

PLACE IN RETURN BOX to remove this checkout from your record.
TO AVOID FINES return on or before date due.
MAY BE RECALLED with earlier due date if requested.

DATE DUE	DATE DUE	DATE DUE

BIODIVERSITY OF TROPICAL SCOLYTINAE (COLEOPTERA:
CURCULIONIDAE)

By

Stephanie Alexandra Dole

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Entomology

2008

ABSTRACT

BIODIVERSITY OF TROPICAL SCOLYTINAE (COLEOPTERA: CURCULIONIDAE)

By

Stephanie Alexandra Dole

A phylogenetic revision of the Xyleborina genus *Xylosandrus* Reitter based on morphological and molecular data sets is presented. The monophyly of the genus was tested using a 43 character morphological data set analyzed separately and in combination with a molecular data set comprised of five independent gene loci: 28S rDNA; the mitochondrial gene cytochrome oxidase I (COI); and the nuclear genes arginine kinase (ArgK), *rudimentary* (CAD), and Elongation Factor 1- α (EF-1 α). The nuclear protein-coding genes CAD and ArgK were used for the first time in phylogenetics of Scolytinae. Both genes demonstrated phylogenetic utility across varying nodal depths. Phylogenetic analyses were performed using Parsimony and Bayesian optimality criteria. *Xylosandrus* was recovered as polyphyletic with the present classification containing species from four different genera: *Amasa* Lea, *Anisandrus* Ferrari, *Cnestus* Sampson, and *Xylosandrus*. Several species of *Xylosandrus* were consistently placed in clades with the genera *Anisandrus* and *Cnestus* with high support values (100% bootstrap support). Among these, was the economically important invasive species *X. mutilatus*, which was consistently recovered as part of the “*Cnestus*” clade. A taxonomic revision of *Xylosandrus* is presented based on these results. The following **new combinations** are given: *Amasa cylindrotomicus* (Schedl), *A. omissus* (Schedl), *A. oralis* (Schedl), *Anisandrus butamali* (Beeson), *A. ursa* (Eggers), *A. ursinus* (Hagedorn).

A. ursulus (Eggers), *Cnestus ater* (Eggers), *C. fijianus* (Schedl), *C. gravidus* (Blandford), *C. improcerus* (Sampson), *C. laticeps* (Wood), *C. mutilatus* (Blandford), *C. orbiculatus* (Schedl), *C. peruanus* (Wood), *C. retifer* (Wood), *C. retusus* (Eichhoff), *C. testudo* (Eggers), *Cyclorhipidion squamulatus* (Beaver and Löyttyniemi), *Xylosandrus amputatus* (Blandford), *X. mixtus* (Schedl), and *X. rotundicollis* (Browne). Two **new species** of *Xylosandrus* are described: *X. borneensis* and *X. hulcri*. An illustrated key to worldwide species of *Xylosandrus* is provided. Biogeography, host plants, diagnosis, and images are presented for each species.

Canopy fogging was used to sample the diversity of bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) at two Western Amazonian rain forest sites in Ecuador. Sampling spanning from 1994-2006 yielded 1,158 samples containing 2,500 scolytine specimens representing more than 400 morphospecies. Here, we analyze a subset of this data representing two ecological groups: true bark beetles (52 morphospecies) and ambrosia beetles (69 morphospecies). A high percentage of these taxa occurred as singletons and doubletons and their species accumulation curves did not reach an asymptote. Diversity estimates placed the total scolytine species richness for this taxon subset present at the two sites between 260 and 323 species. High levels of α - and β -diversity were discovered. However, high β -diversity was found to be an artifact of undersampling and does not appear to be biologically significant. This study demonstrates the utility of canopy fogging methods for the sampling of scolytine richness and for the discovery of new scolytine taxa.

This work is dedicated to my husband, Krishna Peter Dole, who offered constant support during the Ph.D. process and made great sacrifices so that I could achieve my entomological dreams.

ACKNOWLEDGMENTS

This work would not have been possible without the generous support and continued guidance of my major professor, Dr. Anthony Cognato. I would also like to thank my Ph.D. committee members Dr. Richard Merritt, Dr. Therese Poland, Dr. Alan Prather, and Dr. Richard Triemer for their guidance and review. This work was also made possible by the support and advice given by members of the Holistic Insect Systematics Laboratory: Jiri Hulcr, Aaron Smith, and Sarah Smith. Dr. Roger Beaver proved to be an exceptional colleague through his dedication to advising me on this work and his valuable comments on the revision of *Xylosandrus*. I would like to thank Dr. Don Bright, Dr. Bjarte Jordal, Dr. Robert Rabaglia, Dr. Saowapa Sonthichai, and Dr. Stephen Wood for their assistance with this research. I thank Dr. Terry Erwin and Dr. Warren Steiner of the Smithsonian Institute for enabling me to collaborate on their canopy fogging research. I would also like to thank the California Academy of Sciences Department of Entomology for the use of their research facilities and the generous support of their researchers and staff. With tremendous gratitude, I thank my parents, F. Clark and Gabrielle Stephens, for the opportunities they provided me throughout my life that made this achievement possible. This research was supported by NSF-PEET grant (DEB-0328920) to Anthony I. Cognato.

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	ix
CHAPTER 1	
POLYPHYLY OF <i>XYLOSANDRUS</i> REITTER INFERRED FROM NUCLEAR AND MITOCHONDRIAL GENES (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE: XYLEBORINA)	1
Abstract	2
Introduction	3
Materials and Methods	8
Results	14
Discussion	16
CHAPTER 2	
PHYLOGENETIC REVISION OF <i>XYLOSANDRUS</i> REITTER (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE: XYLEBORINA)	45
Abstract	46
Introduction	47
Materials and Methods	55
Results	66
Discussion	68
CHAPTER 3	
DIVERSITY OF SCOLYTINAE (COLEOPTERA: CURCULIONIDAE) IN THE ECUADORIAN RAIN FOREST CANOPY	254
Abstract	255
Introduction	256
Materials and Methods	260
Results and Discussion	266
LITERATURE CITED	286

LIST OF TABLES

Table 1.1: Specimens sequenced, collecting data, and hosts.	25
Table 1.2: PCR primers and annealing temperatures used for the amplification of gene sequences.	28
Table 1.3: Support found for selected clades found by different analyses of the five gene dataset. Numbers represent bootstrap/Bremer supports or posterior probabilities for Bayesian analyses. NA = not applicable or not found in the resulting tree(s).	29
Table 1.4: Contribution of data partitions to the character matrix and to the resolution of the most parsimonious tree found in analysis 1.	30
Table 1.5: Partition branch support based on tree found by phylogenetic analysis 1 (see Materials and Methods). Nodes refer to Figure 1.1.	31
Table 1.6: Partition branch support based on tree found by phylogenetic analysis 2 (see Materials and Methods). Nodes refer to Figure 1.2.	32
Table 1.7: Partition branch support based on tree found by phylogenetic analysis 3 (see Materials and Methods). Nodes refer to Figure 1.3.	33
Table 1.8: Partition branch support based on tree found by phylogenetic analysis 4 (see Materials and Methods). Nodes refer to Figure 1.4.	34
Table 1.9: COI intra- and interspecific distances expressed as the proportion of sites differing between sequences, with interspecific distances given as the average observed between species.	35
Table 2.1: Biogeographic distribution of <i>Xylosandrus</i> species: ● = present; ▲ = present as introduced species.	196
Table 2.2: Morphological character matrix of 43 characters for 73 species. Characters are their scores described in Materials and Methods.	197
Table 2.3: Species data for morphological and molecular characters matrices (● = data available for species).	205
Table 2.4: Contribution of data partitions to the data matrix and to the resolution of the most parsimonious tree found in the analysis of the combined data set.	209
Table 2.5: Partition branch support for the most parsimonious tree found by the analysis of the combined data set. Node numbers refer to Figure 2.2.	210

Table 3.1: Species data, Complementarity Indices (CI) and richness estimators for (A) total data analyzed, (B) bark beetles (Hylesinini), and (C) ambrosia beetles (Xyleborina + Premnobina).	273
Table 3.2: Morphospecies of bark beetles (Hylesinini) found in the canopy fogging samples.	274
Table 3.3: Morphospecies of ambrosia beetles (Xyleborina + Premnobina) found in the canopy fogging samples.	276
Table 3.4: Previous South American generic and species records for various scolytine subtribes compared with taxa collected by this study.	278
Table 3.5: Species numbers and Complementarity Indices (CI) for analyzed subtribes of Scolytinae.	279

LIST OF FIGURES

Figure 1.1: Most parsimonious tree found by parsimony analysis of data aligned using 28S secondary structure (Jordal et al. 2008), with gaps treated as missing data. Numbers above nodes are Bremer support values. Numbers below nodes are bootstrap support values.	36
Figure 1.2: One of three most parsimonious trees found by parsimony analysis of data aligned using 28S secondary structure (Jordal et al. 2008), with gaps treated as a 5 th character state. Clade numbers are given above nodes. Numbers below nodes are bootstrap support values.	37
Figure 1.3: Single most parsimonious tree found by parsimony analysis of data aligned in MUSCLE, with gaps treated as missing data. Clade numbers are given above nodes. Numbers below nodes are bootstrap support values.	38
Figure 1.4: One of two most parsimonious trees found by parsimony analysis of data aligned in MUSCLE, with gaps treated as a 5 th character state. Clade numbers are given above nodes. Numbers below nodes are bootstrap support values.	39
Figure 1.5: One of two post parsimonious trees found by dynamic alignment and analysis using POY, with a gap cost = 2. Numbers above nodes are Bremer support values.	40
Figure 1.6: Bayesian tree found by analysis of data aligned using 28S secondary structure (Jordal et al. 2008). Numbers above nodes are Bayesian posterior probabilities.	41
Figure 1.7: Bayesian tree found by analysis of data aligned in MUSCLE. Numbers above nodes are Bayesian posterior probabilities.	42
Figure 1.8: Relationships between PBS values and nodal distance (maximum likelihood branch length from a given node to the tip of the tree) for the gene partitions: 28S, COI, and EF-1 _α (A), CAD and ArgK (B).	43
Figure 2.1: Strict consensus of 10,000 most parsimonious trees found in parsimony analysis of the morphological data matrix. Bootstrap values are given below the nodes for clades with support ≥ 90%.	211
Figure 2.2: Most parsimonious tree found in the analysis of the combined data matrix. Node numbers given above branches and bootstrap support/Bremer support values given below.	212
Figure 2.3: Lateral habitus of <i>Amasa cylindrotomicus</i> n. comb., female (A) and <i>Amasa bicostatus</i> , female (B).	213

Figure 2.4: Lateral habitus of <i>Anisandrus ursulus</i> n. comb., female (A) and <i>Anisandrus sayi</i> , female (B).	214
Figure 2.5: Lateral habitus of <i>Cnestus improcerus</i> n. comb., female (A) and <i>Cnestus pseudosuturalis</i> , female (B).	215
Figure 2.6: Lateral (A) and dorsal (B) views of <i>Xylosandrus abruptulus</i> , 1.9 – 2.1 mm, female lectotype.	216
Figure 2.7: Lateral (A) and dorsal (B) views of <i>Xylosandrus adherescens</i> , 2.0 mm, female holotype.	217
Figure 2.8: Lateral (A) and dorsal (B) views of <i>Xylosandrus amputatus</i> n. comb., 2.7 – 2.9 mm, female.	218
Figure 2.9: Lateral (A) and dorsal (B) views of <i>Xylosandrus arquatus</i> , 2.3 – 2.5 mm, female.	219
Figure 2.10: Lateral (A) and dorsal (B) views of <i>Xylosandrus assequens</i> , 1.6 – 2.3 mm, female, holotype.	220
Figure 2.11: Lateral (A) and dorsal (B) views of <i>Xylosandrus borealis</i> , 2.0 – 2.1 mm, female.	221
Figure 2.12: Lateral (A) and dorsal (B) views of <i>Xylosandrus borneensis</i> n. sp., 1.5 – 1.6 mm, female holotype.	222
Figure 2.13: Lateral (A) and dorsal (B) views of <i>Xylosandrus brevis</i> , 2.5 – 2.8 mm, female.	223
Figure 2.14: Lateral (A) and dorsal (B) views of <i>Xylosandrus compactus</i> , 1.4 – 1.9 mm, female.	224
Figure 2.15: Lateral (A) and dorsal (B) views of <i>Xylosandrus corthyloides</i> , 2.7 – 3.0 mm, female lectotype.	225
Figure 2.16: Lateral (A) and dorsal (B) views of <i>Xylosandrus crassiusculus</i> , 1.7 – 2.9 mm, female.	226
Figure 2.17: Lateral (A) and dorsal (B) views of <i>Xylosandrus curtulus</i> , 1.3 – 1.5 mm, female holotype of synonym <i>X. biseriatus</i>	227
Figure 2.18: Lateral (A) and dorsal (B) views of <i>Xylosandrus derupteterminatus</i> , 2.0 – 2.3 mm, female holotype.	228

Figure 2.19: Lateral (A) and dorsal (B) views of <i>Xylosandrus deruptulus</i> , 1.8 mm, female lectotype.	229
Figure 2.20: Lateral (A) and dorsal (B) views of <i>Xylosandrus discolor</i> , 1.8 – 2.0 mm, female.	230
Figure 2.21: Lateral (A) and dorsal (B) views of <i>Xylosandrus diversepilosus</i> , 1.8 – 2.3 mm, female holotype.	231
Figure 2.22: Lateral (A) and dorsal (B) views of <i>Xylosandrus eupatorii</i> , 1.8 – 2.1 mm, female cotype.	232
Figure 2.23: Lateral (A) and dorsal (B) views of <i>Xylosandrus ferinus</i> , 1.6 – 1.8 mm, female lectotype.	233
Figure 2.24: Lateral (A) and dorsal (B) views of <i>Xylosandrus germanus</i> , 1.9 – 2.5 mm, female.	234
Figure 2.25: Lateral (A) and dorsal (B) views of <i>Xylosandrus hirsutipennis</i> , 1.9 – 2.2 mm, female paratype.	235
Figure 2.26: Lateral (A) and dorsal (B) views of <i>Xylosandrus hulcri</i> n. sp., 2.4 – 2.7mm, female holotype.	236
Figure 2.27: Lateral (A) and dorsal (B) views of <i>Xylosandrus jaintianus</i> , 3.0 mm, female holotype.	237
Figure 2.28: Lateral (A) and dorsal (B) views of <i>Xylosandrus mancus</i> , 2.9 – 3.3 mm, female.	238
Figure 2.29: Lateral (A) and dorsal (B) views of <i>Xylosandrus mediocris</i> , 1.4 mm, female.	239
Figure 2.30: Lateral (A) and dorsal (B) views of <i>Xylosandrus mesuae</i> , 1.1 – 1.3 mm, female.	240
Figure 2.31: Lateral (A) and dorsal (B) views of <i>Xylosandrus metagermanus</i> , 1.8 mm, female holotype.	241
Figure 2.32: Lateral (A) and dorsal (B) views of <i>Xylosandrus mixtus</i> n. comb., 2.6 – 2.7 mm, female holotype.	242

Figure 2.33: Lateral (A) and dorsal (B) views of <i>Xylosandrus monteithi</i> , 3.0 – 3.4 mm, female paratype.	243
Figure 2.34: Lateral (C) and dorsal (D) views of <i>Xylosandrus monteithi</i> , 2.5 mm, male allotype.	244
Figure 2.35: Lateral (A) and dorsal (B) views of <i>Xylosandrus morigerus</i> , 1.5 – 2.0 mm, female.	245
Figure 2.36: Lateral (A) and dorsal (B) views of <i>Xylosandrus pusillus</i> , 1.5 – 1.7 mm, female holotype.	246
Figure 2.37: Lateral (A) and dorsal (B) views of <i>Xylosandrus pygmaeus</i> , 1.3 – 1.4 mm, female holotype.	247
Figure 2.38: Lateral (A) and dorsal (B) views of <i>Xylosandrus queenslandi</i> , 1.6 – 1.9 mm, female paratype.	248
Figure 2.39: Lateral (A) and dorsal (B) views of <i>Xylosandrus rotundicollis</i> n. comb., 3.7 – 4.1 mm, female holotype.	249
Figure 2.40: Lateral (A) and dorsal (B) views of <i>Xylosandrus subsimiliformis</i> , 2.8 mm, female cotype.	250
Figure 2.41: Lateral (A) and dorsal (B) views of <i>Xylosandrus subsimilis</i> , 2.6 mm, female cotype.	251
Figure 2.42: Lateral (A) and dorsal (B) views of <i>Xylosandrus terminatus</i> , 1.5 – 1.9 mm, female cotype.	252
Figure 2.43: Lateral (A) and dorsal (B) views of <i>Xylosandrus woodi</i> , 2.3 – 2.4 mm, female paratype.	253
Figure 3.1: Species accumulation curves for Onkone Gare + Tiputini for total data (Hylesinini + Xyleborina + Premnobina).	280
Figure 3.2: Species accumulation curves for Onkone Gare + Tiputini for bark beetles (Hylesinini).	281
Figure 3.3: Species accumulation curves for Onkone Gare + Tiputini for ambrosia beetles (Xyleborina + Premnobina).	282
Figure 3.4: Richness estimators for Onkone Gare + Tiputini for total data (Hylesinini + Xyleborina + Premnobina).	283

Figure 3.5: Richness estimators for Onkone Gare + Tiputini for bark beetles (Hylesinini).
..... 284

Figure 3.6: Richness estimators for Onkone Gare + Tiputini for ambrosia beetles
(Xyleborina + Premnobina). 285

CHAPTER 1

**Polyphyly of *Xylosandrus* Reitter inferred from nuclear and mitochondrial genes
(Coleoptera: Curculionidae: Scolytinae)**

ABSTRACT

The monophyly of the Xyleborina ambrosia beetle genus *Xylosandrus* was tested using a data set comprised of multiple gene loci: 28S rDNA; the mitochondrial gene cytochrome oxidase I (COI); and the nuclear genes arginine kinase (ArgK), *rudimentary* (CAD), and Elongation Factor 1- α (EF-1 α). The nuclear protein-coding genes CAD and ArgK were used for the first time in phylogenetics of Scolytinae. Analyses were performed using Parsimony and Bayesian optimality criteria. *Xylosandrus* is a widespread genus containing 54 species, several of which are of economic importance. Our analyses included 43 specimens representing 15 *Xylosandrus* species and 19 species from *Amasa*, *Anisandrus*, *Cnestus*, and *Xyleborus*, and two species from the outgroup genus *Coccotrypes*. All analyses recovered a polyphyletic *Xylosandrus*. Several species of *Xylosandrus* were consistently placed in clades with the genera *Anisandrus* and *Cnestus* with high support values (100% bootstrap support). Among these, was the economically important invasive species *X. mutilatus*, which was consistently recovered as part of the “*Cnestus*” clade. In our analyses, both CAD and ArgK demonstrated phylogenetic utility across varying nodal depths. Despite the selection of genes with signals at complementary phylogenetic depths, the data set used herein did not resolve the phylogeny of *Xylosandrus* and related genera. Since the taxon sample available for molecular work represents only a fraction of *Xylosandrus* species, it is recommended that the genus be the subject of a complete revision that combines molecular and morphological data in total evidence approach.

INTRODUCTION

The beetle subfamily Scolytinae (Coleoptera: Curculionidae) is comprised of 26 tribes containing approximately 225 genera and 6,000 species worldwide (Wood and Bright 1992; Mandelshtam and Beaver 2003). Due to the present classification of Scolytinae as a subfamily of the Curculionidae (Marvaldi 1997; Kuschel et al. 2000) previously recognized tribes (e.g. Xyleborini) are currently treated as subtribes (e.g. Xyleborina). Although the Curculionoidea are a relatively young group (152 MYO), discovery of a fossilized scolytine from Cretaceous amber dates the origin of the subfamily to at least 100 million years ago (Grimaldi and Engel 2005; Cognato and Grimaldi in press). This long history likely contributes to the diversity of Scolytines which occupy two ecological groups: bark beetles and ambrosia beetles. Bark beetles bore into the phloem of trees and feed on tree tissues (Wood and Bright 1992). Ambrosia beetles bore into the xylem and feed on symbiotic fungi, which grows on the walls of their galleries (Beaver 1989; Wood and Bright 1992; Kirkendall 1993). This ambrosial habit has evolved multiple times within the Scolytinae and also in the related weevil subfamily Platypodinae (Farrell et al. 2001). The scolytine subtribe Xyleborina contains approximately 1,300 described species and constitutes one of the largest radiations of ambrosia beetles (Wood and Bright 1992; Jordal 2002). Xyleborina are absent in the Dominican amber fossil record, suggesting that their radiation began in the Miocene (Bright and Poinar 1994; Jordal et al. 2000). The xyleborine mating system, which includes haplodiploidy and extreme inbreeding, is believed to be the cause of this dramatic radiation (Normark et al. 1999). Ambrosia beetles tend to be less host-specific

than their bark beetle counterparts, because adaptation to host secondary chemistry has not influenced their radiation. Hence they are particularly suited for the invasion of new habitats and establishment as introduced exotic species. Ten species of exotic xyleborine beetles became established in the United States between 1985 and 2005 (Haack 2006; Rabaglia et al. 2006). These invasions, along with the interesting biology and ecology of xyleborine beetles, have prompted much research interest. Historically, the classification of the Xyleborina has been chaotic, with Wood (1986) describing his own classification of the tribe as “tentative and flawed.” However, recent taxonomic work has begun to correct this, as the subtribe is finally being studied within a phylogenetic context (Jordal et al. 2000; Jordal 2002; Hulcr et al. 2007).

Xylosandrus Reitter (1913) is a large genus of xyleborine ambrosia beetles with a widespread distribution primarily in tropical, but also in temperate regions of the world. In their worldwide catalog of the Scolytinae, Wood and Bright (1992) list 52 species of *Xylosandrus*. Subsequent descriptions, new synonymies, and new combinations have brought the present number to 54 species (Bright and Skidmore 1997; Saha et al. 2002; Wood 2007; Dole and Beaver in press).

Several *Xylosandrus* species cause economic losses in nursery and agricultural settings in their native and introduced ranges. In Brazil, *X. compactus* causes losses in several economically important host species, including avocado, cacao, coffee, and mango (Oliveira 2008). In North America, three *Xylosandrus* species (*X. compactus*, *X. crassiusculus*, and *X. germanus*) have caused “considerable economic damages” since their introductions (Oliver and Mannion 2001). As an example, nursery managers in Maryland reported individual losses of \$3,650 - \$8,400 in stock to *Xylosandrus* species in

the spring of 2008 alone (R. J. Rabaglia per. com.). A revised understanding of *Xylosandrus* generic boundaries and species diagnosis would aid in the identification and control of these economically important beetles.

Xylosandrus currently contains species with highly variable morphologies, several of which are similar to those of other genera, leading to confusion concerning the generic boundaries of *Xylosandrus* and its relationship to and distinction from the genera *Amasa* Lea, *Anisandrus* Ferrari, and *Cnestus* Sampson. The underlying cause of this confusion has been the incorrect placement of species within *Xylosandrus*, which has blurred the boundaries between it and other genera (Dole and Beaver in press). Commonly cited diagnostic characters for *Xylosandrus* include widely separated procoxae; very stout, cylindrical bodies; and antennal club that is obliquely truncate with the first segment of the antennal club forming a circular costa and with segments two and three not visible on posterior face of the club (Bright 1968; Wood 1986; Hulcr et al. 2007; Dole and Beaver in press). However, even the frequently cited diagnostic character of widely separated procoxae does not function as a synapomorphy for *Xylosandrus* and the genus is presently defined by a collection of homoplastic xyleborine characters (Hulcr et al. 2007).

Both morphological (Dole and Beaver in press) and molecular data suggest that *Xylosandrus* is not monophyletic (Jordal 2002). A cladistic review of the generic taxonomic characters of Xyleborina recovered a monophyletic *Xylosandrus*, but it is important to note that this study did not include species with morphologies that deviate from the *sensu stricto* concept of the genus (Hulcr et al. 2007). In their review of Australian *Xylosandrus*, Dole and Beaver (in press) contributed to the revision of *Xylosandrus* by defining characters that distinguish it from *Cnestus* and moving two

species from *Xylosandrus* to *Cnestus*. This was only a beginning, given the narrow geographic perspective of their review. *Xylosandrus* is in need of a comprehensive phylogenetic revision that includes other suspect genera, such as *Amasa*, *Anisandrus*, and *Cnestus*. The prevalence of homoplastic morphological characters within *Xylosandrus* and related genera necessitates the inclusion of alternative characters, such as DNA, to help reconstruct the phylogeny of this group.

Molecular studies of scolytine phylogenetics have been based mainly on mitochondrial genes (16S, COI), the ribosomal encoding gene 28S, and the nuclear protein encoding genes elongation factor 1 α (EF-1 α) and *Enolase* (Normark et al. 1999; Jordal et al. 2000; Cognato and Vogler 2001; Farrell et al. 2001; Jordal 2002; Jordal and Hewitt 2004; Jordal et al. 2008). Of these genes, EF-1 α has shown the greatest potential for resolving the phylogenetic relationship of Scolytinae (Jordal 2002, 2007). However, use of these genes alone has not resolved a Scolytinae phylogeny. Recent studies have indicated that the use of multiple independent gene loci may be necessary to recover resolved phylogenies (Rokas and Carroll 2005; Edwards et al. 2007; Wild and Maddison 2008). The thousands of protein-coding genes present in the nuclear genomes of eukaryotes offer a rich source of new loci to include in phylogenetic studies of arthropods (Wiegmann et al. 2000; Jordal 2007; Wild and Maddison 2008). Protein-coding nuclear genes have been used in the inference of Lepidoptera phylogenetics for over a decade (Friedlander et al. 1998; Regier et al. 1998; Fang et al. 2000; Friedlander et al. 2000; Mitchell et al. 2000; Wiegmann et al. 2000). They have also proven useful in the reconstruction of higher-level relationships among the Arthropods (Schultz and Regier 2000a; Schultz and Regier 2000b; Regier and Schultz 2001). Nuclear protein-coding

genes are being used in Coleoptera phylogenetics, but a recent literature survey found only 24 studies of beetle molecular phylogenetics (out of a total of 106) that utilized them (Wild and Maddison 2008). Advantages of nuclear protein-coding genes include slower rates of evolution, a lower tendency toward base-composition bias, and ease of alignment (Wiegmann et al. 2000; Wild and Maddison 2008).

Recognizing the underutilized potential of nuclear protein-coding genes, Jordal (2007) screened multiple gene loci for the phylogenetic reconstruction of scolytines. The nuclear genes CAD, also known as *rudimentary*, and arginine kinase (ArgK) were found to be the most promising and were recommended for use in future phylogenetic studies of Scolytinae. The CAD gene codes for several enzymes involved in the de novo synthesis of pyrimidines. In Insecta, the carbamolyphosphate synthetase locus of CAD has been used in phylogenetic studies of Diptera (Moulton and Wiegmann 2004) and Hymenoptera (Danforth et al. 2006). The ArgK gene encodes for a metabolic phosphotransferase enzyme that aids in the maintenance of ATP levels. In Insecta, ArgK has been used in phylogenetic studies of Hymenoptera (Kwakita et al. 2003; Banks and Whitfield 2006).

Wild and Maddison (2008) empirically tested the utility of CAD and ArgK, along with other nuclear protein-coding genes, for the inference of beetle phylogenies against a presumably known phylogeny of Coleoptera which spanned several taxonomic levels. Within this study, CAD was the highest performing gene fragment of the eight tested, because it recovered the greatest number of clades of the known phylogeny and had high support values. ArgK reconstructed deeper clades of the known phylogeny with more accuracy than shallower clades. Also, there is no evidence for the existence of multiple copies of CAD and ArgK within beetle genomes (Jordal 2007; Wild and Maddison

2008). Thus, the inclusion DNA from both genes in a phylogenetic analysis of *Xylosandrus* could help resolve multiple levels of the resulting phylogeny.

Here, we use the CAD and ArgK genes for the first time for phylogenetic inference in the Scolytinae. Using a data set comprised of multiple gene loci (28S, ArgK, CAD, COI, and EF-1 α) we construct a phylogenetic hypothesis of the species relationships within *Xylosandrus*, test the monophyly of the genus, and test the relationships among *Xylosandrus* and the genera *Amasa*, *Anisandrus*, and *Cnestus*.

MATERIALS AND METHODS

Taxa, DNA sequences, and alignment

The majority of *Xylosandrus* species are relatively difficult to collect, thus it was a challenge to include a broad taxon sampling in this study. Specimens for DNA extraction were either collected by the authors in Ecuador, Thailand, Papua New Guinea, and Borneo or obtained from colleagues. In nearly all cases, specimens were stored in 95% ethanol at – 80° C. However, DNA was successfully extracted from several specimens that had been killed in 95% ethanol, but then pinned and stored dried (*X. monteithi* and *X. queenslandi*). We included 43 specimens (Table 1.1) representing 15 *Xylosandrus* species 19 species from the genera *Amasa*, *Anisandrus*, *Cnestus*, *Xyleborus*, and two species from the outgroup genus *Coccotrypes*. Species from a diverse group of genera were chosen in order to test the generic limits of *Xylosandrus*.

DNA was extracted from dissected throacies following protocols of Cognato and Vogler (2001) and the remaining body parts were pinned and vouchered at the A.J. Cook

Arthropod Research Collection, Michigan State University. Using the purified DNA, partial gene regions of mitochondrial cytochrome oxidase I, nuclear ribosomal 28S (D2 and D3 regions), elongation factor-1 α , CAD (rudimentary), and Arginine Kinase (ArgK) were amplified with the listed PCR primers (Table 1.2). All PCR reactions first included published COI, EF-1 α and 28S primers (Normark et al. 1999; Hebert et al. 2003; Jordal et al. 2008) and additional xyleborine specific primers were designed when PCR failed. CAD and ArgK sequences were first generated with degenerate primers designed based on bee sequences (Danforth et. al 2006; Jordal 2007). We used these sequences to subsequently create new xyleborine primers (Table 1.2). Each COI, EF-1a and 28S PCR reaction contained: 29.5 μ l ddH₂O, 10 μ l 5x *Taq* DNA polymerase buffer (Promega, Madison, WI), 5 μ l 25mM Promega MgCl₂, 1 μ l 40 mM deoxynucleotide triphosphates (dNTPs), 0.5 μ l of 5 units/ μ l Promega *Taq* DNA polymerase, 10 picomoles/ μ l of forward and reverse primers and 2 μ l of DNA template (5-50 nanograms). Each CAD and ArgK PCR reactions contained: 17.75 μ l ddH₂O, 2.5 μ l 10x *Taq* DNA polymerase buffer (Qiagen Inc., Santa Clara, CA), 1 μ l 25mM MgCl₂, 0.5 μ l 40 mM deoxynucleotide triphosphates (dNTPs), 0.25 μ l of 5 units/ μ l Qiagen Hotstar *Taq* DNA polymerase, 5 picomoles/ μ l of forward and reverse primers and 2 μ l of DNA template (5-50 nanograms). PCR was performed on a thermal cycler (MJ Research, Waltham, MA) under the following conditions: one cycle for 2 minutes at 95°C (15 min. for Hotstar *Taq*), 34 cycles for 1 min. at 95°C, 0.75 min. at 45-55°C (see Table 1.2 for specific annealing temperatures), 1 min. at 72°C, and a final elongation cycle of 5 min. at 72°C.

PCR products were visualized via electrophoresis. For each reaction, 5.0 μ l of PCR product was mixed with 2.00 μ l 5X loading buffer (Promega, Madison, WI). The 7

μl mixture was applied to an ethidium bromide stained 1.5% agarose gel at 100 volts for 30 minutes. The gel was visualized under an ultraviolet light source and photographed. Unincorporated oligonucleotides and *Taq* were destroyed in each reaction with ExoSAP-IT following the manufacturer's protocols (USB Corp., Cleveland, OH). The clean PCR reactions were directly sequenced using BigDye® Terminator v.1.1 (Applied Biosystems, Foster City, CA) cycle sequencing kit and visualized on an ABI 3730 or 3700 (Applied Biosystems, Foster City, CA) at the Research Technology Support Facility at Michigan State University. Primers used in PCR were used to sequence sense and antisense strands for all reactions.

Sense and antisense DNA sequences were compiled with the computer software Sequencer (Ann Arbor, MI), in order to inspect for ambiguities and create consensus sequences. No sequence length variation was observed among the protein coding genes for the included taxa, however considerable variation occurred in the 28S sequences. These sequences were aligned by two methods; manually with reference to a scolytine-specific secondary structure model (Jordal et al. 2008) and by a multiple progressive pairwise alignment with secondary refinement using the computer software, MUSCLE v.3.52 (Edgar 2004). We did not specify stems and loop regions for the secondary structure alignment. Instead, we used the scolytid secondary structure model to guide the alignment by identifying conserved and length variable regions. For the other alignment, we used the default settings of the web version of MUSCLE (<http://www.ebi.ac.uk/Tools/muscle/index.html>). Nexus files of both alignments are available at <http://www.hisl.ent.msu.edu/research/publications.php>.

Phylogenetic Analyses

We conducted several analyses, which used different optimality criteria, alignments, and accounted for potential bias in nucleotide substitution patterns. Parsimony analyses of data aligned by secondary structure and the MUSCLE software were conducted with the software PAUP* (Swofford 2002). For all parsimony analyses, most-parsimonious reconstructions were obtained by a heuristic search with 300 random stepwise addition replicates using PAUP* default settings. Bootstrap values were determined by performing 1000 pseudo-replicates with simple sequence addition. Bremer support values were calculated by constructing constraint trees with the software TreeRot (Sorensen 1996) followed by subsequent analysis with PAUP. For analyses of both alignments, we considered gap positions as missing data and as a 5th character state because previous studies have showed that gap positions are phylogenetically informative (Cognato and Vogler 2001; Lee 2001).

Several researchers have proposed direct optimization of nucleotide homology during phylogenetic reconstruction given that static nucleotide alignments may not accurately reflect positional homology of nucleotides for all taxa (Kruskal 1983; Sankoff and Cedergren 1983; Wheeler 1996). We performed direct optimization on the data using the program POY ver. 4.0.2881 (Wheeler 1996; Varón et al. 2008) in order to evaluate the relative signal within length variable regions. We used the alignment guided by secondary structure to divide the 28S data into seven input files, which corresponded to conserved and length variable regions. The other gene sequences were kept as separate input files. These files were inputted into POY and analyzed under a parsimony optimality criterion using the following tree search commands:

transform(tcm:(1,2),gap_opening:1), build (300), swap (threshold:5.0), select (),

perturb(transform(static_approx),iterations:15,ratchet:(0.2,3)), select(),

fuse(iterations:200,swap()), select(), report (trees:(total)). An additional analysis

considering gap cost of 3 was conducted with the same tree search strategy as above.

Bremer support values were calculated for the tree recovered in the first analysis using

the following command: *calculate_support(bremer, build(trees:0), swap(tbr, trees:2)).*

Data and command files are available at (<http://www.hisl.ent.msu.edu>

/research/publications.php).

We analyzed the data under maximum likelihood using Bayesian estimation of **phylogeny** as implemented in Mr. Bayes 3.1.2 (Huelsenbeck and **Ronquist** 2001) in order to evaluate the effect of nucleotide substitution models on **phylogenetic** reconstruction. We conducted a separate analysis for each of the static **alignments**. For both analyses, we partitioned the protein coding genes by codon **resulting** in 13 partitions thus allowing each to independently evolve under a general time **reversal** (GTR) model with a proportion of invariant sites and a gamma distribution. Four **Metropolis-Coupled** Markov chain Monte Carlo searches (1 cold, 3 heated) were **performed** twice for 20×10^6 generations each with sampling every 100th iteration. **Approach** to stationarity (“burn-in”) of each search was determined with the graphical **interface** of Tracer v. 1.4 (Rambaut and Drummond 2007) (graph not shown). All **parameters** reached stability within 2,000,000 generations and parameters between runs **did** not vary. Bayesian posterior probabilities were calculated by a majority-rule **consensus** of those trees after the burn-in (for both runs, 180,000 trees).

In order to assess the contribution of support of each gene to the total support of the tree, the dependency of partitioned Bremer support (PBS) and nodal distance (the branch length from a given node to the tip of the tree) were tested for each gene (Baker et al. 1998; Cognato and Vogler 2001). In PAUP*, maximum likelihood was used to fit branch lengths to a molecular clock in order to scale branch lengths throughout the most parsimonious tree found in analysis 1 (Table 1.3). Maximum likelihood estimations were performed using the following settings: general time-reversible model, base frequencies determined empirically, proportion of invariable sites estimated, among-site rate variation approximated to a gamma distribution with 4 rate categories and shape parameter = 0.5, and molecular clock enforced. Linear regression analyses were then performed on the nodal distance versus partitioned Bremer support for each gene using PopTools (Hood 2008).

Intraspecific distances using Jukes-Cantor nucleotide substitution model were calculated for each data partition in PAUP* for all taxa with more than one individual sequenced (*X. compactus*, *X. crassiusculus*, *X. germanus*, *X. morigerus*, and *Xyleborus roundicollis*). Distances for specimens of each of these species were also calculated with respect to *Xyleborus pelliculosus* as a means of comparing intra- and interspecific distances. The presence of pseudogenes can affect analyses of genetic distance if they result in the comparison of non-homologous gene copies (Song et al. 2008). For this reason, the presence of COI pseudogenes was ruled out using several methods. First, sequence chromatograms were checked for the presence of double peaks. The presence of double peaks would indicate the possible amplification of pseudogenes. Next, the COI sequences were translated into amino acids using the invertebrate mitochondrial genetic

code in the software Mesquite (Maddison and Maddison 2006) and checking for stop codons in the sequences. The presence of stop codons throughout the amino acid sequence would indicate that it has been translated from a non-functioning gene copy. Lastly, nucleotide substitution rates were calculated for each codon position. In functioning gene copies, there should be a strong substitution rate bias in the third codon position, whereas this phenomenon may not be observed in non-functioning pseudogene copies.

RESULTS

All analyses recovered a polyphyletic *Xylosandrus* (Table 1.3, Figs. 1.1 – 1.7). The varied placement of the “*Anisandrus*” and “*Cnestus*” clades, along with the placement of several *Xylosandrus* species within these clades, was responsible for rendering the genus polyphyletic. The phylogenetic placement of “*Anisandrus*” and “*Cnestus*” changed, depending on the parameters of the analysis performed, and the various placements were usually weakly supported (e.g. $\leq 50\%$ bootstrap support). The uncertain position of these clades made it impossible to determine the phylogenetic relationships among *Xylosandrus*, *Anisandrus*, and *Cnestus* within the context of this study. While the phylogenetic position of these clades was weakly supported, the placement of several species of *Xylosandrus* within the “*Anisandrus*” and “*Cnestus*” clades had very strong support (e.g. 100% bootstrap support).

Homoplasy as measured by Consistency Indices (CI) and Retention Indices (RI) indicated that homoplasy was the lowest for 28S of all the data partitions (Table 1.4). However, CAD, ArgK, and EF1- α , had similar CI's (0.450 – 0.486) and RI's (0.631 –

0.677). Homoplasy as measured by node and gene partition provided details of character congruence. Bremer supports were affected by the alignment method used and whether gaps were treated as missing data or as a 5th character in the analysis (Tables 1.5 – 1.8). Overall, 28S gave the highest Bremer support values. Static alignment using MUSCLE combined with gaps treated as missing data had a dramatic effect on 28S Bremer support values (Table 1.7). The branch support provided for the various phylogenies by ArgK was also very high (Tables 1.5 – 1.8). The support provided by CAD varied depending on the alignment method used for the 28S data. Alignments informed by secondary structure produced trees with lower CAD Bremer support values (Tables 1.5 and 1.6). However, when the alignment was produced by the software MUSCLE, the CAD Bremer support values were considerably higher (Tables 1.7 and 1.8). The comparison of PBS and nodal distances showed no significant relationship for all of the genes, except for COI, which was significant at $\alpha = 0.05$ ($r = 0.1170$, $P = 0.0307$) (Figs. 1.8). The COI data exhibited stronger support for shallower nodes. The phylogenetic information obtained from the majority of the genes (EF1- α , 28S, ArgK, CAD) occurs throughout the phylogeny, regardless of branch length.

Intra- and interspecific distances were expressed as the proportion of sites differing between sequences, with interspecific distances given as the average observed between species (Table 1.9). Intraspecific distances for EF-1 α , ArgK, CAD, and 28S were relatively low, ranging from 0 – 1.18% of sites differing between sequences. In comparison, the average interspecific distances observed for the five genes in the dataset ranged from 3.39 – 11.48%. Overall, sequences of COI showed high intraspecific distances, ranging from 0 – 13.16%. In comparison, the average interspecific distances

observed for COI ranged from 14.61 – 17.29%. COI sequence chromatograms were clean and without double peaks, translated COI sequences did not contain stop codons, and there was a strong nucleotide substitution rate bias observed for the third codon position. Therefore, the possibility of high COI sequence divergences being artifacts caused by the amplification of non-homologous pseudogenes was ruled out.

DISCUSSION

Phylogenetics of *Xylosandrus*

According to these data, the present classification of *Xylosandrus* contains species from three different genera: *Xylosandrus*, *Anisandrus*, and *Cnestus*. Although tree topologies differed some, depending on analysis type, alignment parameters, and treatment of gaps, the following clades were consistently recovered with high support values: “*Anisandrus*”, “*Cnestus*”, and (((*X. germanus* + *X. n. sp. Borneo*) *X. morigerus*, ~~*X. compactus*~~) (Table 1.3). Membership within these clades is also consistent with morphological characters that separate other xyleborine genera from *Xylosandrus sensu stricto*, such as widely separated procoxae (see Chapter 2). Three additional clades were recovered by multiple analyses with varying levels of support, but were not consistently present on all of the tree topologies: “*Cnestus*” + *X. crassiusculus*, *X. n. sp. PNG* + *X. monteithi*, *X. mancus* + *X. discolor* (Table 1.3).

“*Anisandrus*” Clade

The “*Anisandrus*” clade consists of four species of *Anisandrus* (*A. dispar*, *A. hirtus*, *A. obesus*, and *A. sayi*) along with two species currently classified as *Xylosandrus* (*X. ursa* and *X. ursinus*). This clade was recovered by all phylogenetic analyses with high support values (Table 1.3, Figs. 1.1 – 1.7). Bootstrap support for the “*Anisandrus*” clade was 100% in the four analyses for which bootstrap support was calculated. Likewise, the “*Anisandrus*” clade was recovered by both Bayesian analyses with a posterior probability of 1.00. Bremer supports for this clade ranged from 22 to 67.

The genus *Anisandrus* was recently resurrected in a phylogenetic study of generic taxonomic characters in the Xyleborina (Hulcr et al. 2007). Morphological characters distinguishing *Anisandrus* from *Xylosandrus* include contiguous procoxae and lateral protibial margins with 7 – 8 socketed teeth. In *Xylosandrus sensu stricto* the procoxae are widely separated and the lateral protibial margins bear 4 – 5 socketed teeth (see Chapter 2). The two *Xylosandrus* species included in the “*Anisandrus*” clade are morphologically consistent with *Anisandrus*. This clade is also supported by a molecular synapomorphy in 28S in the form of a 9 – 50 base pair insertion comprised almost exclusively of T’s and C’s.

“*Cnestus*” Clade

The “*Cnestus*” clade consists of two species of *Cnestus* (*C. bimaculatus* and *C. pseudosuturalis*) along with three species currently classified as *Xylosandrus* (*X. ater*, *X. improcerus*, and *X. mutilatus*). This clade was also recovered by all phylogenetic analyses with high support values (Table 1.3, Figs. 1.1 – 1.7). Bootstrap support for the “*Cnestus*” clade was 100% in the four analyses for which bootstrap support was calculated. Likewise, the clade was recovered by both Bayesian analyses with a posterior

probability of 100. Bremer supports for the “*Cnestus*” clade were relatively high, ranging from 53 – 120.

Dole and Beaver (in press) recognized the incorrect placement of *Cnestus* species within *Xylosandrus* and made tentative steps toward correcting these taxonomic errors by transferring two species from *Xylosandrus* to *Cnestus* in their review of the Australian species of *Xylosandrus*. Morphological characters support the placement of the three *Xylosandrus* species within the “*Cnestus*” clade. Characters distinguishing *Cnestus* from *Xylosandrus sensu stricto* include subcontiguous procoxae and a four segmented antennal funicle. In *Xylosandrus sensu stricto* the antennal funicle is always five segmented. Additionally, in *Cnestus* the anterior margin of the pronotum bears four or fewer asperities, with a coarse pair medially, and the pronotum is often produced anteriorly. In *Xylosandrus sensu stricto* the anterior margin of the pronotum bears six or more asperities of approximately equal size and is never produced anteriorly (see Chapter 2). The two *Xylosandrus* species placed in the “*Cnestus*” clade are morphologically consistent with *Cnestus*.

“*Xylosandrus sensu stricto*” Clade

The clade (((*X. germanus* + *X. n. sp.* Borneo) *X. morigerus*) *X. compactus*) was also consistently recovered by all analyses with high support values (Table 1.3, Figs. 1.1 — 1.7). Given that it contains *X. morigerus*, the type species of *Xylosandrus*, this clade is the highest supported grouping of species belonging to *Xylosandrus sensu stricto* resolved by these data. Bootstrap support for this clade was 100% in all analyses for which bootstrap support was calculated. Likewise, this *Xylosandrus sensu stricto* clade

was recovered by both Bayesian analyses with a posterior probability of 100. Bremer supports for this clade ranged from 21 – 28.

The four species included in the *Xylosandrus sensu stricto* clade are all morphologically consistent with the strict definition of the genus. This clade also contains three economically important species of *Xylosandrus*: *X. compactus*, *X. germanus*, and *X. morigerus*.

Xylosandrus sensu lato

Several *Xylosandrus* species included in this analysis varied in their phylogenetic placement: *X. crassiusculus*, *X. discolor*, *X. mancus*, *X. monteithi*, *X. queenslandi*, and *X. n. sp.* Papua New Guinea. These species did not form a larger monophyletic *Xylosandrus* clade along with the *Xylosandrus sensu stricto* clade. However, none of the various placements of these species were supported by the phylogenetic analyses. Despite their unresolved positions in the molecular phylogeny, the placement of these species in *Xylosandrus* may be correct, since their morphologies are consistent with the defining characters of *Xylosandrus sensu stricto*. A phylogenetic analysis of morphological data will be necessary to further test the placement of these species within the genus. In addition, *Xyleborus rotundicollis* was included in this analysis because its morphology is consistent with that of *Xylosandrus* and not *Xyleborus*. This species was never recovered in a clade with other *Xyleborus* species and its possible transfer into *Xylosandrus* should be examined within the context of a morphological study of the genus.

Contributions of Data Partitions

Commonly used genes, such as 28S, COI, and EF-1 α , demonstrated similar phylogenetic utility as compared with other scolytine studies (Normark et al. 1999; Cognato and Sperling 2000; Jordal et al. 2000; Cognato and Vogler 2001; Farrell et al. 2001; Jordal 2002; Jordal and Hewitt 2004; Cognato et al. 2005; Cognato and Sun 2007; Jordal 2007; Jordal et al. 2008). However, all genes included in this analysis, except COI, showed no significant correlation between nodal distance and PBS, indicating that they had utility for resolving multiple levels of the phylogeny (Figs. 1.8). Typically, the ribosomal-encoding gene 28S has been shown to resolve relationships within tribes of Scolytinae, but offers little phylogenetic signal for deeper nodes (Jordal et al. 2008). Furthermore, alignment guided by secondary structure increases the phylogenetic utility of 28S (Jordal 2007; Jordal et al. 2008). Here, we found no significant correlation between nodal distance and PBS for 28S, but these results are not unexpected, given that the relationships being tested were all below the tribal level. Mitochondrial genes, such as COI, typically do not offer much signal for deeper divergences and offer better resolution for shallower, species-level nodes (Normark et al. 1999; Cognato and Sperling 2000; Cognato and Vogler 2001; Farrell et al. 2001; Jordal 2002; Jordal and Hewitt 2004; Cognato et al. 2005; Cognato and Sun 2007; Jordal 2007). For COI, there was a significant correlation between nodal distance and PBS, with higher support for shallower nodes, as is predicted for mitochondrial genes (Fig. 1.8). Interestingly, this significance was largely due to the inclusion of sequences from multiple specimens of several species. With the removal of the data points representing *X. crassiusculus*, *X. germanus*, and *X. morigerus* the regression analysis found no significant relationship between nodal distance and PBS. Nuclear genes, such as EF-1 α , CAD and ArgK, are more slowly

evolving and have demonstrated phylogenetic utility across several levels of divergence (Normark et al. 1999; Jordal et al. 2000; Cognato and Vogler 2001; Farrell et al. 2001; Jordal and Hewitt 2004; Jordal 2007; Wild and Maddison 2008). In our analyses, both CAD and ArgK showed phylogenetic utility across varying nodal distances (Figs. 1.8). Although the genes used herein were chosen for their complementary phylogenetic signals, they did not resolve the phylogeny of *Xylosandrus* and related genera. The unavailability of the majority of *Xylosandrus* species for DNA sequencing may have contributed to the lack of phylogenetic resolution. It is difficult to untangle whether the genes or lack of taxa contributed to the unresolved phylogeny. However, the addition of both could help to remedy this situation (Rokas and Carroll 2005; Edwards et al. 2007; Wild and Maddison 2008).

Genetic Divergence

The results of the comparisons of intra- and interspecific distances for the data partitions provided a few interesting findings (Table 1.9). *Xylosandrus crassiusculus* is the most widespread species of *Xylosandrus*, with an almost circumtropical distribution. Specimens of *X. crassiusculus* from Madagascar and Thailand showed very high COI sequence divergence from specimens collected in North America (10.09 – 10.94%). Similarly, *X. crassiusculus* specimens from Madagascar and Thailand showed a relatively high level of COI sequence divergence (4.44%). The intraspecific divergences of these specimens observed for the other four genes were similar to those observed in other species. The high intraspecific divergences found for COI were consistent with the findings of other studies of the gene in the Scolytinae (Cognato and Sun 2007; Menard

and Cognato 2007). For instance, COI sequence divergences observed for *Ips* DeGeer species range from 0-10.0%, however, cryptic species were suspected in several cases where COI sequence divergences were greater than 10%.

There was no difference observed for the 28S data between *X. crassiusculus* specimens from Madagascar and Thailand. Similarly, specimens from introduced populations in Maryland and North Carolina showed zero sequence divergence for all five genes. The biogeographic history of *X. crassiusculus* is not entirely known and the population genetics of the species is presently being investigated (Cognato et al. unpublished data). However, these findings are consistent with the genetic bottleneck that can occur with exotic species introductions, especially in the case of species with haplodiploidy and extreme inbreeding, such as *Xylosandrus*.

High levels of intraspecific COI sequence divergence were observed in all other species, except for *Xylosandrus germanus*. However, the findings for *X. germanus* were consistent with those for *X. crassiusculus*. The two specimens of *X. germanus* sampled were from introduced populations in North America (Maryland and Michigan) and these showed zero sequence divergence for all genes, except for COI, which had a divergence of 0.34%. The COI divergences for *X. compactus* and *X. morigerus* ranged from 7.35 – 9.74 %. Interestingly, the highest level of COI sequence divergence was observed in the two populations of *Xyleborus rotundicollis* sampled from Papua New Guinea (13.16%). The possibility that this divergence is an artifact of the comparison of non-homologous gene copies due to the presence of pseudogenes was tested and no evidence of pseudogenes was found. These specimens were both collected from the highlands of Papua New Guinea, where a continuous size gradient has been observed in *X.*

rotundicollis. The two specimens sequenced here represent the two extremes of the size range. Further sequencing and comparisons of specimens across the entire size range would be necessary to establish whether *X. rotundicollis* represents a single species or two morphologically similar species with overlapping ranges.

As mentioned in the case of *X. rotundicollis* above, DNA sequences can be used to help resolve species boundaries in cases where morphology provides little taxonomic utility (Simon et al. 1994; Cognato and Sperling 2000; Scheffer and Lewis 2001; Pons et al. 2006; Vogler and Monaghan 2006). However, the findings of this study add to the growing body of evidence suggesting that the implementation of DNA taxonomy must be carefully tailored to suit the genetic characteristics of each taxonomic group (DeSalle et al. 2005; Rubinoff 2006; Cognato 2007; Cognato and Sun 2007). Some authors have proposed using a standard percentage sequence divergence as a means of differentiating species (Hebert et al. 2003, 2004). However, inter- and intraspecific divergences can vary dramatically, depending on the taxa. Furthermore, inter- and intraspecific distances have been found to overlap in many groups of insects (Cognato 2006). Intraspecific divergences in the Scolytinae have been observed to range between 0.04 – 13.16% (Cognato 2006; Cognato and Sun 2007; Menard and Cognato 2007, this study). A haplodiploidy system of inheritance and inbreeding, as is seen in the Xyleborina, could have a dramatic effect on the divergence observed in these beetles. The effective population size of haplodiploid organisms is at least twice that of diploid organisms (Kirkendall 1993), thus new or rare haplotypes can accumulate faster. In addition, the potential for introduced populations founded by a single female could lead to striking patterns of divergence, as may be the case with species such as *X. crassiusculus*.

Therefore, any use of DNA taxonomy in xyleborines needs to take into consideration the effects of haplodiploidy and inbreeding on genetic divergence and haplotype frequency.

Taxonomic Implications and Future Directions

The molecular characters utilized by this study have agreed with previously cited morphological evidence that *Xylosandrus* is polyphyletic and that the current classification of the genus contains species belonging to several genera (Dole and Beaver in press). However, the taxon sample available for molecular work represents only a fraction of the 54 species currently included in *Xylosandrus*. Due to the unavailability of many species for molecular sequencing, morphological data will be the only way to assess the proper generic placement of the majority of *Xylosandrus* species. For instance, several species of *Xylosandrus* have morphologies which suggest that they should be transferred to *Amasa* (see Chapter 2), but these species are so rarely collected that none were available for DNA sequencing. Furthermore, the economic importance of *Xylosandrus* requires the development of a morphology-based classification with clear diagnostic characters and a key to the worldwide species. Such a revision is currently in progress and will include the five gene data set used here in combination with morphology to provide a more complete phylogenetic classification of *Xylosandrus* (see Chapter 2).

Species	Collection locality, date and collector	Host
<i>Amasa bicostatus</i> (Sampson)	Borneo, Danum Valley, June 2006, Huler et al. Coll.	
<i>Amasa resectus</i> (Eggers)	Papua New Guinea, Wannang, March 2006, Huler et al. Coll.	
<i>Amasa schlichti</i> (Stebbing)	Thailand, Kanchanburi Prov., Thong Pha Phoom District, Phu Yae Subdistrict, el. 400, N14.944° E98.674° Cognato, Gillogly & Harlin Coll.	
<i>Amasa striatotruncatus</i> (Schedl)	Papua New Guinea, Wannang, March 2006, Huler et al. Coll.	
<i>Amasa versicolor</i> (Sampson)	Borneo, Danum Valley, June 2006, Huler et al. Coll.	
<i>Amasa</i> n. sp. 1	Madagascar, Réserve Spéciale de Bemarivo, 23.8 km 223° SW Besalamy, 16°55'30"S 044°22'06"E, 19-23 Nov 2002, EF26 at light, B. Fisher	
<i>Amasa</i> n. sp. 301	Papua New Guinea, Wannang, March 2006, Huler et al. Coll.	
<i>Amasa</i> n. sp. 349	Papua New Guinea, Mu, March 2006, Huler et al. Coll.	
<i>Anisandrus dispar</i> (Fabricius)	Russia: St. Petersburg, Pushkin, June 5, 2004, M. Mandelsham Coll.	
<i>Anisandrus hirtus</i> (Hagedorn)	Thailand, Doi Pui, October 2004, S. Sonthichai Coll.	
<i>Anisandrus obesus</i> (LeConte)	USA: OH, Hocking Co., Logan, Ethanol trap, May 1, 2004, R. Rabaglia Coll.	
<i>Anisandrus sayi</i> (Hopkins)	USA: MD, Anne Arundel Co., Annapolis, Ethanol trap, April 22, 2005, R. Rabaglia Coll.	
<i>Cnestus bimaculatus</i> (Eggers)	Papua New Guinea, Madang Prov., Ohu Village, 2004, Huler et al. Coll.	<i>Ficus nodosa</i> (twig)
<i>Cnestus pseudosuturalis</i> (Schedl)	Papua New Guinea, Ohu, March 2006, Huler et al. Coll.	<i>Litsea</i> Lam.
<i>Coccorypes dactyliporda</i> (Fabricius)	USA: Hawaii Oahu, Manoa Falls Trail, N 21.337844, W 157.803558, Ethanol trap August 7, 2007, D. Rubinoff and M. San Jose Coll.	
<i>Coccorypes longior</i> (Eggers)	Papua New Guinea, Madang Prov., Ohu Village, 2004, Huler et al. Coll.	

Table 1.1 (cont. on following pages): Specimens sequenced, collecting data, and hosts.

Species	Collection locality, date and collector	Host
<i>Xyleborus affinis</i> Eichhoff	Costa Rica, La Selva research station, April 2005, Hulcr Coll. USA: MD, Anne Arundel Co. Annapolis. Ethanol trap. April 22, 2005. R. Rabaglia Coll.	
<i>Xyleborus californicus</i> Wood	USA: MD, Anne Arundel Co. Annapolis. Ethanol trap. April 15, 2005. R. Rabaglia Coll.	
<i>Xyleborus pelliculosus</i> Eichhoff		
<i>Xyleborus rotundicollis</i> Browne	Papua New Guinea, Mu, March 2006, Hulcr et al. Coll.	
<i>Xyleborus rotundicollis</i>	Papua New Guinea, Mu, March 2006, Hulcr et al. Coll.	
<i>Xylosandrus ater</i> (Eggers)	Borneo, Danum Valley, June 2006, Hulcr et al. Coll.	<i>Mallotus</i> Lour.
<i>Xylosandrus compactus</i> (Eichhoff)		
<i>Xylosandrus compactus</i>	Brazil: Espírito Santo Prov. September 26, 2006. P. Sergio Voppi Coll.	
<i>Xylosandrus crassiusculus</i> (Motschulsky)	Ghana: Ankasa. 2 July 2005. J. Hulcr Coll.	
<i>Xylosandrus crassiusculus</i>	Thailand: Chiangmai Prov. Doi Inthanon. July 28, 2004. A.I. Cognato Coll. Madagascar: Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo. 15°17'18"S, 049°32'54"E. March 17-21, 2003. B. Fisher et al. Coll.	
<i>Xylosandrus crassiusculus</i>	USA: MD, Anne Arundel Co. Annapolis. Reared from wood. July 11, 2003. P. Merthel Coll.	
<i>Xylosandrus crassiusculus</i>	USA: North Carolina: Henderson Co. August 8, 2004. P. Merthal Coll.	
<i>Xylosandrus discolor</i> (Blandford)	Thailand: Chiangmai Prov., Mae Rim, June 12, 2005. Dole and Beaver Coll.	Mango

Table 1.1 (cont.): Specimens sequenced, collecting data, and hosts.

