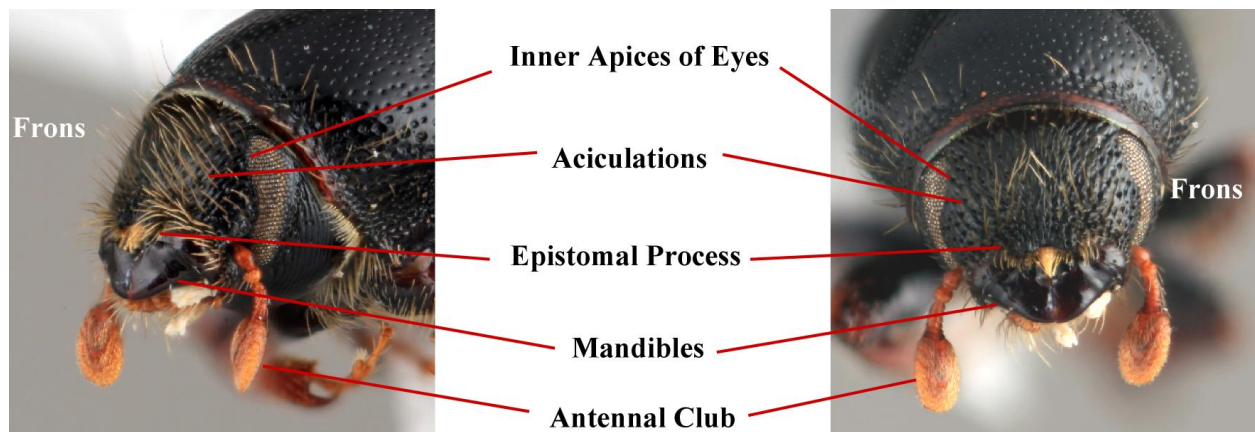


Figure 1.11. General habitus terminology. Terms are defined in the glossary section (*Scolytus fagi* male).

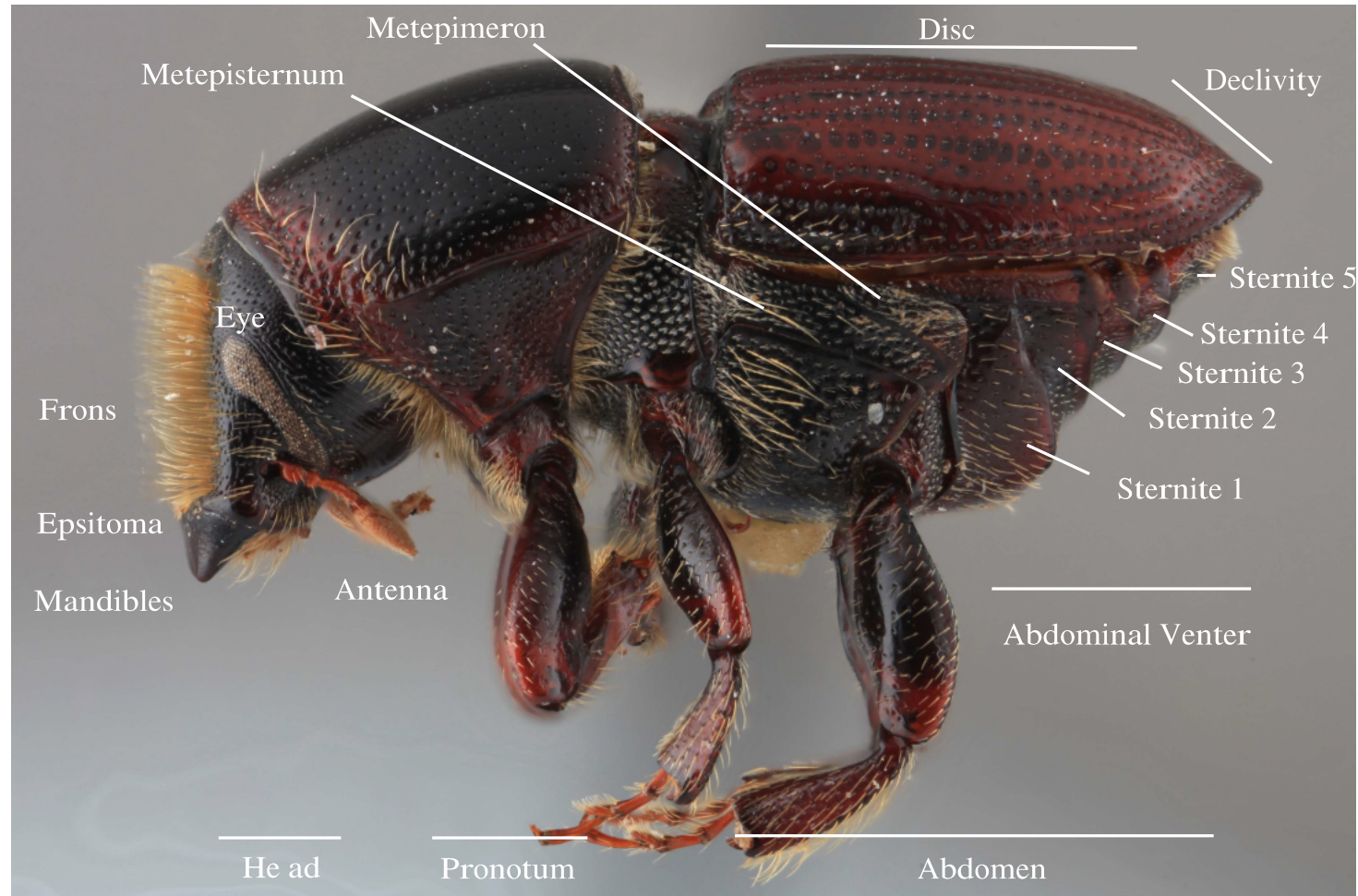


Figure 1.12. Dorsal terminology. Terms are defined in the glossary section (*Scolytus fagi* male).

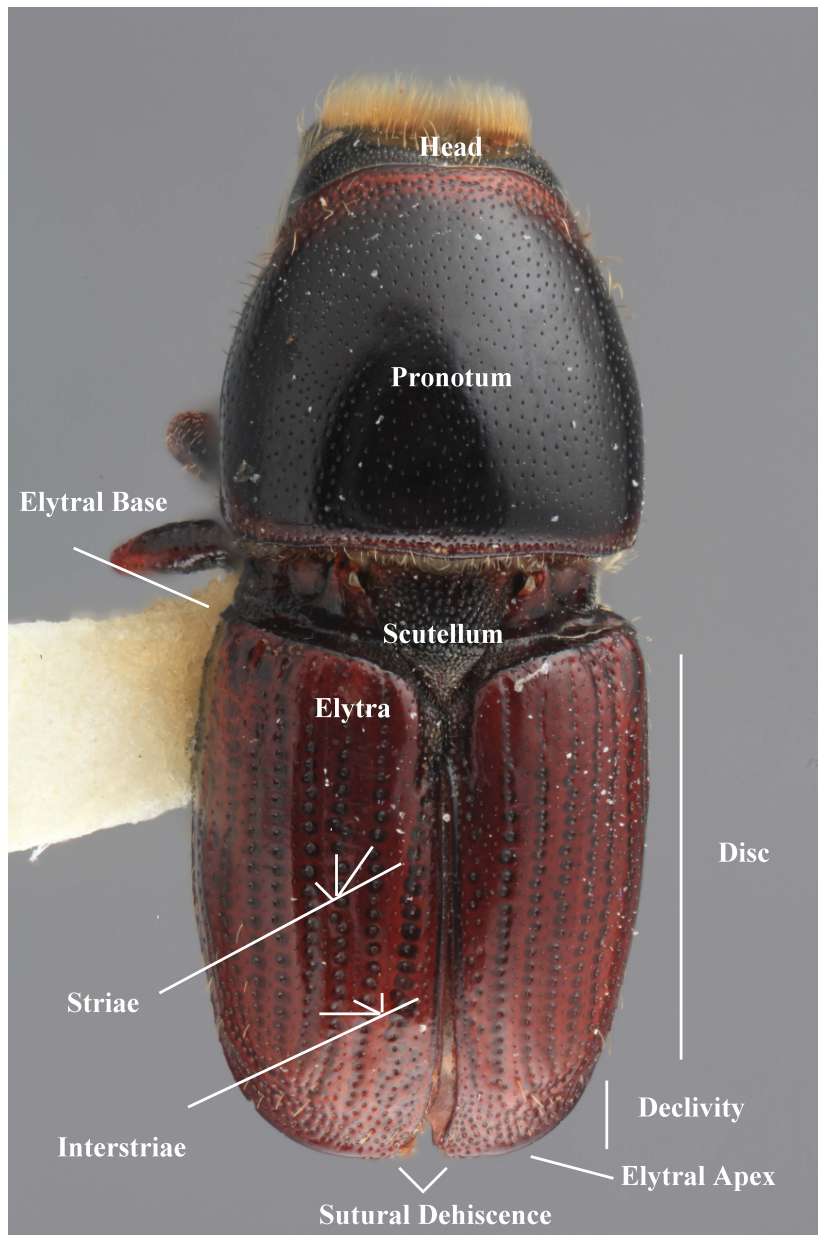


Figure 1.13. Abdominal venter terminology. Terms are defined in the glossary section (*Scolytus ventralis*).

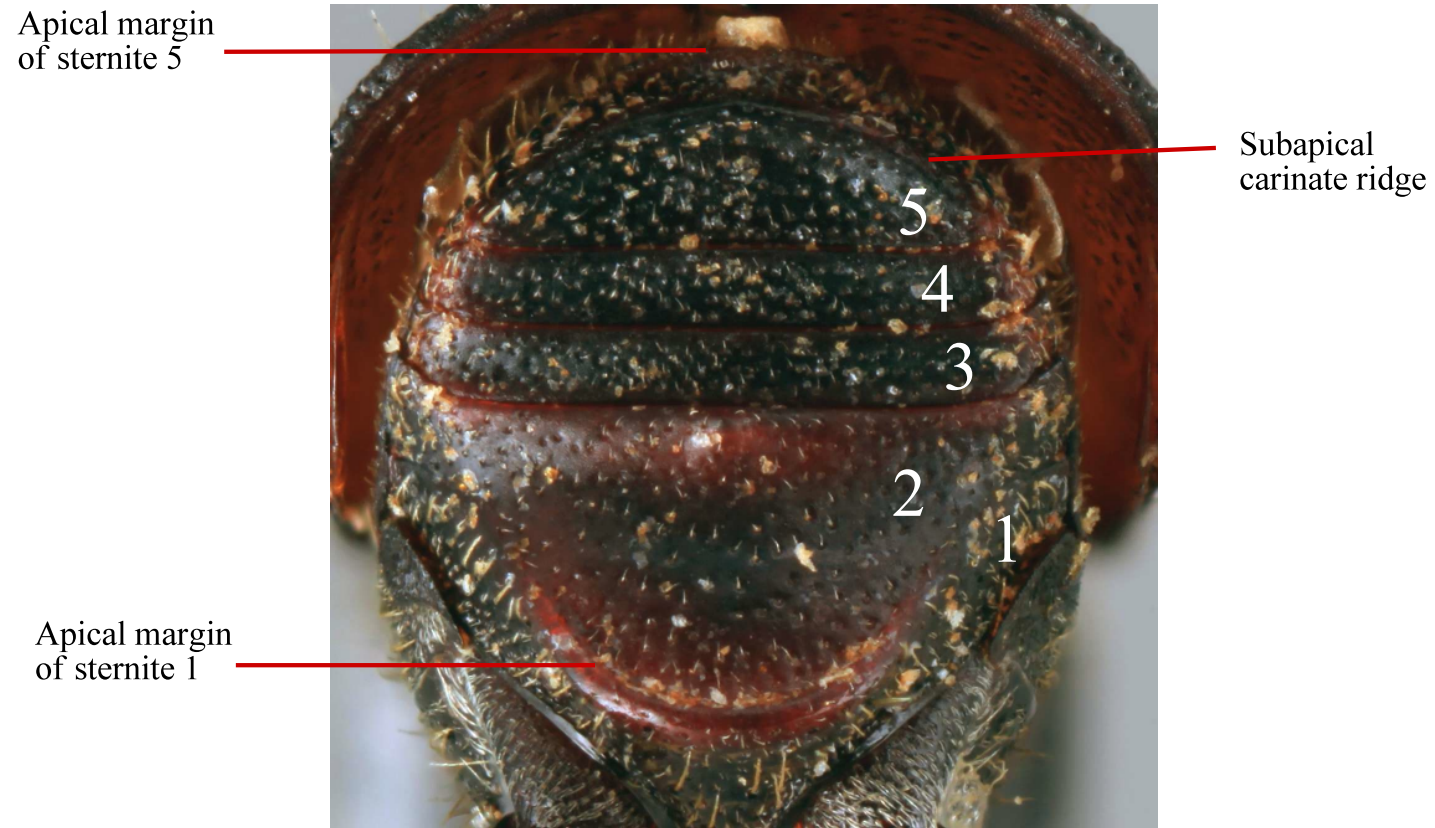


Figure 1.14. Damage pattern. Terms are defined in the glossary section (*Scolytus monticolae*).

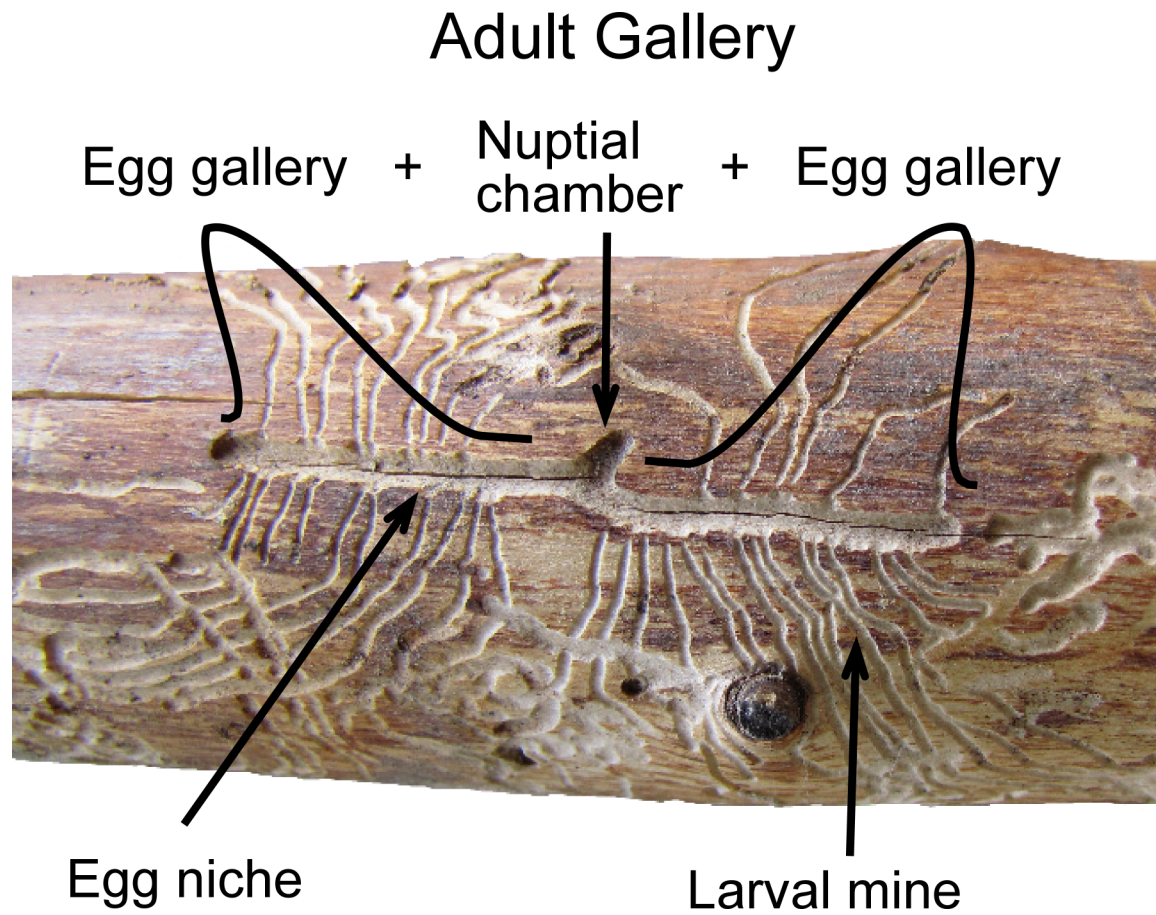


Figure 1.15. Elytral apices consist of two general shapes, rounded (A) (*Scolytus rugulosus*) and truncate (B) (*Scolytus robustus*).



Figure 1.16. Lateral views of *Scolytus mali* male 3.2 – 4.1mm (A) and female 3.0 – 4.2mm (B).

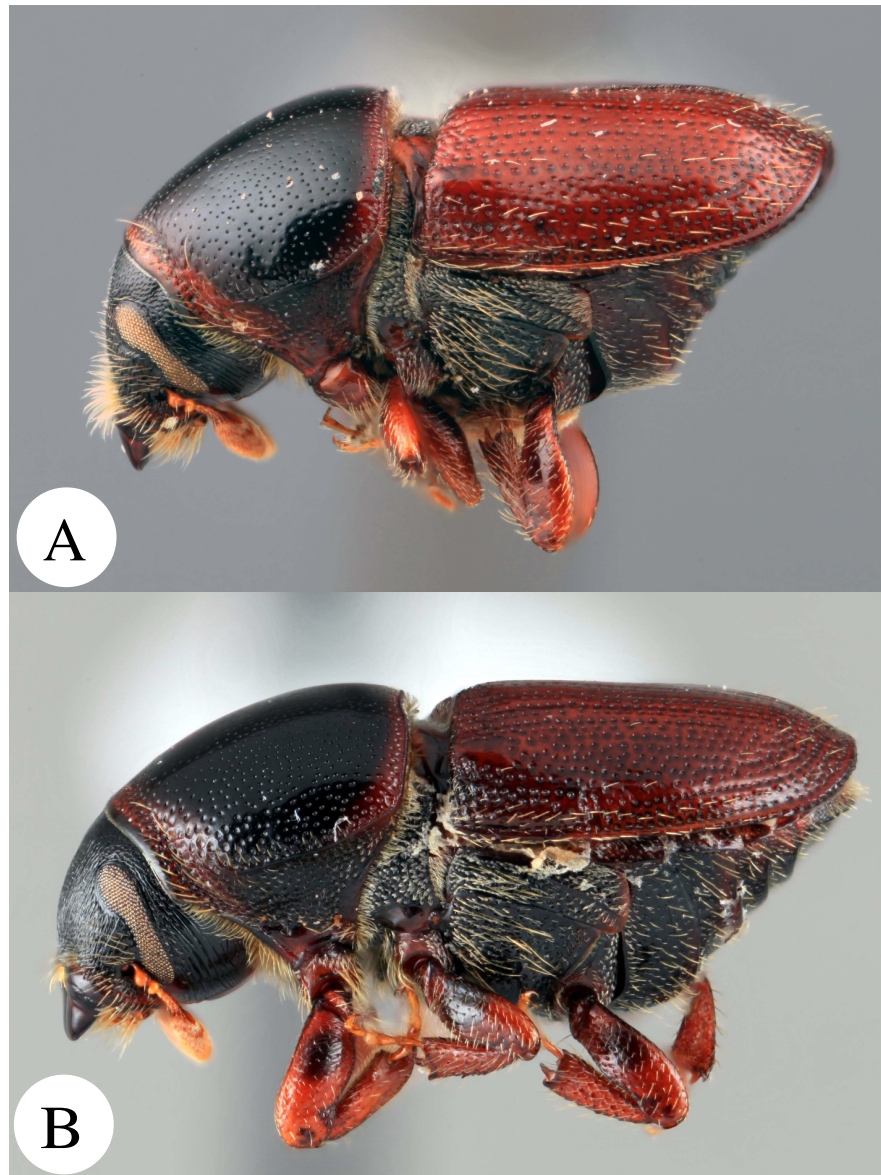


Figure 1.17. Dorsal view of *Scolytus mali* male.



Figure 1.18. Lateral views of *Scolytus multistriatus* male 2.2 – 3.9mm (A) and female 2.4 – 3.3mm (B).



Figure 1.19. Dorsal view of *Scolytus multistriatus* male.



Figure 1.20. Lateral views of *Scolytus rugulosus* male 1.9 – 2.6mm (A) and female 2.0 – 3.1mm (B).

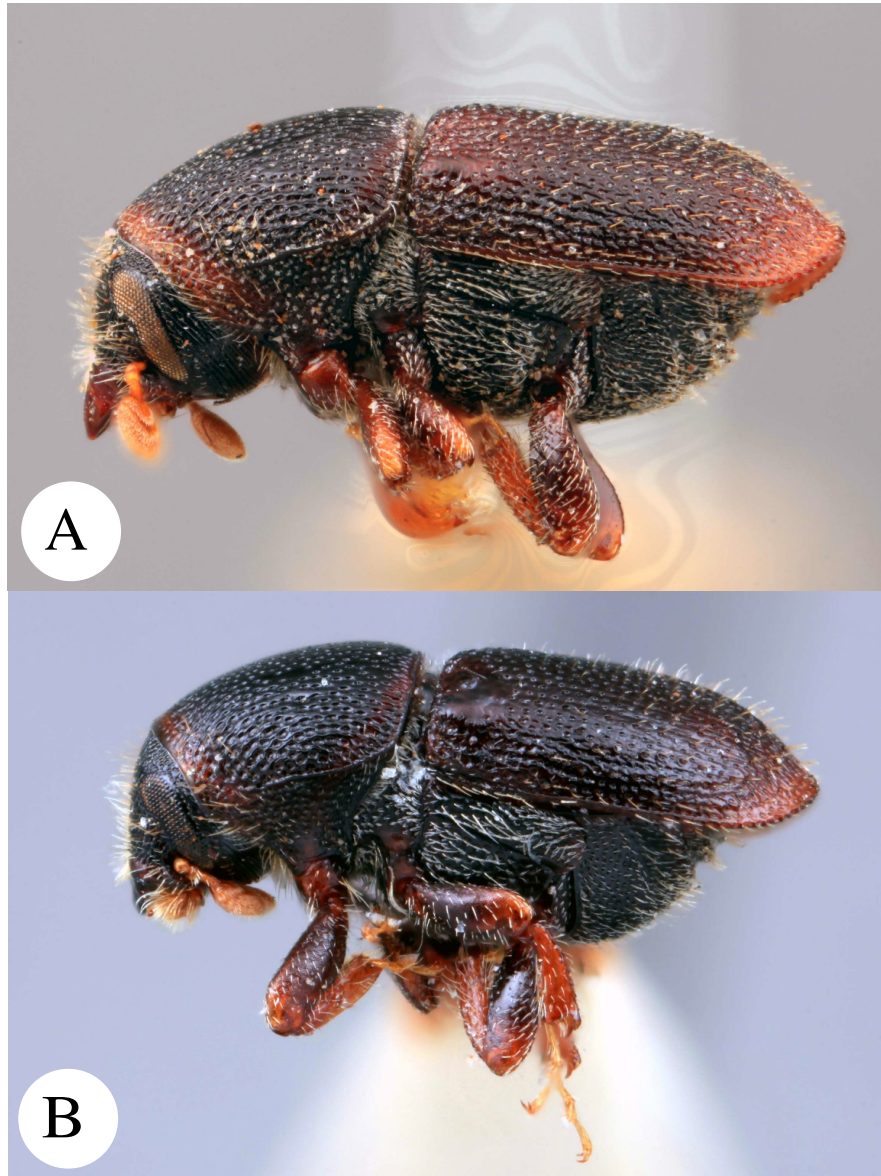


Figure 1.21. Dorsal views of *Scolytus rugulosus* male.



Figure 1.22. Lateral views of *Scolytus schevyrewi* male 2.8 – 3.5mm (A) and female 2.3 – 3.6mm (B).

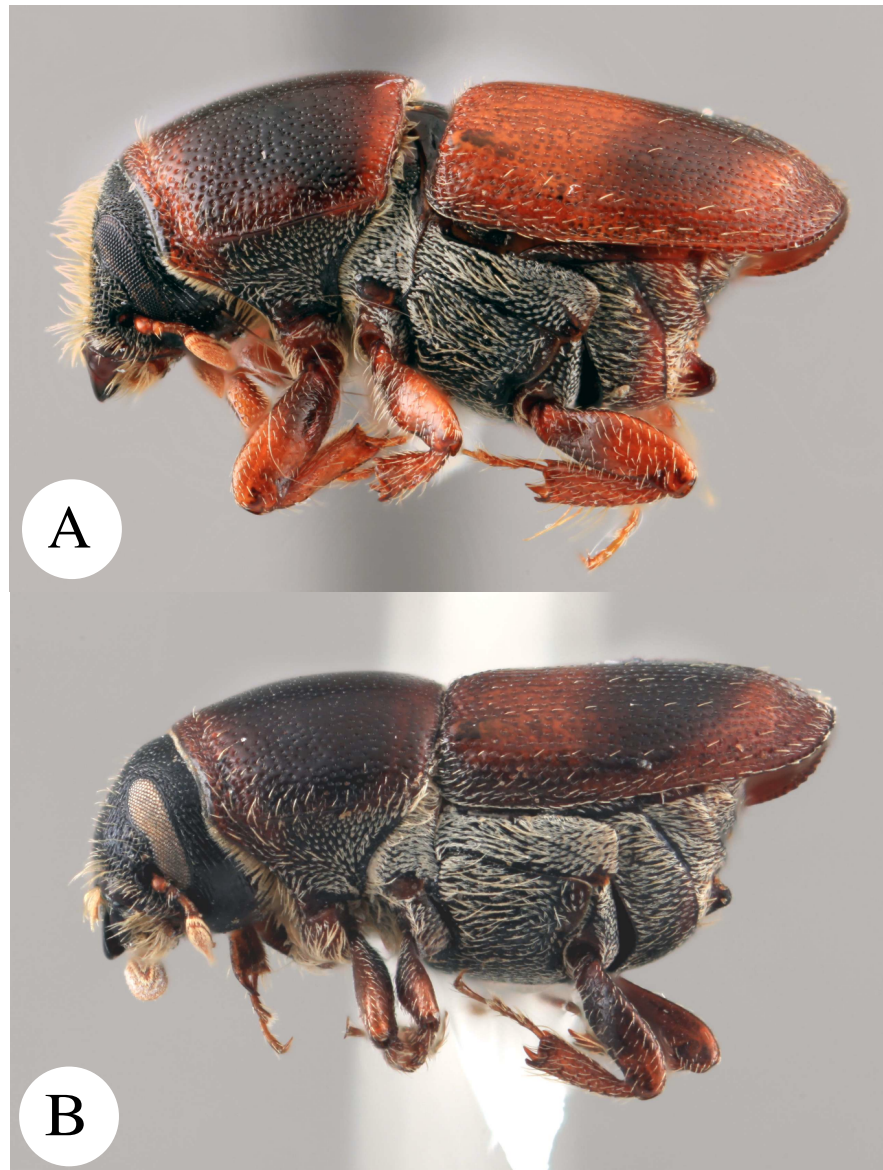


Figure 1.23. Dorsal view of *Scolytus schevyrewi* male.



Figure 1.24. Lateral views of *Scolytus fagi* male 3.3 – 5.5mm (A) and female 3.9 – 5.6mm (B).



Figure 1.25. Dorsal view of *Scolytus fagi* male.



Figure 1.26. Lateral views of *Scolytus muticus* male 2.2 – 5.3mm (A) and female 3.1 – 5.1mm (B).



Figure 1.27. Dorsal view of *Scolytus muticus* male.



Figure 1.28. Lateral views of *Scolytus quadrispinosus* male 2.8 – 4.2mm (A) and female 2.9 – 5.0mm (B).

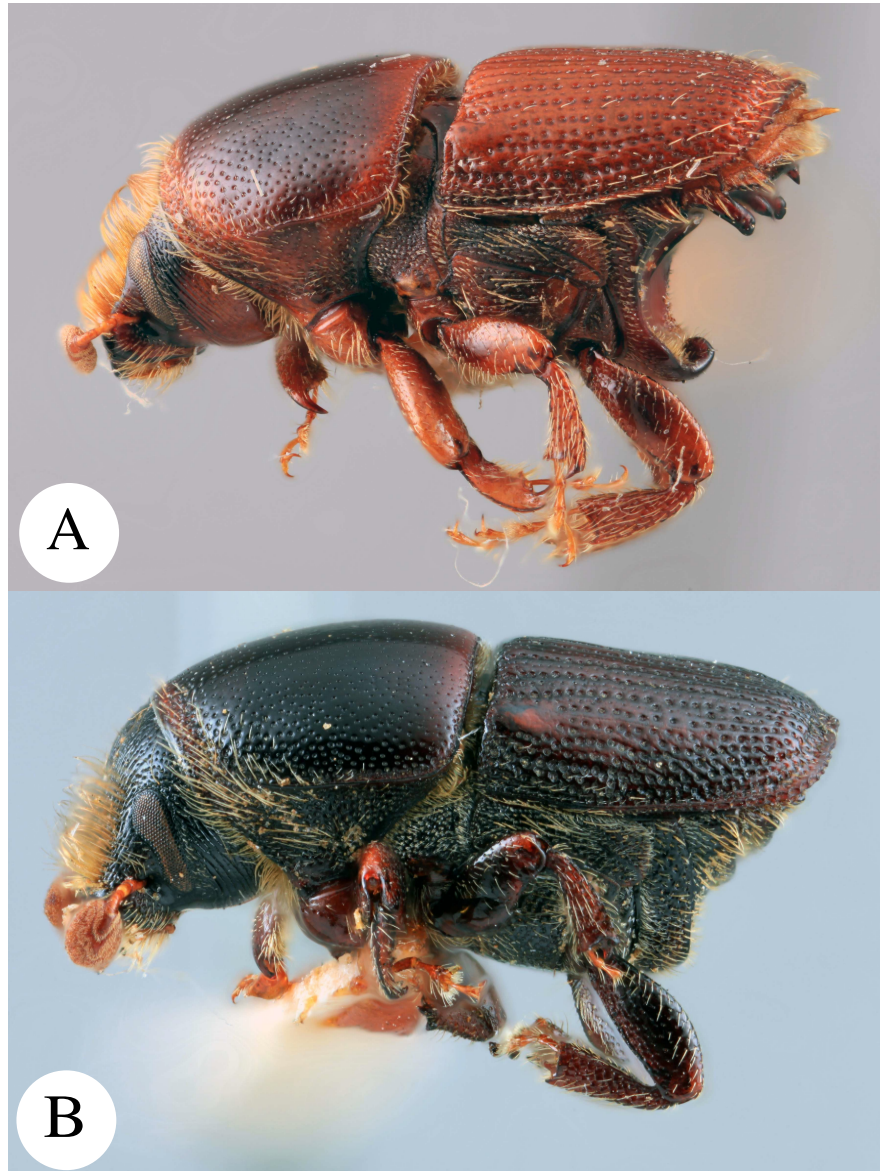


Figure 1.29. Lateral views of *Scolytus quadrispinosus* male.



Figure 1.30. Lateral views of *Scolytus aztecus* male 5.0mm (A) and female 4.6 – 5.9mm (B).



Figure 1.31. Dorsal view of *Scolytus aztecus* male.



Figure 1.32. Lateral views of *Scolytus dentatus* male 3.0 – 4.0mm (A) and female 3.4 – 4.6mm (B).

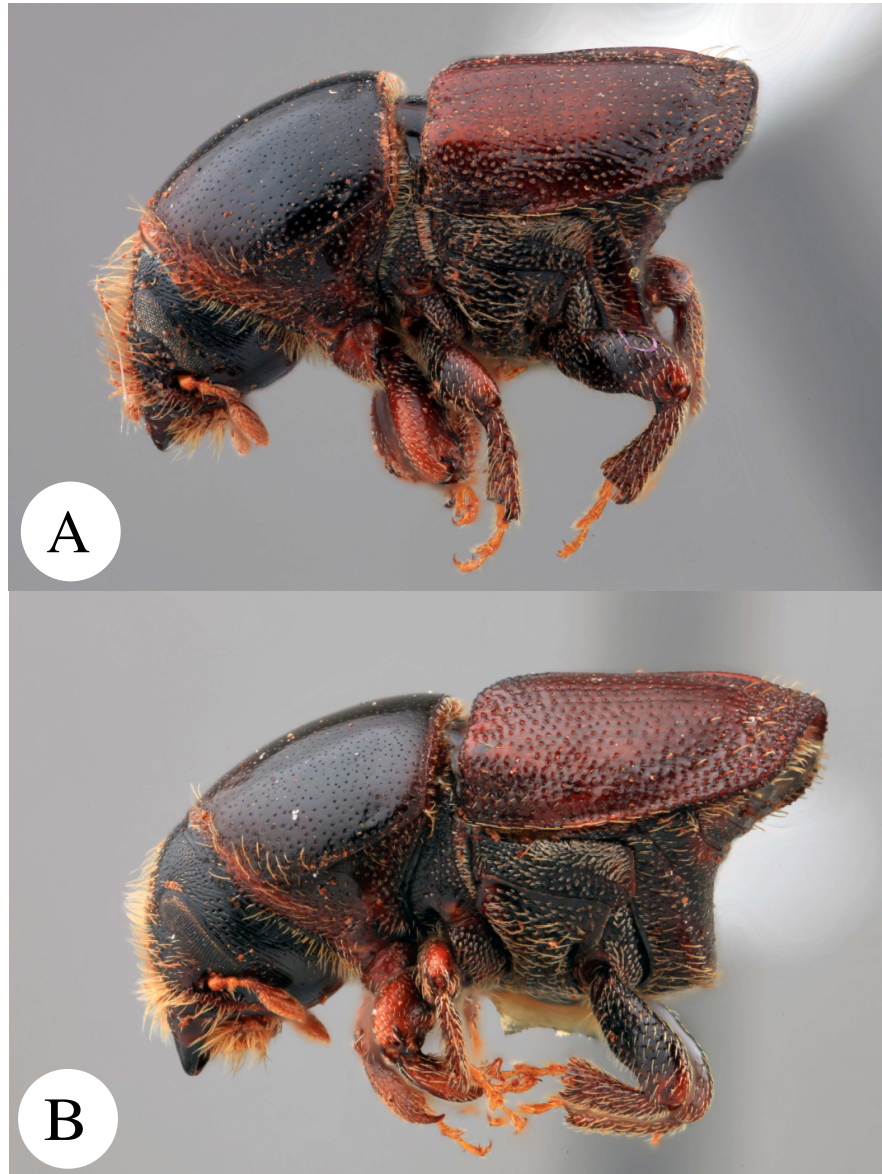


Figure 1.33. Dorsal view of *Scolytus dentatus* male.



Figure 1.34. Lateral views of *Scolytus fiskei* male 2.2 – 2.8mm (A) and female 2.2 – 3.5mm (B).



Figure 1.35. Dorsal view of *Scolytus fiskei* male.



Figure 1.36. Lateral views of *Scolytus hermosus* male 3.0mm (A) and female 2.5 – 3.5mm (B).

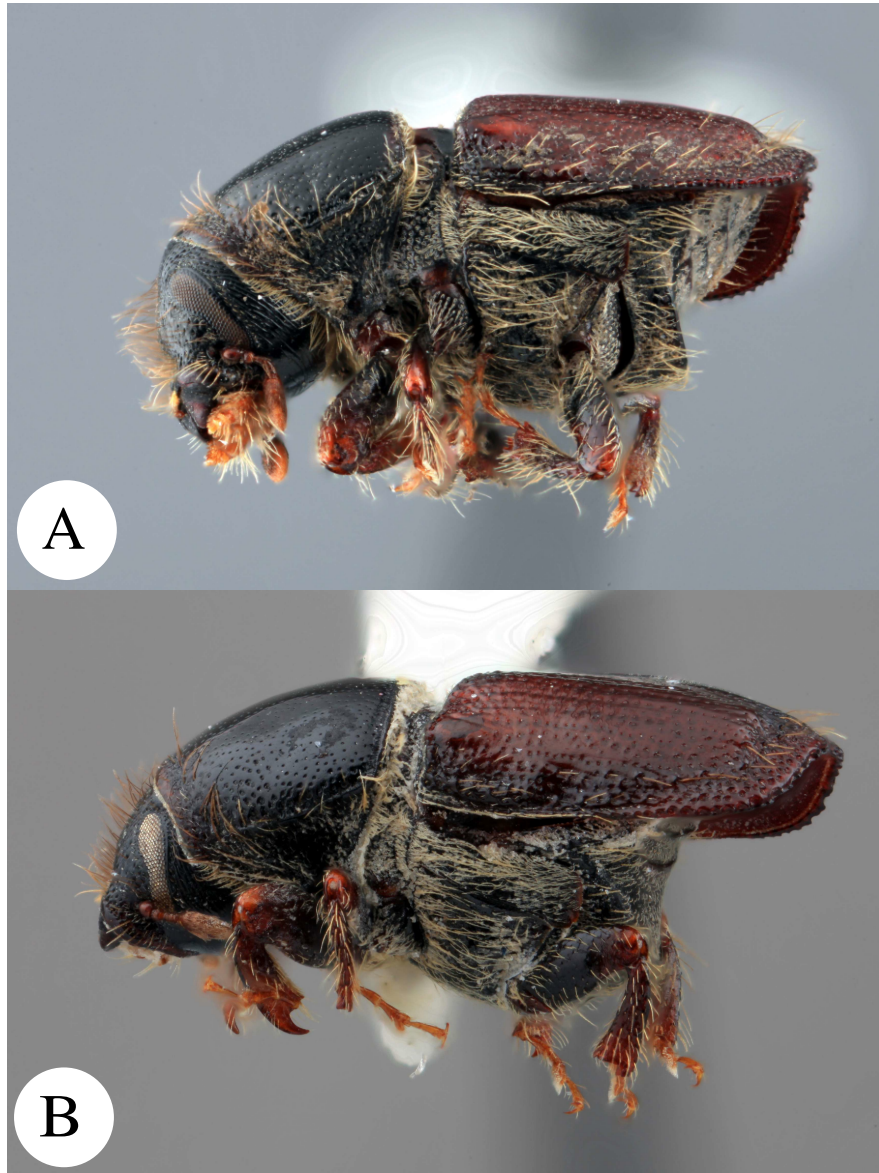


Figure 1.37. Dorsal view of *Scolytus hermosus* male.



Figure 1.38. Lateral views of *Scolytus laricis* male 2.3 – 4.0mm (A) and female 2.6 – 4.0mm (B).

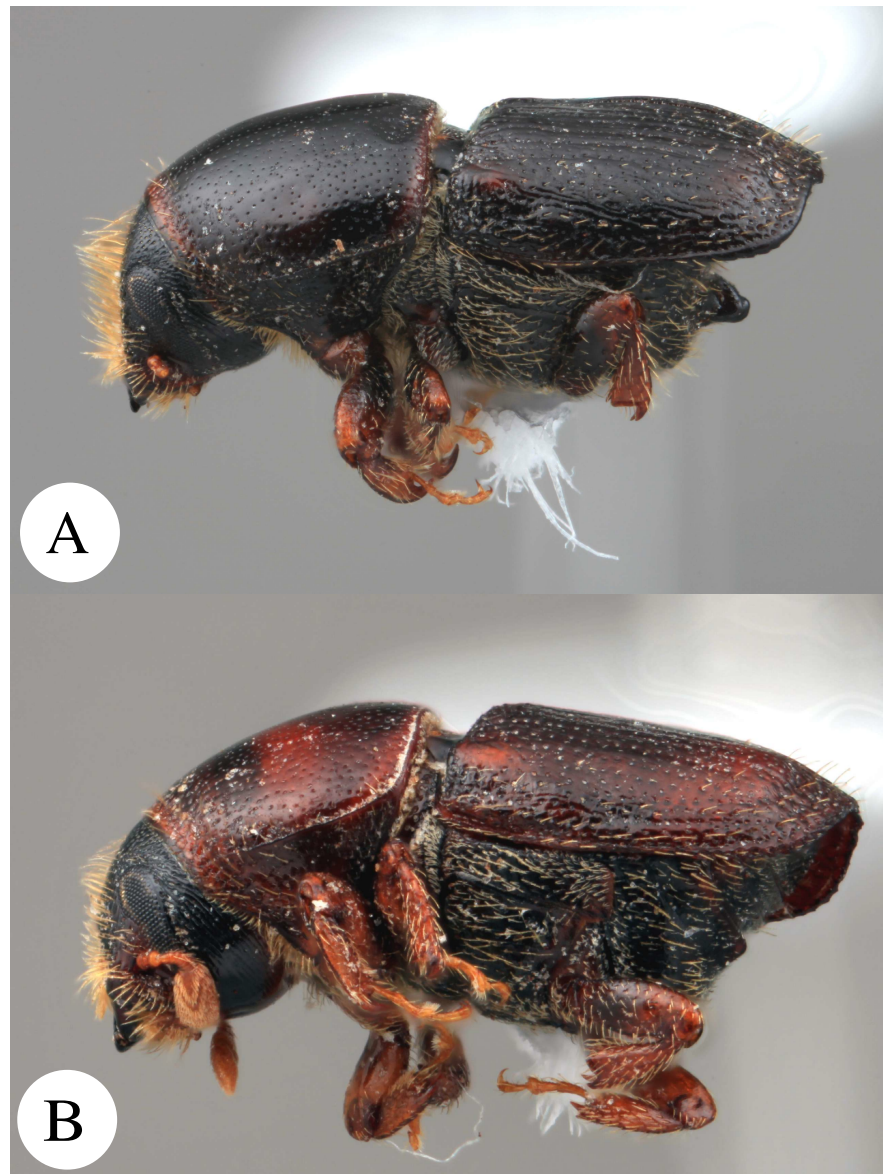


Figure 1.39. Dorsal view of *Scolytus laricis* male.



Figure 1.40. Lateral views of *Scolytus monticolae* male 2.5 – 3.0mm (A) and female 2.3 – 3.5mm (B).

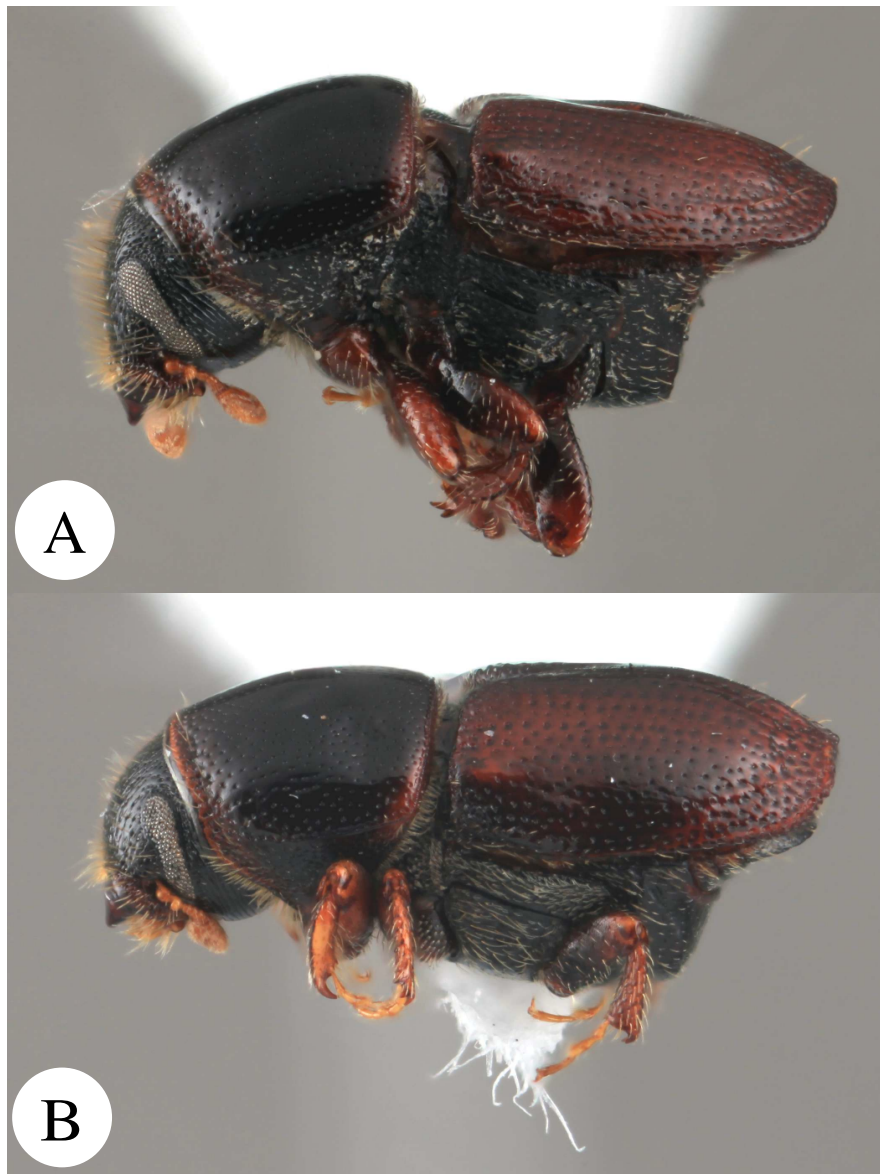


Figure 1.41. Dorsal view of *Scolytus monticolae* male.



Figure 1.42. Lateral views of *Scolytus mundus* male 4.0 – 4.5mm (A) and female 3.3 – 4.6mm (B).

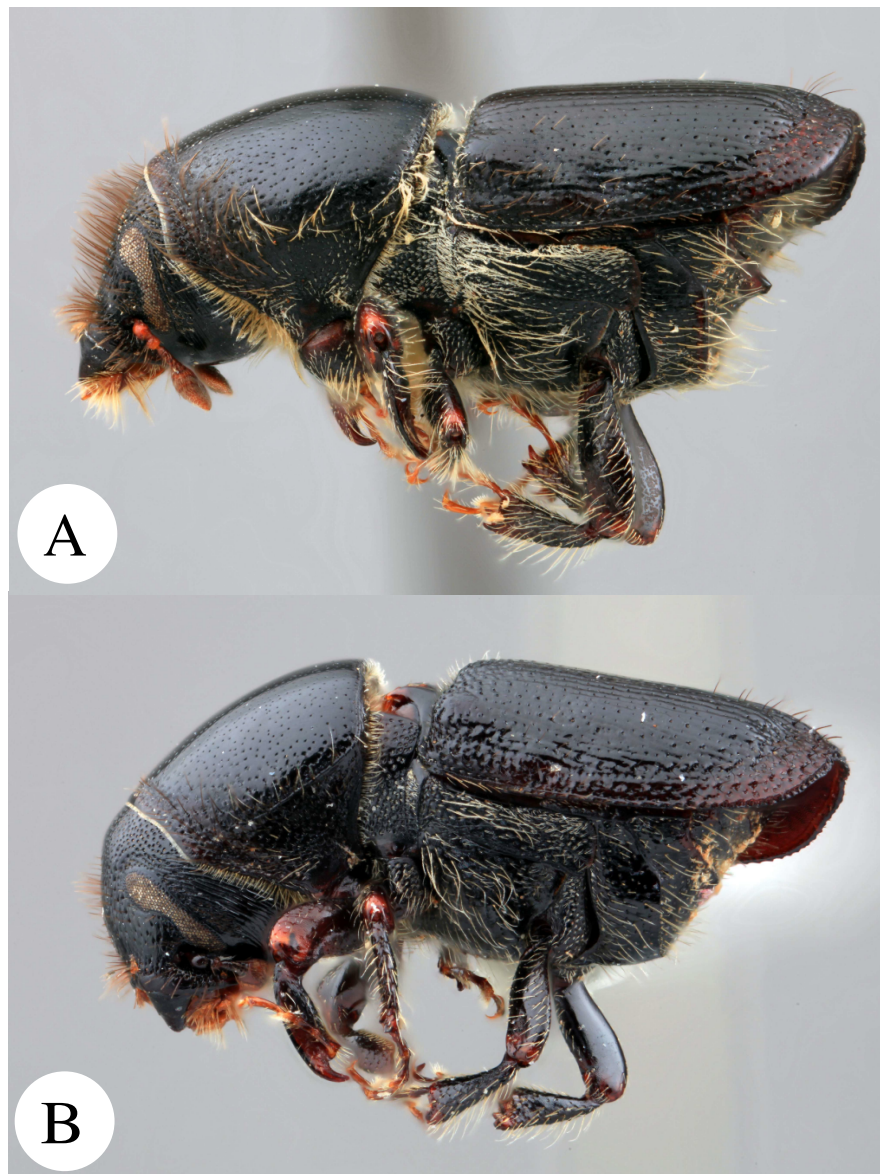


Figure 1.43. Dorsal views of *Scolytus mundus* male.



Figure 1.44. Lateral views of *Scolytus obelus* male 1.8 – 2.9mm (A) and female 1.7 – 3.0mm (B).

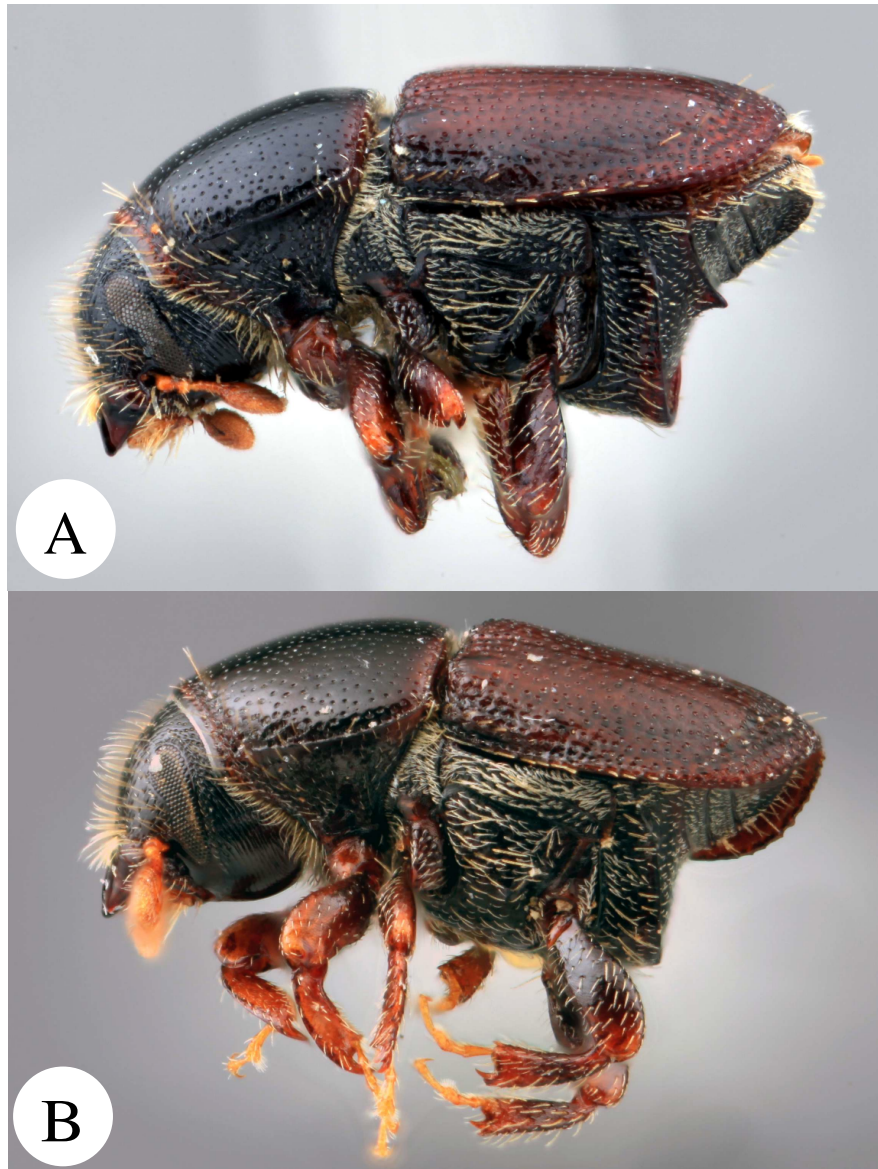


Figure 1.45. Dorsal view of *Scolytus obelus* male.



Figure 1.46. Lateral views of *Scolytus oregoni* male 2.6 – 3.6mm (A) and female 2.8 – 4.0mm (B).

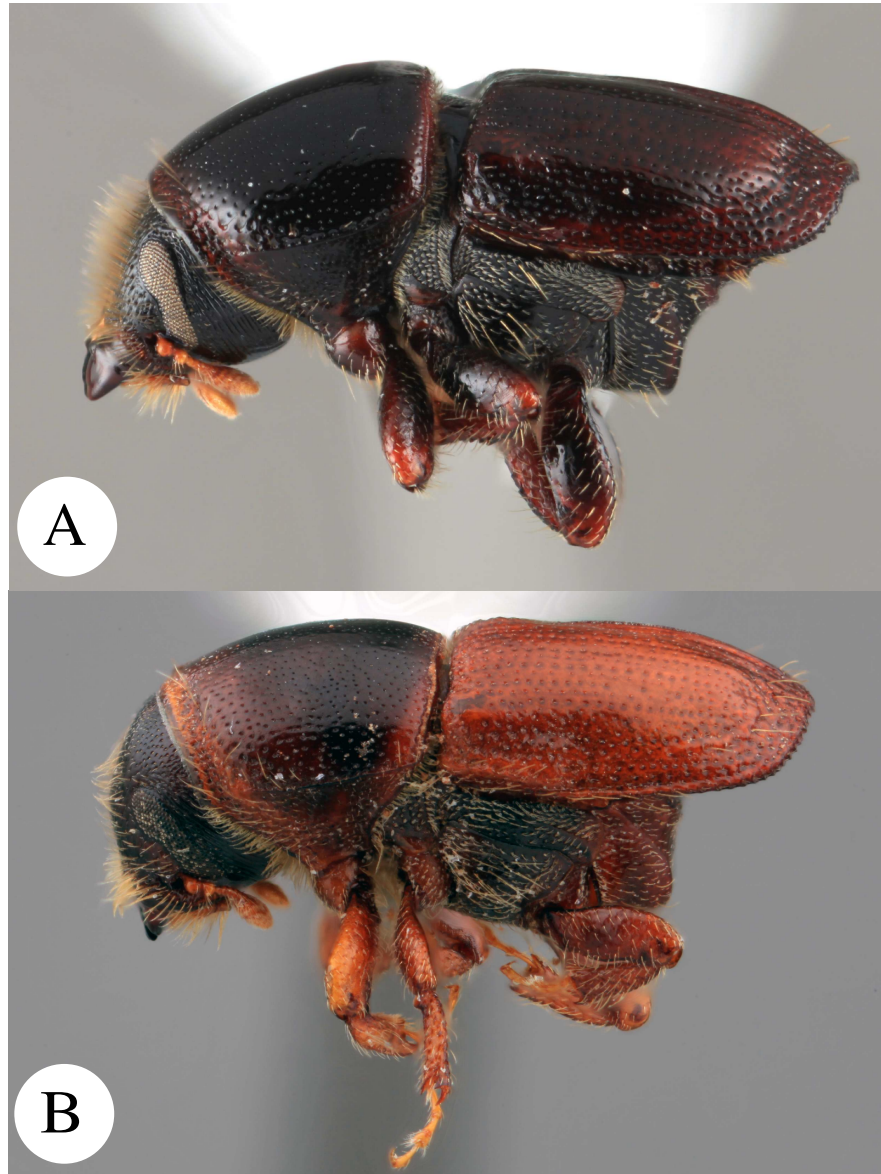


Figure 1.47. Dorsal view of *Scolytus oregoni* male.



Figure 1.48. Lateral views of *Scolytus piceae* male 2.5 – 3.0mm (A) and female 2.3 – 3.0 (B).



Figure 1.49. Dorsal view of *Scolytus piceae* male.



Figure 1.50. Lateral views of *Scolytus praeceps* male 1.8 – 3.2mm (A) and female 1.7 – 3.5mm (B).

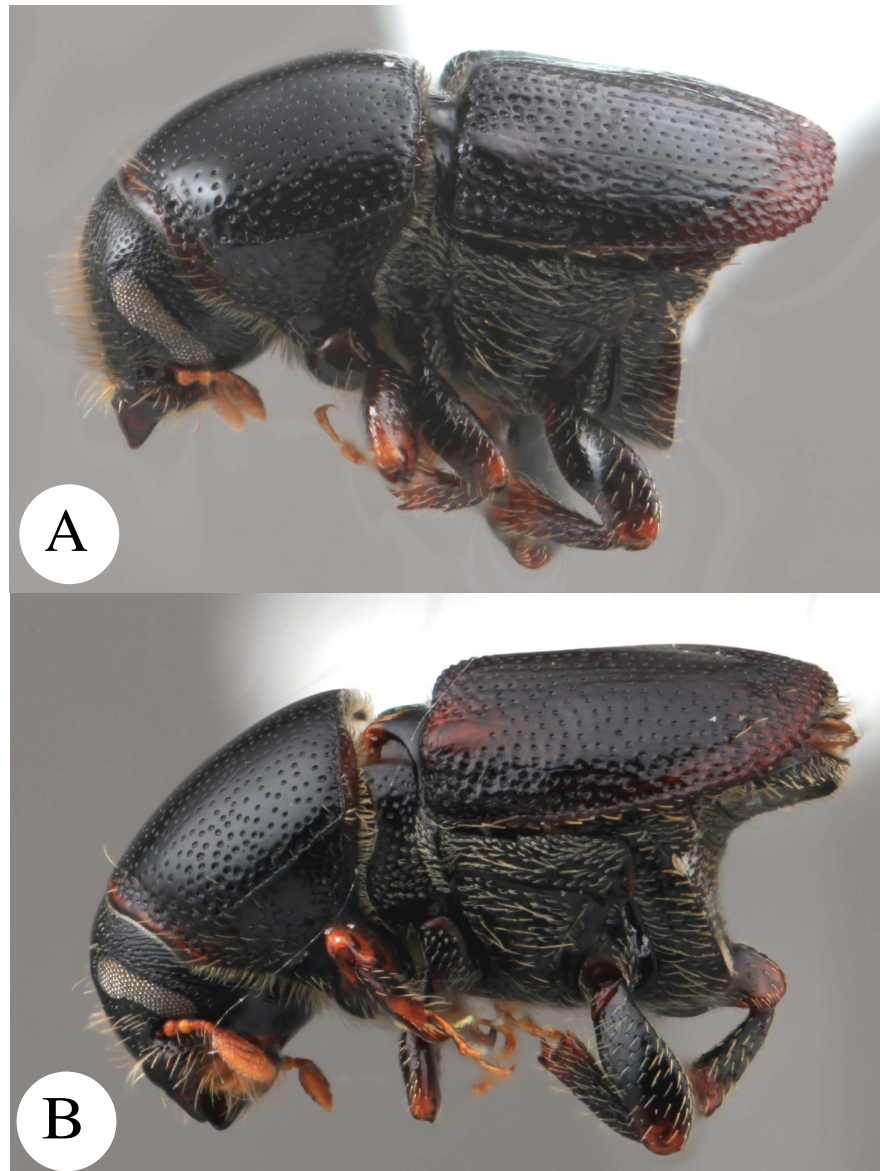


Figure 1.51. Dorsal views of *Scolytus praeceps* male.



Figure 1.52. Lateral views of *Scolytus praeceps* (= *S. abietis*) male (A) and female (B).

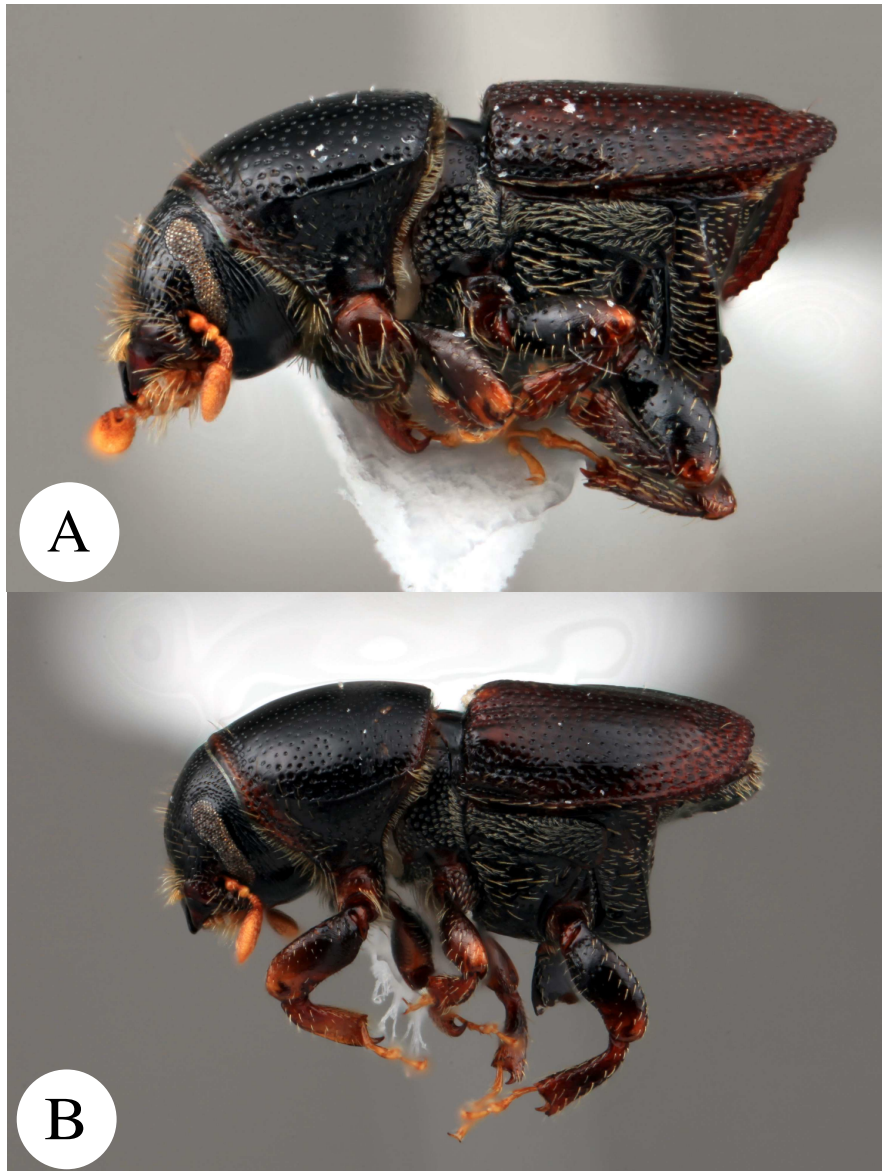


Figure 1.53. Lateral views of *Scolytus praeceps* (= *S. opacus*) male (A) and female (B).

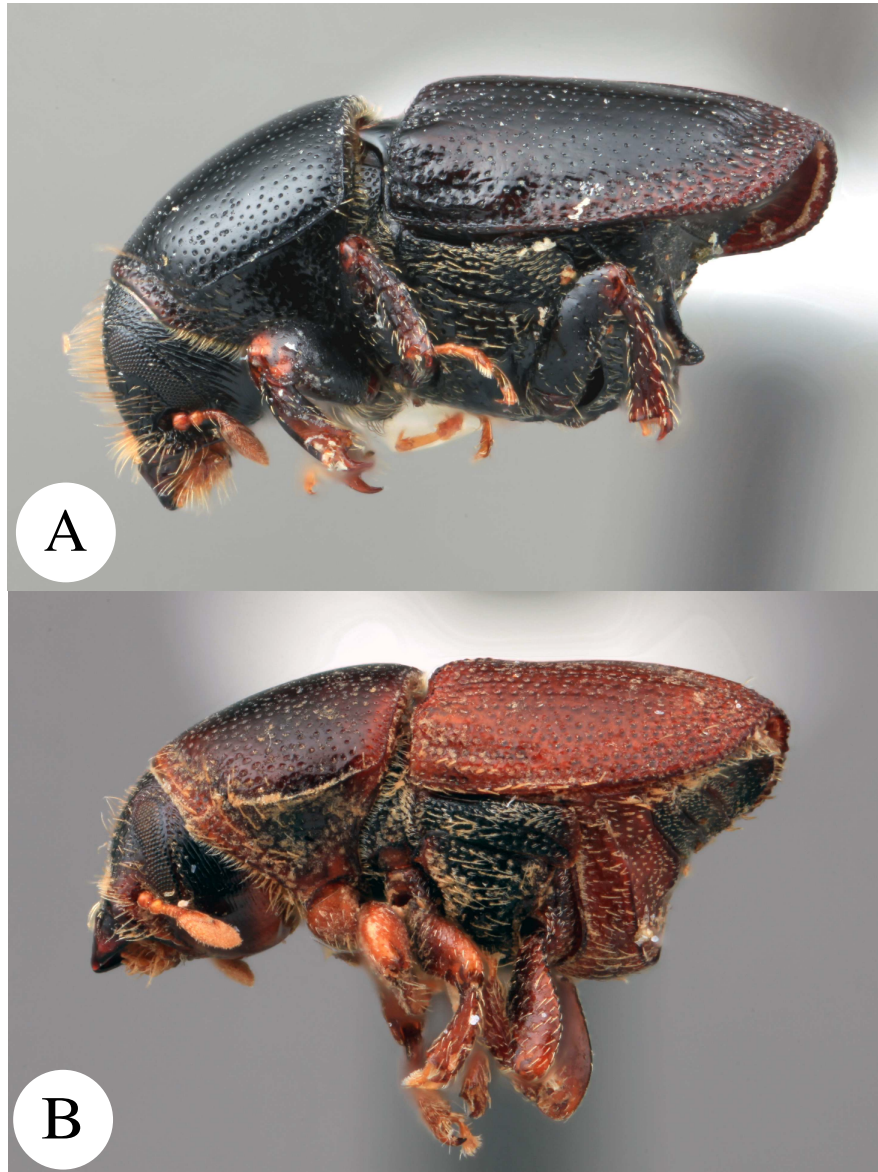


Figure 1.54. Lateral views of male *Scolytus reflexus* with a reflexed sternite 5 (A) and wickhami phenotype without reflexed sternite 5 (B) 2.4 – 3.8mm.



Figure 1.55. Lateral view of *Scolytus reflexus* female 2.5 – 4.0mm (A) and dorsal view of male (B).



Figure 1.56. Lateral views of *Scolytus robustus* male 2.5 – 4.0mm (A) and female 2.2 – 4.1mm (B).



Figure 1.57. Dorsal view of *Scolytus robustus* male.



Figure 1.58. Lateral views of *Scolytus silvaticus* male 3.0mm (A) and female 3.3 – 3.6mm (B).

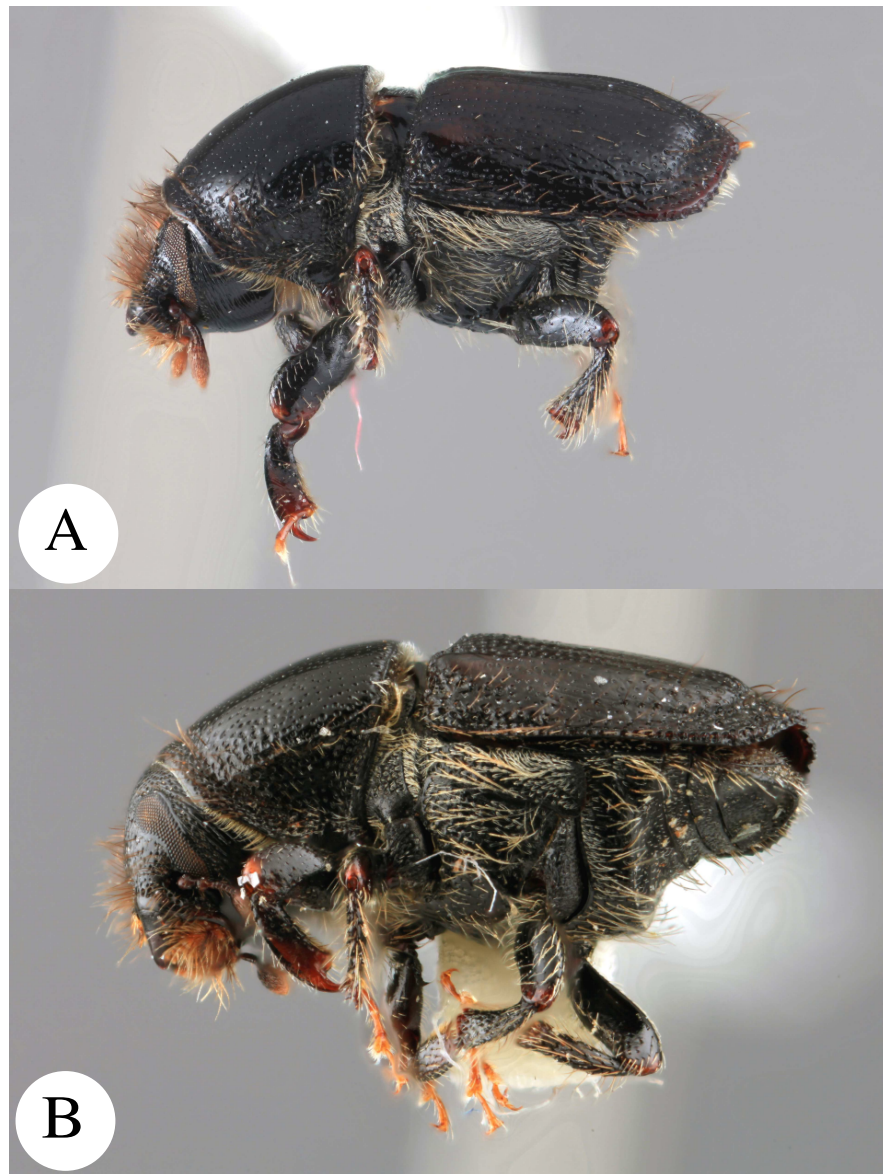


Figure 1.59. Dorsal view of *Scolytus silvaticus* male.



Figure 1.60. Lateral views of *Scolytus subscaber* male 2.0 – 4.3mm (A) and female 3.1 -5.0mm (B).