Species	Collection locality, date and collector	Host
<i>Xylosandrus germanus</i> (Blandford)	USA: MD, Anne Arundel Co. Annapolis. Ethanol trap. April 22, 2005. R. Rabaglia Coll.	
<i>Xylosandrus germanus</i> <i>Xylosandrus improcerus</i> (Sampson)	USA: Michigan: Ingham Co. East Lansing. Ethanol trap. May 7, 2007 A.I. Cognato Coll.	
<i>Xylosandrus mancus</i> (Blandford)	Borneo, Danum Valley, June 2006, Hulcr et al. Coll.	Burseraeae sp. (twig)
<i>Xylosandrus monteithi</i> Dole & Beaver	Thailand: Chumphon Prov., Khao Sok NP, March 24, 2006 Dole et al. Coll.	Rambutan branch
<i>Xylosandrus morigerus</i> (Blandford)	Australia, Queensland, Palmerston, Henrietta Cr., 550 m, Watchua Falls, 24.I.2000, B. Jordal Coll.	
<i>Xylosandrus morigerus</i> <i>Xylosandrus morigerus</i> <i>Xylosandrus mutilatus</i> (Blandford)	Papua New Guinea, Madang, March 2006, Hulcr et al. Coll.	
<i>Xylosandrus queenslandi</i> Dole & Beaver	Ecuador, Napo Prov., Res. Ethnica Waorani, 1 km S. Onkone Gare Camp, Trans. Ent., 00°39'10"S, 076°26'W, January 2006, T. L. Erwin et al. Coll.	
<i>Xylosandrus ursa</i> (Eggers)	Singapore, Bukit Timah, 50 m, 25-27 Oct 1998, B. H. Jordal Coll.	
<i>Xylosandrus ursinus</i> (Hagedorn)	USA: Mississippi: Oktibbeha Co. 3 mi. W. of Adaton. April 23-26, 2004 T.L. Schiefer Coll.	Leguminosae sp. (tree)
<i>Xylosandrus n. sp.</i>	Australia, Queensland, Bunya Mountain NP, 1,100 m, 19.i.2000, B. Jordal & A. Sequeria Coll.	
<i>Xylosandrus n. sp.</i>	Papua New Guinea, Wannang, March 2006, Hulcr et al. Coll.	
	Thailand, Chiangmai Prov., Pong Yaeng, 900m a.s.l. July 2005 Dole and Hulcr Coll.	
	Papua New Guinea, Mu, March 2006, Hulcr et al. Coll.	
	Borneo, Danum Valley, June 2006, Hulcr et al. Coll.	

Table 1.1 (cont.): Specimens sequenced, collecting data, and hosts.

Gene	Primer	Primer Sequence	Annealing Temp	Ampicon size	Reference
COI	LCO 1490	5'-GGTCAACAAATCATAAAGATATTGG-3'	50 C	650 bp	Hebert et al. 2003
	HCO 2198	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	50 C	650 bp	Hebert et al. 2003
28S	D2F1	5'- ACTGTTGGCGACGATGTTCT-3'	50 or 55 C	500 -570 bp	Jordal et al. 2008
	D3R2	5'- TCCTTCGCCCCCTATACCC-3'	50 or 55 C	500 -570 bp	Jordal et al. 2008
	3665	5'-AGAGAGAGTTCAAGAGTACGTG-3'	50 or 55 C	600-750 bp	Jordal et al. 2008
	4048	5'-TTGGTCCGTGTTTCAAGACGGG-3'	50 or 55 C	600-750 bp	Jordal et al. 2008
EF-1 α	efs149	5'-ATCGAGAAAGTTCGAGAAGGAGGCYCARGAAATGGG-3'	48 C	585 bp	Normark et al. 1999
	efa754	5'-CCACCAATTTTGTAGACATC-3'	48 C	585 bp	Normark et al. 1999
	eflafor1	5'- TAGTAAACCATCATTTGATGCTYCC-3'	50 or 55 C	500 bp	This study
	eflarev1	5'-CCTTCTTTACGTTCAATGGACCATCC-3'	50 or 55 C	500 bp	This study
ArgK	forB2	5'-GAYTCCGGWATYGGWATCTAYGCTCC-3'	58 C	620 bp	This study
	revB2	5'-GTATGYTCMCCRCGRGTACCACG-3'	58 C	620 bp	This study
CAD	apCADfor4	5'-TGGAARGARGTGBGARTACGARGTGGTYCG-3'	58 C	740 bp	Danforth et al. 2006
	apCADrev1mod	5'-GCCATYRCYTCBCCVACRCTYTTTCAT-3'	58 C	740 bp	Danforth et al. 2006

Table 1.2: PCR primers and annealing temperatures used for the amplification of gene sequences.

Analysis type	1	2	3	4	5	6	7
Number of most parsimonious trees	1	3	1	2	2	NA	NA
Clades							
"Anisandrus"	100/32	100/47	100/22	100/53	N/A/67	100	100
"Cnestus"	100/60	100/68	100/59	100/53	N/A/120	100	100
"Cnestus" clade + <i>X. crassiusculus</i>	<50/5	98/20	N/A	N/A	N/A	100	100
"Anisandrus" + "Cnestus"	N/A	N/A	<50/1	N/A	N/A	N/A	N/A
<i>X. n. sp. PNG</i> + <i>X. monteithi</i>	97/21	100/26	N/A	60/7	N/A	100	N/A
((<i>X. germanus</i> + <i>X. n. sp. Borneo</i>) <i>X. morigerus</i>)							
<i>X. compactus</i>	100/24	100/24	100/21	100/22	N/A/28	100	100
<i>X. mancus</i> + <i>X. discolor</i>	68/9	<50/18	65	<50/4	N/A/9	100	100
((<i>X. mancus</i> + <i>X. discolor</i>) <i>X. crassiusculus</i>)	N/A	N/A	<50/2	N/A	N/A	N/A	N/A
((<i>X. mancus</i> + <i>X. discolor</i>) "Cnestus")	N/A	N/A	N/A	<50/4	N/A	N/A	N/A
<i>Xylosandrus</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1. Parisomony/static alignment/secondary structure/gaps missing; 2. Parisomony/static alignment/secondary structure/gaps 5th character							
3. Parisomony/static alignment/MUSCLE/gaps missing; 4. Parisomony/static alignment/MUSCLE/gaps 5th character							
5. Parisomony/dynamic alignment/2 gap cost; 6. Bayesian/static alignment/secondary structure/ codons + 28s partitions;							
7. Bayesian/static alignment/MUSCLE/codons + 28s partitions							

Table 1.3: Support found for selected clades found by different analyses of the five gene dataset. Numbers represent bootstrap/Bremer supports or posterior probabilities for Bayesian analyses. NA = not applicable or not found in the resulting tree(s).

	Matrix Size	Variable Sites	Informative Sites	Gaps	Contribution to Tree Length	Consistency Index (CI)	Retention Index (RI)	Mean Branch Length
EF-1α	555	163	116	N/A	414	0.486	0.631	5.494
COI	585	257	237	N/A	2180	0.205	0.339	27.542
ArgK	594	199	165	N/A	613	0.476	0.677	8.012
CAD	714	232	184	N/A	664	0.45	0.64	8.59
28S	1048	318	236	473	779	0.614	0.769	9.964
Combined	3496	1169	938	473	4650	0.369	0.549	59.602

Table 1.4: Contribution of data partitions to the character matrix and to the resolution of the most parsimonious tree found in analysis 1.

	Gene Partion					Total
	EF-1 α	COI	ArgK	CAD	28S	
node						
1	7.75	-0.50	9.25	13.25	9.25	39.00
2	5.75	-1.25	13.00	8.13	10.38	36.00
3	4.00	-3.00	0.67	-2.00	1.33	1.00
4	7.40	12.10	26.40	13.30	0.80	60.00
5	0.00	14.00	1.00	0.00	1.00	16.00
6	3.80	24.00	3.60	1.40	1.20	34.00
7	14.00	7.67	10.67	12.00	18.67	63.00
8	0.00	3.67	0.67	0.00	0.67	5.00
9	-4.00	7.50	2.00	2.00	1.50	9.00
10	3.60	-2.00	3.40	-4.40	2.40	3.00
11	2.00	-0.50	0.17	0.00	0.33	2.00
12	2.00	-0.50	3.50	1.00	8.00	14.00
13	3.00	0.00	6.33	5.33	13.33	28.00
14	2.00	-1.57	0.43	-0.57	2.71	3.00
15	3.25	-2.25	7.75	7.25	16.00	32.00
16	3.60	-2.00	3.40	-4.40	2.40	3.00
17	7.00	-10.33	0.00	-1.00	25.33	21.00
18	-1.00	-1.00	-1.00	-1.00	5.00	1.00
19	2.33	2.67	3.67	-1.67	18.00	25.00
20	2.82	-3.27	1.55	-1.73	3.64	3.00
21	3.80	7.40	6.80	-1.00	7.00	24.00
22	1.71	3.79	-0.07	1.00	1.57	8.00
23	-0.50	17.00	5.50	-0.50	5.50	27.00
24	6.77	33.46	3.92	3.85	8.00	56.00
25	1.67	-1.33	2.33	2.00	4.33	9.00
26	-0.50	-3.00	1.50	3.50	2.50	4.00
27	6.00	-3.00	3.00	11.00	3.00	20.00
28	3.09	-3.73	1.45	-1.45	3.64	3.00
29	9.05	-0.20	1.25	-0.30	-5.80	4.00
30	1.20	3.80	-0.60	-1.20	-0.20	3.00
31	0.00	1.00	-3.00	-1.00	5.00	2.00
32	0.00	-3.00	0.00	-1.00	11.00	7.00
33	0.00	6.00	0.00	0.00	9.00	15.00
34	2.00	0.00	0.00	-1.00	0.00	1.00
35	0.00	-7.00	7.00	0.00	2.00	2.00
36	0.00	-1.00	19.00	0.00	6.00	24.00
37	0.00	7.00	3.00	0.00	-1.00	9.00
38	2.00	-4.00	4.00	6.00	1.00	9.00
39	0.00	3.00	0.00	0.00	0.00	3.00
40	3.00	4.00	0.00	6.00	0.00	13.00
Total	108.59	103.61	151.53	72.78	204.48	641.00

Table 1.5: Partition branch support based on tree found by phylogenetic analysis 1 (see Materials and Methods). Nodes refer to Figure 1.1.

node	Gene Partition					Total
	EF-1 α	COI	ArgK	CAD	28S	
1	1.33	2.33	6.33	16.33	8.67	35.00
2	2.33	2.33	14.33	10.33	8.67	38.00
3	1.33	-1.67	0.33	-0.67	0.67	0.00
4	11.33	11.33	30.83	13.83	0.67	68.00
5	-2.67	17.33	0.33	0.33	-0.33	15.00
6	-2.67	28.33	1.83	4.83	-0.33	32.00
7	6.33	13.33	11.33	16.33	28.67	76.00
8	0.33	5.33	4.83	7.83	1.67	20.00
9	1.33	1.33	0.33	10.33	25.67	39.00
10	-0.79	0.46	-1.04	-3.67	14.04	9.00
11	-1.27	-0.47	-1.67	-5.27	17.67	9.00
12	-0.67	-0.33	2.67	4.00	11.33	17.00
13	1.33	-0.67	6.33	3.33	36.67	47.00
14	-2.00	2.00	1.00	1.00	0.00	2.00
15	-0.67	-5.67	0.33	1.33	30.67	26.00
16	0.33	2.00	2.67	5.33	9.67	20.00
17	14.33	9.83	0.83	1.33	32.67	59.00
18	1.33	-1.67	2.33	1.33	3.67	7.00
19	4.33	4.33	9.33	-0.67	6.67	24.00
20	1.33	6.33	-0.67	-0.67	0.67	7.00
21	1.33	11.33	8.33	3.33	2.67	27.00
22	6.33	33.33	4.33	4.33	8.67	57.00
23	1.53	2.13	2.53	1.73	1.07	9.00
24	0.00	-1.00	2.00	4.00	-1.00	4.00
25	9.33	-3.33	4.50	8.17	5.33	24.00
26	2.00	-4.50	1.50	1.00	3.00	3.00
27	0.00	3.00	3.50	0.50	-2.00	5.00
28	0.33	-2.17	3.83	-0.67	8.67	10.00
29	-0.67	-0.17	0.83	-0.67	1.67	1.00
30	4.33	4.33	7.33	1.33	0.67	18.00
31	4.33	4.33	7.33	1.33	0.67	18.00
32	-0.67	-0.17	3.83	0.33	14.67	18.00
33	1.33	4.33	0.33	-0.67	29.67	35.00
34	1.33	-1.67	0.33	-0.67	0.67	0.00
35	1.33	-8.67	7.33	-0.67	2.67	2.00
36	1.33	-3.67	19.33	-0.67	6.67	23.00
37	-0.67	7.83	2.83	0.33	-1.33	9.00
38	2.33	-4.67	4.33	5.33	1.67	9.00
39	-0.67	3.83	-0.17	0.33	-0.33	3.00
40	2.33	4.83	-0.17	6.33	-0.33	13.00
Total	73.47	145.46	176.66	121.30	321.11	838.00

Table 1.6: Partition branch support based on tree found by phylogenetic analysis 2 (see Materials and Methods). Nodes refer to Figure 1.2.

node	Gene Partition					Total
	EF-1 α	COI	ArgK	CAD	28S	
1	3.00	6.00	11.00	12.00	1.00	33.00
2	6.00	7.00	13.00	12.00	3.00	41.00
3	5.33	-2.67	-1.67	-0.67	2.67	3.00
4	6.00	8.00	31.00	18.00	-4.00	59.00
5	2.00	4.50	-2.00	-0.50	0.00	4.00
6	4.00	3.00	-2.00	0.00	5.00	10.00
7	2.75	6.75	4.75	0.50	8.25	23.00
8	4.00	1.00	-5.00	-3.00	4.00	1.00
9	0.00	4.00	6.00	3.00	9.00	22.00
10	4.00	2.00	-5.50	-2.50	3.00	1.00
11	-1.00	14.00	9.00	-3.00	9.00	28.00
12	4.00	2.00	-5.50	-2.50	3.00	1.00
13	4.00	2.00	-5.50	-2.50	3.00	1.00
14	-0.67	0.33	5.00	3.33	-6.00	2.00
15	3.00	7.50	9.00	0.00	4.50	24.00
16	0.00	14.00	1.00	-1.00	-5.00	9.00
17	0.00	21.00	7.33	-0.67	-0.67	27.00
18	5.00	39.00	6.00	4.00	2.00	56.00
19	2.60	6.20	1.40	-0.60	-0.60	9.00
20	0.00	3.00	4.00	3.00	-4.00	6.00
21	7.00	2.00	2.00	10.00	0.00	21.00
22	1.33	13.67	5.67	1.67	-7.33	15.00
23	0.00	25.00	6.00	9.00	-12.00	28.00
24	11.80	11.10	13.70	15.90	12.50	65.00
25	-6.00	1.00	13.00	0.00	-2.00	6.00
26	-0.67	0.33	5.00	3.33	-6.00	2.00
27	2.00	3.50	-1.75	-1.75	-1.00	1.00
28	-0.67	0.33	5.00	3.33	-6.00	2.00
29	-0.50	-1.00	6.00	2.50	-5.00	2.00
30	0.00	10.00	-0.67	-3.33	-2.00	4.00
31	0.00	3.33	2.33	-0.67	-4.00	1.00
32	-1.00	-5.00	11.00	1.00	-2.00	4.00
33	-0.50	10.00	4.50	-1.50	2.50	15.00
34	0.00	5.00	2.00	-1.00	-5.00	1.00
35	0.00	-6.00	6.00	0.00	1.00	1.00
36	1.40	2.80	18.00	-1.60	5.40	26.00
37	0.00	7.00	3.00	0.00	0.00	10.00
38	3.40	-1.80	2.60	4.60	-0.80	8.00
39	0.00	3.00	0.00	0.00	0.00	3.00
40	3.00	4.00	0.00	6.00	0.00	13.00
Total	74.60	236.87	184.69	86.37	5.42	588.00

Table 1.7: Partition branch support based on tree found by phylogenetic analysis 3 (see Materials and Methods). Nodes refer to Figure 1.3.

	Gene Partition					Total
	EF-1 α	COI	ArgK	CAD	28S	
node						
1	-3.00	0.00	10.00	11.00	6.00	24.00
2	6.00	0.00	14.00	10.00	8.00	38.00
3	5.00	-5.00	1.00	-1.00	3.00	3.00
4	6.00	9.00	26.00	13.00	-1.00	53.00
5	-4.00	5.50	2.00	0.00	0.50	4.00
6	-4.00	5.50	2.00	0.00	0.50	4.00
7	-4.00	8.00	4.00	-4.00	10.00	14.00
8	-2.17	20.50	3.83	4.67	4.17	31.00
9	-1.00	25.00	14.00	22.00	-1.00	59.00
10	-3.00	-11.50	3.00	0.00	12.50	1.00
11	14.00	17.00	0.00	5.00	4.00	40.00
12	-2.00	-14.00	-1.00	3.00	21.00	7.00
13	-0.50	-5.00	-0.50	2.50	6.50	3.00
14	-1.50	-2.25	1.50	1.00	9.25	8.00
15	0.00	0.00	3.00	4.00	4.00	11.00
16	-3.00	-8.50	3.00	12.00	30.50	34.00
17	0.00	-2.00	1.00	0.00	8.00	7.00
18	-3.00	1.00	7.00	0.00	48.00	53.00
19	-3.00	-11.50	3.00	0.00	12.50	1.00
20	-3.00	-11.50	3.00	0.00	12.50	1.00
21	3.00	8.00	7.00	0.00	6.00	24.00
22	0.00	1.00	1.00	4.00	0.00	6.00
23	0.00	15.00	6.00	0.00	4.00	25.00
24	6.33	28.33	6.00	9.00	12.33	62.00
25	1.00	-4.00	3.00	5.00	1.00	6.00
26	0.00	-5.00	2.00	4.00	1.00	2.00
27	4.00	-7.50	5.00	8.00	12.50	22.00
28	-3.00	-11.50	3.00	0.00	12.50	1.00
29	-3.00	-11.50	3.00	0.00	12.50	1.00
30	-1.00	8.00	-1.00	0.00	0.00	6.00
31	-2.00	-5.25	1.25	-0.25	7.25	1.00
32	-3.00	-17.00	6.00	0.00	17.00	3.00
33	0.00	5.00	0.00	0.00	18.00	23.00
34	0.00	1.00	0.00	0.00	-1.00	0.00
35	0.00	-8.00	7.00	0.00	4.00	3.00
36	0.00	-2.00	19.00	0.00	9.00	26.00
37	0.00	7.00	3.00	0.00	3.00	13.00
38	2.00	-6.00	4.00	6.00	1.00	7.00
39	0.00	2.00	0.00	0.00	1.00	3.00
40	3.00	3.00	0.00	6.00	1.00	13.00
Total	1.17	20.83	175.08	124.92	321.00	643.00

Table 1.8: Partition branch support based on tree found by phylogenetic analysis 4 (see Materials and Methods). Nodes refer to Figure 1.4.

	EF-1 α	COI	ArgK	CAD	28S
<i>Xylosandrus compactus</i>					
Brazil vs. Ghana	0.0018	0.0769	0.0064	N/A	0.0061
Ave. Dist. <i>Xyleborus pelliculosus</i>	0.0961	0.1461	0.1033	0.063	0.0355
<i>Xylosandrus crassiusculus</i>					
Madagascar vs. Thailand	0.0092	0.0444	0.0026	0.0014	0
Madagascar vs. Maryland	0.0031	0.1094	0.0051	0.0084	0.0013
Madagascar vs. N. Carolina	0.0031	0.1094	0.0051	0.0084	0.0014
Maryland vs. N. Carolina	0	0	0	0	0
Maryland vs. Thailand	0.0121	0.1009	0.0098	0.007	0.0013
N. Carolina vs. Thailand	0.0118	0.1009	0.0097	0.007	0.0013
Ave Dist. <i>Xyleborus pelliculosus</i>	0.0706	0.1726	0.1104	0.0676	0.0665
<i>Xylosandrus germanus</i>					
Maryland vs. Michigan	0	0.0034	0	0	0
Ave. Dist. <i>Xyleborus pelliculosus</i>	0.0976	0.1729	0.0918	0.0728	0.0339
<i>Xylosandrus morigerus</i>					
Papua New Guinea vs. Ecuador	0.0018	0.0735	0.0042	0.007	0.004
Singapore vs. Papua New Guinea	N/A	0.0855	0.0106	N/A	0.0016
Singapore vs. Ecuador	N/A	0.0974	0.0106	N/A	0.0031
Ave. Dist. <i>Xyleborus pelliculosus</i>	0.0932	0.1573	0.0969	0.0742	0.0351
<i>Xyleborus rotundicollis</i>					
Papua New Guinea 1 vs. Papua New Guinea 2	0.0234	0.1316	N/A	N/A	0.0069
Ave. Distance <i>Xyleborus pelliculosus</i>	0.1006	0.1658	0.1148	0.0714	0.0528

Table 1.9: COI intra- and interspecific distances expressed as the proportion of sites differing between sequences, with interspecific distances given as the average observed between species.

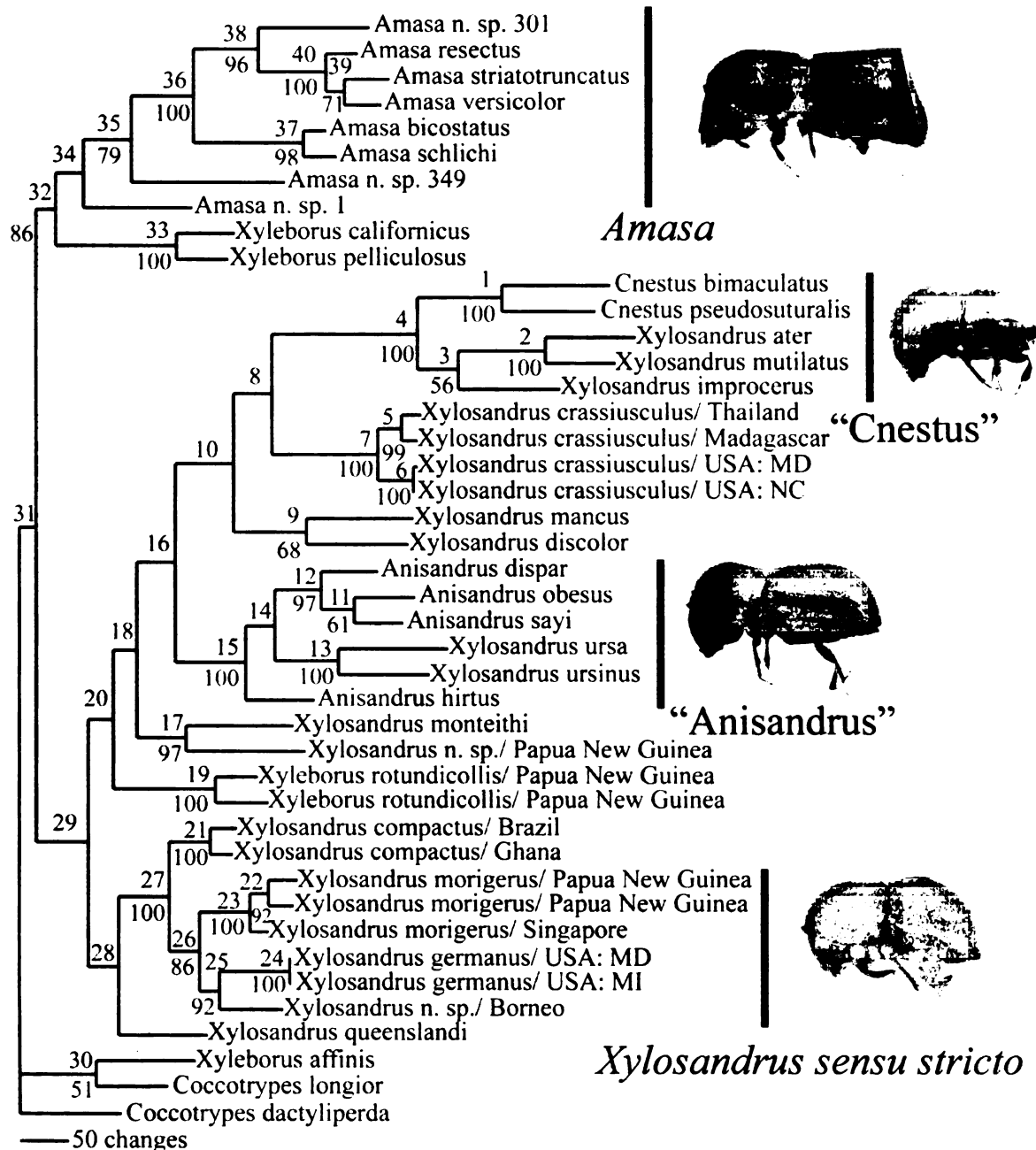


Figure 1.1: Most parsimonious tree found by parsimony analysis of data aligned using 28S secondary structure (Jordal et al. 2008), with gaps treated as missing data. Clade numbers are given above nodes. Numbers below nodes are bootstrap support values.

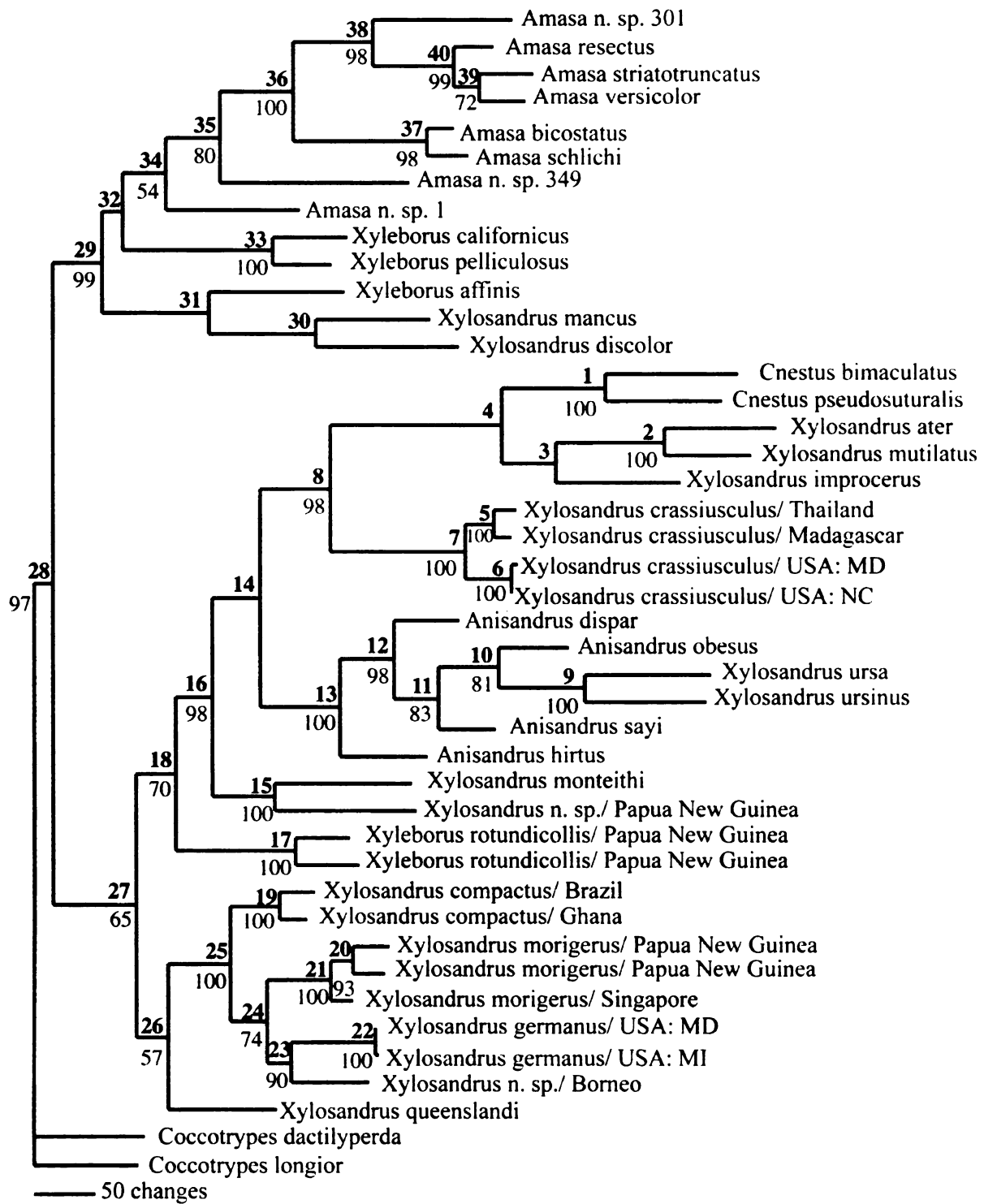


Figure 1.2: One of three most parsimonious trees found by parsimony analysis of data aligned using 28S secondary structure (Jordal et al. 2008), with gaps treated as a 5th character state. Clade numbers are given above nodes. Numbers below nodes are bootstrap support values.

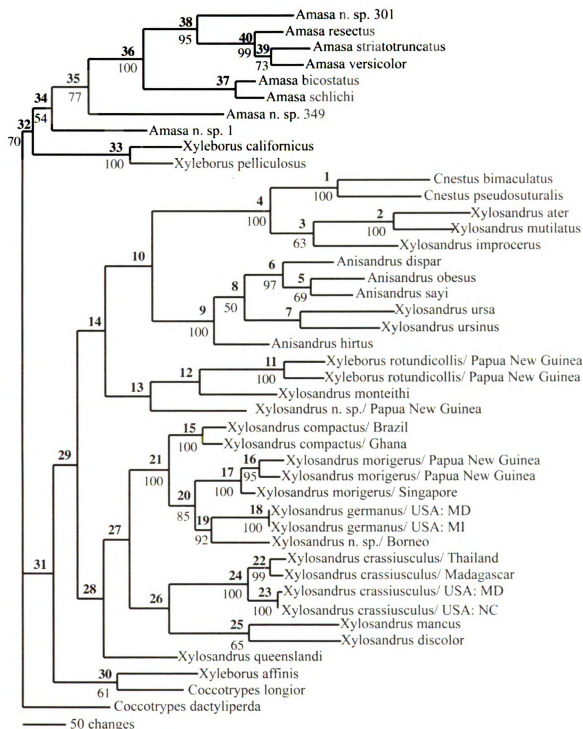


Figure 1.3: Single most parsimonious tree found by parsimony analysis of data aligned in MUSCLE, with gaps treated as missing data. Clade numbers are given above nodes. Numbers below nodes are bootstrap support values.

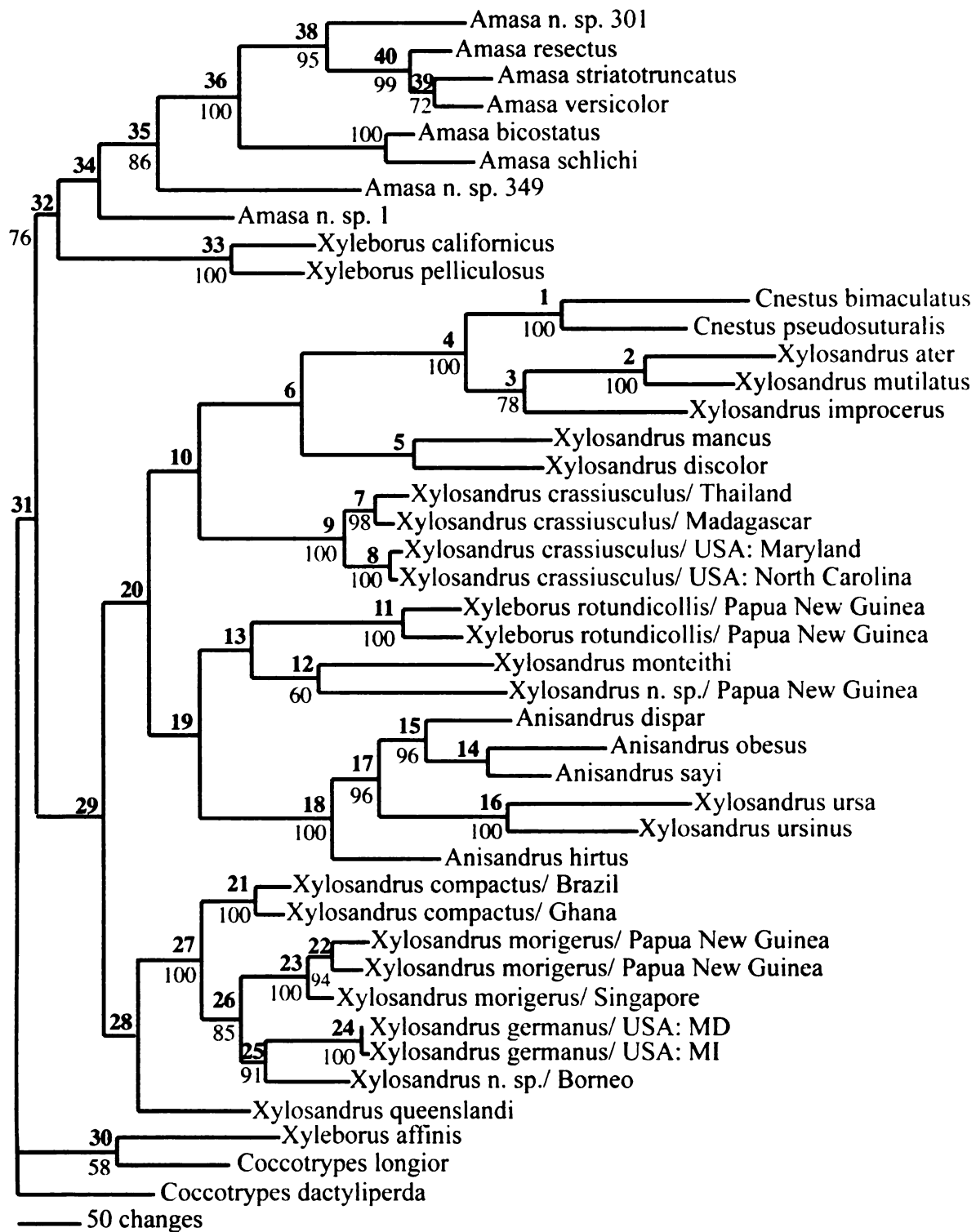


Figure 1.4: One of two most parsimonious trees found by parsimony analysis of data aligned in MUSCLE, with gaps treated as a 5th character state. Clade numbers are given above nodes. Numbers below nodes are bootstrap support values.

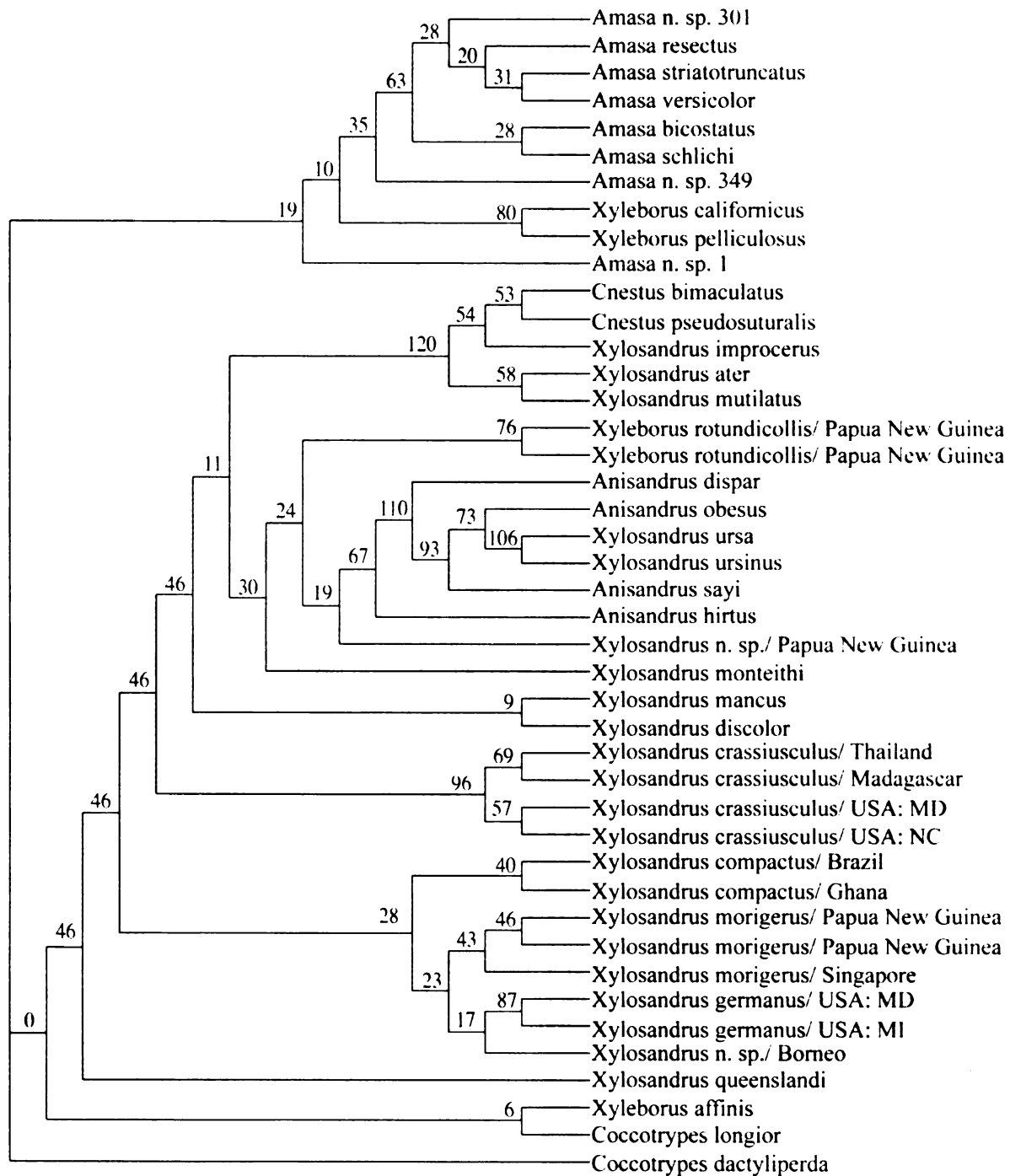


Figure 1.5: One of two post parsimonious trees found by dynamic alignment and analysis using POY, with a gap cost = 2. Numbers above nodes are Bremer support values.

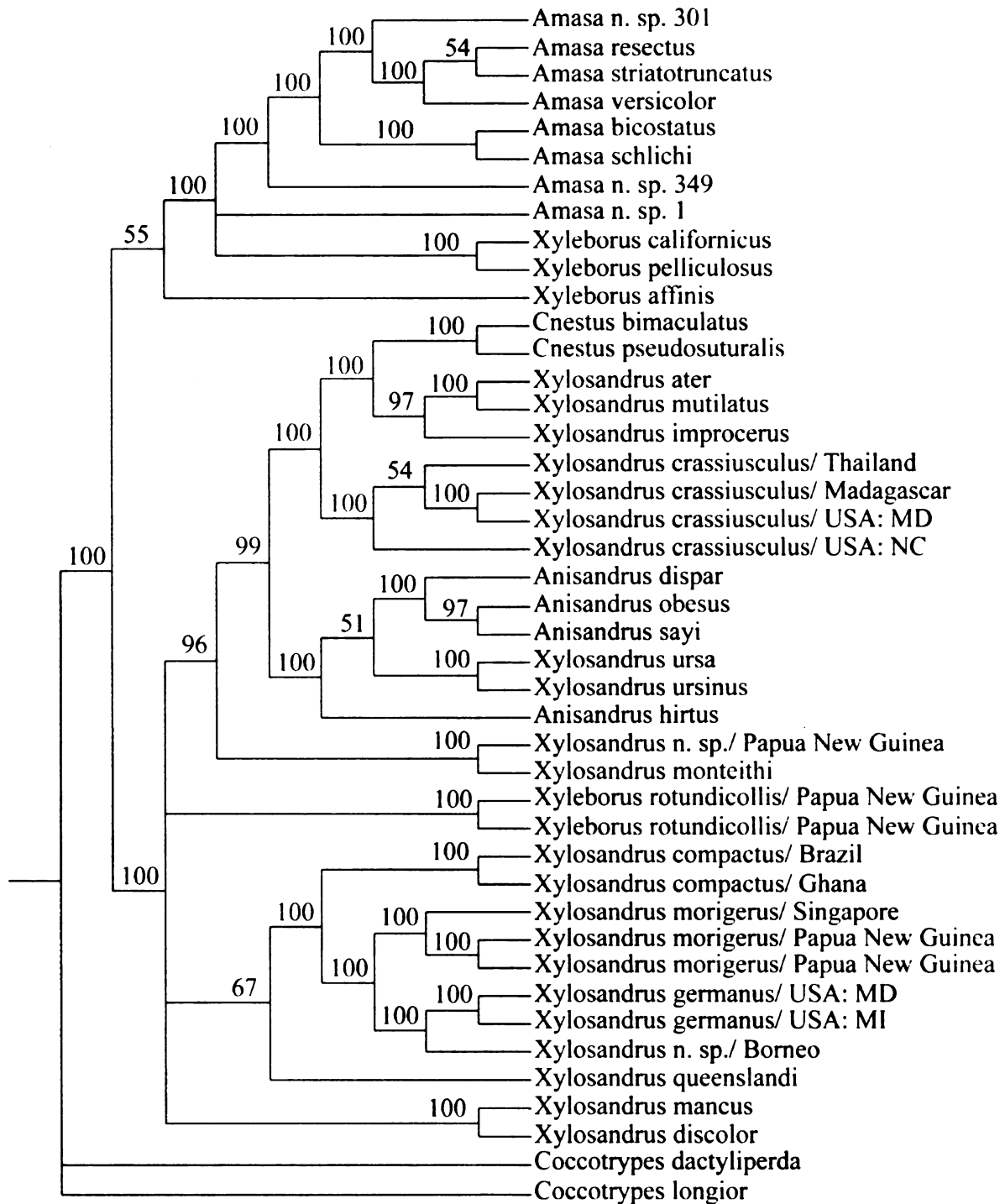


Figure 1.6: Bayesian tree found by analysis of data aligned using 28S secondary structure (Jordal et al. 2008). Numbers above nodes are Bayesian posterior probabilities.

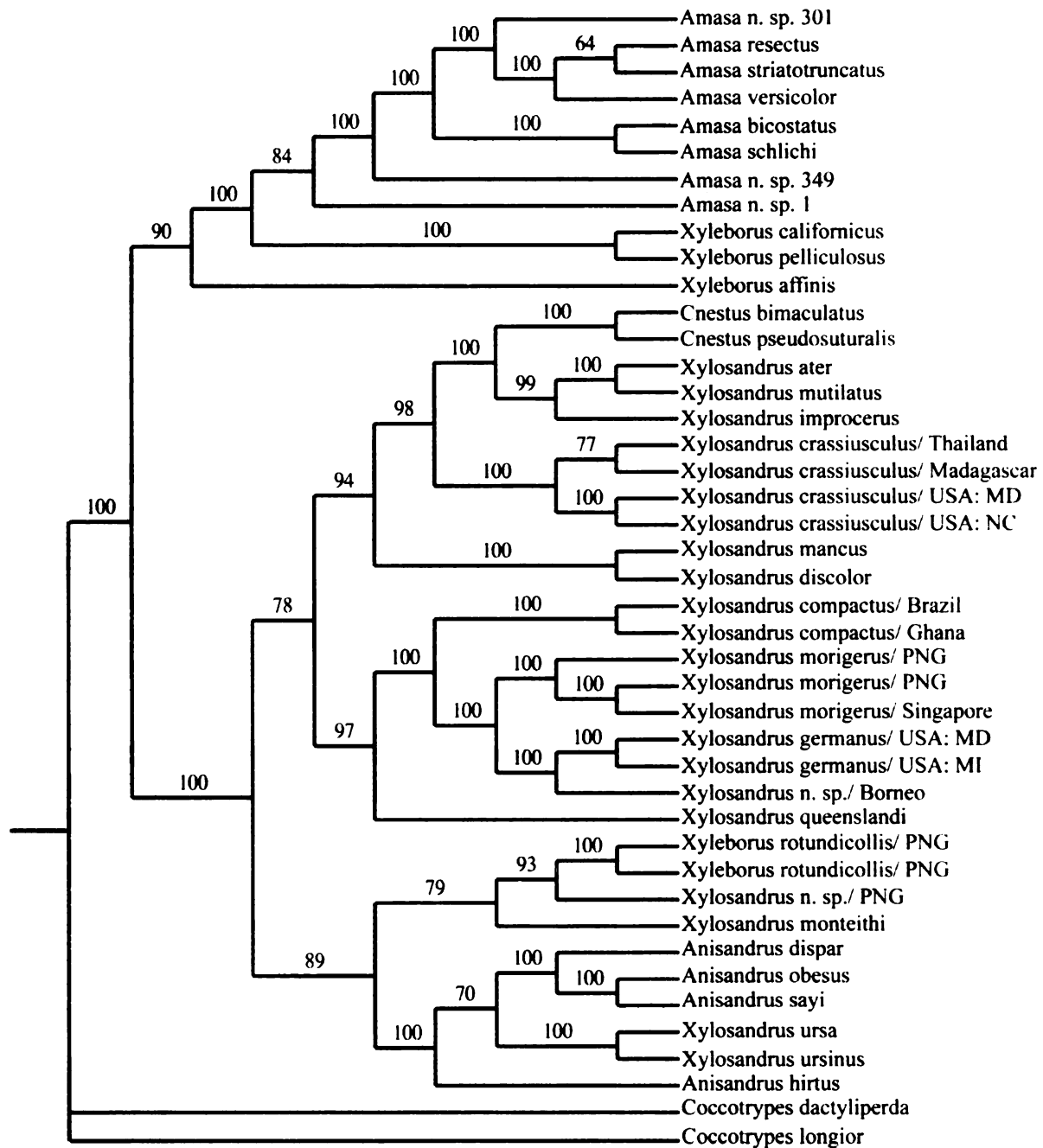


Figure 1.7: Bayesian tree found by analysis of data aligned in MUSCLE. Numbers above nodes are Bayesian posterior probabilities.

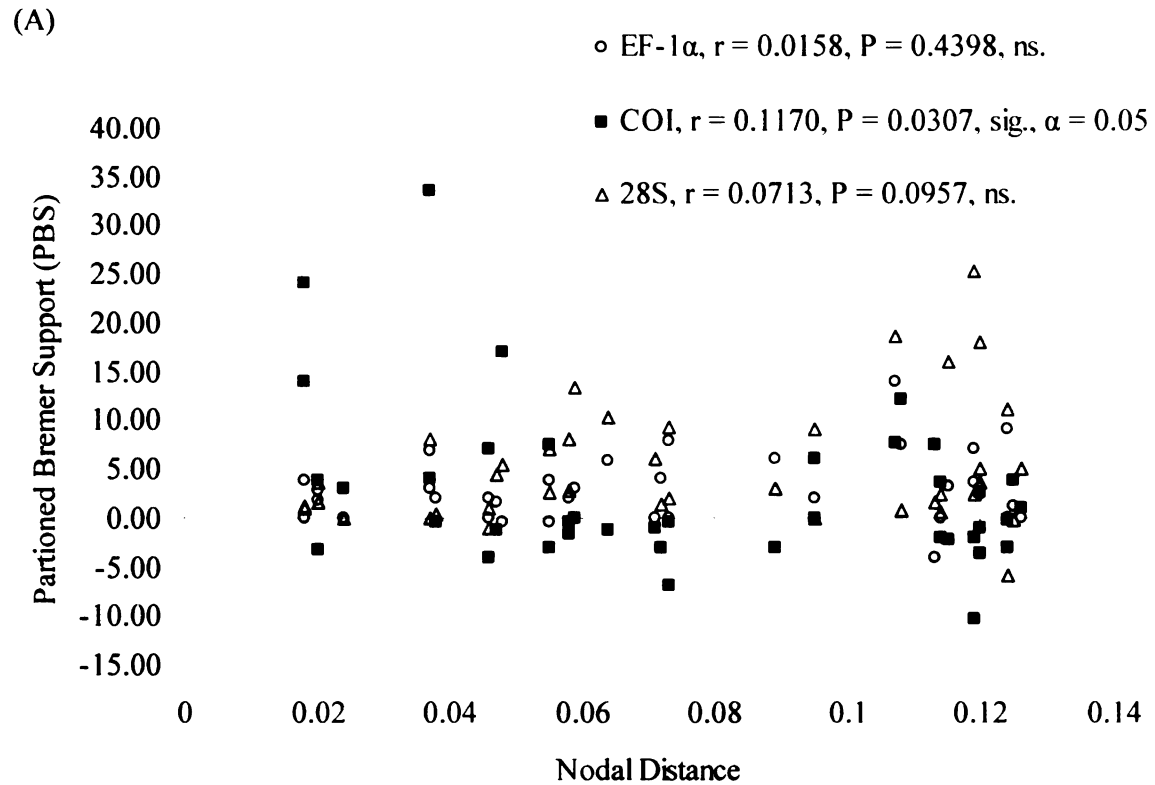


Figure 1.8 (Cont. on next page): Relationships between PBS values and nodal distance (maximum likelihood branch length from a given node to the tip of the tree) for the gene partitions: 28S, COI, and EF-1 α (A), CAD and ArgK (B).

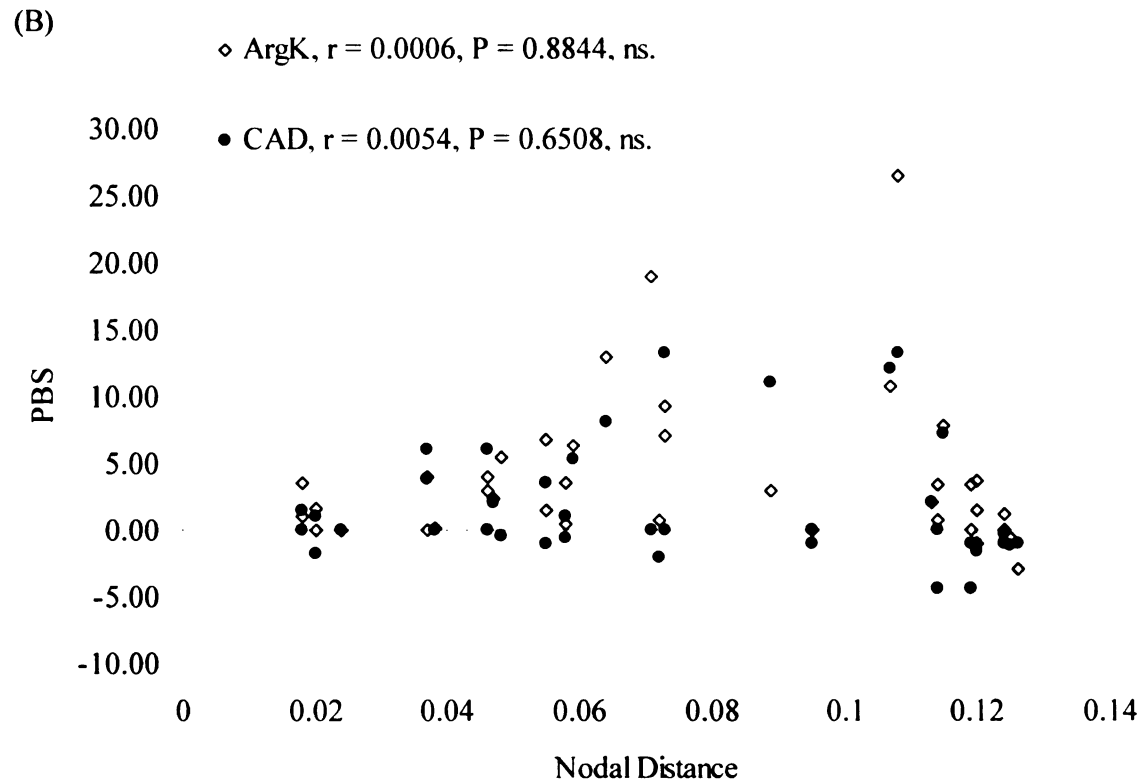


Figure 1.8 (Cont.): Relationships between PBS values and nodal distance (maximum likelihood branch length from a given node to the tip of the tree) for the gene partitions: 28S, COI, and EF-1 α (A), CAD and ArgK (B).

CHAPTER 2

Phylogenetic revision of *Xylosandrus* Reitter (Coleoptera: Curculionidae: Scolytinae: Xyleborina)

ABSTRACT

A phylogenetic revision of the Xyleborina genus *Xylosandrus* Reitter based on morphological and molecular data sets is presented. The monophyly of the genus was tested using a 43 character morphological data set analyzed separately and in combination with a molecular data set comprised of five independent gene loci: 28S rDNA; the mitochondrial gene cytochrome oxidase I (COI); and the nuclear protein-coding genes arginine kinase (ArgK), CAD (rudimentary), and elongation factor 1- α (EF-1 α). *Xylosandrus* was recovered as polyphyletic with the present classification containing species from four different genera: *Amasa* Lea, *Anisandrus* Ferrari, *Cnestus* Sampson, and *Xylosandrus*. A taxonomic revision of *Xylosandrus* is presented based on these results. The following **new combinations** are given: *Amasa cylindrotomicus* (Schedl), *A. omissus* (Schedl), *A. oralis* (Schedl), *Anisandrus butamali* (Beeson), *A. ursa* (Eggers), *A. ursinus* (Hagedorn), *A. ursulus* (Eggers), *Cnestus ater* (Eggers), *C. fijianus* (Schedl), *C. gravidus* (Blandford), *C. improcerus* (Sampson), *C. laticeps* (Wood), *C. mutilatus* (Blandford), *C. orbiculatus* (Schedl), *C. peruanus* (Wood), *C. retifer* (Wood), *C. retusus* (Eichhoff), *C. testudo* (Eggers), *Cyclorhipidion squamulatus* (Beaver and Löyttyniemi), *Xylosandrus amputatus* (Blandford), *X. mixtus* (Schedl), and *X. rotundicollis* (Browne). Two **new species** of *Xylosandrus* are described: *X. borneensis* and *X. hulcri*. An illustrated key to worldwide species of *Xylosandrus* is provided. Biogeography, host plants, diagnosis, and images are presented for each species.

INTRODUCTION

The scolytine subtribe Xyleborina contains approximately 1,300 described species and constitutes one of the largest radiations of ambrosia beetles (Wood and Bright 1992; Jordal 2002). The xyleborine mating system, which includes haplodiploidy and extreme inbreeding, is believed to be the cause of this dramatic radiation (Normark et al. 1999). Xyleborina are absent from the Dominican amber fossil record, suggesting that their radiation began in the Miocene (Bright and Poinar 1994; Jordal et al. 2000). Ambrosia beetles bore into the xylem of host trees and feed on symbiotic fungus, which grows on the walls of their galleries. This ambrosial feeding habit has evolved multiple times within the Scolytinae and also in the related weevil subfamily Platypodinae (Jordal et al. 2000; Farrell et al. 2001). Ambrosia beetles tend to be less host-specific than their bark beetle counterparts because adaptation to host secondary chemistry has not likely influenced their radiation. This lack of host specificity, along with their haplodiploidy mating system and inbreeding, make Xyleborina beetles particularly suited for the invasion of new habitats and establishment as introduced exotic species. In theory, a single female beetle could establish an invasive population of beetles. Furthermore, low host specificity means that invasive beetles do not need to locate a specific host and can infest multiple species. The economic importance of invasive xyleborines, along with their interesting biology and ecology, has prompted much research interest in the subtribe. Recently, the classification of the Xyleborina has been studied within a phylogenetic context to update their classification within an evolutionary framework (Jordal et al. 2000; Jordal 2002; Hulcr et al. 2007).

Xylosandrus Reitter (1913) is a large genus of xyleborine ambrosia beetles with a widespread distribution primarily in tropical and also in temperate regions throughout the world. In their worldwide catalog of the Scolytinae, Wood and Bright (1992) list 52 species of *Xylosandrus*. Subsequent descriptions, new synonymies, and new combinations have brought the present number to 54 species (Bright and Skidmore 1997, 2002; Saha et al. 1992; Wood 2007; Dole and Beaver in press). Several *Xylosandrus* species cause economic losses in nursery and agricultural settings in their native and introduced ranges. In Brazil, *X. compactus* (Eichhoff) causes losses in several economically important host species, including avocado, cacao, coffee, and mango (Oliveira 2008). *Xylosandrus crassiusculus* may potentially impact native tropical fauna, as the species is present as an invasive in Costa Rican primary forests (Kirkendall and Ødegaard 2007). Five *Xylosandrus* species currently occur in North America and of these, only one is native, *X. curtulus* (Eichhoff). The other four, *X. compactus*, *X. germanus* (Blandford), *X. crassiusculus* (Motschulsky), and *X. multilatus* (Blandford) have been introduced from the Old World tropics (Rabaglia 2002; Rabaglia et al. 2006). In North America, three *Xylosandrus* species (*X. compactus*, *X. crassiusculus*, and *X. germanus*) have caused “considerable economic damages” since their introductions (Oliver and Mannion 2001). It is difficult to get exact figures on the economic losses attributed to *Xylosandrus* species, since these numbers are often grouped with damage caused by other xyleborines. As an example, nursery managers in Maryland reported individual losses of \$3,650 - \$8,400 in nursery stock to *Xylosandrus* species in the spring of 2008 alone (R. J. Rabaglia per. com.).

The current classification of *Xylosandrus* contains species with highly variable morphologies, several of which are similar to those of other xyleborine genera (Hulcr et al. 2007; Dole and Beaver in press). Recent phylogenetic analyses of molecular data have also suggested that *Xylosandrus* is polyphyletic (Jordal 2002; see Chapter 1). *Xylosandrus* requires the development of a revised classification based on morphological and molecular evidence given the apparent taxonomic ambiguities and the economic importance of this group (Dole and Beaver in press; see Chapter 1). Furthermore, clear diagnostic characters and a key to worldwide species are necessary for the classification to be a predictive and useful tool in identification and control of invasive *Xylosandrus* species.

In this study, we define 43 morphological characters in an effort to resolve taxonomic ambiguities among *Xylosandrus* species and related genera. We conduct a combined phylogenetic analysis of these taxa using these morphological characters and molecular data in order to guide a revision of *Xylosandrus*.

Systematics

Xylosandrus was established as a monotypic genus by Reitter in 1913, with *Xylosandrus morigerus* designated as the type species. The genus remained monotypic for many years until Hoffmann (1941) transferred *Xyleborus germanus* into *Xylosandrus*. Following this, Nunberg (1959) transferred *Xyleborus compactus* into *Xylosandrus* and scolytine taxonomists began to take notice of the genus. In 1962, Schedl disagreed with the designation of the genus and listed *Xylosandrus* as a synonym of *Xyleborus* Eichhoff. Browne (1963) noted character differences that he felt justified the genus, chiefly the

“broad, obtuse prosternal process separating the front coxae” and transferred 14 species from *Xyleborus* to *Xylosandrus*. Schedl (1964) agreed with Browne’s assessment and transferred 8 more species from *Xyleborus* to *Xylosandrus*. Later, Schedl (1971) described the first species originally described as *Xylosandrus*, rather than being transferred from *Xyleborus*: *X. adherescens* and *X. assequens*.

In 1982, Wood began transferring species into *Xylosandrus*, chiefly from *Xyleborus*, and within a decade the genus grew to include 52 species (Wood 1982, 1984; Wood and Bright 1992). At this point in its taxonomic history, the generic limits and defining characters of *Xylosandrus* were blurred. Many species transferred to *Xylosandrus* by Wood and Bright (1992) have subcontiguous or contiguous procoxae, along with many other characters that set them apart from the species originally included in the genus. Since Wood and Bright gave no discussion of characters supporting their new combinations, it is difficult to ascertain their reasoning. Since 1992, additional species have been described in or transferred to *Xylosandrus*, only some of which fit the characters that originally defined the genus (Beaver 1998; Saha et al. 1992; Wood 2007; Dole and Beaver in press).

The incorrect placement of many species within *Xylosandrus* has created some taxonomic confusion between *Xylosandrus* and the genera *Amasa* Lea (1893) and *Cnestus* Sampson (1911). In addition to this, the recent resurrection of the genus *Anisandrus* Ferrari (1867) has highlighted similarities between it and several species of *Xylosandrus* (Hulcr et al. 2007). In their review of the Australian species of *Xylosandrus*, Dole and Beaver (in press) made tentative steps toward correcting the taxonomy of *Xylosandrus* by defining characters that separate *Xylosandrus sensu stricto* from *Cnestus*

and transferring two species, *Cnestus pseudosolidus* (Schedl) and *C. solidus* (Eichhoff) from *Xylosandrus* to *Cnestus*.

Xylosandrus sensu stricto can be distinguished from other xyleborine genera by the following combination of characters: stout body, usually about twice as long as wide, widely separated procoxae, flat scutellum that is flush with the surface of elytra, and obliquely truncate antennal club with the first segment forming a circular costa and dense pubescence on the oblique portion of the club (Reitter 1913; Browne 1963; Bright 1968; Wood 1986; Hulcr et al. 2007; Dole and Beaver in press).