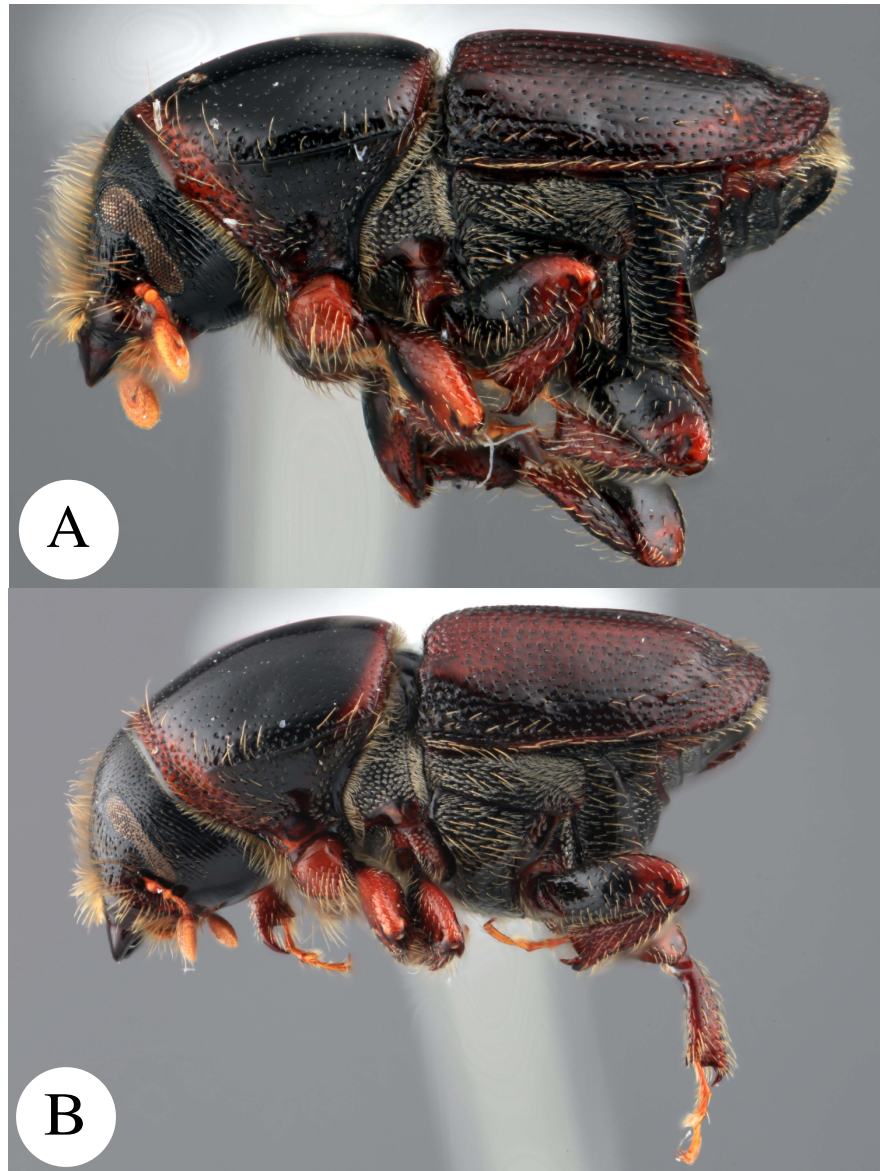


Figure 1.61. Dorsal view of *Scolytus subscaber* male.



Figure 1.62. Lateral views of *Scolytus tsugae* male 2.8 – 3.4mm (A) and female 2.3 – 3.5mm (B).

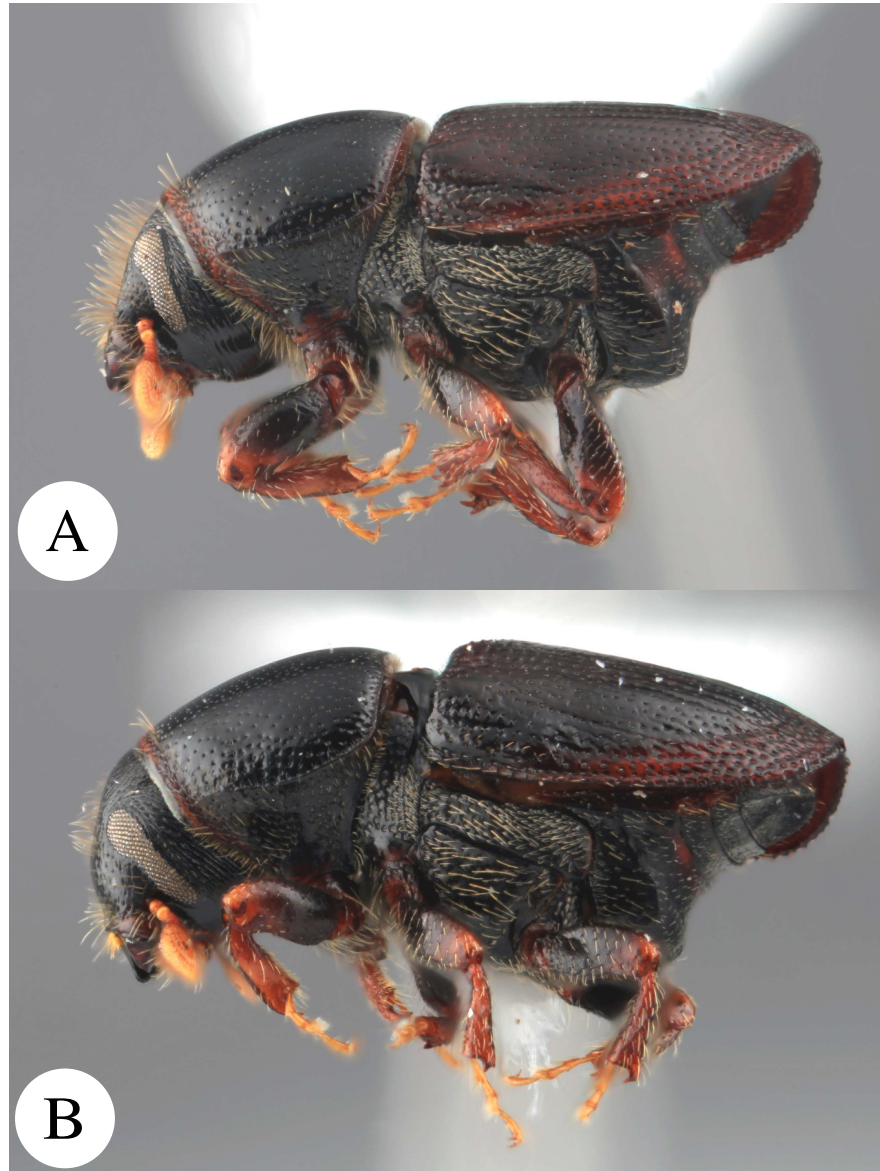


Figure 1.63. Dorsal view of *Scolytus tsugae* male.



Figure 1.64. Lateral views of *Scolytus unispinosus* male 2.2 – 3.2mm (A) and female 2.2 – 3.0 (B).

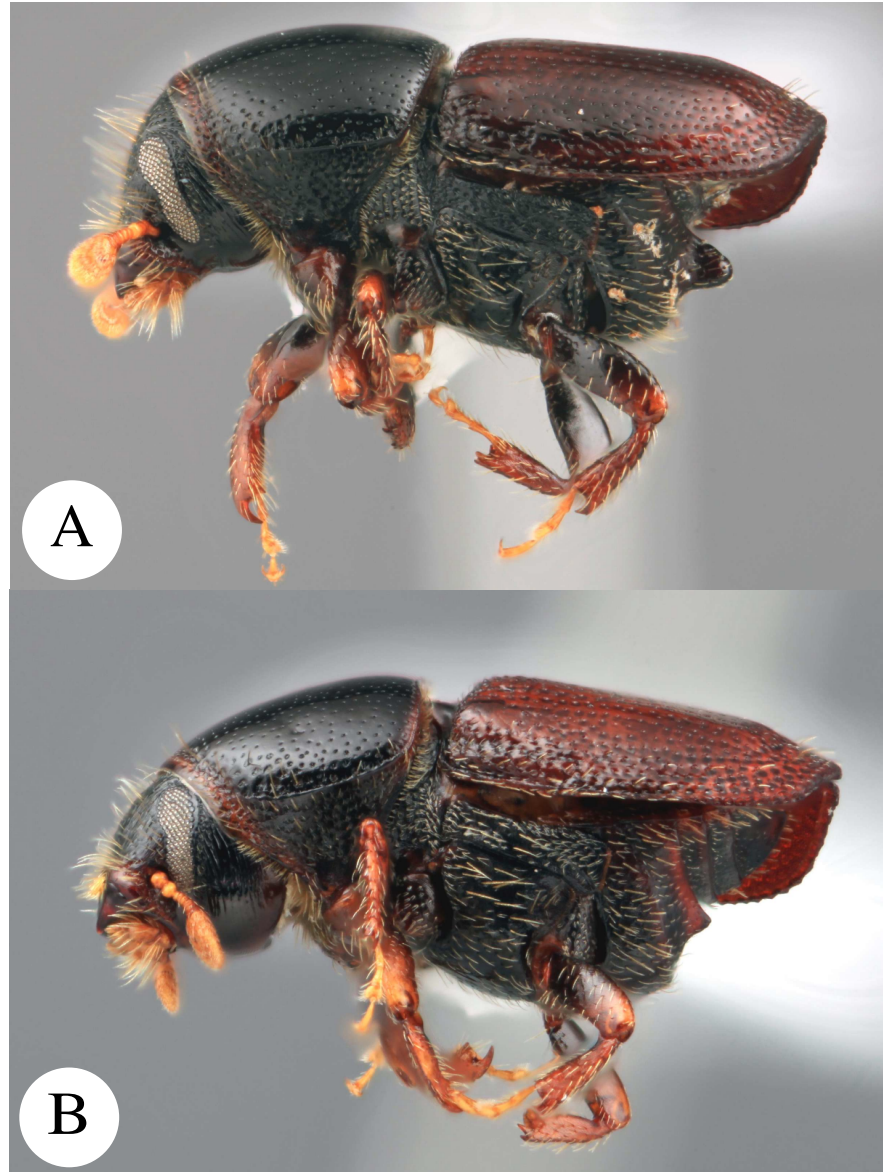


Figure 1.65. Dorsal view of *Scolytus unispinosus* male.



Figure 1.66. Lateral views of *Scolytus ventralis* male 3.0 – 4.0mm (A) and female 2.2 – 4.6 mm (B).

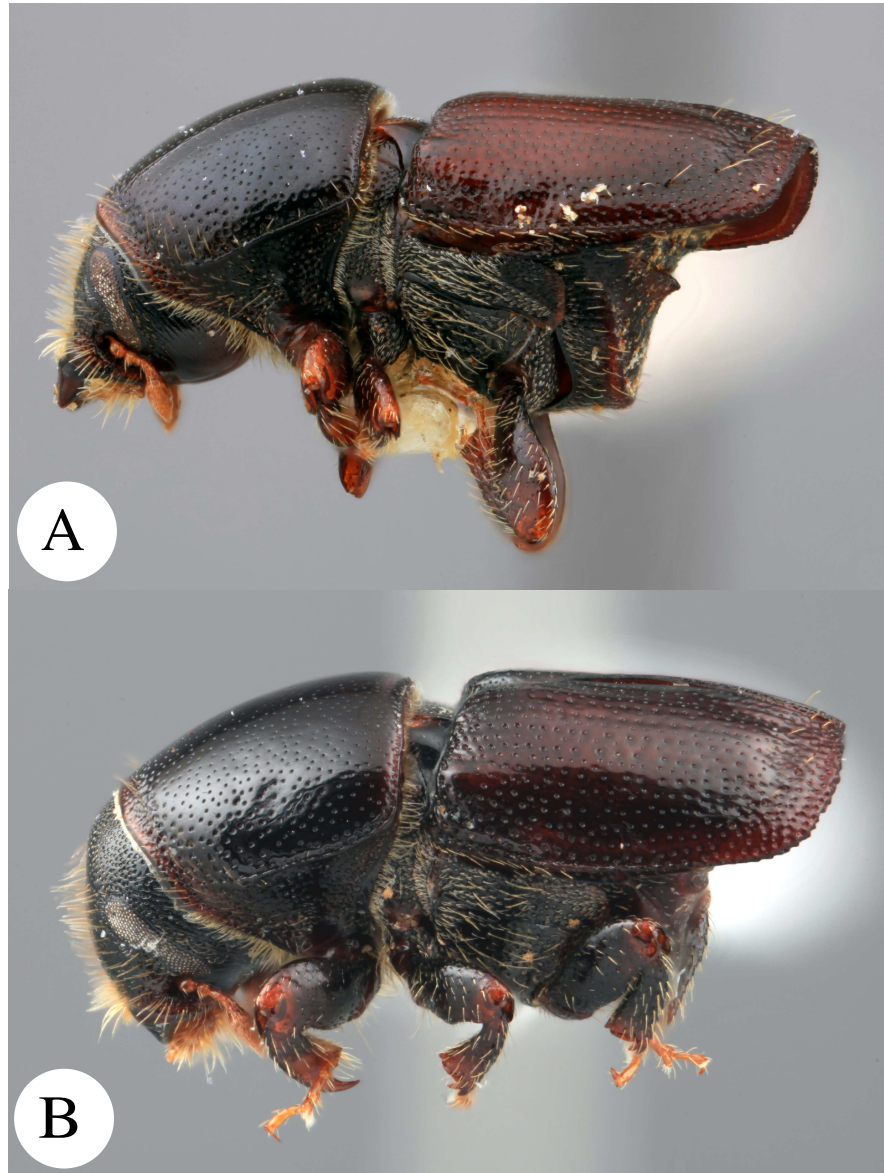


Figure 1.67. Dorsal views of *Scolytus ventralis* male.



APPENDIX B:
Tables and Figures for Chapter 2

Table 2.2. Table of Scolytini specimens sequenced, the collection locality, collector, host, matrix names and extraction names.

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Coptonotus cyclopus</i>	Costa Rica: Puntarenas: Coto Brus: Las Cruces Biological Station, N8°47.7', W82°57.32', 1200m, 16.VI.2010, S.M. Smith coll.	Copt cyc 69	SMS 69
<i>Coptonotus cyclopus</i>	Costa Rica: Herida [GenBank]	Copt cyc BJ	
<i>Camptocerus aeneipennis</i>	Guyana: Region 8: Iwokrama Forest, 4.671822, -58.684114, 66m, 4-9.III.2007, Cognato, Dole, Hulcr, Smith, McCall coll., Ex. <i>Ocotea oblonga</i>	Cam aen 1	Cam aen 1
<i>Camptocerus aeneipennis</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 14.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Protium amazonicum</i>	Cam aen 27	Cam aen 27
<i>Camptocerus aeneipennis</i>	Panama: Panama: Pipeline Rd, N9°10.315' W79°45.213', 94m, 3.IX.2008, S.M. Smith, A.D. Smith, A.R. Gillogly coll. Ex. <i>Protium</i> sp.	Cam aen 29	Cam aen 29
<i>Camptocerus aterrimus</i>	Peru: Madre de Dios: Los Amigos Biological Station, S12°34.9' W70°6.04', 15.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Protium amazonicum</i>	Cam ate 6	Cam ate 6
<i>Camptocerus auricomus</i>	Costa Rica: Heredia: Puerto Viejo, La Selva Biological Station, N10°26' W83°59', 4.VII.2010, S.M. Smith coll, Ex. <i>Protium</i> sp.	Cam aur 23	SMS 23
<i>Camptocerus auricomus</i>	Panama: Panama: Pipeline Rd, N9°10.315' W79°45.213', 94m, 3.IX.2008, S.M. Smith, A.D. Smith, A.R. Gillogly coll. Ex. <i>Protium</i> sp.	Cam aur 1	Cam aur 1

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Camptocerus coccoformus</i>	Ecuador: Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, lot 3125, trans. 3, sta. 5, I.2006, T.L. Erwin et al. coll., Ex. canopy fogging	Cam cocco	Cam cocco 1
<i>Camptocerus costatus</i>	Guyana: Region 8: Iwokrama Forest, 4.671822, -58.684114, 66m, 4-9.III.2007, Cognato, Dole, Hulcr, Smith, McCall coll, Ex. <i>Ocotea oblonga</i>	Cam cos	Cam sp. 2
<i>Camptocerus costatus</i>	Peru: Loreto: 25km SE from Iquitos to Rio Momon (Shimbilo), 5km from Pte Allegre, 109m, S3°33.094" W73°30.967", 14.IV.2012, A. Petrov coll.	Cam cos 173	SMS 173
<i>Camptocerus latipllis</i>	Ecuador: Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, lot 3293, trans. 9, sta. 3, VII.2006, T.L. Erwin et al. coll., Ex. canopy fogging	Cam lat	Cam D 1
<i>Camptocerus latipllis</i>	Peru: Loreto: 58 km SSW from Iquitos to Nauta, Rio Itaya, 120m, 6.III.2007, A. Petrov coll.	Cam lat 52	SMS 52
<i>Camptocerus mallopterus</i>	Ecuador: Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, lot 3129, trans. 3, sta. 9, I.2006, T.L. Erwin et al. coll., Ex. canopy fogging	Cam mall 1	Cam mall 1

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Camptocerus noel</i>	Guyana: Region 8: Iwokrama Forest, 4.671822, -58.684114, 66m, 4-9.III.2007, Cognato, Dole, Hulcr, Smith, McCall coll., Ex. <i>Ocotea oblonga</i>	Cam noel 2	Cam aen 2
<i>Camptocerus noel</i>	Ecuador: Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, lot 3283, trans. 8, sta. 3, VII.2006, T.L. Erwin et al. coll., Ex. canopy fogging	Cam noel 7	Cam aen 7
<i>Camptocerus noel</i>	Peru: Madre de Dios: Manu Los Amigos Biological Station, S12°34.9' W70°6.04', 14.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Protium amazonicum</i>	Cam noel 26	Cam aen 26
<i>Camptocerus opacicollis</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 15.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Protium amazonicum</i>	Cam opa 1	Cam opa 1
<i>Camptocerus pilifrons</i>	Ecuador: Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, lot 3187, trans. 9, sta. 7, I.2006, T.L. Erwin et al. coll., Ex. canopy fogging	Cam pil 1	Cam pil 1
<i>Camptocerus pseudoangustior</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 15.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Protium amazonicum</i>	Cam pse 5	Cam ate 5

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Camptocerus suturalis</i>	Guyana: Region 8: Iwokrama Forest, 4.671822, -58.684114, 66m, 4-9.III.2007, Cognato, Dole, Hulcr, Smith, McCall coll, Ex. <i>Ocotea oblonga</i>	Cam sut sp 1	Cam sp. 1
<i>Camptocerus suturalis</i>	Ecuador: Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, lot 3265, trans. 7, sta. 5, VII.2006, T.L. Erwin et al. coll., Ex. canopy fogging	Cam sut 1	Cam sut 1
<i>Camptocerus suturalis</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 15.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Protium amazonicum</i>	Cam sut 2	Cam sut 2
<i>Ceratolepsis amazonicus</i>	Ecuador: Orellana: Tiputini Biodiversity Station, S00°38.189' W76°08.965', 223m, 3-9.VI.2011, S.M. Smith coll. Ex. window trap	Cne ama 77	SMS 77
<i>Ceratolepsis amazonicus</i>	Peru: Loreto: 25km SE from Iquitos to Rio Momon (Shimbilo), 5km from Pte Allegrre, 109m, S3°33.094" W73°30.967, 10.V.2012, A. Petrov coll.	Cne ama 174	SMS 174
<i>Ceratolepsis insignis</i>	Panama: Panama: BCNM: Barro Colorado Island, 9°9'N, 79°50'W, 50-120m, 29.VIII.2012, S.M. Smith, N.A. Barc coll. Ex. <i>Virola sebifera</i>	Cne ins 175	SMS 175
<i>Cnemonyx exiguus</i>	Panama: Panama: BCNM: Barro Colorado Island, 9°9'N, 79°50'W, 50-120m, 29.VIII.2012, S.M. Smith, N.A. Barc coll. Ex. <i>Protium panamense</i>	Cne exi 177	SMS 177

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Cnemonyx panamensis</i>	Panama: Panama: BCNM: Barro Colorado Island, 9°9'N, 79°50'W, 50-120m, 27.VIII.2012, S.M. Smith, N.A. Barc coll. Ex. <i>Trichila hiruta</i>	Cne pan 176	SMS 176
<i>Cnemonyx rugulosus</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 12.V.2008, S.M. Smith, J. Hulcr coll.	Cne rug 5	Cne rug 5
<i>Cnemonyx rugulosus</i>	Ecuador: Orellana: Tiputini Biodiversity Station, S00°38.189' W76°08.965', 223m, 3-9.VI.2011, S.M. Smith coll.	Cne rug 76	SMS 76
<i>Cnemonyx setulosus</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 12.V.2008, S.M. Smith, J. Hulcr coll.	Cne pan	Cne sp 2
<i>Cnemonyx vismiacolens</i>	Guyana: Region 8: Iwokrama Forest, 4.671822, -58.684114, 66m, 4-9.III.2007, Cognato, Dole, Hulcr, Smith, McCall coll.	Cne vis	Cne sp. 1
<i>Loganius flavicornis</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 4.V.2008, S.M. Smith, J. Hulcr coll.	Cne fla 1	Cne fla 1
<i>Loganius gracilens</i>	Mexico: Oaxaca: Matalán, 10 km SSE; 16.76519, -96.34564; 19.X.2011, T.H. Atkinson coll., THA-954, Ex. <i>Euphorbia schlechtendali</i>	Cne gra 152	SMS 152
<i>Loganius opacus</i>	Panama: Panama: Pan-American Highway, N8°55.598' W79°33.936', 13m, 17.VIII.2008, A.D. Smith, A.R. Gillogly coll.	Cne opa 1	Cne opa 1

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus aztecus</i>	Mexico: Nuevo Leon: San Antonio de las Alazanas: Santa Catarina, G. Cuellar coll., Ex. <i>Pseudotsuga menziesii</i>	Sco aze 161	SMS 161
<i>Scolytus carpini</i>	Czech Republic: Moravia: Břeclav Kamci obora, 2004, K. Novakova coll.	Sco car 61	SMS 61
<i>Scolytus cristatus</i>	Peru: Junin: Perene River, 8 km NNE from Puerto Ocopa, Cananeden vill., S11°06' W73°60', 1100m, 2.II.2008, A. Petrov coll.	Sco cris 150	SMS 150
<i>Scolytus dimidiatus</i>	Panama: Panama: Gamboa Rd, N9°07'09.24" W79°42'51.98", 36m, 14.VIII.2008, S.M. Smith, A.D. Smith, A.R. Gillogly coll.	Sco dimi	Sco casp 1
<i>Scolytus ecksteini</i>	Iran: Gilan: Rasht, N37°11'55" E49°38'27", 16.VIII.2011, S. Amini coll., Ex. <i>Ulmus</i> sp.	Sco eck 166	SMS 166
<i>Scolytus ecksteini</i>	Iran: Gilan: Rasht, N37°11'55" E49°38'27", 16.VIII.2011, S. Amini coll., Ex. <i>Ulmus</i> sp.	Sco eck 167	SMS 167
<i>Scolytus ensifer</i>	Czech Republic: Moravia: Břeclav Kamci obora, 2004, K. Novakova coll.	Sco ens 58	SMS 58
<i>Scolytus ensifer</i>	Iran: Gilan: Rasht, N37°11'55" E49°38'27", 16.VIII.2011, S. Amini coll., Ex. <i>Ulmus</i> sp.	Sco ens 163	SMS 163
<i>Scolytus excavatus</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 22.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Pterocarpus rohrii</i>	Sco exc 1	Sco exc 1

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus fagi</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco fagi 2	Sco fagi 2
<i>Scolytus fagi</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco fagi 1	Sco fagi 1
<i>Scolytus fiskei</i>	USA: Colorado: Mesa Co: Grand Mesa overlook, 8.VIII.2008, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i> branches	Sco uni 1	Sco uni 1
<i>Scolytus fiskei</i>	USA: Colorado: Larimer Co.: Roosevelt National Forest, 9 km E Estes Park, Hwy 34, Big Thompson Canyon, N40°24.456' W105°24.565', 2143m, 5.V.2010, S.M. Smith, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 37	SMS 37
<i>Scolytus fiskei</i>	USA: Idaho: Boise Co.: Boise National Forest, Bogus Basin, NF275, N43°44.347' W116°07.099', 6042ft, 8.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 38	SMS 38
<i>Scolytus fiskei</i>	USA: Idaho: Latah Co.: Univeristy of Idaho experimental forest, N46°51.764' W116°43.786', 2855ft, 10.VIII.2010, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 41	SMS 41

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus intricatus</i>	Sweden: Smaaland: Karlsburg, 15.VII.2005, B.H. Jordal coll., Ex. <i>Quercus</i> sp.	Sco int 64	SMS 64
<i>Scolytus intricatus</i>	Sweden: Smaaland: Oskarshamn [GenBank]	Sco int BJ	
<i>Scolytus japonicus</i>	Russia: Primorsky: Anisimovka, 14.VII.2008, B.H. Jordal coll.	Sco jap 59	SMS 59
<i>Scolytus koltzei</i>	Russia: Far East, Shkotovskiy reg., 7 km S from Anisimovka vill., 20.VI.2008, A. Napolov coll., Ex. <i>Tilia</i> sp.	Sco kol 157	SMS 157
<i>Scolytus laevis</i>	Denmark, Rødby Havn, 24.VIII.2005, J. Pedersen leg.	Sco laevis	
<i>Scolytus laricis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.197' W116°13.068', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Larix occidentalis</i>	Sco lar 12	SMS 12
<i>Scolytus laricis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Larix occidentalis</i>	Sco lar 2	SMS 2
<i>Scolytus mali</i>	USA: Pennsylvania: Lebanon Co.: Mt. Gretna, N40.242501 W76.462406, IV-VIII.2009, S.E. Spichiger coll., Ex. Lindgren funnel trap	Sco mal 1	Sco mal 1

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus monticolae</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 33	SMS 33
<i>Scolytus monticolae</i>	USA: Idaho: Soshone Co.: Coeur D'Alene National Forest, Placer Creek Rd N47°25.746' W115°53.601', 3547ft, 15.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 34	SMS 34
<i>Scolytus monticolae</i>	USA: Idaho: Boise Co.: Boise Natioanl Forest, Bogus Basin, NF275, N43°44.347' W116°07.099', 6042ft, 8.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Pseudotsuga menziesii</i>	Sco mon 35	SMS 35
<i>Scolytus mozolevskae</i>	Ecuador: Orellana: Tiputini Biodiversity Station, S00°38.189' W76°08.965', 223m, lot 3024, T.L. Erwin et al. coll., Ex. canopy fogging	Sco mozo 54	SMS 54
<i>Scolytus multistriatus</i>	Denmark: Storstrøm: Rødbyhavn, 24.VIII.2005, J. Pedersen coll.	Sco mul 65	SMS 65
<i>Scolytus multistriatus</i>	USA: Michigan: Kalamazoo Co.: Gourdneck Lake State Game Area, 19.VI.2011, A.I. Cognato coll., Ex. <i>Ulmus</i> sp.	Sco mul 82	SMS 82
<i>Scolytus multistriatus</i>	Russia: Moscow Oblast: Dolgoprudnly, N55°58.266', E37°30.191', 570m, 28.VII.2011, A.V. Petrov coll., Ex. <i>Ulmus laevis</i>	Sco mul 147	SMS 147

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus muticus</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 29.V.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco mut 1	Sco mut 1
<i>Scolytus muticus</i>	USA: Michigan: Wayne Co.: Grosse Ile, N42.17060 W83.14496, 7-20.VI.2007, R. Mech coll., Ex. Lindgren funnel trap	Sco mut 2	Sco mut 2
<i>Scolytus muticus</i>	USA: South Carolina: Columbia, 26.X.2011, W. Jones coll., Ex. <i>Celtis</i> sp.	Sco mut 169	SMS 169
<i>Scolytus obelus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°55.987' W109°16.331', 7022ft, 22.V.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco obe 18	SMS 18
<i>Scolytus obelus</i>	USA: New Mexico: Torrance Co.: Cibola National Forest, W. Manzano, N34°37.226' W106°24.752', 7999ft, 11.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco obe 44	SMS 44
<i>Scolytus oregoni</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, Rogue River gorge viewpoint, Hwy 62 1/4 mi N Union Creek Rd, N42°54.540' W122°26.733', 3489ft, 21.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ore 5	SMS 5

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus oregoni</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, Rogue River gorge viewpoint, Hwy 62 1/4 mi N Union Creek Rd, N42°54.540' W122°26.733', 3489ft, 21.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ore 71	SMS 71
<i>Scolytus orientalis</i>	Turkmenistan: Central Kopet Dag Mountains, 16 km S from Batken, Ipay Kala, 700m, 15.V.1996, A. Petrov coll, Ex. <i>Ulmus</i> sp.	Sco orien 148	SMS 148
<i>Scolytus piceae</i>	USA: Michigan: Livingston Co.: Howell, 431 Bishop Rd, N42.5076 W83.85698, 25.VI.2009, R. Mech coll., Ex. Lindgren funnel trap	Sco pic 1	Sco mul 1
<i>Scolytus piceae</i>	USA: Idaho: Latah Co.: University of Idaho Experimental Forest, N46°51.164' W116°44.838', 2939ft, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Picea engelmanni</i>	Sco pic 7	SMS 7
<i>Scolytus piceae</i>	USA: South Dakota: Lawrence Co.: Brownsville Rd near Leads, N44.2922 W103.7828, 27.VII.2004, 5650ft, K.P. Dole coll., Ex. <i>Picea glauca</i>	Sco pic 73	SMS 73
<i>Scolytus piceae</i>	USA: Wyoming: Carbon Co.: Medicine Bow National Forest, Snowy Mountains, WY130, Lake Marie, N41°19.965' W106°19.516' 3208m, 26.VII.2011, S.M. Smith, D.E. Bright, B.A Barr coll., Emerged 1-5.IX.2011, Ex. <i>Picea engelmannii</i> branches	Sco pic 83	SMS 83

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus praeceps</i>	USA: California: Siskiyou Co.: Klamath National Forest, FR 41N16, N41°14.822' W122°53.562', 5081ft, 28.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco abi 14	SMS 14
<i>Scolytus praeceps</i>	USA: Idaho: Bonner Co.: Kaniksu National Forest, FR 232, N48°20.609' W116°20.507', 2717ft, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies grandis</i>	Sco abi 16	SMS 16
<i>Scolytus praeceps</i>	USA: Idaho: Latah Co.: Univeristy of Idaho experimental forest, N46°51.372' W116°44.038', 2857ft, 10.VIII.2010, S.M. Smith, A.R. Gillogly, M.M. Furniss coll., Ex. <i>Abies lasiocarpa</i>	Sco opa 21	SMS 21
<i>Scolytus praeceps</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.200' W116°13.067', 2696ft 13.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies lasiocarpa</i>	Sco opa 68	SMS 68
<i>Scolytus praeceps</i>	USA: California: El Dorado Co.: El Dorado National Forest, nr. Ice House Reservoir, N38°50.002' W120°21.160', 5413ft, 25.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco pra 29	SMS 29
<i>Scolytus praeceps</i>	USA: California: Siskiyou Co.: Shasta Trinity National Forest, Mt. Shasta, N41°20.844' W122°16.691', 4892ft, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco pra 30	SMS 30

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus praeceps</i>	USA: Wyoming: Albany Co.: Snowy Mountains, Medicine Bow National Forest, Spruce campground, 6.IX.2010, D.E. Bright, B.A. Barr coll., Ex. <i>Abies concolor</i>	Sco pra 91	SMS 91
<i>Scolytus propinquus</i>	Mexico: Oaxaca: Huatulco, 15.76234, -96.12885, 41m, 23.VI.2009, T.H. Atkinson coll., THA 874, Ex. legume tree	Sco pro 1	Sco pro 1
<i>Scolytus propinquus</i>	Mexico: Oaxaca: Huatulco, 15.76234, -96.12885, 41m, 23.VI.2009, T.H. Atkinson coll., THA 874, Ex. legume tree	Sco pro 2	Sco pro 2
<i>Scolytus proximus</i>	Bolivia: Santa Cruz: nr. Samaipata, above Achira camp, 10.XI.2009, N.P. Lord coll.	Sco prox 3	Sco prox 3
<i>Scolytus proximus</i>	Peru: Madre de Dios: Manu: Los Amigos Biological Station, S12°34.9' W70°6.04', 22.V.2008, S.M. Smith, J. Hulcr coll., Ex. <i>Pterocarpus rohrii</i>	Sco prox 2	Sco sasp 2
<i>Scolytus pygmaeus</i>	Czech Republic: Moravia: Břeclav Kamci obora, 2004, K. Novakova coll.	Sco pyg 62	SMS 62
<i>Scolytus pygmaeus</i>	Denmark: Storstrøm: Rødbyhavn, 24.VIII.2005, J. Pedersen coll.	Sco pyg 67	SMS 67
<i>Scolytus quadrispinosus</i>	USA: Pennsylvania: Cumberland Co.: Roadway Dr @ Schenider Dr., 24.VII.2009, L.R. Donovall coll., Ex. Lindgren funnel trap	Sco qua 1	Sco qua 1

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus quadrispinosus</i>	USA: Maryland: Ann Aruridel Co.: Annapolis, 26.V.2012, R.J. Rabaglia coll., Ex. Lindgren funnel trap	Sco qua 170	SMS 170
<i>Scolytus ratzeburgii</i>	Russia: Primorsky: Anisimovka, 12.VII.2008, B.H. Jordal coll.	Sco ratz 60	SMS 60
<i>Scolytus reflexus</i>	USA: Arizona: Pima Co.: Coronado National Forest, Santa Catalina Mountains, N32°24.529' W110°42.678', 7869ft, 22.V.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco ref 26	SMS 26
<i>Scolytus reflexus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°54.915' W109°16.040', 8196ft, 20.V.2010, S.M. Smith coll. Ex. <i>Pseudotsuga menziesii</i>	Sco ref 27	SMS 27
<i>Scolytus reflexus</i>	USA: Colorado: Larimer Co.: Roosevelt National Forest, 9 km E Estes Park, Hwy 34, Big Thompson Canyon, N40°24.456' W105°24.565', 2143m, 5.V.2010, S.M. Smith, D.E. Bright, B.A. Barr coll. Ex. <i>Pseudotsuga menziesii</i>	Sco ref 32	SMS 32
<i>Scolytus reflexus</i>	USA: Colorado: Boulder Co.: Roosevelt National Forest, St. Vrain canyon, N40°10.072' W105°23.623', 2127m, 24.VII.2011, S.M. Smith, D.E. Bright, B.A. Barr coll., Ex. <i>Pseudotsuga menziesii</i>	Sco ref 85	SMS 85

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus reflexus</i>	Mexico: Nuevo Leon: San Antonio de las Alazanas: Santa Catarina, G. Cuellar coll., Ex. <i>Pseudotsuga menziesii</i>	Sco vir 162	SMS 162
<i>Scolytus reflexus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°55.360' W109°15.702', 7882ft, 20.V.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco wick 24	SMS 24
<i>Scolytus reflexus</i>	USA: New Mexico: Otero Co.: Lincoln National Forest, Apache Point observatory, N32°47.046' W105°48.841', 9116ft, 16.V.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco wick 25	SMS 25
<i>Scolytus reflexus</i>	USA: New Mexico: Colfax Co.: Highway 64 near Ute Park, N36°33'9.26" W105°07'6.74", 2242m, 24.VI.2004, A.I. Cognato, S.A. Stephens coll., Ex. <i>Pinus ponderosa</i>	Sco wick 74	SMS 74
<i>Scolytus robustus</i>	USA: Arizona: Graham Co.: Coronado National Forest, Pinaleno Mountains, N32°37.702' W109°49.472', 7896ft, 23.V.2010, S.M. Smith coll. Ex. <i>Abies concolor</i>	Sco rob 3	SMS 3
<i>Scolytus robustus</i>	USA: New Mexico: Taos Co.: Carson National Forest, Agua Piedra campground, Hwy 75, N36°07.960' W105°31.828', 8477 ft, 13.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco rob 43	SMS 43

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus robustus</i>	USA: Arizona: Cochise Co.: Coronado National Forest, Chiricahua Mountains, N31°54.665' W109°16.336', 2445m, 5.VIII.2012, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco rob 178	SMS 178
<i>Scolytus rugulosus</i>	Hungary: Győr-Moson-Sopron: Sopron, 2003, F. Lakatos coll.	Sco rug 66	SMS 66
<i>Scolytus rugulosus</i>	Morocco: 30 km S. Asni, Tizi'n'Test, 18.IV.2002, B.H. Jordal coll., Ex. <i>Prunus dulcis</i>	Sco rug 72	SMS 72
<i>Scolytus rugulosus</i>	Czech Republic: South Bohemia: Jindřichův Hradec env. Číměř, 23.VII.2011, M.Knížek lgt., Ex. <i>Prunus</i> sp.	Sco rug 79	SMS 79
<i>Scolytus rugulosus</i>	Iran: Gilan: Khoshkestalkh, N37°27'01" E49°42'06", 17.VII.2011, S. Amini coll., Ex. <i>Malus</i> sp.	Sco rug 165	SMS 165
<i>Scolytus schevyrewi</i>	USA: Missouri: Saint Louis Co.: Maryland Heights, 22.V.2008, Ex. Lindgren funnel trap	Sco sch 2	Sco sch 2
<i>Scolytus scolytus</i>	Denmark: NEJ, Tofte Skov [GenBank]	Sco sco BJ	
<i>Scolytus semenovi</i>	Russia: Primorsky, N43°00'34" E134°07'43", 17-21.VIII.2007, A. Napolov coll.	Sco sem 156	SMS 156
<i>Scolytus sinopiceus</i>	China: Qinghai: MaiXiu Forest Preserve, N35°16.288' E101°55.904', 2927m, 21.V.2008, A.I. Cognato coll., Ex. Lindgren funnel trap	Sco sin 1	Sco sin 1
<i>Scolytus sinopiceus</i>	China: Sichuan: Highway 213 near Zhangla, 9.VII.2004, A.I. Cognato coll., Ex. <i>Picea purpurea</i>	Sco sin 70	SMS 70

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus subscaber</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.197' W116°13.068', 2748ft 13.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies lasiocarpa</i>	Sco sub 51	SMS 51
<i>Scolytus subscaber</i>	USA: California: Alpine Co., Toiyabe National Forest, 11.6 miles E of Markleeville, N38°39.906' W119°38.540', 24.VII.2010, S.M. Smith coll., Ex. <i>Abies magnifica</i>	Sco sub 6	SMS 6
<i>Scolytus sulcifrons</i>	Russia: Moscow Oblast: Dolgoprudny, N55°58.266', E37°30.191', 570m, 28.VII.2011, A.V. Petrov coll., Ex. <i>Ulmus laevis</i>	Sco sul 146	SMS 146
<i>Scolytus triarmatus</i>	Sweden: Uppsala: Tierp, WGS 84, N60°18.310' E17°28.716', 8.VI.2012, Å. Lindelöw coll., Ex. reared from bark of standing <i>Ulmus glabra</i>	Sco tri 171	SMS 171
<i>Scolytus tsugae</i>	USA: Idaho: Soshone Co.: St. Joe National Forest, N47°00.790' W116°12.359', 3192ft, 15.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Tsuga occidentalis</i>	Sco tsu 10	SMS 10
<i>Scolytus tsugae</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, N48°40.911' W116°34.345', 4353ft, 12.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Tsuga heterophylla</i>	Sco tsu 11	SMS 11

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus unispinosus</i>	USA: Oregon: Deschutes Co.: Deschutes National Forest, Black Butte Rd, Black Butte, N40°24.924' W121°38.323', 4212ft, 1.VIII.2010 S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco fis 1	SMS 1
<i>Scolytus unispinosus</i>	USA: Oregon: Hood River Co.: Mount Hood National Forest, Sherwood Campground, Hwy 35, N45°19.278' W121°37.104', 4293ft, 2.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 39	SMS 39
<i>Scolytus unispinosus</i>	USA: Oregon: Klamath Co.: Deschutes National Forest, NF 4672, N43°30.474' W121°52.147', 4923ft, 31.VII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 42	SMS 42
<i>Scolytus unispinosus</i>	USA: Oregon: Jackson Co.: Rogue River National Forest, NF 60, N42°53.926' W122°19.177', 4547ft, 30.VII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 40	SMS 40
<i>Scolytus unispinosus</i>	USA: Oregon: Marion Co.: Williamette National Forest, Breitenbush Rd, N44°47.200' W121°56.557', 2645ft, 1.VIII.2010, S.M. Smith coll., Ex. <i>Pseudotsuga menziesii</i>	Sco uni 151	SMS 151

Table 2.2 (cont'd).

Species	Collection locality, date, collector and host	Matrix name	Extraction name
<i>Scolytus ventralis</i>	USA: Idaho: Boundary Co.: Kaniksu National Forest, Robinson Lake campground, N48°58.385' W116°13.351', 2748ft, 11.VIII.2010, S.M. Smith, A.R. Gillogly coll., Ex. <i>Abies lasiocarpa</i>	Sco ven 22	SMS 22
<i>Scolytus ventralis</i>	USA: New Mexico: Torrance Co.: Cibola National Forest, W. Manzano, N34°37.325' W106°24.642', 8026ft, 11.V.2010, S.M. Smith, A.I. Cognato coll., Ex. <i>Abies concolor</i>	Sco ven 48	SMS 48
<i>Scolytus ventralis</i>	USA: California: El Dorado Co.: El Dorado National Forest, nr. Ice House Reservoir N38°50.002' W120°21.160', 5413ft, 25.VII.2010, S.M. Smith coll., Ex. <i>Abies concolor</i>	Sco ven 49	SMS 49
<i>Scolytus ventralis</i>	USA: Arizona: Coconino Co.: Arizona Snowbowl, N36°24.381' W112°05.619', 8923ft, 30.V.2010 S.M. Smith, K. Bush coll., Ex. <i>Abies lasiocarpa</i>	Sco ven 50	SMS 50

Table 2.3. Properties of the data included in the Bayesian analysis of all genes and the model of nucleotide evolution selected by the AIC criterion in MrModel test. PI = parsimony informative characters; Steps = the shortest parsimony tree produced by analysis of the partition for included taxa; CI = consistency index for included taxa.

Partition	Taxa	Characters	PI	Steps	CI	Best model	Mr Bayes model
COI	111	615	288	3199	0.204	GTR+I+G	GTR+I+G
28S	127	557	339	1121	0.57	TVM+G	GTR+I+G
CAD	114	690	309	1800	0.32	TrN+I+G	GTR+I+G
ArgK	106	692	252	1197	0.343	TIMEf+I+G	GTR+I+G
CAD+ArgK	122	1382	561	3831	0.331	TIM+I+G	GTR+I+G
COI+28S+CAD+ArgK	131	2554	1188	7616	0.302	TIM+I+G	GTR+I+G

Table 2.4. *Camptocerus* species distribution, known host families and genera.

		Magnoliids	Eurosid I	Eurosid II		Genera
		Laurales	Malpighiales	Sapindales		
		Lauraceae	Chrysobalanaceae	Burseraceae	Meliaceae	
Species	Region					
<i>aeneipennis</i>	Central & South America	X		X		<i>Protium; Ocotea</i>
<i>aterrimus</i>	South America			X		<i>Protium</i>
<i>auricomus</i>	Central & South America	X		X	X	<i>Protium; Cedrela; Ocotea</i>
<i>coccoformus</i>	South America					
<i>costatus</i>	South America	X				<i>Ocotea</i>
<i>latipilis</i>	South America					
<i>mallopterus</i>	South America					
<i>niger</i>	South America		X	X		<i>Protium; Hirtella; Licania</i>
<i>noel</i>	South America	X		X		<i>Protium; Ocotea</i>
<i>opacicollis</i>	Central & South America		X	X		<i>Protium</i>
<i>pilifrons</i>	South America					
<i>pseudoangustior</i>	South America			X		<i>Protium</i>
<i>suturalis</i>	South America	X		X		<i>Protium; Ocotea</i>

Table 2.5. *Ceratolepsis*, *Cnemonyx* and *Loganius* species distribution, known host families and genera.

			Angiosperms					Genera
			Magnoliids	Eurosid I		Eurosid II		
			Magnoliales	Malpighiales		Sapindales		
Genus	Species	Region	Myristicaceae	Clusiaceae	Euphorbiaceae	Burseraceae	Meliaceae	
<i>Ceratolepsis</i>	<i>amazonicus</i>	South America	X					<i>Virola</i> <i>Protium</i> ; <i>Vismia</i> ; <i>Trichila</i> <i>Protium</i>
<i>Ceratolepsis</i>	<i>insignis</i>	Central & South America						
<i>Cnemonyx</i>	<i>panamensis</i>	Central & South America		X		X	X	
<i>Cnemonyx</i>	<i>exiguus</i>	Central America				X		
<i>Cnemonyx</i>	<i>setulosus</i>	Mexico & Central America						<i>Tetragastris</i> ; <i>Trichilia</i> <i>Vismia</i>
<i>Cnemonyx</i>	<i>rugulosus</i>	South America				X	X	
<i>Cnemonyx</i>	<i>vismiacolens</i>	South America		X				
<i>Loganius</i>	<i>flavicornis</i>	South America			X			
<i>Loganius</i>	<i>gracilens</i>	Mexico						
<i>Loganius</i>	<i>opacus</i>	Central America				X		<i>Hippomane</i>

Table 2.6. *Scolytus* species distribution, known host families and genera.

		Pinopsida	Angiosperms															
		Pinales	Eudicots															
			Ranunculales	Core Eudicots														
				Caryophyllales	Saxifragales	Eurosid I												
						Fabales	Fagales		Malpighiales			Rosales						
		Pinaceae	Ranunculaceae	Polygonaceae	Hamamelidaceae	Fabaceae	Betulaceae	Fagaceae	Juglandaceae	Combretaceae	Euphorbiaceae	Malpigiaceae	Saliceae	Elaeagnaceae	Cannabaceae	Rhamnaceae	Rosaceae	Ulmaceae
<i>Scolytus</i> species	Region																	
<i>aztecus</i>	Nearctic	X																
<i>fagi</i>	Nearctic							X							X			
<i>fiskei</i>	Nearctic	X																
<i>laricis</i>	Nearctic	X																
<i>monticolae</i>	Nearctic	X																
<i>muticus</i>	Nearctic														X		X	
<i>obelus</i>	Nearctic	X																
<i>oregoni</i>	Nearctic	X																
<i>piceae</i>	Nearctic	X																
<i>praeceps</i>	Nearctic	X																
<i>quadrispinosus</i>	Nearctic								X									
<i>reflexus</i>	Nearctic	X																
<i>robustus</i>	Nearctic	X																
<i>subscaber</i>	Nearctic	X																
<i>tsugae</i>	Nearctic	X																
<i>unispinosus</i>	Nearctic	X																
<i>ventralis</i>	Nearctic	X																

Table 2.6 (cont'd).

		Pinopsida	Angiosperms															
		Pinales	Eudicots															
			Ranunculales	Core Eudicots														
				Caryophyllales	Saxifragales	Eurosid I												
						Fabales	Fagales		Malpighiales			Rosales						
<i>Scolytus</i> species	Region	Pinaceae	Ranunculaceae	Polygonaceae	Hamamelidaceae	Fabaceae	Betulaceae	Fagaceae	Juglandaceae	Combretaceae	Euphorbiaceae	Malpigaceae	Saliceae	Elaeagnaceae	Cannabaceae	Rhamnaceae	Rosaceae	Ulmaceae
<i>cristatus</i>	Neotropical		X			X						X						
<i>dimidiatus</i>	Neotropical					X										X		
<i>excavatus</i>	Neotropical					X												
<i>mozolevskae</i>	Neotropical																	
<i>propinquus</i>	Neotropical					X												
<i>proximus</i>	Neotropical					X												
<i>carpini</i>	Paelarctic						X	X										X
<i>ecksteini</i>	Paelearctic																	X
<i>ensifer</i>	Paelearctic																X	X
<i>intricatus</i>	Paelearctic				X		X	X					X				X	X
<i>japonicus</i>	Paelearctic																X	X
<i>koltzei</i>	Paelearctic																	
<i>laevis</i>	Paelearctic						X	X									X	X
<i>mali</i>	Paelearctic																X	X

Table 2.6 (cont'd).

		Pinopsida	Angiosperms																			
		Pinales	Eudicots																			
			Ranunculales	Core Eudicots																		
				Caryophyllales	Saxifragales	Eurosid I																
						Fabales	Fagales		Malpighiales			Rosales										
Scolytus species	Region	Pinaceae	Ranunculaceae	Polygonaceae	Hamamelidaceae	Fabaceae	Betulaceae	Fagaceae	Juglandaceae	Combretaceae	Euphorbiaceae	Malpigaceae	Saliceae	Elaeagnaceae	Cannabaceae	Rhamnaceae	Rosaceae	Ulmaceae				
multistriatus	Paelearctic	X		X		X	X	X					X			X		X				
orientalis	Paelearctic																					X
pygmaeus	Paelearctic											X	X									X
ratzeburgii	Paelearctic											X	X	X				X				X
rugulosus	Paelearctic																					X
schevyrewi	Paelearctic										X	X							X			X
scolytus	Paelearctic											X		X								X
semenovi	Paelearctic																				X	X
sinopiceus	Paelearctic																					
sulcifrons	Paelearctic												X									X
triarmatus	Paelearctic																					

Table 2.6 (cont'd).

		Angiosperms					Genera
		Eudicots					
		Eurosid II		Euasterid II			
		Malvales	Sapindales	Dipsacales	Lamiales		
<i>Scolytus</i> species	Region	Malvaceae	Sapindaceae	Caprifoliaceae	Oleaceae	Verbenaceae	
<i>aztecus</i>	Nearctic						<i>Abies; Pseudotsuga</i>
<i>fagi</i>	Nearctic						<i>Fagus; Celtis</i>
<i>fiskei</i>	Nearctic						<i>Pseudotsuga</i>
<i>laricis</i>	Nearctic						<i>Larix</i>
<i>monticolae</i>	Nearctic						<i>Pseudotsuga</i>
<i>muticus</i>	Nearctic						<i>Celtis; Gleditsia</i>
<i>obelus</i>	Nearctic						<i>Abies</i>
<i>oregoni</i>	Nearctic						<i>Pseudotsuga</i>
<i>piceae</i>	Nearctic						<i>Picea</i>
<i>praeceps</i>	Nearctic						<i>Abies</i>
<i>quadrispinosus</i>	Nearctic						<i>Carya</i>
<i>reflexus</i>	Nearctic						<i>Pseudotsuga</i>
<i>robustus</i>	Nearctic						<i>Abies</i>
<i>subscaber</i>	Nearctic						<i>Abies</i>
<i>tsugae</i>	Nearctic						<i>Tsuga</i>
<i>unispinosus</i>	Nearctic						<i>Pseudotsuga</i>
<i>ventralis</i>	Nearctic						<i>Abies</i>

Table 2.6 (cont'd).

		Angiosperms					Genera
		Eudicots					
		Eurosid II		Euasterid II			
		Malvales	Sapindales	Dipsacales	lamiales		
<i>Scolytus</i> species	Region	Malvaceae	Sapindaceae	Caprifoliaceae	Oleaceae	Verbenaceae	
<i>cristatus</i>	Neotropical					X	<i>Lonchocarpus; Heteropterys; Clematis, Petrea</i>
<i>dimidiatus</i>	Neotropical						<i>Lonchocarpus; Rhamnus</i>
<i>excavatus</i>	Neotropical						<i>Pterocarpus</i>
<i>mozolevskae</i>	Neotropical						
<i>propinquus</i>	Neotropical						<i>Inga; Lonchocarpus</i>
<i>proximus</i>	Neotropical						<i>Lonchocarpus</i>
<i>carpini</i>	Paelarctic						<i>Carpinus; Ostrya; Fagus; Corylus; Quercus;</i>
<i>ecksteini</i>	Paelearctic						<i>Ulmus; Zelkova</i>
<i>ensifer</i>	Paelearctic						<i>Ulmus; Prunus; Zelkova</i>
<i>intricatus</i>	Paelearctic		X				<i>Ostrya; Castanea; Parrotia; Ulmus; Quercus;</i> <i>Zelkova; Populus; Salix; Aesculus; Sorbus;</i> <i>Betula; Fagus</i>
<i>japonicus</i>	Paelearctic		X	X			<i>Prunus; Pyrus; Ulmus; Zelkova; Malus;</i> <i>Lonicera; Acer</i>
<i>koltzei</i>	Paelearctic	X					<i>Tilia</i>
<i>laevis</i>	Paelearctic	X	X				<i>Ulmus; Alnus; Corylus; Fagus; Quercus; Tilia;</i> <i>malus; Prunus; Pyrus; Acer</i>
<i>mali</i>	Paelearctic						<i>Malus; Prunus; Pyrus; Cotoneaster; Crataegus;</i> <i>Sorbus; Ulmus</i>

Table 2.6 (cont'd).

		Angiosperms					Genera
		Eudicots					
		Eurosid II		Euasterid II			
		Malvales	Sapindales	Dipsacales	miales		
<i>Scolytus</i> species	Region	Malvaceae	Sapindaceae	Caprifoliaceae	Oleaceae	Verbenaceae	
<i>multistriatus</i>	Paelearctic				X		<i>Ulmus</i>
<i>orientalis</i>	Paelarctic						<i>Ulmus</i> , <i>Zelkova</i>
<i>pygmaeus</i>	Paelearctic				X		<i>Ulmus</i> ; <i>Carpinus</i> ; <i>Fagus</i> ; <i>Quercus</i> ; <i>Prunus</i> ; <i>Olea</i>
<i>ratzeburgii</i>	Paelearctic				X		<i>Betula</i> ; <i>Ulmus</i> ; <i>Carpinus</i> ; <i>Corylus</i> ; <i>Prunus</i> ; <i>Zelkova</i> ; <i>Populus</i> ; <i>Juglans</i> ; <i>Salix</i> ; <i>Fraxinus</i>
<i>rugulosus</i>	Paelearctic						<i>Malus</i> ; <i>Pyrus</i> ; <i>Prunus</i> ; <i>Amelanchier</i> ; <i>Crataegus</i> ; <i>Sorbus</i> ; <i>Cotoneaster</i> ; <i>Cydonia</i> ; <i>Mespilus</i>
<i>schevyrewi</i>	Paelearctic						<i>Ulmus</i> ; <i>Salix</i> ; <i>Eleagnus</i> ; <i>Caragana</i> ; <i>Prunus</i> ; <i>Armeniaca</i> ; <i>Caragana</i> ; <i>Persica</i>
<i>scolytus</i>	Paelearctic				X		<i>Ulmus</i> ; <i>Quercus</i> ; <i>Amalygdalus</i> ; <i>Fraxinus</i> ; <i>Juglans</i> ; <i>Corylus</i>
<i>semenovi</i>	Paelearctic						<i>Ulmus</i> ; <i>Malus</i>
<i>sinopiceus</i>	Paelearctic						<i>Picea</i>
<i>sulcifrons</i>	Paelearctic						<i>Ulmus</i> ; <i>Quercus</i>
<i>triarmatus</i>	Paelarctic						<i>Ulmus</i>
<i>sinopiceus</i>	Paelearctic						<i>Picea</i>
<i>sulcifrons</i>	Paelearctic						<i>Ulmus</i> ; <i>Quercus</i>
<i>triarmatus</i>	Paelarctic						<i>Ulmus</i>

Table 2.7. Estimates of clade ages in millions of years ago (mya) and 95% highest posterior density (HDP) ranges generated using a Bayesian relaxed molecular clock in BEAST with fossil calibrations of the oldest Scolytini at 100 mya (A) and 120 mya (B).

Node	Clade	Analysis A		Analysis B	
		Median	95% HDP	Median	95% HDP
1	Scolytini	94	139-53	113	158-68
2	<i>Loganius</i>	26	42-13	32	47-14
3	<i>Ceratolepsis</i>	21	33-11	26	37-14
4	<i>Camptocerus s.l.</i>	30	45-17	39	57-23
5	<i>Camptocerus s.s.</i>	34	49-20	43	59-26
6	<i>Scolytus</i>	50	70-30	59	78-38
7	Neotropical <i>Scolytus</i>	21	35-7	22	35-12
8	Holarctic <i>Scolytus</i>	32	47-19	38	52-24
9	Tubuloscolytus	9	17-3	12	21-6
10	Nearctic conifer <i>Scolytus</i>	16	24-9	20	27-11

Table 2.1. Scolytini genera, diversity, distribution, feeding habits and common host families.

Genus	Species count	Distribution	Feeding habit	# Conifer feeders	Common hosts
<i>Camptocerus</i>	31	Neotropical	fungus	0	Burseraceae, Lauraceae
<i>Ceratolepsis</i>	6	Neotropical	phloem	0	Myristicaceae
<i>Cnemonyx</i>	22	Neotropical	phloem	0	Burseraceae, Clusiaceae, Euphorbiaceae
<i>Loganius</i>	19	Neotropical	phloem	0	Euphorbiaceae
<i>Scolytopsis</i>	6	Neotropical	phloem	0	Combretaceae
<i>Scolytus</i>	44	Neotropical	phloem	0	Fabaceae
<i>Scolytus</i>	21	Nearctic	phloem	18	Pinaceae, Cannabaceae, Fagaceae, Juglandaceae, Ulmaceae, Rosaceae,
<i>Scolytus</i>	62	Paleartic	phloem	4	Betulaceae, Fagaceae, Sapindaceae, Julandaceae, Malvaceae, Pinaceae
Total	211			22	

Figure 2.1. Bayesian tree derived by analysis of data set I with all genes treated as a single partition with GTR+I+ Γ . Posterior probabilities are listed above nodes (** ≥ 95 , * ≥ 90).

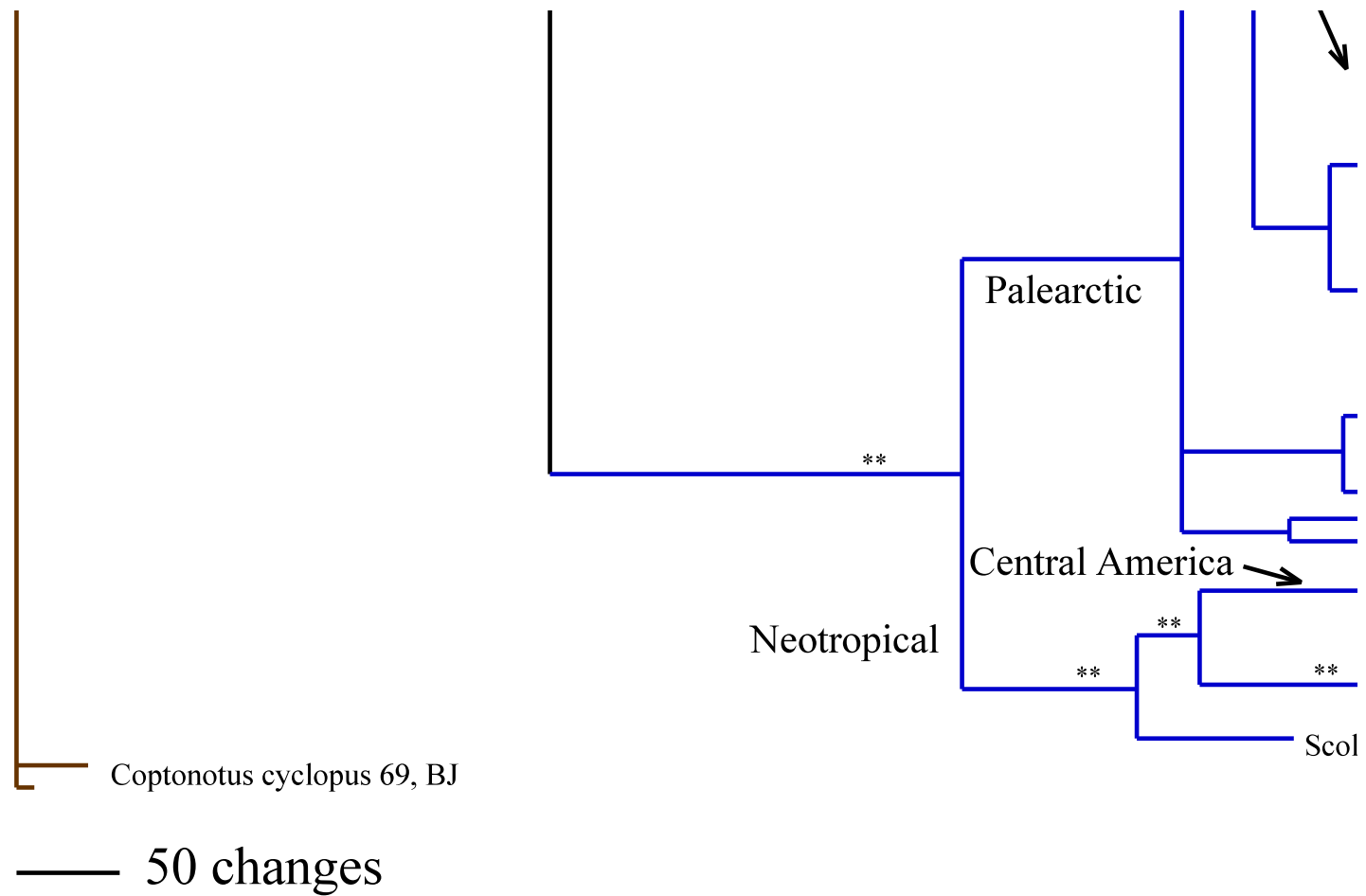


Figure 2.1 (cont'd).

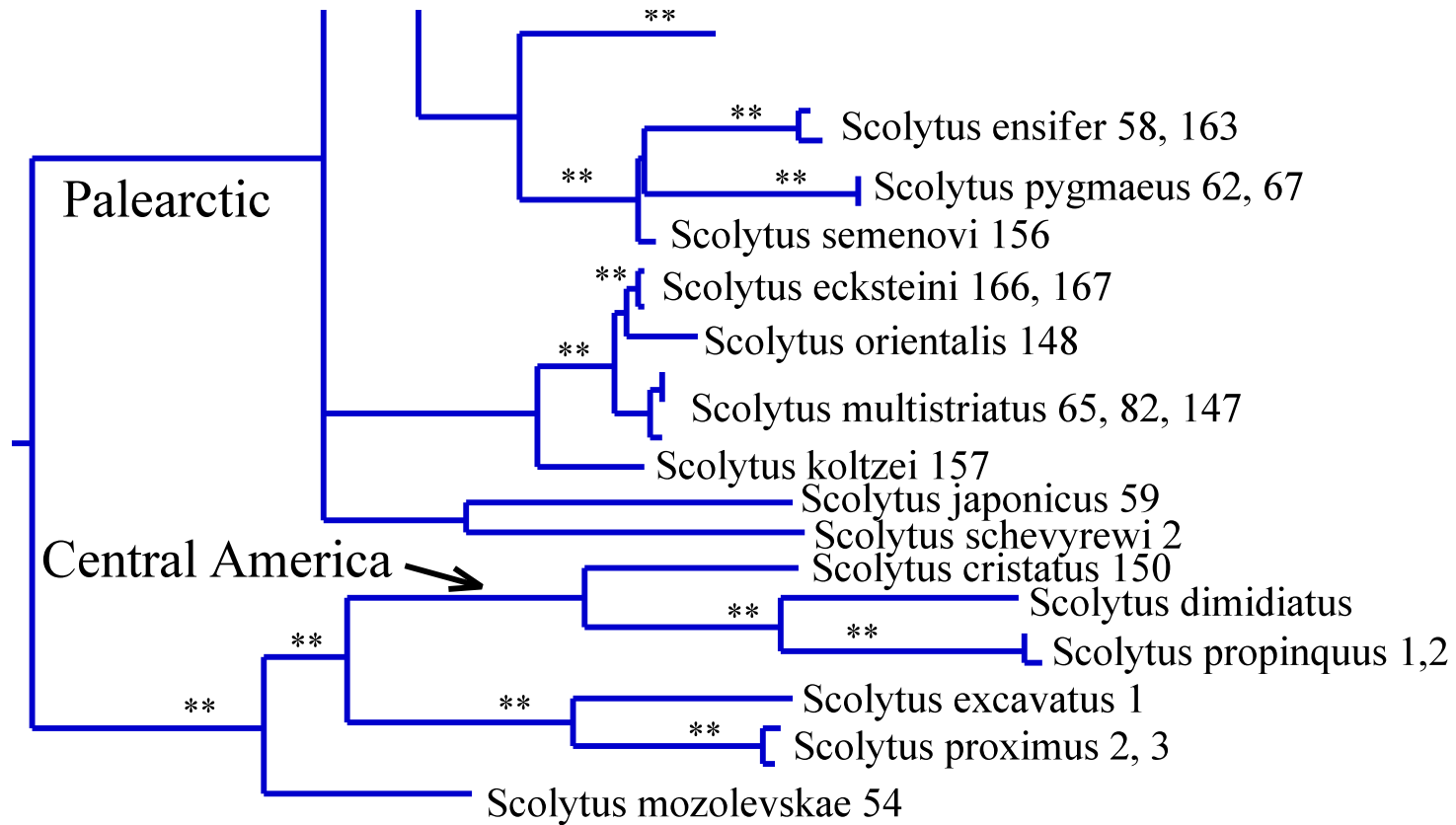


Figure 2.1 (cont'd).

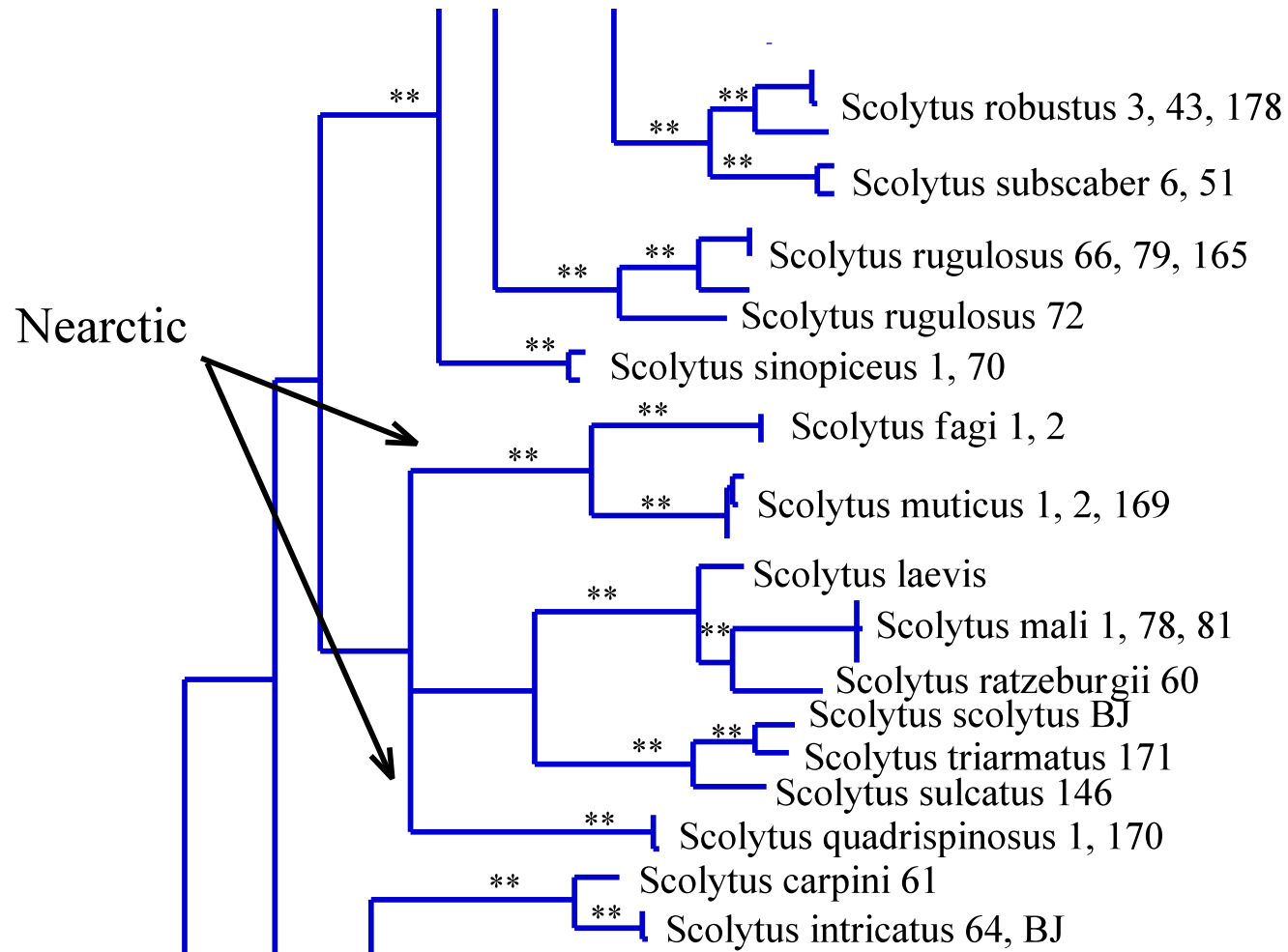


Figure 2.1 (cont'd).

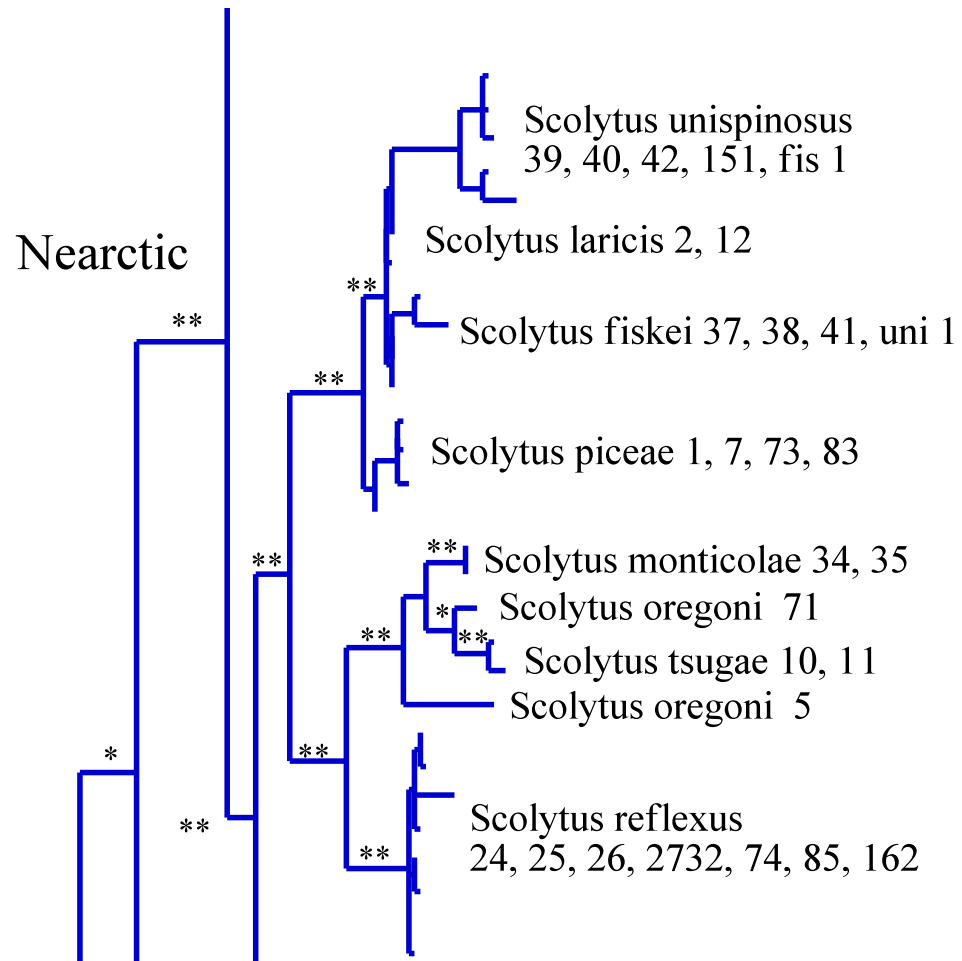


Figure 2.1 (cont'd).

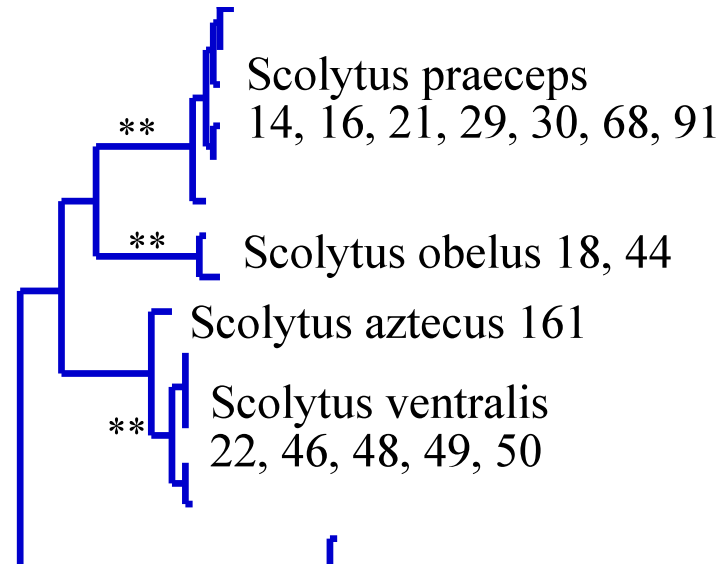


Figure 2.1 (cont'd).