Amasa can best be distinguished from *Xylosandrus* by its antennal club, which is oval, not truncate, with prominent 1st and 2nd segments, separated by sutures that are visible on both the anterior and posterior face (Lea 1893; Wood 1986; Hulcr et al. 2007). In all *Xylosandrus*, the antennal club is obliquely truncate, with the first segment forming a circular costa, lacking sutures posteriorly and with segment one covering the entire posterior face. *Amasa* also have contiguous procoxae (Lea 1893; Wood 1986; Hulcr et al. 2007). In all *Xylosandrus sensu stricto*, the procoxae are separated by an intercoxal piece that is at least half the width of the coxae.

Anisandrus can be distinguished from *Xylosandrus* by the contiguous procoxae (Hulcr et al. 2007). The lateral margin of the protibiae of *Anisandrus* are armed with 6 – 7 socketed teeth. In *Xylosandrus sensu stricto* there are always only 4 – 5 socketed teeth on the lateral margin of the protibiae. *Anisandrus* species also have pronotal lateral margins that are rounded, a character which separates them from *Cnestus*, which has carinate lateral margins (Hulcr et al. 2007). *Xylosandrus sensu stricto* contains species with both rounded and carinate lateral margins of the pronotum.

Cnestus can be distinguished from *Xylosandrus* by the subcontiguous procoxae (Sampson 1911; Hulcr et al. 2007). *Cnestus* also have antennae with four funicular segments, whereas *Xylosandrus* species have five. Additionally, in *Cnestus* the anterior margin of the pronotum bears 4 or fewer asperities, with a pair of coarse asperities medially, and the pronotum is often produced anteriorly. In *Xylosandrus* the anterior margin of the pronotum bears 6 or more smaller asperities of approximately equal size and is never produced anteriorly. Many species of *Cnestus* have elytra that are wider than they are long, a character which is never observed in *Xylosandrus sensu stricto*.

Recent taxonomic work has examined the classification of xyleborine genera within a phylogenetic context (Jordal et al. 2000; Jordal 2002; Hulcr et al. 2007; see Chapter 1). A cladistic review of the generic taxonomic characters of Xyleborina recovered a monophyletic *Xylosandrus*, but it is important to note that this study did not include species with morphologies that deviate from the *sensu stricto* concept of the genus (Hulcr et al. 2007). Dole and Beaver (in press) were the first to treat the classification of problematic *Xylosandrus* species by defining characters that distinguish *Xylosandrus* from *Cnestus*. Phylogenetic analyses of DNA sequence data have also recovered a non-monophyletic *Xylosandrus*. Jordal (2002) used the nuclear gene Elongation Factor -1 α (EF-1 α) to test the monophyly of the Xyleborina and, while the subtribe was recovered as monophyletic, *Xylosandrus* was found to be paraphyletic with respect to *Cnestus*. Phylogenetic reconstruction of a subset of *Xylosandrus* taxa using data from mitochondrial and nuclear genes recovered a polyphyletic *Xylosandrus* with the placement of *Anisandrus* and *Cnestus* among *Xylosandrus* species (see Chapter 1). In addition, several *Xylosandrus* species were placed within the “*Anisandrus*” and

“*Cnestus*” clades with strong support (e.g., 100% bootstrap support), further indicating the need for a taxonomic revision of *Xylosandrus*.

Biogeography

Xylosandrus is widely distributed in primarily tropical, but also in temperate regions worldwide. Whereas the inclusion of the problematic species discussed above does not change the overall distribution in terms of biogeographical regions, the biogeography discussed herein will pertain to *Xylosandrus* as it is defined in this taxonomic revision (Table 2.1). Three species of *Xylosandrus* have almost circumtropical distributions: *X. compactus*, *X. crassiusculus*, and *X. morigerus*. A fourth species, *Xylosandrus germanus* is less widely distributed, occurring in the Nearctic Region, Oceania, the Oriental Region, and the Palearctic Region. These four species were all introduced as exotic invasive species into temperate regions of the world. *Xylosandrus* has a high level of regional endemism, with 71% of species occurring in only one biogeographical region. The Oriental Region is the most species rich, with 76% of *Xylosandrus* species present and a high occurrence of endemic species. The next richest is the Australian Region, with 29% of *Xylosandrus* species present. The Afrotropical Region and Oceania each contain 13%, and the Palearctic Region contains 16% of *Xylosandrus* species. Contrary to its tendency towards remarkable levels of species diversity, the Neotropical Region contains the same number of *Xylosandrus* species as the Nearctic (where the vast majority of species are introduced). This is congruent with the biogeography of the rest of Xyleborina, which tend to have their

highest levels of diversity in the Old World Tropics (Beaver 1979; Wood and Bright 1992).

Natural History

As is typical of ambrosial feeding scolytines, *Xylosandrus* beetles are usually not host specific (Beaver 1979). Known host plants are listed for each species herein. All xyleborine beetles are haplodiploid, inbreeding and sexually dimorphic (Figs. 2.33 and 2.34). The diploid males are dwarfed, flightless and bear little resemblance to their female counterparts. All *Xylosandrus* species are xylomycetophagous. The female carries ambrosial fungi within a mycangium between the pronotum and mesonotum. Colonization of a host tree begins when a female beetle locates a suitable host and initiates gallery construction. As she bores into the tree, the female inoculates the woody tissue lining the gallery tunnels with a suite of microorganisms, including the ambrosial fungi. Once the fungi have begun to grow along the walls of the gallery, the female beetle lays eggs in small clusters at the end of the main tunnel. *Xylosandrus* larvae and adults will feed exclusively on the ambrosial fungi. If the establishing female was unmated, she will produce only male offspring. In this case, as soon as they have pupated into adults, the flightless and dwarfed males (Fig. 2.34) will mate with their mother to produce female offspring. If the establishing female had mated prior to gallery construction, she will produce both male and female offspring, but with a highly skewed sex ratio (Kirkendall 1993). In Xyleborina beetles, the female to male sex ratio has been observed to be as high as 30:1 (Bright 1968; Krikendall 1993). When both male and

female offspring have been produced, the males will mate with their sisters to produce the next generation of beetles (Kirkendall 1993).

MATERIALS AND METHODS

Approximately 1,300 specimens were studied from entomological collections.

The following acronyms are used for collections referenced in the text:

AMNH	American Museum of Natural History, New York, New York, USA.
BMNH	The Natural History Museum, London, United Kingdom.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
CAS	California Academy of Sciences, San Francisco, California, USA.
CSCA	California State Collection of Arthropods, Sacramento, California, USA.
FICB	Forest Research Centre, Lae, Papua New Guinea.
FMNH	Field Museum of Natural History, Chicago, Illinois, USA.
FRCS	Forest Research Centre, Sabah, Sandakan, Malaysia.
FRI	Indian Forest Research Institute, Dehra Dun, Uttar Pradesh, India.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Belgium, Brussels.
IZM	Institute of Zoology, Moscow, Russia.
MNB	Museum für Naturkunde der Humboldt University, Berlin, Germany.
MRCB	Musée Royal du Congo Belge, Tervuren, Belgium.
MSUC	Michigan State University Collection, East Lansing, Michigan, USA.
MTD	Museum für Tierkunde, Dresden, Germany.
MZLU	Lund University, Lund, Sweden.

MZUSP	Museum de Zoologia, Universidade de Sao Paulo, Sao Paulo, Brazil.
NHMW	Naturhistorisches Museum Wien, Wien, Austria.
NHR	Naturhistoriska riksmuseet, Stockholm, Sweden.
NZSI	Zoological Survey of India, National Zoological Collection, Calcutta, India.
RAB	Roger A. Beaver, personal collection, Chiang Mai, Thailand.
UCDC	R. M. Bohart Museum of Entomology, University of California, Davis, California, USA.
USNM	National Museum of Natural History, Washington, D.C., USA (Including Stephen L. Wood Collection).
ZFMK	Zoologische Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

Plant host species were compiled from the following publications: Bright and Skidmore (1997, 2002), Cibrián et al. (1995), Ohno (1990), Schedl (1962), Wood and Bright (1992). Hosts recorded since the publication of Bright and Skidmore (2002) were collected from the literature by the authors and provided by Dr. Don Bright (per. com.). Plant author names, when missing, were added using the International Plant Names Index (www.ipni.org).

Morphological Characters

A total of 43 external morphological characters (24 binary, 19 multistate) were coded and used in the phylogenetic analysis. Morphological characters were scored for

females only, since the morphological classification of Xyleborina beetles is based entirely on females and males are rare or unknown for many species. Characters were scored for 52 species of *Xylosandrus* (Table 2.2). In order to test the generic limits of *Xylosandrus*, a diversity of taxa were included in the morphological analysis: three *Anisandrus*, nine *Amasa*, three *Cnestus*, one *Coccotrypes* and three *Xyleborus* species (Table 2.2). Characters coded were distributed as follows: two habitus characters (five states), five head characters (14 states), 14 pronotal characters (35 states), two elytral characters (five states), and 20 elytral declivity characters (51 states). Characters that were ambiguous or difficult to see on the specimen(s) examined were coded as “?” and treated as missing data. Inapplicable characters were coded as “?” and treated as missing data. All characters were treated as non-additive and unweighted in the phylogenetic analysis.

The following morphological characters and character states were used in the phylogenetic analysis. The character data matrix (Table 2.2) was prepared and coded using the program MX (Yoder et al. 2006-Present).

Habitus

1. *Body ratio*

0 = less than 2.0 times longer than wide

1 = more than 2.0 times longer than wide

2. *Pronotal to elytra color*

0 = roughly the same color

1 = elytra distinctly darker than pronotum

2 = overall, same color, but elytra with testaceous patches

Head

3. Frons sculpture

0 = punctuate

1 = finely granulate

2 = reticulate or rugose

? = ambiguous or difficult to see

4. Frons median keel

0 = absent

1 = present

? = ambiguous or difficult to see

5. Antennal funicular segment count

0 = 4-segmented

1 = 5-segmented

2 = 6-segmented

? = ambiguous or difficult to see

6. Antennal club type

0 = circle absent

1 = circle closed anteriad

2 = circle closed posteriad

? = ambiguous or difficult to see

7. Segments visible on posterior face of antennal club

0 = segments 2 and 3 not visible, segment 1 covering whole face

1 = segment 2 visible, segment 1 covering most of face

2 = segments 1, 2, and 3 visible on face

? = ambiguous or difficult to see

Pronotum

8. *Pronotum ratio*

0 = Pronotum wider than long

1 = pronotum of equal length and width

2 = pronotum longer than wide

9. *Pronotal type dorsal*

0 = rounded (type 1, Hulcr et al. 2007)

1 = basic (type 2, Hulcr et al. 2007)

10. *Pronotal type laterally*

0 = basic

1 = rounded

2 = prolonged anteriorly

3 = prolonged posteriorly

11. *Pronotal vestiture*

0 = erect, hair-like setae

1 = semi-appressed, hair-like setae

12. *Pronotal basal setae*

0 = glabrous, without setae (except for mycangium, when present)

1 = moderately setose, with basal setae being less dense than anterior

2 = densely setose, with basal setae being at least as dense as anterior

13. *Pronotal mycangial setae*

0 = absent

1 = present

? = ambiguous

14. *Pronotal basal sculpture*

0 = punctate

1 = asperate-granulate

15. *Pronotal basal sculpture density*

0 = moderate sculpture, punctures or granules separated by a distance greater than their size

1 = dense sculpture, punctures or granules separated by a distance equal to or less than their size

16. *Pronotal anterior serrations count*

0 = 4 or fewer serrations

1 = 6 or more serrations

17. *Pronotal anterior serrations course median pair*

0 = absent

1 = present

? = only two anterior serrations present

18. *Pronotal anterior margin produced*

0 = not produced

1 = produced

19. *Pronotal lateral carina*

0 = absent

1 = present

20. *Procoxal separation*

0 = widely separated, intercoxal piece at least 1/3 the width of coxae

1 = narrowly separated to subcontiguous

2 = contiguous

? = procoxae not visible

21. *Protibial teeth*

0 = 4 or 5 socketed teeth

1 = 6 socketed teeth

2 = 7 socketed teeth

3 = 8 socketed teeth

? = ambiguous or difficult to see

Elytra

22. *Elytral ratio*

0 = elytra longer than wide

1 = elytra of equal length and width

2 = elytra wider than long

23. *Discal interstrial sculpture distribution*

0 = uniseriate

1 = multiseriate, including biseriate

Elytral Declivity

24. *Declivital origin*

0 = declivity originating less than 1/3 the length of elytra from base

1 = declivity originating $\geq 1/2$ the length of elytra from base

25. *Declivital slope*

0 = elytral disc gradually curving into declivity

1 = declivital face abrupt and steeply separated from disc

26. *Declivital shape*

0 = not circular

1 = circular

27. *Declivital surface*

0 = convex

1 = flattened

2 = concave, at least in part

28. *Declivital carina*

0 = absent, rounded

1 = granulate

2 = carinate

3 = serriate

29. *Declivital carina length*

0 = carina not extending beyond 7th interstriae

1 = carina extending beyond 7th interstriae, forming a circumdeclivital ring

? = absent

30. *Declivital striae count*

0 = 3 striae visible on declivity

1 = 3 striae visible on declivity

2 = 4 striae visible on declivity

3 = 5 striae visible on declivity

4 = 6 striae visible on declivity

? = ambiguous

31. *Declivital strial impression*

0 = not impressed

1 = impressed

32. *Declivital strial sculpture*

0 = punctuate

1 = granulate

33. *Declivital strial sculpture distribution*

0 = straight

1 = confused

34. *Declivital strial setae type*

0 = absent

1 = hair-like

2 = scale-like

? = ambiguous

35. *Declivital strial setae length*

0 = length less than or equal to the width of second declivital interstriae

1 = length greater than the width of second declivital interstriae

2 = length at least 2 times the width of second declivital interstriae

? = absent or ambiguous

36. *Declivital strial setae profile*

0 = appressed or semi-appressed

1 = erect

? = absent or ambiguous

37. *Declivital interstrial sculpture*

0 = punctuate

1 = coarsely granulate

2 = finely granulate

38. *Declivital interstrial sculpture distribution*

0 = uniseriate

1 = multiseriate, including biseriate

39. *Declivital interstrial setae type*

0 = absent

1 = hair-like

2 = scale-like

? = ambiguous

40. *Declivital interstrial setae length*

0 = length less than or equal to the width of second declivital interstriae

1 = length greater than the width of second declivital interstriae

2 = Length at least twice the width of second declivital interstriae

? = absent or ambiguous

41. *Declivital interstrial setae profile*

0 = appressed or semi-appressed

1 = erect

? = absent, ambiguous

42. *First interstriae elevated at apex of elytra*

0 = not elevated

1 = elevated

43. *Granules or tubercles near apex of first interstriae*

0 = absent

1 = present

Molecular Characters

The molecular data set used herein (see Chapter 1) is comprised of multiple gene loci, chosen for their complementary phylogenetic signals at varying nodal depths: 28S rDNA; the mitochondrial gene cytochrome oxidase I (COI); and the nuclear protein-coding genes arginine kinase (ArgK), CAD (rudimentary), and Elongation Factor -1 α (EF-1 α). For extraction, sequencing and alignment protocols see Chapter 1. For our combined analysis, we used the molecular data set aligned manually with reference to a scolytine-specific secondary structure model (Jordal et al. 2008). The resulting combined data set included only taxa for which both morphological and molecular data were available (Table 2.3). This combined data set includes 27 taxa, representing 15 *Xylosandrus* species, 12 species belonging to the genera *Amasa*, *Anisandrus*, *Cnestus*, *Xyleborus*, and the outgroup genus *Coccotrypes* (Table 2.3).

Phylogenetic Analysis

Phylogenetic analysis of the morphological data set was conducted with the software TNT (Goloboff et al. 2003). A new technology driven search was employed for the parsimony analysis with all search modules employed: sectorial search (RSS and CSS), ratchet, drift, and tree fusing. Default TNT settings were used, with the following exceptions: tree fusion was conducted globally after every hit and the search was set to end after the minimal tree length was found 10 times. Traditional (heuristic) search methods were then used to conduct tree bisection and reconnection branch swapping on the 43 most parsimonious trees found in the new technology search. Maximum trees being held by TNT was set to 10,000. Bootstrap support values were calculated by performing 1,000 pseudo-replicates with simple sequence addition in the program Winclada (Nixon 1999).

Phylogenetic analysis of the combined data set was conducted with the software PAUP* (Swofford 2002). A heuristic search was employed with 300 random stepwise addition replicates using PAUP* default settings. Gaps were treated as missing data in the analysis. Bootstrap values were calculated by performing 1,000 pseudo-replicates with simple addition sequence in PAUP*. Bremer support values for each data partition were calculated by constructing a constraint tree with the software TreeRot (Sorensen 1996) followed by subsequent analysis with PAUP*.

RESULTS

Xylosandrus was recovered as polyphyletic by analyses of both the morphological and the combined data set. Phylogenetic analysis of the morphological data set produced

10,000+ equally parsimonious trees of 318 steps (max trees in TNT set to 10,000) (Fig 2.1). The strict consensus tree was mostly unresolved, but recovered several clades with high support values. The monophyly of the clade containing *Amasa*, *Anisandrus*, *Cnestus*, and *Xylosandrus* with respect to the genus *Xyleborus* was recovered with 100% bootstrap support (see discussion of *Xyleborus rotundicollis* below). The unresolved placement of the “*Amasa*”, *Anisandrus*, and “*Cnestus*” clades, as well as the placement of several species of *Xylosandrus* within these clades, was responsible for rendering *Xylosandrus* paraphyletic. While morphology did not resolve their phylogenetic placement, the data did support the monophyly of the “*Amasa*” and “*Cnestus*” clades and the inclusion of several *Xylosandrus* species within them. These clades were both recovered with 100% bootstrap support. *Anisandrus* was recovered as monophyletic with 100% bootstrap support. The Consistency Index (CI) indicates that the occurrence of homoplasy is high in the morphological data set (CI = 0.190). Furthermore, the Retention Index (RI) indicates that character state changes are occurring predominantly on the internal nodes (RI = 0.671).

Phylogenetic analysis of the combined data set recovered a single most parsimonious tree of 4524 steps (Fig. 2.2). This tree was well resolved, with high support values (e.g. $\geq 90\%$ bootstrap support) toward the terminal nodes and poorer support (e.g. $\leq 74\%$ bootstrap support) for the deeper relationships among the clades. The placement of the “*Anisandrus*”, and “*Cnestus*” clades, the inclusion of several *Xylosandrus* species within these clades, as well as the placement of *Xylosandrus mancus* and *X. discolor* in a clade with *Amasa* and *Xyleborus*, rendered *Xylosandrus* polyphyletic. The low support for deeper nodes made it impossible to determine the phylogenetic relationships among

Xylosandrus, *Amasa*, *Anisandrus*, *Cnestus*, and *Xyleborus*. However, the placement of several species of *Xylosandrus* within the “*Anisandrus*” and “*Cnestus*” clades had very strong support (e.g. 100% bootstrap support). The genus *Amasa* and a *Xylosandrus sensu stricto* clade (containing the type species *X. morigerus*) were also recovered with 100% bootstrap support.

Homoplasy as measured by CI and RI indicated that homoplasy was lowest for the 28S data partition (Table 2.4). The nuclear protein-coding genes ArgK, CAD, and EF-1 α had similar CI's (0.474 – 0.522) and RI's (0.460 – 0.600). The mitochondrial gene COI had the highest level of homoplasy (CI = 0.265, RI = 0.246). The low RI value for COI indicates that the character state changes for this gene largely occurred towards the terminal nodes of the tree. The morphological data demonstrated lower levels of homoplasy in the combined analysis (CI = 0.346) than it did when analyzed alone (CI = 0.200). However, the RI observed for the morphological data was lower in the combined analysis (RI = 0.492), indicating that the occurrence of character state changes shifted more toward the terminal nodes when the data were combined with molecular data. Overall, 28S gave the highest bremer support values, with CAD having the next highest values (Table 2.5). Interestingly, the overall bremer supports for COI and morphology were similar.

DISCUSSION

All analyses conducted herein recovered a polyphyletic *Xylosandrus*, with the present classification of the genus containing species from at least four different genera: *Xylosandrus*, *Amasa*, *Anisandrus*, and *Cnestus*. These findings are consistent with those

of other studies of *Xylosandrus* (Jordal 2002; Dole and Beaver in press; see Chapter 1). Separate and combined analyses of morphological and molecular data sets have recovered the following clades with high support values: “*Anisandrus*”, “*Amasa*”, “*Cnestus*” and “*Xylosandrus sensu stricto*” (see Chapter 1). However, even a data set combining morphology and five gene partitions was not sufficient to resolve the relationships among these genera (Fig. 2.2). Despite this, these trees provide a valuable framework with which to revise the present classification of *Xylosandrus*.

***Amasa* Clade**

The “*Amasa*” clade has been consistently recovered by all parsimony analyses (Bayesian and POY analyses of molecular data recovered an unresolved or polyphyletic *Amasa*, with respect to *Xyleborus*) (see Chapter 1) (Figs. 2.1 and 2.2). The genus is rendered monophyletic by the inclusion of three *Xylosandrus* species: *X. cylindrotomicus*, *X. omissus*, and *X. oralis* (Fig. 2.1). The placement of these species within *Amasa* is supported by the morphological characters used to define *Amasa* and distinguish it from other Xyleborina genera (Hulcr et al. 2007) (Fig. 2.3). Similarly, the species *A. mixtus* and *A. amputatus* were included among *Xylosandrus* species, rather than *Amasa*, by the analysis of the morphological data set. The transfer of these species into *Xylosandrus* is consistent with the characters defining *Xylosandrus sensu stricto*. The combined phylogenetic analyses have indicated that *Amasa* is more closely related to *Xyleborus* than it is to *Anisandrus*, *Cnestus*, and *Xylosandrus*. Thus, it appears that confusion between *Xylosandrus* and *Amasa* was simply the result of taxonomic error and not an indication of close phylogenetic relationship.

***Anisandrus* Clade**

The “*Anisandrus*” clade has been recovered by all analyses that included molecular data (see Chapter 1) (Fig. 2.2). The only analysis that did not recover this clade was that of morphological data alone (Fig. 2.1). However, the membership of species included in this clade is consistent with characters that support the separation of *Anisandrus* from other Xyleborina genera (Hulcr et al. 2007) (Fig. 2.4). All other analyses recovered the “*Anisandrus*” clade with high support (100% bootstrap support, Bayesian posterior probability of 100, and Bremer supports ranging from 22-67) (see Chapter 1) (Fig. 2.2; Table 2.5). The genus *Anisandrus* is rendered monophyletic by the inclusion of three *Xylosandrus* species: *X. ursa*, *X. ursinus*, *X. ursulus*. Transfer of these species to *Anisandrus* is also supported by the morphological characters that distinguish the genus (Hulcr et al. 2007). *Xylosandrus butamali* is a fourth species with the morphological characteristics of *Anisandrus* rather than those of *Xylosandrus*. This species was not available for DNA sequencing and was only included in the morphological analysis. This analysis placed *X. borealis* in a larger clade with the “*Anisandrus*” and “*Cnestus*” clades with 93% bootstrap support, but the relationships within this clade were unresolved in the strict consensus tree. Based on this phylogenetic evidence, in combination with the morphological characters that distinguish *Anisandrus*, *X. borealis* is transferred to *Anisandrus* herein.

***Cnestus* Clade**

The “*Cnestus*” clade has been recovered by all phylogenetic analyses (see Chapter 1) (Figs. 2.1 and 2.2). The genus is rendered monophyletic by the inclusion of 11 *Xylosandrus* species: *X. ater*, *X. fijianus*, *X. gravidus*, *X. improcerus*, *X. laticeps*, *X. mutilatus*, *X. orbiculatus*, *X. peruanus*, *X. retifer*, *X. retusus*, and *X. testudo*. These are in addition to two species already transferred from *Xylosandrus* to *Cnestus* by Dole and Beaver (in press): *X. pseudosolidus* and *X. solidus*. The inclusion of these species in *Cnestus* is also supported by morphological characters used to distinguish the genus (Hulcr et al. 2007; Dole and Beaver in press) (Fig. 2.5). Support values for the “*Cnestus*” clade were very high (100% bootstrap support, Bayesian posterior probability of 100, and Bremer supports ranging from 53-120).

The transfer of the above species from *Xylosandrus* to *Cnestus* is of some importance to scolytine control, considering the establishment of *X. mutilatus* as an invasive species in North America. The inclusion of *X. mutilatus* in *Cnestus* constitutes a new generic record for North America (Rabaglia et al. 2006). Likewise, the transfer of several South American species (*X. laticeps*, *X. peruanus*, *X. retifer*, *X. retusus*) to *Cnestus* establishes, for the first time, the presence of the genus in the Neotropics (Wood 2007).

***Xylosandrus sensu stricto* Clade**

The “*Xylosandrus sensu stricto*” clade was consistently recovered by all analyses that included molecular data (see Chapter 1) (Fig. 2.2). The analysis of morphological data did not recover this clade, but the resolution for all *Xylosandrus* species not placed in clades with other genera was poor (Fig. 2.1). The “*Xylosandrus sensu stricto*” clade is

comprised of (((*X. germanus* + *X. borneensis* n. sp.) *X. morigerus*) *X. compactus*). Given that it contains *X. morigerus*, the type species of *Xylosandrus*, this clade is the highest supported grouping of species belonging to *Xylosandrus sensu stricto* found by phylogenetic analyses of the genus. Support values for this clade were very high (100% bootstrap support, Bayesian posterior probabilities of 100, Bremer supports ranging from 21-28). The species included in this clade are morphologically consistent with the strict definition of the genus. This clade also contains three economically important species of *Xylosandrus*: *X. compactus*, *X. germanus*, and *X. morigerus*.

Xylosandrus sensu lato

The phylogenetic placement of the remaining *Xylosandrus* species was largely unresolved by these analyses. However, a couple of clades were recovered by the combined data analysis with high support (≥ 92 % bootstrap support): *X. hulcri* n. sp. + *X. moteithi* and *X. discolor* + *X. mancus* (Fig. 2.2). The placement of a few species calls into question the monophyly of *Xylosandrus*, even after this revision. The placement of *X. crassiusculus* as sister to *Cnestus*, which has been recovered by multiple analyses with high support (≥ 97 % bootstrap support, Bayesian posterior probabilities of 100), would render the genus paraphyletic (see Chapter 1) (Fig. 2.2). Because of the wide distribution and economic importance of the species any taxonomic changes to *X. crassiusculus* should be made with strong phylogenetic support. A study of the species' relationship to other Xyleborina genera not considered in this analysis should be made before it is hastily established as a monotypic genus. Furthermore, *Xylosandrus crassiusculus* forms a morphologically distinct group with *X. hirsutipennis* and any analysis of its phylogenetic

placement should consider this species as well. A phylogenetic study of Xyleborina genera is presently being completed and may shed more light on this taxonomic issue (Cognato et al. in prep.).

Several *Xylosandrus* species groups may require further consideration as the phylogenetics of Xyleborina genera is resolved. The species *X. amputatus*, *X. beelsoni*, *X. borealis*, *X. brevis*, *X. discolor*, *X. diversepilosus*, *X. jaintianus*, *X. mancus*, *X. squamulatus*, *X. subsimilis*, and *X. subsimiliformis* all form a distinct morphological group with declivital faces that are steep and abruptly separated from the elytral disc. This grouping was recovered in a clade with *Amasa* by the analysis of morphological data with 97% bootstrap support. Phylogenetic analysis of the combined data set recovered a subset of these species (*X. discolor* + *X. mancus*) as more closely related to *Xyleborus affinis* (92% bootstrap support) and to a clade containing *Amasa* + *Xyleborus californicus* (64 % bootstrap support) than to *Xylosandrus*. Within this species group, *X. amputatus*, *X. mancus*, and *X. squamulatus* form perhaps the most distinct group of *Xylosandrus* species. These three species have lateral declivital margins with a carina or a raised rim of granules that extends beyond the 7th declivital interstriae, forming a circumdeclivital ring, a character often observed in *Amasa*. However, these species have *Xylosandrus*-type antennae and pronotal-mesonotal mycangia, two characters that are never observed in *Amasa*. Future work on the phylogenetics of *Xylosandrus* and the generic classification of Xyleborina should address these issues with more thorough taxon sampling and the expansion of DNA data sets.

Key to the females of the species of *Xylosandrus*

- 1 Margin of elytral declivity carinate or with a raised rim of granules. ...2
 - Margin of elytral declivity rounded, tuberculate, or serrate but without a continuous carina or rim. ...32

- 2 Margin of elytral declivity carinate to 7th interstriae. ...3
 - Margin of elytral declivity with carina extending beyond 7th interstriae, forming a circumdeclivital ring. ...37

- 3 (2) Declivital face of elytra steep and abruptly separated from disc. ...4
 - Elytral disc gradually curving into declivity. ...16

- 4 (3) Declivital striae punctate. Five or six striae visible on declivity. ...5
 - Declivital striae granulate. Four or five striae visible on declivity. ...9

- 5 (4) Declivital striae impressed. ...6
 - Declivital striae not impressed. ...7

- 6 (5) Elytral declivity with deeply impressed striae, giving the appearance of six distinct ridges on face. Six striae visible on declivity. Declivital striae with very appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae very finely granulate, giving the declivity a matte appearance, with erect, hair-like setae, shorter than the width of second declivital interstriae.

Pronotum with a lateral costa, but not carinate. 1.5 – 1.6 mm long. Oriental Region. ...*X. boreensis* n. sp. (Fig. 2.12)

- Elytral declivity with striae less impressed. Five striae visible on declivity. Declivital striae with erect or semi-erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae more coarsely granulate, declivity shining. Pronotum with a lateral costa and carina. 1.3 – 1.5 mm long. Oriental Region. ...*X. pygmaeus* (Eggers) (Fig. 2.38)

7 (5) Elytral declivity flattened. Five striae visible on declivity. ...8

- Elytral declivity convex. Six striae visible on declivity. Declivital striae with setae. Interstriae uniseriate punctate, with erect, hair-like setae, longer than twice the width of second declivital interstriae. 1.2 – 1.8 mm long. Afrotropical Region, Australian Region, Neotropical Region, Oceania, Oriental Region, Palearctic Region. ...*X. morigerus* (Blandford) (Fig. 2.35)

8 (7) Declivital striae without setae. Interstriae uniseriate granulate, with erect, hair-like setae, longer than the width of second declivital interstriae. Larger species, 2.0 – 2.3 mm long. Oriental Region. ...*X. derupteterminatus* (Schedl) (Fig. 2.18)

- Declivital striae without setae. Interstriae uniseriate punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Smaller species, 1.5 – 1.9 mm long. Oriental Region. ...*X. terminatus* (Eggers) (Fig. 2.41)

- 9 (4) Declivity covered with a dense vestiture of appressed, flattened, scale-like setae.
 Striae and interstriae granulate. Pronotum granulate and pubescent basally.
 Lateral pronotum costate and carinate. Frons rugose. 2.6 mm long. Oriental
 Region. ...*X. subsimilis* (Eggers) (Fig. 2.41)
- Declivital setae hair-like, not flattened. ...10
- 10 (9) Lateral pronotum costate and carinate. ...11
- Lateral pronotum costate, but without a carina. ...14
- 11 (10) Pronotum uniformly convex dorsally. Declivital face convex. Smaller species, 1.5
 – 2.0 mm long. Australian Region, Oceania, Oriental Region. ...*X. discolor*
 (Blandford) (Fig. 2.20)
- Pronotum with conspicuous summit on basal third. Declivital face flattened,
 convex, or sometimes depressed in areas. Larger species, 2.8 – 3.0 mm long.
 ...12
- 12 (11) Four striae visible on elytral declivity. Declivital interstriae without a row of
 longer, erect setae, bearing only a vestiture of short, appressed setae. ...13
- Five striae visible on elytral declivity, with striae 4 and 5 forming a loop.
 Declivital interstriae with a single row of long, erect, hair-like setae, along with a
 dense vestiture of shorter appressed setae. 2.8 – 2.9 mm long. Oriental Region.
 ...*X. beasoni* Saha, Maiti, and Chakraborti (Illustrated in Saha et al. 1992)

- 13 (12) First and second declivital interstriae elevated toward apex, with depressed areas on each side of raised interstriae. Frons rugose, with a distinct median keel. 3.0 mm long. Oriental Region, Palearctic Region. ...*X. jaintianus* (Schedl) (Fig. 2.27)
- Declivital face flattened, without interstriae elevated toward apex. Frons punctate, without a distinct median keel. 2.8 mm long. Oriental Region. ...*X. subsimiliformis* (Eggers) (Fig. 2.40)
- 14 (10) Declivital striae and interstriae granulate with appressed, hair-like setae. ...15
- Declivital striae coarsely granulate, without setae. Interstriae granulate, with erect, hair-like setae, longer than twice the width of second declivital interstriae. 1.8 – 2.3 mm long. Oriental Region. ...*X. diversepilosus* (Eggers) (Fig. 2.21)
- 15(14) Granules on interstriae dense and closely placed, giving the declivity a matte appearance. Smaller species, 2.0 – 2.1 mm long. Oriental Region. Palearctic Region. ...*X. borealis* Nobuchi (Fig. 2.11)
- Granules on interstriae less densely and closely placed, giving the declivity a shining appearance. Larger species, 2.5 – 2.8 mm long. Oriental Region, Palearctic Region. ...*X. brevis* (Eichhoff) (Fig. 2.13)
- 16 (3) Declivital striae and interstriae densely, finely, and confusedly granulate. Pronotum of equal length and width. ...17

- Declivital striae and interstriae not densely, finely, and confusedly granulate.
Striae punctate. Pronotum wider than long. ...18

- 17 (16) Pronotum with a lateral costa, but without a carina. Elytral disc multiseriate punctate. Six striae visible on elytral declivity. Striae with erect, hair-like setae, shorter than the width of second declivital interstriae. Interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Frons rugose. 1.7 – 2.9 mm long. Afrotropical Region, Australian Region, Nearctic Region, Neotropical Region, Palearctic Region, Oceania, Oriental Region. ...***X. crassiusculus* (Motschulsky)** (Fig. 2.16)

- Pronotum with a lateral costa and carina. Elytral disc uniseriate punctate. Five striae visible on elytral declivity. Striae and interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Frons punctate. 1.9 – 2.2 mm long. Afrotropical Region. ...***X. hirsutipennis* (Schedl)** (Fig. 2.25)

- 18 (16) Pronotum with a lateral costa and carina. ...19

- Pronotum with a lateral costa, but without a carina. ...27

- 19 (18) At least first interstriae on elytral disc multiseriate punctate. ...20

- All interstriae on elytral disc uniseriate punctate. ...21

- 20 (19) Elytral disc with interstriae densely punctured. Declivital interstriae multiseriate granulate. Declivital surface matte in appearance. Stouter species, 2.0 times

longer than wide; elytra of equal length and width. 1.6 – 2.3 mm long. Oriental Region. ...***X. assequens* Schedl** (Fig. 2.10)

- Elytral disc with interstriae more sparsely punctured, multiseriate only on first interstriae. Declivital interstriae uniseriate granulate. Declivital surface shining. More elongate species, 2.2 times longer than wide; elytra 1.4 times longer than wide. 1.8 mm long. Oriental Region. ...***X. deruptulus* (Schedl)** (Fig. 2.19)

21 (19) Declivital striae with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. ...22

- Declivital striae without setae. ...24

22 (21) Pronotal disc glabrous, except for a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium. Elytra strongly arched from base to middle of declivity. 1.3 – 1.5 mm long. Nearctic Region, Neotropical Region. ...***X. curtulus* (Eichhoff)** (Fig. 2.17)

- Pronotal disc more evenly pubescent, with a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium. Elytra more evenly arched from middle of disc to apex. ...23

23 (22) Body very stout, 1.9 times as long as wide. 1.5 – 1.7 mm long. Oriental Region. ...***X. pusillus* (Schedl)** (Fig. 2.36)

- Body less stout, 2.3 times longer than wide. 1.4 – 1.9 mm long. Afrotropical Region, Nearctic Region, Neotropical Region, Oceania, Oriental Region. ...***X. compactus* (Eichhoff)** (Fig. 2.14)
- 24 (21) Smaller species, 1.4 mm long. Pronotum of equal length and width. Declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than the width of second declivital interstriae. Oriental Region. ...***X. mediocris* (Schedl)** (Fig. 2.29)
- Larger species, 1.8 – 2.5 mm long. ...25
- 25 (24) Pronotum wider than long or of equal length and width. Pronotal disc glabrous, except for a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium. ...26
- Pronotum 1.1 times longer than wide. Pronotal disc more evenly pubescent, with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. 1.9 – 2.5 mm long. Nearctic Region, Oceania, Oriental Region, Palearctic Region. ...***X. germanus* (Blandford)** (Fig. 2.24)
- 26 (25) Pronotum wider than long. Declivital interstriae uniseriate granulate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. 2.0 mm long. Oriental Region. ...***X. adherescens* Schedl** (Fig. 2.7)
- Pronotum of equal length and width. Declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of second declivital

interstriae. 1.8 – 2.1 mm long. Oriental Region. ...*X. eupatorii* (Eggers) (Fig. 2.22)

27 (18) Body bicolored, with pronotum distinctly lighter than elytra or with a testaceous patch on elytra basally and laterally. ...28

– Body uniformly colored, light to dark brown. ...31

28 (27) Pronotum and elytral apices dark brown, elytra with a testaceous patch basally and laterally. Elytral disc with interstriae mutliseriate. Declivital interstriae multiseriate punctate, with erect, hair-like setae, longer than twice the width of second declivital interstriae. 2.4 – 2.7 mm long. Australian Region. ...*X. hulcri* n. sp. (Fig. 2.26)

– Pronotum distinctly lighter than elytra; elytra without a testaceous patch. ...29

29 (28) Smaller species, 1.1 – 1.3 mm long. Declivital striae with setae. Interstriae with erect, hair-like setae, longer than the width of second declivital interstriae. Australian Region, Oriental Region. ...*X. mesuae* (Eggers) (Fig. 2.30)

– Larger species, 1.6 – 2.5 mm long. ...30

30 (29) Six striae visible on elytral declivity. Declivital striae with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae punctate. Pronotum distinctly lighter than elytra; pronotum light brown and elytra black.

Body 2.3 times longer than wide. Larger species, 2.3 – 2.5 mm long. Oriental Region. ...***X. arquatus* (Sampson)** (Fig. 2.9)

- Five striae visible on elytral declivity. Declivital striae without setae. Interstriae granulate. Pronotum distinctly lighter than elytra; pronotum light brown and elytra dark brown. Smaller species, 1.6 – 1.8 mm long. Oriental Region. ...***X. ferinus* (Schedl)** (Fig. 2.23)

31 (27) Five striae visible on elytral declivity. Declivital striae with semi-appressed, hair-like setae. Interstriae multiseriate. Larger species, 2.6 – 2.7 mm long. Australian Region. ...***X. mixtus* (Schedl)** (Fig. 2.32)

- Six striae visible on elytral declivity. Declivital striae without setae. Interstriae uniseriate. Smaller species, 1.8 mm long. Oriental Region. ...***X. metagermanus* (Schedl)** (Fig. 2.31)

32 (1) Margin of elytral declivity rounded or with a discontinuous row of small tubercles. Elytral disc with multiseriate interstitial punctures. ...33

- Margin of elytral declivity serrate. Elytral disc with uniseriate interstitial punctures. ...35

33 (32) Margin of elytral declivity with a discontinuous row of small tubercles. Five striae visible on declivity. Smaller species, 2.3 – 2.4 mm long. Australian Region. ...***X. woodi* Dole and Beaver** (Fig. 2.42)

- Margin of elytral declivity rounded. Six striae visible on declivity. Larger species 3.0 – 4.1 mm long. ...34
- 34 (33) Basal pronotum lacking a dense patch of setae. Declivital striae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae multiseriate granulate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Smaller species, 3.0 – 3.4 mm long. Australian Region. ...*X. monteithi* **Dole and Beaver** (Fig. 2.33)
- Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Declivital striae with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of second declivital interstriae. Larger species, 3.7 – 4.1 mm long. Australian Region. ...*X. rotundicollis* (**Browne**) (Fig. 2.39)
- 35 (32) Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Body unicolorous. Six striae visible on elytral declivity. Striae granulate. Smaller species, 1.6 – 2.1 mm long. ...36
- Basal pronotum lacking a dense patch of setae. Body bicolored, pronotum distinctly darker than elytra. Five striae visible on elytral declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae multiseriate granulate, with erect, hair-like setae, longer

than the width of second declivital interstriae. Larger species, 2.7 – 3.0 mm long.

Oriental Region. ...*X. corthyloides* (Schedl) (Fig. 2.15)

36 (35) Elytral disc gradually curving into declivity. Declivity shining. Declivital striae

with appressed, hair-like setae, shorter than the width of second declivital

interstriae. 1.9 – 2.1 mm long. Australian Region. ...*X. abruptulus* (Schedl)

(Fig. 2.6)

– Declivital face steep and abruptly separated from disc. Declivity matte. Striae

with erect, acutely tapering, hair-like setae, shorter than the width of second

declivital interstriae. 1.6 – 1.9 mm long. Australian Region. ...*X. queenslandi*

Dole and Beaver (Fig. 2.38)

37 (2) Declivital striae with a row of large, shallow punctures, arranged in a somewhat

wavy line. Declivital interstriae shining, not densely granulate. Stouter species,

1.2 – 1.4 times as long as wide. Smaller species, 2.9 – 3.3 mm long. Afrotropical

Region and Oriental Region. ...*X. mancus* (Blandford) (Fig. 2.28)

– Declivital striae with smaller punctures arranged in perfectly straight rows.

Declivital interstriae densely and finely granulate-punctate, giving the declivity a

matte appearance. More elongate species, 2.5 times as long as wide. 2.7 – 2.9

mm long. ...*X. amputatus* (Blandford) **n. comb.** (Fig. 2.8)

Taxonomy

Genus *Xylosandrus* Reitter

Xylosandrus Reitter 1913: 80, 83. Type-species: *Xylosandrus morigerus* Blandford.

Apoxyloborus Wood 1980: 90. Type-species: *Xyleborus mancus* Blandford, original designation. Synonymy: Wood 1984: 229.

Diagnosis. *Xylosandrus sensu stricto* can be distinguished from other xyleborine genera by the following combination of characters: the stout body, usually about twice as long as wide, widely separated procoxae, flat scutellum that is flush with the surface of elytra, and obliquely truncate antennal club with the first segment forming a circular costa and dense pubescence on the oblique portion of the club.

Xylosandrus abruptulus (Schedl)

(Fig. 2.6)

Xyleborus abruptulus Schedl, 1953: 81. Lectotype ♀: Australia, Wongabel, 2 May 1941, A. R. Brimblecombe, from *Loranthus* sp.; NHMW; designated by Schedl, 1979a: 9.

Xylosandrus abruptulus (Schedl): Schedl, 1964: 213.

Notes. Schedl (1953) failed to designate a holotype in his original description of *X. abruptulus* and subsequently designated a lectotype (Schedl 1979a).

Diagnosis. Female 1.9 – 2.1 mm long; 2.1 times longer than wide. Body brown; antennae and legs same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed hair-like setae; setae less dense on disc. Basal pronotum with a dense

patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae with 7 – 8 socketed teeth. Elytra 1.3 times longer than wide; 1.7 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margin with coarse serrations. Six striae visible on declivity. Striae granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of three *Xylosandrus* with lateral declivital marigins that are marked by coarse serrations: *X. abruptulus*, *X. corthyloides* (Fig. 2.15), and *X. queenslandi* (Fig. 2.38). *Xylosandrus abruptulus* can be distinguished from these species by the following characters: body unicolorous; basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium; elytral disc gradually curving into declivity; six striae visible on elytral declivity; and declivital striae punctate with appressed, hair-like setae, shorter than the width of second declivital interstriae.

Distribution. AUSTRALIAN REGION: Queensland.

Hosts. *Loranthus* L. sp.

Specimens Examined. (12 ♀; 0 ♂)

Type material: Lectotype *Xyleborus abruptulus* (♀; NHMW). Syntype: Australia, Wongabel, 2 May 1941, A. R. Brimblecombe, from *Loranthus* sp. (♀; BMNH).

Other material: **AUSTRALIAN REGION: Queensland:** N. Qld., Mt Finnigan Summit via Helenvale, 28-30 Nov 1985, G. Monteith and D. Cook, Pitfall traps, rainforest (1 ♀; RAB); N. QLD, Wallaman Falls Rd, 600 m, 14 Dec 1986 - 2 Jan 1987, Monteith, Thompson, and Hamlet, RF, Flight intercept trap (1 ♀; RAB); N. Qld., Mossman Bluff Track, 5-10 km W Mossman, Site 9, 1260 m, 1-17 Jan 1989, Monteith, Thompson, and Anzsies, flt. intercept (2 ♀; RAB); N. Qld., Mossman Bluff Track, 5-10 km W Mossman, Site 7, 7100 m, 20 Dec 1989 - 15 Jan 1990, Monteith, Thompson, and Anzsies, flt. intercept (1 ♀; RAB); N. E. QLD, Cardwell Range, Upper Broadwater Ck Valley, 750 m, 17-20 Dec 1986, Monteith, Thompson, and Hamlet, Flight intercept trap (1 ♀; RAB); NEQ: 17°26'S, 145°42'E, Hughes Road, Topaz, 650 m, 6 Dec 1993 - 25 Feb 1994, Monteith, Cook, Janetzki, RF Pitfalls (1 ♀; RAB); NEQ: 16°24'Sx145°17'E, Upper High Falls Ck., 1000 m, 25 Jan - 12 Feb 1996, R. Wertz, Flight intercept trap (1 ♀; RAB); N. E. Qld, Kirrama Range, (Douglass Ck Rd, 800 m), 10 Dec 1986 - 11 Jan 1987, Monteith, Thompson, and Hamlet, RF, Flight intercept trap (2 ♀; RAB).

Xylosandrus adherescens Schedl

(Fig. 2.7)

Xylosandrus adherescens Schedl, 1971: 375. Holotype ♀: Hui (?), Chuo Chan [Tonkin], Nov. 03; NHMW.

Diagnosis. Female 2.0 mm long; 2.0 times longer than wide. Body light brown to brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide.

Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimen examined with. Elytra 1.3 times longer than wide; 1.5 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margin carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. eupatorii* (Fig. 2.22) and *X. germanus* (Fig. 2.24). These three species share the following characters: elytral disc gradually curving into declivity; pronotum with a lateral carina; interstriae on elytral disc uniseriate punctate; and declivital striae with semi-appressed, hair-like setae, shorter than the width of the second declivital interstriae. *Xylosandrus adherescens* can be distinguished from these species by the following characters: pronotum wider than long; pronotal disc glabrous, except for a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium; and declivital interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

Distribution. ORIENTAL REGION: Vietnam (Tonkin Island).

Hosts. Unknown.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Holotype *Xylosandrus adherescens* (♀; NHMW).

Xylosandrus amputatus (Blandford), **new combination**

(Fig. 2.8)

Xyleborus amputatus Blandford, 1894b: 575. Holotype ♀: Japan: Higo; BMNH.

Amasa amputatus (Blandford): Wood and Bright, 1992: 682.

Notes. This species was first included in *Amasa* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Diagnosis. Female 2.7 – 2.9 mm long; 2.5 times longer than wide. Body light brown to brown; declivity distinctly darker than rest of elytra; legs and antennae the same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 1.0 – 1.1 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely punctate, with punctures separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; meso- and metatibiae with 11 socketed teeth. Elytra 1.3 times longer than wide; 2.3 – 2.4 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital

face of elytra steep and abruptly separated from disc. Declivity concave, lateral margins carinate, with carina extending beyond 7th interstriae, forming a circumdeclivital ring. Four striae visible on declivity. Striae punctate, without setae. Interstriae finely granulate-punctate, without setae.

This species is one of two *Xylosandrus* with the margin of the elytral declivity with a carina that extends beyond the 7th interstriae, forming a circumdeclivital ring: *X. amputatus* and *X. mancus* (Fig. 2.28). *Xylosandrus amputatus* can be distinguished from *X. mancus* by the following characters: 2.5 times as long as wide; declivity without setae; declivital striae with smaller punctures arranged in perfectly straight rows; and declivital interstriae densely and finely granulate-punctate, giving the declivity a matte appearance.

Distribution. ORIENTAL REGION: China, Japan, Taiwan.

Hosts. *Acer* L. sp., *Cinnamomum mairei* H. Lév., *Cinnamomum* L. sp., *Machilus* Nees sp., *Pelargonium hortorum* L. H. Bailey, *Ziziphus jujuba* Lam.

Specimens Examined. (3 ♀; 0 ♂)

Type material: Unable to examine type material.

Other material: **ORIENTAL REGION: China** Gang-keu, SW. Fukien, S, China, VII-26-36, L. Gressitt Collection (1 Homotype ♀; USNM); **Japan:** Okinawa Id, June 23, 1945, F. N. Young, No 54 (1 ♀; USNM); Japan: Kagoshima Pref., Tarumizu Oonohara. Broadleaf forest, 425 m, 14 Aug 2000, Yoshikazu Sato Coll., Ex; ETOH-baited trap (1 ♀; USNM).

Xylosandrus arquatus (Sampson)

(Fig. 2.9)

Xyleborus arquatus Sampson, 1912: 246. Holotype ♀: Ceylon [Sri Lanka]; BMNH.

Xylosandrus arquatus (Sampson): Schedl, 1964: 213.

Diagnosis. Female 2.3 – 2.5 mm long; 2.3 times longer than wide. Pronotum distinctly lighter than elytra; pronotum light brown and elytra black; antennae and legs light brown. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum basic (type 2, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Base of pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately granulate. Pronotum moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 8 socketed teeth; metatibiae with 8 socketed teeth. Elytra 1.4 times longer than wide; 1.5 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae punctate, uniseriate, with erect, hair-like setae, shorter than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus*, *X. discolor* (Fig. 2.20), *X. ferinus* (Fig. 2.23), and *X. mesuae* (Fig. 2.30). *Xylosandrus arquatus* can be distinguished from *X. discolor* by the

following characters: elytral disc gradually curving into declivity. *Xylosandrus arquatus* can be distinguished from *X. ferinus* and *X. mesuae* by the following characters: 2.3 – 2.5 mm long; pronotum light brown and elytra black; six striae visible on elytral declivity; declivital striae with erect, hair-like setae; and declivital interstriae punctate.

Distribution. ORIENTAL REGION: Sri Lanka.

Hosts. *Cinnamomum* L. spp., “*Kududavula* sp.” (Sri Lanka), *Symplocos loha* Buch.-Ham. ex D. Don.

Specimens Examined. (29 ♀; 0 ♂)

Type material: Unable to examine type material.

Other material: **ORIENTAL REGION: Sri Lanka:** Ceylon [Sri Lanka] (1 ♀; NHMW); Sri Lanka: Bad. Dist., Pattopola, 200 mtrs., 3 June 1975, S. L. Wood, *Kududavula* sp. (2 ♀; USNM); Sri Lanka: Mat. Dist., Enselwatte, 800 mtrs., 25 May 1975, S. L. Wood, misc. hosts (1 ♀; USNM); Sri Lanka: N. E. Dist., 11 km SE Nuara Eliya, 1 June 1975, 2000 m. S. L. Wood, collected from branches (1 ♀; USNM); Sri Lanka: N. E. Dist., 11 km SE Nuara Eliya, 1 June 1975, 2000 m. S. L. Wood. Host: *Symplocos loha* (18 ♀; USNM); Sri Lanka: N. E. Dist., 11 km SE Nuara Eliya, 1 June 1975, 2000 m. S. L. Wood, collected from twigs (6 ♀; USNM).

Xylosandrus assequens Schedl

(Fig. 2.10)

Xylosandrus assequens Schedl, 1971: 376. Holotype ♀: Malaya, Kelantan, Bukit Kabong, 14.ii.1947, in *Xanthophyllum* sp., F. G. Browne.; BMNH.

Diagnosis. Female 1.6 – 2.3 mm long; 2.0 times longer than wide. Body brown to dark brown; antennae and legs light brown. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Pronotum punctate basally; lacking a dense patch of setae. Pronotal disc densely punctate, with punctures separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 9 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.3 times longer than wide; 1.7 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate; striae and interstriae confused on disc. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. deruptulus* (Fig. 2.19). *Xylosandrus assequens* can be distinguished from *X. deruptulus* by the following characters: 2.0 times longer than wide; elytra of equal length and width; elytral disc with interstriae densely punctured; declivital interstriae multiseriate; and declivital surface matte in appearance.

Distribution. ORIENTAL REGION: Brunei, Malaysia.

Hosts. *Xanthophyllum* Roxb. sp.

Specimens Examined. (7 ♀; 0 ♂)

Type material: Holotype *Xylosandrus assequens* (♀; BMNH).

Other material: **ORIENTAL REGION: Brunei:** BRUNEI: Temburong: Nr. K.

Belalong Field Study Centre 150 m, 4°33'N 155°09'E, 5-8.iii.1992, R. A. Beaver,

RGS/UBD Exped. Pitfall trap (1 ♀; RAB); BRUNEI: Temburong: Nr. K. Belalong Field

Study Centre 100 m, 4°33'N 155°09'E, 12-14.iii.1992, R. A. Beaver, RGS/UBD Exped. (2

♀; RAB); BRUNEI: Temburong: Nr. K. Belalong Field Study Centre 150 m, 4°33'N

155°09'E, 22-24.ii.1992, R. A. Beaver, RGS/UBD Exped. Pitfall trap (1 ♀; RAB);

BRUNEI: Temburong: Nr. K. Belalong Field Study Centre 150 m, 4°33'N 155°09'E, 26-

29.ii.1992, R. A. Beaver, RGS/UBD Exped. Pitfall trap (1 ♀; RAB); **Malaysia:**

MALAYSIA: Sabah Sipitang, Mendolong, T6/R, 31.iii.1989, leg. S. Abdebratt (1 ♀;

RAB).

Xylosandrus beelsoni Saha, Maiti, and Chakraborti

(Illustrated in Saha et al. 1992)

Xylosandrus beelsoni Saha, Maiti, and Chakraborti, 1992: 11. Holotype ♀: India:

Rangirum (1846 m), Darjiling Dist., coll. J. C. M. Gardner, 8.ix.1929, ex. “*Symplocos*

theaeifolia” [*Symplocos theifolia*].

Diagnosis. Female 2.8 – 2.9 mm long; 2.0 times as long as wide. Body yellowish brown. Frons reticulate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum wider than long. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc densely setose.

setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; meso- and metatibiae with 8 socketed teeth. Elytra longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytral steep and abruptly separated from disc. Declivity convex, lateral margins carinate to 7th interstriae. Five striae visible on declivity with striae 4 and 5 forming a loop. Striae granulate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with a single row of long hair-like setae along with a dense vestiture of shorter appressed setae.

This species is morphologically similar to *X. discolor* (Fig. 2.20), *X. jaintianus* (Fig. 2.27), and *X. subsimiliformis* (Fig. 2.40). *Xylosandrus beelsoni* can be distinguished from these species by the following characters: declivital face convex, five striae visible on declivity with striae 4 and 5 forming a loop, and declivital interstriae with a single row of long, erect, hair-like setae, along with a dense vestiture of shorter appressed setae.

Distribution. ORIENTAL REGION: India.

Hosts. *Symplocos theifolia* D. Don.

Specimens Examined. (0 ♀; 0 ♂)

Type material: Unable to examine type material.

Discussion. This species was described by Saha, Maiti, and Chakraborti (1992) from 4 female specimens from a single collecting event. All specimens are deposited in

collections in India (FRI and ZSI) and were not available for examination as part of this revision. However, based on the original species description and corresponding images, this *X. beelsoni* is clearly a member of the *Xylosandrus* sensu stricto group. The species description was also detailed enough that it could be utilized to score morphological characters for the phylogenetic analysis.

Xylosandrus borealis Nobuchi

(Fig. 2.11)

Xylosandrus borealis Nobuchi, 1981: 34. Holotype ♀: Honshu, Kyushu (Japan); Nobuchi Collection, Ibaraki, Japan.

Diagnosis. Female 2.0 – 2.1 mm long; 1.8 – 1.9 times as long as wide. Body yellowish brown to light brown; antennae and legs the same color as body. Frons rugose with a distinct median keel. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by a distance less than or equal to their size. Lateral aspect of pronotum prolonged anteriorly (type 9, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae with 8 socketed teeth. Elytra 1.0 – 1.3 times longer than wide; 1.1 times longer than pronotum. Discal

striae punctate; interstriae multiseriate punctate. Declivital face of elytral steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, hair-like setae shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. brevis* (Fig. 2.13). *Xylosandrus borealis* can be distinguished from *X. brevis* by the matte appearance of its elytral declivity, due to dense and closely placed interstitial granules, and by its smaller size of 2.0 – 2.1 mm.

Distribution. **ORIENTAL REGION:** Japan. **PALEARCTIC REGION:** Korea.

Hosts. *Camellia sasanqua* Thunb., *Styrax obassia* Siebold and Zucc.

Specimens Examined. (4 ♀; 0 ♂)

Type material: Unable to examine type material.

Other material: **ORIENTAL REGION: Japan:** Okusa, Japan, 20.VII.1935, Coll. K. Baba (4 ♀; USNM).

Xylosandrus borneensis Dole and Cognato, **new species**

(Fig. 2.12)

Description. Female (Fig. 2.12): 1.5 – 1.6 mm long, 2.1 times longer than wide, with pronotum yellowish brown, slightly darker toward apex, elytra brown, ventral side and appendages yellowish brown. Frons convex, shining, coriaceous, punctate between eyes, with deep, vertically elongate punctures, a single hair-like setae originating from each

puncture. Epistoma with row of short hair-like setae along lower margin. Eyes emarginate. Antennal funicle 5-segmented, scape and funicle with sparse, short, hair-like setae; club obliquely truncate, first segment sclerotized, forming a circular costa (type 1, Hulcr et al. 2007), circular costa closed anteriorly, oblique part of club densely pubescent, second segment not corneous; posterior face of club covered entirely by first segment (type 1, Hulcr et al. 2007). Pronotum of equal length and width, basic shape dorsally (type 2, Hulcr et al. 2007), widest about two-thirds pronotal length from base, anterior third broadly rounded toward apex, basal angles rounded, anterior margin with 8-10 asperities; anterior slope asperate, asperities smallest at summit and increasing in size toward anterior margin; disc moderately punctate, patch of denser punctures medially at base, hair-like setae originating from punctures, background sculpture finely granulate; lateral aspect of pronotum basic (type 0, Hulcr et al. 2007), lateral costa extending two-thirds pronotal length, lateral carina present only in basal $\frac{1}{4}$ of pronotum; pronotal vestiture of short, semi-appressed, hair-like setae. Scutellum triangular, flush with surface of elytra. Elytra 1.1 times longer than wide, 1.1 times as long as pronotum, parallel-sided on basal two-thirds and then broadly rounded toward apex; disc shining; declivity matte in appearance. Striae impressed beginning slightly before declivital origin and becoming more deeply impressed on declivity, shallowly and regularly punctate, punctures becoming less distinct on declivity, with very short, appressed setae originating from punctures. Interstriae equal the width of striae, finely granulate, giving a matte appearance, short (less than or equal to width of interstria), erect, hair-like setae in uniseriate rows; interstriae 4 - 6 not reaching apex of the declivity. Declivity commencing behind mid-point of elytra, abruptly and steeply separated from disc; lateral

margins carinate to 7th interstriae. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 7 - 8 socketed teeth; metatibiae with 8 - 9 socketed teeth. Abdominal ventrites evenly punctured, punctures with short and long, moderately appressed, hair-like setae.

Specimens Examined. (11 ♀; 0 ♂)

Type Material. Holotype ♀: MALAYSIA, Sabah, Danum Valley, 120 m asl. July 2006 Hulcr coll. Burseraceae, twig. Vial 1694. In MSU.

Paratypes ♀: MALAYSIA, Sabah, Danum Valley, 120 m asl. July 2006 Hulcr coll. Burseraceae, twig. Vial 1694. One paratype in FRCS. Nine paratypes in MSU. One paratype female was used for DNA extraction and remains are vouchered in MSU.

BRUNEI [DARUSSALAM]: Temburong: nr. K[uala] Belalong Field Stud[ies]. Centre, 4.33°N 115.09°E, 150m, 21.ii.1992 (R.A.Beaver). One paratype in RAB. MALAYSIA: Sabah, Sipitang, Mendolong, 11.v.1988 (2); 10.iii.1989 (1); 14.iii.1989 (2) (S.Adebratt). Three paratypes in MZLU; two in RAB.

Male: Unknown

Etymology. This species is named *borneensis* after the type locality.

Diagnosis. This species can be distinguished from all other known *Xylosandrus* by the deeply impressed declivital striae, which form six distinct ridges on the declivity. It is morphologically similar to *X. pygmaeus* (Fig. 2.38). *Xylosandrus borneensis* can be distinguished from *X. pygmaeus* by the following characters: pronotum without lateral carina; declivital striae more deeply impressed; six striae visible on elytral declivity; declivital striae without setae; and declivital interstriae finely granulate, giving the

declivital face a matte appearance, with erect, hair-like setae, shorter than the width of second declivital interstriae.

Distribution. ORIENTAL REGION: Malaysia (Sabah).

Hosts. Burseraceae.

Discussion. This species was found in association with the mycocleptes species *Xyleborus mucronatulus* Eggers (Hulcr 2008).

Xylosandrus brevis (Eichhoff)

(Fig. 2.13)

Xyleborus brevis Eichhoff, 1877: 121. Syntypes ♀: Nipon (Hagi Hiller) and Nipon Insula Asiatica; IRSNB.

Xylosandrus brevis (Eichhoff): Browne, 1965: 204.

Xyleborus cucullatus Blandford, 1894c: 121. Syntypes ♀: Kurigahara, and Konose in Higo, Japan; BMNH. Synonymy: Murayama 1954: 176.

Diagnosis. Female 2.5 – 2.8 mm long; 2.1 times longer than wide. Body dark brown; antennae and legs light brown. Frons rugose, with distinct median keel between eyes. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of dense, semi-appressed, hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by a distance less than or equal to their size.

Lateral aspect of pronotum prolonged anteriorly (type 9, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae with 10 – 11 socketed teeth. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity convex, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. borealis* (Fig. 2.11). *Xylosandrus brevis* can be distinguished from *X. borealis* by the shining appearance of its elytral declivity and by its larger size of 2.5 – 2.8 mm.

Distribution. ORIENTAL REGION: Japan, Taiwan, Thailand. **PALEARCTIC REGION:** China (Xizang [Tibet]), Korea, Nepal.

Hosts. *Berberis* L. sp., *Camellia japonica* L., *C. sasanqua* Thunb., *Cinnamomum japonicum* Siebold, *Diospyros kaki* Thunb., *Fagus crenata* Blume, *Grevillia* Knight sp., *Hamamelis* L. sp., *Lindera* Thunb. spp., *Machilus japonica* Siebold and Zucc., *Machilus thunbergii* Siebold and Zucc., *Maesa tenera* Mez, *Meliosma cuneifolia* Franch., *Parabenzoin praecox* Nakai, *Quercus* L. spp., *Smilax china* L., *Styrax obassia* Siebold and Zucc., *Viburnum* L. sp., *Weigela hortensis* C. A. Mey.

Specimens Examined. (25 ♀; 0 ♂)

Type material: Unable to examine type material.

Other material: **ORIENTAL REGION: Japan:** Japan: Kagoshima Pref., Tarumizu Oonohara, Broadleaf forest, 425 m, 14 May 2001, Yoshikazu Sato Coll. Ex; ETOH-baited trap (4 ♀; MSU); Japan, Ookusa, 20.VI.1933. Coll. K. Baba (3 ♀; USNM); JAPAN: RYUKYUS, Mt. Yonaha-dake, Okinawa-honto Is., 5.VI.1997, H. Goto leg.. Host tree: *Michilus japonica* sleb. Et Zucc. (4 ♀; RAB); Japan, Tamagowa, 29.VII.1980, *Fagus crenatus* (3 ♀; USNM); Japan, Tokyo, Takao, VII.31.1957, Coll. A. Nobuchi (4 ♀; USNM). **Taiwan:** TAIWAN: Taichung, Hsien: Shei-Pa N.P., 10.5.2004, J-T. Yang, Pitfall (5 ♀; RAB). **PALEARCTIC REGION: Nepal:** Nepal: Sikha 83°40'E, 28°26'N, 8000 ft. 24–26.v.1954. K. H. Hyatt. Litter in oak forest (2 ♀; BMNH).

Xylosandrus compactus (Eichhoff)

(Fig. 2.14)

Xyleborus compactus Eichhoff, 1875: 201. Syntypes 2 ♀, 1 ♂: Japan; NHMW (syntypes in Hamburg Museum lost).

Xylosandrus compactus (Eichhoff): Nunberg, 1959: 434.

Xyleborus morstatti Hagedorn, 1912: 37. Syntypes ♀: Amani, Deutsch-Ostafrika; Hamburg Museum, lost.

Xylosandrus morstatti (Hagedorn): Browne, 1963:55. Synonymy: Murayama and Kalshoven, 1962: 247.

Diagnosis. Female 1.4 – 1.9 mm long; 2.3 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal

aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 7 socketed teeth; metatibiae with 8 socketed teeth. Elytra 1.3 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae punctate-granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. curtulus* (Fig. 2.17) and *X. pusillus* (Fig. 2.36). It can be distinguished from *X. curtulus* by a pronotal disc that is evenly pubescent, rather than mostly glabrous. *Xylosandrus compactus* is nearly morphologically identical to *X. pusillus*. The only character distinguishing the two species is the degree of body stoutness, with *X. compactus* being 2.3 times as long as wide and *X. pusillus* being 1.9 times as long as wide. However, this is too large a disparity to warrant synonymizing the two species without further investigation.

Distribution. AFROTROPICAL REGION: Cameroon, Cameroon Islands (Grande Comoro), Equatorial Guinea, Fernando Poo, Gabon, Ghana, Ivory Coast, Liberia, Madagascar, Mauritania, Nigeria, Reunion Islands, Senegal, Seychelles Islands, Sierra Leone, South Africa, Tanzania, Uganda. **NEARCTIC REGION (Introduced)** United

States (Alabama, Florida, Louisiana, Mississippi North Carolina, East Texas).

NEOTROPICAL REGION: Brazil, Cuba, Peru, Puerto Rico, Virgin Islands.

OCEANIA: Hawaiian Islands (Hawaii, Kauai, Lanai, Maui, Molokai, Oahu), Samoan

Islands. **ORIENTAL REGION:** Bonin Islands, China (Guangdong), India (Tamil Nadu), Indonesia (Java), Japan, Malaya, Malaysia (Sabah), Philippine Islands, Ryukyu Islands, Sri Lanka, Taiwan, Thailand, Vietnam (Tonkin Island).

Hosts. *Acacia mangium* Willd., *Acalypha* L. sp., *Acer* L. sp., *Acrocarpus fraxinifolius* Wight and Arn., *Adenanthera pavonina* L., *Albizia chinensis* Merr., *A. lebeck* Benth., *A. zygia* (DC.) Macbride, *Ardisia paniculata* Roxb., *Aucoumea klaineana* Pierre, “Bamboo Orchid” (Hawaii), *Bauhinia* L. sp., *B. tomentosa* L., *Bombax malabaricum* DC., *Cajanus cajan* (L.) Millsp., *Camellia sinensis* Kuntze, *Cassia hirta* Wild., *C. mutijuna* Rich., *C. siamea* Lam., *C. tora* L., *Cattleya* Lindl. sp., *Cinnamomum camphora* (L.) J. Presl, *C. iners* Reinw., *C. zeylanicum* Broyn., *Clerodendron* Burm. sp., *Coffea* L. sp., *C. arabica* L., *C. bukobensis* Zimmermann, *C. canephora* Pierre., *C. liberica* Bull., *C. quillon* Wester, *C. robusta* L. Lind., *C. stenophylla* G. Don., *Cola nitida* (Vent.) Schott and End., *Crotalaria* L. sp., *Cryptocaria* Gay sp., *Dendrobium* Sw. sp., *D. phalaenopsis* Fitz., *D. veratrifolium* Lindl., *Desmodium ovalifolium* Guill., *Drypetes phyllanthoides* (Rock) Sherff, *Elaeis guineensis* Jacq., “Elderberry” (Singapore), *Enthandrophragma utile* Sprague, *Erythroxylon novagranatense* Hieron., *Eupatorium pallescens* DC., *Eusideroxylon zwageri* Teijsm., *Ficus aurea* Nutt., *F. soroceoides* Bar., *Gossypium* L. sp., *Haasia* Nees. sp., *Hopea parviflora* Bedd., *Ichthyomethia communis* S. F. Blake, *Indigofera suffruticosa* Mill., *Jacobinia* Moric. sp., *Khaya grandifoliola* C. DC., *K. senegalensis* A. Juss., *Leucaena glauca* Benth., *Litsaea cassiaefolia* Blume, *Mangifera*

indica L., *M. odorata* Griff., *Melia azedarach* L., *Muntingia calabura* L., *Myrciaria dubia* (H. B. and K.) McVaugh, *Nectandra angustifolia* Nees. and Mart., *Olea europaea* L., *Persea* Mill. sp., *Persa Americana* Miller, *P. gratissima* Gaertn., *P. indica* Sprang., “*Prosopis nudiflora*” (Java: Schedl 1962), *Quercus myrsinaefolia* Blume, *Rhizophora* L. sp., *Sambucus* L. sp., *S. canadensis* L., *S. javanica* Reinw., *Shorea* Roxb. ex. C. F. Gaertn. sp., *S. sumatrana* (Slooten) Desch., *Spathodea campanulata* P. Beauv., *Swietenia macrophylla* King, *S. mahagoni* Jack., *Tephrosia maxima* Pres., *Thea sinensis* L., *Theobroma cacao* L., *Toona sureni* Merr., *Turraeanthus africana* Pellegr., *Vanda coerula* Griff., *V. teres* Lindl., *V. tricolor* Lindl., *Vitex* L. sp., “Wild Grape” (Florida)..

Specimens Examined. (123 ♀; 8 ♂)

Type material: Syntypes *Xyleborus compactus* (2 ♀, 1 ♂; NHMW).

Other material: **AFROTROPICAL REGION: Ghana:** Ghana: Kumasi, 12.9.61 (6 ♀, 1 ♂; USNM). **Madagascar:** Madagascar: Prov. Flanarantsoa, 7 km W Ranomafana, 1100 m, 1-7 November 1988, W. E. Steiner (1 ♀; USNM). **NEARCTIC REGION: United States:** Florida: Dade Co. Coral Gables, Matheson Hammock Pk., 27 June 1980, O’Brien and Wibmer (1 ♀; CAS); Florida: Key Largo, 6.25.1951, Price Beamers – Wood, *Ichthyomethia communis* (1 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers – Wood (4 ♀, 1 ♂; USNM); Florida: Key Largo, 6.25.1951, Price Beamers – Wood, taken on wild grape (7 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers – Wood, *Ardisia paniculata* (4 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers – Wood, *Cajanus cajan* (6 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers – Wood, taken on *Ficus aurea* (1 ♀; USNM); Florida: Tallahassee, Fall, 1979, C. W. O’Brien, reared ex dogwood flags, emer. Sum 1980 (23 ♀; CAS); Florida, W.

Palm Beach, I.27.61 (6♀; USNM). **NEOTROPICAL REGION: Peru:** Perou-Loreto, Iquitos, Juin 1990, G. Couturier Col., Plante – Hôte, *Myrciaria dubia* (1 ♀; USNM). **Peurto Rico:** Peurto Rico: Carite St. For., VII.28.1999, C. W. O'Brien, P. Kovarik (1 ♀; CAS). **OCEANIA: Hawaiian Islands:** Hawaii: Mt. Puu Puae, Waianae Mts., Cahu 425 m., in twigs of *Drypetes phyllanthrides*, 1.VII.1970. W. C. Gagne Collector (1 ♀; NHMW); Hawaii: Oahu, Kailua, I. 1962, Ex *Vitex* sp. (10 ♀; CAS); Hawaii: Oahu, Kailua, I.2.62., ex. *Vitex* sp. Roy Hirata Coll. (2 ♀, 3 ♂; USNM); Hawaii: Oahu, Nuuanu, May 8, 1931, H. L. Lyon, Elderberry stems imported from Singapore (1♀; USNM); USA: HI: O'ahu I., N. Halawa Valley, NW of Honolulu, 390 m, 21o25'N, 157o51'W, 11-29.VI.1991, FMHD#91-4, Met. Polym.-Psidium-Hibiscus mixed nat./exotic forest, A. Newton and M. Thayer, #869, window trap (4 ♀; FMNH); Quarantine from Hawaii at Carpenteria, California, VI.20.2001, Ex. Bamboo Orchid (2 ♀; CSCA). **ORIENTAL REGION: India:** India: Coffee Research Station, Chilemagalur dist., Mysore, 2.I.1966 (7 ♀; CAS); South India: Nilgiri Hills, Devala, 3200 ft., XI.60, P. S. Nathan (23 ♀; 2 ♂; USNM). **Indonesia:** Java: Boger, VIII.1964, N. L. H. Krauss, Coffee (1 ♀; USNM); E. Java, Ma Lang, 10.1951, Planta nutrix, Coffea (4 ♀; USNM). **Sri Lanka:** Sri Lanka: Col. Dist., Labugama, 23 June 1975, S. L. Wood, collected from branches (1 ♀; USNM).

Xylosandrus corthyloides (Schedl)

(Fig. 2.15)

Xyleborus corthyloides Schedl, 1934: 86. Lectotype ♀: Java, Mount Gede, 800 m, ex Zingiberaceae; NHMW; designated by Schedl, 1979a: 66.

Xylosandrus corthyloides (Schedl): Wood and Bright 1992: 790.

Xyleborus percorthyloides Schedl, 1957: 85. Lectotype ♀: Java, Mount Gede, 800 m; NHMW; designated by Schedl, 1979a: 66. Synonymy: Wood and Bright 1992: 790.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a “new combination.” *Xyleborus percorthyloides* was also listed as a synonym (an “unneeded replacement of *corthyloides*”) by Wood and Bright (1992), but was not indicated as a “new synonymy.”

Diagnosis. Female 2.7 – 3.0 mm long; 2.1 times longer than wide. Body bicolored, pronotum distinctly darker than elytra; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Lacking a dense patch of setae at base of pronotum. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibial teeth not visible on specimens examined; metatibiae with 10 socketed teeth. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins with small serrations. Five striae visible on declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of three *Xylosandrus* with lateral declivital margins that are marked by coarse serrations: *X. abruptulus* (Fig. 2.6), *X. corthyloides*, and *X. queenslandi* (Fig. 2.38). *Xylosandrus corthyloides* can be distinguished from these species by the following characters: 2.7 – 3.0 mm long; basal pronotum lacking a dense patch of setae; body bicolored, pronotum distinctly darker than elytra; five striae visible on elytral declivity; and declivital striae punctate.

Distribution. ORIENTAL REGION: Indonesia (Java).

Hosts. Lingiberaceae, Zingiberaceae.

Specimens Examined. (2 ♀; 1 ♂)

Type material: Holotype *Xyleborus corthyloides* (♀; NHMW). Paratype *Xyleborus percorthyloides* Java: Mt. Gede, 14-IX-1922, 800 m, L. G. E. Kalshoven, Lingiberaceae (♀; NHMW). Allotype *Xyleborus percorthyloides* Java: Mt. Gede, 14-IX-1922, 800 m, L. G. E. Kalshoven, Lingiberaceae (♂; NHMW).

Xylosandrus crassiusculus (Motschulsky)

(Fig. 2.16)

Phlaeotrogus crassiusculus Motschulsky, 1866: 403. Syntypes ♀: published as Des Montagnes de Nura-Ellia, Ceylon types labeled India Occidentale; IZM.

Xylosandrus crassiusculus (Motschulsky): Wood, 1982: 766.

Xyleborus semiopacus Eichhoff, 1878: 334. Syntypes ♀: Nipom insula Japonica; Hamburg Museum, lost. Synonymy: Wood, 1969: 119.

Xyleborus semigranosus Blandford, 1896a: 211. Holotype ♀: Sumatra; BMNH.

Synonymy: Schedl 1959: 496.

Xyleborus ebriosus Niisima, 1909: 154. Holotype ♀: Sapporo, Japan; Nobuchi Collection, Ibaraki. Synonymy: Choo, 1983: 98.

Dryocoetes bengalensis Stebbing, 1908: 12. Syntypes ♀: Goalpara, Assam; FRI. Synonymy: Beeson, 1915: 297.

Xyleborus mascarenus Hagedorn, 1908: 379. Syntypes ♀: Mauritius, and Bomole et Amani in Deutsch-Ostafrika; NHMW (syntypes in Hamburg Museum lost). Synonymy: Eggers, 1923: 130.

Xyleborus okoumeensis Schedl, 1935: 271. Syntypes ♀: imported Okoume logs, Carlshafen, Hessen-Nassau [Germany]; NHMW. Synonymy: Schedl, 1959: 496.

Xyleborus declivigranulatus Schedl, 1936: 30. Lectotype ♀: Selangor, Malay Peninsula; NHMW; designated by Schedl, 1979a: 76. Synonymy: Schedl, 1959: 496.

Diagnosis. Female 1.7 – 2.9 mm long; 2.2 times longer than wide. Body light to dark brown; antennae and legs yellowish brown. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely punctate, with punctures separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated, though less so than in most *Xylosandrus* species. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae

with 14 – 16 socketed teeth. Elytra 1.2 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, carinate to 7th interstriae. Six striae visible on declivity. Striae granulate, with erect, hair-like setae, shorter than twice the width of second declivital interstriae. Interstriae granulate, multiseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. hirsutipennis* (Fig. 2.25). Both species have a declivital face that is matte in appearance due to densely, finely, and confusedly granulate striae and interstriae. *Xylosandrus crassiusculus* can be distinguished from *X. hirsutipennis* by the following characters: frons rugose; pronotum without a lateral carina; elytral disc multiseriate punctate; six striae visible on the elytral declivity; declivital striae with erect, hair-like setae shorter than the width of second declivital interstriae; and declivital interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

Distribution. **AFROTROPICAL REGION:** Cameroon, Congo, Equatorial Guinea, Fernando Poo, Gabon, Ghana, Ivory Coast, Kenya, Madagascar, Mauritania, Nigeria, Sierra Leone, Seychelles Islands, Tanzania, Zaire. **AUSTRALIAN REGION:** New Guinea. **NEARCTIC REGION (Introduced):** United States (Alabama, Delaware, Florida, Georgia, Kansas, Louisiana, Maryland, Mississippi, North Carolina, Oregon, South Carolina, Tennessee, Texas). **NEOTROPICAL REGION:** Costa Rica, Panama. **OCEANIA:** Hawaiian Islands (Hawaii, Kauai, Maui, Oahu), Micronesia (Palau Islands), New Caladonia, Samoan Islands. **ORIENTAL REGION:** Bonin Islands, Burma, Hong Kong (Fujian), China (Hunan, Sichuan), India (Andaman Islands, Assam, Bengal,

Himachal Pradesh, Madhya Pradesh, Maharashtra, Tamil Nadu, Uttar Pradesh), Indonesia (Borneo, Celebes, Java, Sumatra), Japan, Malaya, Malaysia (Sabah, Sarawak), Philippine Islands, Sri Lanka, Taiwan, Thailand, Vietnam. **PALEARCTIC REGION:** Bhutan, China (Xizang [Tibet]), Germany, Korea, Nepal.

Hosts. *Acacia* Mill. sp., *A. decurrens* Willd., *A. mangium* Willd., *Acrocarpus* J. R. Forst and G. Forst spp., *Adina rubescens* Hemsl., *Adinandra dumosa* Jack., *Adinobotrys atropurpureus* Dunn., *Afzelia bipindensis* Harms, *Agathis* Salisb. sp., *Albizia* Durazz. sp., *A. chinensis* Merr., *A. ferruginea* Benth., *A. gummifera* (Gmel.) C. A. Sm., *A. lebbek* L., *A. moluccana* Miq., *A. stipitata* Boivin, *A. zygia* (DC.) Macbride, *Alnus* Mill. sp., *Alstonia* R. Br. sp., *Altingia excelsa* Nor., *Amoora* Roxb. sp., *Angylocalyx pynaertii* De Wild., *Anisoptera* Korth. sp., *Anthonota fragrans* Baker, *Antiaris africana* Engl., *Antrocaryon micraster* A. Chev. and Guill., *Artocarpus* J. R. Forst. and G. Forst. sp., *A. chaplasha* Roxb., *Aucoumea klaineana* Pierre, *Barteria nigritiana* Hook., *Bauhinia tomentosa* L., *Bischofia javanica* Blume, *Buchanania arborescens* Blume, *B. sessilifolia* Blume, *Cacao* Mill. sp., *Calamus* L. sp., *Calophyllum tetrapterum* Miq., *Camelia sinensis* (L.) O. Kuntze., *C. thea* Link., *Canarium* L. sp., *Cannabis sativa* L., *Carapa procera* DC., *Carica papaya* L., *Carya illinoensis* (Wangenh.) Koch, *Caryota* L. sp., *Castanea argentea* Bl., *C. javanica* Blume, *Castanopsis* (D. Don) Spach spp., *Castilla elastica* Cerv., *Casuarina equisetifolia* L., *Cecropia* L. leaf petiole, *Cedrela toona* Roxb. ex Rottler and Willd., *Ceiba pentandra* Gaertn., *C. thoningii* A. Chev., *Celtis brownii* Rendl., *C. luzonicus* Warb., *C. mildbraedii* Engl., *C. zenkeri* Engl., *Chlorophora excelsa* Benth. and Hook., *Chloroxylon swietenia* DC., *Chrysophyllum* L. sp., *Cinchona* L. sp., *Cinnamaum camphora* (L.) J. Presl, *Cinnamomum* L. sp., *C. camphora* L., *Cistanthera* K.

Schum. sp., *Cleistopholis patens* Benth., *Coelocaryon preussii* Warb., *Coffea* L. sp., *C. robusta* L. Linden, *Cylicodiscus gabunensis* Harms, *Cynometra hankie* Harms, *Dacryodes pubescens* (Vermoesen) H. J. Lam., *Dactylocladus stenostachya* Oliv., *Dalbergia latifolia* Roxb., *D. sissoo* Roxb., *Dialium corbisieri* Staner, *D. pachyphyllum* Harms, *Dillenia pentagyna* Roxb., *Dimocarpus longan* Lour., *Dipterocarpus* C. F. Gaertn. spp., *D. baudii* Korth., *Distemonanthus benthamianus* Baill., *Doona zeylanica* Thwaites., *Dryobalanops* C. F. Gaertn. sp., *Drypetes leonensis* Pax. Var. *glabra* J. Léonard, *Elaeis guineensis* Jacq. (leafstalks), *Elaeocarpus sericeus* Stapf., “*Elaeocarpus tetrapterum*” (Wood and Bright 1992), *E. tuberculatus* Roxb., *Entandrophragma angolense* C. DC., *E. cylindricum* Sprague, *E. utile* Sprague, *Erythrina* L. spp., *E. lithosperma* Miq. var. *inermis* Kds. and Val., *Erythrophleum guineense* G. Don, *Eucalyptus deglupta* Blume, *Eucalyptus* L’Hér. sp., *E. robusta* Sm., *Eugenia caryophylla* St. Lag., *E. jambolana* Lam., *Eupatorium pallescens* DC., *Fagara macrophylla* (Oliv.) Engl., *Fagus crenata* Blume, *Ficus* L. spp., *Garcinia polyantha* Oliv., *G. punctata* Oliv., *Gliricidia maculate* H. B. and K., *Gluta tourtour* Marchand, *G. travancorica* Bedd., *Gmelina arborea* Roxb., *Gossweilerondendron balsamiferum* Harms, *Grevillea* Knight sp., *G. robusta* A. Cunn., *Guarea cedrata* A. Chev., *G. laurentii* De Wild., *Hannoa klaineana* Pierre, *Haronga paniculata* (Pert.) Lodd., *Hevea brasiliensis* (Willd. ex A. Juss) Müll. Arq., *Holigarna arnottiana* Hook., *Hopea beccariana* Burck, *H. ferrea* Heim, *H. odorata* Roxb., *H. parviflora* Bedd., *H. wightiana* Wall., “*Ilteocafus baudii*” [?] (China), *Julbernardia sereti* (De Wild.), *Khaya ivorensis* A. Chev., *Kayea floribunda* Wall., *Koompassia malaccensis* Maingay, *Lagerstroemia flos-reginae* Retz., *L. speciosa* Pres., *Lannea grandis* Enql., *Lasiococca* Hook. sp., Lauraceae sp., *Lecanodiscus*

cupanoides Planch., *Leea crispa* L., *L. sambucina* (L.) Willd., “Liana” [woody vine] (Sri Lanka), *Lithocarpus wallichiana* Rehder, *Lophira procera* A. Chev., *Lovoa klaineana* Pierre, *L. trichiliodes* Harms, *Luffa* Mill. sp., *Macaranga monandra* Müll.-Arg., *Machilus odoratissima* Nees., *Macrolobium* Schreb. sp., *M. macrophyllum* Harms, *Malus pumila* Mill., *Mangifera indica* L., *Mansonia altissima* A. Chev., *Melanorrhoea* Wall. sp., *Melochia umbellata* Stapf., *Microcos coriacea* (Mast.) Burret, *M. pinnatifida* (Mast.) Burret, *Mitragyna stipulosa* O. Ktze. Rev., *Murraya koenigii* Spreng., *Musanga cecropoides* R. Br., *Myrianthus arboreus* P. Beauv., *Myristica* L. sp., *Myristica dactyloides* Wall., *Napoleana imperialis* P. Beauv., *Nauclea (Sarcocephalus) diderichii* De Wild., “Nayabu” (Sri Lanka), *Ochthocosmus africanus* Hook., “*Octomeles sumatrana*” (Ohno 1990), *Ongokea gore* Engl., *Pachylobus deliciosus* Pellegr., *Palaquium gutta* Burck., *Pancovia laurentii* De Wild., *Parinari kerstingii* Engl., *Parishia* Hook. f. sp., *Parkia bicolor* A. Chev., *Pithecollobium lobatum* Benth., *Piptadenia africana* Hook., *Piptadeniastrum africanum* Benth., *Protium pittieri* Engl., *Pycnanthus angolensis* (Welw.) Exell., *Quercus* L. sp., *Q. serrata* Roxb., *Randia congolana* De Wild. and Th. Dur., *Ricinodendron heudelotii* (Baill.) Pierre, *Saccharum officinarum* L., *Sagraea laurina* Dalz., *Sandoricum* Cav. sp., *Sapium* P. Browne sp., Sapotaceae sp., *Scorodophloeus zenkeri* Harms, *Shorea* Roxb. ex. C. F. Gaertn. sp., *S. guiso* (Blanco) Blume, *S. macroptera* Dyer, *S. robusta* Gaertn., *Sindora* Miq. sp., *Sorindeia lameirei* De Wild., *Staidtia stipitata* Warb., *Sterculia macrophylla* Vent., *S. oblonga* Mater, *S. villosa* Roxb., *Strombosia glaucesens* Engl., *Strombosiopsis tetrandra* Engl., *Styrax bensoin* Dryand., *Swietenia macrophylla* King., *Synsepalum subcordatum* De Wild., *Tarieta utilis* Sprague, *Tectona grandis* L., *Terminalia ivorensis* A. Chev., *T. superba* Engl., *T.*

tomentosa W. and A., *Tessmannia africana* Harms, *T. anomala* Harms, *Tetrapleura* (Thonn.) Taub., *Thalia geniculata* L., *Thea sinensis* L., *Theobroma cacao* L., *Topobea maurofernandeziana* Cogn., *Trichilia heudelotii* Planch., *T. prieureana* Juss., *Triplochiton scleroxylon* K. Schum., *Turraneanthus africana* Benth., *Vernonia arborea* Ham., *V. conferta* Benth., *Vitis* L. sp., *Vochysia ferruginea* Mart., *Xanthophyllum affine* Korth.

Specimens Examined. (104 ♀; 2 ♂)

Type material: Lectotype *Xyleborus declivigranulatus* (♀; NHMW). Holotype *Xyleborus mascarenus* (♀; NHMW). Lectotype *Xyleborus okoumeensis*: In Okumé (♀; NHMW). Paratype *Xyleborus okoumeensis*: W. Africa: Gabun-vinde (♀; NHMW). Allotype *Xyleborus okoumeensis*: Germany: Carlshafen, Hess. Nassau, 17.8.28 (♂; NHMW). Neotype *Xyleborus semiopacus*: Formosa, Akau, 1-10.XII.1907, Hans Sauter leg., vend. 23.IV.1908 (♀; NHMW).

Other material: **AFROTROPICAL REGION: Congo:** Yangambi, 1952, C. Donis, z. 1345, Coll. R. Mayne, Com. Ét Bois Congo, R. 2598 (1 ♀; USNM). **NEOTROPICAL REGION: United States:** Alabama: Baldwin Co., Mobile – Apr 88, C. Kouskelekas (2 ♀; USNM); Quarentine from Florida at Costa Mesa, California, IX.5.2000, Ex.

Dimocarpus longan (1 ♀; CSCA); Mississippi: Harrison Co., Gulfport, 29 March 1985, John Davis, ex peach (healthy) (1 ♀; USNM); Mississippi: Stone Co. 29 March 1985, G. Weaver, ex plum (healthy) (1 ♀; USNM); Mississippi: Stoneville, Amer. Elm, 6-23-86, J. D. Solomon (2 ♀; USNM). **OCEANIA: Hawaiian Islands:** Hawaii, Hilo, Hav. Fern Wood, V-16-'53, Working in cut wood, C. J. Davis (1 ♀; USNM); Hawaii, Hilo, X-17-62, ex *Eucalyptus robusta*, R. Nelson (1 ♀; USNM); Oahu, Haleauau Val., 7-54, E. J.

Ford Collector (1 ♀; USNM); Oahu: Waianae Mts., 2-55, Ford (3 ♀; CAS); USA: HI: O'ahu I., N. Halawa Valley, NW of Honolulu, 390 m, 21°25'N, 157°51'W, 11-29.VI.1991, FMHD#91-4, Met. Polym.-Psidium-Hibiscus mixed nat./exotic forest. A. Newton and M. Thayer, #869, window trap (6 ♀; FMNH). **Micronesia:** Koror I., Palau Islds., Limestone ridge N. of inlet, 16 Jan. 1948 (1 ♀; USNM). **ORIENTAL REGION:** **Burma:** Burma: Mogaung, X.4.44, Cpt. L. C. Kuitert (1 ♀; USNM). **China:** China: Suisapa, 1000 m., Lichuan Distr., W. Hupah, VIII.21.48 (1 ♀; CAS); Salango, Kafang, 3.X.1949., F. G. Browne, ex *Ilteoeafus baudii* [?] (1 ♀; USNM). **India:** India: Dehra Dun. U. P., C. F. C. Beeson, 25.X.1915, ex *Cinnamaum cambhora* (1 ♀; USNM); S. India: Animalia Hills, April 1956, Cichona 3500 ft., P. S. Nathan (2 ♀; USNM); South India: Animalia Hills, Cincohona, V-60, 3500 ft., P.S. Nathan (1 ♀; USNM); S. India: Cinchona, Anamalai Hills, 3500 ft., V.1959, P. S. Nathan (1 ♀; NHMW); S. India: Coffee Re. Sta., 12-29 '59, *Coffea robusta* Lot 60-13752 (1 ♀; USNM); S. India: Madras. Coimbatore, IV-1956 1400 ft., P. S. Nathan (4♀; USNM); South India: Nilgiri Hills, Devala, 3200 ft., X-60, P. S. Nathan (2 ♀; USNM). **Indonesia:** Java, Leg. Kalshoven (2 ♀; USNM); Java, Bantam, Leg. Kalshoven, *Planta nutrix* Hena (10 ♀; USNM). **Japan:** Japan: Matskawa, 27-VII-1980, S. L. Wood (1 ♀; USNM); Okinawa: ID, Nov 16, 1945, F. N. Young (2 ♀; USNM); Japan: Tamagowa, 29-VII-1980, S. L. Wood *Fagus crenatus* (7 ♀; USNM); Japan: Tokyo, Takao, VIII.31.1957, Coll. Akira Nobuchi (2 ♀; USNM). **Philippine Islands:** Philippines, Mindanao, 1965, Krauss, Cacao trunk (1 ♀, 1 ♂; USNM). **Taiwan:** Taiwan: Raisya, 24.XI.1934, S. Issiki (1 ♀; NHMW). **Thailand:** Thailand: Chiangmai Prov., E. Fk. Mae Ping, 56 km N. Chiangmai, 1300', 24-Xi-1964, W. L. and J. G. Peters, at light (1 ♀; CAS). **Sri Lanka:** Sri Lanka: Col Dist., Labugama,

23 June 1975, S. L. Wood, Collected from branches (10 ♀; USNM); Sri Lanka: Col Dist., Labugama, 23 June 1975, S. L. Wood, Collected from twigs (2 ♀; USNM); Sri Lanka: Col. Dist., Labugama, 23 June 1975, S. L. Wood, Collected from *Liana* (1 ♀; USNM); Sri Lanka: Col Dist., Labugama 23 June 1975, S. L. Wood, Misc. hosts (1 ♀; USNM); Sri Lanka: Gal. Dist., Ugugama, Kanneliya Jungle, 400 ft., 6-12-X-1973, at black light, K. V. Krombein, P. E. Karunarante, P. Fernando, J. Fernando (1 ♀; USNM); Sri Lanka: Kal. Dist., Morapitiya, 250 mtrs., 27 May 1975, S. L. Wood, Misc. hosts (3 ♀; USNM); Sri Lanka: Ceylon: Kan. Dist., Kandy, 1-15 March 1971, Piyadasa and Sompala (1 ♀; USNM); Sri Lanka: Keg. Dis., Kitulhala, 200 m, 30 May 1975, S. L. Wood, Host: Nayabu (1 ♀; USNM); Sri Lanka: Keg. Dist., Kitulgala, 250 m., 27 May 1975, S. L. Wood, Collected from pole (1 ♀; USNM); Sri Lanka: Keg. Dist., Kitulgala, 200 m., 30 May 1975, S. L. Wood, Host: *Doona* sp. (2 ♀; USNM); Sri Lanka: Mat. Dist., Enselwatte, 800 mtrs. 25 May 1975, S. L. Wood, Misc. hosts (7 ♀; USNM); Sri Lanka: Rat, Dist., Gilimale, 17 May 1975, S. L. Wood, Host: *Myristica dactyloides* (3 ♀; USNM); Sri Lanka: Rat. Dist. Gilimale, 17 May 1975, S. L. Wood, Collected from pole (1 ♀; USNM). **PALEARCTIC REGION: Germany:** Germany: Carlshafen, Hess. Nassau, 17.8.28 (3 ♀; NHMW).

Xylosandrus curtulus (Eichhoff)

(Fig. 2.17)

Xyleborus curtulus Eichhoff, 1869: 281. Holotype ♀: Brazil: Patria; IRSNB.

Xylosandrus curtulus (Eichhoff): Wood, 1982: 770.

Xyleborus curtuloides Eggers, 1941a: 102. Holotype ♀: Guadeloupe (Gourbeyre); Eggers Collection (not listed by Anderson and Anderson, 1971 or Schedl, 1979a). Synonymy: Wood, 1982: 770.

Xyleborus biseriatus Schedl, 1963: 226. Holotype ♀: Nova Teutonia, Santa Catarina, Brazil; NHMW. Synonymy: Wood, 1973: 187.

Xylosandrus strumosus Schedl, 1972: 73. Holotype ♀: Brasilien, Corcovado, Guanabara; NHMW. Synonymy: Wood and Bright, 1992: 793.

Anisandrus zimmermanni Hopkins 1915: 67. Holotype ♀: Biscayne, Florida; USNM. Synonymy: Wood, 2007: 467.

Xylosandrus zimmermanni (Hopkins): Wood, 1962: 79.

Notes. Wood and Bright (1992) first list *Xylosandrus strumosus* as a synonym of *Xylosandrus curtulus*. The synonymy is referenced as “Wood 1992: (in press)”, but the synonymy did not appear in another publication.

Diagnosis. Female 1.3 – 1.5 mm long; 2.1 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae

with 7 socketed teeth. Elytra 1.3 times longer than wide; 1.5 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. compactus* (Fig. 2.14) and *X. pusillus* (Fig. 2.36). *Xylosandrus curtulus* can be distinguished from these species by the following characters: pronotal disc glabrous, except for a dense patch of short, erect, hair-like setae basally, indicating the presence of a pronotal-mesonotal mycangium; and elytra strongly arched from base to middle of declivity.

Distribution. NEARCTIC REGION (Introduced): United States (Florida).

NEOTROPICAL REGION: Antilles Islands (Guadeloupe), Brazil, Colombia, Costa Rica, Guatemala, Honduras, Mexico (Chiapas, Colima, Hidalgo, Nayarit, Oaxaca, San Luis Potosi, Varacruz), Venezuela.

Hosts. *Acer rubrum* L., “Anonillo” (Guatemala), *Ardisia* Gaertn. sp., *Byrsonima cotinifolia* H. B. and K., *Calliandra confusa* Sparque and Riley, *Cedrela odorata* L., *Chrysobalanus* L. sp., *Coffea canephora* var. *robusta* (Linden) A. Chev., *Cupania guatemalensis* Radlk., *Ficus* L. spp., *Inga* Scop. sp., *Nectandra* Roll. ex Rottb. sp., *Phoradendron robustissimum* Eichler, *Phoradendron* Nutt. spp., *Rheedia edulis* Planch. and Triana., *Serjania* Mill. sp., *Spondias mombin* L., *Tabebuia* Gomes ex. DC. sp., *Ocotea catesbyana* Sarq., *Dodonaea viscosa* Jacq..

Specimens Examined. (86 ♀; 3 ♂)

Type material: Holotype *Xyleborus biserialatus*; (♀; NHMW). Holotype *Xylosandrus strumosus* (♀; NHMW). Holotype *Anisandrus zimmermanni* (♀; USNM).

Other material: **NEARCTIC REGION: United States:** Florida: Sebring, 6-20-1951,

Price Beamers – Wood (1 ♀; USNM); Florida: Sebring, 6-20-1951, Price Beamers – Wood, *Ardisia* (7 ♀, 1 ♂; USNM); Florida: Sebring, 6-20-1951, Price Beamers – Wood, *Ocotea catsibiana* (1 ♀; USNM); Florida: Sebring, 6-20-1951, Price Beamers – Wood,

Red Maple (2 ♀, 1 ♂; USNM). **NEOTROPICAL REGION: Colombia:** Colombia:

Caicedonia near Sevilla, Aug. 1959, Coffee branches, Leg. Duque (1 ♀; USNM);

Colombia: El Bosque, Caicedonia (V.), Junio 1959, J. Restrepo, en Café (11 ♀, 1 ♂;

USNM); Colombia: 1959, leg. Beteem (1 ♀; USNM). **Costa Rica:** Costa Rica: Guapiles,

Lim. 300 ft., VIII-22-'66, S. L. Wood, unknown vine (2 ♀; USNM); Costa Rica: Santa

Ana, S. J., 4000 ft., VII-1-1963, S. L. Wood, Coffee (1 ♀; USNM); Costa Rica: Santa

Ana, S. J., 4000 ft., VIII-30-1963, S. L. Wood, *Rheedia edulis* (1 ♀; USNM); Costa Rica:

Santa Ana, S. J., 4000 ft., VIII-30-1963, S. L. Wood, unknown sapling (3 ♀; USNM);

Costa Rica: Santa Ana, S. J., 400 ft., VIII-1-1963, S. L. Wood, *Cupania guatemalensis* (9

♀; USNM); Costa Rica: San Ignacio, S. J., 4700 ft., VIII-5-1963, S. L. Wood, unknown

sapling (1 ♀; USNM); Costa Rica: Pandora, Lim., 150 ft., VIII-23-1963, S. L. Wood,

unknown shrub (4 ♀; USNM); Costa Rica: Tapnti Cart., 400 ft., VIII-17-1963, S. L.

Wood, *Calliandra confusa* (1 ♀; USNM). **Guatemala:** Guatemala: Palin, Esquintla, 100

ft., V-19-1964, S. L. Wood, *Anonillo* (1 ♀; USNM); Guatemala: Rodeo Esquintla, 500

ft., VI-4-1964, S. L. Wood, Unknown vine (1 ♀; USNM); Guatemala: Volcan de Agua,

3000 ft., V-19-1964, S. L. Wood, unknown twigs (1 ♀; USNM); Guatemala: Volcan de

Agua, 3000 ft., V-19-1964, S. L. Wood, unknown broken branch (1 ♀; USNM).

Honduras: Honduras: Zamorano, Moraz, 2200 ft., IV-18-1964, S. L. Wood, *Phoradendron robustissimum* (1 ♀; USNM); Honduras: Zamorano, Moraz, 2200 ft., *Serjania* (1 ♀; USNM). **Mexico:** Mexico: 2 mi W Armeria, Col., VI-28-1965, 200 ft., S. L. Wood, *Phoradendron* (2 ♀; USNM); Mexico: El Salto, S. L. P., VI-19-53, taken on *Ficus* (1 ♀; USNM); Mexico: Morelos, Ruinas de Xochicalco, S-322, 22E 82, 1200 m, Col Atkinson and Equihua, Hosp. *Dodonaea viscosa* (1 ♀; USNM); Mexico: Laguna Sta. Maria N., VII-6-1965, 3000 ft., S. L. Wood, unknown vine (1 ♀; USNM); Mexico: Romero 12 mi S, VI-24-1967, OAX, S. L. Wood, *Phoradendron* (1 ♀; USNM); Mexico: 5 mi N Rosamorada N., VII-15-1965, 300 ft., S. L. Wood, unknown broken branch (2 ♀; USNM); Mexico: Romeo, 23 mi N VC, 300 ft., S. L. Wood, unknown branch (1 ♀; USNM); Mexico: Tapachula Chis, 21 VIII 82, Col. A. B. Celis, *Coffea coneophora* var. *robusta* (1 ♀; USNM); Mexico: Vera Cruz, 16 mi S Tecolutla, VI-26.53 (8♀; USNM).

Venezuela: Venezuela: S. of Barrancas, Barinas, 150 m., XI-5-69, S. L. Wood, *Spondias mombin* (1 ♀; USNM); Venezuela: 9 km S. of Barrancas, Barinas, 150 m., XI-15-69, S. L. Wood, *Inga* (1 ♀; USNM); Venezuela 40 km, E. Canton-Barinas, III-8-1970, 70 m., S. L. Wood, unknown vine (1 ♀; USNM); Venezuela: 20 km SW El Vigia, Merida, XII-10 69, el. 50 m., S. L. Wood (1 ♀; USNM); Venezuela: Rancho Grande, Aragua, 1100 m., IV-9-1970, S. L. Wood, *Tabebuia* (3 ♀; USNM); Venezuela: Rancho Grande, Aragua, 1100 m., IV-9-1970, S. L. Wood, *Nectandra* sp. (5 ♀; USNM); Venezuela: 40 km SE Socopo, Barinas, I-25-1970, 150 m., S. L. Wood, Bejuco Blanco (1 ♀; USNM).

Xylosandrus derupteterminatus (Schedl)

(Fig. 2.18)

Xyleborus derupteterminatus Schedl, 1951: 64. Holotype ♀: Java, Mount Gede

IX.1932L. G. E. Kalshoven Coll., NHMW.

Xylosandrus derupteterminatus (Schedl): Schedl, 1964: 213.

Diagnosis. Female 2.0 – 2.3 mm long; 2.0 times longer than wide. Body dark brown to black; antennae and legs same color as body. Frons punctate, with distinct median keel between eyes. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with dense patch of short, erect setae indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae with 13 socketed teeth. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face of elytra steep, abruptly separated from disc. Declivity flattened, lateral margin carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. morigerus* (Fig. 2.35) and *X. terminatus* (Fig. 2.41). *Xylosandrus derupteterminatus* can be distinguished from *X. morigerus* by the following characters: face of elytral declivity flattened; and 5 striae

visible on declivity. *Xylosandris derupteterminatus* can be distinguished from *X.*

terminatus by the following characters: larger species, 2.0 – 2.3 mm long; declivital striae with erect, hair-like setae; and declivital interstriae multiseriate granulate.

Distribution. ORIENTAL REGION: Indonesia (Java, Moluccas, Sulawesi).

Hosts. Unknown.

Specimens Examined. (10 ♀; 0 ♂)

Type material: Holotype *Xyleborus derupteterminatus* (♀;NHMW).

Other material: **ORIENTAL REGION: Indonesia:** INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot A, ca 200 m Lowland forest, May-85, Flight intercept trap (4 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot A, ca 200 m Lowland forest, Dec. 1985, suspended carrion (1 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, Apr-85, Flight intercept trap (2 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, Feb-85, Flight intercept trap (1 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., G.Mogogonipa summit, 1008 m., 22-24.x.85, yellow plate (1 ♀; RAB).

Xylosandrus deruptulus (Schedl)

(Fig. 2.19)

Xyleborus deruptulus Schedl, 1942b: 37. Lectotype ♀: Java, Mount Dede, 800 m, VIII-1923, Nr 54, Kalshoven; NHMW; designated by Schedl, 1979a: 78.

Xylosandrus deruptulus (Schedl): Schedl, 1964: 213.

Diagnosis. Female 1.8 mm long; 2.2 times longer than wide. Body brown; antennae and legs light brown. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of appressed, hair-like setae; setae less dense on disc. Specimen examined too damaged to determine whether pronotal mycangial setae are present. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Pro-, meso- and metatibial teeth not visible on specimen examined. Elytra 1.4 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate. Interstriae granulate, uniseriate. Specimen examined too damaged to determine states of declivital setae and setae not mentioned in original description (Schedl 1942b).

This species is morphologically similar to *X. assequens* (Fig. 2.10). *Xylosandrus deruptulus* can be distinguished from *X. assequens* by the following characters: more elongate, 2.2 times longer than wide; elytral disc with interstriae more sparsely punctured, multiseriate only on first interstriae; declivital interstriae uniseriate granulate; and declivital surface shining, not matte.

Distribution. ORIENTAL REGION: Indonesia (Java).

Hosts. Unknown.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Lectotype *Xyleborus deruptulus* (♀; NHMW).

Xylosandrus discolor (Blandford)

(Fig. 2.20)

Xyleborus discolor Blandford, 1898: 429. Holotype ♀: Ceylon, E. E. Green; BMNH.

Xylosandrus discolor (Blandford): Browne, 1963: 55.

Xyleborus posticestriatus Eggers, 1939b: 119. Lectotype ♀: Formosa (Taihoku); USNM; designated by Anderson and Anderson, 1971: 26. Synonymy: Schedl, 1958:149.

Xylosandrus posticestriatus (Eggers): Nunberg, 1959: 434.

Diagnosis. Female 1.8 – 2.0 mm long; 1.8 times longer than wide. Body bicolored; pronotum distinctly lighter than elytra; pronotum light brown and elytra dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of erect, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-punctate, with sculpture separated by distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 – 5 socketed teeth on lateral margin; meso- and metatibiae with 8 – 9 socketed teeth. Elytra of equal length and width; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriata punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity

flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, with appressed hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus* (Fig. 2.9), *X. discolor*, *X. ferinus* (Fig. 2.23), and *X. mesuae* (Fig. 2.30). *Xylosandrus discolor* can be distinguished from these species by the following characters: elytral declivity steep and abruptly separated from disc, and declivital striae and interstriae with a dense vestiture of appressed setae.

Distribution. AUSTRALIAN REGION: Queensland. OCEANIA: Micronesia.

ORIENTAL REGION: Burma, China (Fujian, Guangdong, Sichuan, Yunnan), India (Andaman Islands, Assam, Tamil Nadu, Uttar Pardesh), Indonesia (Java), Malaysia, Sri Lanka, Taiwan, Thailand.

Hosts. *Ailanthus altissima* (Mill.) Swingle, *Albizia* Benth. sp., “Avocado” (Java), *Bauhinia variegata* L., *Camellia sinensis* Kuntze, *Cassia multijuga* Rich., *Castanopsis fargesii* Franch., *Cedrela toona* Roxb. ex Rottler and Willd., *Chloroxylon swietenia* DC., *Coffea* L. spp., *Coffea Arabica* L., *C. robusta* L. Linden, *Cinnamomum camphora* (L.) J. Presl., *Eupatorium* L. sp., *Grevillea robusta* A. Cunn., *Hevea brasiliensis* (Willd. ex A. Juss) Müll. Arq., “Igall sp.” (Thailand), *Juglans nigra* L., “Liana” [woody vine] (Sri Lanka) sp., *Machilus indica* Kurz., “Mango” (Thailand), *Pterospermum acerifolium* Willd., “Rukaththana” (Sri Lanka), *Rhus chinensis* Mill., *Sophora japonica* L., *Swietenia mahagoni* (L.) Jacq., *Tephrosia candida* DC., *Terminalia myriocarpa* Van Heurck and Müll. Arq., *T. procera* Roxb., *Theobroma cacao* L., *Vitis vinifera* L.

Specimens Examined. (61 ♀; 4 ♂)

Type material: Lectotype *Xyleborus posticestriatus*: Formosa: Taihoku, 10.VII.1934, Col. M. Chujo (♀; NHMW). Cotype *Xyleborus posticestriatus*: XI.1926 (locality unreadable) (♂; NHMW).

Other material: **AUSTRALIAN REGION: Queensland:** AUSTRALIA: N. QLD, Iron Range, 26-31.X.1991, Wood, Dunn, and Hasenpusch (3 ♀; RAB); NE.Q: 16°54'S x 145°42'E, Whitefield Range, 550 m, 28 Aug - 19 Oct 1991, Monteith and Janetzki, Pitfall and Intercept traps (1 ♀; RAB). **ORIENTAL REGION: Indonesia:** Java, 565 m., Bandjar, VII.32, L. G. E. Kalshoven (1 ♀; NHMW); Java, Boger, VIII-1964, N. L. H. Krauss, avocado branch (4 ♀; USNM); W. Java: 800 m Mount Gedeh, 7.1933, Leg. Kalshoven, *Planta nutrix*, *Eupatorium* (1 ♀; USNM). **Malaysia:** Koror, Palau Is. Apr 1953, J. W. Beardsley (1 ♀; USNM). **Sri Lanka:** Ceylon [Sri Lanka], Hantane, XII.1962, Dr. D. Calnaido (1 ♀; NHMW); Ceylon [Sri Lanka]: Perdadeiya, 11.VII.1914, A. Rutherford (2 ♀; USNM); Ceylon [Sri Lanka], Sabargamuva, 12.XI.1950, E. Judenko (1 ♀; NHMW); Sri Lanka: Col. Dist., Labugama, 23 June 1975, S. L. Wood, Misc. hosts (4 ♀; USNM); Sri Lanka: Col. Dist., Labugama, 23 June 1975, S. L. Wood, collected from twigs (1 ♀; USNM); Sri Lanka: Mate. Dist., 48 km N Naula, 200 mtrs., 14 June 1975, S. L. Wood, Host: Rukaththana (1 ♀; USNM); Sri Lanka: Matte. Dist., 48 km, N Naula, 200 mtrs., 14 June 1975, S. L. Wood, collected from log (1 ♀; USNM); Sri Lanka: Mon. Dist., 8 km NW Bibile, 50 mtrs, 7 June 1975, S. L. Wood, collected from tree seedling (13 ♀; USNM); Sri Lanka: Mon. Dist., 8 km NW Bibile, 50 mtrs, 7 June 1975, S. L. Wood, collected from pole (2 ♀; USNM); Sri Lanka: Mon Dist. 8 km NW Bibile, 50 mtrs, 7 June 1975, S. L. Wood, collected from *Liana* (2 ♀; USNM); Sri Lanka: Rat.

Dist., Ratnapura, Resthouse, 200-300 ft., 24-X-1976, black light, Collected by: G. F. Hevel, R. E. Dietz, W. S. Karunaratne, D. W. Balasooriya (1 ♀; USNM). **Thailand:** THAILAND: Chiang Mai, 2.vii.72, R. A. Beaver, ex *Bauhinia variegata* (1 ♀; RAB); Thailand: Chiang Mai: Doi Inthanon, 5.viii.02, R. A. Beaver and K. Koivisto (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 13-14.iv.00, R. A. Beaver (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 12.x.93, R. A. Beaver, At light (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 1-3.I.2000, R. A. Beaver, M.T. (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 5.v.94, R. A. Beaver, At light (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 29-31.x.95, R. A. Beaver, M.T. (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 28.xi.02, R. A. Beaver, FIT (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 9.x.96, R. A. Beaver, ex mango twig (2 ♀; RAB); Thailand: Chiang Mai: Maerim, 5.x.96, R. A. Beaver, ex mango twig (1 ♀, 1 ♂; RAB); Thailand: Chiang Mai: Maerim, 21.ix.96, R. A. Beaver, ex mango twig (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 3.xii.96, R. A. Beaver, ex mango twig (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 16.x.96, R. A. Beaver, ex mango twig (1 ♂; RAB); Thailand: Chiang Mai: Maerim, 26.viii.99, R. A. Beaver, ex *Igall* sp. (1 ♀, 1 ♂; RAB); Thailand: Chiang Mai: Maerim, 23.vii.03, R. A. Beaver, FIT (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 10.xii.02, R. A. Beaver, FIT (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 18.xi.03, R. A. Beaver, FIT (1 ♀; RAB); THAILAND: Chiang Mai 300 m, Maerim, 16.I.92, R. A. Beaver (1 ♀; RAB); THAILAND: Chiang Mai 300 m, Maerim, 15.I.92, R. A. Beaver (1 ♀; RAB).

Xylosandrus diversepilosus (Eggers)

(Fig. 2.21)

Xyleborus diversepilosus Eggers, 1941b: 224. Holotype ♀: China, Prov. Fukien (Kuatun, 2300 m), 1.5.1938, L. J. Klapperich; ZMFK.

Xylosandrus diversepilosus (Eggers): Browne, 1963: 55.

Diagnosis. Female 1.8 – 2.3 mm long; 2.1 times longer than wide. Body light brown; antennae and legs yellowish brown. Frons not visible on specimen examined. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotal disc densely asperate-granulate, with sculpture separated by distance less than or equal to their size. Pronotum with lateral costa, carinate. Procoxae not visible on specimen examined. Pro-, meso- and metatibial teeth not visible on specimen examined. Elytra 1.2 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, without setae. Interstriae granulate, biseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. borealis* (Fig. 2.11) and *X. brevis* (Fig. 2.13). *Xylosandrus diversepilosus* can be distinguished from these species by the following characters: declivital striae coarsely granulate, without setae; and interstriae

granulate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

Distribution. **ORIENTAL REGION:** China (Fukian).

Hosts. Unknown.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Holotype *Xyleborus diversepilosus* (♀; ZMFK).

Xylosandrus eupatorii (Eggers)

(Fig. 2.22)

Xyleborus eupatorii Eggers, 1940: 140. Holotype ♀: Java (Tjibodas, G. Gedeh); Kalshoven Collection.

Xylosandrus eupatorii (Eggers): Schedl, 1964: 213.

Diagnosis. Female 1.8 – 2.1 mm long; 2.2 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimen examined. Elytra 1.2 times longer than wide; 1.2 times

longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital intrstriae.

This species is morphologically similar to *X. adherescens* (Fig. 2.7) and *X. germanus* (Fig. 2.24). *Xylosandrus eupatorii* can be distinguished from these species by the following characters: pronotum of equal length and width; pronotal disc glabrous, except for mycangial setae; and declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

Distribution. ORIENTAL REGION: Indonesia (Java).

Hosts. “*Eupatorium tjibeureum*” (Java).

Specimens Examined. (1 ♀; 0 ♂)

Type material: Cotype *Xyleborus eupatorii*: Java: Gedeh, 1700 M., VI.32, leg. H. R. A. Muller, *Eupatorium tjibeureum* (♀; NHMW).

Xylosandrus ferinus (Schedl)

(Fig. 2.23)

Xyleborus ferinus Schedl, 1936: 31. Lectotype ♀: India: Travancore Mt. Estate, Tamil Nadu, VII.1934, S. A. Ran, on red gum; NHMW; designated by Schedl, 1979a: 96.

Xylosandrus ferinus (Schedl): Browne, 1963: 55.

Notes. Schedl (1936) failed to designate a holotype in his original description of *X. ferinus* and subsequently designated a lectotype (Schedl 1979a).

Diagnosis. Female 1.6 – 1.8 mm long; 2.2 times longer than wide. Body bicolored, pronotum distinctly lighter than elytra; pronotum light brown and elytra brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 8 socketed teeth; metatibial teeth not visible on specimens examined. Elytra 1.4 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; insterstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, shorter than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus* (Fig. 2.9), *X. discolor* (Fig. 2.20), *X. ferinus*, and *X. mesuae* (Fig. 2.30). *Xylosandrus ferinus* can be distinguished from *X. discolor* by the following characters: elytral disc gradually curving into declivity. *Xylosandrus arquatus* can be distinguished from *X. mesuae* by its larger size of 1.6 – 1.8 mm long. *Xylosandrus ferinus* can be distinguished from *X. arquatus* by the following characters: five striae

visible on the elytral declivity; declivital striae without setae; and lighter color, with pronotum light brown and elytra brown.

Distribution. ORIENTAL REGION: India (Tamil Nadu).

Hosts. Red gum.

Specimens Examined. (2 ♀; 0 ♂)

Type material: Lectotype *Xyleborus ferinus* (♀; NHMW). Syntype *Xyleborus ferinus*:

India: Travancore Mt. Estate, Tamil Nadu, VII.1934, S. A. Ran, on red gum (♀; NHMW).

Xylosandrus germanus (Blandford)

(Fig. 2.24)

Xyleborus germanus Blandford, 1894c: 106. Syntypes (sex?); Oyayama, Nikko, Subashiri, Kiga, Miyanashita: BMNH.

Xylosandrus germanus (Blandford): Hoffmann, 1941: 38.

Xyleborus orbatus Blandford, 1894c: 123. Holotype ♀: Kurigahara, Japan; BMNH.

Synonymy: Choo, 1983: 100.

Notes on types: Browne (1963) wrongly lists *X. germanus* as the type species for *Xylosandrus*.

Diagnosis. Female 1.9 – 2.5 mm long; 2.3 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 1.1 times longer than wide.

Dorsal aspect of pronotum rounded (type1, Hulcr et al. 2007). Pronotal vestiture of semi-

appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 11 – 12 socketed teeth; metatibiae with 12 – 13 socketed teeth. Elytra 1.1 times longer than wide; 1.1 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. adherescens* (Fig. 2.7) and *X. eupatorii* (Fig. 2.22). *Xylosandrus germanus* can be distinguished from these species by the following characters: pronotum longer than wide; and pronotal disc evenly pubescent, not glabrous.

Distribution. NEARCTIC REGION (Introduced): Canada (British Columbia, Ontario, Quebec), United States (Connecticut, Delaware, Florida, Illinois, Indiana, Kentucky, Maine, Massachusetts, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, Virginia, West Virginia). **OCEANIA:** Hawaiian Islands. **ORIENTAL REGION:** China (Anhui, Fujian, Shanxi, Xizang [Tibet], Yunnan), Japan, Ryukyu Islands, Taiwan, Vietnam. **PALEARCTIC REGION (Introduced):** Austria, Belgium, France, Germany, Italy, Korea, Switzerland, Yugoslavia.