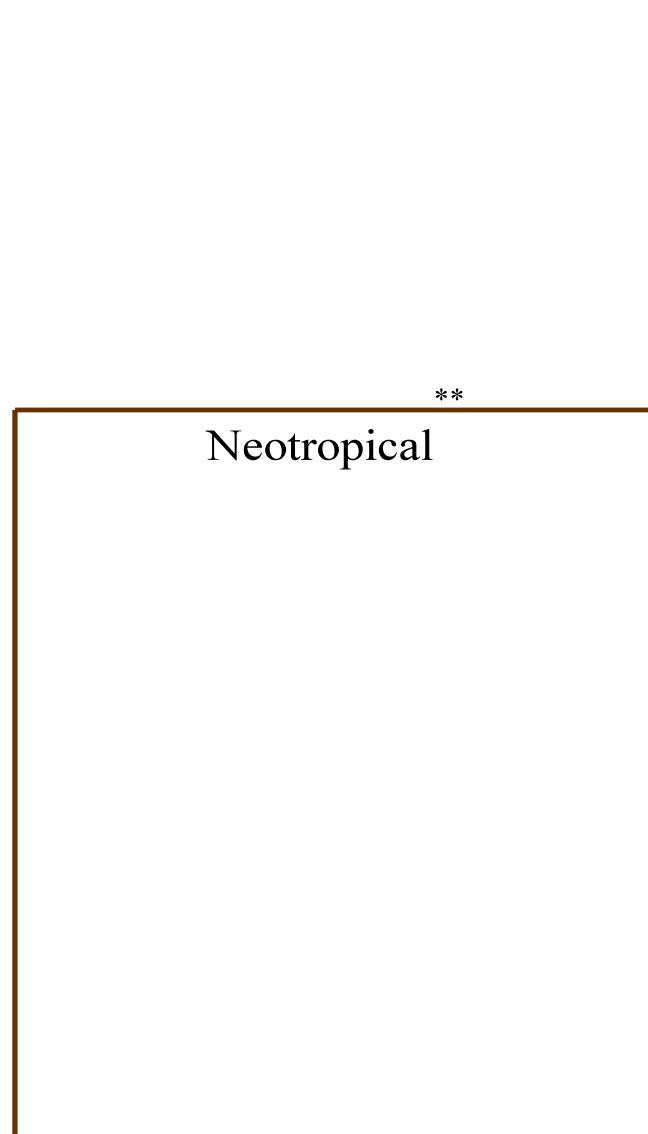


Figure 2.1 (cont'd).

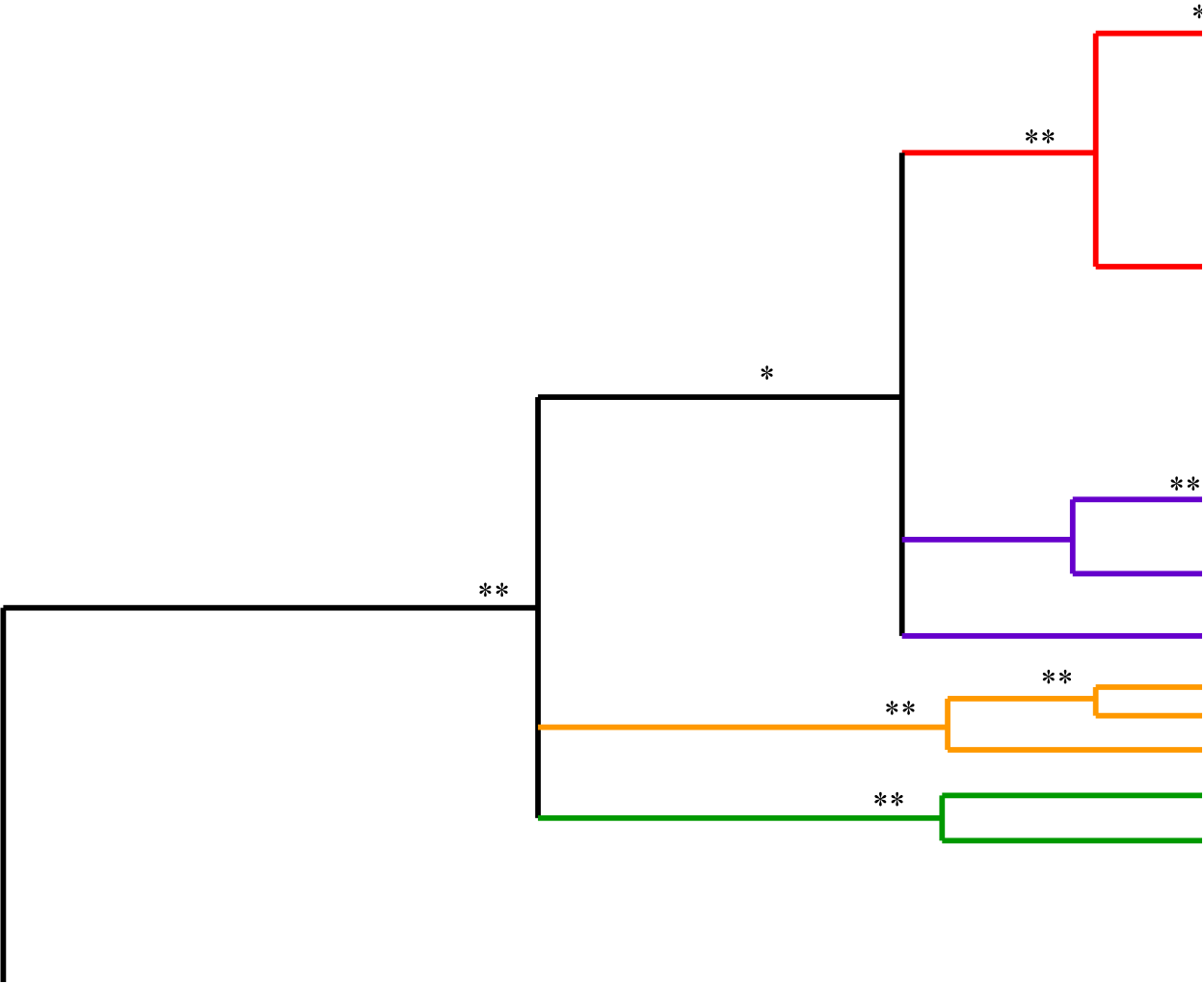


Figure 2.1 (cont'd).

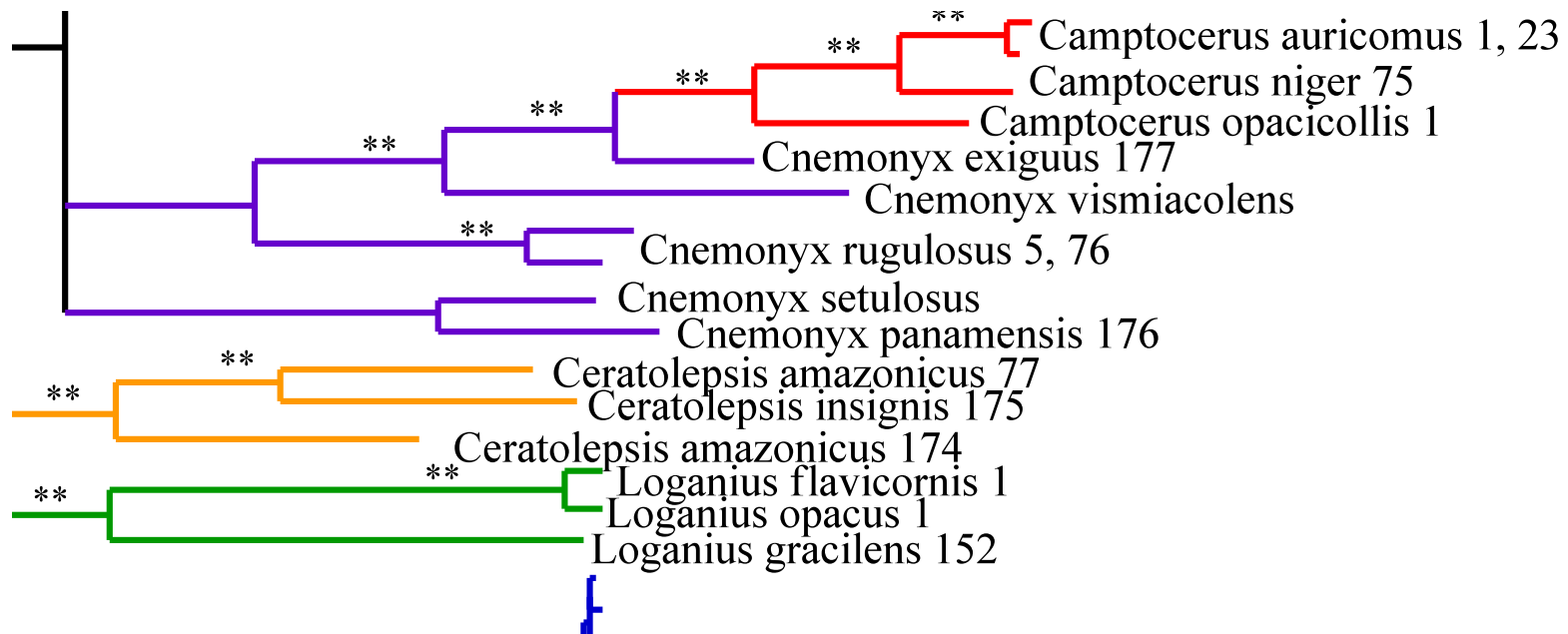


Figure 2.1 (cont'd).

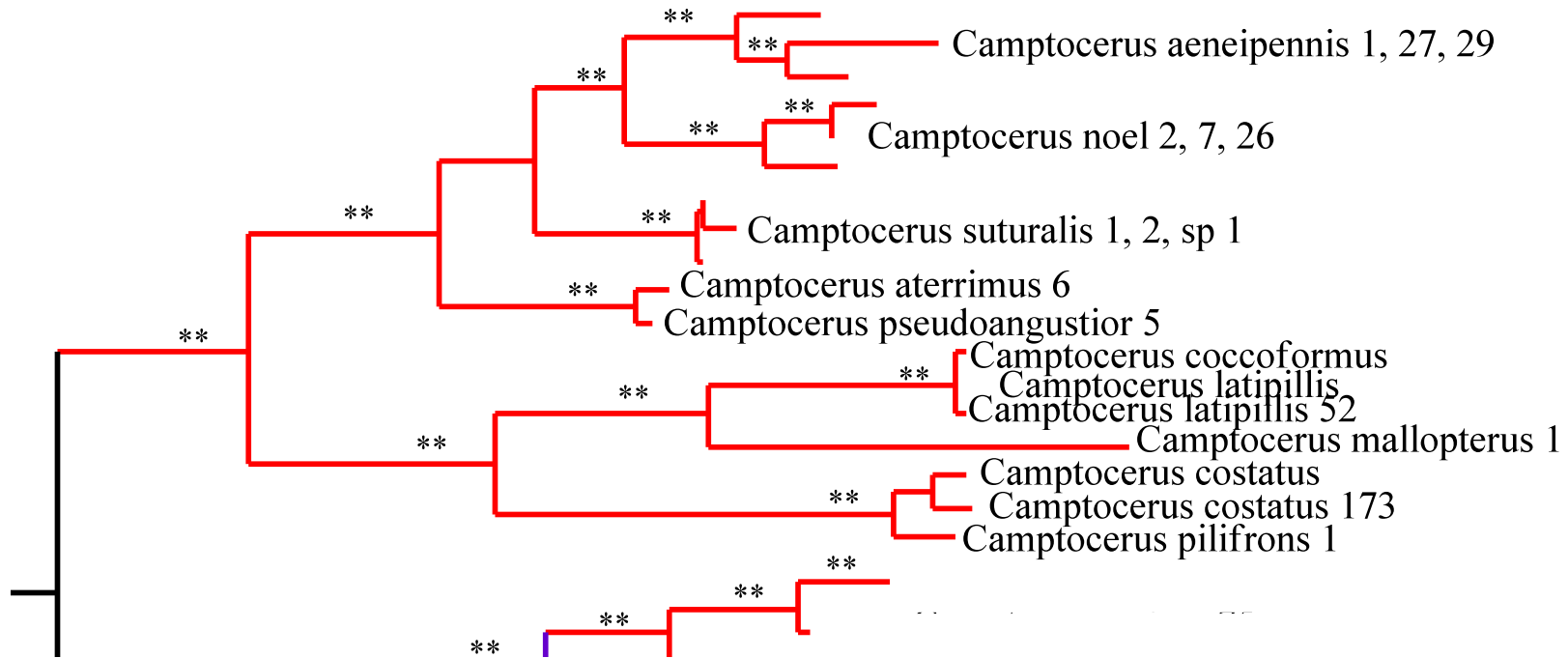


Figure 2.2. Bayesian tree derived by analysis of data set II with all genes treated as a single partition with GTR+I+ Γ . Posterior probabilities are listed above nodes (** ≥ 95 , * ≥ 90).

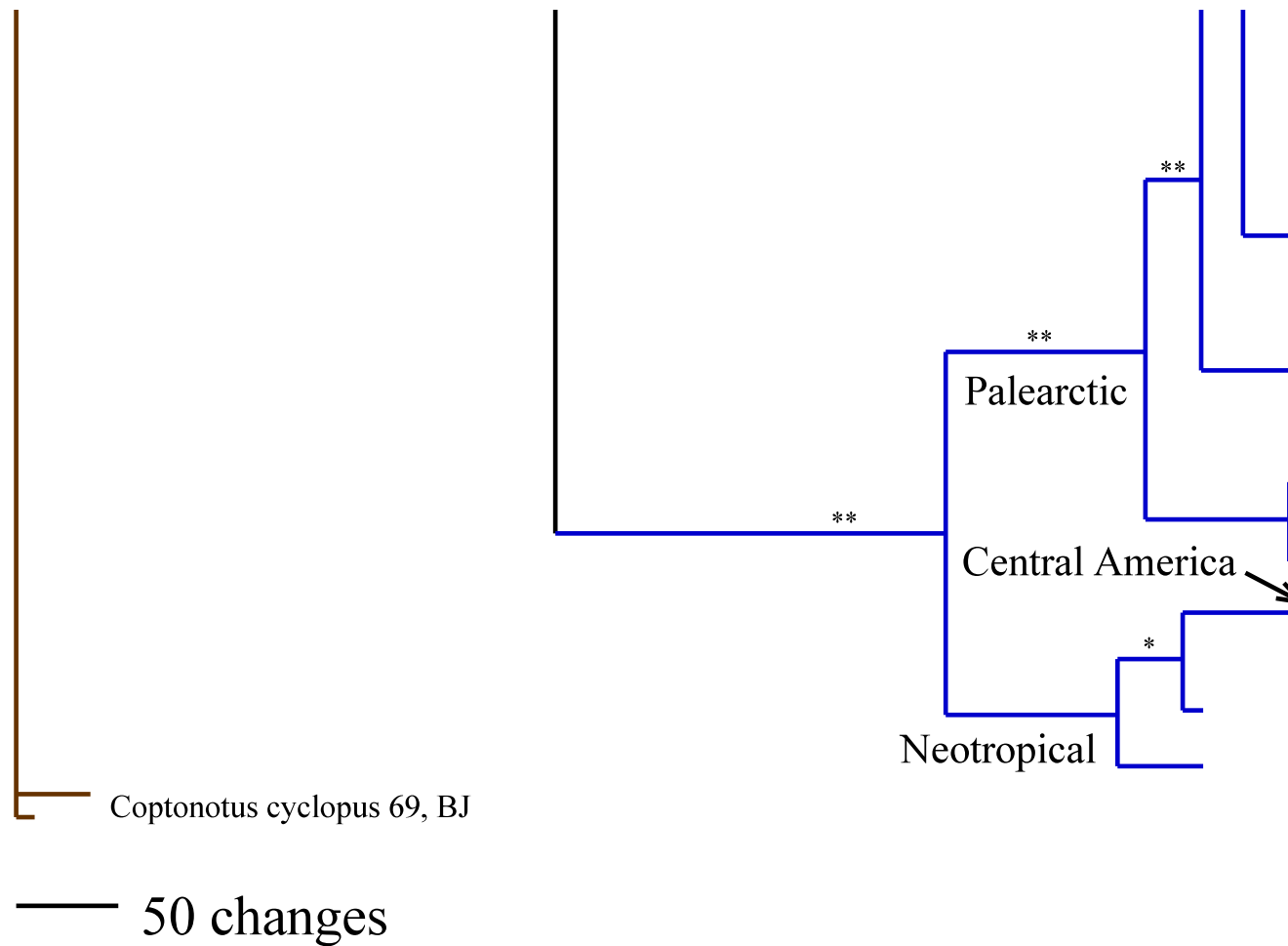


Figure 2.2 (cont'd).

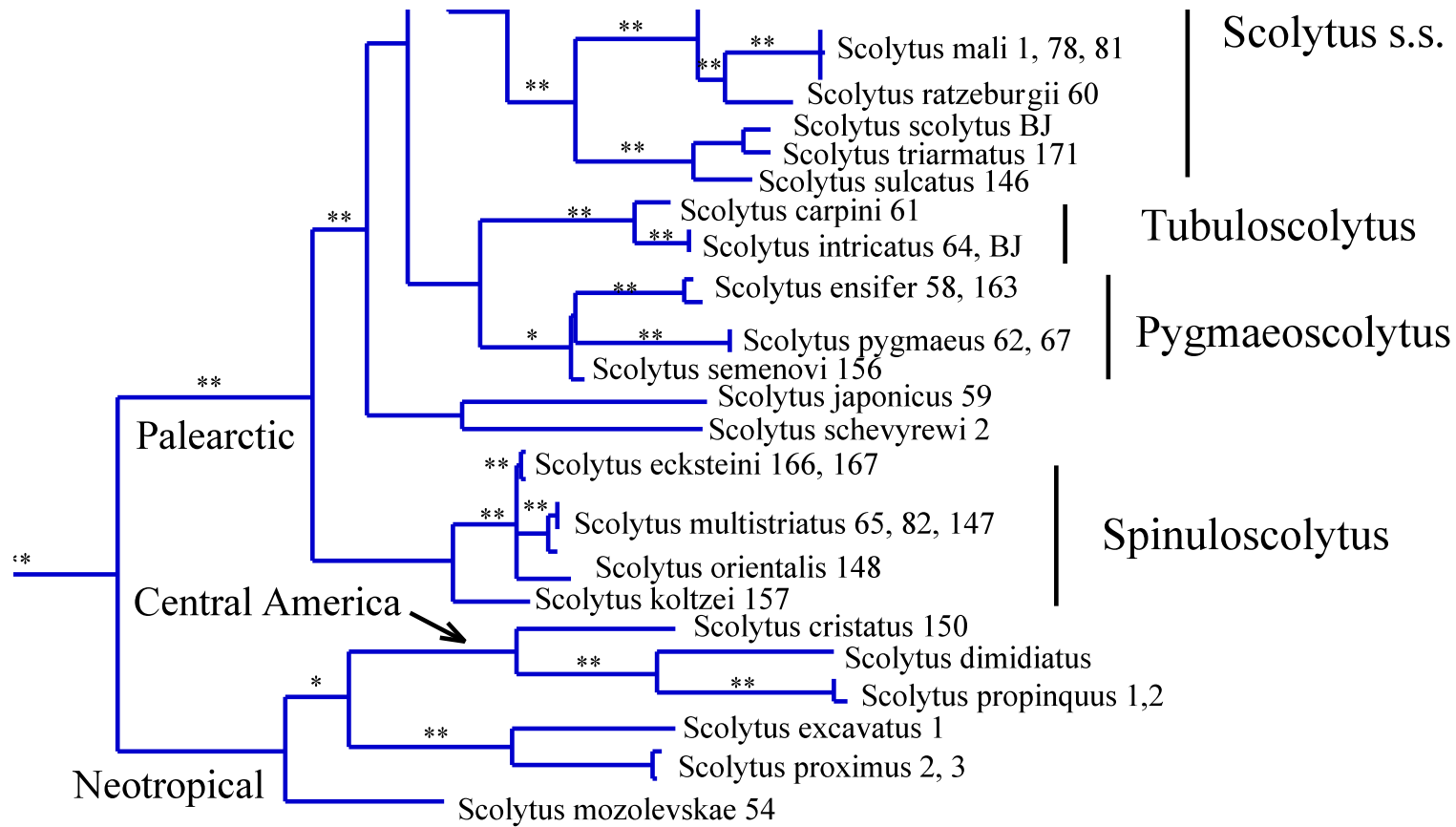


Figure 2.2 (cont'd).

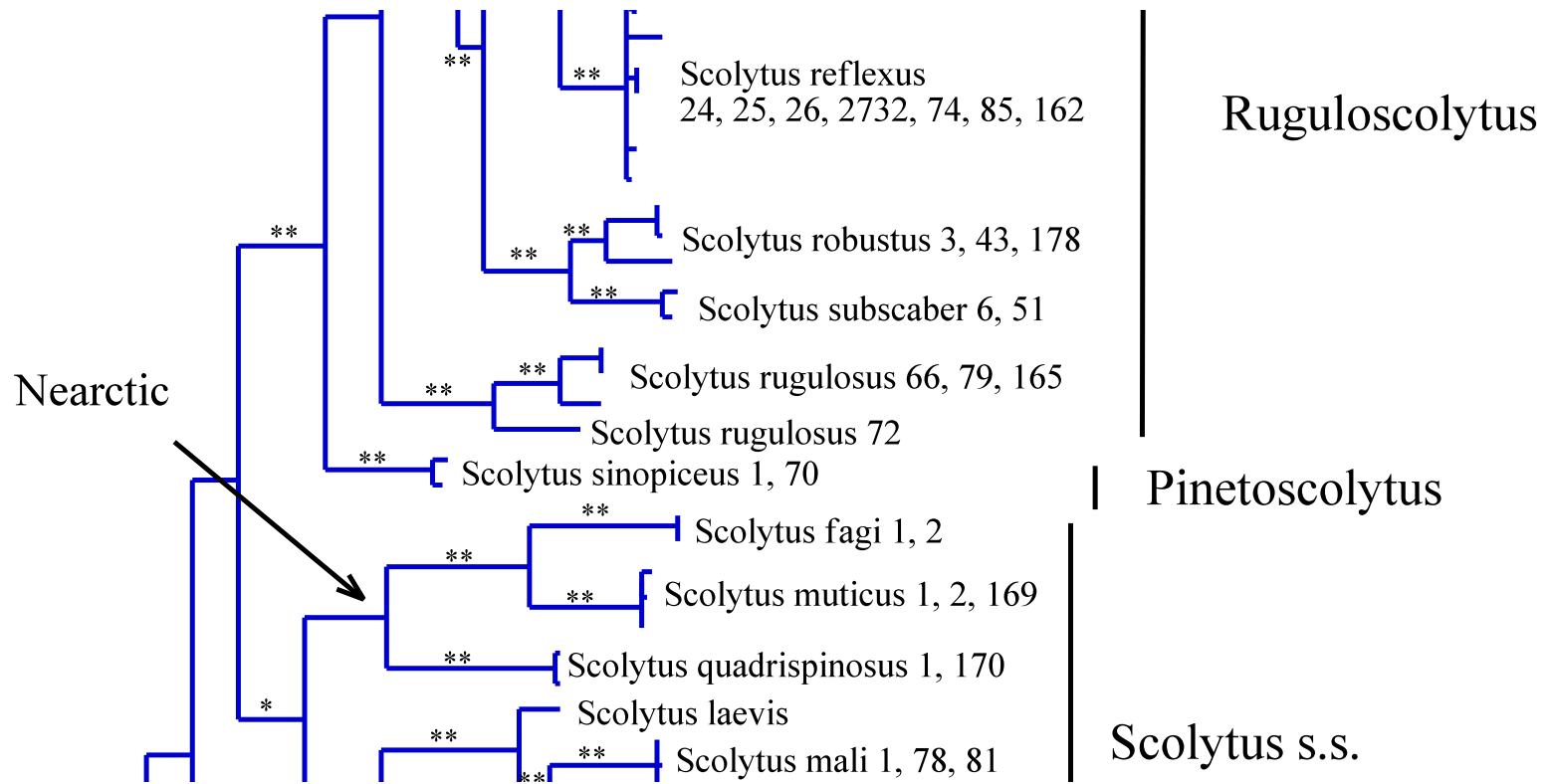


Figure 2.2 (cont'd).

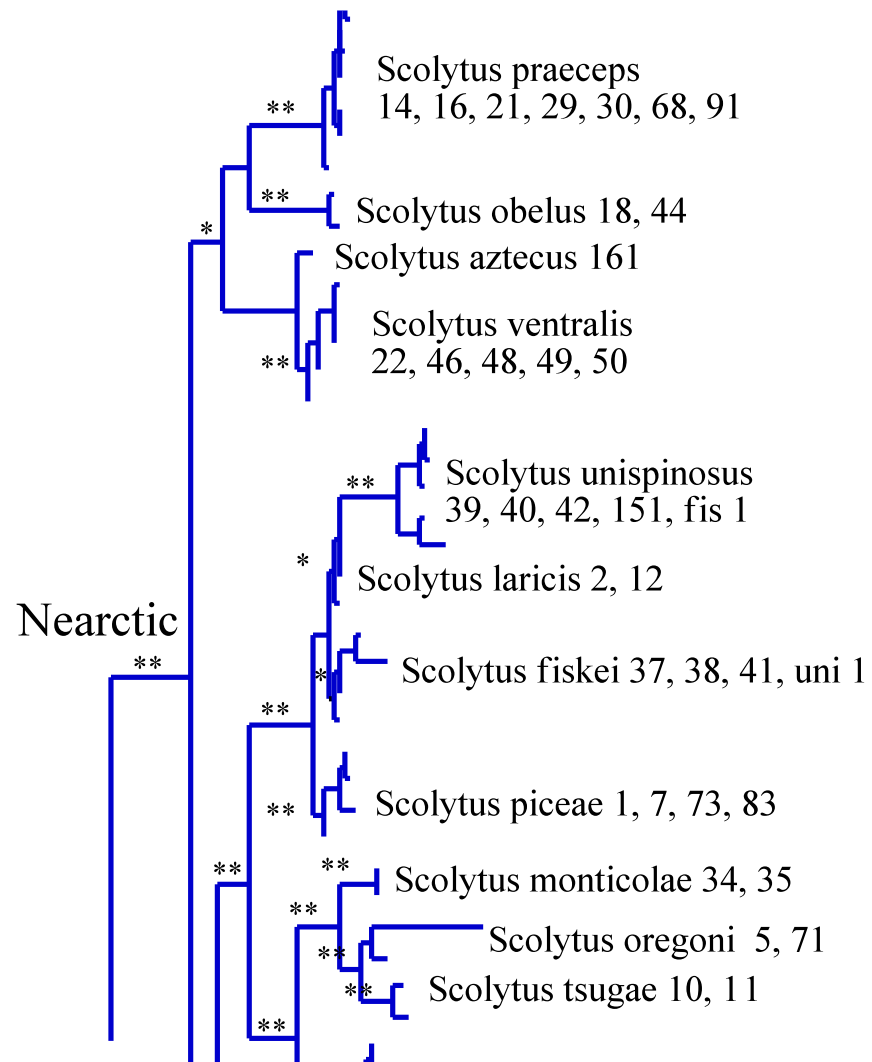


Figure 2.2 (cont'd).

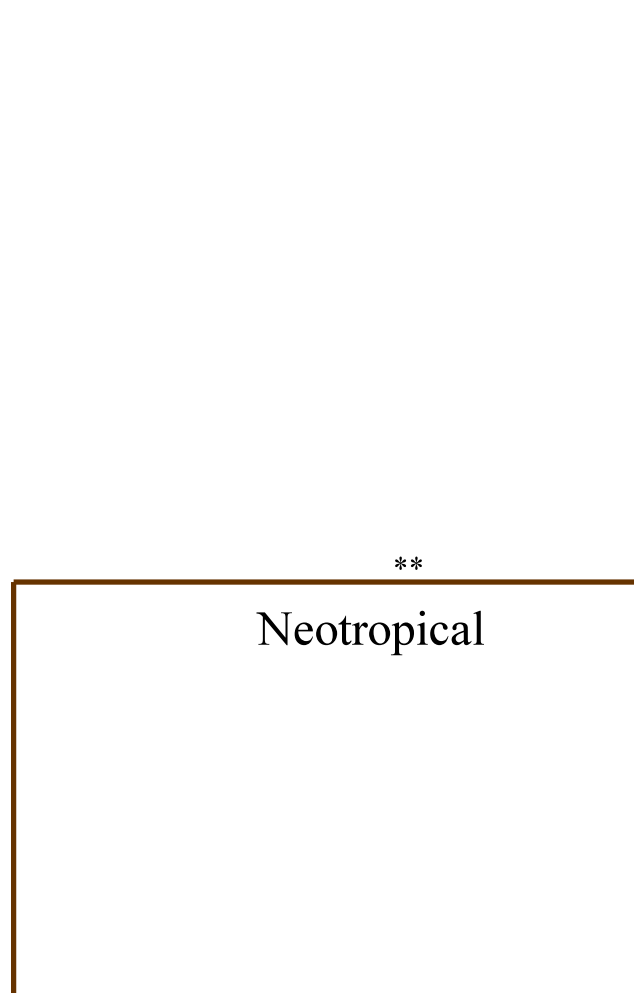


Figure 2.2 (cont'd).

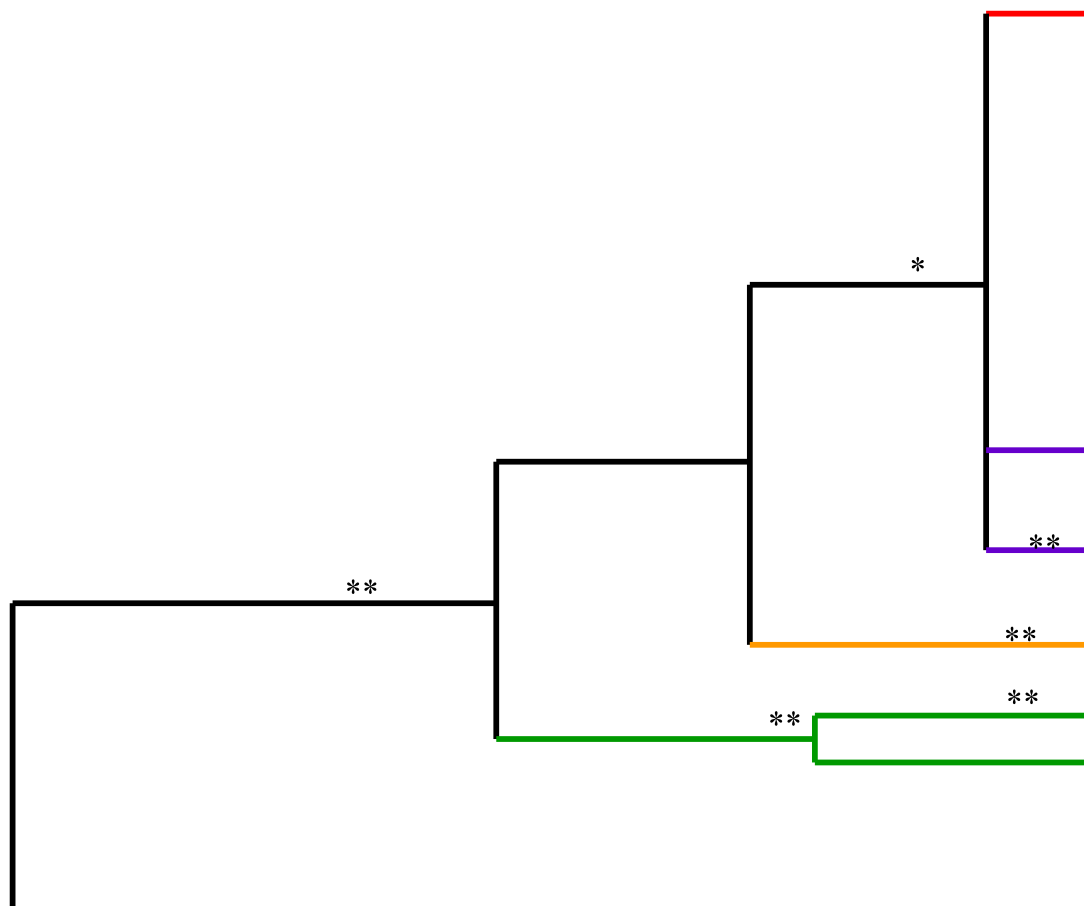


Figure 2.2 (cont'd).

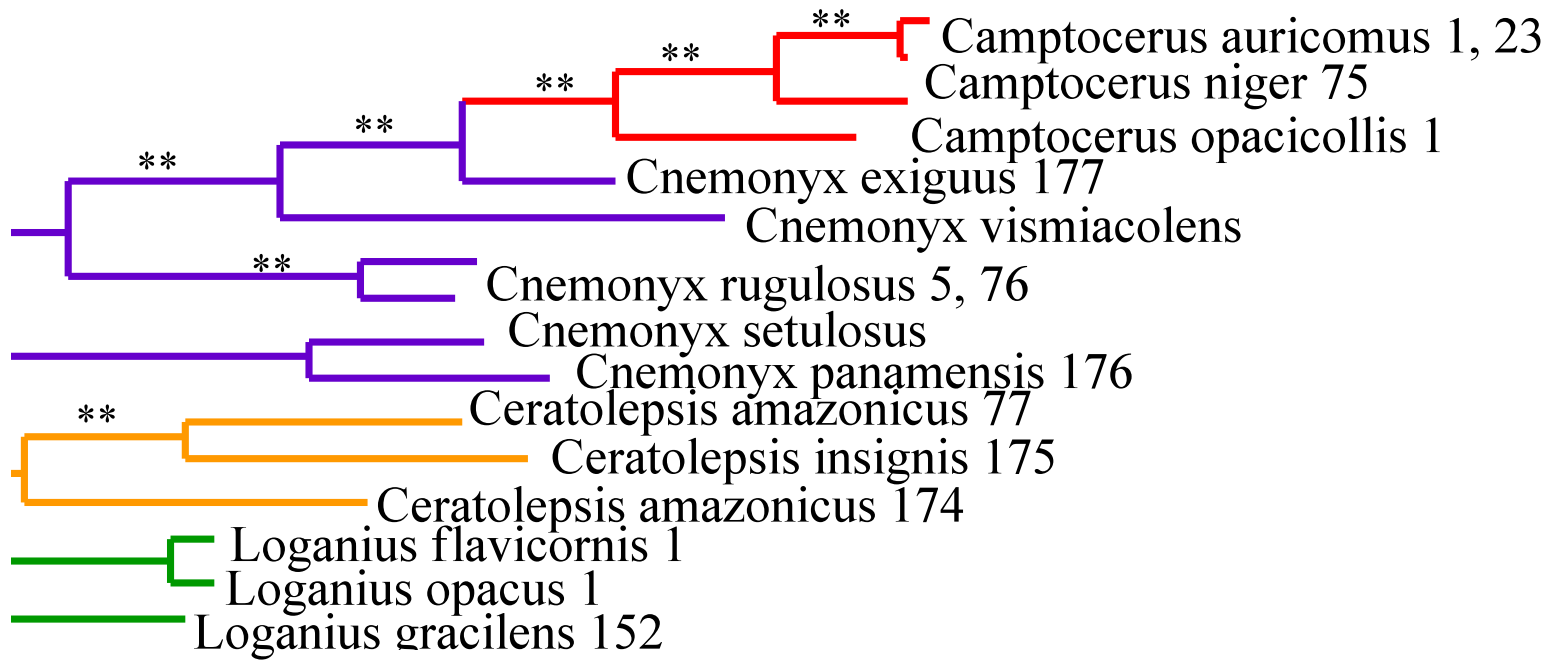


Figure 2.2 (cont'd).