Hosts. *Abies fabric* (Masters) Craib, *A. pectinata* Poir., *Acer* L. spp., *A. platanoides* L., *A. pseudoplatanus* Falk., *Alnus glutinosa* (L.) Gaertn., *Alnus* Mill. sp., *Betula verrucosa* Ehrh., *Carpinus betulus* L., *C. laxiflora* (Siebold and Zucc.) Blume, *Carya* Nutt. sp., *Cassia siamea* Lam., *Castanea crenata* Siebold and Zucc., *Castanopsis* (D. Don) Spach sp., *Celtis tenuifolia* Nutt., *Chamaecyparis obtuse* Siebold and Zucc., *Cleyera japonica* Siebold and Zucc., *Cornus florida* L., *Diospyros kaki* Thunb., *Fagus crenata* Blume, *Fagus multinervis* Nakai, *F. sylvatica* L., *Fraxinus* L. spp., *Juglans regia* L., *Juglans* L. sp., *Myrica carolinensis* Mill., *Myrica* L. sp., *Lindera erythrocarpa* Makino, *Liriodendron tulipifera* L., *Machilus* Nees sp., *Morus* L. spp., *Nyssa aquatica* L., *Picea abies* (L.) K. Harst., *P. excelsa* Link, *Pinus densiflora* Siebold and Zucc., *P. pentaphylla* Carrière, *P. strobes* L., *Pinus* L. sp., *Prunus avium* (L.) L., *P. cerasus* L., *Prunus scrotina* Ehrh., *Prunus* L. spp., *Pyrus serotina* Rehder, *Pyrus* L. sp., *Rhus chinensis* Mill., *Quercus rubra* L., *Q. sessiliflora* Salisb., *Quercus* L. spp., *Robinia pseudoacacia* L., *Schima superba* Gardn. and Champ., *Styrax obassia* Siebold and Zucc., *S. japonicus* Siebold and Zucc., *Taxodium distichum* Rich., *Ulmus effuse* Willd., *Ulmus* L. spp., *Vitis* L. sp., “young chestnut” (Japan), *Ziziphus jujuba* Mill..

Specimens Examined. (66 ♀; 6 ♂)

Other material: NEARCTIC REGION: **United States:** Indiana: Turkey Run St. Park, VI-10-1967, L. and C. W. O’Brien (1 ♀; USNM); Indiana: W. Lafayette, McCormick Woods, V.26-1968, Collectors L. and C. W. O’Brien (1 ♀; USNM); IND., W. Lafayette, Tippercanoe Co., 12 Apr. 1981, M. and N. Deyrup, in pan trap below Malaise trap (2 ♀; RAB); Maryland: Takoma Park, Montgomery Co., 17-IV-1969, W. H. Tyson (1 ♀; USNM); North Carolina: McDowell Co., 10.20.1976, B. C. Weber collector (1 ♂;

USNM); North Carolina: McDowell Co., 7-21 1977, B. C. Weber collector (1 ♀, 1 ♂; USNM); North Carolina: McDowell Co., 10-19 1976, B. C. Weber collector (2 ♀; USNM); North Carolina: McDowell Co., 10.20.1976, B. C. Weber collector (9 ♀; USNM); North Carolina: Raleigh, 25.6.63, *Prunus scrotina* (1 ♀; NHMW); New Jersey: Norwood, Apl 11 1944, Schott, from branches of *Myrica carol* (6 ♀; USNM); New Jersey: Princeton, 2 June 1971, R. J. Gouger, *Fagus sylvatica* (4 ♀; USNM); New York: Kingston, Jun 8, 1939, Esselbaugh, H. R. Dodge Collection (1 ♀; USNM); New York: New Rochelle, IV.20.1932, L. Lacey collector (3 ♀; USNM); Ohio: Chillicothe, 28-VI-50, *Liriodendron tulipifera* (3 ♀; USNM); Ohio: Moreland Hills, 3.VIII.1981, W. V. Miller (1 ♀; CAS); Virginia: Albemarle Co., Ivy ex *Vitis*, cane tunnels, 29 Apr 1983, D. G. Pfeiffer coll. (2 ♀; USNM). **ORIENTAL REGION: China:** S. China: Fukien, Shaowu, Tachulan, V.14.1942, T. Maa (2 ♀; CAS). **Japan:** Japan: III-1917, Van Dyke Collection, in trunk of young chestnut (1 ♀; CAS); Japan, Hokkaido, Gamushi, VI.9.1956, Akira Nobuchi (2 ♀; USNM); JAPAN: HONSHU, Higashiaraya, Kushibikimachi, Yamagata Pref., 13.Vi.1996, K. Domon leg., Host tree: *Pyrus serotina* Rehder (1 ♀, 2 ♂; RAB); JAPAN: KYUSHU, Shiiya-touge Pass, Miyazaki-Kumamoto Pref., 25.Vi.1994, H. Goto leg. (1 ♀; RAB); Japan: Matsukawa, 27-VII-1980, S. L. Wood (1 ♀; USNM); Japan: Tamagowa, 29-VII-1980, S. L. Wood, *Fagus cranatus* (6 ♀; USNM); Japan: Tokyo, Mt. Takao, IX.22.1950, Akira Nobuchi (2 ♀; USNM). **Thailand:** Thailand: Chiang Mai: Doi Suthep, 7.Viii.02, Beaver, K. Koivisto (2 ♀; RAB).

PALEARCTIC REGION: Germany: Germania (Hessen) 28.8.52, Darmst-Kranichst, Geishecke, leg. F. Groschike, *Quercus* (1 ♂; NHMW, 1 ♂; BMNH); IGB – Sengscheid, SAAR, Wald, 18.6.90, leg. Mosbacher (4 ♀; RAB). **Switzerland:** Helvetia, Arlesheim,

1988, In traps (2 ♀; RAB). **OCEANIA: Hawaiian Islands:** USA: HI: O'ahu I., N. Halawa Valley, NW of Honolulu, 390 m, 21°25'N, 157°51'W, 11-29.VI.1991, FMHD#91-4, Met. Polym.-Psidium-Hibiscus mixed nat./exotic forest, A. Newton and M. Thayer, #869, window trap (4 ♀; FMNH).

Xylosandrus hirsutipennis (Schedl)

(Fig. 2.25)

Xyleborus hirsutipennis Schedl, 1961b: 144. Holotype ♀: Madagascar, Perinet, Montagne d'Ambre, Antaniditra: IRSM.

Xylosandrus hirsutipennis (Schedl): Wood and Bright, 1992: 796.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a “new combination.”

Diagnosis. Female 1.9 – 2.2 mm long; 2.3 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 7 socketed teeth; metatibiae with 7 socketed teeth. Elytra 1.3 times longer than wide; 1.3

times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Five striae visible on declivity. Striae granulate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. crassiusculus* (Fig. 2.16). Both species have a declivital face that is matte in appearance due to densely, finely, and confusedly granulate striae and interstriae. *Xylosandrus hirsutipennis* can be distinguished from *X. crassiusculus* by the following characters: frons punctate; pronotum with a lateral carina; pronotal disc glabrous, except for mycangial setae; elytral disc uniseriate punctate; five striae visible on elytral declivity; and declivital striae and interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

Distribution. AFROTROPICAL REGION: Madagascar.

Hosts. *Cassipourea* Aubl. sp., *Ficus soroceoides* Baker var. *macrophlebia* H. Perrier, *Harungana madagascariensis* Poir., *Psychotria* L. sp., *Urophyllum lyallii* Baker, *Vernonia* Schreb. sp.

Specimens Examined. (3 ♀; 1 ♂)

Type material: Paratypes *Xyleborus hirsutipennis*: Madagascar, Perinet, 21.XI.1952, Dr. K. E. Schedl (2 ♀; NHMW); Madagascar, Montagne d'Ambre, 7.XII.1952, Dr. K. E. Schedl (1 ♂; NHMW); Madagascar, Montagne d'Ambre, 5.XII.1952, Dr. K. E. Schedl (1 ♀; NHMW).

Xylosandrus hulcri Dole and Cognato, **new species**

(Fig. 2.26)

Description. Female (Fig. 2.26): Body oval, 2.4 - 2.7 mm long, 2.0 times longer than wide, bicolored, with pronotum and elytral apices dark brown, dorsal 1/3 and lateral 2/3 of elytra yellowish brown, ventral side and appendages dark brown. Frons convex, coriaceous, sparsely punctate between eyes, long erect hair-like setae originating from punctures, weak ridge at middle of frons just above epistoma. Epistoma with dense row of long and short hair-like setae along lower margin. Eyes emarginate. Antennal funicle 5-segmented, scape and funicle with sparse, short, hair-like setae; club obliquely truncate, first segment sclerotized, forming a circular costa (type 1, Hulcr et al. 2007), circular costa closed posteriad, oblique part of club densely pubescent, second segment not corneous; posterior face of club covered entirely by first segment (type 1, Hulcr et al. 2007). Pronotum 0.9 times longer than wide, rounded dorsally (type 1, Hulcr et al. 2007), widest about one-half pronotal length from base, anterior half broadly rounded and then tapering slightly toward apex, basal angles rounded, anterior margin with 4-6 asperities; anterior slope densely asperate, asperities smallest at summit and increasing in size toward anterior margin; disc moderately punctate, lacking a patch of denser punctures medially at base, background sculpture finely granulate; lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007), lateral costa extending approximately two-thirds pronotal length, lateral carina absent; pronotal vestiture of long and short, moderately appressed, hair-like setae. Scutellum triangular, yellowish-brown to dark brown, flush with surface of elytra. Elytra 1.2 times longer than wide, 1.4 times as long

as pronotum, shining, parallel-sided on basal two-thirds and then broadly rounded toward apex. Striae not impressed, shallowly and regularly punctuate, long erect hair-like setae originating from punctures. Interstriae twice the width of striae, finely punctuate, confused, long (1.5 - 2 times width of interstria) and short (less than width of interstria) erect hair-like setae originating from punctures. Declivity commencing behind mid-point of elytra, gradually separating from disc; lateral margins carinate to 7th interstriae. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 7 - 8 socketed teeth; metatibiae with 8 socketed teeth. Abdominal ventrites evenly punctured, punctures with long, erect, hair-like setae.

Specimens Examined. (4 ♀; 0 ♂)

Type Material. Holotype ♀: PAPUA NEW GUINEA, Chimbu, Mu Village, March 2006, 1600 m asl. Hulcr and Coganto coll. *Ficus mollior*. Vila 1462. In MSU. Paratypes ♀: PAPUA NEW GUINEA, Chimbu, Mu Village, March 2006, 1600 m asl. Hulcr and Coganto coll. *Ficus mollior*. Vila 1462. One paratype in FICB. Three paratypes in MSU. One paratype female was used for DNA extraction, and remains are vouchered at MSU.

Male: Unknown.

Etymology. This species is named for Jiri Hulcr (Michigan State University), who collected the type series and whose collecting efforts have contributed greatly to our knowledge of tropical scolytine fauna.

Diagnosis. This species can be readily distinguished from all other known *Xylosandrus* species by its distinct color pattern, with a testaceous patches on the elytra basally and laterally.

Distribution. AUSTRALIAN REGION: Papua New Guinea.

Hosts. *Ficus mollior* Benth.

Discussion. This species is known from a single collecting event. Specimens were collected at the same locality, but from galleries in several host trees. This species is mycocleptes and has been found in association with and stealing ambrosial fungus from *Xylosandrus rotundicollis*. Phylogenetic analysis places it as sister to the Australian species, *X. queenslandi*.

Xylosandrus jaintianus (Schedl)

(Fig. 2.27)

Xyleborus jaintianus Schedl, 1967: 161. Holotype ♀: Shillong, Assam, C. F. C. Beeson, 22.V.1925; NHMW.

Xylosandrus jaintianus (Schedl): Wood and Bright, 1992: 796.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a “new combination.”

Diagnosis. Female 3.0 mm long; 2.0 times longer than wide. Body brown; antennae and legs same color as body. Frons rugose, with distinct median keel between eyes. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by distance less than or equal to their width. Lateral aspect of pronotum basic

(type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae with 11 – 12 socketed teeth. Elytra 1.1 times longer than wide; 1.1 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity with depressed areas on each side of raised interstriae, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. beelsoni* (Illustrated in Saha et al. 1992), *X. discolor* (Fig. 2.20), and *X. subsimiliformis* (Fig. 2.40). *Xylosandrus jaintianus* can be distinguished from these species by the following characters: first and second declivital interstriae elevated toward apex, with depressed areas on each side of raised interstriae; frons rugose with a distinct median keel.

Distribution. ORIENTAL REGION: Burma, India (Assam). **PALEARCTIC REGION:** Nepal.

Hosts. Unknown.

Specimens Examined. (4 ♀; 0 ♂)

Type material: Holotype *Xyleborus jaintianus* (♀; NHMW). Paratype *Xyleborus*

jaintianus: N. E. Burma: Kambaiti, 7000ft., 23/5/1934, R. Malaise (♀; BMNH).

Other material: **PALEARCTIC REGION: Nepal:** NEPAL-HIMALAYA Annapurna mts. N-Pokhara, Madi-Khola-Tal, 1850m, 2.v.1996, leg. O. Jäger (1 ♀; RAB); NEPAL,

Kali Gandaki Tai 2 km SO Narcheng oberth. Rele Khola, HO-Hang, 2300 m, N28°30'40", E83°41'33", 25.v.2001, leg. O. Jäger (1 ♀; RAB).

Xylosandrus mancus (Blandford)

(Fig. 2.28)

Xyleborus mancus Blandford, 1898: 428. Holotype ♀: Ceylon, E. E. Green; BMNH.

Apoxyleborus mancus (Blandford): Wood 1980: 90.

Xylosandrus mancus (Blandford): Wood 1984: 229.

Xyleborus abruptus Sampson, 1914: 388. Syntypes ♀: Seychelles, Mahe: high forest of Morne Blanc, and Cascade Estate; BMNH. Synonymy: Schedl, 1951: 51.

Xyleborus mancus formosanus Eggers, 1930: 186. Holotype ♀: Formosa: Taihoku; FRI. Synonymy: Schedl, 1952: 61.

Notes. This species was first included in *Xylosandrus*, when Wood (1984) synonymized *Apoxyleborus* with *Xylosandrus*.

Diagnosis. Femle 2.9 – 3.3 mm long; 1.2 – 1.4 times longer than wide. Body yellowish brown to brown; elytra darker brown at apex and declivity; legs and antennae the same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming circular costa; segment one covering entire posterior face. Of approximately equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with

lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae with 12 socketed teeth. Elytra 1.2 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins carinate, with carina extending beyond 7th interstriae, forming a circumdeclivital ring. Four striae visible on declivity. Striae punctate, without setae. Interstriae granulate, without setae.

This species is one of two *Xylosandrus* with the margin of the elytral declivity with a carina or rim of granules that extends beyond the 7th interstriae, forming a circumdeclivital ring: *X. amputatus* (Fig. 2.8) and *X. mancus*. *Xylosandrus mancus* can be distinguished from *X. amputatus* by the following characters: 2.9 – 3.3 mm long; 1.2 – 1.4 times as long as wide; declivital striae with a row of large, shallow punctures, arranged in a somewhat wavy line; and declivital interstriae shining, not densely granulate.

Distribution. **AFROTROPICAL REGION:** Madagascar, Mauritania, Seychelles Islands, Tanzania. **ORIENTAL REGION:** China (Gansu, Xizang [Tibet]), Maharashtra, India (Tamil Nadu), Indonesia (Java, Sumatra), Japan, Malaya, Philippine Islands, Sri Lanka, Taiwan, Vietnam.

Hosts. *Adenanthera pavonina* L., *Albizia* Benth. sp., *Anacardium occidentale* L., *Aphanamixis rohituka* Pierre, *Artocarpus dadak* Miq., *Brackenridgea hookeri* (Planch.) A. Gray, *Buchanania lanzan* Spreng., *B. latifolia* Roxb., *Butea frondosa* Wall., *Calophyllum inophyllum* L., *Cassia fistula* L., *Cordia dichotoma* G. Forst., *Cordia myxa* L., *Dalbergia latifolia* Roxb., *Dryobalanops aromatica* Gaertn., *D. oblongifolia* Dyer,

Gomphia serrata (Gaertn.) Kanis, *Grewia paniculata* Roxb., *Hibiscus macrophyllus* Roxb., *Hopea beccariana* Burck, *H. ferrea* Heim, *Hullettia dumosa* King, *Khaya senegalensis* Juss., *Litsea megacarpa* Gamble, *Magnifera indica* L., *Melanorrhoea* Wall. sp., *Nephelium lappaceum* L., *Palaquium gutta* Burk., *Pometia pinnata* J. R. Forst. and G. Forst., *Quercus* L. sp., *Shorea bracteolata* Dyer, *S. leprosula* Miq., *S. macroptera* Dyer, *S. sumatrana* (Slooten) Desch, *Styrax benzoin* Dryand., *Swietenia macrophylla* King, *S. mahagoni* (L.) Jacq., *Tectona grandis* L., *Theobroma cacao* L., *Toonia sureni* Merrill., *Tristania whitiana* Griff., *Vateria copallifera* (Retz.) Alston, *Vitex pubescens* Vahl.

Specimens Examined. (69 ♀; 2 ♂)

Type material: Holotype *Xyleborus mancus* (♀; BMNH).

Other material: **AFROTROPICAL REGION:** D. O. Africa (1 ♀; NHMW).

Madagascar: Madagascar, Ambila, 28.XI.1952, K. E. Schedl (1 ♀, 1 ♂; NHMW).

Seychelles: Seychelles: P. R. Dupont, 1915, attacking Cashew (3 ♀; BMNH).

ORIENTAL REGION: China: Salagar, Kafang, ex *Clenderai*, 5. XII.1948, F. G.

Browne (3 ♀; USNM). **Indonesia:** Java: Kediri Forest, II.1925, L. G. E. Kalshoven (2

♀; USNM); Java: Kediri, III.1925, L. G. E. Kalshoven (1 ♀; NHMW). **Japan:** Japan:

Kagoshima Pref., Tarumizuy, Oonohara, Broadleaf forest, 425 m, 14 May 2001,

Yoshikazu Sato coll., ex. ETOH-baited trap (2 ♀; MSU); Japan: Kagoshima Pref.,

Tarumizuy, Oonohara, Broadleaf forest, 425 m, 3 July 2001, Yoshikazu Sato coll., ex.

ETOH-baited trap (1 ♀; MSU). **Malaysia:** Sarawak, Bako National Park, 29 Oct – 2

Nov 1998, 50 m, B. Jordal coll. (1 ♀; MSU); Malaya, Selangor, Kepong, 8.IV.1934,

Selenager Mus., ex. *Styrax benzoin* (1 ♀; NHMW). **Philippine Islands:** Manila, Philippine

Islands, Colln PC, McGregow (1 ♀; USNM); Philippine Islands: Puerto Princesa. Palawan Is., sea level, 2nd growth forest, IV.29.47, H. Hoogstraal leg. (1 ♀; FMNH). **Singapore:** Singapore, Bukit Timah, 50 m, 25–27 Oct 1998, B. H. Jordal coll., *Cinnamomum* (1 ♀; MSU). **Sri Lanka:** Sri Lanka: Bad. Dist., Buttala, 5 June 1975, S. L. Wood, collected from *Liana* (5 ♀; USNM); Sri Lanka: Bad. Dist., Butatala, 5 June 1975, S. L. Wood, collected from pole (8 ♀, 1 ♂; USNM); Sri Lanka: Bat. Dist., Unnichchai, 9 June 1975, S. L. Wood, collected from *Liana* (2 ♀; USNM); Ceylon [Sri Lanka]: Col. Dist. Tunmodera, 200 ft, 17-XI-1970, O. S. Flint, Jr. (2 ♀; USNM); Sri Lanka: Gal. Dist., Kanneliya, 250 mtrs., 23 May 1975, S. L. Wood, Collected from pole (9 ♀; USNM); Ceylon [Sri Lanka]: Hantane, XII.1962, D. Calnaido (1 ♀; NHMW); Ceylon [Sri Lanka]: Kan. Dist., Kandy, 1-15 March 1971, Piyadasa and Somapala (4 ♀; USNM); Ceylon [Sri Lanka]: Kan. Dist., 5 mi NW Mahiyangana, 30 Mar-9 Apr 1971, P. and P. Spangler (2 ♀; USNM); Sri Lanka: Keg. Dist., Kitulgala, 200 m, 30 May 1975, S. L. Wood, host: *Osbeckia aspera* (1 ♀; USNM); Sri Lanka: Matte. Dist., 5 km SE Naula, 200 mtrs, 14 June 1975, S. L. Wood, misc. hosts (4 ♀; USNM); Sri Lanka: Matte. Dist., 5 km SE Naula, 200 mtrs, 14 June 1975, S. L. Wood, collected from *Liana* (1 ♀; USNM); Sri Lanka: Mon. Dist. 8 km NW Bibile, 50 mtrs, 7 June 1975, S. L. Wood, collected from pole (5 ♀; USNM); Sri Lanka: Mon. Dist., Buttala, 50 mtrs, 6 June 1975, S. L. Wood, collected from pole (1 ♀; USNM); Sri Lanka: Pol. Dist. 32 km N Polonnaruwa, 11 June 1975, S. L. Wood, collected from pole (1 ♀; USNM); Sri Lanka: Rat. Dist. Gilimale, 17 May 1975, S. L. Wood, host: *Myristica dactyloides* (1 ♀; USNM); Ceylon [Sri Lanka]: Rat. Dist., Uggaalkaltota 350 ft., irrigation bungalow, 31 Jan – 8 Feb 1970, Davis and

Rowe (1 ♀; USNM); Ceylon [Sri Lanka], Sabagamuva, Millawitiya Est., 3-10.Vii.1956,

E. Judenko (1 ♀; NHMW).

Xylosandrus mediocris (Schedl)

(Fig. 2.29)

Xyleborus mediocris Schedl, 1942a: 185. Lectotype ♀: Malaya, N.S. Pasoh Forest Reserve, 12-II-1938, ex *Shorea dasyphylla*; NHMW.

Xylosandrus mediocris (Schedl): Browne, 1963: 55.

Diagnosis. Female 1.4 mm long; 2.3 times longer than wide. Body brown; antennae and legs yellowish brown. Frons not visible on specimen examined. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae not visible on specimen examined. Pro-, meso- and metatibial teeth not visible on specimen examined. Elytra 1.3 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. adherescens* (Fig. 2.7), *X. eupatorii* (Fig. 2.22), and *X. germanus* (Fig. 2.24). *Xylosandrus mediocris* can be distinguished from these species by the following characters: 1.4 mm long; pronotum of equal length and width; and declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than the width of second declivital interstriae.

Distribution. **ORIENTAL REGION:** Malaysia.

Hosts. *Dipterocarpus cornutus* Dyer, *Shorea dasyphylla* Foxw..

Specimens Examined. (1 ♀; 0 ♂)

Type material: Lectotype *Xyleborus mediocris* (♀; NHMW).

Xylosandrus mesuae (Eggers)

(Fig. 2.30)

Xyleboruss mesuae Eggers, 1930: 182. Holotype ♀: Bengal (Kalimpong), Aug. 1910 on *Mesua ferra*; FRI.

Xylosandrus mesuae (Eggers): Browne, 1963: 55.

Diagnosis. Female 1.1 – 1.3 mm long; 2.2 times longer than wide. Body bicolored, pronotum distinctly lighter than elytra; pronotum light brown and elytra dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium.

Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 6 socketed teeth; metatibiae with 8 socketed teeth. Elytra 1.3 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae uniseriate, very finely punctate. Elytral disc gradually curving into declivity. Declivity convex, carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus* (Fig. 2.9), *X. discolor* (Fig. 2.20), *X. ferinus* (Fig. 2.23), and *X. mesuae*. *Xylosandrus mesuae* can be distinguished from *X. discolor* by the following characters: elytral disc gradually curving into declivity. *Xylosandrus mesuae* can be distinguished from *X. arquatus* and *X. ferinus* by the following characters: 1.1 – 1.3 mm long; declivital striae with setae; declivital interstriae with erect, hair-like setae, longer than the width of second declivital interstriae.

Distribution. **AUSTRALIAN REGION:** Papua New Guinea. **ORIENTAL REGION:** India (Bengal, Uttar Pradesh), Sri Lanka.

Hosts. *Diptericarpus zeylanicus* Thwaites., *Macaranga* Thou. sp., *Mesua ferrea* L., *Osbeckia aspera* Benth., *Shorea robusta* Roth.

Specimens Examined. (102 ♀; 1 ♂)

Type material: Cotype *Xyleborus mesuae*: Bengal, Kalimpong on *Mesua ferra* (♀; NHMW).

Other material: **AUSTRALIAN REGION: Papua New Guinea:** Papua New Guinea, Lae, 15 km S Lae, 100 m, 13.2.2003, B. Jordal and A. Sequeira leg. ex *Macaranga petoles* (3 ♀; RAB). **ORIENTAL REGION: Sri Lanka:** Ceylon [Sri Lanka]: 10-16.VII.1956, Sabargamuva, Millawitiya Est., E. Judenko (1 ♀; NHMW); Sri Lanka: Col. Dist. Labugama, 23 June 1975, S. L. Wood, collected from legume tree (2 ♀; USNM); Sri Lanka: Col. Dist. Labugama, 23 June 1975, S. L. Wood, collected from twigs (64 ♀; USNM); Sri Lanka: Col. Dist. Labugama, 23 June 1975, S. L. Wood, host: *Dictyocarpus zeylanicus* (25 ♀, 1 ♂; USNM); Sri Lanka: Keg. Dis. Kitulgala, 200 m, 30 May 1975, S. L. Wood, host: *Osbeckia aspera* (6 ♀; USNM).

Xylosandrus metagermanus (Schedl)

(Fig. 2.31)

Xyleborus metagermanus (Schedl), 1951: 58. Holotype ♀: U. Dihing Res., Lakhimpur Assam, 6. VIII. 1931, ex *Gmelina arborea*, C. F. C. Beeson; NHMW.

Xylosandrus metagermanus (Schedl): Browne, 1963: 55.

Diagnosis. Female 1.8 mm long; 2.0 times longer than wide. Body light brown to brown; antennae and legs same color as body. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum

basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimen examined. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. mixtus* (Fig. 2.32). *Xylosandrus metagermanus* can be distinguished from *X. mixtus* by the following characters: 1.8 mm long; six striae visible on declivity; declivital striae without setae; declivital interstriae uniseriate granulate.

Distribution. ORIENTAL REGION: India (Assam).

Hosts. *Gmelina arborea* Roxb.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Holotype *Xyleborus metagermanus* (♀; NHMW).

Xylosandrus mixtus (Schedl), **new combination**

(Fig. 2.32)

Xyleborus mixtus Schedl, 1979b: 108. Holotype ♀: Papua, Butolo, Morobe Distr., Upper Monki, L. A., 16.3.1973, sticky trap Nr. 1604, F. R. Wylie and P. Shanahan; NHMW.

Amasa mixtus (Schedl): Wood and Bright, 1992: 683.

Notes. This species was first included in *Amasa* by Wood and Bright (1992), but the authors failed to indicate it as a “new combination.”

Diagnosis. Female 2.6 – 2.7 mm long; 2.4 times longer than wide. Body light brown; antennae and legs same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae narrowly, but completely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 9 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.4 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae mutliseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, mutiseriatae, with erect, hair-like setae, more than twice as long as width of second declivital interstriae.

This species is morphologically similar to *X. metagermanus* (Fig. 2.31).

Xylosandrus mixtus can be distinguished from *X. metagermanus* by the following characters: 2.6 – 2.7 mm long; five striae visible on elytral declivity; declivital striae with semi-appressed, hair-like setae; declivital interstriae multiseriate granulate.

Distribution. AUSTRALIAN REGION: New Guinea.

Hosts. Unknown.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Holotype *Xyleborus mixtus* (♀; NHMW).

Xylosandrus monteithi Dole and Beaver

(Fig.2.33 and 2.34)

Xylosandrus monteithi Dole and Beaver, in press. Holotype ♀: AUSTRALIA, Queensland, Palmerston, Henrietta Cr., 550m, ex unknown tree, 22.1.2000 (B. Jordal). In QMB (Accession # T144402).

Diagnosis. Female 3.0 – 3.4 mm long; 2.1 times longer than wide. Body dark brown or blackish, base of pronotum and elytra lighter brown, ventral side and appendages yellowish brown. Frons reticulate with coarse punctures. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of erect and semi-appressed long hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Pronotum lacking a dense patch of setae at base of pronotum. Pronotal disc moderately punctate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin, meso- and metatibiae with 7 – 9 socketed teeth. Elytra 1.2 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae mutliseriata punctate, becoming granulate toward declivity. Elytral disc gradually curving into declivity. Declivity convex, lateral margins

rounded, without a carina or a row of tubercles or serrations. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is one of two *Xylosandrus* with the margin of the elytral declivity rounded: *X. monteithi* and *X. rotundicollis* (Fig. 2.39). *Xylosandrus monteithi* can be distinguished from *X. rotundicollis* by the following characters: 3.0 – 3.4 mm long; basal pronotum lacking a dense patch of setae; declivital striae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae; and declivital interstriae multiseriate granulate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. *Xylosandrus monteithi* may also be confused with *X. woodi*, but the latter species has small tubercles marking the lateral declivital margin.

Distribution. AUSTRALIAN REGION: Queensland.

Hosts. Unknown.

Specimens Examined. (1 ♀; 1 ♂)

Type material: Paratype *Xylosandrus monteithi*: Australia, Queensland, Palmerston, Watchua Falls, Jan. 2000, 550 m, ex unknown tree, 24.1 B. Jordal leg (♀; MSU).

Allotype Xylosandrus monteithi: Australia, Queensland, Palmerston, Watchua Falls, Jan. 2000, 550 m, ex unknown tree, 24.1 B. Jordal leg. (♂; MSU).

Xylosandrus morigerus (Blandford)

(Fig. 2.35)

Xyleborus morigerus Blandford, 1894a: 264. Syntypes ♀: probably New Guinea; BMNH.

Xylosandrus morigerus (Blandford): Reitter, 1913: 83.

Xyleborus coffeae Wurth, 1908: 199. Syntypes ♀: Java; type location unknown.

Synonymy: Strohmeier, 1910: 86.

Xyleborus luzonicus Eggers, 1923: 174. Lectotype ♀: Mt. Makiling, Insel Luzon, Philippinen; USNM.

Xylosandrus luzonicus (Eggers): Browne, 1963: 55. Synonymy: Wood, 1974: 287.

Xyleborus difficilis Eggers, 1923: 174. Lectotype ♀: Java, Hagedorn coll., 1915; USNM.

Xylosandrus difficilis (Eggers): Browne, 1963: 55. Synonymy: Synonymy Bright and Skidmore 1997: 4, 169.

Xyleborus abruptoides Schedl, 1955: 298. Holotype ♀: Fiji: Viti Levu, Navai Mill, near Nandarivatu, 2500 ft., 15.IX.1938, beating shrubbery; BPBM.

Xylosandrus abruptoides (Schedl): Browne, 1963: 55. Synonymy (= *Xylosandrus difficilis*) Beaver 1995: 17.

Diagnosis. Female 1.5 – 2.0 mm long; 2.1 times longer than wide. Body light to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with a lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 8 – 10 socketed teeth;

metatibiae with 10 socketed teeth. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face steep and abruptly separated from disc. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with erect hair-like setae, shorter than the width of second declivital interstriae. Interstriae punctate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. derupteterminatus* (Fig. 2.18) and *X. terminatus* (Fig. 2.41). *Xylosandrus morigerus* can be distinguished from these species by the following characters: elytral declivity convex; six striae visible on declivity; declivital striae with setae; and declivital interstriae uniseriate punctate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

Distribution. **AFROTROPICAL REGION:** Gabon, Madagascar, Mauritius Islands, Zaire. **AUSTRALIAN REGION:** New Britain Island, New Guinea, Solomon Islands Queensland. **NEOTROPICAL REGION:** Brazil, Colombia, Costa Rica, Ecuador (Santa Cruz in Galapagos Islands), Honduras, Mexico (Campeche, Chiapas, Oaxaca, Tabasco, Varacruz), Panama, Puerto Rico, Tobago, Venezuela. **OCEANIA:** Fiji Islands, Hawaiian Islands, Micronesia (Caroline Islands, Timor in Mariana Islands), Samoan Islands, Tonga (Vava'u). **ORIENTAL REGION:** India (Bengal, Tamil Nadu), Indonesia (Borneo, Celebes, Java, Sumatra), Malaysia (Sarawak), Philippine Islands, Sri Lanka, Taiwan, Vietnam (Tonkin Island, Vietnam). **PALEARCTIC REGION (Introduced):** Austria, Czechoslovakia, England, France, Italy, Jordan, Lebanon.

Hosts. *Acacia gaumeri* S. F. Blake, *Acalypha* L. sp., *Actinophora fragrans* Wall., *Adenanthera pavonina* L., *Albizzia falcate* (L.) Backer, *A. glauca* Benth., *A. procera*

Benth, Albizia Durazz. sp., Alseis yucatanensis Standl., Altingia excelsa Noronha,
Arthrophyllum diversifolium Blume, Amomum L. sp., Aspidosperma Mart and Zucc. sp.,
Astronium graveolens Jacq., Bixa orellana L., Boehmeria Jacq. sp., Bridelia Willd. sp.,
Brosimum alicastrum Sw., Bursera simaruba (L.) Sarq., Butea monosperma Kuntze,
Calamus L. sp., C. caesius Blume, Calophyllum brasiliense Camb., Camellia sinensis
Kuntze, C. thea Link., C. theifera Dyer, Cassia multijuga Rich., Castanea argentea
Blume, Castanopsis (D. Don.) Sprach. sp., Cattleya Lind. sp., Cedrela odorata L.,
Cedrela P. Borne sp., Cecropia obtusifolia Bertol., Ceiba pentandra (L.) Gaertn. ,
Centrosema plumieri Benth., Cecropia Loefl. sp., Chrysophyllum cainito L., Cinchona L.
sp., Claoxylon polot Merr., Clidemia hirta Don., Cocos nucifera L., Coffea arabica L.,
Coffea excelsa Cheval., "C. hybrida" (Java: Schedl 1962) , C. liberica Bull. ex Schum.,
C. robusta L. Linden, Cola acuminata Schott and Endl., Cordia dodecandra DC.,
Crotalaria L. sp., C. anagyroides Kunth, C. usaramoensis Baker , Dalbergia latifolia
Roxb., Dendrobium Sw. sp., D. phalaenopsis Fitzq., D. superbum Rchb., D. veratrifolium
Lindl., Derris microphylla (Miq.) B. D. Jacks, Didymopanax Decne. and Planch. sp.,
Dryobalanops oblongifolia Dyer, Endospermum malaccense Muell.-Arg., Epidendrum
stamfordianum Bateman , Erythrina lithosperma Miq. Var, inermis Kds. and Val.,
Erythroxylon novogranatense Hieron., Esenbeckia pentaphylla Griseb., Eugenia
polyantha Phil., Eupatorium pallescens DC., Eusideroxylon zwageri Teijsm. and Binn.,
Ficus L. sp., Ficus ampelas Burm., Fissistigma elegans Merr., Flemingia strobilifera
(L.) W. T. Aiton, Freycinetia hombroni Martelli, Fuchsia L. sp., Glochidion J. R. Forst.
and G. Forst. sp., Grewia laevigata Vahl, Gynotroches onillaris Blume, Hevea
brasiliensis Muell.-Arg., Intsia palembanica Miq., "Laurel roja" (Venezuela), Lecythis

Loefl. sp., *Leucaena glauca* Benth., *Licania hypoleuca* Benth., *Lonicera caprifolium* L., *Macaranga* Thou. sp., *Machaerium cirrhiferum* Pittier, “Mahogany” (Fiji), *Marumia muscosa* Blume, *Melia azedarach* L., *Miconia trinervia* Coqn., *Ochroma lagopus* Sw., “Palito negro” (Venezuela), *Persea gratissima* Gaertn., *Phalaenopsis* Blume sp., *Pometia pinnata* Forst., *Pouteria sapota* (Jacq.) H. E. Moore and Stearn, *Quararibea* Aubl. sp., *Renathera storiei* Rchb., *Sambucus javanica* Reinw. ex Blume, *Schizolobium parahyba* (Vell.) Blake, *Schleichera oleosa* Merr., *Serjania* Mill. sp., *Shorea* Roxb. ex C. F. Gaertn sp., *S. leprosula* Mil., *Spondias mombin* L., *Swietenia macrophylla* King, *S. mahagoni* (L.) Jacq., *Tabebuia rosea* DC., *Tarenna incerta* Koord. and Valetton, *Tectona grandis* L., *Tephrosia* Pers. sp., *T. maxima* Pers., *T. vogelii* Hook, *Thea sinensis* L., *Theobroma cacao* L., *Terminalia amazonica* (J. F. Gmel.) Exell, *Trema micrantha* (L.) Blume, *T. orientale* Blume, *Vanda* Jones ex. R.Br. sp., *V. coerulea* Griff. ex Lindl., *V. teres* Lindl., *V. tricolor* Lindl., *Vitis* L. sp.

Specimens Examined. (197 ♀; 13 ♂)

Type material: Lectotype *Xyleborus difficilis* (♀; USNM). Allotype *Xylosandrus difficilis*: Java, Bnadya, VII-33, L. G. E. Kalshoven (♂; NHMW). Cotype *Xyleborus difficilis*: Java: Coll. Hagedorn, 1915 (♀; NHMW). Lectotype *Xyleborus luzonicus*: Mt. Makiling, Luzon, Baker, Eggers collection 1948 (♀; USNM). Paratype *Xyleborus apruptoides*: Fiji: Viti Levu, Navai Mill, Nr. Nandarivatu, 2500 ft., 15.IX.1938, beating shrubbery (♀; NHMW).

Other material: **AUSTRALIAN REGION: Australia:** In *Phalaenopsis* sp. VI-17-35 (17 ♀, 1 ♂; USNM); Australia, on *Vanda coerulea*, VI-25-1938 (3 ♀; USNM); Australia: In *Vanda coerulea*, VII-7-36 (9 ♀, 3 ♂; USNM); Australia, Fullaway, Nov. 26 1934,

Dendrobium phalaenopsis (1 ♀; USNM); Australia: Brisbane, S. F., 3/1/49. In Quar.,
Dendrobium phalenopsis host, collector Art Retan (4 ♀, 1 ♂; CAS). **Soloman Islands:**
Solomon Islands: Guadaleanel, Mt. Auston. 11 Jan 1984, M. Bigger, boring in *Pometia*
pinnata midrib (1 ♀; BMNH). **NEARCTIC REGION: United States:** New Jersey,
Bound Brook, Aug 14/16, B. Weiss Harry colr., *Cattleya* (6 ♀, 3 ♂; USNM).
NEOTROPICAL REGION: Colombia: Colombia: 24 km E Barbosa, VII-18-70,
Antioquia, el. 1200 m, S. L. Wood, Lauraceae (1 ♀; USNM); Colombia: 24 km E
Barbosa, VII-18-70, Antioquia, el. 1200 m, S. L. Wood, *Xelopia* sp. (2 ♀; USNM);
Colombia: 8 km S Colonia V. de Cauca, VII-9-70, el. 30 m, S. L. Wood, *Aspidosperma*
sp. (5 ♀; USNM); Colombia: 8 km S Colonia V. de Cauca, VII-9-70, el. 30 m, S. L.
Wood, *Lecythis* sp. (1 ♀; USNM); Colombia: 8 km S Colonia V. de Cauca, VII-9-70, el.
30 m, S. L. Wood, *Chrysophyllum catmito* (1 ♀; USNM). **Costa Rica:** Costa Rica:
Pandora lim., 150 ft., VIII-23-1963, S. L. Wood, *Cecropia* sp. leaf petioles (1 ♀;
USNM); Costa Rica: San Jose, Santa Ana, 4000 ft., X 4-1963, S. L. Wood, unknown
limb (1 ♀; USNM). **Ecuador:** Ecuador: Galap: St. Cruz, 1.7 km N St. Rosa, 1-30.V.91,
550 m, Scalesia, mal-FIT, S. and J. Peck (2 ♀; CAS); Ecuador, Napo Prov., Rees.
Ethnica Waorani, 1 km S. Onkone Gare Camp, Trans. Ent. 00°39'10"S, 076°26'W, 220
m. elev., July 1995, T. L. Erwin, et al collectors (1 ♀; USNM); Ecuador, Napo Prov.,
Rees. Ethnica Waorani, 1 km S. Onkone Gare Camp, Trans. Ent. 00°39'10"S, 076°26'W,
220 m. elev., January 1996, T. L. Erwin, et al collectors (1 ♀; USNM); Ecuador, Napo
Prov., Rees. Ethnica Waorani, 1 km S. Onkone Gare Camp, Trans. Ent. 00°39'10"S,
076°26'W, 220 m. elev., July 1996, T. L. Erwin, et al collectors (3 ♀; USNM); Ecuador,
Napo Prov., Tiputini Biodiversity Station, 220-250 m, October 1998, 00°37'55"S.

076°08'39"W, T. L. Erwin, et al collectors (3 ♀; USNM). **Honduras:** Honduras, at Tampa, 28-III-1968, J. Jordan, in orchid plnt. stem (1 ♀; USNM); Honduras: Zamorano, Moraz, 2200 ft., IV-18-1946, S. L. Wood, *Serjania* (2 ♀; USNM). **Mexico:** Mexico: OAX, Romero 18 mi N, 400 ft, VI-29-1967, S. L. Wood, unknown twig (1 ♀; USNM); Mexico: OAX, Romero 18 mi N, 400 ft, VI-29-1967, S. L. Wood, unknown branch (1 ♀; USNM); Mexico: OAX, Romero 23 mi N, VI-29-1967, 300 ft., S. L. Wood, unknown branch (1 ♀; USNM); Mexico: VC, Coatzacoalcos, 18 mi E, VI-26-1967, el. 100ft., S. L. Wood, unknown log (2 ♀; USNM); Mexico, Vera Cruz, and Oaxaca, 24-VIII-66, Cool. G. Schwenke, Orchids and bromeliads (8 ♀; USNM). **Nicaragua:** Finca San Pedro, Matagalpa, 10-IV-81, en tallo de Cacao, Coll. J. A. Estrada (4 ♀; USNM). **Panama:** Ancon, C. I., 18.VII-45, *Epidendrum stamfordianum* Broelle (1 ♀; USNM), Barro Colorado, CZ Panama, 16, 19, 21/5 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 25, 28, 30. IV.1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 22, 24, 26. IX. 1986, Henk Wolda (6 ♀; UCDC); Barro Colorado, CZ Panama, 28, 31/3. 2/4. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 20-24.X.1986, Henk Wolda (4 ♀; UCDC); Barro Colorado, CZ Panama, 25-29.V.1987, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 1-5.VI.1987, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 1-5.XII.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 23-27.II.1987, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 15, 17, 19. IX.1986, Henk Wolda (3 ♀; UCDC); Barro Colorado, CZ Panama, 4, 8, 9. IV. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 14, 17, 19, .III. 1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 9, 12, 14. V. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 1, 3, 5.IX.1986, Henk

Wolda (13 ♀; UCDC); Barro Colorado, CZ Panama, 25, 27. VIII. 1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 18, 21, 23. IV. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 29.IX/1,3.X.1986, Henk Wolda (6 ♀; UCDC); Barro Colorado, CZ Panama, 8-12.XII.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 11, 14, 16/4.1986, Henk Wolda (3 ♀; UCDC); Barro Colorado, CZ Panama, 2, 5, 7/5. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 31-I/3-II.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 6, 9, 11.VI.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 7, 9, 11.VII.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 18, 20, 22.VIII. 1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 13, 15, 17.X.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 21, 23, 25.VII.1986, Henk Wolda (1 ♀; UCDC); Panama: Barro Colo Is. OZ, I-II-45, J. Zetek (3 ♀; USNM); Baro Colo. Is., CZ, Mar. Apr. 49, Zetek (1 ♀; USNM); Barro Colorado Isl., CZ, XII-46-II-47 J Zetek collector (1 ♀; USNM); Panama: Barro Colorado Island, CZ, VII-23-1966, S. L. Wood, unknown log (1 ♀; USNM); CZ Panama, Lion Hill, VI 21 1982, R. B. Kimsey Col. (1 ♀; UCDC); Panama: CZ, Ft Amador, VII-27-66, S. L. Wood, unknown twigs (4 ♀; USNM); Panama: CZ, Gatun Dam, 40 ft., XII-31-1963, S. L. Wood, *Cecropia* sp. leaf petioles (2 ♀; USNM); Panama: Panama Prov., 6-8 km N El Llano on El Llano-Carti Road, VI-6-1994, F. Andrews and A. Gilbert (1 ♀; CSCA); Panama: Panama Prov. 9 km N El Llano, V-21-1993, F. Andrews and A. Gilbert (1 ♀; CSCA). **Venezuela:** Venezuela 9 km S of Barrancas, Barinas, 150 m, XI-5-69, S. L. Wood, *Spondias mombin* (2 ♀; USNM); Venezuela: 9 km S of Barrancas, Barinas, 150 m, XI-5-69, S. L. Wood, *Inga* (1 ♀; USNM); Venezuela: 8 km SW Bumbum, Barinas, II-11-1970, 150 m, S. L. Wood,

Cucurbitaceae (1 ♀; USNM); Venezuela: 20 km SE El Vigia Merida, XII-10 69, el. 50 m.

S. L. Wood, unknown vine (1 ♀; USNM); Venezuela: Finca Monasterios, Cacaugua, Mir., 1971, *Theobroma cacao* (1 ♀; USNM). Sanat Domingo, 25-I-1980, Coffee. J. Esenbar (1 ♀; USNM); Venezuela: 40km SE Socopo, Barinas, I-25-1970, 150 m, S. L. Wood, Palito negro (1 ♀; USNM); Venezuela: 40 km SE Socopo, Barinas, I-25-1970, 150 m, S. L. Wood, Laurel roja (1 ♀; USNM). **OCEANIA: Fiji Islands:** Fiji, Viti Levu, Nadarivatu, VIII.1955, B. A. O'Connor, young mahogany (2 ♀; NHMW). **Samoa Islands:** Samoa: Afiamalu, Upolu, VII-10-40, beating dead branches, F. C. Zimmerman collector (1 ♀; NHMW). **ORIENTAL REGION: Indonesia:** Java, Bnadya, VII-33, L. G. E. Kalshoven (2 ♀; NHMW). India: Coffee Res Sub-station, Chethalli, Karnataka. Sp. 70. on *Coffea robusta* (1 ♀; BMNH); Java: W Bandjar, 1933, leg. Kalshoven, *Tectona* (2 ♀; USNM). La Reunion, Saint Pierre, 17.X.1989, Orchidee, S. Quilici (3 ♀; USNM). **Malaysia:** Malaya: Kelantan, I:VII:1947, F. G. Browne (3 ♂; BMNH). **Philippine Islands:** Philippines, X-23-63, E. Shiroma and E. Davidson, in orchid sp. (1 ♀; USNM); Philippine Is., Apr. 2, 1940, In *Ranathera storiei* (1 ♀; USNM); Philippine Is., *Dendrobium superbum*, E. Arbios, Sept.19.1933 (1 ♀; USNM). **Sri Lanka:** Ceylon [Sri Lanka]: Peradeniya, 29.VII.1914, A. Rutherford (1 ♀; NHMW); Sri Lanka: Kal. Dist., Morapitiya, 250 mtrs., 27 May 1975, S. L. Wood (1 ♀; USNM). **PALEARCTIC REGION: England:** England, St. Albans, *Dendrobium phalenopsis*, IV-25-30, E. Rannells, intercepted Washington D.C. (3 ♀, 4 ♂; USNM).

Xylosandrus nanus (Blandford), **nomen dubium**

(Fig. 2.36)

Xyleborus nanus Blandford, 1896b: 242. Holotype ♀: Noumea (Delauney); Location of holotype unknown.

Xylosandrus nanus (Blandford): Browne, 1963: 55.

Notes. *Xylosandrus nanus* was described from a single specimen by Blandford in 1896. When Browne (1963) transferred the species to *Xylosandrus*, he noted that it was “probably at most a variation of *X. morigerus*.” Furthermore, Wood and Bright (1992) incorrectly cite the holotype as being housed in the BMNH. Since Blandford did not indicate where the holotype was deposited in his original description, the location of the holotype is unknown. Therefore, the authors were unable to examine any specimens of *X. nanus*. Blandford separated it from *X. morigerus* by the characters of minute granules and setae on the elytral declivity. In several hundred specimens examined from New Caledonia, not a single one corresponded to *X. nanus* (Beaver per comm). Given that after over 100 years, *X. nanus* is still only known from the holotype, the validity of this species is doubtful.

Distribution. OCEANIA: New Caledonia.

Hosts. Unknown.

Specimens Examined. Unable to examine any specimens (see notes above).

Xylosandrus pusillus (Schedl)

(Fig. 2.36)

Xyleborus pusillus Schedl, 1961a: 91. Holotype ♀: Luzon, Rizal, Mt. Irid; NHMW.

Xylosandrus pusillus (Schedl): Schedl, 1964: 213.

Diagnosis. Female 1.5 – 1.7 mm long; 1.9 times longer than wide. Body light brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with a lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibial teeth not visible on specimen examined; metatibiae with 10 socketed teeth. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. compactus* (Fig. 2.14) and *X. curtulus* (Fig. 2.17). It can be distinguished from *X. curtulus* by a pronotal disc that is evenly pubescent, rather than mostly glabrous. *Xylosandrus pusillus* is nearly morphologically identical to *X. compactus*. The only character distinguishing the two species is the degree of body stoutness, with *X. pusillus* being 1.9 times as long as wide

and *X. compactus* being 2.3 times as long as wide. However, this is too large a disparity to warrant synonymizing the two species without further investigation.

Distribution. ORIENTAL REGION: Philippine Islands (Luzon).

Hosts. Unknown.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Holotype *Xyleborus pusillus* (♀; NHMW).

Xylosandrus pygmaeus (Eggers)

(Fig. 2.38)

Xyleborus pygmaeus Eggers, 1940: 142. Holotype ♀: Ost-Java (Alas Tbedek) leg.

Bedemann; NHMW.

Xylosandrus pygmaeus (Eggers): Browne, 1963: 55.

Diagnosis. Female 1.3 – 1.4 mm long; 2.3 times longer than wide. Body light brown to brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 6 socketed teeth; metatibiae with 5 socketed teeth. Elytra times 1.2 longer than

wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. boreensis* (Fig. 2.12). *Xylosandrus pygmaeus* can be distinguished from *X. boreensis* by the following characters: elytral declivity with striae less impressed; five striae visible on declivity; declivital striae with erect or semi-erect, hair-like setae, longer than the width of the second declivital interstriae; and pronotum with a lateral costa, but not carinate.

Distribution. ORIENTAL REGION: Indonesia (Java), Malaysia, Sri Lanka.

Hosts. *Litsea amara* Blume, *Vitex pubescens* Vahl.

Specimens Examined. (11 ♀; 0 ♂)

Type material: Holotype *Xyleborus pygmaeus* (1 ♀; NHMW).

Other material: **ORIENTAL REGION: Indonesia:** E. Java: Bangelan, 14.5.1932 (1 ♀; USNM); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot B, ca 300 m Lowland Forest, Mar-85, Flight intercept trap (1 ♀; RAB). **Malaysia:** BRUNEI: Temburong: Nr. K. Belalong Field, Study Centre 150 m, 4°33'N 155°09'E, 21.ii.1992, R. A. Beaver, RGS/UBD Exped. (1 ♀; RAB); MALAYSIA: Sabah Sipitang, Mendolong, T6/R, 14.iii.1989, leg. S. Abdebratt (1 ♀; RAB); MALAYSIA: Sabah Sipitang, Mendolong, T5/R, 10.iii.1989, leg. S. Abdebratt (1 ♀; RAB); MALAYSIA: Sabah Sipitang, Mendolong, T6/R, 14.iii.1989, leg. S. Abdebratt (1 ♀; RAB); MALAYSIA: Sabah Sipitang, Mendolong, T6/R, 11.v.1988, leg. S. Abdebratt (1 ♀; RAB);

MALAYSIA: Sabah Sipitang: Mendolong, T5/R, 28.iv.1988, leg. S. Abdebratt, comps.
Sp'm det. F. G. Browne (1 ♀; RAB). **Sri Lanka:** Ceylon [Sri Lanka]: W. Prov.,
Labugama, 24 miles ESE Colombo, 21.I.62, in sweep net (1 ♀; NHMW). **OTHER**
(uncertain): Selega (?), Kefang (?), 25. 1. 1949, F. G. Browne, ex *Vitex pubescens* (1 ♀;
BMNH).

Xylosandrus queenslandi Dole and Beaver

(Fig. 2.38)

Xylosandrus queenslandi Dole and Beaver, in press. Holotype ♀: AUSTRALIA,
Queensland, Bunya Mountain NP, 1100m, ex Leguminosae tree, 19.i.2000 (B. Jordal and
A. Sequeira); QMB.

Diagnosis. Female 1.6 – 1.9 mm long; 2.2 times longer than wide. Body light brown to
brown; elytra slightly darker than pronotum; antennae and appendages light brown.
Frons reticulate and sparsely punctate. Antennae with 5 funicular segments. Antennal
club obliquely truncate; first segment forming a circular costa; segment one covering
entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum
rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae;
setae less dense on disc. Basal pronotum with a dense patch of short, erect setae,
indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc moderately
punctate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with
lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on
lateral margin, meso- and metatibiae with 7 – 9 socketed teeth. Elytra 1.2 times longer
than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate

punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margin marked by a row of coarse, closely placed serrations. Six striae visible on declivity. Striae coarsely granulate, with erect, tapered hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of three *Xylosandrus* with lateral declivital margins that are marked by coarse serrations: *X. abruptulus* (Fig. 2.6), *X. corthyloides* (Fig. 2.15), and *X. queenslandi*. *Xylosandrus queenslandi* can be distinguished from *X. corthyloides* by the presense of a dense patch of mycangial setae on the basal pronotum. *Xylosandrus queenslandi* can be distinguished from *X. abruptulus* by the following characters: declivital face steep and abruptly separated from disc; declivity matte; and declivital striae with erect, acutely tapering, hair-like setae, shorter than the width of the second declivital interstriae.

Distribution. AUSTRALIAN REGION: Queensland.

Hosts. *Argyrodendron actinophyllum* (Bailey) Edlin.

Specimens Examined. (2 ♀; 0 ♂)

Type material: Paratypes *Xylosandrus queenslandi*: Australia: Queensland, Bunya mountains National Park, Jan. 2000, 1100 m, ex. Leguminosae tree, 19.1 B. Jordal and A. Sequeira leg. (2 ♀; MSU).

Xylosandrus rotundicollis (Browne), **new combination**

(Fig. 2.39)

Xyleborus rotundicollis Browne, 1984: 73. Holotype ♀: New Guinea: Morobe District, Mount Kaindi, 2350 m, 4.XI.1972; BMNH.

Diagnosis. Female 3.7 – 4.1 mm long; 2.2 – 2.6 times longer than wide. Body dark brown; antennae and legs light brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 – 1.0 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae narrowly, but completely separated. Protibiae with 4 – 5 socketed teeth on lateral margin; mesotibiae with 10 socketed teeth; metatibiae with 11 socketed teeth. Elytra 1.2 – 1.7 times longer than wide; 1.2 – 1.8 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins rounded, without a carina or a row of tubercles or serrations. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. monteithi* (Fig. 2.33). *Xylosandrus rotundicollis* can be distinguished from *X. monteithi* by the following characters: 3.7 – 4.1 mm long; basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium; declivital striae with semi-appressed, hair-

like setae, shorter than the width of the second declivital interstriae; and declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of the second declivital interstriae.

Distribution. AUSTRALIAN REGION: Papua New Guinea.

Hosts. *Ficus* L. sp., *F. mollior* Benth., *Gordonia* Ellis sp., *Meliosma* Blume sp., *Schefflera* sp. J. R. Forst and G. Forst.

Specimens Examined. (56 ♀; 0 ♂)

Type material: Holotype *Xyleborus rotundicollis* (♀; BMNH).

Other material: AUSTRALIAN REGION: Papua New Guinea: Papua New Guinea, Mu village, March 2006, 1600 m asl, Hulcr and Cognato coll. (54 ♀; MSU). Papua New Guinea, Kupa Range, Morobe, 2000 m., glue trap, Roberts coll. (1 ♀; FICB).

Xylosandrus subsimiliformis (Eggers)

(Fig. 2.41)

Xyleborus subsimiliformis Eggers, 1939a: 11. Holotype ♀: Nordostbirma (Kaim, 7000 Fuss) 17.V.1934; NHR (Eggers Cotype in NHMW).

Xylosandrus subsimiliformis (Eggers): Wood and Bright, 1992: 800.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a “new combination.”

Diagnosis. Female 2.8 mm long; 2.1 times longer than wide. Body brown; antennae and legs same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering

entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture or semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely aspirate-granulate, with sculpture separated by distance less than or equal to their width. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 10 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.2 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae finely granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. beelsoni* (Illustrated in Saha et al. 1992), *X. discolor* (Fig. 2.20), and *X. jaintianus* (Fig.2.27). *X. subsimiliformis* can be distinguished from these species by the following characters: declivity flattened; pronotum with a conspicuous summit on basal third; four striae visible on elytral declivity; and frons punctate, without a distinct median keel.

Distribution. ORIENTAL REGION: Burma.

Hosts. Unknown.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Cotype *Xyleborus subsimiliformis*: N. E. Burma, Nambaiti, 7000 ft., 12.5.1924, R. Malaise (♀; NHMW).

Xylosandrus subsimilis (Eggers)

(Fig. 2.41)

Xyleborus subsimilis Eggers, 1930: 186. Holotype ♀: Assam (Shillong, 6000 ft); FRI.

Xylosandrus subsimilis (Eggers): Wood and Bright, 1992: 800.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a “new combination.”

Diagnosis. Female 2.6 mm long; 2.0 times longer than wide. Body brown; antennae and legs same color as body. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi- appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by distance less than or equal to their width. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 - 5 socketed teeth on lateral margin; mesotibiae with 9 – 11 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on

declivity. Striae coarsely granulate, with appressed, scale-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, scale-like setae shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. beesoni* (Illustrated in Saha et al. 1992), *X. discolor* (Fig. 2.20), *X. jaintianus* (Fig. 2.27), and *X. subsimiliformis* (Fig. 2.41). However, *X. subsimilis* can easily be distinguished from these species by its declivital vestiture of dense, flattened, scale-like setae.

Distribution. ORIENTAL REGION: China, India (Assam, Bengal), Thailand.

Hosts. *Cinnamomum obtusifolium* Nees., *Tectona grandis* L., *Terminalia myriocarpa* Van Heurck and Müll. Arq..

Specimens Examined. (8 ♀; 1 ♂)

Type material: Cotype *Xyleborus subsimilis*: Shillong, 6000 ft, C. F. C. Beeson, 14.V.1925, ex. unknown wood (1 ♀; NHMW).

Other material: **ORIENTAL REGION: China:** China, 1962.VII (2 ♀; USNM). **India:** Samsingh 1800, Kalimpong, Bengal, 4.X.33, C. F. C. Beeson. ex. *Cinnamomum obtusifolium* branches (2 ♀; USNM). **Thailand:** Thailand: Chiang Mai: Doi Pui, 16.I.05, R. A. Beaver (1 ♀; RAB); Thailand: Chiang Mai, Doi Suthep, c.1400m, 18.x.04, R. A. Beaver (2 ♀, 1 ♂; RAB).

Xylosandrus terminatis (Eggers)

(Fig. 2.42)

Xyleborus terminatis Eggers, 1930: 182. Holotype ♀: Coorg (Virojapet, Sidapur); FRI.

Xylosandrus terminatis (Eggers): Browne, 1963: 55.

Diagnosis. Female 1.5 – 1.9 mm long; 2.1 times longer than wide. Body dark brown to black; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimens examined. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Striae punctate, without setae. Interstriae punctate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. derupteterminatus* (Fig. 2.18) and *X. morigerus* (Fig. 2.35). *Xylosandrus terminatus* can be distinguished from *X. morigerus* by the following characters: elytral declivity flattened; and five striae visible on declivity. *Xylosandrus terminatus* can be distinguished from *X. derupteterminatus* by the following characters: smaller species, 1.5 – 1.9 mm long; declivital striae without setae; and declivital interstriae uniseriate punctate.

Distribution. ORIENTAL REGION: India (Karnataka, Maharashtra, Tamil Nadu).

Hosts. *Holigarna arnottiana* Hook, *Lantana* L. sp., *Swietenia macrophylla* King.

Specimens Examined. (3 ♀; 0 ♂)

Type material: Cotype *Xyleborus terminatis*: Coorg, Virojapet, Sidapur, Y. R. Rao coll., 9. XI.1917, boring into twigs of *Lantana* (♀; NHMW).

Other material: **ORIENTAL REGION: India:** Chandanthode, Wynadd, Madras. Research Forester., 8.XII.1938, ex *Swietenia macrophylla* stump (2 ♀; USNM).

Xylosandrus woodi Dole and Beaver

(Fig.2.42)

Xylosandrus woodi Dole and Beaver, in press. Holotype ♀: [AUSTRALIA], NEQ[ueensland], 16°30'S x 145°19'E, Mt Demi summit, 1100 m, flight intercept, 17.xii.1995-22.i.1996 (Monteith, Thompson and Ford). In QMB (Accession # T144404).

Diagnosis. Female 2.3 – 2.4 mm long; 2.1 times longer than wide. Body dark brown; antennae and legs light brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed hair-like setae; pronotal disc densely setose, with setae as dense as on anterior pronotum. Lacking a dense patch of setae at base of pronotum. Pronotal disc densely asperate-granulate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4-5 socketed teeth on lateral margin; meso- and metatibiae with 7-8 socketed teeth. Elytra 1.3 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex,

lateral margin with discontinuous row of small tubercles, some of these towards apex with carinate tip. Five striae visible on declivity. Striae punctate, with appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed hair-like setae, longer than the width of second declivital interstriae.

This species can be distinguished from all other known *Xylosandrus* by its lateral declivital margin which is marked by a discontinuous row of small tubercles.

Xylosandrus woodi may be confused with *X. monteithi* (Fig. 2.33) and *X. rotundicollis* (Fig. 2.39), but these two species have lateral declivital margins that are rounded and without a row of tubercles.

Distribution. AUSTRALIAN REGION: Queensland.

Hosts. Unknown.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Paratype *Xylosandrus woodi*: Australia: NEQ, 19°07'S, 146°23'E, Mt Halifax summit, 1050m, heath, rainforest, pitfalls, 19-21.iii.1991, G. Monteith and D. Cook (1 ♀; MSU).

New Combinations, *Amasa*

Amasa cylindrotomicus (Schedl), **new combination**

Pseudoxyleborus cylindrotomicus Schedl, 1939: 40. Lectotype ♀: Sumatra, Benkoelen. 23-6-31, leg. Shuller; NHMW; designated by Schedl, 1979a: 74.

Xylosandrus cylindrotomicus (Schedl): Wood and Bright, 1992: 793.

Xyleborus semitruncatus Schedl, 1942b: 35. Lectotype ♀: Sumatra, Manna, 15-IX-34: NHMW; designated by Schedl, 1979a: 224. Synonymy: Wood, 1989: 177.

Xyleborus truncatellus Schedl, 1951: 79. Lectotype ♀: Z. Sumatra, Poelau Pisang, and Manna; NHMW; designated by Schedl 1979a: 256. Synonymy: Kalshoven, 1959: 95.

Xyleborus jucundus Schedl, 1954: 138. Lectotype ♀: Z. Sumatra, Poelau Pisang, and Manna; NHMW; designated by Schedl, 1979a: 256. Synonymy: Kalshoven, 1959: 95.

Xyleborus ramulorum Schedl, 1957: 115. Holotype ♀: Congo Belge: Yangambi; MRCB. Synonymy: Wood, 1989: 177.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. **AFROTROPICAL REGION:** Zaire. **ORIENTAL REGION:** Indonesia (Sumatra).

Specimens Examined. (4 ♀; 1 ♂)

Type material: Lectotype *Pseudoxyleborus cylindrotomicus* (♀; NHMW). Lectotype *Xyleborus semitruncatus* (♀; NHMW). Lectotype *Xyleborus truncatellus* (♀; NHMW). Allotype *Xyleborus truncatellus*: Sumatra, Manna, 25-IX-1934 (♂; NHMW).

Other material: **ORIENTAL REGION: Indonesia:** Sumatra, Benkoelen, 23-6-31, leg. Shuller (1 ♀; NHMW).

Discussion. Based on the contiguous procoxae, antennal club with 3 segments visible on the anterior and posterior face, the declivital face that is steep and abruptly separated from the elytral disc and the circular costa forming a complete circumdeclivital ring, this species is here transferred to *Amasa*.

Amasa omissus (Schedl), **new combination**

Xyleborus omissus Schedl, 1961b: 153. Holotype ♀: Madagascar, Antaniditra pres Perinet, 18 November 1952, K. E. Schedl; IRSM.

Xylosandrus omissus (Schedl): Wood and Bright, 1992: 799.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. **AFROTROPICAL REGION:** Madagascar.

Specimens Examined. (2 ♀; 0 ♂)

Type material: Paratypes *Xyleborus omissus*: Madagascar, Perinet, 17.XI.1952, K. E. Schedl (2 ♀; NHMW)

Discussion. Based on the contiguous procoxae, antennal club with 3 segments visible on the anterior and posterior face, the declivital face that is steep and abruptly separated from the elytral disc and the circular costa forming a complete circumdeclivital ring, this species is here transferred to *Amasa*.

Amasa oralis (Schedl), **new combination**

Xyleborus oralis Schedl, 1961b: 154. Holotype ♀: Madagascar, Antaniditra pres Perinet, 18 November 1952, K. E. Schedl; IRSM.

Xylosandrus oralis (Schedl): Wood and Bright, 1992: 799.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. AFROTROPICAL REGION: Madagascar.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Paratype *Xyleborus oralis*: Madagascar, Perinet, 17.XI.1952, K. E.

Schedl (♀; NHMW).

Discussion. Based on the contiguous procoxae, antennal club with 3 segments visible on the anterior and posterior face, and the declivital face that is steep and abruptly separated from the elytral disc, this species is here transferred to *Amasa*.

New Combinations, *Anisandrus*

Anisandrus butamali (Beeson), **new combination**

Xyleborus butamali Beeson, 1930: 40. Syntypes ♀: Bombay: Agsur, South Kanara, and Dandeli, North Kanara, B. M. Bhatia, Nov.; FRI.

Xylosandrus butamali (Beeson): Wood and Bright, 1992: 788.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. ORIENTAL REGION: India (Maharaashtra, Tamil Nadu).

Specimens Examined. (7 ♀; 0 ♂)

Type material: Paratypes *Xyleborus butamali*: Bombay, Agsur, S. Kanara Div., 13.XI.29, B. M. Bhatia, ex. *Dillenia pentagyna* (2 ♀; NHMW).

Other material: **ORIENTAL REGION: India:** S. India: Anamalis Hills, Cinohona, 3500 ft, April 1956, P. S. Nathan (1 ♀; USNM); Kattiyur, Wynaad, Madras, F. R. J. Project, 25.12.1945 (3 ♀; USNM); Manantoddy, N. Malabar, G. C. Robinson, 8.XI.1930. ex *Tectona grandis* (1 ♀; USNM).

Discussion. Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment one covering the entire posterior face. protibiae with 6 socketed teeth, and rounded lateral pronotal margins this species is here transferred to *Anisandrus*.

Anisandrus ursa (Eggers), **new combination**

Xyleborus ursa Eggers, 1923: 172. Lectotype ♀: Haveri, N. Guinea, S. E., Havari, Loria, VII-XI-93; USNM; designated by Anderson and Anderson, 1971: 35.

Xylosandrus ursa (Eggers): Wood and Bright, 1992: 801.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. **AUSTRALIAN REGION:** New Guinea, Solomon Islands. **ORIENTAL REGION:** Malaya, Indonesia (Celebes, Sumatra), Philippine Islands (Luzon).

Specimens Examined. (8 ♀; 0 ♂)

Type material: Lectotype *Xyleborus ursa* (♀; USNM).

Other material: **ORIENTAL REGION: Indonesia:** INDONESIA. *Irian Jaya:* PT., Freeport Concession Wapoga, camp. 03.14°S 136.57°E, 3600 ft., 19-29 April 1998, R. R. Snelling, Malaise trap montane primary rainforest (1 ♀; RAB); INDONESIA:

SULAWESI UTARA, Dumoga-Bone N.P., 1008 m G. mogongonipa summit, Aug-85, Malaise Trap (1 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P. G.Mogogonipa summit, 1008 m., Sep-85, Pitfall trap (1 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P. G.Mogogonipa summit, 1008 m., May-85, Malaise Trap (2 ♀; RAB). **Philippine Islands:** Luzon, P. I. Baguio Mt. Sto, Tomas W. Schultze (2 ♀; NHMW).

Discussion. Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment one covering the entire posterior face, protibiae with 7 socketed teeth, and rounded lateral pronotal margins this species is here transferred to *Anisandrus*.

Anisandrus ursinus (Hagedorn), **new combination**

Xyleborus ursinus Hagedorn, 1908: 381. Holotype ♀: Sumatra, Si-Ramve; MNB.

Xylosandrus ursinus (Hagedorn): Wood and Bright, 1992: 801.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. **ORIENTAL REGION:** Indonesia (Boreo/Soemba Island, Sumatra), Philippine Islands (Mindoro).

Specimens Examined. (9 ♀; 0 ♂)

Type material: Unable to examine type material.

Other material: **ORIENTAL REGION: Indonesia:** Dammerman, N. O. Soemba, Kambera, III.1925 (1 ♀; NHMW); Sumatra: Solok, Coll. F. Schneiber, 1911 (1 ♀;

MTD). **Philippine Islands:** Philippine Islands: Glog Riv., Mt. Apo, Mindanao, IX.29,30, Altitude 6000 ft., Coll. by C. F. Clagg (2 ♀; FMNH); Philippine Islands: La Lun Mts. Davao Prov., Mindanao, I.1.31, Coll. by C. F. Clagg, at light (1 ♀; FMNH); Mindoro. Port Galera, Mc Gregor (2 ♀; USNM); Mt. Makiling, Laguna P. I., 7-21-22, F. C. Hagedorn Collection (1 ♀; USNM); Philippine Islands: Seliban Riv., Mt. Apo, Mindanao, VII.30.30, Altitude 6000 ft., Coll. by C. F. Clagg (1 ♀; FMNH).

Discussion. Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment one covering the entire posterior face, protibiae with 7 socketed teeth, and rounded lateral pronotal margins this species is here transferred to *Anisandrus*.

Anisandrus ursulus (Eggers), new combination

Xyleborus ursulus Eggers, 1923: 173. Holotype ♀: Ost Bali, Kintamani, E. Sundainseln, 1913; MTD.

Xylosandrus ursulus (Eggers): Wood and Bright, 1992: 801.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. ORIENTAL REGION: China (Fujian), India (Bengal, Nicobar Islands), Malaya, Thailand, Indonesia (Bali, Borneo, Java, Sumatra, Sunda Island), Philippine Islands (Luzon).

Specimens Examined. (29 ♀; 1 ♂)

Type material: Holotype *Xyleborus ursulus* (♀; MTD). Cotype *Xyleborus ursulus*: Java: Batoerranden, G. Slamet, F. C. Drescher, 19.VII.1930 (♂; NHMW).

Other material: **ORIENTAL REGION: India:** Samasingh, Kalimpong, Bengal, III.1934, Mohal Lall. (3 ♀; USNM); Kamsingh, 1800, Kalimpong, Bengal, 22.III.34, C. F. C. Beeson, ex *Sterculia colorata* or *Sapium eugeniaefolium* (2 ♀; USNM). **Indonesia:** Java: Batoerraden, G. Slamet, F. C. Drescher, 22.III.1930 (5 ♀; USNM); Java: Batoerranden, G. Slamet, F. C. Drescher, 10.IV.1930 (2 ♀; NHMW); Java: Mount Gede, 1900 m, XI-1932, L. G. E. Kalshoven (1 ♀; USNM); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot B, ca 300 m Lowland Forest, Apr-85. Flight intercept trap (2 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., G.Mogogonipa summit, 1008 m, May-85, Malaise Trap (1 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Oct-85 (1 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, Apr-85, Flight intercept trap (2 ♀; RAB); INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, May-85, Flight intercept trap (1 ♀; RAB).

Malaysia: MALAYA: Pahang: Palau, Tioman: Kampong Tekek, to Kampong Juara, 20.iii.1962, K. J. Kuncheria Collector BISHOP, In Jungle (1 ♀; RAB); Mlay Penin: Pabang. F. M. S., Fraseas [?] Hill, 4200 ft, 28-6-1931 (1 ♀; NHMW); MALAYSIA: Penang, Pencing Hill. 1701, 10.viii.77, R. A. Beaver, Ex. Pitfall trap (1 ♀; RAB); SABAH: Poring Spring, *Xanthophyllum affine*, Lower montane, 650 m, Mixed dipterocarp Fst., 20. Vi. 1992, A. Floren, Fog Za4/F1 (1 ♀; RAB). **Thailand:** Thailand: Chiang Mai, Doi Chiang Dao, 12-13.vii.02, A. Cognato, ex ETOH trap on dead tree (1 ♀; RAB); Thailand: Kanchanaburi, 14.70N 98.87E, 17.vii.02, A. Cognato (3 ♀; RAB).

Discussion. Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment one covering the entire posterior face, protibiae with 7 socketed teeth, and rounded lateral pronotal margins this species is here transferred to *Anisandrus*.

New Combinations, *Cnestus*

***Cnestus ater* (Eggers), new combination**

Xyleborus ater Eggers, 1923: 210. Holotype ♀: Batoe Insel (Tanah Masa); Natura Artis Magistra.

Xylosandrus ater (Eggers): Wood and Bright, 1992: 787.

Xyleborus retusiformis Schedl, 1936: 31. Holotype ♀: Borneo; NHMW. Synonymy: Wood, 1989: 177.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. ORIENTAL REGION: China (Fujian), Malaya, Indonesia (Batoe Island, Borneo).

Specimens Examined. (6 ♀; 0 ♂)

Type material: Holotype *Xyleborus retusiformis* (♀; NHMW).

Other material: **ORIENTAL REGION: Brunei:** BRUNEI: Temburong: Nr. K.

Belalong Field, Study Centre 300m, 4°33'N 155°09'E, 10.ii.1992, R. A. Beaver,

RGS/UBD Exped. Ex. Rattan Calamus Daeninorops (2 ♀; RAB); BRUNEI: Temburong:

Nr. K. Belalong Field, Study Centre 300m, 4°33'N 155°09'E, 10.ii.1992, R. A. Beaver,

RGS/UBD Exped. Ex. Calamus Daeninorops sp. (2 ♀; RAB). **Indonesia:** Padang, ex. Ljengkeh [?], 14.Xii.35, Kalshoven (1 ♀; NHMW).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with 6 socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus fijianus (Schedl), **new combination**

Xyleborus fijianus Schedl, 1938: 50. Lectotype ♀: Fiji Islands, Taverne Quilai, 800 feet, October 18, 1924, H. S. Evans; NHMW.

Xylosandrus fijianus (Schedl): Wood and Bright, 1992: 794-795.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. **OCEANIA:** Fiji Islands.

Specimens Examined. (9 ♀; 2 ♂)

Type material: Lectotype *Xyleborus fijianus* (♀; NHMW).

Other material: **OCEANIA: Fiji:** Fiji, Lami Quarry, Nr. Suva, VII-24-38, E. C.

Zimmerman collector, beating shrubs, 10', 250' (1 ♀; NHMW)l Fijji. Viti Levu, Suva, 22.xi.88, R. A. Beaver, ex *Swietenia macrophylla* (1 ♀; RAB); FIJI, Viti Levu, Savura Creek, 29.iii.83, R. A. Beaver, ex *Serianthea melanesica* (1 ♀; RAB); FIJI, Viti Levu, Namosi 10km, 19-20. V. 85, R. A. Beaver (2 ♀; RAB); FIJI, Viti Levu, Savura Creek,

19.iii.83, R. A. Beaver, ex *Canarium vitiense* (2 ♀; RAB)l; FIJI, Viti Levu, Savura Creek, v.83, R. A. Beaver, ex *Canarium vitiense* (1 ♂; RAB); Fiji, Suva, ex. *Swietenia macrophylla* (1 ♂; BMNH). Fiji, Colo-I-Suva, Static Trap 71, Mahongany plantation. Cpt 23, 10/10/2006, K. Wotherspoon.

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with 7 socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus gravidus (Blandford), **new combination**

Xyleborus gravidus Blandford, 1898: 427. Holotype ♀: Chittagong Hills [Bangladesh]; BMNH.

Xylosandrus gravidus (Blandford): Wood and Bright, 1992: 796.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. **ORIENTAL REGION:** Bangladesh, Burma, India (Assam, Bengal), Laos, Sri Lanka, Thailand, Vietnam (Tonkin). **PALEARCTIC REGION:** China (Xizang [Tibet]).

Specimens Examined. (2 ♀; 0 ♂)

Type material: Unable to examine type material.

Other material: **ORIENTAL REGION: Vietnam:** Nord Vietman, L. Thainguyen, VII.1969, leg. Le. Van. Nong (1 ♀; NHMW); Phovi, S 07 (1 ♀; NHMW).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering most of the posterior face, the presence of a coarse median pair of asperities on the anterior margin of the pronotum, the protibiae with 7 socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus improcerus (Sampson), **new combination**

Xyleborus improcerus Sampson, 1921: 33. Holotype ♀: Siam; BMNH.

Xylosandrus improcerus (Sampson): Beaver, 1998: 183.

Distribution. **ORIENTAL REGION:** Brunei, India, Indonesia (Borneo), Malaya, Thailand.

Specimens Examined. (7 ♀; 0 ♂)

Type material: Unable to examine type material.

Other material: **ORIENTAL REGION:** Brunei. BRUNEI: Temburong: Nr. K. Belalong Field, Study Centre 250 m, 4°33'N 155°09'E, 7.ii.1992, R. A. Beaver, RGS/UBD Exped. (3 ♀; RAB); BRUNEI: Temburong: Nr. K. Belalong Field, Study Centre 250 m, 4°33'N 155°09'E, 21.ii.1992, R. A. Beaver, RGS/UBD Exped. (1 ♀; RAB); Lagleari [?] BC. Sarak, 20:X:1948, F. G. Browne (1 ♀; USNM); Malaya, Kelantan, E. G. B., 6.10.1946 (1 ♀; USNM); MALAYA, Teneguann, Besut Dist., V-1958, R. Traub, 400 ft. (1 ♀; USNM).

Discussion. Based on the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with 6 socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus laticeps (Wood), **new combination**

Xyleborus laticeps Wood, 1977: 219. Holotype ♀: 20 km SW El Vigia, Merida, Venezuela; USNM.

Xylosandrus laticeps (Wood): Wood and Bright, 1992: 796.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. NEOTROPICAL REGION: Venezuela.

Specimens Examined. (51 ♀; 12 ♂)

Type material: *Xyleborus laticeps* (♀; USNM).

Other material: **NEOTROPICAL REGION: Venezuela:** Venezuela: 9 km S

Barrancas, 150 m, X-1-69, S. L. Wood, *Protium tenuifolium* (13 ♀; USNM); Venezuela:

9 km S of Barrancas, Barinas, 150 m, X-5-69, S. L. Wood (2 ♀; USNM); Venezuela: 9

km S. of Barrancas, Barinas, 150 m, XI-5-69, S. L. Wood, *Spondias mombin* (5 ♀;

USNM); Venezuela: 9 km S. of Barrancas, Barinas, 150 m, XI-5-69, S. L. Wood,

Dendropanax arboreum (1 ♀; USNM); Venezuela: 9 km S Barrancas, Barinas, XII-2-69,

el. 150 m, S. L. Wood, *Melicococcus bijugata* (1 ♀; USNM); Venezuela: 8 km SW

Bumbum, Barinas, II-11-1970, 150 m, S. L. Wood, *Tartaguito* sp. (2 ♀; USNM);
 Venezuela: 40 km, E Canton, Barinas, III-8-1970, 70 m, S. L. Wood, *Protium tenuifolium*
 (1 ♀; USNM); Venezuela: 40 km E Canton, Barinas, III-8-1970, 70 m, S. L. Wood,
Palito negro (1 ♀; USNM); Venezuela: 40 km E Canton, Barinas, III-8-1970, 70 m, S. L.
 Wood, tree seedling (1 ♀; USNM); Venezuela: 40 km E Canton, Barinas, III-8-1970, 70
 m, S. L. Wood, *Pouteria anibaefolia* (1 ♀; USNM); Venezuela: 5 km W El Pino, 10 m,
 Zulia, X-20-69, S. L. Wood, unknown tree (2 ♀; USNM); Venezuela: 20 km SW El
 Vigio, Merida, XI-21-69, el. 50 m, S. L. Wood, *Jacaranda* sp. (10 ♀; USNM);
 Venezuela: Merida, 1700 m, IX-22-69, S. L. Wood (4 ♀, 12 ♂; USNM); Venezuela: 40
 km SE Socopo, Barinas, I-25-1970, 150 m, S. L. Wood, *Protium* sp. (1 ♀; USNM);
 Venezuela: 17 km SE of Miri, Barinas, XII-17-69, 150 m, S. L. Wood, *Protium* sp. (1 ♀;
 USNM); Venezuela: 10 km SE of Miri, Barinas, II-8-1970, 150 m, S. L. Wood, *Inga* sp.
 (1 ♀; USNM); Venezuela: 7 km NW Socopo, Barinas, II-13-1970, 200 m, S. L. Wood,
Protium sp. (1 ♀; USNM); Venezuela: Valle de Choroní, IV-3-1964, J. L. Saunders,
Theobroma cacao (3 ♀; USNM).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle,
 obliquely truncate antennal club with first segment forming a circular costa and segment
 one covering the entire posterior face, the presence of a coarse median pair of asperities
 on the produced anterior margin of the pronotum, the protibiae with 6 socketed teeth, and
 the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus mutilatus (Blandford), **new combination**

Xyleborus mutilatus Blandford, 1894c: 103. Holotype ♀: Japan; BMNH.

Xylosandrus mutilatus (Blandford): Wood and Bright, 1992: 799.

Xyleborus sampsoni Eggers, 1930: 184. Holotype ♀: Assam (Haflong, Cachar); FRI.

Synonymy: Wood, 1989: 177.

Xyleborus banjoewangi Schedl, 1939: 41. Lectotype ♀: Banjoewangi, 270 m.

Tjoerahlele, 25-II-36; NHMW. Synonymy: Kalshoven, 1960: 63.

Xyleborus taitonus Eggers 1939b: 118. Holotype ♀: Formosa, Taito; Chujo Collection.

Synonymy: Wood and Bright, 1992: 799.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer. *Xyleborus taitonus* was also listed as a synonym by Wood and Bright (1992), but was not indicated as a “new synonymy.” Wood and Bright (1992) indicate that “Specimens in the FRI, Dehra Dun labeled by Eggers as *taionus* are *mutilatus*; synonymy needs confirmation”, but this author was unable to examine the specimens referred to.

Distribution. **AUSTRALIAN REGION:** New Guinea. **NEARCTIC REGION:** United States (Florida, Mississippi, Texas). **ORIENTAL REGION:** Burma, China (Anhui, Sichuan, Yunnan, Zhejiang), India (Andaman Islands, Assam), Indonesia (Batoe, Boreneo, Java, Sumatra), Japan, Malaya, Sri Lanka, Taiwan, Thailand. **PALEARCTIC REGION:** Korea.

Specimens Examined. (34 ♀; 3 ♂)

Type material: Paratype *Xyleborus mutilatus*: Malaya, Salagor, 16:XI:1948, F.G.

Browne ex wood of *Adenanthera tauonina* (♂; BMNH). Lectotype *Xyleborus*

banjoewangi (♀; NHMW). Allotype *Xyleborus banjoewangi*: Banjoewangi, II-1936, leg. Baschwesen [?] (1 ♂; NHMW).

Other material: **ORIENTAL REGION: Japan:** JAPAN: Okinawa I., Mt. Oppadake,

20.vi.95, H. Goto, ex *Rhus succedanea* (2 ♀, 1 ♂; RAB); JAPAN: RYUKYUS, Mt.

Oppadake, Okinawa Is., emerged from the logs, 19.vii.1995, H. Goto leg., Host tree:

Rhus succedanea L. (1 ♀, 1 ♂; RAB). **NEARCTIC REGION: United States:**

Mississippi, Oktibbeha Co., 3 mi W. of Adaton, 33°29'00"N 88°58'13"W, 23-26 April

2004, T. L. Schiefer coll (39 ♀; MSU); Miss., Oktibbeha Co., 3 mi W. of Adaton,

33°29'00"N 88°58'13"W, 17-19 April 2002, T. L. Schiefer, in Lindgren funnel trap (1 ♀; MSU).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with 7 socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus orbiculatus (Schedl), **new combination**

Xyleborus orbiculatus Schedl, 1942a: 186. Holotype ♀: Borneo; NHMW.

Xylosandrus orbiculatus (Schedl): Wood and Bright, 1992: 800.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. **ORIENTAL REGION:** Indonesia (Borneo).

Specimens Examined. (2 ♀; 0 ♂)

Type material: Holotype *Xyleborus orbiculatus* (♀; NHMW).

Other material: **ORIENTAL REGION: Borneo:** BRITISH N. BORNEO, Tenompok, 15.II.1959, T. C. Maa Collector (1 ♀; RAB).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering most the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus peruanus (Wood), **new combination**

Xylosandrus peruanus Wood, 2007: 468. Holotype ♀: Satipo [Junin], Peru, V-VI.1942, Paprzycki; USNM.

Distribution. **NEOTROPICAL REGION:** Peru (Junin).

Specimens Examined. (1 ♀; 0 ♂)

Type material: Holotype *Xylosandrus peruanus* (♀; USNM).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering most the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, and the protibiae with 6 socketed teeth this species is here transferred to *Cnestus*.

Cnestus retifer (Wood), **new combination**

Xylosandrus retifer Wood, 2007: 468. Holotype ♀: Fazenda Laminit, Itinga do Maranhão, Brazil; MZUSP.

Distribution. NEOTROPICAL REGION: Brazil.

Specimens Examined. (1 ♀; 0 ♂)

Type material: Paratype *Xylosandrus retifer* BR-MA-Itinga do Maranhão, Fazenda Laminit, 6-yr old *Schizolobium nicum* stand, ethanol baited FIT, Ataíde, J. A. col. VII/2002 (♀; USNM).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus retusus (Eichhoff), **new combination**

Xyleborus retusus Eichhoff, 1868: 151. Syntypes ♀: N. Freiburg [Brazil]; Hamburg Museum, lost.

Xylosandrus retusus (Eichhoff): Wood and Bright, 1992: 800.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. NEOTROPICAL REGION: Argentina, Brazil.

Specimens Examined. (120 ♀; 0 ♂)

Type material: Unable to examine type specimens.

Other material: **NEOTROPICAL REGION: Brazil:** Brazil: Nova Teutonia, Sta. Cat., X-56, Plaumann (19 ♀; USNM); Brazil: Nova Teutonia, 27°11'8".52°23'1", F. Plaumann, 300-500 m, XI.1956 (1 ♀; USNM); Brazil: Nova Teutonia, 27°11'8" 52°23'1", F. Plaumann, 300-500 m, I-1.1957 (1 ♀; USNM); Brazil: Nova Teutonia, 1944, F. Plaumann coll. (5 ♀; USNM); Brasil, Nova Teutonia, Santa Catarina, IX-18-1944, 27°11'La., 52°23'Lo., Fritz Plaumann collector (1 ♀; AMNH); Brazil: Nova Teutonia, 28 Oct 1951, F. Plaumann coll. (10 ♀; FMNH); Brazil: Nova Teutonia, 25 Oct 1951, F. Plaumann coll. (7 ♀; FMNH); Brazil: Nova Teutonia, 27°11' B. 52°23' L., 500m, XI.1947, Fritz Plaumann (8 ♀; FMNH); Brazil, Nova Teutonia, Sta. Catharina, VII.14.1944 (1 ♀; FMNH); Brasil: Nova Teutonia, 1944, F. Plaumann coll. (3 ♀; NHMW); Brasil, Rio Claro-S. Paulo, Mat no. 5, III-947 [?] (1 ♀; USNM)l Brasil, Rio Claro-S. Paulo, Mat no. 2 III-946[?] (1 ♀; USNM); Brazil: Santa Catharina, Nova Teutonia, 300-500 m, 27°11'-52°23', XI-1947, leg. F. Plaumann (60 ♀; FMNH); Brasil, Varginha, M Gerais, M. Alvarenga leg., III.1972 (1 ♀; NHMW); RS/RGS Exp. Brazil. 12o49'S 51o46'W, 29.xi.1968, R. A. Beaver (1 ♀; RAB).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with 6 socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus testudo (Eggers), **new combination**

Xyleborus testudo Eggers, 1939b: 116. Lectotype ♀: Formosa, Trichu, XI.1930., col. T.

Mitono; USNM; designated by Anderson and Anderson, 1971: 34.

Xylosandrus testudo (Eggers): Wood and Bright, 1992: 801.

Notes. This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a “new combination” or cite any characters justifying its transfer.

Distribution. ORIENTAL REGION: Taiwan, Thailand, Vietnam.

Specimens Examined. (3 ♀; 0 ♂)

Type material: Lectotype *Xyleborus testudo* (♀; USNM).

Other material: **ORIENTAL REGION: Thailand:** THAILAND: Chiang Mai 600 m, Fang., 17.iii.74, R. A. Beaver, comp. Paralectotyps ex. TARI. (1 ♀; RAB). **Vietnam:** Tonkin, Reg De Moa binn, A. De Looman, 1929 (1 ♀; NHMW).

Discussion. Based on the subcontiguous procoxae, the 4-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment one covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with 7 socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

New Combinations, *Cyclorhipidion*

Cyclorhipidion squamulatus (Beaver and Löyttyniemi), **new combination**

Apoxyleborus squamulatus Beaver and Löyttyniemi, 1985: 69. Holotype ♀: Zambia: Lusaka, 21.i.1980, light trap. R. A. Beaver coll; BMNH.

Xylosandrus squamulatus (Beaver and Löyttyniemi): Wood, 1984: 229.

Notes. Beaver and Löyttyniemi (1985) described this species in the genus *Apoxyleborus*. However, Wood (1984) had synonymized *Apoxyleborus* with *Xylosandrus*. The species was listed in *Xylosandrus* by Wood and Bright (1992).

Distribution. AFROTROPICAL REGION: Zambia.

Hosts. Unknown.

Specimens Examined. (2 ♀; 0 ♂)

Type material: Holotype *Apoxyleborus squamulatus* (♀; BMNH). Paratype

Apoxyleborus squamulatus: ZAMBIA, Lusaka, 2052, 8-9.v.80, R. A. Beaver, trap light (♀; RAB).

Discussion. Based on the contiguous procoxae, antennal club with segment one not forming a circular costa (type 3, Hulcr et al. 2007), and arched protibiae with 8 socketed teeth, this species is herein transferred to *Cyclorhipidion*. This species was compared with the holotype of the type species of *Cyclorhipidion*: *C. pelliculosus*. The inclusion this species, along with *Cylcorhipidion pelliculosus* Eggers, in the phylogenetic analysis of morphological data caused the strict consensus tree to become completely unresolved. Since *Cyclorhipidion* has not historically been confused with *Xylosandrus*, the genus was not included in the phylogenetic analysis.

Species	Afrotropical Region	Australian Region	Nearctic Region	Neotropical Region	Oceania	Oriental Region	Palaearctic Region
<i>X. abruptulus</i>		●					
<i>X. adherescens</i>						●	
<i>X. amputatus</i> n. comb.						●	
<i>X. arquatus</i>						●	
<i>X. assequens</i>						●	
<i>X. beesoni</i>						●	
<i>X. borealis</i>						●	●
<i>X. boreensis</i> n. sp.						●	
<i>X. brevis</i>						●	●
<i>X. compactus</i>	●		▲	●	●	●	
<i>X. corthyloides</i>						●	
<i>X. crassiusculus</i>	●	●	▲	●	●	●	▲
<i>X. curtulus</i>			●	●			
<i>X. derupteterminatus</i>						●	
<i>X. deruptulus</i>						●	
<i>X. discolor</i>		●			●	●	
<i>X. diversepilosus</i>						●	
<i>X. eupatorii</i>						●	
<i>X. ferinus</i>						●	
<i>X. germanus</i>			▲		●	●	▲
<i>X. hirsutipennis</i>	●						
<i>X. hulcri</i> n. sp.		●					
<i>X. jaintianus</i>						●	●
<i>X. mancus</i>	●					●	
<i>X. mediocris</i>						●	
<i>X. mesuae</i>		●				●	
<i>X. metagermanus</i>						●	
<i>X. mixtus</i> n. comb.		●					
<i>X. monteithi</i>		●					
<i>X. morigerus</i>	●	●		●	●	●	▲
<i>X. pusillus</i>						●	
<i>X. pygmaeus</i>						●	
<i>X. queenslandi</i>		●					
<i>X. rotundicollis</i> n. comb.		●					
<i>X. subsimiliformis</i>						●	
<i>X. subsimilis</i>						●	
<i>X. terminatus</i>						●	
<i>X. woodi</i>		●					

Table 2.1: Biogeographic distribution of *Xylosandrus* species: ● = present: ▲ = present as introduced species.

Species	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Amasa anomalus</i>	1	0	0	0	1	0	2	1	0	3	1	0	0	0	0	2	0	0	0	?
<i>A. bicoastatus</i>	1	0	1	0	1	0	2	2	0	3	1	0	0	0	0	2	0	0	1	2
<i>A. cylindriciformis</i>	1	0	1	0	?	?	?	2	0	3	1	0	0	0	0	2	0	0	0	2
<i>A. cylindrotomicus</i>	1	0	0	0	1	0	2	0	0	0	1	0	0	0	0	2	0	0	0	2
<i>A. fulgens</i>	1	0	1	0	?	0	2	2	0	3	1	0	0	0	0	2	0	0	0	?
<i>A. omissus</i>	1	0	0	0	?	0	2	2	0	3	1	0	0	0	0	2	0	0	0	2
<i>A. oralis</i>	1	0	2	0	1	0	2	2	0	3	1	0	0	0	0	2	0	0	1	?
<i>A. striatotruncatus</i>	1	0	1	0	1	0	2	1	0	0	1	0	0	0	0	2	0	0	0	1
<i>A. umbratulus</i>	1	0	1	0	1	0	2	0	0	3	1	0	0	0	0	2	0	0	0	?
<i>A. versicolor</i>	1	1	1	0	1	0	2	2	0	3	1	0	0	0	0	2	0	0	0	2
<i>Anisandrus butamali</i>	0	0	0	0	1	1	0	2	0	1	0	1	1	1	0	2	1	0	0	2
<i>A. dispar</i>	1	0	0	0	1	1	0	0	0	1	1	2	1	0	0	1	0	0	0	2
<i>A. obesus</i>	1	0	0	0	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	1
<i>A. sayi</i>	1	0	0	0	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	2
<i>A. ursa</i>	1	0	0	0	2	1	0	0	0	1	0	2	1	0	1	2	1	0	0	2
<i>A. ursinus</i>	1	0	0	0	2	1	0	0	0	1	1	1	1	0	1	2	1	0	0	2
<i>A. ursulus</i>	1	0	0	0	2	1	0	0	0	1	1	2	1	0	1	2	1	0	0	2

Table 2.2 (cont. following pages): Morphological character matrix of 43 characters for 73 species. Characters are their scores 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
<i>Cnestus ater</i>	0	0	0	0	0	2	1	0	0	1	1	1	1	0	1	1	1	1	1	1
<i>C. bimaculatus</i>	0	2	0	0	0	1	0	1	0	1	1	0	1	0	1	1	1	0	1	1
<i>C. fijianus</i>	0	0	0	0	0	2	1	0	0	1	1	2	1	0	1	1	1	1	1	1
<i>C. gravidus</i>	0	0	0	0	0	2	1	0	0	1	1	0	1	0	0	1	1	0	1	1
<i>C. improcerus</i>	0	2	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	1	1	0
<i>C. laticeps</i>	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	0	1
<i>C. mutilatus</i>	0	0	2	1	0	2	1	0	0	1	1	2	1	0	1	1	1	1	1	1
<i>C. orbiculatus</i>	0	0	0	0	0	2	0	1	0	1	1	0	1	0	0	1	1	1	1	1
<i>C. peruanus</i>	1	0	0	0	0	1	0	0	0	1	1	2	1	0	1	1	1	1	0	1
<i>C. pseudosolidus</i>	0	0	0	0	0	2	0	1	0	1	1	1	1	0	0	1	1	0	0	1
<i>C. pseudosuturalis</i>	1	2	0	0	0	2	0	1	0	1	1	1	1	0	0	1	1	1	1	1
<i>C. retifer</i>	0	0	0	0	0	1	0	2	0	1	1	0	1	0	0	1	1	1	0	1
<i>C. retusus</i>	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	1	0	1
<i>C. solidus</i>	0	1	0	0	0	2	0	0	0	1	1	2	1	0	1	1	1	0	0	1
<i>C. testudo</i>	0	0	2	0	0	2	1	0	0	1	1	1	1	0	1	1	1	1	1	1
<i>C. triangularis</i>	1	0	0	0	0	2	0	2	0	1	1	1	1	1	1	1	1	1	1	1
<i>Coccotrypes dactyliperda</i>	1	0	2	0	0	2	1	2	1	0	1	2	0	1	1	0	?	0	0	2
<i>Xyleborus affinis</i>	1	0	0	0	1	2	1	2	0	0	1	1	0	0	0	0	?	0	0	2
<i>X. californicus</i>	1	0	0	0	1	2	1	2	0	0	1	1	0	0	0	0	?	0	0	2

Table 2.2 (cont.): Morphological character matrix of 43 characters for 73 species. Characters are their scores 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
<i>Xylosandrus adherescens</i>	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0
<i>X. amputatus</i>	1	0	0	1	1	1	0	0	0	0	1	1	1	0	1	2	0	0	0	0
<i>X. arquatus</i>	1	1	?	0	?	1	0	0	1	0	1	1	1	1	0	2	0	0	0	0
<i>X. assequens</i>	1	0	2	0	1	1	0	0	0	0	1	1	0	0	1	2	0	0	1	0
<i>X. beesonii</i>	1	0	2	0	1	1	0	0	0	0	1	2	1	1	1	2	0	0	1	0
<i>X. borealis</i>	1	0	2	1	1	1	0	2	0	2	1	2	1	1	1	2	0	0	0	0
<i>X. borneensis</i>	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0
<i>X. brevis</i>	1	0	2	1	1	1	0	0	0	0	1	2	1	1	1	2	0	0	0	0
<i>X. compactus</i>	1	0	0	0	1	1	0	1	0	0	1	1	1	0	0	2	0	0	1	0
<i>X. corthyloides</i>	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	2	0	0	0	0
<i>X. crassiusculus</i>	1	0	2	0	1	1	0	1	0	0	1	2	1	0	1	2	0	0	0	1
<i>X. curtulus</i>	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	2	0	0	1	0
<i>X. derupteterminatus</i>	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0
<i>X. deruptulus</i>	1	0	2	0	?	?	?	0	0	0	1	1	?	0	1	2	0	0	1	0
<i>X. discolor</i>	0	1	0	0	1	1	0	0	0	0	1	1	1	1	1	2	0	0	1	0
<i>X. diversepilosus</i>	1	0	?	?	?	?	?	0	0	0	1	1	1	1	1	2	0	0	0	?
<i>X. eupatorii</i>	1	0	0	0	1	1	0	1	0	1	1	0	1	0	0	2	0	0	1	0
<i>X. ferinus</i>	1	1	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	0	0
<i>X. germanus</i>	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	1	0

Table 2.2 (cont.): Morphological character matrix of 43 characters for 73 species. Characters are their scores 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
<i>X. hirsutipennis</i>	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	2	0	0	0	0
<i>X. hulcri</i>	1	2	0	0	1	1	0	0	0	1	1	1	0	0	0	2	0	0	0	0
<i>X. jainianus</i>	1	0	2	1	1	1	0	0	0	0	1	1	1	1	1	2	0	0	1	0
<i>X. mancus</i>	1	3	0	0	1	1	0	1	0	0	1	1	1	0	0	2	0	0	0	0
<i>X. mediocris</i>	1	0	?	0	?	?	?	1	0	0	1	1	1	0	0	2	0	0	1	?
<i>X. mesuae</i>	1	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	0	0
<i>X. metagermanus</i>	1	0	2	0	?	1	0	0	0	0	1	0	1	0	0	2	0	0	0	0
<i>X. mixtus</i>	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	0	1
<i>X. montethi</i>	1	0	0	0	1	1	0	0	0	1	1	2	0	0	0	2	0	0	0	0
<i>X. morigerus</i>	1	0	0	0	1	1	0	0	0	1	1	1	1	0	0	2	0	0	1	0
<i>X. pusillus</i>	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	1	0
<i>X. pygmaeus</i>	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	2	0	0	1	0
<i>X. queenstandi</i>	1	0	2	0	1	1	0	0	0	1	1	1	1	0	0	2	0	0	0	0
<i>X. rotundicollis</i>	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	0	1
<i>X. subsimilis</i>	1	0	2	0	1	1	0	0	0	0	1	1	1	1	1	2	0	0	1	0
<i>X. subsimiliformis</i>	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1	2	0	0	0	0
<i>X. terminatis</i>	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0
<i>X. woodi</i>	1	0	0	0	1	1	0	0	0	1	1	2	0	1	1	2	0	0	0	0

Table 2.2 (cont.): Morphological character matrix of 43 characters for 73 species. Characters are their scores described in Materials and Methods.

Species	Characters																						
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
<i>Amasa anomalus</i>	1	0	1	1	1	1	1	2	1	2	0	0	0	2	0	0	2	1	2	0	0	0	0
<i>A. bicostatus</i>	1	0	1	1	1	1	1	2	1	1	0	0	0	0	?	?	0	1	0	?	?	1	1
<i>A. cylindriiformis</i>	?	0	1	1	1	1	2	2	1	0	0	0	0	0	?	?	2	1	0	?	?	1	1
<i>A. cylindrotomicus</i>	0	0	0	1	1	1	1	2	1	1	0	0	0	0	?	?	1	1	0	?	?	0	0
<i>A. fulgens</i>	?	0	0	1	1	1	1	2	1	1	0	0	0	1	0	0	2	1	1	1	0	1	1
<i>A. omissus</i>	?	0	1	1	1	1	1	2	1	3	0	0	0	0	?	?	1	1	1	0	1	0	0
<i>A. oralis</i>	0	0	1	1	1	1	1	2	0	?	0	0	1	?	?	?	1	1	1	0	0	1	1
<i>A. striatotruncatus</i>	2	0	1	1	1	1	1	2	1	1	0	0	0	0	?	?	0	1	0	?	?	0	0
<i>A. umbratulus</i>	1	0	1	1	1	1	1	2	1	1	0	0	0	0	?	?	2	1	0	?	?	0	1
<i>A. versicolor</i>	1	0	1	1	1	1	1	2	1	1	0	0	0	0	?	?	2	1	0	?	?	0	1
<i>Anisandrus butamali</i>	1	2	1	1	0	0	0	0	?	4	0	0	0	0	?	?	1	1	1	1	1	0	0
<i>A. dispar</i>	1	0	0	1	0	0	0	1	?	4	0	0	0	1	0	1	1	1	1	1	1	0	0
<i>A. obesus</i>	2	0	1	1	0	0	0	3	?	4	1	0	0	1	0	1	1	0	1	1	1	0	0
<i>A. sayi</i>	2	0	1	1	0	0	0	1	?	4	1	0	0	0	?	?	1	0	1	1	1	0	0
<i>A. ursa</i>	1	0	1	1	0	0	0	0	?	3	0	0	0	0	?	?	1	1	1	1	1	0	0
<i>A. ursinus</i>	1	0	1	1	0	0	0	0	?	3	0	0	0	0	?	?	1	1	1	1	1	0	0
<i>A. ursulus</i>	1	0	1	1	0	0	0	0	?	3	0	0	0	0	?	?	1	1	1	1	1	0	0

Table 2.2 (cont.): Morphological character matrix of 43 characters for 73 species. Characters are their scores described in Materials and Methods.

Characters		21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Species		3	2	1	0	1	1	0	2	0	3	0	1	1	1	0	0	1	1	1	0	0	0	0
<i>Cnestus ater</i>		0	2	1	1	0	0	0	2	0	3	0	0	0	0	?	?	0	1	0	?	?	0	0
<i>C. bimaculatus</i>		2	2	1	0	1	0	0	2	0	?	0	1	1	1	1	0	1	1	1	1	0	0	0
<i>C. fijianus</i>		0	2	1	1	1	0	0	2	0	3	0	0	0	1	1	0	1	1	1	1	0	1	0
<i>C. gravidus</i>		1	2	1	0	1	0	0	2	0	?	0	0	0	1	1	0	1	1	1	1	0	0	0
<i>C. improcerus</i>		1	2	1	0	1	0	0	2	1	?	0	0	1	0	?	?	1	1	0	?	?	0	0
<i>C. laticeps</i>		2	2	1	0	1	1	0	2	0	?	0	0	1	1	1	0	1	1	1	1	0	0	0
<i>C. mutilatus</i>		?	2	1	0	1	0	0	2	0	3	1	0	0	0	?	?	1	1	0	?	?	0	0
<i>C. orbiculatus</i>		1	0	1	1	0	0	0	2	0	3	0	0	0	1	1	1	1	1	1	1	1	1	0
<i>C. peruanus</i>		0	2	1	1	1	0	0	2	0	4	1	0	0	1	?	0	1	1	1	1	0	0	0
<i>C. pseudosolidus</i>		?	0	1	1	0	0	0	2	0	3	0	0	0	0	?	?	0	0	1	1	1	0	0
<i>C. pseudosuturalis</i>		?	2	1	1	1	0	0	2	0	?	0	0	1	0	?	?	0	1	0	?	?	1	1
<i>C. retifer</i>		1	2	1	1	1	1	0	2	0	?	0	1	1	0	?	?	1	1	0	?	?	0	0
<i>C. retusus</i>		1	2	1	1	1	0	0	2	0	4	1	0	0	1	0	1	1	1	1	1	0	0	0
<i>C. solidus</i>		2	2	1	0	1	1	0	2	0	3	0	0	0	1	0	0	1	1	1	1	0	0	0
<i>C. testudo</i>		1	0	1	1	1	0	0	2	0	3	0	0	0	?	?	?	1	0	1	1	1	0	0
<i>C. triangularis</i>		0	0	0	1	0	0	0	0	?	?	0	0	0	1	0	0	1	0	1	1	1	0	0
<i>Coccotrypes dactyliperda</i>		0	0	0	1	0	0	0	1	?	4	0	0	0	0	?	?	1	0	1	1	1	0	0
<i>Xyleborus affinis</i>		2	0	0	1	0	0	0	0	?	4	0	0	0	0	?	?	1	0	1	1	1	0	0
<i>X. californicus</i>																								

Table 2.2 (cont.): Morphological character matrix of 43 characters for 73 species. Characters are their scores described in Materials and Methods.

Characters		21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Species																								
<i>Xylosandrus adhaerescens</i>		0	0	0	1	0	0	0	2	0	4	1	0	0	0	?	?	1	0	1	1	0	0	0
<i>X. amputatus</i>		0	0	1	1	1	1	2	2	1	2	0	0	0	0	?	?	2	1	0	?	?	1	0
<i>X. arquatus</i>		0	0	0	1	0	0	0	2	0	4	0	0	0	1	1	1	0	0	1	0	1	0	0
<i>X. assequens</i>		0	0	1	1	0	0	0	2	0	4	0	0	0	1	1	1	1	1	1	1	1	0	0
<i>X. beesoni</i>		0	0	1	1	1	1	0	2	0	3	0	1	0	1	0	0	1	1	1	?	?	0	0
<i>X. borealis</i>		0	0	1	1	1	1	1	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
<i>X. borneensis</i>		0	0	0	1	1	0	0	2	0	4	1	0	0	1	0	0	1	1	1	0	1	1	0
<i>X. brevis</i>		0	0	1	1	1	1	0	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
<i>X. compactus</i>		0	0	0	1	0	0	0	2	0	4	0	0	0	1	0	0	0	0	1	3	1	0	0
<i>X. corthyloides</i>		0	0	0	1	1	1	1	3	?	3	0	0	0	1	1	1	1	1	1	1	1	0	0
<i>X. crassiusculus</i>		0	0	1	1	0	0	0	2	0	4	0	1	0	1	2	1	1	1	1	1	0	0	0
<i>X. curtulus</i>		0	0	0	1	0	0	0	2	0	4	0	0	0	1	0	0	1	0	1	1	1	0	0
<i>X. derupteterminatus</i>		0	0	0	1	1	0	1	2	0	3	0	0	0	0	?	?	1	0	1	0	1	0	0
<i>X. deruptulus</i>		?	0	1	1	0	0	0	2	0	4	0	0	0	?	?	?	1	0	?	?	?	0	0
<i>X. discolor</i>		0	1	1	1	1	1	1	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
<i>X. diversepilosus</i>		?	0	1	1	1	1	1	2	0	2	0	1	0	0	?	?	1	1	1	3	1	0	0
<i>X. eupatorii</i>		0	0	0	1	0	0	0	2	0	4	0	0	0	0	?	?	1	0	1	3	1	0	0
<i>X. ferinus</i>		0	0	0	1	0	0	0	2	0	3	0	0	0	0	?	?	1	0	1	0	1	0	0
<i>X. germanus</i>		0	0	0	1	0	0	0	2	0	4	0	0	0	0	?	?	1	0	1	1	1	0	0

Table 2.2 (cont.): Morphological character matrix of 43 characters for 73 species. Characters are their scores described in Materials and Methods.

Species	Characters																						
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
<i>X. hirsutipennis</i>	0	0	0	1	0	0	0	2	0	3	0	1	0	1	1	0	1	1	1	1	0	0	0
<i>X. hulcri</i>	0	0	1	1	0	0	0	2	0	3	0	0	0	1	0	1	1	1	1	1	1	0	0
<i>X. jaintianus</i>	0	0	1	1	1	1	2	2	0	2	0	1	0	1	0	0	1	1	1	0	0	1	0
<i>X. mancus</i>	0	0	1	1	1	1	1	2	1	2	0	0	0	0	?	?	1	1	0	?	?	1	0
<i>X. mediocris</i>	?	0	0	1	0	0	0	2	0	4	1	0	0	0	?	?	1	0	1	1	1	0	0
<i>X. mesuae</i>	0	0	0	1	0	0	0	2	0	4	0	0	0	1	0	0	1	0	1	1	1	0	0
<i>X. metagermanus</i>	0	0	0	1	0	0	0	2	0	4	0	0	0	0	?	?	1	0	1	1	1	0	0
<i>X. mixtus</i>	0	0	1	1	0	0	0	2	0	3	0	0	0	1	0	0	1	1	1	3	1	0	0
<i>X. montethi</i>	0	0	1	1	0	0	0	0	?	4	0	0	0	1	1	0	1	1	1	1	0	0	0
<i>X. morigerus</i>	0	0	0	1	1	0	0	2	0	4	0	0	0	1	0	1	0	0	1	3	1	0	0
<i>X. pusillus</i>	0	0	0	1	0	0	0	2	0	4	0	0	0	1	0	0	1	0	1	3	1	0	0
<i>X. pygmaeus</i>	0	0	0	1	1	0	1	2	0	3	1	0	0	0	?	?	1	0	1	1	1	0	0
<i>X. queenslandi</i>	0	0	0	1	1	0	1	3	?	4	0	1	0	1	0	1	1	0	1	1	1	0	0
<i>X. rotundicollis</i>	1	0	1	1	0	0	0	0	?	4	0	0	0	1	0	0	1	0	1	3	1	0	0
<i>X. subsimilis</i>	0	0	1	1	1	1	1	2	0	2	0	1	0	2	0	0	1	1	2	0	0	0	0
<i>X. subsimiliformis</i>	0	0	1	1	1	1	1	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
<i>X. terminatis</i>	0	0	0	1	1	0	1	2	0	3	0	0	0	0	?	?	0	0	1	1	1	0	0
<i>X. woodi</i>	0	0	1	1	0	0	0	1	?	3	1	0	0	1	1	0	1	1	1	1	0	0	0

Table 2.2 (cont.): Morphological character matrix of 43 characters for 73 species. Characters are their scores described in Materials and Methods.

Species	Morphology	28S	COI	ArgK	CAD	EF-1a
<i>Amasa anomalus</i> (Schedl)	●					
<i>Amasa bicostatus</i> (Sampson)	●	●	●	●	●	●
<i>Amasa cylindriciformis</i> (Schedl)	●					
<i>Amasa cylindrotomicus</i> (Schedl) n. comb.	●					
<i>Amasa fulgens</i> (Schedl)	●					
<i>Amasa omissus</i> (Schedl)	●					
<i>Amasa oralis</i> (Schedl)	●					
<i>Amasa striatotruncatus</i> (Schedl)	●	●	●	●	●	
<i>Amasa umbratulus</i> (Schedl)	●					
<i>Amasa versicolor</i> (Sampson)	●	●	●	●	●	●
<i>Anisandrus butamali</i> (Beeson) n. comb.	●					
<i>Anisandrus dispar</i> (Fabricius)	●	●	●	●	●	●
<i>Anisandrus obesus</i> (LeConte)	●	●	●	●	●	
<i>Anisandrus sayi</i> (Hopkins)	●	●	●	●	●	●
<i>Anisandrus ursa</i> (Eggers) n. comb.	●	●	●	●	●	●
<i>Anisandrus ursinus</i> (Hagedorn) n. comb.	●	●	●	●	●	●
<i>Anisandrus ursulus</i> (Eggers) n. comb.	●					

Table 2.3 (Cont. on following pages): Species data for morphological and molecular characters matrices (● = data available for species).

Species	Morphology					28S	COI	ArgK	CAD	EF-1 α
<i>Cnestus ater</i> (Eggers), n. comb.	•	•	•	•	•	•	•	•	•	•
<i>Cnestus bimaculatus</i> (Eggers)	•	•	•	•	•	•	•	•	•	
<i>Cnestus fijianus</i> (Schedl) n. comb.	•									
<i>Cnestus gravidus</i> (Blandford) n. Comb.	•									
<i>Cnestus improcerus</i> (Sampson) n. comb.	•	•	•	•	•	•	•	•	•	•
<i>Cnestus laticeps</i> (Wood) n. comb.	•									
<i>Cnestus mutilatus</i> (Blandford) n. comb.	•	•	•	•	•	•	•	•	•	•
<i>Cnestus orbiculatus</i> (Schedl) n. comb.	•									
<i>Cnestus peruanus</i> (Wood) n. comb.	•									
<i>Cnestus pseudosolidus</i> (Schedl)	•									
<i>Cnestus pseudosuturalis</i> Schedl	•	•	•	•	•	•	•	•	•	•
<i>Cnestus retifer</i> (Wood) n. comb.	•									
<i>Cnestus retusus</i> (Eichhoff) n. comb.	•									
<i>Cnestus solidus</i> (Eichhoff)	•									
<i>Cnestus testudo</i> (Eggers) n. comb.	•									
<i>Cnestus triangularis</i> (Schedl)	•									
<i>Coccotrypes dactyliperda</i> (Fabricius)	•	•	•	•	•	•	•	•	•	•
<i>Xyleborus affinis</i> Eichhoff	•	•	•	•	•	•	•	•	•	•
<i>Xyleborus californicus</i> Wood	•	•	•	•	•	•	•	•	•	•

Table 2.3 (Cont.): Species data for morphological and molecular characters matrices (• = data available for species).

Species	Morphology	28S	COI	ArgK	CAD	EF-1 α
<i>Xylosandrus abruptulus</i> (Schedl)	●					
<i>Xylosandrus adherescens</i> Schedl	●					
<i>Xylosandrus amputatus</i> (Blandford) n. comb.	●					
<i>Xylosandrus arquatus</i> (Sampson)	●					
<i>Xylosandrus assequens</i> Schedl	●					
<i>Xylosandrus beesoni</i> Saha, Maiti, & Chakraborti	●					
<i>Xylosandrus borealis</i> Nobuchi	●					
<i>Xylosandrus borneensis</i> n. sp.	●	●	●	●	●	●
<i>Xylosandrus brevis</i> (Eichhoff)	●					
<i>Xylosandrus compactus</i> (Eichhoff)	●	●	●	●	●	●
<i>Xylosandrus corhyloides</i> (Schedl)	●					
<i>Xylosandrus crassiusculus</i> (Motschulsky)	●	●	●	●	●	●
<i>Xylosandrus curtulus</i> (Eichhoff)	●					
<i>Xylosandrus derupteterminatus</i> (Schedl)	●					
<i>Xylosandrus deruptulus</i> (Schedl)	●					
<i>Xylosandrus discolor</i> (Blandford)	●	●	●	●	●	●
<i>Xylosandrus diversepilosus</i> (Eggers)	●					
<i>Xylosandrus eupatorii</i> (Eggers)	●					
<i>Xylosandrus ferinus</i> (Schedl)	●					
<i>Xylosandrus germanus</i> (Blandford)	●	●	●	●	●	●

Table 2.3 (Cont.): Species data for morphological and molecular characters matrices (● = data available for species).

Species	Morphology	28S	COI	ArgK	CAD	EF-1 α
<i>Xylosandrus hirsutipennis</i> (Schedl)	●					
<i>Xylosandrus hulcr</i> n. sp.	●	●	●	●	●	●
<i>Xylosandrus jainianus</i> (Schedl)	●					
<i>Xylosandrus mancus</i> (Blandford)	●		●	●	●	●
<i>Xylosandrus mediocris</i> (Schedl)	●					
<i>Xylosandrus mesuae</i> (Eggers)	●					
<i>Xylosandrus metagermanus</i> (Schedl)	●					
<i>Xylosandrus mixtus</i> (Schedl) n. comb.	●					
<i>Xylosandrus monteithi</i> Dole & Beaver	●	●	●	●	●	●
<i>Xylosandrus morigerus</i> (Blandford)	●	●	●	●	●	●
<i>Xylosandrus pusillus</i> (Schedl)	●					
<i>Xylosandrus pygmaeus</i> (Eggers)	●					
<i>Xylosandrus queenslandi</i> Dole & Beaver	●	●	●	●	●	●
<i>Xylosandrus rotundicollis</i> (Browne) n. comb.	●	●	●	●	●	●
<i>Xylosandrus subsimiliformis</i> (Eggers)	●					
<i>Xylosandrus subsimilis</i> (Eggers)	●					
<i>Xylosandrus terminatus</i> (Eggers)	●					
<i>Xylosandrus woodi</i> Dole & Beaver	●					

Table 2.3 (Cont.): Species data for morphological and molecular characters matrices (● = data available for species).

	Matrix		Variable		Informative		Gaps		Contribution		Consistency		Retention		Mean Branch Length	
	Size		Sites		Sites				to Tree Length		Index (CI)		Index (RI)			
EF-1α	555		151		102		N/A		371		0.493		0.46		7.98	
COI	585		247		219		N/A		1549		0.265		0.246		31.39	
ArgK	594		195		153		N/A		529		0.522		0.6		11.04	
CAD	714		226		172		N/A		607		0.474		0.527		12.72	
28S	1048		463		335		473		1283		0.631		0.759		26.29	
Morphology	43		43		40		N/A		185		0.346		0.492		3.94	
Combined	3539		1325		1021		473		4524		0.449		0.536		93.37	

Table 2.4: Contribution of data partitions to the data matrix and to the resolution of the most parsimonious tree found in the analysis of the combined data set.