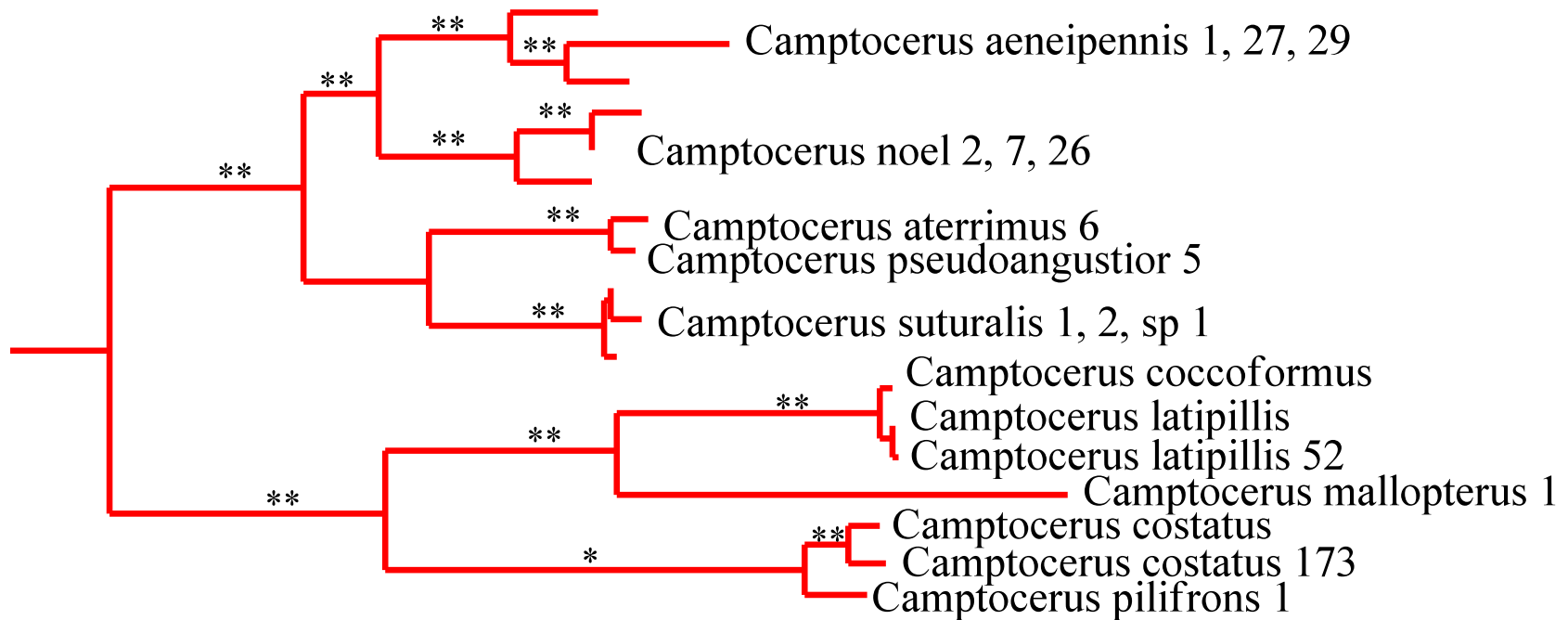


Figure 2.3. Bayesian tree derived by analysis of data set III with three data partitions COI, 28S and (ArgK+CAD) with GTR+I+ Γ . Posterior probabilities are listed above nodes (** ≥ 95 , * ≥ 90).

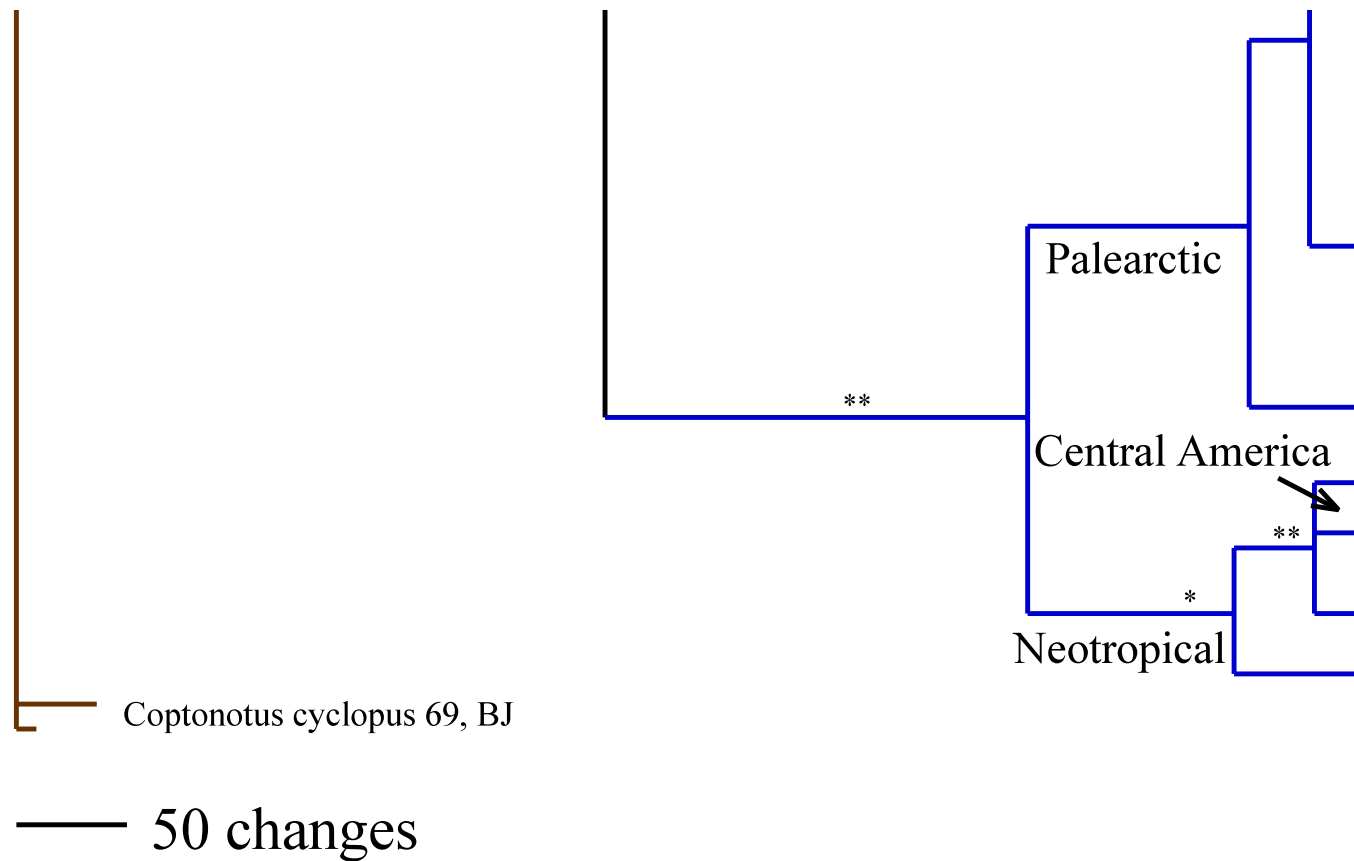


Figure 2.3 (cont'd).

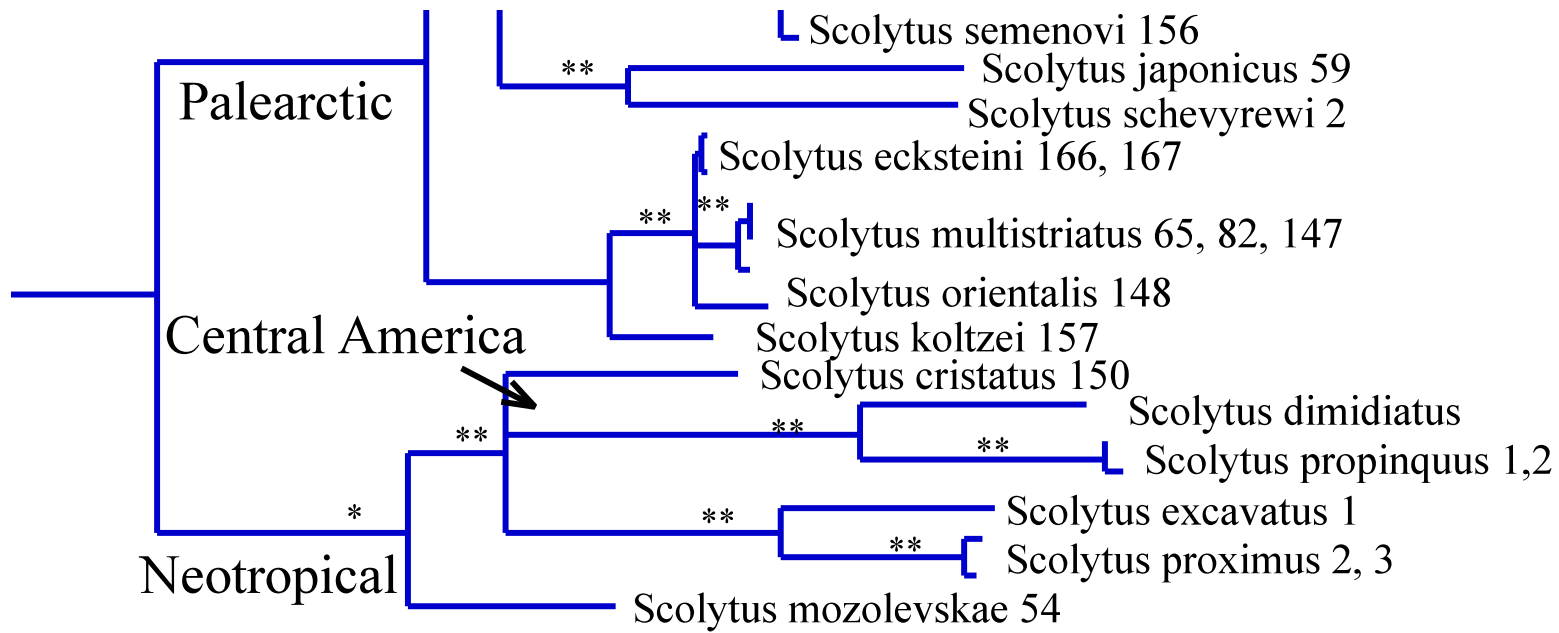


Figure 2.3 (cont'd).

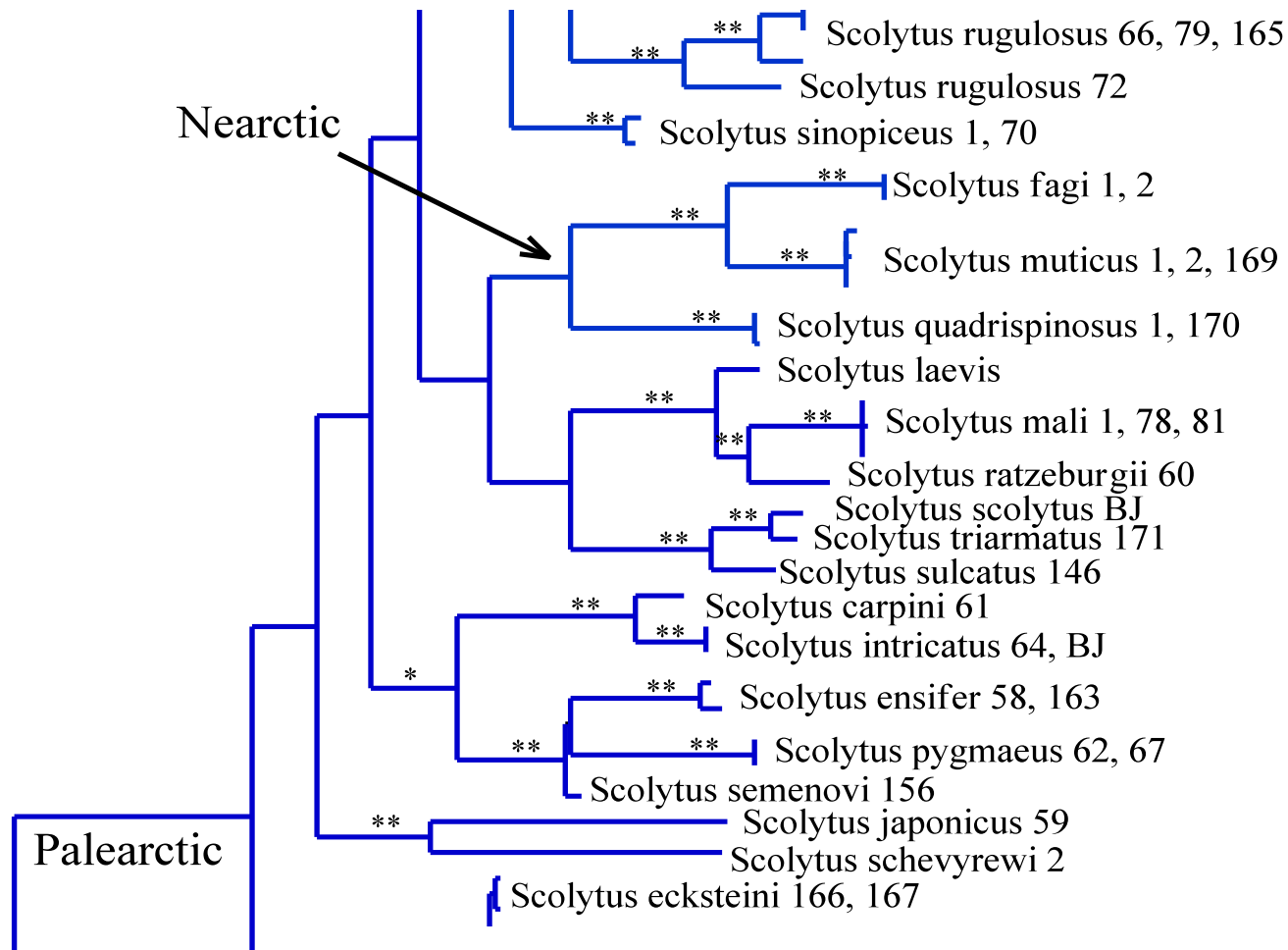


Figure 2.3 (cont'd).

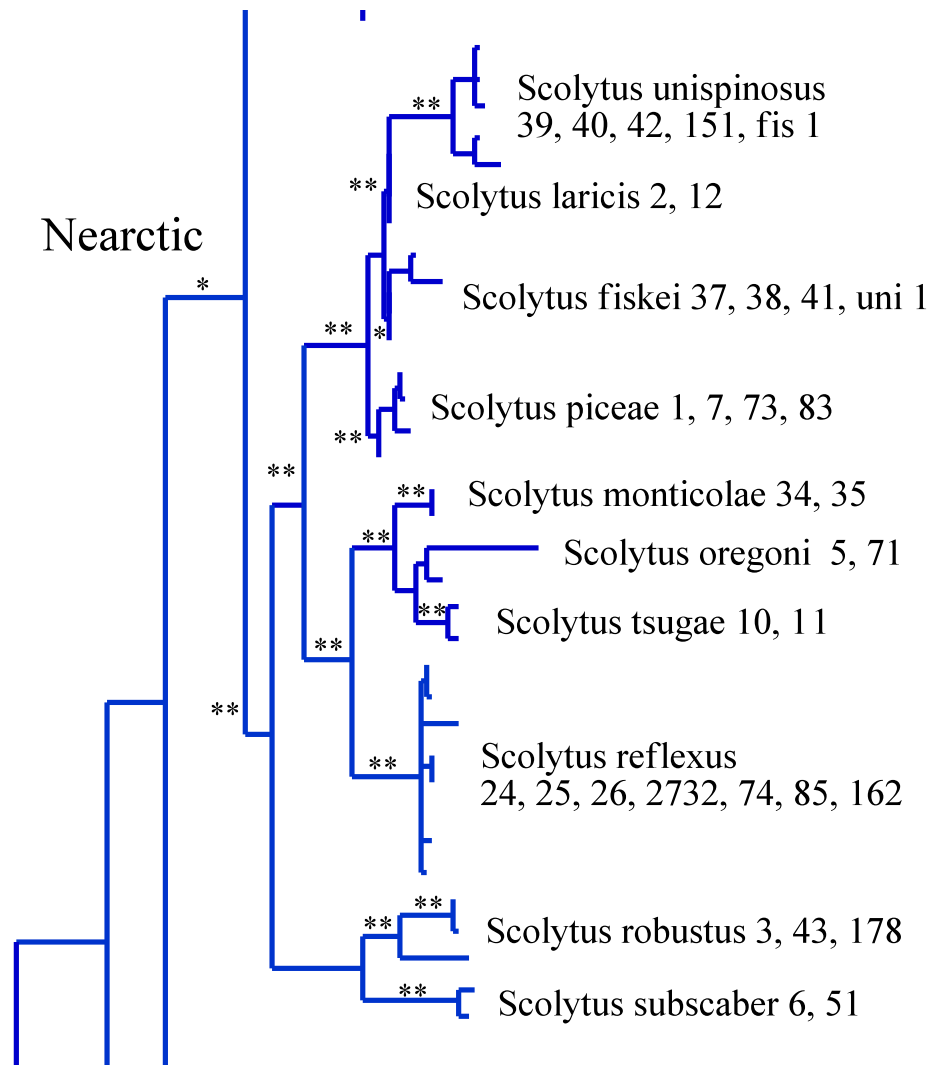


Figure 2.3 (cont'd).

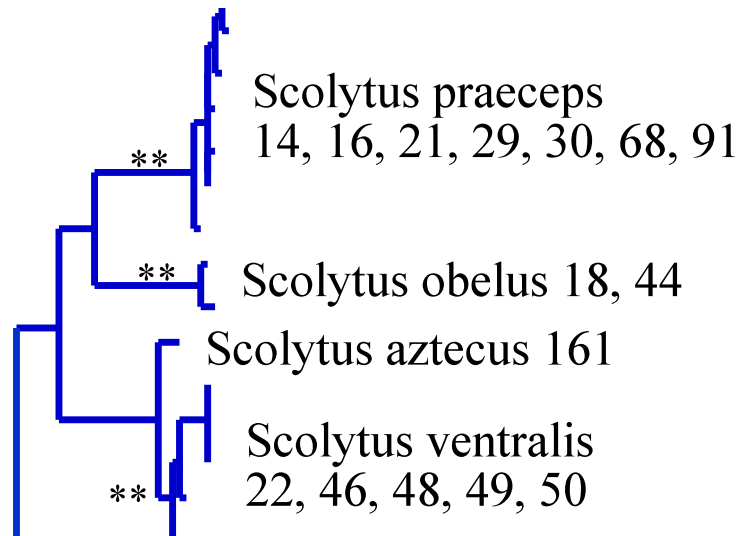


Figure 2.3 (cont'd).

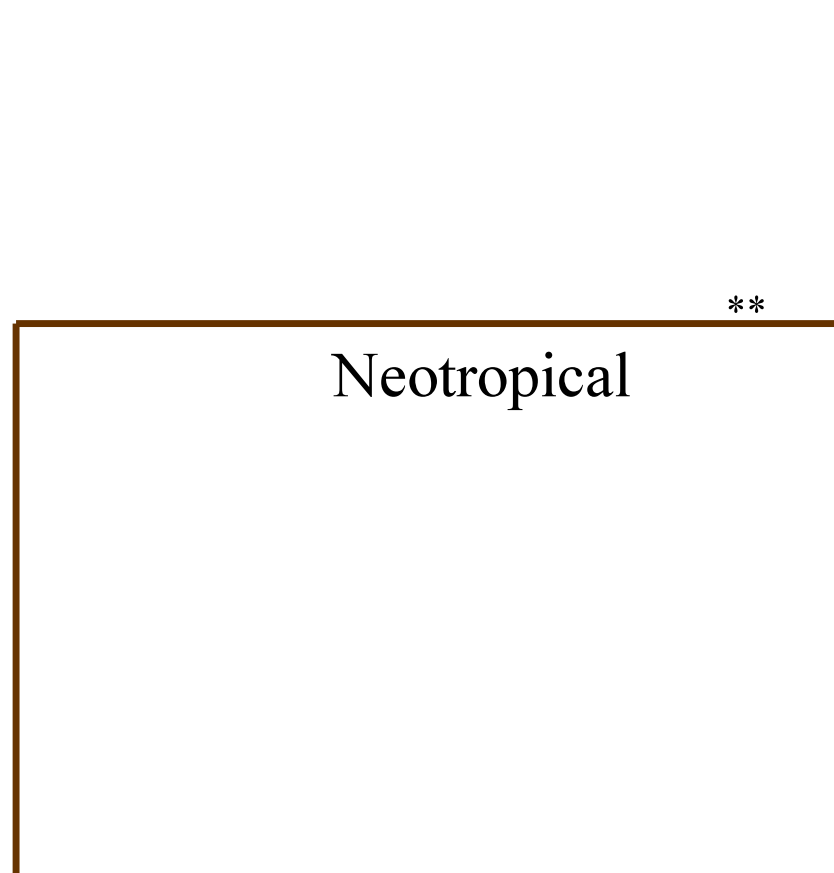


Figure 2.3 (cont'd).

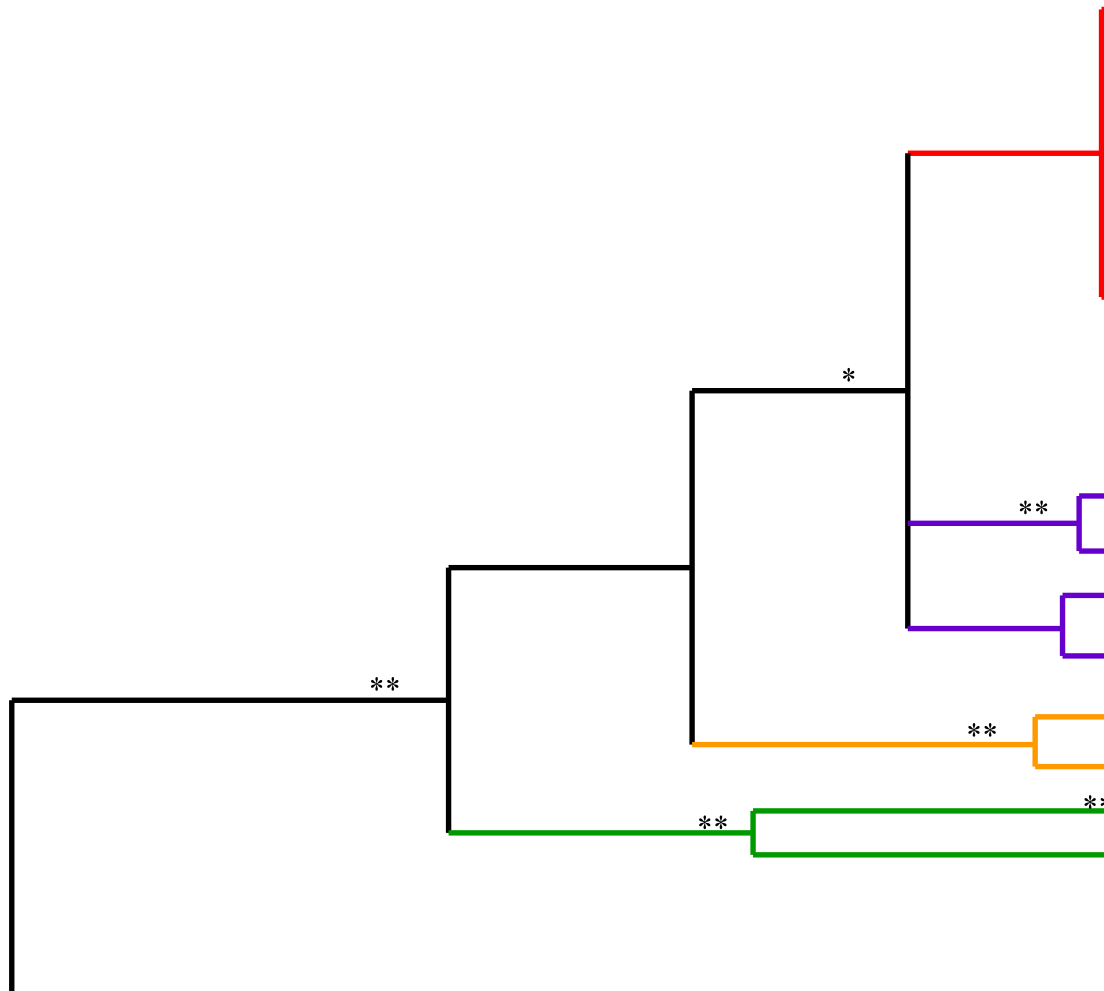


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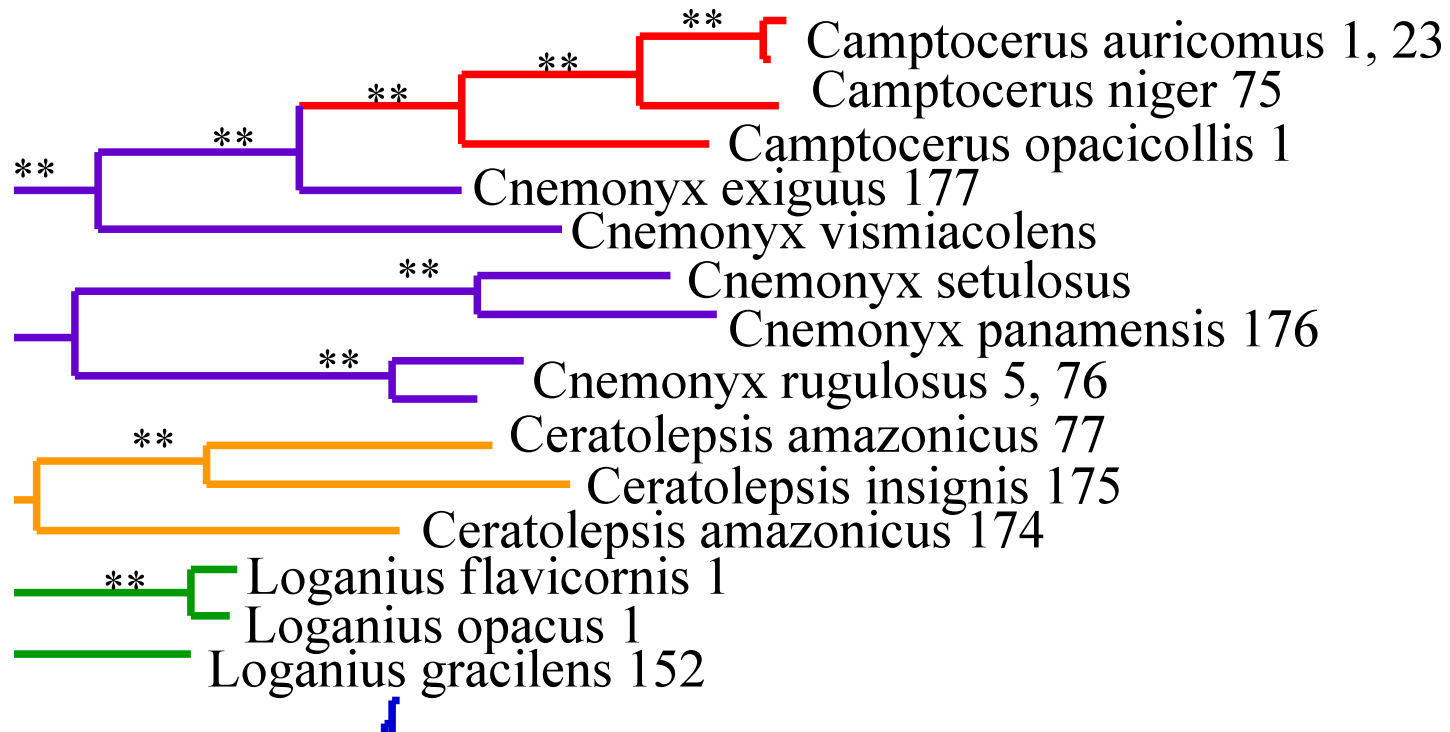


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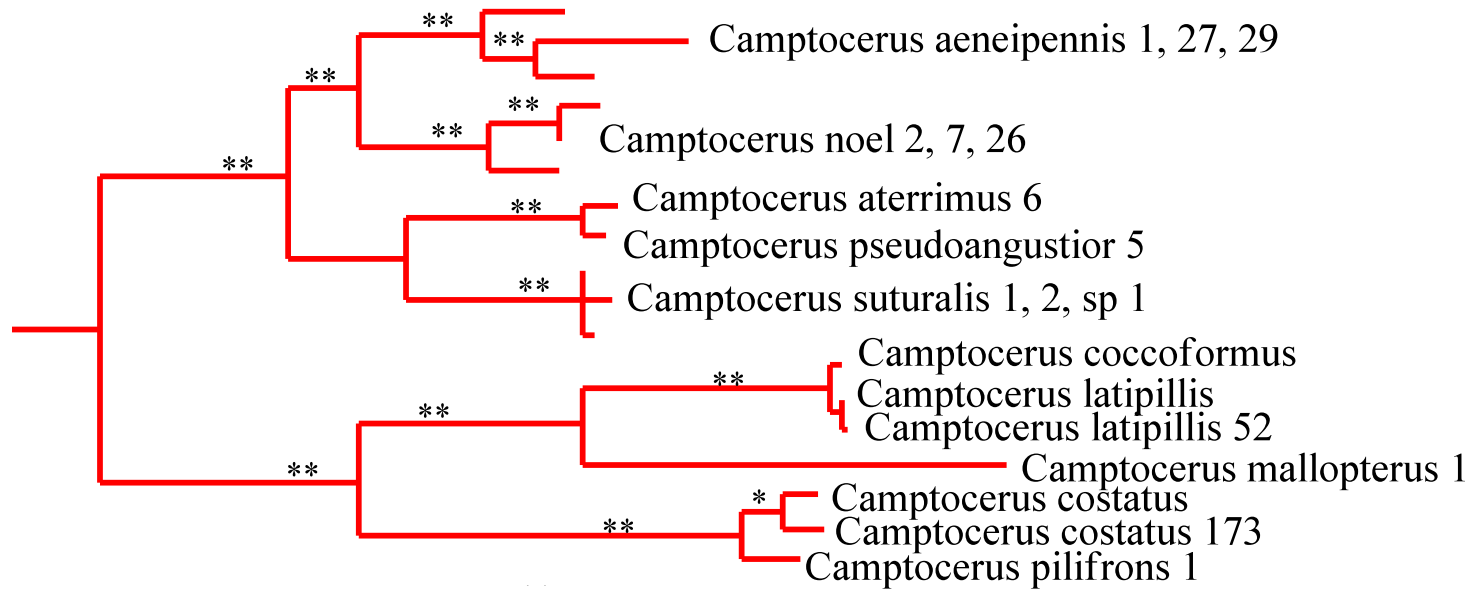


Figure 2.4. Ancestral state reconstruction of feeding habit among the Scolytini calculated by likelihood estimation with the Mk-1 model over the analysis II consensus tree topology (Figure 2.2). Taxa known to bore into sapwood are marked in black and taxa known to mine the phloem are marked in white.

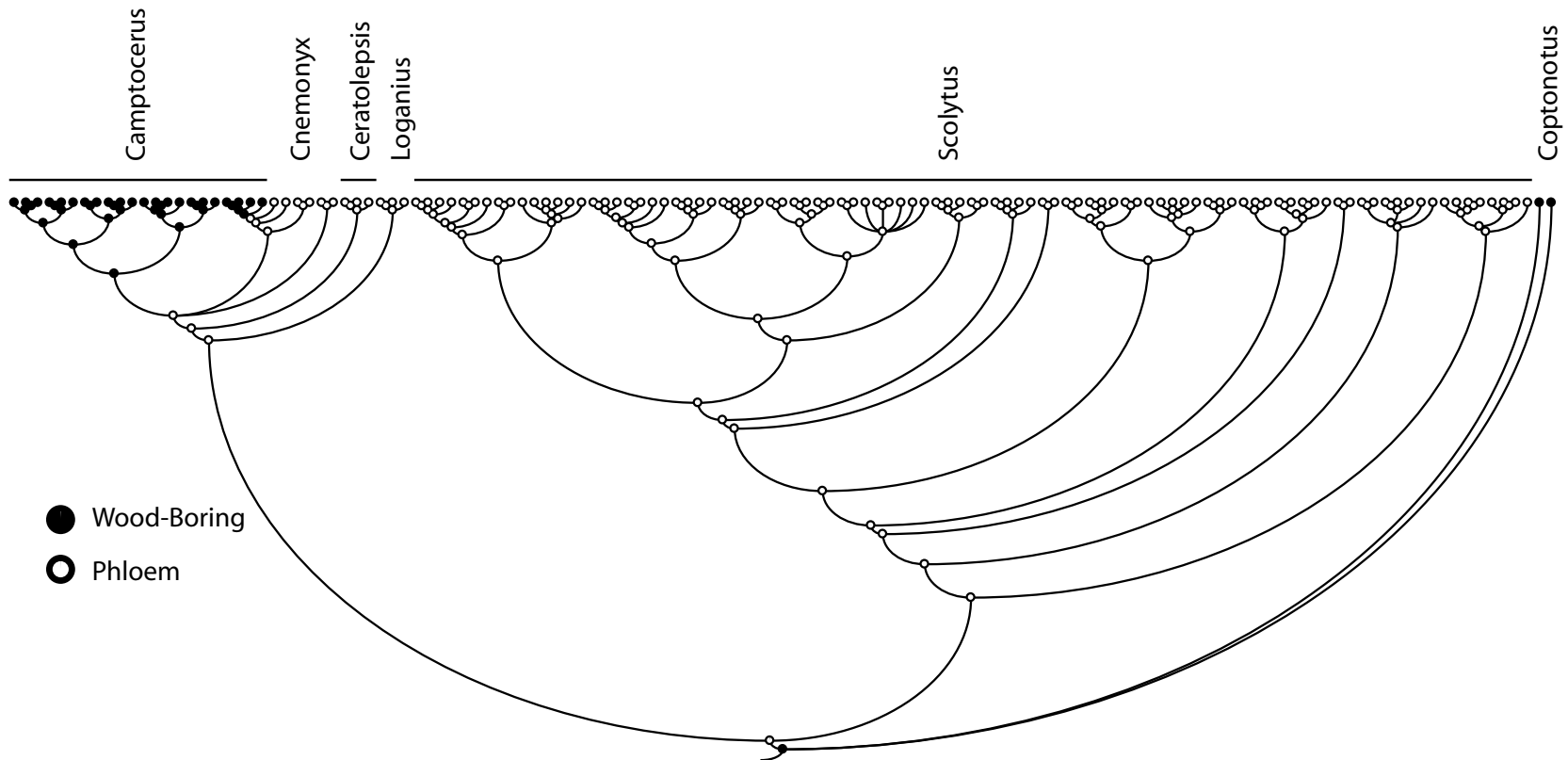


Figure 2.5. Ancestral state reconstruction of host-use among the Scolytini calculated by likelihood estimation with the Mk-1 model over the analysis II consensus tree topology (Figure 2.2). Only most common host family was scored for each species. Only those taxa with host records were scored.