	Gene Partition						
	Ef-1 α	COI	ArgK	CAD	28S	Morphology	
node							
1	3.00	2.00	5.00	8.00	0.00	5.00	23
2	3.00	2.00	5.00	8.00	0.00	5.00	23
3	1.00	4.00	2.00	0.00	1.00	-1.00	7
4	0.00	-2.00	2.00	4.00	-2.00	0.00	2
5	8.00	-1.50	7.50	11.00	-1.00	-2.00	22.00
6	3.00	0.00	-1.00	0.00	4.00	0.00	6.00
7	2.00	0.00	-4.00	-2.00	36.00	-4.00	28.00
8	0.00	5.00	0.00	11.00	25.00	5.00	46.00
9	0.00	2.00	-3.00	-4.00	15.00	-4.00	6.00
10	0.00	2.00	-3.00	-4.00	15.00	-4.00	6.00
11	5.00	6.00	2.00	-1.00	63.00	-4.00	71.00
12	2.00	-1.00	-1.00	-1.00	2.00	0.00	1.00
13	5.00	0.00	15.00	10.00	11.00	5.00	46.00
14	3.00	-2.00	1.00	-2.00	2.00	1.00	3.00
15	0.00	1.00	10.00	15.00	8.00	1.00	35.00
16	13.00	5.67	29.67	13.33	8.33	7.00	77.00
17	3.00	2.00	5.00	8.00	0.00	5.00	23.00
18	-1.00	-3.00	-3.00	0.00	26.00	0.00	19.00
19	2.00	0.00	1.00	0.00	5.00	1.00	9.00
20	0.00	-0.50	4.00	5.00	2.00	2.50	13.00
21	2.00	-2.00	-1.00	2.00	5.00	0.00	6.00
22	3.00	-2.00	0.00	10.00	3.00	0.00	14.00
23	8.50	2.50	-0.50	18.50	3.00	11.00	43.00
24	0.00	11.00	7.00	7.00	2.00	-3.00	24.00
Total	65.50	31.17	79.67	116.83	233.33	26.50	442.00

Table 2.5: Partition branch support for the most parsimonious tree found by the analysis of the combined data set. Node numbers refer to Figure 2.2.

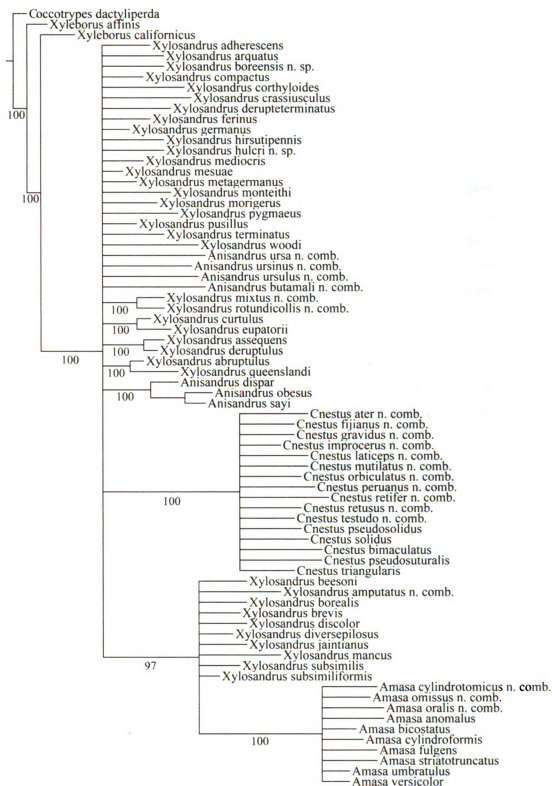


Figure 2.1: Strict consensus of 10,000 most parsimonious trees found in parsimony analysis of the morphological data matrix. Bootstrap values are given below the nodes for clades with support $\geq 90\%$.

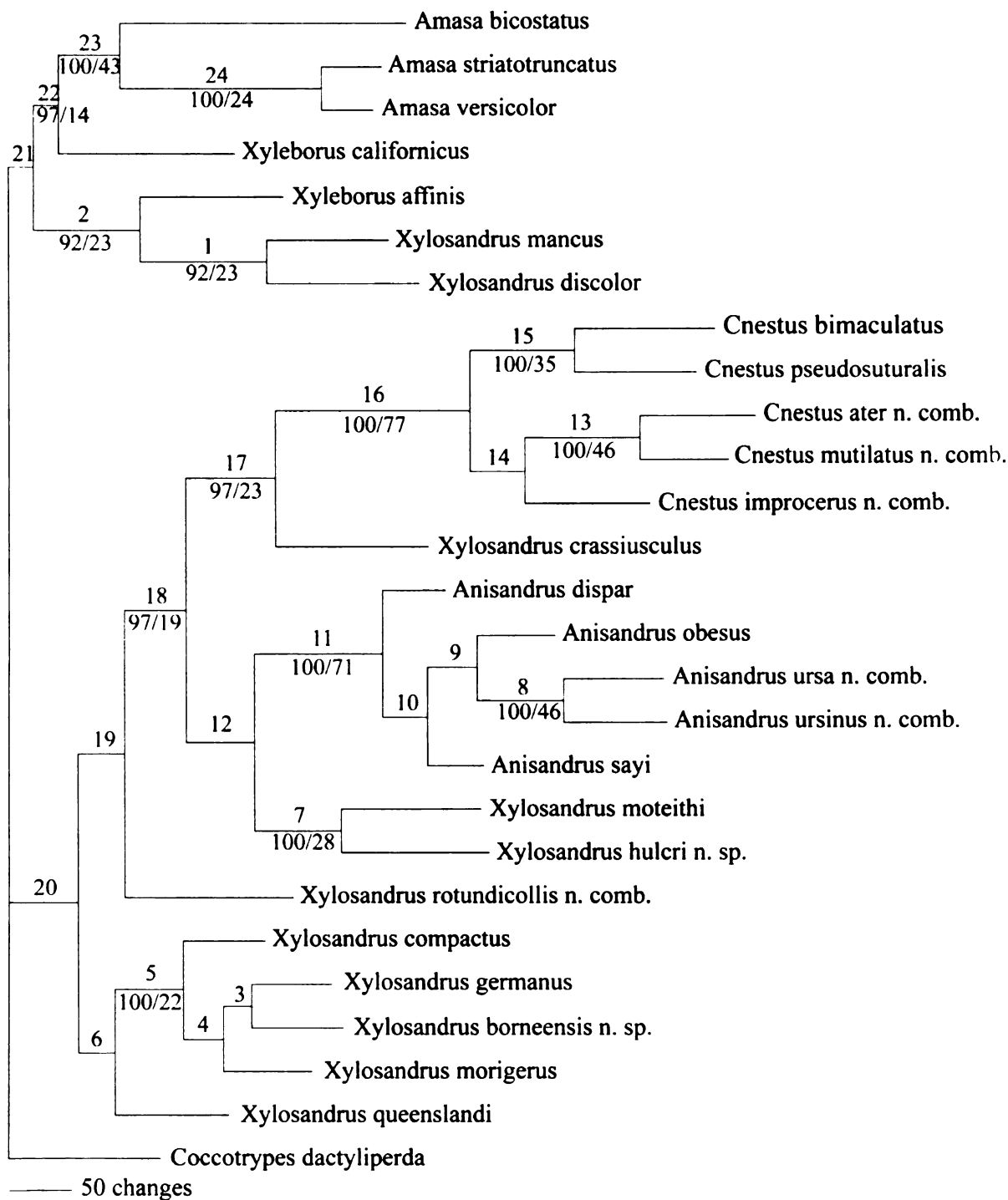


Figure 2.2: Most parsimonious tree found in the analysis of the combined data matrix. Node numbers given above branches and bootstrap support/Bremer support values given below.

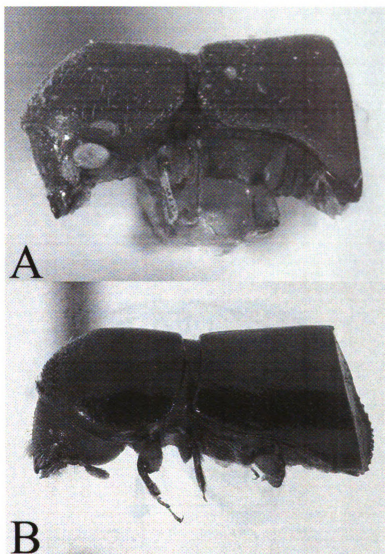


Figure 2.3: Lateral habitus of *Amasa cylindrotomicus* n. comb., female (A) and *Amasa bicostatus*, female (B).

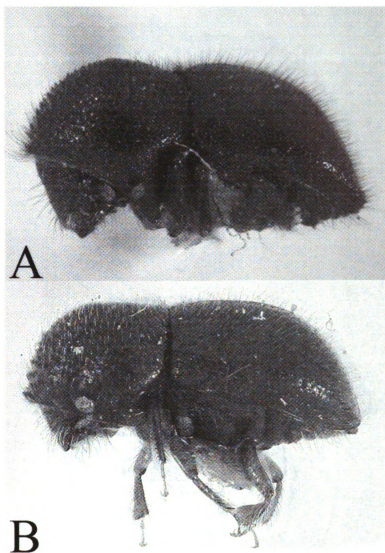


Figure 2.4: Lateral habitus of *Anisandrus ursulus* n. comb., female (A) and *Anisandrus sayi*, female (B).

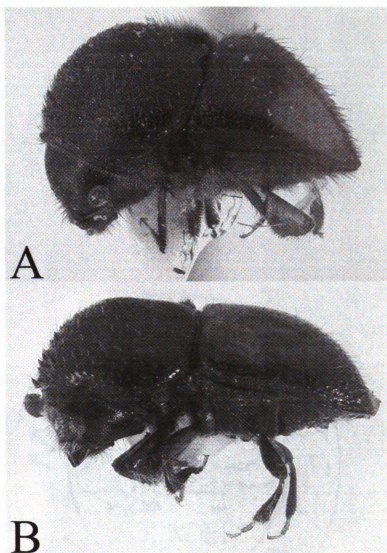


Figure 2.5: Lateral habitus of *Cnestus improcerus* n. comb., female (A) and *Cnestus pseudosuturalis*, female (B).

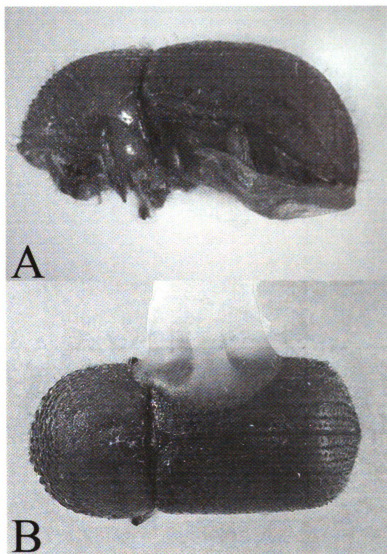


Figure 2.6: Lateral (A) and dorsal (B) views of *Xylosandrus abruptulus*, 1.9 – 2.1 mm, female lectotype.

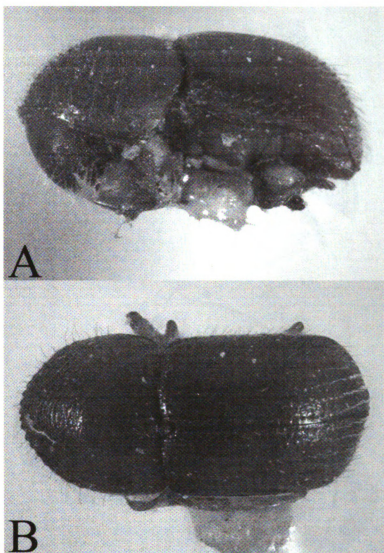


Figure 2.7: Lateral (A) and dorsal (B) views of *Xylosandrus adherescens*, 2.0 mm, female holotype.

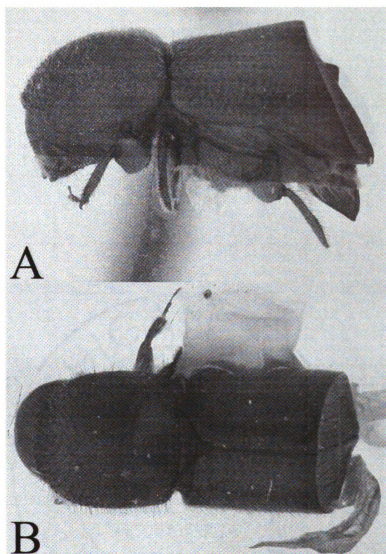


Figure 2.8: Lateral (A) and dorsal (B) views of *Xylosandrus amputatus* n. comb., 2.7 – 2.9 mm, female.

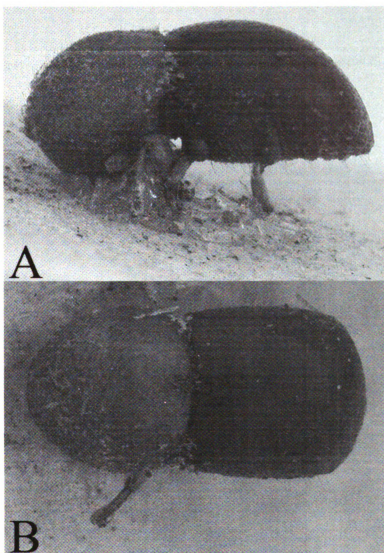


Figure 2.9: Lateral (A) and dorsal (B) views of *Xylosandrus arquatus*, 2.3 – 2.5 mm, female.

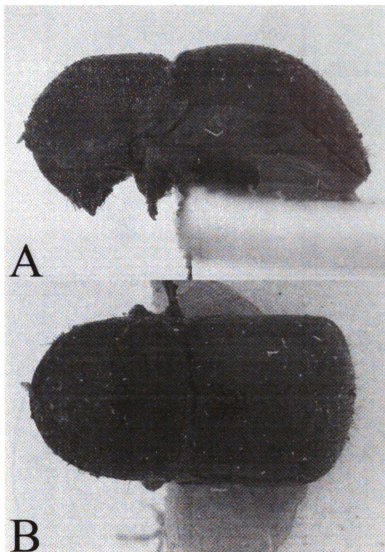


Figure 2.10: Lateral (A) and dorsal (B) views of *Xylosandrus assequens*, 1.6 – 2.3 mm, female, holotype.

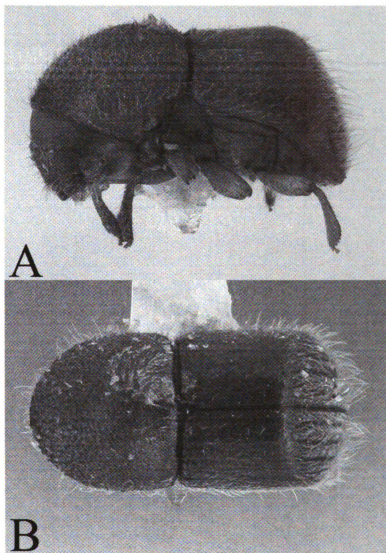


Figure 2.11: Lateral (A) and dorsal (B) views of *Xylosandrus borealis*, 2.0 – 2.1 mm, female.

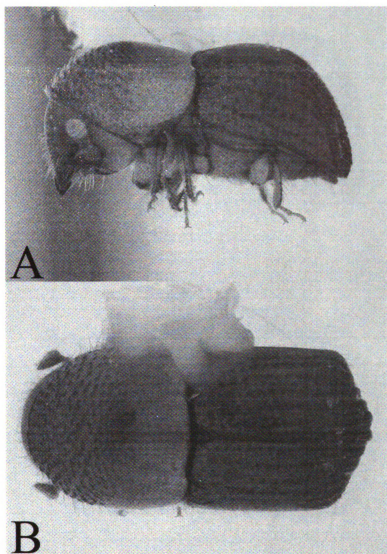


Figure 2.12: Lateral (A) and dorsal (B) views of *Xylosandrus borneensis* n. sp., 1.5 – 1.6 mm, female holotype.

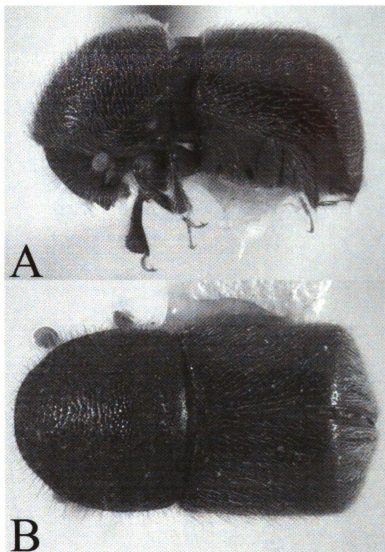


Figure 2.13: Lateral (A) and dorsal (B) views of *Xylosandrus brevis*, 2.5 – 2.8 mm, female.

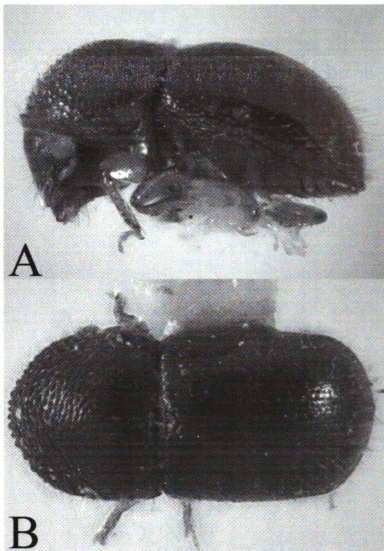


Figure 2.14: Lateral (A) and dorsal (B) views of *Xylosandrus compactus*, 1.4 – 1.9 mm, female.

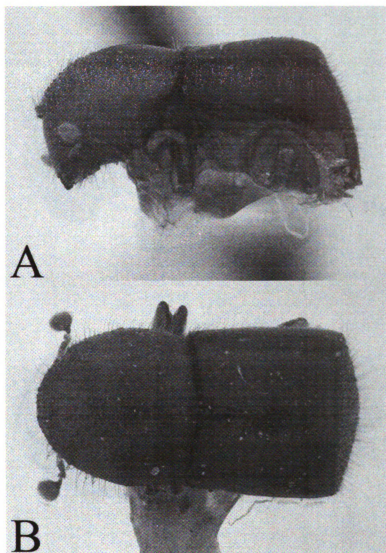


Figure 2.15: Lateral (A) and dorsal (B) views of *Xylosandrus corthyloides*, 2.7 – 3.0 mm, female lectotype.

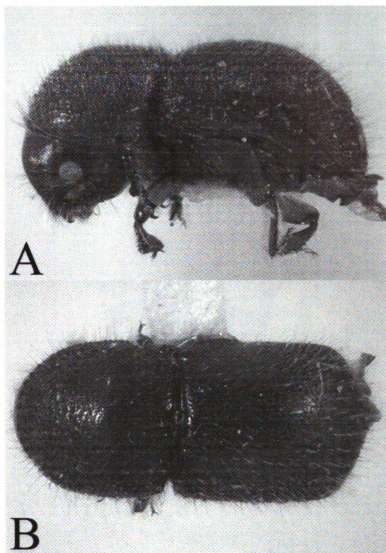


Figure 2.16: Lateral (A) and dorsal (B) views of *Xylosandrus crassiusculus*, 1.7 – 2.9 mm, female.

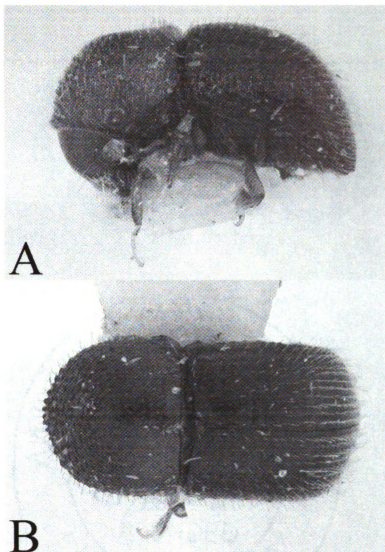


Figure 2.17: Lateral (A) and dorsal (B) views of *Xylosandrus curtulus*, 1.3 – 1.5 mm, female holotype of synonym *X. biseriatus*.

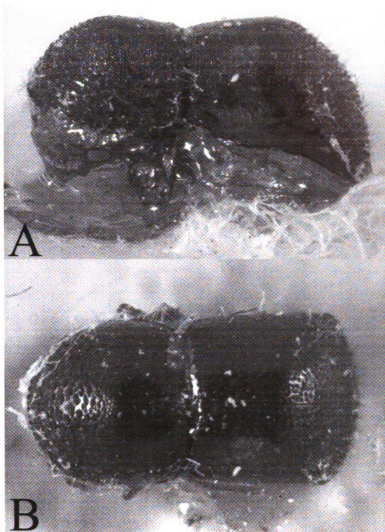


Figure 2.18: Lateral (A) and dorsal (B) views of *Xylosandrus derupteterminatus*, 2.0 – 2.3 mm, female holotype.

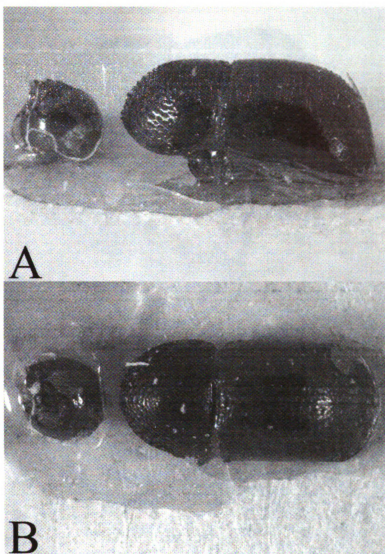


Figure 2.19: Lateral (A) and dorsal (B) views of *Xylosandrus deruptulus*, 1.8 mm, female lectotype.

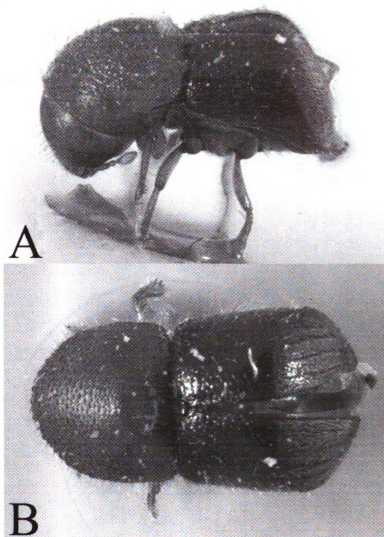


Figure 2.20: Lateral (A) and dorsal (B) views of *Xylosandrus discolor*, 1.8 – 2.0 mm, female.

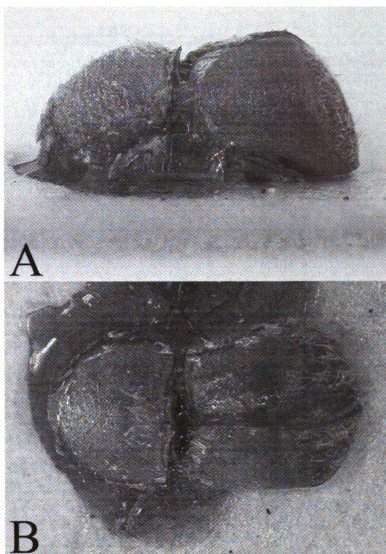


Figure 2.21: Lateral (A) and dorsal (B) views of *Xylosandrus diversepilosus*, 1.8 – 2.3 mm, female holotype.

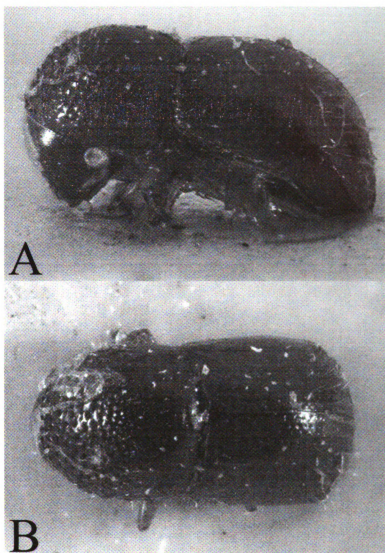


Figure 2.22: Lateral (A) and dorsal (B) views of *Xylosandrus eupatorii*, 1.8 – 2.1 mm, female cotype.

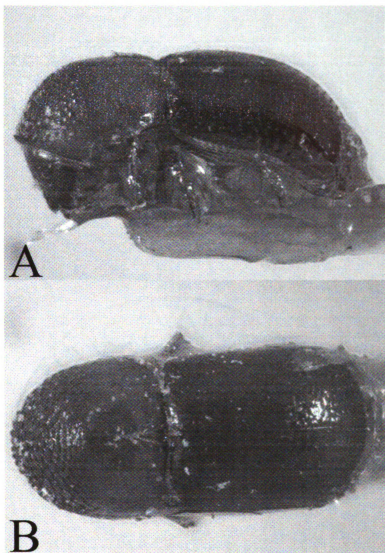


Figure 2.23: Lateral (A) and dorsal (B) views of *Xylosandrus ferinus*, 1.6 – 1.8 mm, female lectotype.

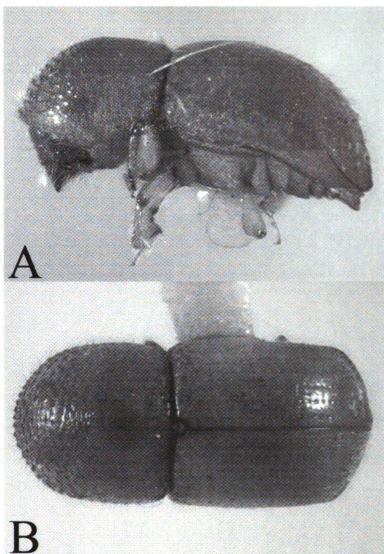


Figure 2.24: Lateral (A) and dorsal (B) views of *Xylosandrus germanus*, 1.9 – 2.5 mm, female.

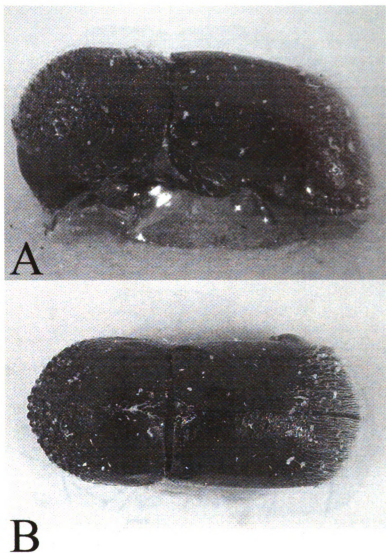


Figure 2.25: Lateral (A) and dorsal (B) views of *Xylosandrus hirsutipennis*, 1.9 – 2.2 mm, female paratype.

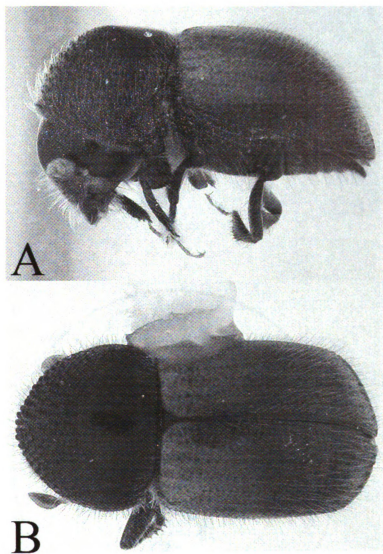


Figure 2.26: Lateral (A) and dorsal (B) views of *Xylosandrus hulcri* n. sp., 2.4 – 2.7mm, female holotype.

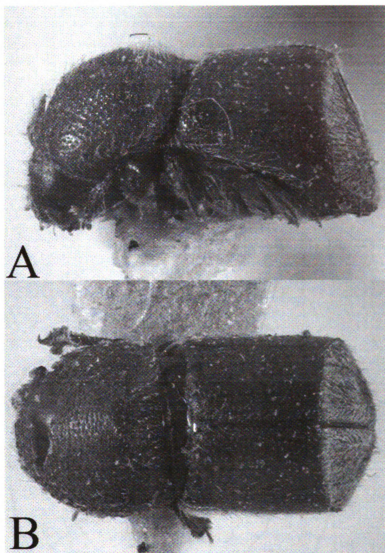


Figure 2.27: Lateral (A) and dorsal (B) views of *Xylosandrus jaintianus*, 3.0 mm, female holotype.

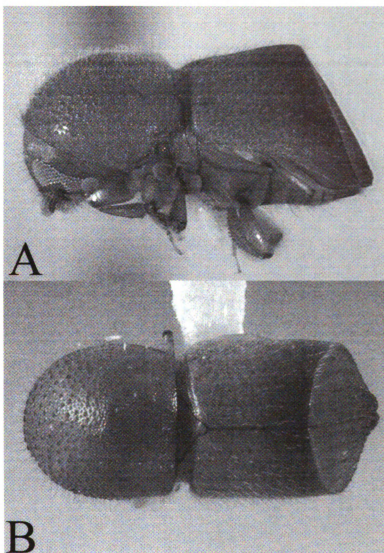


Figure 2.28: Lateral (A) and dorsal (B) views of *Xylosandrus mancus*, 2.9 – 3.3 mm, female.

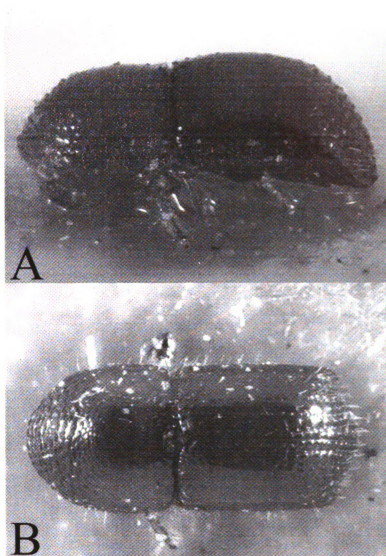


Figure 2.29: Lateral (A) and dorsal (B) views of *Xylosandrus mediacris*, 1.4 mm, female.

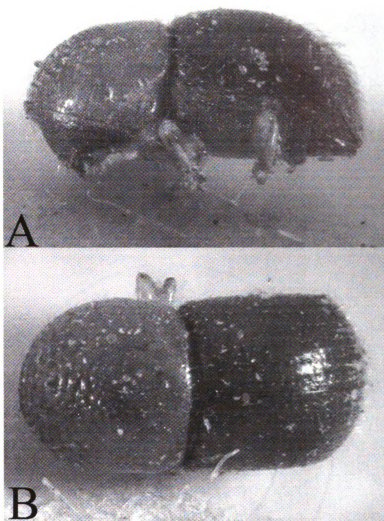


Figure 2.30: Lateral (A) and dorsal (B) views of *Xylosandrus mesuae*, 1.1 – 1.3 mm, female.

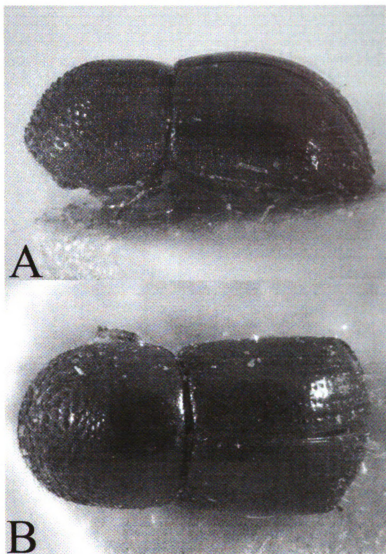


Figure 2.31: Lateral (A) and dorsal (B) views of *Xylosandrus metagermanus*, 1.8 mm, female holotype.

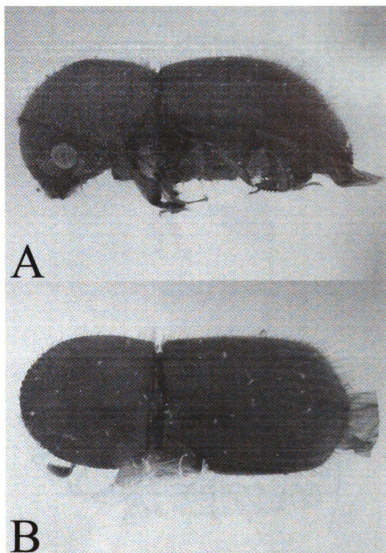


Figure 2.32: Lateral (A) and dorsal (B) views of *Xylosandrus mixtus* n. comb., 2.6 – 2.7 mm, female holotype.

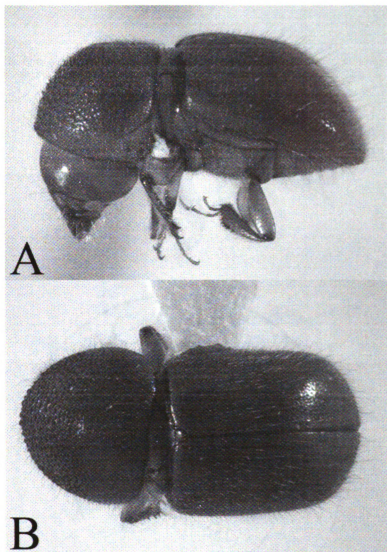


Figure 2.33: Lateral (A) and dorsal (B) views of *Xylosandrus monteithi*, 3.0 – 3.4 mm, female paratype.

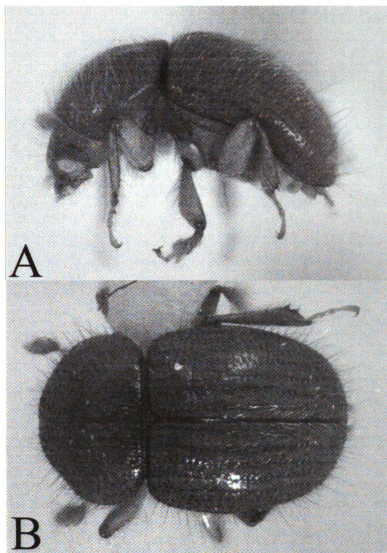


Figure 2.34: Lateral (C) and dorsal (D) views of *Xylosandrus monteithi*, 2.5 mm, male allotype.

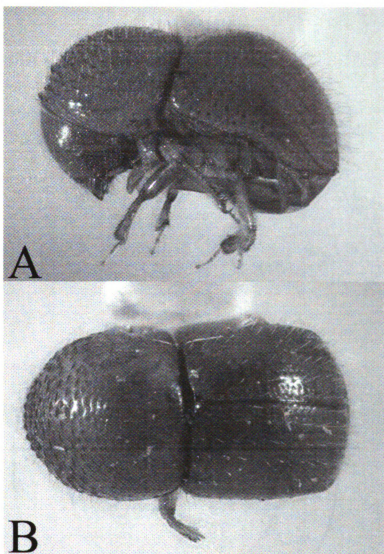


Figure 2.35: Lateral (A) and dorsal (B) views of *Xylosandrus morigerus*, 1.5 – 2.0 mm, female.

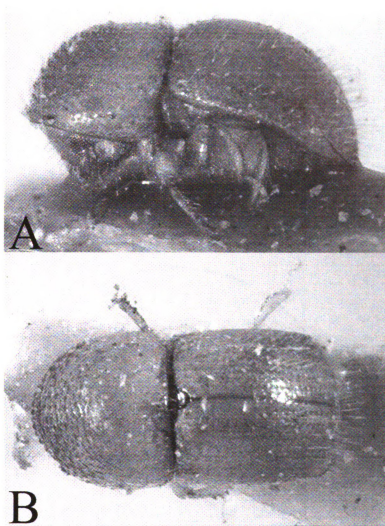


Figure 2.36: Lateral (A) and dorsal (B) views of *Xylosandrus pusillus*, 1.5 – 1.7 mm, female holotype.

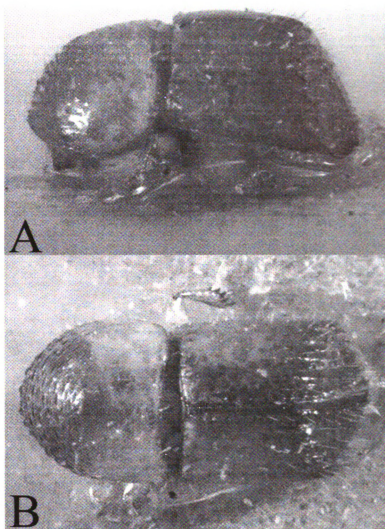


Figure 2.37: Lateral (A) and dorsal (B) views of *Xylosandrus pygmaeus*, 1.3 – 1.4 mm, female holotype.

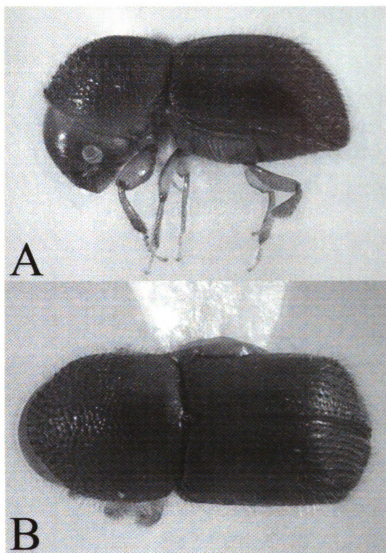


Figure 2.38: Lateral (A) and dorsal (B) views of *Xylosandrus queenslandi*, 1.6 – 1.9 mm, female paratype.

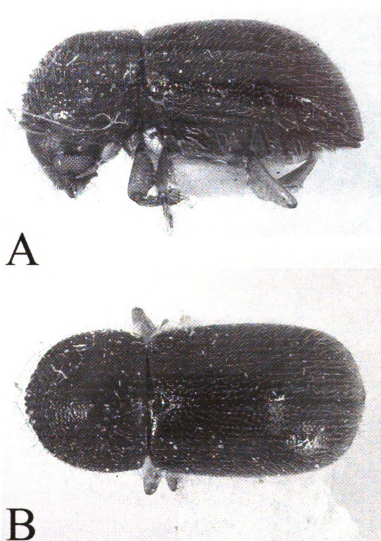


Figure 2.39: Lateral (A) and dorsal (B) views of *Xylosandrus rotundicollis* n. comb., 3.7 – 4.1 mm, female holotype.

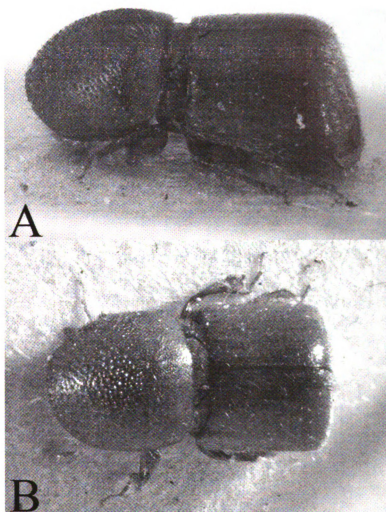


Figure 2.40: Lateral (A) and dorsal (B) views of *Xylosandrus subsimiliformis*, 2.8 mm, female cotype.

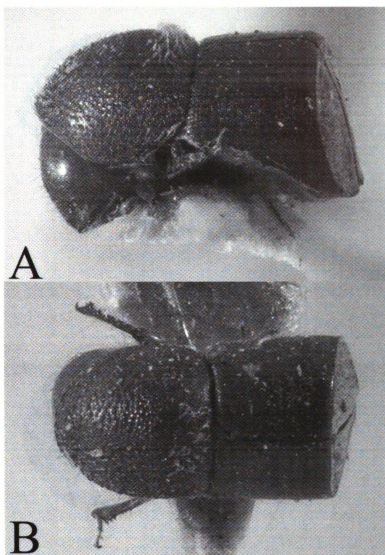


Figure 2.41: Lateral (A) and dorsal (B) views of *Xylosandrus subsimilis*, 2.6 mm, female cotype.

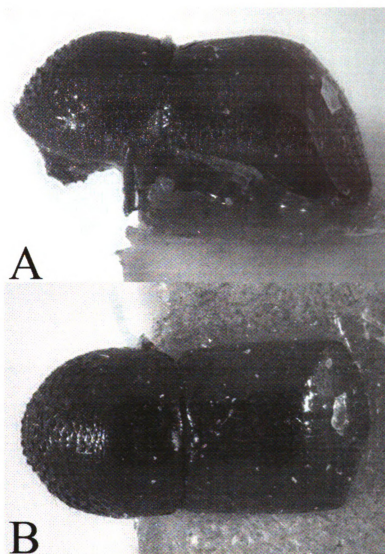


Figure 2.42: Lateral (A) and dorsal (B) views of *Xylosandrus terminatus*, 1.5 – 1.9 mm, female cotype.

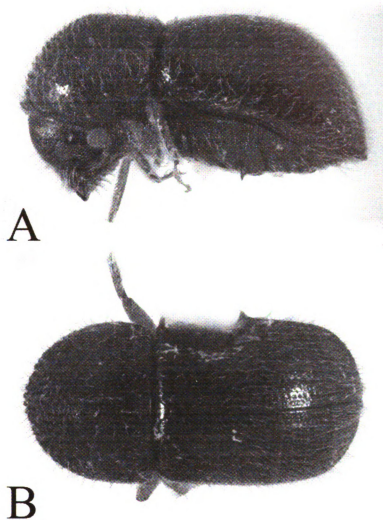


Figure 2.43: Lateral (A) and dorsal (B) views of *Xylosandrus woodi*, 2.3 – 2.4 mm, female paratype.

CHAPTER 3

Diversity of Scolytinae (Coleoptera: Curculionidae) in the Ecuadorian rain forest canopy

ABSTRACT

Canopy fogging was used to sample the diversity of bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) at two Western Amazonian rain forest sites in Ecuador. Sampling spanning from 1994-2006 yielded 1,158 samples containing 2,500 scolytine specimens representing more than 400 morphospecies. Here, we analyze a subset of this data representing two ecological groups: true bark beetles (52 morphospecies) and ambrosia beetles (69 morphospecies). A high percentage of these taxa occurred as singletons and doubletons and their species accumulation curves did not reach an asymptote. Diversity estimates placed the total scolytine species richness for this taxon subset present at the two sites between 260 and 323 species. High levels of α - and β -diversity were discovered. However, high β -diversity was found to be an artifact of undersampling and does not appear to be biologically significant. This study demonstrates the utility of canopy fogging methods for the sampling of scolytine richness and for the discovery of new scolytine taxa.

INTRODUCTION

Studies of tropical canopy ecosystems have documented the richness of this habitat and its potential for the discovery of new arthropod species (Erwin 1982, 1983a 1983b, 1988; Lowman and Witman 1996; Erwin et al. 2005). Erwin's studies of arthropod diversity in tropical forest canopies resulted in the controversial estimate of 30-50 million arthropod species (Erwin 1982). Subsequently, several authors were critical of this estimate (May 1988; Adis 1990; Gaston 1991), which was actually intended to spark discussion of the use of hypothesis driven data analysis for global species estimation and the adequacy of current sampling methods, rather than be an authoritative estimation of global biodiversity (Erwin 1991). Nevertheless, Erwin's estimate highlighted the under-explored biodiversity contained in the canopy ecosystem and the need to document and describe canopy species in light of tropical deforestation.

The subfamily Scolytinae (Coleoptera: Curculionidae) is comprised of approximately 225 genera containing 6,000 species worldwide (Wood and Bright 1992). Scolytine species feed sub-cortically on a wide variety of woody and herbaceous plants. The typical life cycle of scolytines consists of a brief dispersal flight period after adult emergence, followed by colonization of new hosts. Once a suitable host has been located, adults bore galleries into the host tissue, where eggs are laid, and larvae complete their development into the next generation of adults.

Scolytine beetles can be divided into two ecological groups: bark beetles and ambrosia beetles. The degree to which scolytines specialize on specific hosts varies considerably depending on these ecological groups. Bark beetles bore into the phloem of trees, feed on tree tissues, and tend to have more specialized host preferences. Ambrosia

beetles bore into the xylem, feed on species of symbiotic fungi which grow along the walls of their galleries, and tend to have more generalized tree host preferences (Beaver 1979; Kirkendall 1993). The majority of scolytine diversity occurs in tropical regions of the world, with much of this species richness believed to be undescribed.

First pioneered by Southwood (1961) in temperate forests and then later adapted for tropical research by numerous others (Lowman and Witman 1996), canopy fogging methods use insecticide to collect arthropods from the upper architecture of the forest habitat. These methods have become widely used in surveying arthropod diversity, particularly in lowland rain forests (Basset 2001). For a more than a decade, Erwin and colleagues have sampled arthropod diversity in the Ecuadorian Amazon rain forest canopy at two lowland rain forest sites, separated by 21km of contiguous primary forest, using a standardized insecticidal fogging protocol (Erwin 1983a, 1983b; Erwin et al. 2005). Sampling has taken place during dry, wet, and transitional seasons to measure temporal turnover in species composition. Tree data were also recorded for fogging stations within the two study sites (Pitman et al. 2001). Canopy fogging samples collected in these surveys offer a potentially rich source of new scolytine specimens because collecting scolytines directly from their hosts can require great effort and can also be limited by the abundance and accessibility of colonized hosts. Thus canopy fogging may provide taxonomists access to species which complement those collected using traditional, ground-based, hand-collecting methods.

Remarkably few studies have looked at the spatial and temporal turnover of scolytine species (β -diversity) (Deyrup and Atkinson 1987; Thunes 1988; Peltonen et al. 1998; Hulcr et al. 2007, in press). The majority of studies have focused on the

composition of the scolytine fauna of temperate regions and examined the distributions of a few economically important species (Deyrup and Atkinson 1987; Jakus 1998; Peltonen et al., 1998; Oliver and Mannion 2001; Gaylord et al. 2006). Several studies in the tropics have attempted to determine the effects of seasonal changes in rainfall and temperature to the composition of scolytine communities (Beaver and Löyttyniemi 1991; Madoffe and Bakke 1995; Morales et al. 2000; Flethmann et al. 2001; Hulcr et al. in press). Studies in Malaysian forests have examined the spatial distribution of scolytines across horizontal (Maeto et al. 1999; Chung 2004) and vertical gradients (Maeto and Fukuyama 2003; Simon et al. 2003). Recent studies in Papua New Guinea (Hulcr et al. 2007) and Thailand (Hulcr et al. in press) have used quantitative sampling schemes to examine scolytine community composition and attempt to determine the proximate causes of the distribution of species in tropical habitats. Scolytine communities in lowland Papua New Guinean rain forests have been found to have low β -diversity, thus contradicting the expected trend of high β -diversity in the tropics. Novotny et al. (2007) similarly demonstrated low species turnover for insect communities when examined on a large scale across New Guinean forests. In Thailand, two study sites separated by only 5 km were found to have significantly different scolytine species composition (Hulcr et al. in press). Correspondence analysis found that differences in mean annual temperature and humidity, rather than seasonal fluctuations, explained the differing species composition at the two sites. However, the Thailand study sites differed from each other greatly, one being a mixed evergreen forest located at 1,410 meters altitude and the other a deciduous dipterocarp forest at the edge of the city of Chiang Mai at 350 meters altitude. Such habitat variation did not exist in the study of lowland New Guinean rain

forests or the two Amazonian study sites examined herein. Thus, it is uncertain whether Amazonian forests will produce the same trend of low β -diversity seen in Papua New Guinea or high β -diversity, as was observed between different Thai forests.

In tropical ecosystems, an increase in host specificity combined with an increase in plant diversity is often used to explain high levels of species diversity. However, bark and ambrosia beetles show a reverse trend, with a decrease in host specificity in tropical regions. This is largely due to the greater abundance of ambrosial feeding scolytines which, as discussed above, tend to be relative host generalists (Beaver 1979).

Nevertheless, most scolytine groups have higher species diversity in tropical regions than they do in temperate ones (Beaver 1979; Deyrup and Atkinson 1987; Wood and Bright 1992). It is therefore expected that canopy fogging will yield a high number of scolytine species, but that the β -diversity of scolytines across the Amazonian canopy may not necessarily be high.

In his 2007 taxonomic monograph of the bark and ambrosia beetles of South America, Wood lists less than 50 scolytine species records from Ecuador (Wood 2007). Most scolytine taxonomists would doubt that this paucity of species records represents the true scolytine diversity contained within the rich tropical ecosystems of the Ecuadorian Amazon. What, then, is the true extent of scolytine diversity in Ecuador and what sampling methods can be utilized to uncover the uncollected and undescribed diversity that remains?

In this study, we use a subset of scolytine subtribes representing both the bark beetle (Hylesinini: Bothrosternina, Phloeosinina, Phloeotribina, Phrixosomina) and ambrosia beetle (Xyleborina, Premnobina) ecological groups to assess the diversity of

scolytines at two Western Amazonian forest study sites. We use this data to assess the value of canopy fogging as a source of scolytine specimens, determine the spatial turnover of scolytine species, and use the data collected from these foggings to predict the scolytine species richness at the two sites. Alpha taxonomy for newly discovered genera and species is a longer-term component of this research and is being undertaken in conjunction with this work as well (Dole and Cognato 2007).

MATERIALS AND METHODS

Field Sites and Sampling

The two study sites in this investigation were typical lowland rain forest habitats in the western Amazon Basin at the margin of Yasuní National Park, separated by 21 km of contiguous primary forest: Onkone Gare Station (cited as “Piraña” in Pitman et al. 2001 and Erwin et al. 2005) (0° 39' 25.685" S, 76° 21' 10.813" W; 216 m) and Tiputini Biodiversity Station (0° 37' 55.397" S, 76° 08' 39.205" W; 216 m). The Onkone Gare and Tiputini study plots were established in 1994 and 1997, respectively. The study sites receive an average of 2.7 m of rainfall per year (Erwin et al. 2005). Precipitation at the two sites is seasonal, with the wet season occurring from May to October and the dry season occurring from November to April.

Tree data were recorded for collecting stations within Erwin's canopy fogging study transects. Trees with a diameter at breast height (diameter measured at 1.33 m from tree base) greater than 10 cm that had at least part of a branch hanging over the collecting sheet were tagged by Erwin's team and subsequently identified by Pitman and

colleagues (Pitman et al. 2001). In terms of trees, the Onkone Gare and Tiputini sites are very different at the species level (73% occurring at only one site), moderately dissimilar at the generic level (53% occurring at only one site), and fairly similar at the family level (26% occurring at only one site). With approximately 250 species each, the two study sites represent individually 21.26% (Onkone Gare) and 21.42% (Tiputini) and collectively 34% of the regional tree diversity (Erwin et al. 2005).

The fogging protocol used was one that has been developed by Erwin (Erwin 1983a, 1983b). The study plot area at each site (100 m x 1000 m) was divided into 10 transects (10 m x 100 m). Each transect consisted of 10 collecting stations (3 m x 3 m), which were randomly arrayed on both sides of the transect centerline. Each station is constructed of a sampling sheet tied and suspended 1 m off the ground, on which fogged arthropods fall from the canopy, and a collecting jar attached to the center of the sheet. The total area of these collecting stations was 9250 m², which represented just 1.11% of the entire transect at each site.

Fogging took place three times per year: January/February (dry), June/July (wet), and October (transitional). Fogging took place at Onkone Gare from 1994-1996 and from 2005-2006. Fogging took place at Tiputini from 1998-2002 (intermittent research funding and social unrest in Ecuador interrupted the research at Tiputini after the plot had been established). The pyrethroid insecticide resmethrin was fogged for 60 seconds in a column from just above the sheet to a height that was then recorded for each fogging event (for details on fogging techniques and equipment used see Lucky et al. 2002). Foggings took place at 0345-0500 hr in order to minimize insecticidal drift outside of the column due to air currents. Previous studies had demonstrated that arthropod

repopulation occurs within 10 days after fogging (Lucky et al. 2002). Hence, the same stations could be resampled at each seasonal collecting event without an effect on sampling.

The samples examined herein represent only a subset (1,158 samples) of the total (1,400+ samples) taken during the decade of canopy fogging conducted. Samples from several collecting expeditions have yet to be exported from Ecuador and were therefore not available for this study. Samples were sorted and 14 target taxa for the larger canopy arthropod diversity study were extracted, including adult Coleoptera. Scolytines were extracted from the adult Coleoptera samples, sorted to morphospecies, and identified using published keys (Wood 2007).

Statistical Analysis

A goal of the statistical analyses was to obtain results that were comparable to those of other analyses conducted on samples from the same foggings and to similar studies of scolytine β -diversity (Hulcr et al. 2007, in press). For this reason, statistics used were determined by previous studies (Lucky et al. 2002; Erwin et al. 2005; Hulcr et al. 2007, in press) and by a selection of the most robust methods currently available in β -diversity research.

Species accumulation curves and richness estimators

EstimateS Version 7.5 software (Colwell 2004) was used to calculate species accumulation curves and richness estimators for the fogging data. For all analyses, the term “singletons” is used in reference to species represented by a single specimen from a

sample, while “doubletons” are defined as species represented by two specimens from a sample.

Species accumulation curves and richness estimators were used to assess the completeness of the sampling effort and to predict the overall diversity of scolytines occurring in the canopy habitat. Richness estimators employ the same principles as mark-release-recapture techniques used to estimate animal populations. Just as large populations are indicated by capturing new individuals, rather than the same ones over and over again, species diversity is indicated by capturing new species rather than individuals of the same species over and over again. Hence, richness estimators recognize that different information about diversity is contained within the rare units of the sample (singletons and doubletons) than in the most abundant units (species represented by multiple specimens). However, these estimators also recognize that rare species can skew estimates of diversity and, therefore, several richness estimators treat the rarer species differently in their calculations than they do the more abundant ones.

There are two categories of richness estimators: abundance-based and incidence-based. The two abundance-based richness estimators used were Chao1 (Chao 1984) and the Abundance-based Coverage Estimator (ACE) (Chao and Lee 1992; Chao et al. 1993). The two incidence-based richness estimators used were Chao2 (Chao 1987) and the Incidence-based Coverage Estimator (ICE) (Lee and Chao 1994). ACE and ICE consider two classes of species for their calculations: those that are rare and those that are not rare. For analytical purposes, ACE and ICE consider species with fewer than 10 individuals in the sample to be rare. The choice of the number 10 is arbitrary and is merely the value suggested by EstimateS (Colwell 2004). Chao1 and Chao2 treat all species (rare and not

rare) the same in their calculations. These estimates also attempt to account for the effect of unseen rare species (rare species that were not sampled). The default bias-corrected option was used to calculate Chao1 and Chao2 in EstimateS (Colwell 2004). This analysis estimated the critical value for the abundance distribution to be > 0.5 for all subsets of the data analyzed. In cases such as these, Chao recommends that the Chao1, Chao2, ACE, and ICE be recalculated using the Classic option instead. Thus, the richness estimators reported herein were calculated using the Classic option under diversity settings in EstimateS (Colwell 2004).

In addition to the above richness estimators, a second-order jackknife (Burnham and Overton 1978, 1979) was calculated using EstimateS (Colwell 2004). This measure is based on the number of species that occur in one sample, as well as those that occur in exactly two samples. Colwell and Coddington (1994) have shown the second-order jackknife to be one of the more reliable predictors of species diversity.

Similarity Estimators

Several measures of diversity were used to analyze these samples to determine the distinctness of the species composition in each sample. The simplest of these measures is the Complementarity Index (CI) (Colwell and Coddington 1994) that expresses the distinctness or dissimilarity between two samples. This calculation is based on the observed species for each sample, the total species richness, and the number of species unique to either sample. Complementarity Index values range from 0 to 1.0, where $CI = 0$ means that the compared samples have all species in common while a $CI = 1.0$ means that they do not share any species. Complementary indices were calculated for each of

the subtribes examined herein, as well as for the Xyleborina + Premnobina, Hylesinini, and for the total sample (Hylesinini and Xyleborina + Premnobina) for Onkone Gare and Tiputini.

More sophisticated measures of shared species attempt to estimate the similarity of species composition of the samples based on the observed data. These measures include the classic Jaccard and Sørensen indices (Chao et al. 2005, 2006). However, these measures are notoriously sensitive to sample size, especially when rare species are present in the samples. They are also based solely on incidence (presence-absence) data and cannot account for unseen shared species. The more accurate Chao-Sørensen abundance-based and incidence-based estimators correct for this by incorporating the effect of unseen shared species (Chao et al. 2005, 2006).

The Onkone Gare study site was sampled more than twice as much as the Tiputini site. To correct for this, the Onkone Gare sample was rarified to contain the same total number of individuals and a similar distribution of abundances as the Tiputini site [Tiputini mean (SD) = 1.93 (12.21); rarified Onkone Gare mean (SD) = 1.93 (12.70)]. The total number of individual specimens for both the Tiputini and the rarified Onkone Gare samples equaled 230. Two subsequent statistical analyses (Monte Carlo and Chao-Sørensen analyses) used this rarified data.

We performed a Monte Carlo analysis on the total (Hylesinini and Xyleborina + Premnobina) dataset to test the hypothesis that the observed similarity is not statistically significant, but rather a result of random sampling of individuals from similar or identical scolytine communities. In each replicate of this test individuals of each species were

randomly distributed between the two sites. This randomized dataset was then used to calculate the Chao-Sørensen similarity index and the procedure was repeated 100 times.

RESULTS AND DISCUSSION

A total of 1,158 canopy fogging samples were analyzed from the Ecuadorian Amazon study transects (Table 3.1). Of these, 965 were from the Onkone Gare study site and 293 were from the Tiputini study site. These samples contained a total of 2,500 individual scolytines, representing more than 400 morphospecies. Scolytines were found in 60% of the Onkone Gare samples, 75% of the Tiputini samples, and 69% of the total samples for both sites. The canopy fogging samples contained a large number of rare species occurring as singletons and doubletons. The subset of taxa examined here represented 688 individuals and 121 species from this larger dataset (Tables 3.2 and 3.3).

Bark beetles

Bark beetles belonging to the tribe Hylesinini were represented by four subtribes in the canopy fogging samples: Bothrosternina, Phloeosinina, Phloeotribina, and Phrixosomina. A total of 183 specimens representing 9 genera and 52 morphospecies of hylesines were collected (Tables 3.2 and 3.4). In his monograph of South American Scolytinae Wood (2007) records 13 genera and 207 species of Hylesinini from the region. Assuming that none of the genera or species collected were previously undiscovered, canopy fogging yielded 69% of the known genera and 25% of the known species from South America. However, at least one genus found by the foggings was previously

undiscovered: *Akrobothrus* Dole and Cognato (2007) (Bothrosternina) and several species have been identified as undescribed. These discoveries suggest that canopy fogging is not only a useful method for the collection of known scolytine fauna, but also an effective means for discovering new taxa.

Ambrosia beetles

Ambrosia beetles were represented in our analyses by two subtribes: Xyleborina and Premnobina. Xyleborines exhibit highly skewed sex ratios (Bright 1968; Kirkendall 1993), with males rarely being collected, and the taxonomic classification of the subtribe is based on female morphology. Although 18 specimens of xyleborine males were collected by this study, it was impossible to associate these with their female counterparts with any certainty. Therefore, these individuals were not included in the analysis. A total of 504 specimens representing 8 genera and 68 species of Xyleborina were collected via canopy fogging (Tables 3.3 and 3.4). Wood (2007) records 11 genera and 233 species of Xyleborina from South America. Thus, with the exception of any undescribed genera or species, fogging yielded 73% of the known genera and 29% of the known xyleborina species from the region. However, as with the subtribes of Hylesinini, several morphospecies of Xyleborina appear to represent previously undiscovered taxa.

A single species belonging to the xyleborine genus *Amasa* was collected via the canopy foggings. Wood (2007) noted that the existence of *Amasa* in South America had been based on an erroneous record but still included the genus in his key to xyleborine genera of the region. Therefore, this collection represents the first confirmed record of *Amasa* from South America. Comparison of this species with known *Amasa* from other

regions will be necessary to assess whether it is likely a native or introduced species, as invasive xyleborines have been known to inhabit primary Neotropical forests (Kirkendall and Ødegaard 2007). A single genus and species of Premnobina was collected:

Premnobius clavipennis Eichhoff. Premnobina is a monogeneric subtribe containing three South America species (Wood 2007).

Species Accumulation Curves and Richness Estimators

Species accumulation curves for both sites combined and for each site individually have yet to asymptote at the current sampling levels (Figs. 3.1-3.3). The steadily increasing species accumulation curves are correlated with a continued occurrence of rare species (singletons and doubletons) in the samples. This indicates that our sampling was not adequate to sample the entire scolytine species composition of the two study sites.

Estimates of true species richness differed between abundance-based and incidence-based statistics (Table 3.1; Figs. 3.4-3.6). For the two sites combined, the abundance-based ACE and Chao1 estimated a total scolytine species richness of 301 and 308 species, respectively. The incidence-based ICE and Chao2 gave the higher estimates of 323 and 311 species. Abundance-based and incidence-based estimates of species richness for the Onkone Gare overlapped slightly. For Onkone Gare, ACE estimated the total scolytine fauna to be 275 species and Chao1 estimated 296 species. Incidence-based estimates were slightly higher, with ICE estimating 292 species and Chao2 estimating 309 species. Abundance-based and incidence-based statistics arrived at similar estimates for the Tiputini site. ACE estimated the total richness to be 90 species and Chao1

estimated 85 species. The incidence-based statistics, ICE and Chao2 estimated greater species diversity, with a total of 96 and 90 species, respectively.

The second-order Jackknife estimated a scolytine species richness of 260 species for both study sites (Table 3.1; Figs. 3.4-3.6). For Onkone Gare, the second-order Jackknife estimated 217 species and for Tiputini it estimated 95 species.