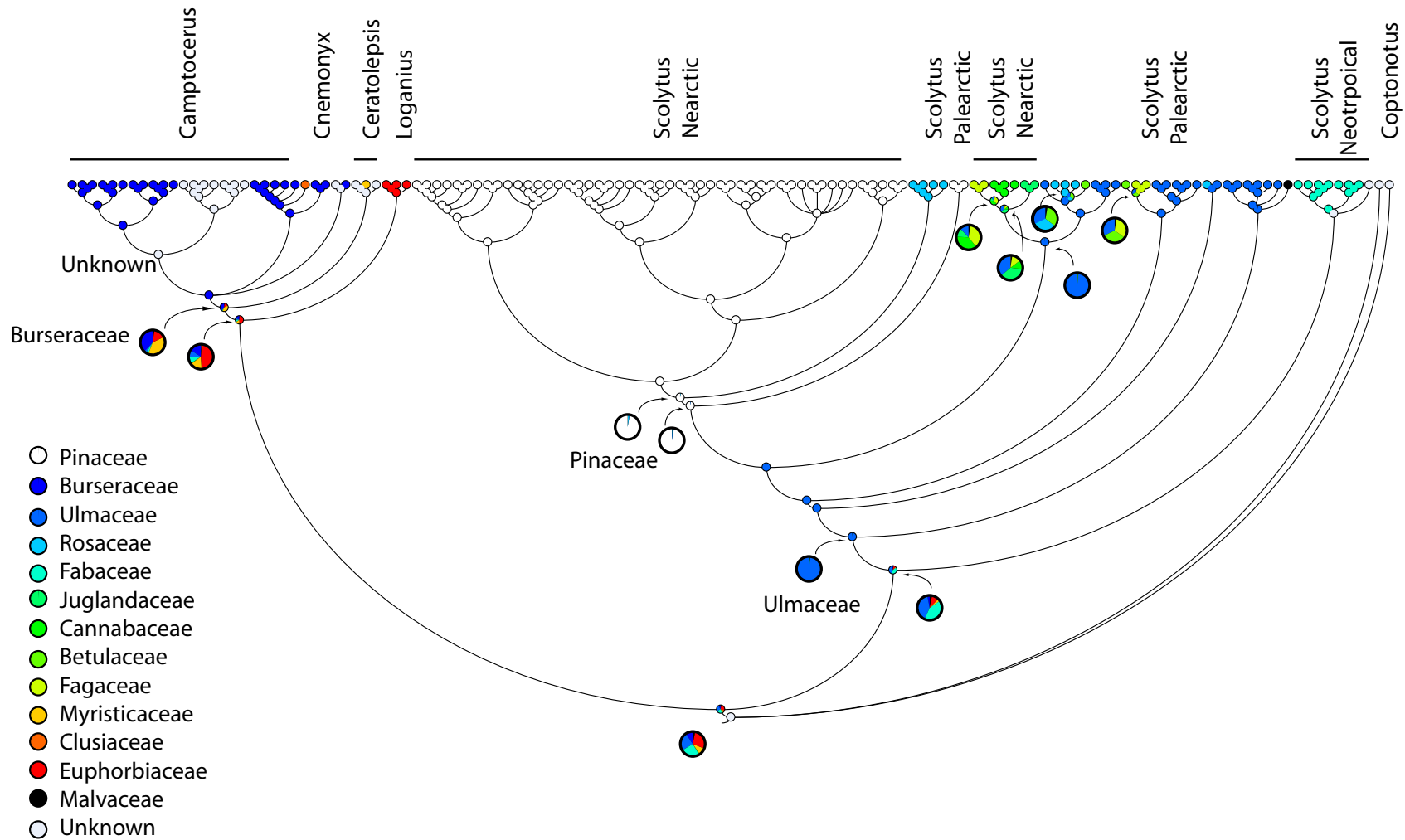


Figure 2.6. Ancestral state reconstruction of conifer-feeding *Scolytus* by host genus, calculated by likelihood estimation with the Mk-1 model over a pruned analysis II consensus tree topology (Figure 2.2) with non-*Scolytus* genera removed. Only coniferous genera were scored for each species while angiosperm feeders are marked in black.

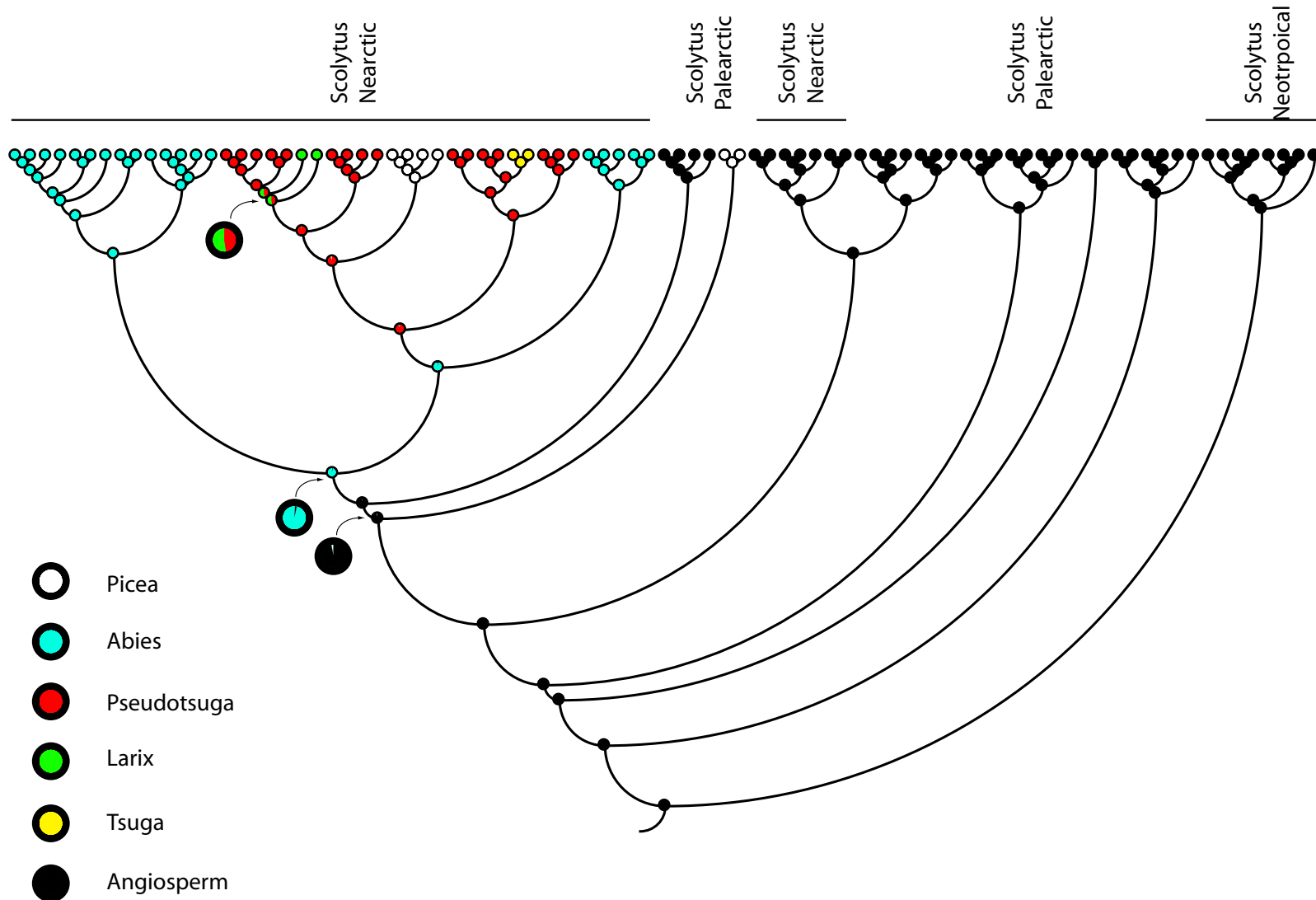


Figure 2.7. Maximum clade credibility tree (in part) for Scolytini based on the minimum age Bayesian analysis (analysis A). 95% confidence intervals for the ages of clades indicated with blue bars. Numbers correspond to clades listed in Table 2.8. ** denotes the Quaternary period and * denotes the Pliocene epoch.

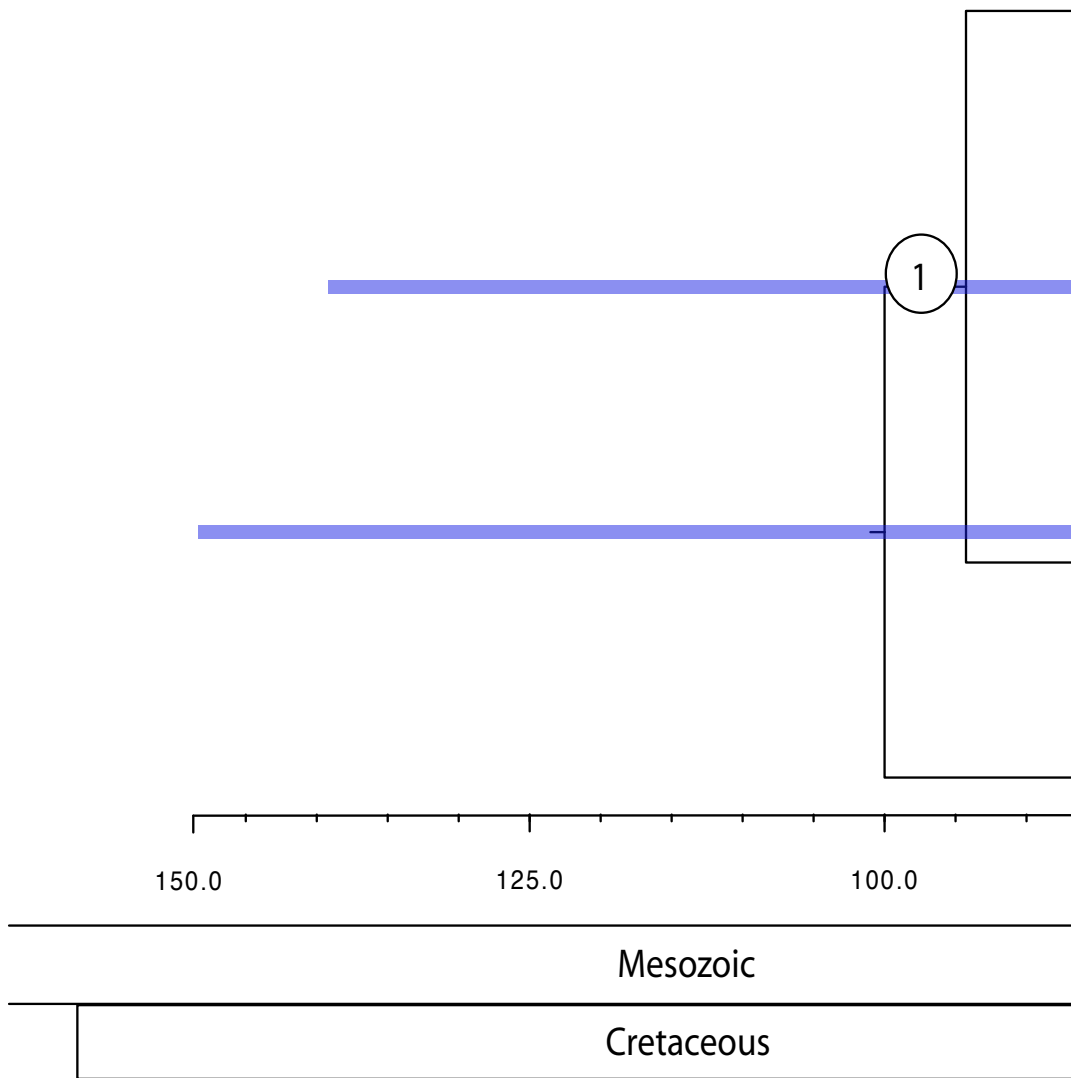


Figure 2.7 (cont'd).

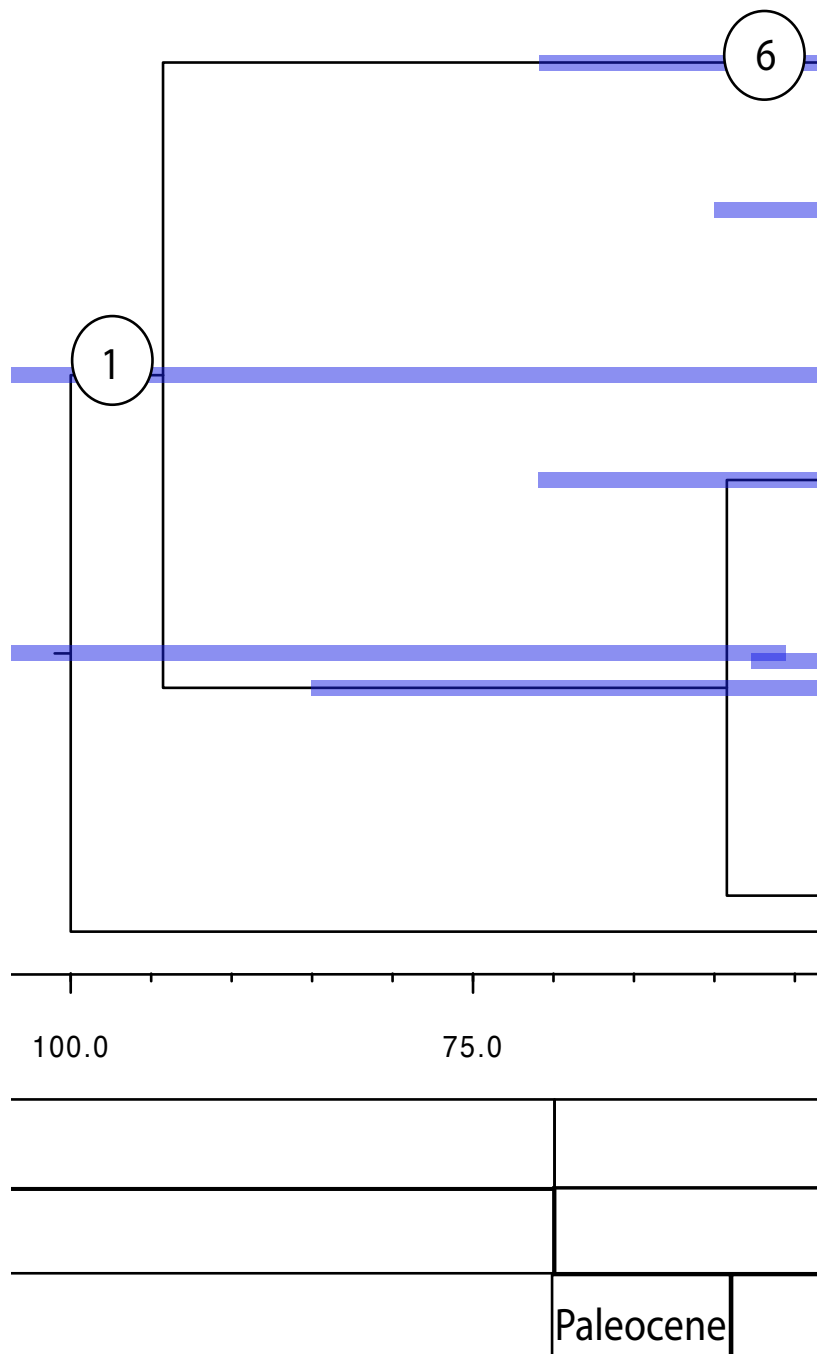


Figure 2.7 (cont'd).

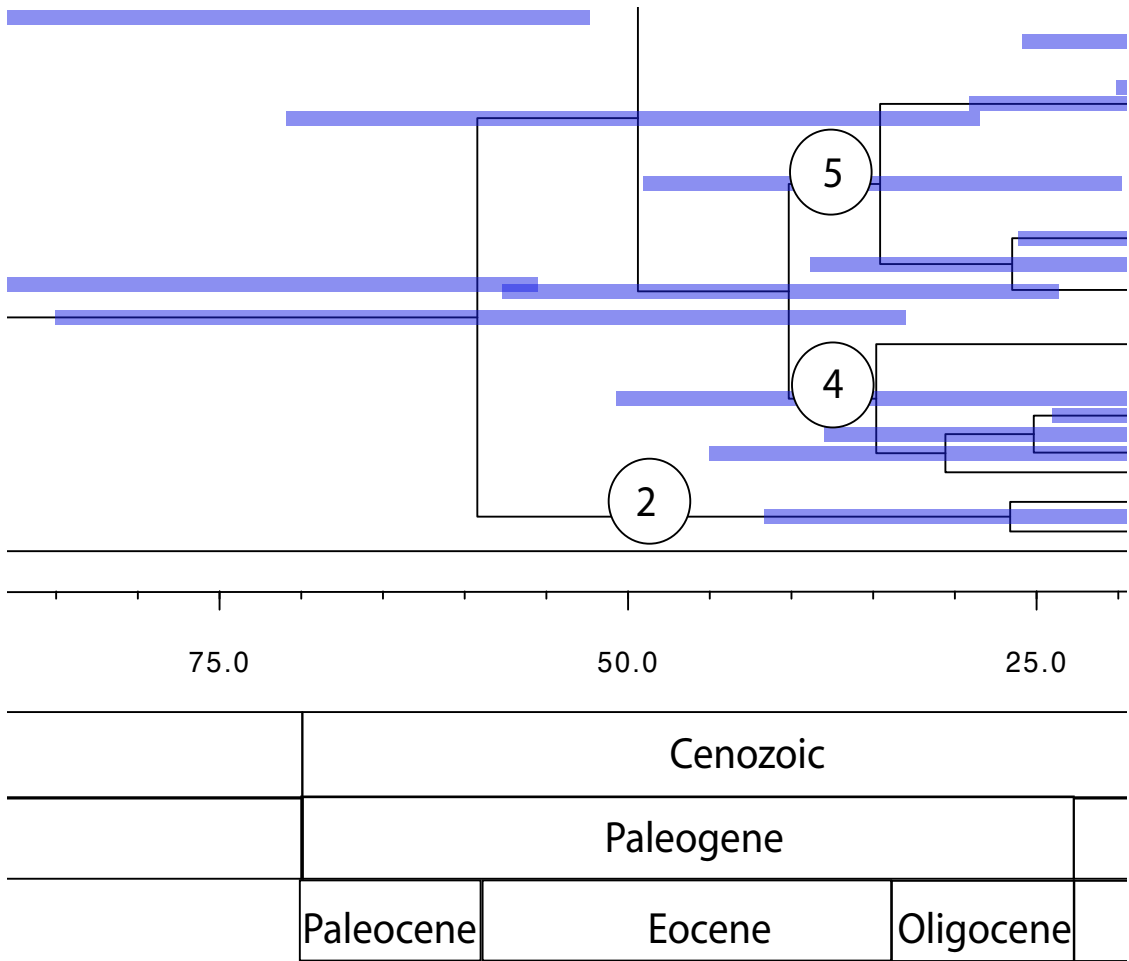


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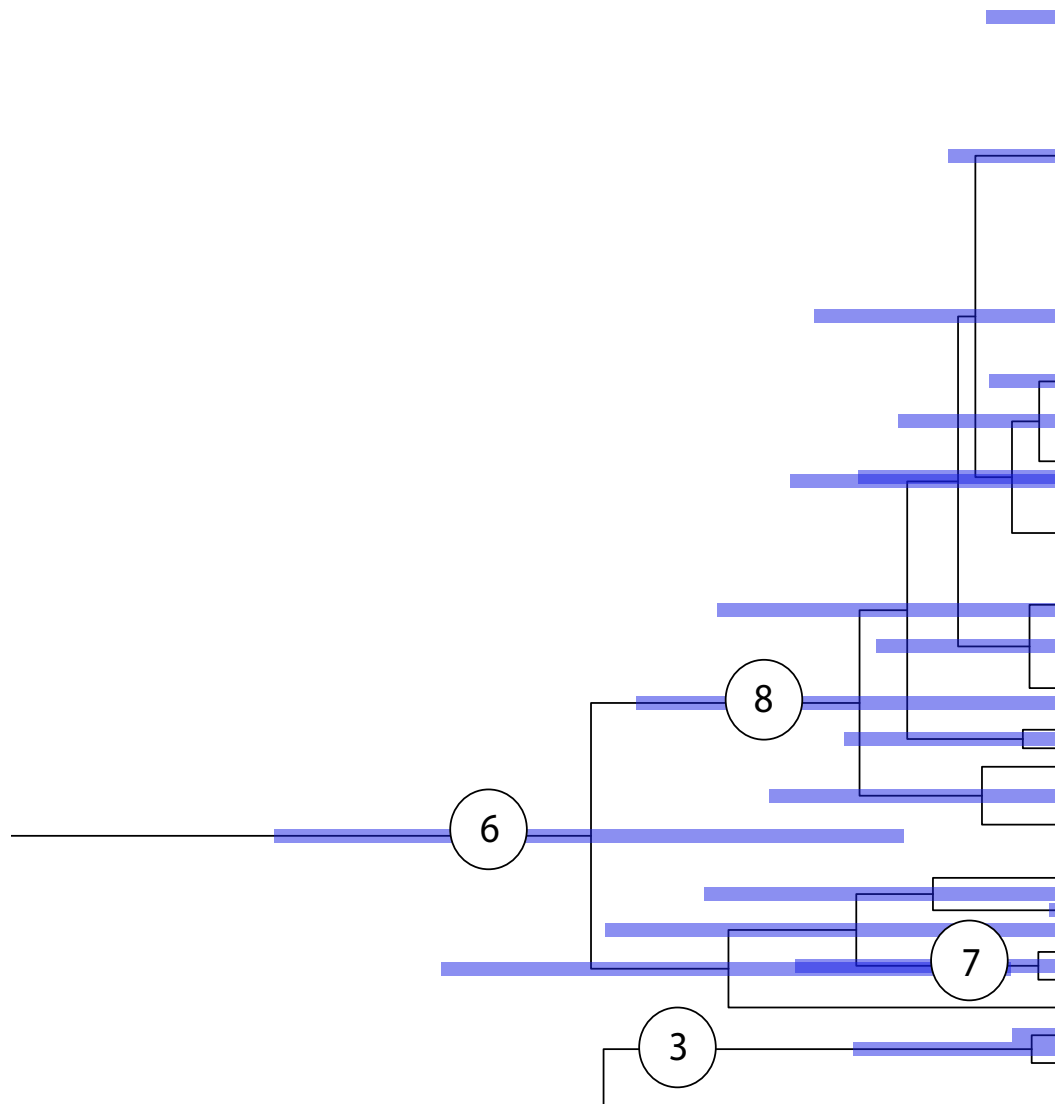


Figure 2.7 (cont'd).

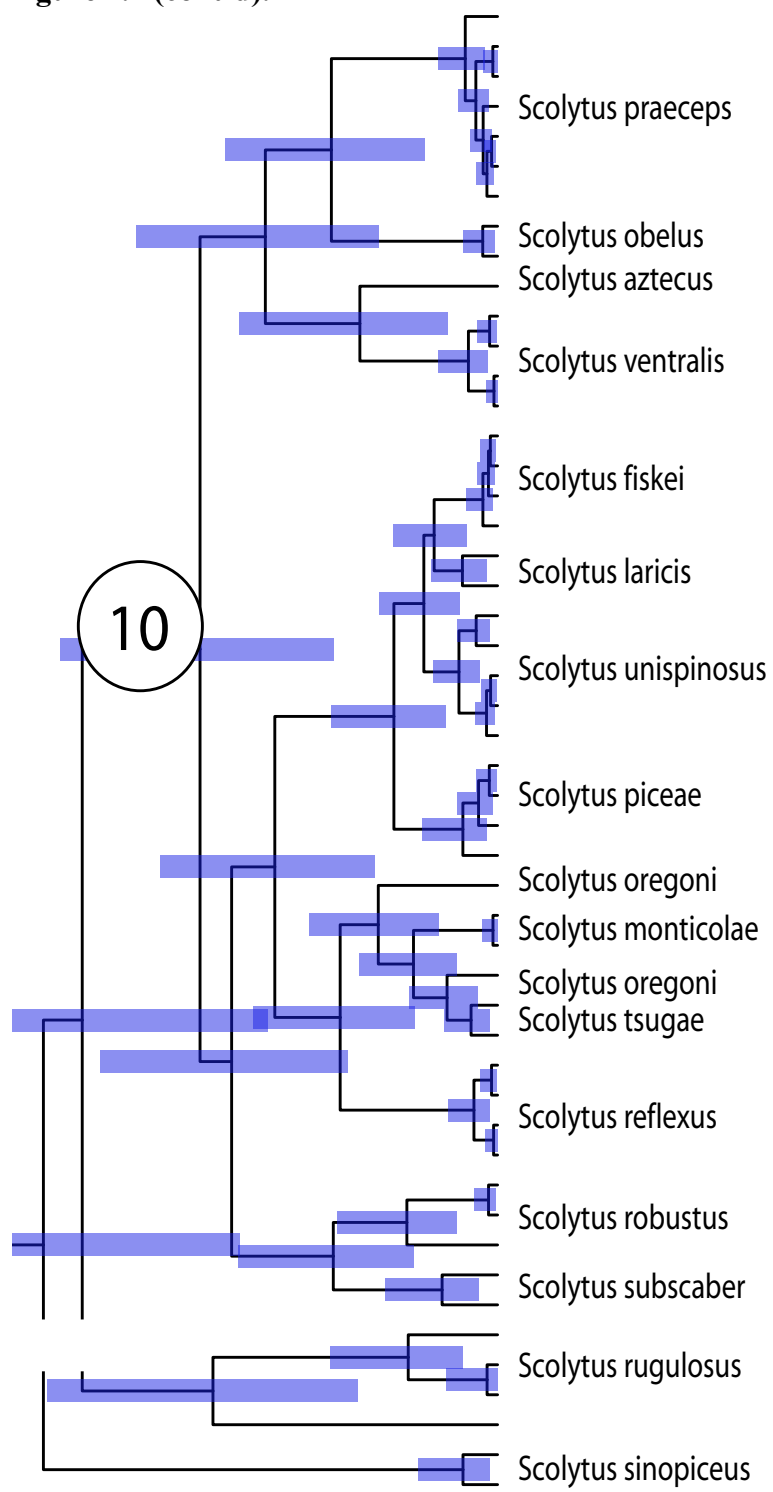


Figure 2.7 (cont'd).

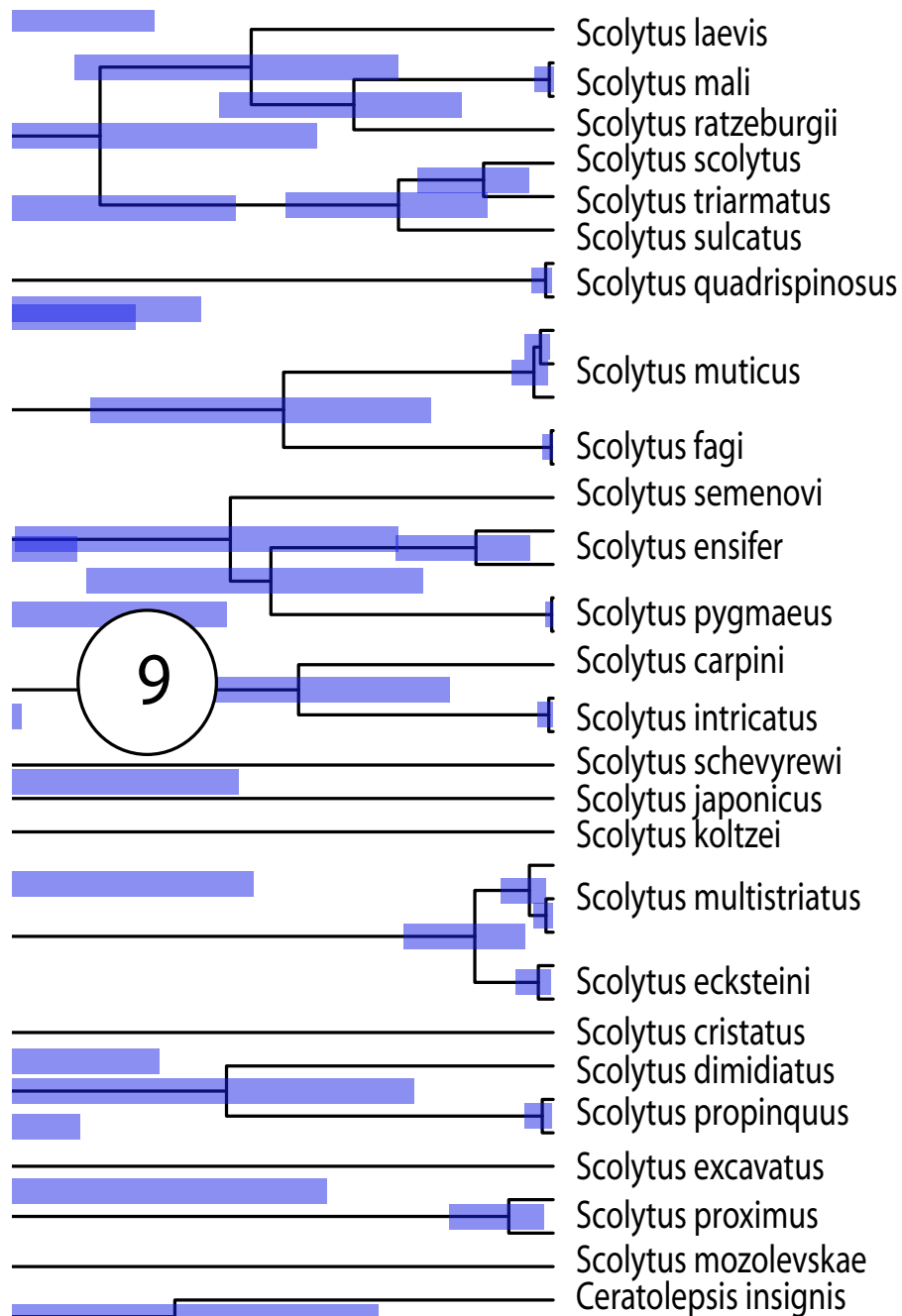


Figure 2.7 (cont'd).

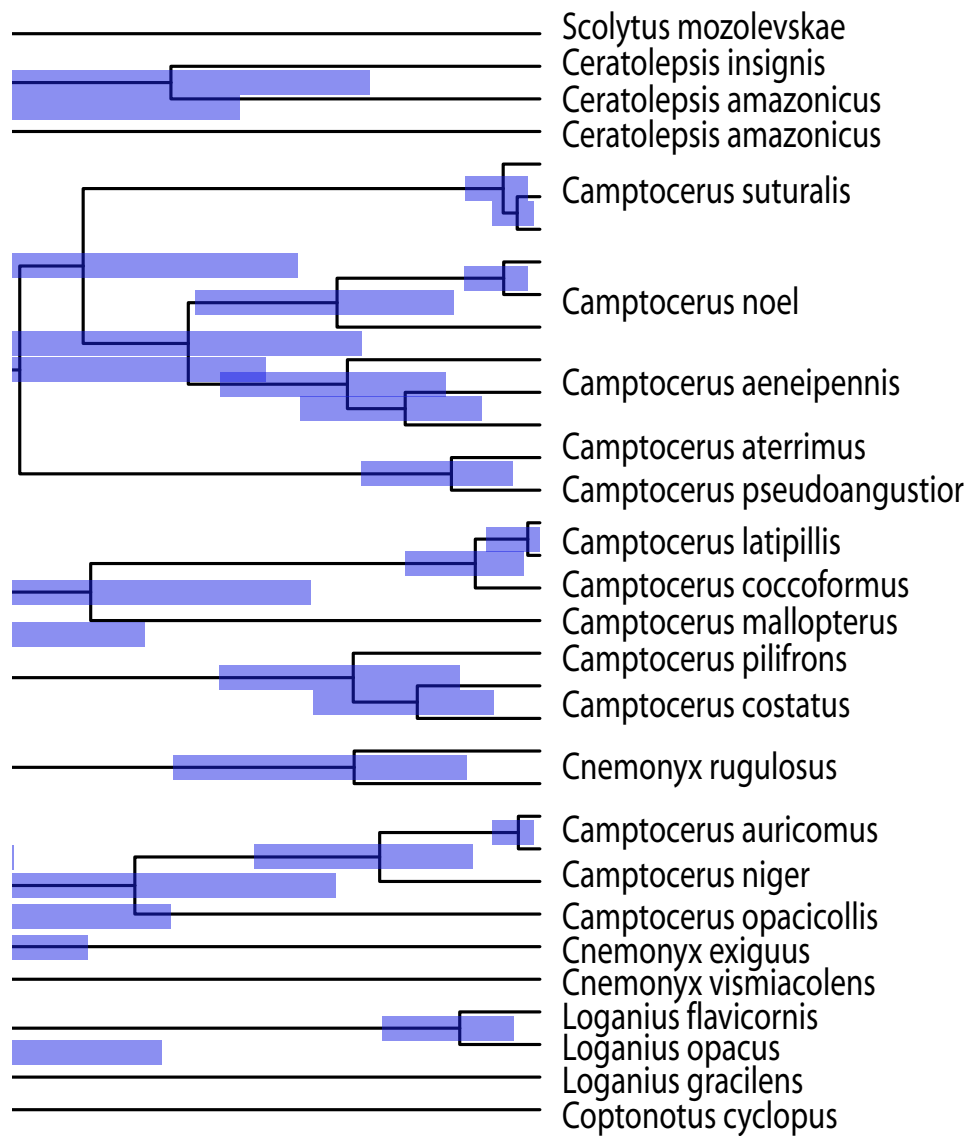
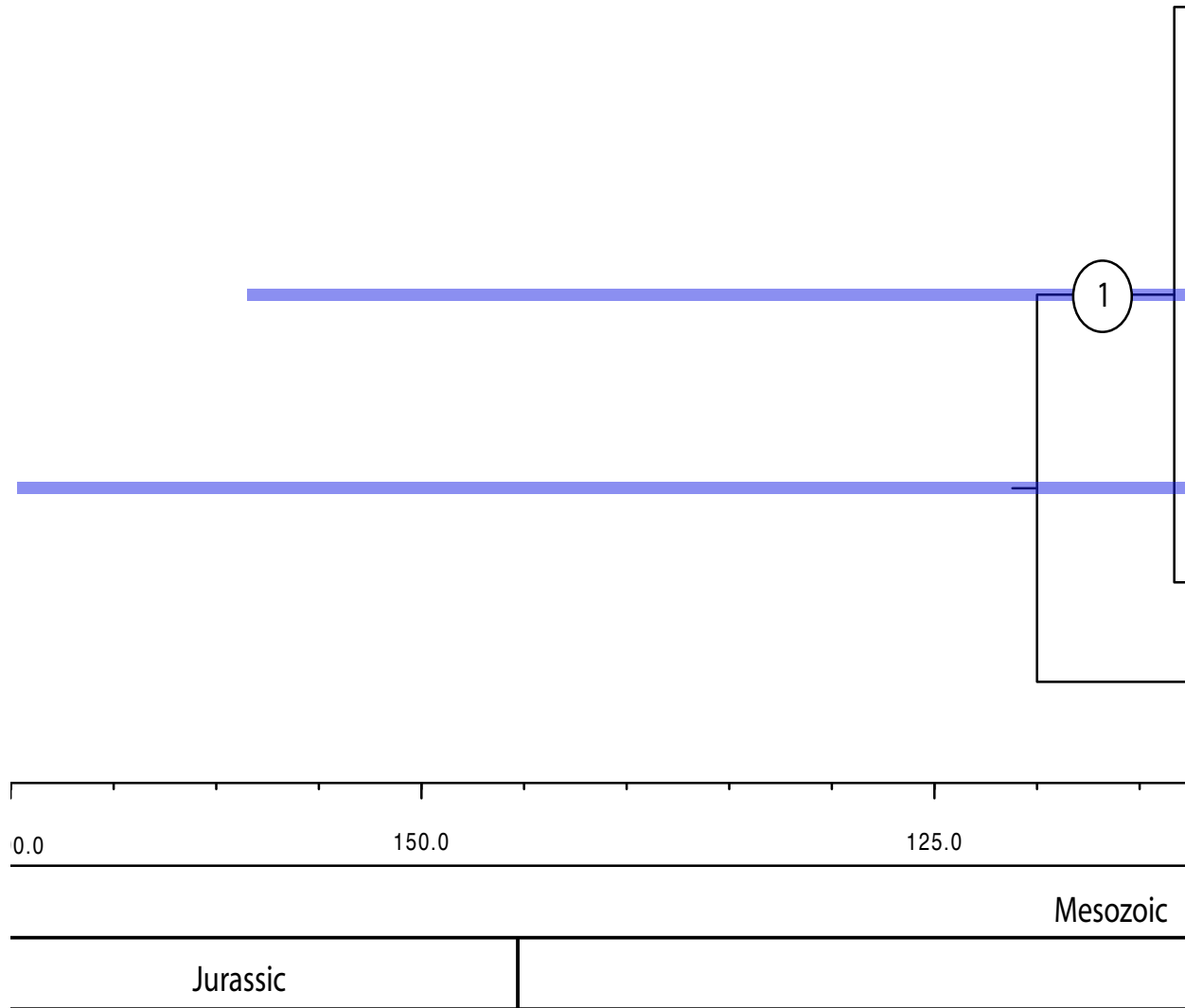


Figure 2.8. Maximum clade credibility tree (in part) for Scolytini based on the maximum age Bayesian analysis (analysis B). 95% confidence intervals for the ages of clades are indicated with blue bars. Numbers correspond to clades listed in Table 2.8. ** denotes the Quaternary period and * denotes the Pliocene epoch.



A horizontal bar chart with five bars of varying lengths. The x-axis is labeled 'Cretaceous' and has tick marks at 100.0 and 75.0. The y-axis has five horizontal lines. The bars are blue and represent the percentage of species in each period. The first bar is at the top, the second is at the second line from the top, the third is at the third line from the top, the fourth is at the fourth line from the top, and the fifth is at the bottom line.

Period	Percentage
Period 1	~95.0
Period 2	~95.0
Period 3	~95.0
Period 4	~75.0
Period 5	~100.0

Figure 2.8 (cont'd).

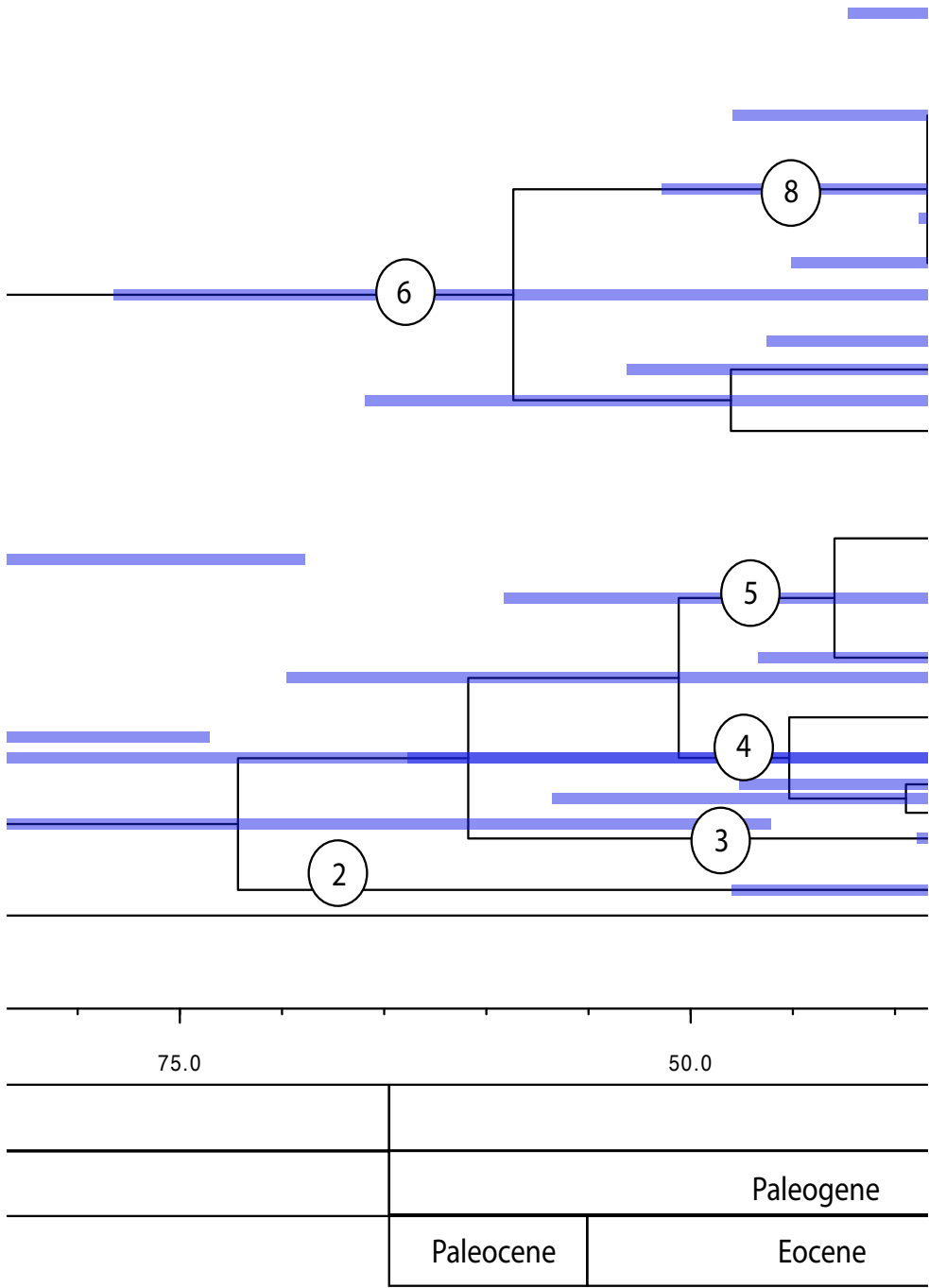


Figure 2.8 (cont'd).

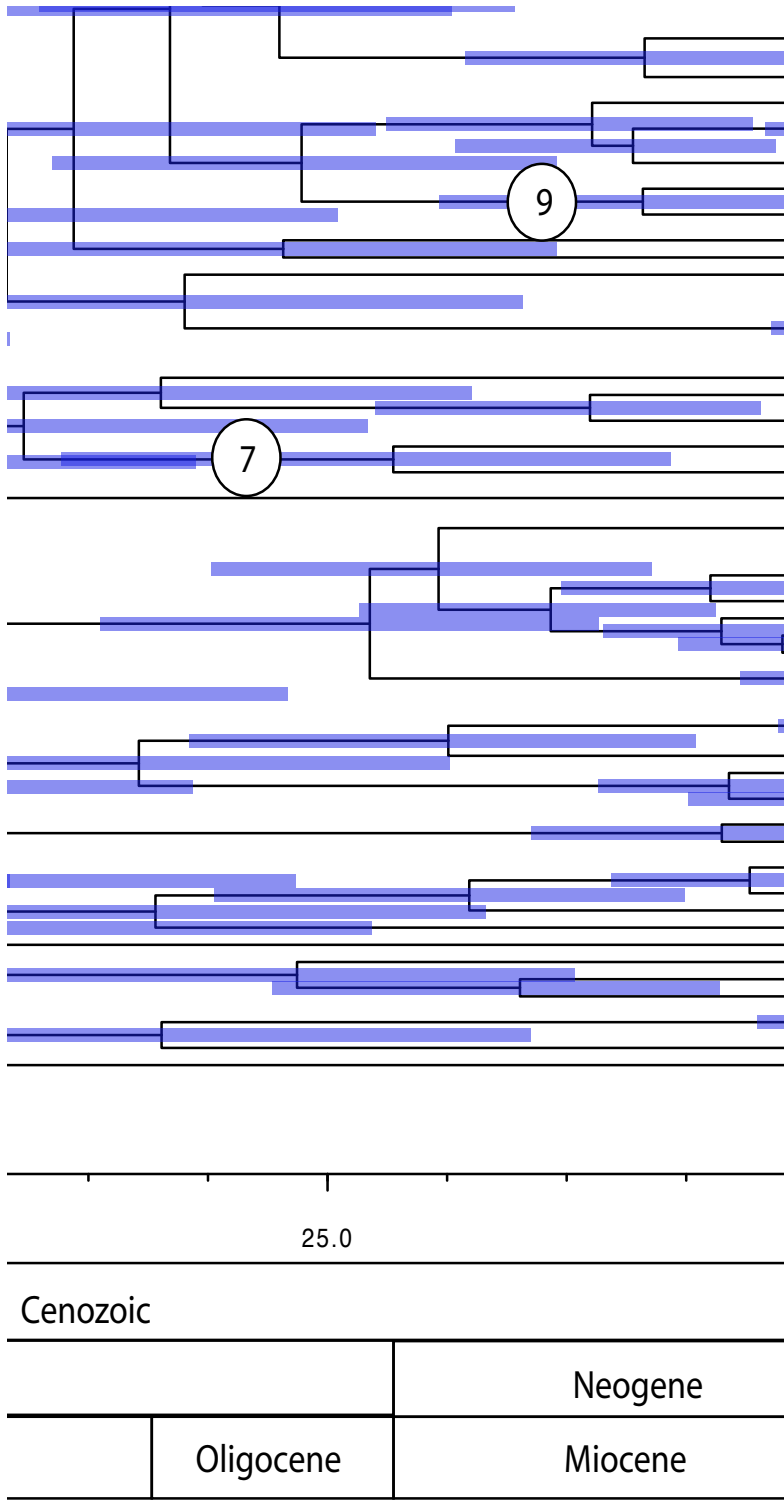


Figure 2.8 (cont'd).

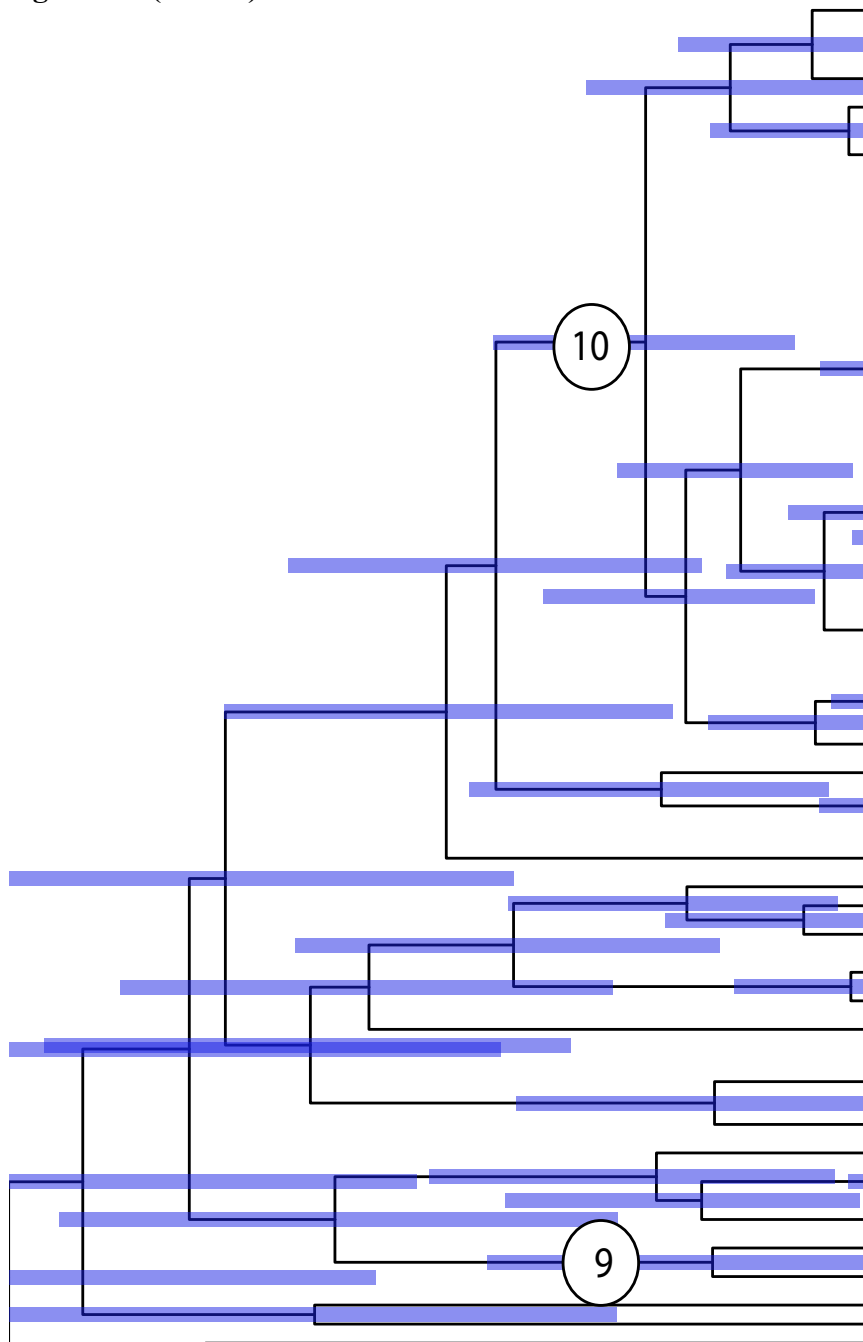


Figure 2.8 (cont'd).

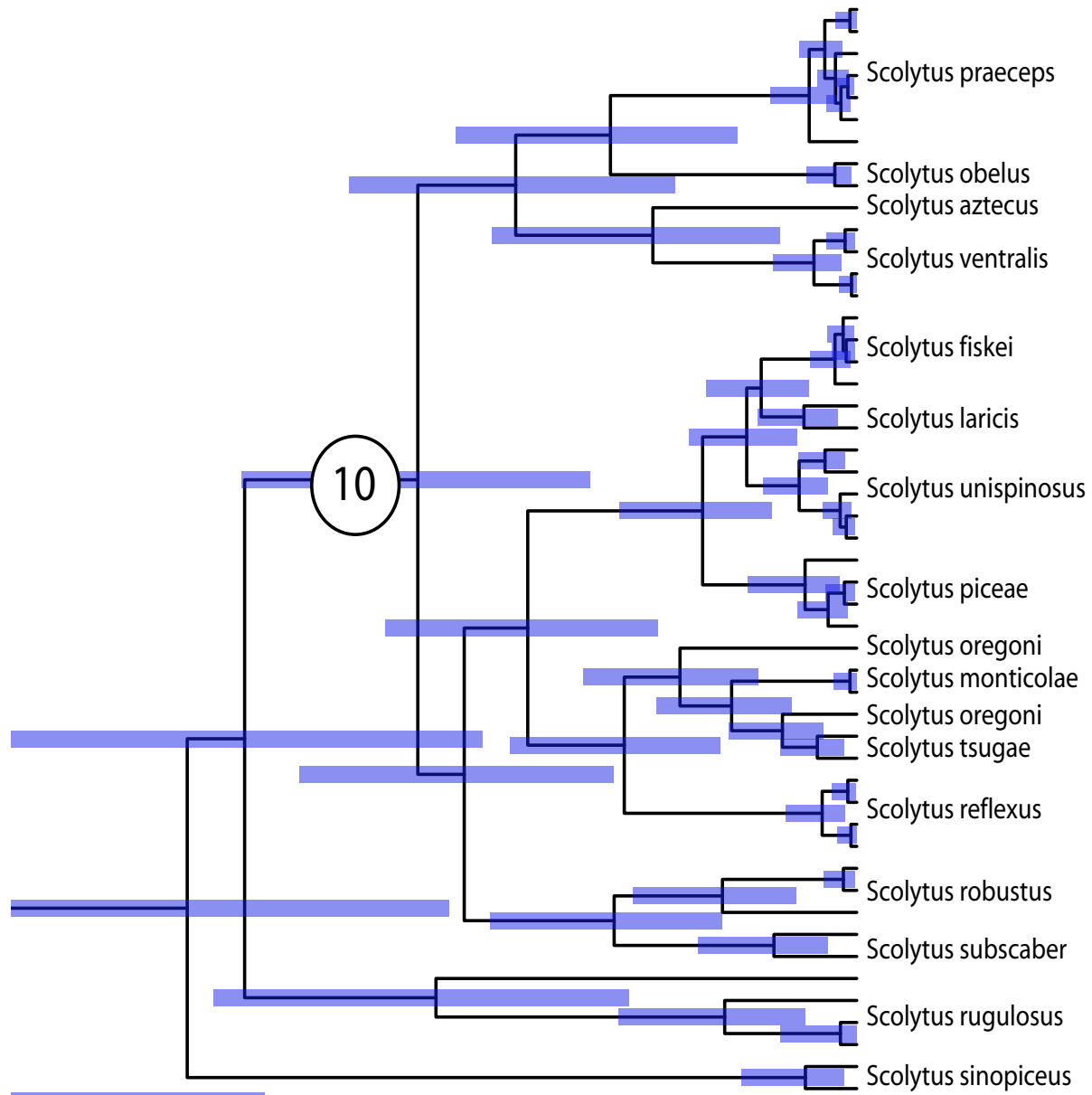


Figure 2.8 (cont'd).

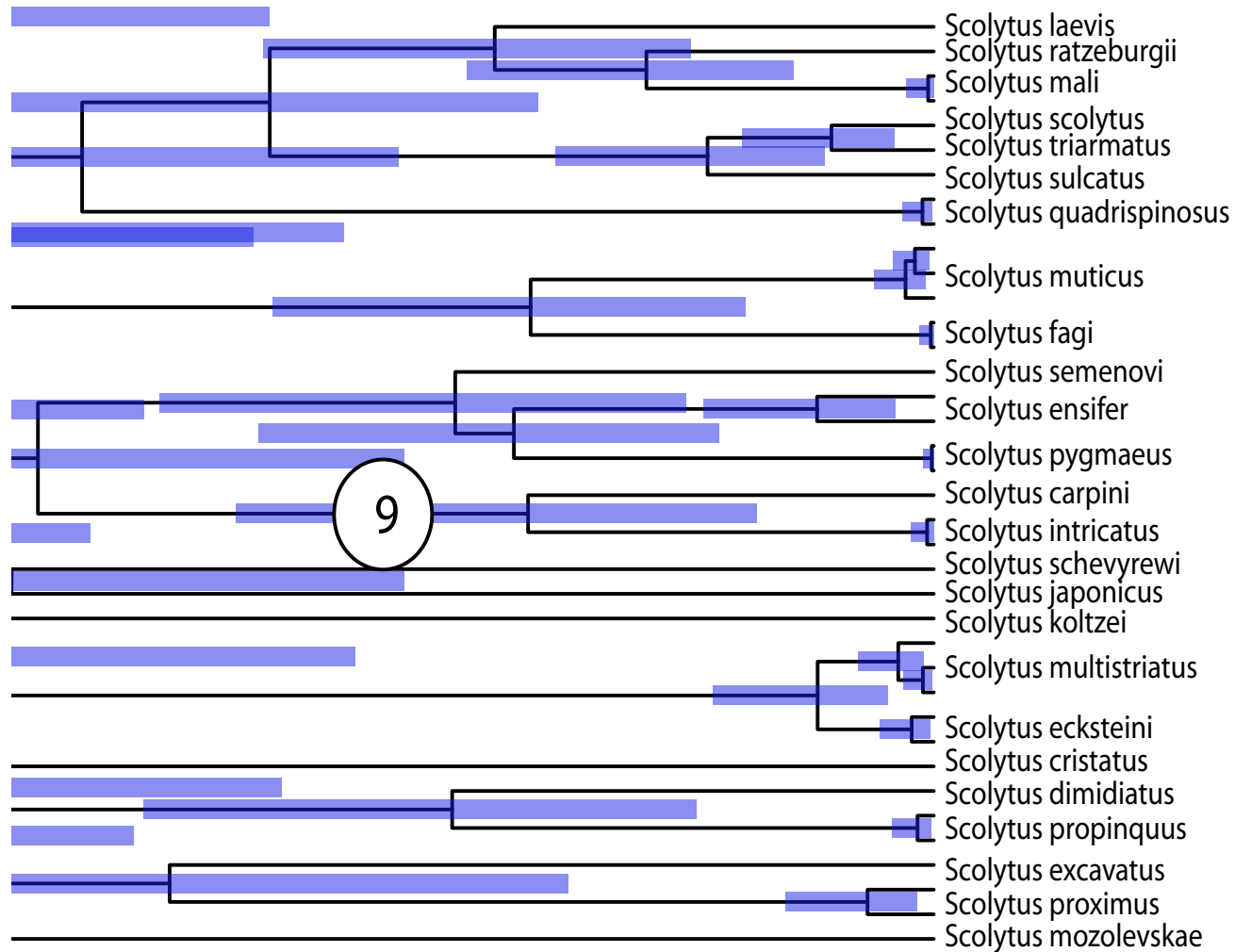
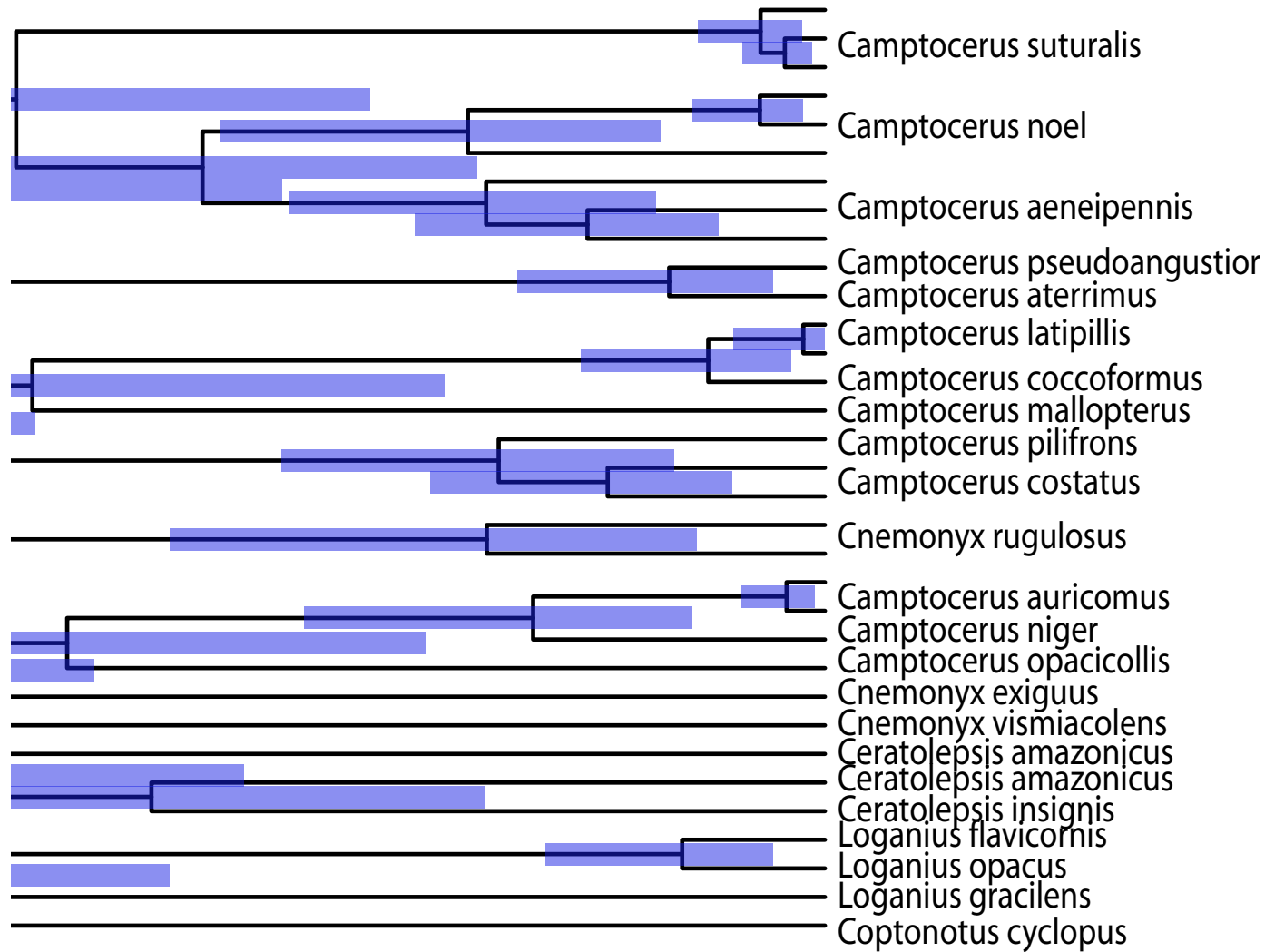


Figure 2.8 (cont'd).



APPENDIX C:
Tables and Figures for Chapter 3

Figure 3.1. *Ceratolepsis* diagnostic characters including the shape and setae on the antennal club and funicle (A), the apical margins of the meso- and metathoracic tibiae unnamed with supplemental denticles (B), the shape of the mesosternum (C) and the slightly impressed frons in both sexes (D).

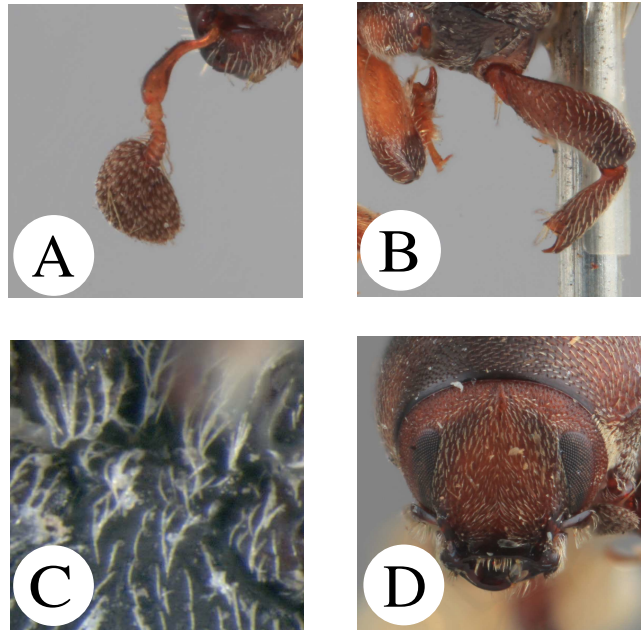


Figure 3.2. *Ceratolepsis jucundus* lateral (A) and dorsal view (B).

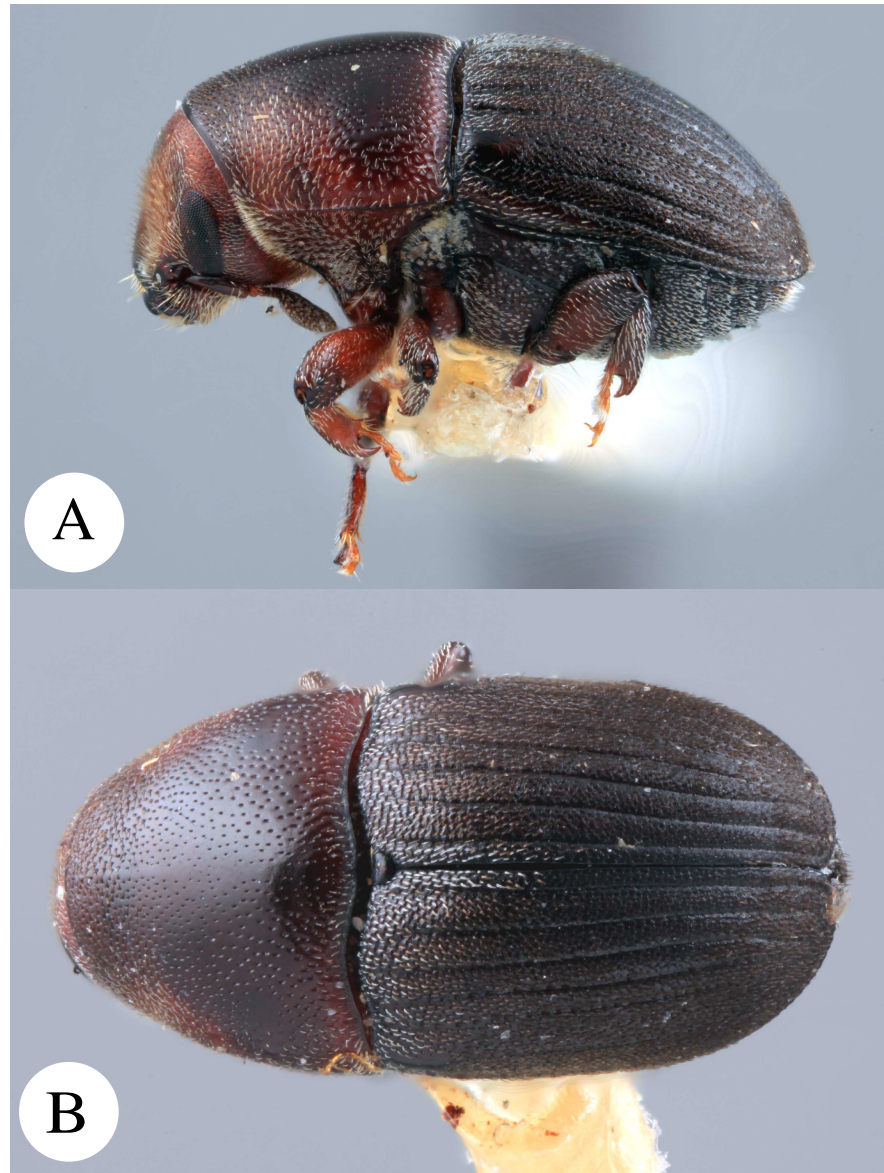


Figure 3.3. *Scolytus rabagliatus* male, 3.0-3.2 mm long, lateral (A) and dorsal view (B).



Figure 3.4. *Scolytus rabagliatus* female, 2.0-3.0 mm long, lateral (A) and dorsal view (B).



Figure 3.5. *Scolytus rabagliatus* male venter posterior (A) and posterior oblique (B); female venter posterior (C) and posterior oblique (D).

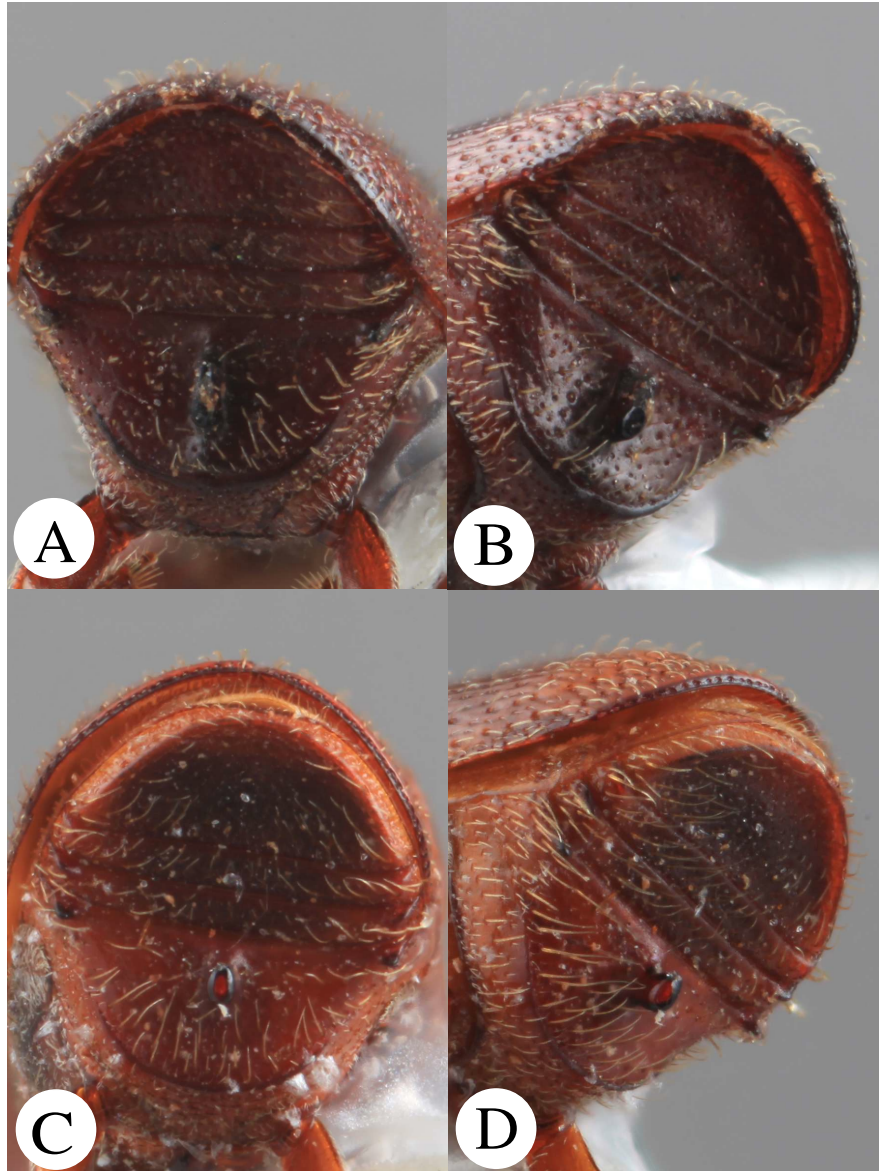
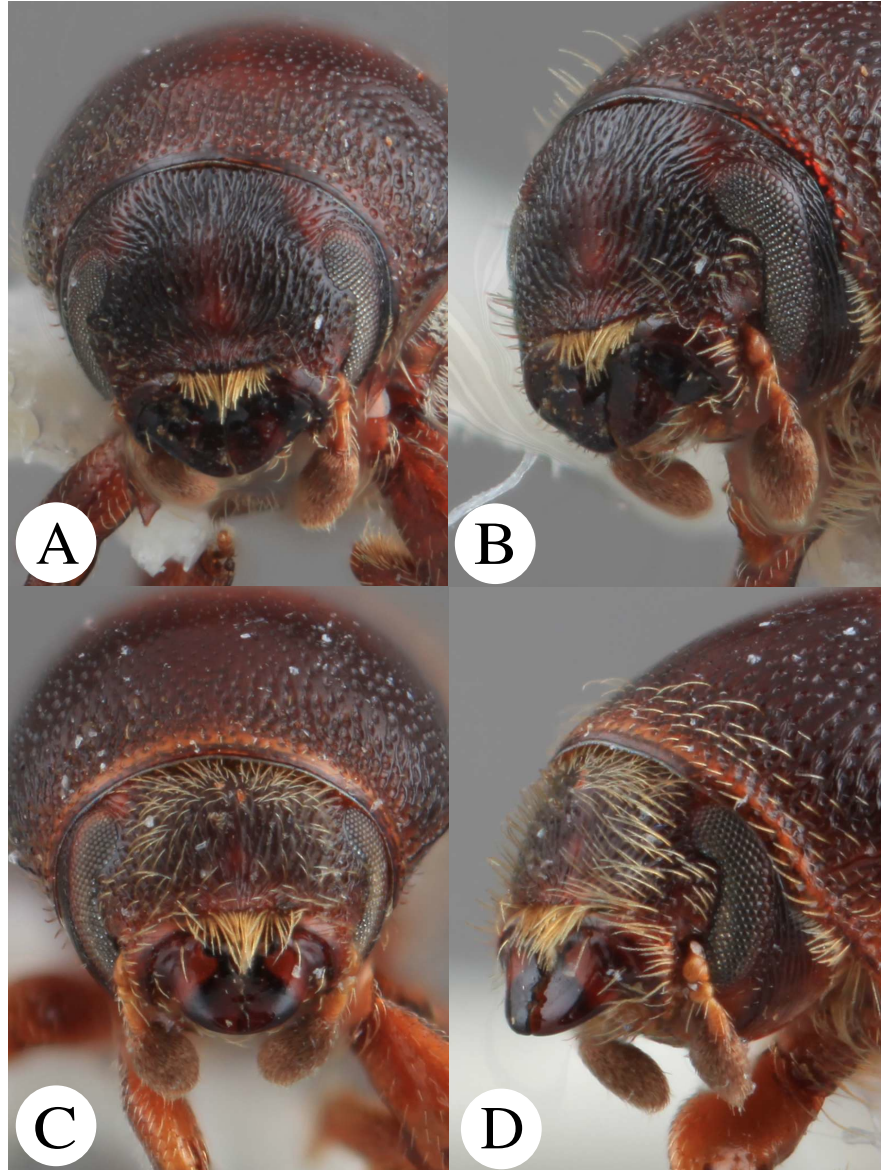


Figure 3.6. *Scolytus rabagliatus* male head anterior (A) and anterior oblique (B); female head anterior (C) and anterior oblique view (D).



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