Shared Species Estimators

Simple Complementarity Indices found that the composition of the scolytine fauna was markedly different for the two study sites. Onkone Gare and Tiputini had a $CI = 0.81$ for the total analyzed subset of scolytine subtribes (Table 3.1). Complementarity Indices for various subtribes of Scolytinae ranged from 0.73 to 1.00 (Table 3.5). In the samples, at least half of all the species occurring at either site were unique to that site: 76% of species at Onkone Gare and 50% of species at Tiputini (Table 3.1). However, the Monte Carlo test concluded that the observed difference between the two sites was due to stochastic sampling error and does not appear to be biologically significant. The Monte Carlo radonmization test returned a probability of 0.374 [median modeled similarity $L' = 0.77$ (lower and upper 2.5% quantiles = 0.634 and 0.836)]. These results conclude that it would be impossible to assess whether the actual dissimilarity between Onkone Gare and Tiputini is biologically significant without further sampling. Since the species accumulation curves for Onkone Gare and Tiputini have not assymptoted, any comparison of the two study sites must be considered preliminary and cannot be seen as statistically valid result.

Our results indicate that even a large scale, long-term sampling effort, such as this one, was not adequate for uncovering the true scolytine species richness contained in the

rain forest canopy at two Western Amazonian sites. Despite over 1,100 individual fogging events (representing 14 fogging expeditions), which collected 688 individual beetles representing 121 species, the species accumulation curves did not reach an asymptote (Figs. 3.1-3.3). Likewise, the occurrence of rare species in the form of singletons and doubletons did not decline. These phenomena were observed from the individual data collected for each study transect and for the collective species data for the two sites.

Since the levels of scolytine β -diversity observed herein were found to not be biologically significant and species accumulation curves have not asymptoted, it would be invalid to compare our results with those of other studies. The different levels of β -diversity found by studies of Papua New Guinean and Thai scolytine faunas suggests that patterns in scolytine β -diversity may vary regionally within tropical forest ecosystems (Hulcr et. al 2007, in press). Previous canopy fogging studies have found significant differences in the species composition of different forest types. In Manaus, Brazil, 83% of beetle species in canopy fogging samples were found in only one type of forest (Erwin 1983a). Of the four forest types characterized and studied by Erwin, “mixed-water” forests were found to be the most species rich. However, “terre firme” (non-floodplain) forests had the second highest number of species and the highest number of restricted species (β -diversity). Both sites sampled in this study were “terre firme” forest. Erwin also found that “terre firme” forests carry a high load of smaller insect species (1 mm class, as defined for his study). This offers another predictor of the true scolytine diversity in this habitat, as most scolytine species are within the 1-3 mm range. If scolytnes follow the same general patterns found for all Amazonian insects, we can

predict that further sampling would uncover an even richer scolytine fauna with possibly many species not found in other forest types.

One goal of this study was to assess the value of canopy fogging as a source of scolytine specimens. Prior to this work, there were less than 50 scolytine species records from Ecuador (Wood 2007). Our entire collection of scolytines from the foggings represented over 400 morphospecies, the inclusion of these species into the faunal record will dramatically increase the number of species that are known from Ecuador and the two Amazonian sites used in this study represent only one of the many habitat types known to occur in the region. Although extensive floral data exists for the two study sites (Pitman et al. 2001), caution must be taken when making associations of scolytine species with particular hosts based on tree data from the sampling sites. It is unlikely that scolytines would actually be extracted from their galleries by the insecticide used in fogging. The typical scolytine reaction to disturbance is to move deeper into the gallery, rather than to vacate it. Therefore, it is most likely that scolytines collected by canopy fogging are those in flight or on the surfaces of trees and other canopy vegetation. It would be erroneous to assume that scolytines fogged from a particular tree utilize that tree as their host. However, general correlations between tree and beetle diversity could be made using the data collected via canopy fogging. Therefore, despite the fact that some data critical to understanding of scolytine ecology is lost with the use of canopy fogging methods, we have demonstrated that fogging offers a method for sampling scolytine diversity that can uncover many species missed by traditional hand-collecting methods. For large-scale sampling of scolytine diversity, canopy fogging offers a quantitative method that can be repeated multiple times at a single site.

Large-scale sampling of tropical habitats offers a rich source of previously unknown species, but as this study demonstrates, even the most ambitious sampling schemes may not be enough to adequately assess the true species richness of hyper-diverse groups. In addition to this, the proper application of statistical tools is necessary to avoid erroneous conclusions and over estimates of β -diversity based on stochastic sampling (Hulcr et al. 2007, Lewinsohn and Roslin 2008). Scolytines demonstrate that a single taxon can show multiple patterns of diversity, even within tropical ecosystems. Based on the sampling of a single Amazonian habitat, we have uncovered a level of scolytine α -diversity that increases the known fauna of Ecuador nearly ten-fold. Ultimately relating this figure to the β -diversity of the region could help reveal how the composition of Neotropical scolytine communities are affected by habitat changes.

(A) Total data									
Site	No. Samples	Species Observed	Unique Species	CI	ACE	ICE	Chao1	Chao2	Jack2
Onkone Gare	965	98	74	NA	275	292	296	309	217
Tiputini	293	47	24	NA	90	96	85	90	95
Both Sites	1158	121	NA	0.81	301	323	308	311	260

(B) Bark beetles									
Site	No. Samples	Species Observed	Unique Species	CI	ACE	ICE	Chao1	Chao2	Jack2
Onkone Gare	965	42	32	NA	95	90	154	109	83
Tiputini	293	20	10	NA	38	35	32	30	35
Both Sites	1158	52	NA	0.81	121	119	154	137	109

(C) Ambrosia beetles									
Site	No. Samples	Species Observed	Unique Species	CI	ACE	ICE	Chao1	Chao2	Jack2
Onkone Gare	965	56	42	NA	179	184	153	208	128
Tiputini	293	27	14	NA	51	61	55	67	58
Both Sites	1158	69	NA	0.81	183	211	161	174	150

Table 3.1: Species data, Complementarity Indices (CI) and richness estimators for (A) total data analyzed, (B) bark beetles (Hylesinini), and (C) ambrosia beetles (Xyleborina + Premnobina).

Subtribe	Genus	Species	Locality(ies)	No. Specimens
Bothrosternina	<i>Akrobothrus</i>	<i>ecuadoriensis</i>	Onkone Gare	3
		n. sp.. nr.	Onkone	
Bothrosternina	<i>Bothrosternus</i>	<i>truncatus</i>	Gare/Tiputini	8
Bothrosternina	<i>Bothrosternus</i>	sp.	Tiputini	1
Bothrosternina	<i>Bothrosternus</i>	sp.	Onkone Gare	1
Bothrosternina	<i>Bothrosternus</i>	sp.	Onkone Gare	1
Bothrosternina	<i>Bothrosternus</i>	sp.	Onkone Gare	1
Bothrosternina	<i>Cnesinus</i>	sp.	Onkone Gare	4
Bothrosternina	<i>Cnesinus</i>	sp.	Onkone Gare	6
Bothrosternina	<i>Cnesinus</i>	sp.	Tiputini	1
Bothrosternina	<i>Cnesinus</i>	sp.	Tiputini	2
Bothrosternina	<i>Cnesinus</i>	sp.	Tiputini	2
			Onkone	
Bothrosternina	<i>Cnesinus</i>	sp.	Gare/Tiputini	4
			Onkone	
Bothrosternina	<i>Cnesinus</i>	sp.	Gare/Tiputini	4
Bothrosternina	<i>Cnesinus</i>	sp.	Onkone Gare	1
			Onkone	
Bothrosternina	<i>Cnesinus</i>	sp.	Gare/Tiputini	5
Bothrosternina	<i>Cnesinus</i>	sp.	Onkone Gare	1
			Onkone	
Bothrosternina	<i>Eupagiocerus</i>	sp..	Gare/Tiputini	2
			Onkone	
Bothrosternina	<i>Pagiocerus</i>	sp.	Gare/Tiputini	4
Bothrosternina	<i>Sternobothrus</i>	sp.	Tiputini	2
Bothrosternina	<i>Sternobothrus</i>	sp.	Onkone Gare	1
Bothrosternina	<i>Sternobothrus</i>	sp.	Onkone Gare	1
Bothrosternina	<i>Sternobothrus</i>	sp.	Onkone Gare	1
Phloeosinina	<i>Chramesus</i>	sp.	Onkone Gare	1
Phloeosinina	<i>Chramesus</i>	sp.	Tiputini	1
Phloeosinina	<i>Chramesus</i>	sp.	Onkone Gare	1
Phloeosinina	<i>Chramesus</i>	sp.	Tiputini	1
Phloeosinina	<i>Chramesus</i>	sp.	Onkone Gare	1
Phloeosinina	<i>Chramesus</i>	sp.	Onkone Gare	1

Table 3.2 (cont. on next page): Morphospecies of bark beetles (Hylesinini) found in the canopy fogging samples.

Subtribe	Genus	Species	Locality(ies)	No. Specimens
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare/Tiputini	31
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	20
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare/Tiputini	6
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare/Tiputini	21
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	4
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	2
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Tiputini	2
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Tiputini	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare/Tiputini	7
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	13
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Tiputini	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phloeotribina	<i>Phloeotriubus</i>	sp.	Onkone Gare	1
Phrixosimina	<i>Phrixosoma</i>	sp..	Onkone Gare	1
Phrixosimina	<i>Phrixosoma</i>	sp.	Onkone Gare	1
Phrixosimina	<i>Phrixosoma</i>	sp.	Onkone Gare	1

Table 3.2 (cont.): Morphospecies of bark beetles (Hylesinini) found in the canopy fogging samples.

Subtribe	Genus	Species	Locality(ies)	No. Specimens
Xyleborina	<i>Amasa</i>	sp.	Onkone Gare	1
Xyleborina	<i>Ambrosiodmus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare/Tiputini	6
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	2
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare/Tiputini	16
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare/Tiputini	11
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare/Tiputini	2
Xyleborina	<i>Coptoborus</i>	sp.	Tiputini	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare/Tiputini	2
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare/Tiputini	5
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare/Tiputini	6
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	3
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Tiputini	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Coptoborus</i>	sp.	Onkone Gare	2
Xyleborina	<i>Coptoborus</i>	<i>vespatorius</i>	Onkone Gare	1
Xyleborina	<i>Dryocoetoides</i>	sp.	Onkone Gare	6
Xyleborina	<i>Dryocoetoides</i>	sp.	Onkone Gare	1
Xyleborina	<i>Dryocoetoides</i>	sp.	Onkone Gare	1
Xyleborina	<i>Dryocoetoides</i>	sp.	Onkone Gare	1
Xyleborina	<i>Dryocoetoides</i>	sp.	Onkone Gare	2

Table 3.3 (cont. on next page): Morphospecies of ambrosia beetles (Xyleborina + Premnobina) found in the canopy fogging samples.

Subtribe	Genus	Species	Locality(ies)	No. Specimens
Xyleborina	<i>Theoborus</i>	sp.	Tiputini	1
Xyleborina	<i>Theoborus</i>	sp.	Tiputini	3
Xyleborina	<i>Theoborus</i>	sp.	Onkone Gare/Tiputini	5
Xyleborina	<i>Theoborus</i>	nr. <i>micarius</i>	Onkone Gare	1
Xyleborina	<i>Theoborus</i>	sp.	Onkone Gare	3
Xyleborina	<i>Theoborus</i>	sp.	Tiputini	1
Xyleborina	<i>Theoborus</i>	sp.	Onkone Gare/Tiputini	8
Xyleborina	<i>Theoborus</i>	sp.	Tiputini	1
Xyleborina	<i>Theoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Theoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Theoborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborinus</i>	sp.	Tiputini	2
Xyleborina	<i>Xyleborus</i>	sp.	Tiputini	21
Xyleborina	<i>Xyleborus</i>	<i>spathipennis</i>	Onkone Gare/Tiputini	2
Xyleborina	<i>Xyleborus</i>	<i>affinis</i>	Onkone Gare/Tiputini	317
Xyleborina	<i>Xyleborus</i>	sp.	Tiputini	1
Xyleborina	<i>Xyleborus</i>	nr. <i>ferrugineus</i>	Onkone Gare/Tiputini	12
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	2
Xyleborina	<i>Xyleborus</i>	sp.	Tiputini	8
Xyleborina	<i>Xyleborus</i>	sp.	Tiputini	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Tiputini	1
Xyleborina	<i>Xyleborus</i>	sp.	Tiputini	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	2
Xyleborina	<i>Xyleborus</i>	sp.	Tiputini	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	2
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xyleborus</i>	sp.	Onkone Gare	1
Xyleborina	<i>Xylosandrus</i>	<i>morigerus</i>	Onkone Gare/Tiputini	12
Premnobina	<i>Premnobius</i>	<i>clavipennis</i>	Onkone Gare	1

Table 3.3 (cont.): Morphospecies of ambrosia beetles (Xyleborina + Premnobina) found in the canopy fogging samples.

Subtribe	SA Generic Records	SA spp. Records	Genera Collected	Species Collected
Xyleborina	11	233	8	68
Premnobina	1	3	1	1
Bothrosterminal	6	82	6	22
Phloeosinina	5	61	1	6
Phloeotribina	1	54	1	21
Phrixosomina	1	10	1	3

Table 3.4: Previous South American generic and species records for various scolytine subtribes compared with taxa collected by this study.

Subtribe	Samples with Taxon	% Occurrence in Samples	Onkone Gare spp.	Tiputini spp.	Total spp.	Shared spp.	Unique spp.	CI
Xyleborina	314	27	56	27	68	14	55	0.81
Premnobina	1	0.09	1	0	1	0	1	1.00
Bothrostermina	50	4.32	17	11	22	6	16	0.73
Phloeosinina	6	0.52	4	2	6	0	6	1.00
Phloeotribina	89	7.69	18	7	21	4	17	0.81
Phrixosomina	3	0.26	3	0	3	0	3	1.00

Table 3.5: Species numbers and Complementarity Indices (CI) for analyzed subtribes of Scolytinae.

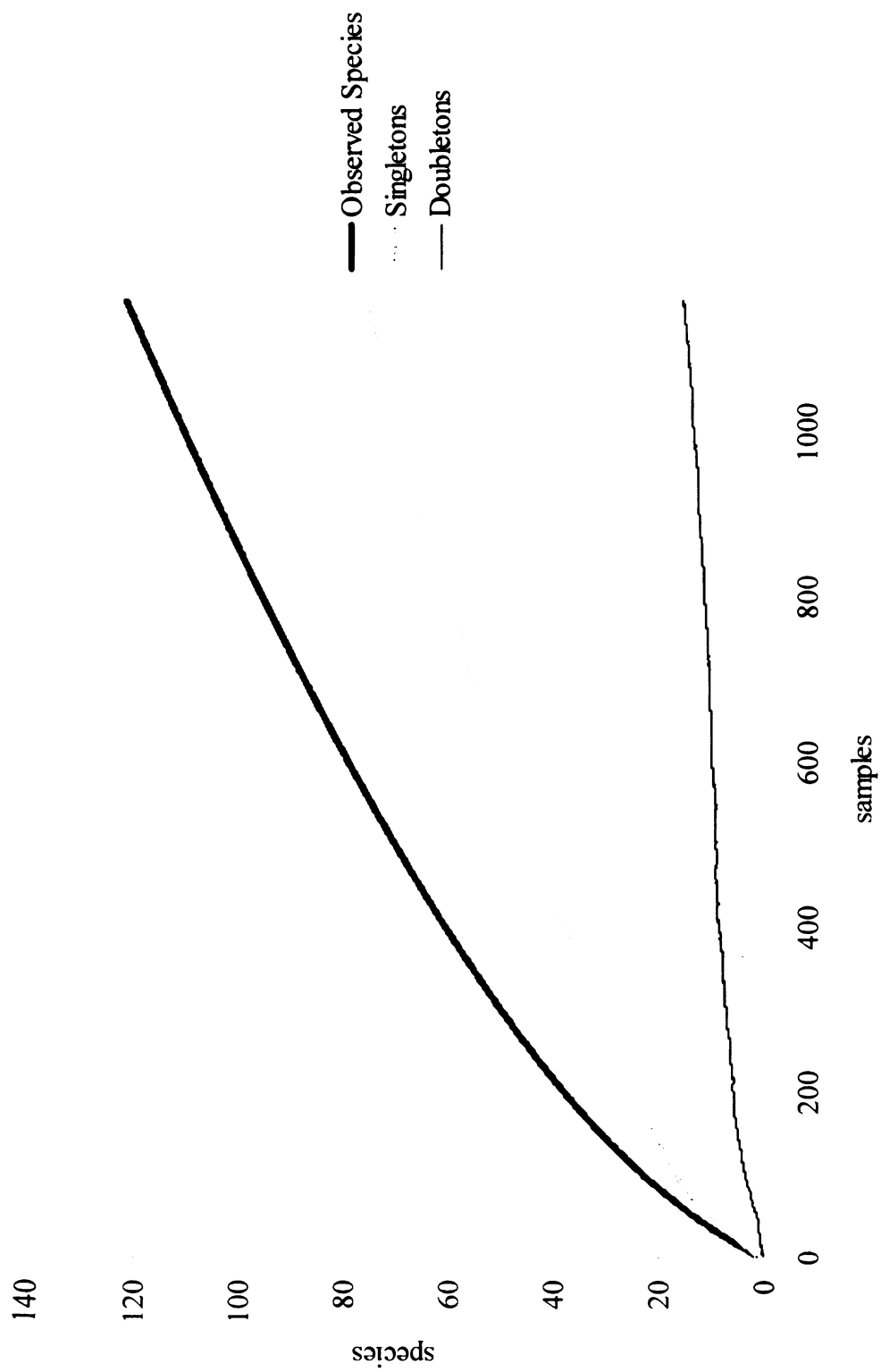


Figure 3.1: Species accumulation curves for Onkone Gare + Tiputini for total data (Hylesinini + Xyleborina + Premnobina).

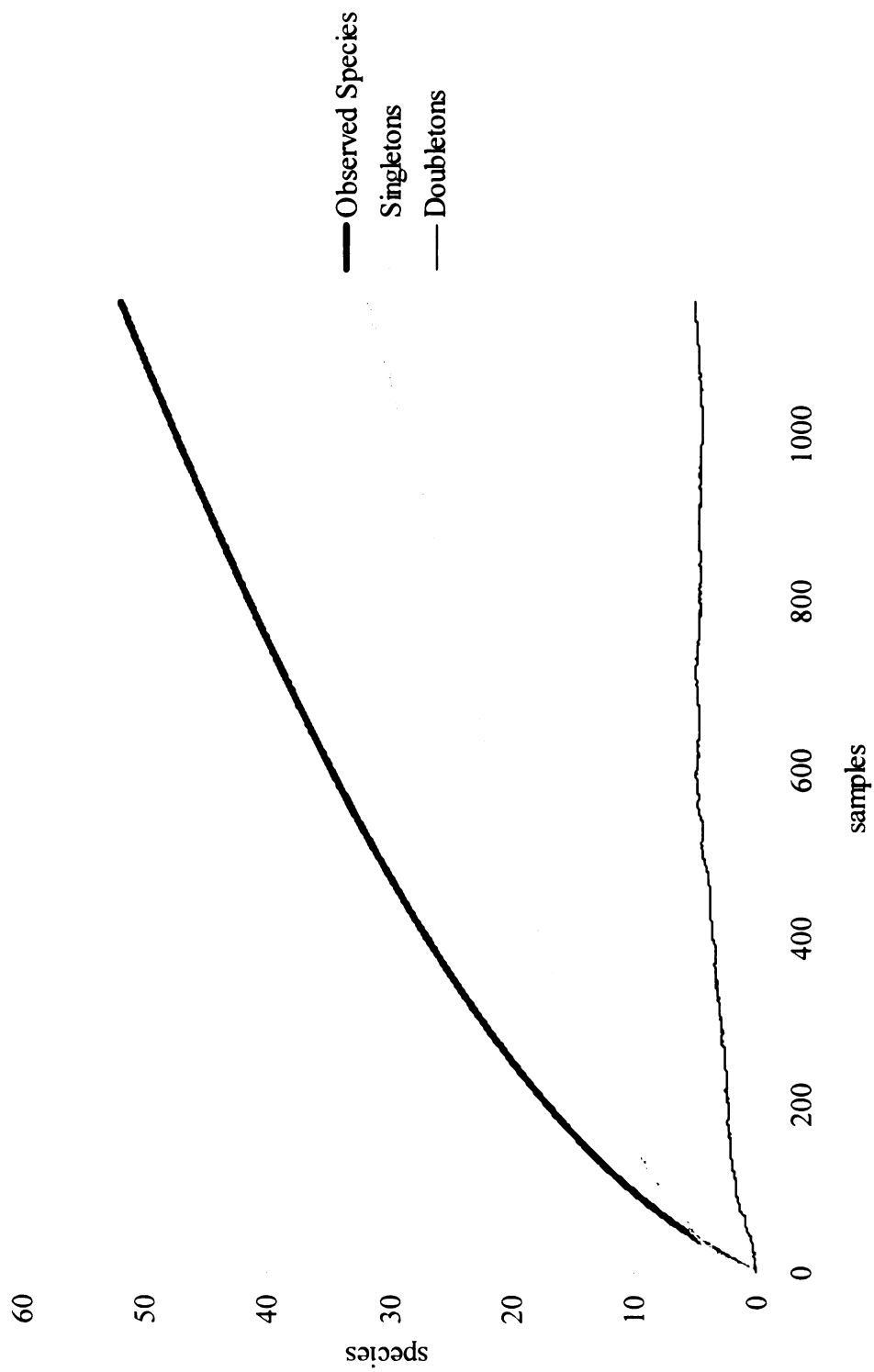


Figure 3.2: Species accumulation curves for Onkone Gare + Tiputini for bark beetles (Hylesinini).

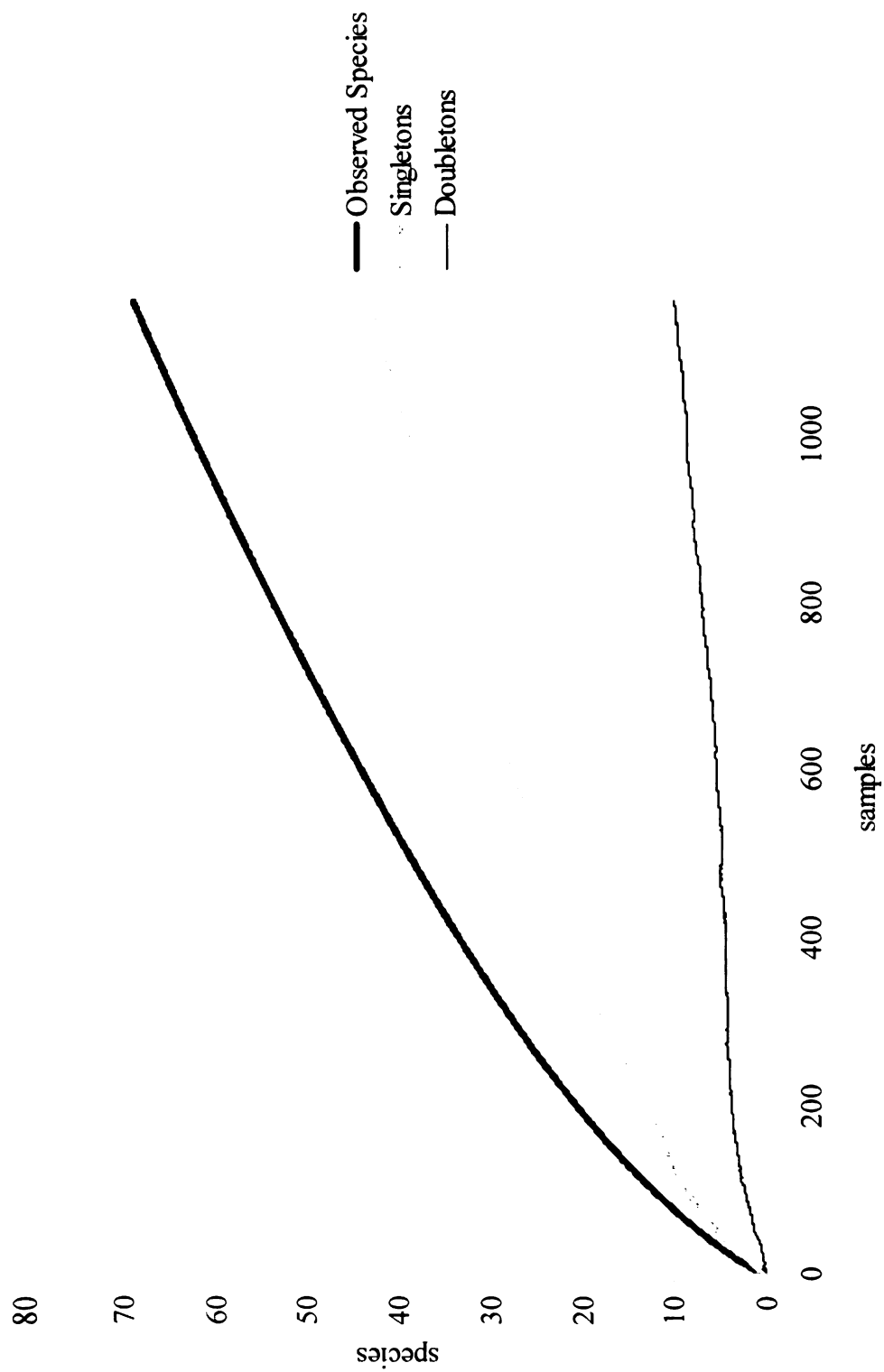


Figure 3.3: Species accumulation curves for Onkone Gare + Tiputini for ambrosia beetles (Xyleborina + Premnobina).

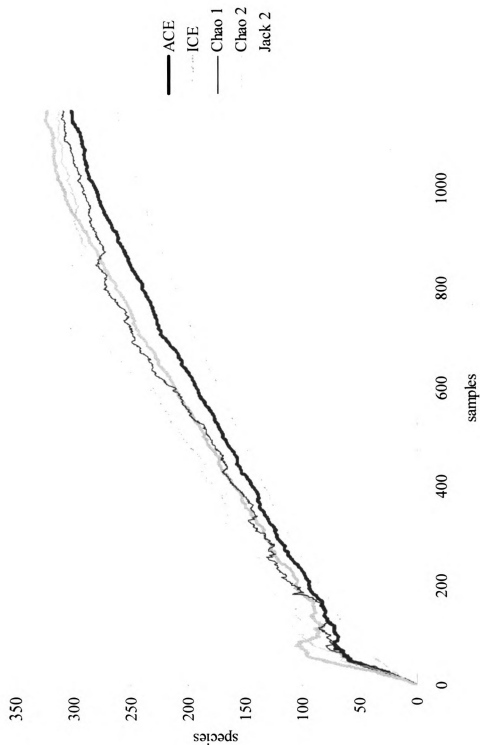


Figure 3.4: Richness estimators for Onkone Gare + Tiputini for total data (Hylesinini + Xyleborina + Premnobina).

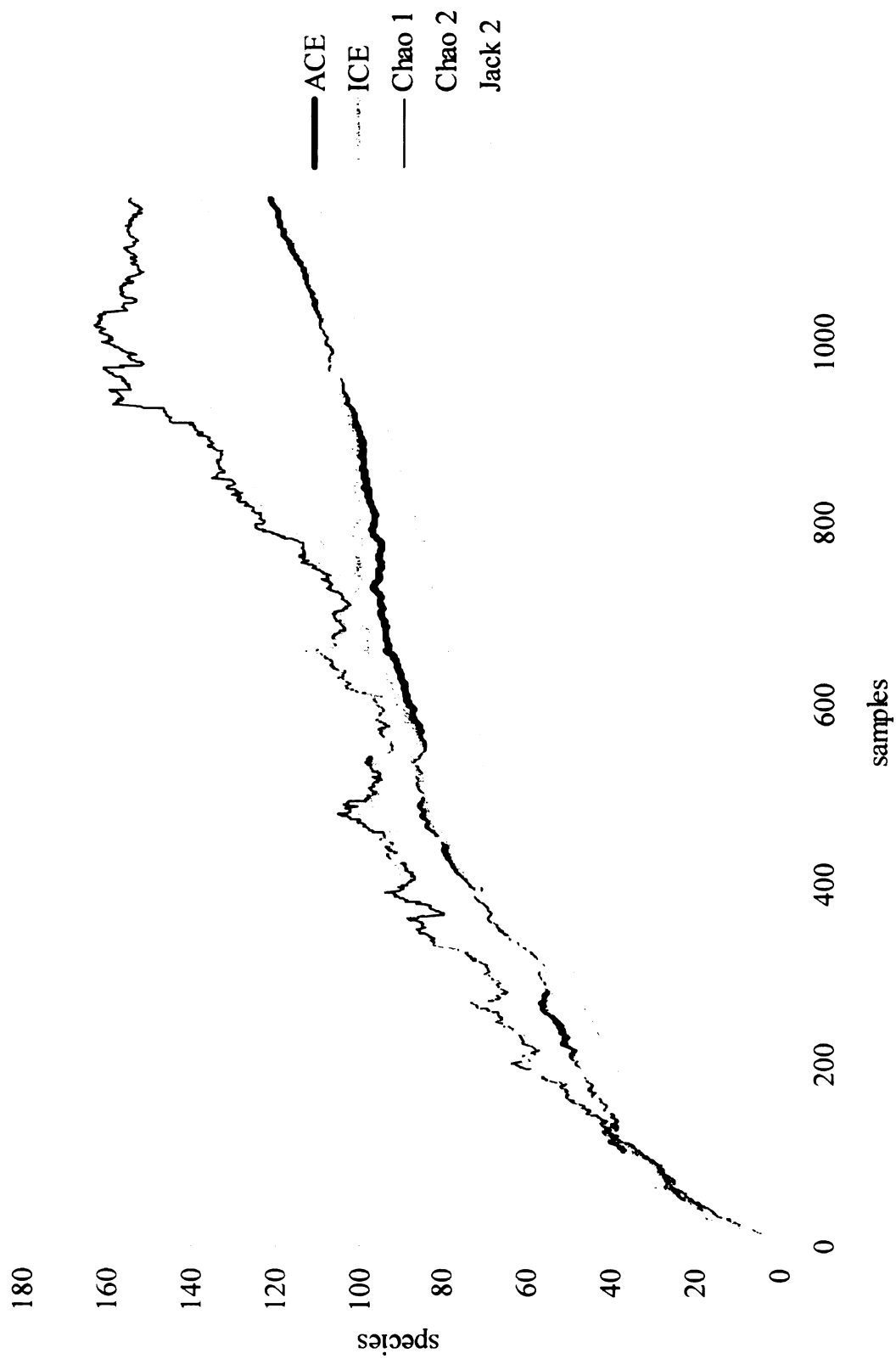


Figure 3.5: Richness estimators for Onkone Gare + Tiputini for bark beetles (Hylesinini).

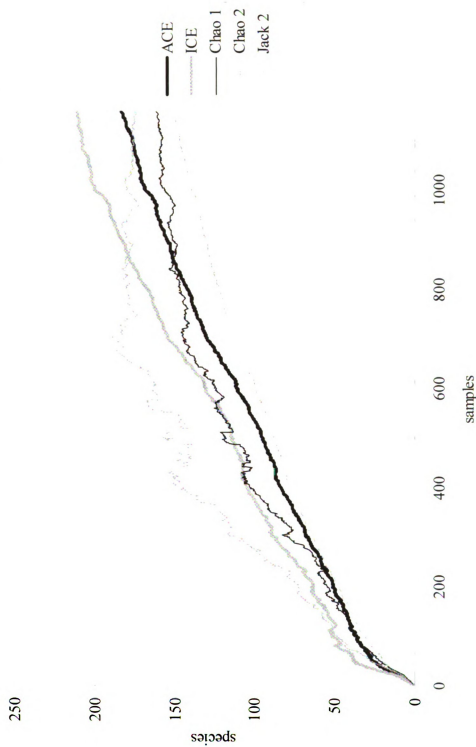


Figure 3.6: Richness estimators for Onkone Gare + Tiputini for ambrosia beetles (Xyleborina + Premnobina).

LITERATURE CITED

- Adis, J. 1990.** Thirty million arthropod species – too many or too few? *Journal of Tropical Ecology* 6:115-118.
- Anderson, W. H. and D. M. Anderson. 1971.** Type specimens in the Hans Eggers collection of scolytid beetles (Coleoptera). *Smithsonian Contributions to Zoology* 94: 1-38.
- Baker, R. H., X. B. Yu, and R. DeSalle. 1998.** Assessing the relative contribution of molecular and morphological characters in simultaneous analysis trees. *Molecular Phylogenetics and Evolution* 9: 427-436.
- Banks, J. C. and J. B. Whitfield. 2006.** Dissecting the ancient rapid radiation of microgastrine wasp genera using additional nuclear genes. *Molecular Phylogenetics and Evolution* 41: 690-703.
- Basset, Y. 2001.** Invertebrates in the canopy of tropical rain forests. How much do we really know? *Plant Ecology* 153: 87-107.
- Beaver, R. A. 1979.** Host specificity of temperate and tropical animals. *Nature* 281:139-141.
- Beaver, R. A. 1985.** Bark and ambrosia beetles (Coleoptera: Scolytidae) of Zambia. *Revue de Zoologie Africaine* 99: 63-85.
- Beaver, R. A. 1989.** Insect-fungus relationships in the bark and ambrosia beetles. *In: N. Wilding, N. M. Collins, P. M. Hammond, and J. F. Webber (Eds.) Insect Fungus Interactions.* Academic Press, London: pp. 121-143.
- Beaver, R. A. 1995.** New synonymy and taxonomic changes in Oriental and Australasian Scolytidae and Platypodidae (Coleoptera). *Annalen des Naturhistorischen Museums in Wien, Series B* 97B: 197-204.
- Beaver, R. A. 1998.** New synonymy, new combinations and taxonomic notes on Scolytidae and Platypodidae (Insecta: Coleoptera). *Annalen des Naturhistorischen Museums in Wien* 100B: 179-192.
- Beaver, R. A. and K. Löyttyniemi. 1991.** Annual flight patterns and diversity of bark and ambrosia beetles (Col., Scolytidae and Platypodidae) attracted to bait logs in Zambia. *Journal of Applied Entomology* 112: 505-511.
- Beeson, C. F. C. 1915.** Notes on some Indian forest beetles. *Indian Forester* 16: 294-299.
- Beeson, C. F. C. 1930.** The biology of the genus *Xyleborus*, with more new species. *Indian Forest Records* 14(10): 209-272.

- Blandford, W. F. H. 1894a.** Notes on Scolytidae and their food-plants. *Insect Life* 6: 260-265.
- Blandford, W. F. H. 1894b.** Supplementary notes on the Scolytidae of Japan, with a list of species. *Entomological Society of London, Transactions* 1894: 575-580.
- Blandford, W. F. H. 1894c.** The Rhynchophorous Coleoptera of Japan. Part III. Scolytidae. *Entomological Society of London, Transactions* 1894: 53-141.
- Blandford, W. F. H. 1896a.** Descriptions of new Scolytidae from the Indo-Malayan and Austro-Malayan regions. *Entomological Society of London, Transactions* 1896: 191-228.
- Blandford, W. F. H. 1896b.** Scolytides de la Nouvelle Calédonie. *Société Entomologique de Belgique, Annales* 40: 241-245.
- Blandford, W. F. H. 1898.** On some Oriental Scolytidae of economic importance, with descriptions of five new species. *Entomological Society of London, Transactions* 1898: 423-430.
- Bright, D. E. 1968.** Review of the tribe Xyleborini in America North of Mexico (Coleoptera: Scolytidae). *The Canadian Entomologist*. 100: 1288-1323.
- Bright, D. E. and G. O. Poinar. 1994.** Scolytidae and Platypodidae (Coleoptera) from Dominican Republic amber. *Annals of the Entomological Society of America* 87: 170-194.
- Bright, D. E. and R. E. Skidmore. 1997.** A Catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 1 (1990-1994). NRC Research Press, Ottawa, Ontario, Canada: 368 pp.
- Bright, D. E. and R. E. Skidmore. 2002.** A Catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 2 (1995-1999). NRC Research Press, Ottawa, Ontario, Canada. 523 pp.
- Browne, F. G. 1963.** Taxonomic notes on Scolytidae (Coleoptera). *Entomologische Berichten* 23(3): 53-59.
- Browne, F. G. 1965.** On some Scolytidae and Platypodidae (Coleoptera), mainly from Africa and the Oriental Region. *Zoologische Mededelingen, Leiden* 40(22): 187-209.
- Browne, F. G. 1984.** Some new species of Platypodidae and Scolytidae (Coleoptera) from Papua New Guinea. *South Pacific Journal of Natural Science* 4: 55-75.
- Burnham, K. P. and W. S. Overton. 1978.** Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65: 623-633.

Burnham, K. P. and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60: 927-936.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11: 265-270.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783-791.

Chao, A., R. L. Chazdon, R. K. Colwell, and T.-J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* 8: 148-159.

Chao, A., R. L. Chazdon, R. K. Colwell, and T.-J. Shen. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62: 361-371.

Chao, A. and S. M. Lee. 1992. Estimating the number of classes via sample coverage. *Journal of American Statistical Association* 87: 210-217.

Chao, A., M.C. Ma, and M. C. K. Yang. 1993. Stopping rules and estimation for recapture debugging with unequal failure rates. *Biometrika* 80: 193-201.

Choo, H. Y. 1983. Taxonomic studies on the Platypodidae and Scolytidae (Coleoptera) from Korea. Dissertation. Seoul National University, Seoul, Korea. 128pp.

Chung, A. Y. C. 2004. Vertical stratification of beetles (Coleoptera) using flight intercept traps in a lowland rainforest of Sabah, Malaysia. *Sepilok Bulletin* 1: 27-39.

Cibrián T. D., J.T. Méndez Montiel, R. Campos Bolaños, H.O. Yates III, and J.F. Lara. 1995. *Insectos Forestales de Mexico/Forest Insects of Mexico*. Universidad Autonoma Chapingo, Chapingo, Mexico. 453 pp.

Cognato, A. I. 2006. Standard percent DNA sequence difference for insects does not predict species boundaries. *Journal of Economic Entomology* 99: 1037-1045.

Cognato, A. I., N. E. Gillette, R. C. Bolaños, F. A. H. Sperling. 2005. Mitochondrial phylogeny of pine cone beetles (Scolytinae, *Conophthorus*) and their affiliation with geographical area and host. *Molecular Phylogenetics and Evolution* 36: 494-508.

Cognato, A.I. and D. Grimaldi. In Press. One hundred million years of morphological conservation in a bark beetle (Coleoptera: Curculionidae: Scolytinae). *Systematic Entomology*.

- Cognato, A. I. and F. A. H. Sperling. 2000.** Phylogeny of *Ips* DeGeer species (Coleoptera Scolytidae) inferred from mitochondrial cytochrome oxidase I DNA sequences. *Molecular Phylogenetics and Evolution* 14(3): 445-460.
- Cognato, A. I. and J. H. Sun. 2007.** DNA based cladograms augment the discovery of a new *Ips* species from China (Coleoptera: Curculionidae: Scolytinae). *Cladistics* 23: 539-551.
- Cognato, A. I. and A. P. Vogler. 2001.** Exploring data interaction and nucleotide alignment in a multiple gene analysis of *Ips* (Coleoptera: Scolytinae). *Systematic Biology* 50(6): 758-780.
- Colwell, R. K. 2004.** EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application e-published at: <http://viceroy.eeb.uconn.edu/estimates>
- Colwell, R. K. and J. A. Coddington. 1994.** Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London, Series B*, 345: 101-118.
- Danforth, B. N., J. Fang, and S. Sipes. 2006.** Analysis of family-level relationships in bees (Hymenoptera: Apiformes) using 28S and two previously unexplored nuclear genes: CAD and RNA polymerase II. *Molecular Phylogenetics and Evolution* 39: 358-372.
- DeSalle, R., M. G. Egan, and M. Siddall. 2005.** The unholy trinity: taxonomy, species delimitation and DNA barcoding. *Philosophical Transactions of the Royal Society, B*: 360: 1905-1916.
- Deyrup, M. and Atkinson, T. H. 1987.** Comparative biology of temperate and subtropical bark and ambrosia beetles (Coleoptera: Scolytidae, Platypodidae) in Indiana and Florida. *The Great Lakes Entomologist* 20(2):59-66.
- Dole, S. A. and R. A. Beaver. In Press.** A Review of the Australian Species of *Xylosandrus* Reitter (Coleoptera: Curculionidae: Scolytinae). *The Coleopterists' Bulletin*.
- Dole, S. A. and A. I. Coganto. 2007.** A New Genus and Species of Bothrosternina (Coleoptera; Curculionidae: Scolytinae) from Ecuador. *The Coleopterists' Bulletin* 61(2): 318-325.
- Edgar, R. C. 2004.** MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792-1797.
- Edwards, S. V., L. Liu, and D. K. Pearl. 2007.** High-resolution species tree without concatenation. *Proceedings of the National Academy of Sciences, USA* 104: 5936-5941.

Eggers, H. 1923. Neue indomalayische Borkenkafer (Ipidae). Zoologische Mededeelingen 7: 129-220.

Eggers, H. 1930. Neue Xyleborus-Arten (Col. Scolytidae) aus Indien. India Forest Records, Entomology 14(9): 177-208.

Eggers, H. 1939a. Entomological results from the Swedish expedition 1934 to Burma and British India. Coleoptera: Ipidae, gesammelt von Rene Malaise. Arkiv for Zoologi 31A (4): 1-14.

Eggers, H. 1939b. Japanische Borkenkafer, II. Arbeiten uber Morphologische und Taxonomische Entomologie 6: 4-123.

Eggers, H. 1940. Neue indomalayische Borkenkafer (Ipidae). III. Nachrag (Forstsetzung). Tijdschrift voor Entomologie 83: 132-154.

Eggers, H. 1941a. Borkenkafer aus Sudamerika (Col. Ipid.) IX. Insel Guadeloupe. Arbeiten uber Morphologische und Taxonomische Entomologie 8: 99-109.

Eggers, H. 1941b. Neue Borkenkafer (Ipidae, Col.) aus China. Entomologische Blatter 37: 222-226.

Eichhoff, W. J. 1868. Neue amerikanische Borkenkafer-Gattung und Arten. Berliner Entomologische Zeitschrift 12: 145-152.

Eichhoff, W. J. 1869. Neue Borkenkafer. Berliner Entomologische Zeitschrift 12: 273-280.

Eichhoff, W. J. 1875. Felicien Chapuis et W. Eichhoff, Scolytides recueillis au Japan par M. C. Lewis. Societe Entomologique de Belgique, Annales 18: 195-203.

Eichhoff, W. J. 1877. Japanische Scolytidae. Deutsche Entomologische Zeitschrift 21(1): 117-128.

Eichhoff, W. J. 1878. Ratio, descriptio, emendatio eorum Tomicinorum qui sunt in Dr. Medin. Chapuisi et autoris ipsius collectionibus et quos praeterea recognovit. Societe Entomologique de Liege, Memoires 8(2): 1 + iv + 531 pp.

Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopterists' Bulletin 36(1):74-75.

Erwin, T. L. 1983a. Tropical forest canopies, the last biotic frontier. Bulletin of the Entomological Society of America 29(1):14-19.

- Erwin, T. L. 1983b.** Beetles and other arthropods of the tropical forest canopies at Manaus, Brasil, sampled with insecticidal fogging techniques, pp. 59-75. In, Sutton, S. L., T. C. Whitmore and A. C. Chadwick (Eds.). *Tropical Rain Forests: Ecology and Management*. Blackwell Scientific Publications. Oxford, United Kingdom.
- Erwin, T. L. 1988.** The tropical forest canopy: The heart of biotic diversity, pp. 123-129. In, Wilson, E. O. (Ed.). *Biodiversity*. National Academy Press. Washington, DC.
- Erwin, T. L. 1991.** How many species are there?: Revisited. *Conservation Biology* 5(3):330-333.
- Erwin, T. L., M. C. Pimienta, O. E. Murillo, and V. Aschero. 2005.** Mapping Patterns of β -Diversity for Beetles Across the Western Amazon Basin: A Preliminary Case for Improving Inventory Methods and Conservation Strategies. *Proceedings of the California Academy of Sciences*, ser. 4, 56(Suppl. I): 72-85.
- Fang, Q. Q., A. Mitchell, J. C. Regier, C. Mitter, T. P. Friedlander, and R. W. Poole. 2000.** Phylogenetic utility of the nuclear gene dopa decarboxylase in noctuid moths (Insecta: Lepidoptera: Noctuoidea). *Molecular Phylogenetics and Evolution* 15(3): 473-486.
- Farrell, B. D., A. S. Sequeira, B. C. O'Meara, B. B. Normark, J. H. Chung, and B. H. Jordal. 2001.** The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). *Evolution* 55(10): 2011-2027.
- Ferrari, J. A. 1867.** Die Forst- und Baumzuchtschadlichen Borkenkafer (Tomicides Lac.) aus der Familie der Holzverderber (Scolytides Lac.). Carl Gerold's Sohn, Wien, 96 p.
- Flechtmann, C. A. H., A. L. T. Ottati, and C. W. Berisford. 2001.** Ambrosia and bark beetles (Scolytidae: Coleoptera) in pine and eucalypt stands in southern Brazil. *Forest Ecology and Management* 142: 183-191.
- Friedlander, T. P., K. R. Horst, J. C. Regier, C. Mitter, R. S. Peigler, and Q. Q. Fang. 1998.** *Molecular Phylogenetics and Evolution* 9(1): 131-140.
- Friedlander, T. P., J. C. Regier, C. Mitter, D. L. Wagner, and Q. Q. Fang. 2000.** Evolution of heteroneuran Lepidoptera (Insecta) and the utility of dopa decarboxylase for Cretaceous-age phylogenetics. *Zoological Journal of the Linnean Society* 130: 213-234.
- Gaston, K. J. 1991.** The magnitude of global insect species richness. *Conservation Biology* 5(3):283-296.

- Gaylord, M. L., T. E. Kolb, K. F. Wallin, and M. R. Wagner. 2006.** Seasonality and lure preference of bark beetles (Curculionidae: Scolytinae) and associates in a Northern Arizona ponderosa pine forest. *Environmental Entomology* 35: 37-47.
- Goloboff, P., J. Farris, and K. Nixon. 2003.** Tree Analysis using new technology. Program and documentation available from the authors, and at www.zmuc.dk/public/phylogeny.
- Grimaldi, D. and M. S. Engel. 2005.** Evolution of the Insects. Cambridge University Press, Cambridge, U.K., 755pp.
- Haack, R. A. 2006.** Exotic bark and wood-boring Coleoptera in the United States; recent establishments and interceptions. *Canadian Journal of Forest Research* 36(2): 269-288.
- Hagedorn, J. M. 1908.** Diagnosen bisher umbeschriebener Borkenkäfer. *Deutsche Entomologische Zeitschrift* 1908(3): 369-382.
- Hagedorn, J. M. 1912.** Ipiden als Kaffeeschadlinge. *Entomologische Blätter* 8: 33-43.
- Hebert, P. D. N., A. Cywinska, S. L. Ball, and J. R. deWard. 2003.** Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London, B*: 270: 313-321.
- Hebert, P. D. N., M. Y. Stoeckle, T. S. Zemlak, and C. M. Francis. 2004.** Identification of birds through DNA barcodes. *PLoS Biology* 2: e312.
- Hoffmann, C. H. 1941.** Biological observations on *Xylosandrus germanus* (Bldfd.). *Journal of Economic Entomology* 34: 38-42.
- Hood, G. M. 2008.** PopTools, version 3.0.6. Available on the internet. URL <http://cse.csiro.au/poptools>.
- Hopkins, A. D. 1915.** Classification of the Cryphalinae with descriptions of new genera and species. United States Department of Agriculture Report 99: 75 pp.
- Hulcr, J. 2008.** Frequent evolution of theft in fungus-farming ambrosia beetles. Evolution 2008 meeting, University of Minnesota, Minneapolis, MN, June 20-24, 2008.
- Hulcr, J., R. A. Beaver, W. Puranaskul, S. A. Dole, and S. Sonthichai. In Press.** A comparison of bark and ambrosia beetle communities in two forest types in Northern Thailand (Coleoptera: Curculionidae: Scolytinae and Platypodinae). *Environmental Entomology*.

- Hulcr, J., S. A. Dole, R. A. Beaver, and A. I. Cognato. 2007.** A cladistic review of generic taxonomic characters in Xylebroina (Coleoptera: Curculionidae: Scolytinae). *Systematic Entomology* 32(3):568-584.
- Hulcr, J., V. Novotny, B. A. Maurer, and A. I. Cognato. 2007.** Low beta diversity of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae) in lowland rainforests of Papua New Guinea. *Oikos* 117(2): 214-222.
- Hulsenbeck, J. P. and F.R. Ronquist. 2001.** MrBayes: Bayesian inference of phylogeny, *Biometrics* 17: 754-755.
- Jakus, R. 1998.** Patch level variation on bark beetle attack (Col., Scolytidae) on snapped and uprooted trees in Norway spruce primeval natural forest in endemic conditions: species distribution. *Journal of Applied Entomology* 122 (2-3): 65-70.
- Jordal, B. H. 2002.** Elongation Factor 1 α resolves the monophyly of the haplodiploid ambrosia beetles Xyleborini (Coleoptera: Curculionidae). *Insect Molecular Biology* 11(5): 453-465.
- Jordal, B. H. 2007.** Reconstructing the phylogeny of Scolytinae and close allies: major obstacles and prospects for a solution. In: Bentz, B., A. Cognato, and K. Raffa (Eds.), *Proceedings from the Third Workshop on Genetics of Bark Beetles and Associated Microorganisms*. Proc. RMRS-P-45. Fort Collins, CO., US. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 3-9.
- Jordal, B., J. J. Gillespie, and A. I. Cognato. 2008.** Secondary structure alignment and direct optimization of 28S rDNA sequences provide limited phylogenetic resolution in bark and ambrosia beetles (Curculionidae: Scolytinae). *Zoologica Scripta* 37(1): 43-56.
- Jordal, B. H. and G. M. Hewitt. 2004.** The origin and radiation of Macroneasian beetles breeding in *Euphorbia*: The relative importance of multiple data partitions and population sampling. *Systematic Biology* 53(5): 711-734.
- Jordal, B. H., B. J. Normark, and B. D. Farrell. 2000.** Evolutionary radiation of an inbreeding haplodiploid beetle lineage (Curculionidae: Scolytinae). *Biological Journal of the Linnean Society* 71: 483-499.
- Kawakita, A., T. Sota, J. S. Ascher, M. Ito, H. Tanaka and M. Kato. 2003.** Evolution and phylogenetic utility of alignment gaps within intron sequences of three nuclear genes in bumble bees (*Bombus*). *Molecular Biology and Evolution* 20: 87-92.
- Kalshoven, L. G. E. 1959.** New cases of synonymy in Indomalayan scolytids. *Entomologische Berichten* 19: 93-97.
- Kalshoven, L. G. E. 1960.** Two new cases of synonymy in Indomalayan Platypodidae and Scolytidae. *Entomologische Berichten* 20(3): 63-64.

Kirkendall, L. R. 1993. Ecology and evolution of biased sex ratios in bark and ambrosia beetles. In: Wrensch, D. L. and M. A. Ebbert. *Evolution and Diversity of Sex Ratio in Insects and Mites*. Chapman and Hall, New York.

Kirkendall, L. R. and F. Ødegaard. 2007. Ongoing invasions of old-growth tropical forests: establishment of three insectivorous beetle species in southern Central America (Curculionidae: Scolytinae). *Zootaxa* 1588: 53-62.

Kruskal, J. B. 1983. An overview of sequence comparison. In: Sankoff, D., Kruskal, J.B. (Eds.), *Time Warps, String Edits, and Macromolecules: The Theory and Practice of Sequence Comparison*. Addison-Wesley, Reading, Massachusetts, pp. 1-45.

Kuschel, G., R. A. B. Leschen, and E. C. Zimmermann. 2000. Platypodidae under scrutiny. *Invertebrate Taxonomy* 14: 771-805.

Lea, Arthur Mills, 1893. Description of new species of Bostrychidae. *Linnean Society of New South Wales, Proceedings* 8: 317-323.

Lee, M.S.Y. 2001. Unalignable sequences and molecular evolution. *Trends Ecol. Evol.* 16: 681-685.

Lee, S. M., and A. Chao. 1994. Estimating population size via sample coverage for closed capture-recapture models. *Biometrics* 50: 88-97.

Lewinsohn, T. M. and T. Roslin. 2008. Four ways toward tropical herbivore megadiversity. *Ecological Letters* 11: 398-416.

Lowman, M. D. and P. K. Wittman. 1996. Forest Canopies: Methods, Hypotheses, and Future Directions. *Annual Review of Ecology and Systematics* 27: 55-81.

Lucky, A., T. L. Erwin, and J. D. Witman. 2002. Temporal and Spatial Diversity and Distribution of Arboreal Carabidae (Coleoptera) in a Western Amazonian Rain Forest. *Biotropica* 34(3): 376-386.

Maddison, W. P. and D. R. Maddison. 2006. Mesquite: a modular system for evolutionary analysis. Version 1.12. Available from: <<http://mesquiteproject.org>>.

Madoffe, S. S. and A. Bakke. 1995. Seasonal fluctuations and diversity of bark and wood-boring beetles in lowland forest: implications for management practice. *South African Forestry Journal* 173: 9-15.

Maeto, K. and K. Fukuyama. 2003. Vertical stratification of ambrosia beetle assemblages in a lowland forest at Pasoh, peninsular Malaysia, pp. 325-336. *In* T.

Okuda, N. Manokaran, Y. Matsumoto, K. Niiyama, S. C. Thomas, and P. S. Ashton (eds.), Pasoh: ecology of a lowland rain forest in Southeast Asia. Springer, Tokyo, Japan.

Maeto, K., K. Fukuyama, and L. G. Kirton. 1999. Edge effects on ambrosia beetle assemblages in a lowland forest, bordering oil palm plantations in peninsular Malaysia. *Journal of Tropical Forest Science* 11: 537-547.

Mandelshtam, M. Y. and R. A. Beaver. 2003. *Amphiscolytus* — a new genus, and Amphiscolytini — a new tribe of Scolytidae (Coleoptera) for *Dacryophthorus capensis* Schedl. *Zootaxa*, 298: 1-8.

Marvaldi, A. E. 1997. Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. *Cladistics* 13: 285-312.

May, R. M. 1988. How many species are there on Earth? *Science* 241:1441-1449.

Menard, K. L. and A. I. Cognato. 2007. Mitochondrial haplotypic diversity of pine cone beetles (Scolytinae: *Conophthorus*) collected on food sources. *Molecular Ecology and Evolution* 36 (4): 962-966.

Mitchell, A., C. Mitter, and J. C. Regier. 2000. More taxa or more characters revisited: Combining data from nuclear protein-encoding genes for phylogenetic analysis of Noctuoidea (Insecta: Lepidoptera). *Systematic Biology* 49(2): 202-224.

Morales, N. E., J. C. Zanuncio, D. Pretissoli, and A. S. Fabres. 2000. Fluctuación poblacional de Scolytidae (Coleoptera) en zonas reforestadas con *Eucalyptus grandis* (Myrtaceae) en Minas Geraes, Brasil. *Revista de Biología Tropical* 48: 101-107.

Motschulsky, V. von. 1866. Neue Borkenkafer de Ceylon [In French]. *Moskov Obschch Isp. Prirody Biol. Biul.* (Bulletin de la Societe Imperiale des Naturalistes de Moscou) 39: 401-404.

Moulton, J. K. and B. M. Wiegmann. 2004. Evolution and phylogenetic utility of CAD (rudimentary) among Mesozoic-aged Eremoneuran Diptera (Insecta). *Molecular Phylogenetics and Evolution* 31: 363-378.

Murayama, J. J. 1954. Scolytid-fauna on the northern half of Honshu with a distribution table of all the scolytid-species described from Japan. Yamaguti University, Faculty of Agriculture, Bulletin 5: 149-212.

Murayama, J. J. and L. G. E. Kalshoven. 1962. *Xyleborus morstatti* Hag., a synonym of *X. compactus* Eichh. (Col., Scolytidae). *Entomologische Berichten* 22: 247-250.

Niisima, Y. 1909. Die Scolytiden Hokkaidos unter Berücksichtigung ihrer Bedeutung für Forstschaden. Tohoku Imperial University, Sapporo, *Journal of the College of Agriculture* 3: 109-179.

- Nixon, K. C. 1999.** Winclada (Beta), Version 0.9.9. Published by the author.
- Nobuchi, A. 1981.** Studies on Scolytidae XXIII. The ambrosia beetles of the genus *Xylosandrus* Reitter from Japan (Coleoptera). Forestry and Forestry Products Research Institute, Bulletin 314: 27-37.
- Normark, B. B., B. H. Jordal, and B. D. Farrell. 1999.** Origin of a haplodiploidy beetle lineage. Proceedings of the Royal Society of London, Series B, 266: 2253-2259.
- Novotny, V., S. E. Miller, J. Hulcr, R. A. Drew, Y. Basset, M. Janda, G. P. Setliff, K. Darrow, A. J. A. Stewart, J. Auga, B. Isua, K. Molem, M. Manumbor, E. Tamtiai, M. Mogia, and G. Weiblen. 2007.** Low beta diversity of herbivorous insects in tropical forests. *Nature (Lond.)* 448: 692-697.
- Nunberg, M. 1959.** Die Gattung *Xyleborus* Eichhoff (Coleoptera: Scolytidae). Ergänzungen. Berichtigungen und Erweiterung der Diagnosen. I. Teil [The genus *Xyleborus* additions, corrections and expansion of diagnoses. Part 1]. *Beiträge zur Entomologie* 9(3/4): 413-466.
- Ohno, S. 1990.** The Scolytidae and Platypodidae (Coleoptera) from Borneo found in logs at Nagoya Port 1. *Research Bulletin of the Plant Protection Service (Japan)* 26: 83-94.
- Oliveira, C. M. 2008.** First record of *Xylosandrus compactus* (Eichhoff) (Coleoptera: Curculionidae: Scolytinae) on soursop, *Annona muricata* L. (Annonaceae) in Brazil, with a list of host plants. *The Coleopterists' Bulletin* 62(1): 45-48.
- Oliver, J. B. and C. M. Mannion. 2001.** Ambrosia beetle (Coleoptera: Scolytidae) species attacking chestnut and captured in ethanol-baited traps in middle Tennessee. *Population Ecology* 30(5): 909-918.
- Peltonen, M., Heliövaara, K., Väisänen, R., and Keronen, J. 1998.** Bark beetle diversity at different spatial scales. *Ecography* 21:510-517.
- Pitman, N. C. A., J. W. Terborgh, M. R. Silman, P. Núñez V., D. A. Neill, C. E. Cerón, W. A. Palacios, and M. Aulestia. 2001.** Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82(8): 2101-2117.
- Pons, J., T. G. Barraclough, J. Gomez-Zurita, A. Cardoso, D. P. Duran, S. Hazell, S. Kamoun, W. D. Sumlin, and A. F. Vogler. 2006.** Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* 55(4): 595-609.
- Rabaglia, R. J. 2002.** Curculionidae: Scolytinae Latreille 1807. *In*: R. H. Arnett et al. (Eds.) *American Beetles, Volume 2*. CRC Press, Boca Raton.

Rabaglia, R. J., S. A. Dole, and A. I. Cognato. 2006. A review of the Xyleborina (Coleoptera: Curculionidae: Scolytinae) in America North of Mexico, with an Illustrated Key. *Annals of the Entomological Society of America* 99(6): 1034-1056.

Rambaut, A., Drummond, A.J. 2007. Tracer v1.4, Available from <http://beast.bio.ed.ac.uk/Tracer>

Regier, J. C., Q. Q. Fang, C. Mitter, R. S. Peigler, T. P. Friedlander, and M. A. Solis. 1998. Evolution and phylogenetic utility of the *period* gene in Lepidoptera. *Molecular Biology and Evolution* 15(9): 1172-1182.

Regier J. C. and J. W. Schultz. 2001. Elongation factor-2: A useful gene for arthropod phylogenetics. *Molecular Phylogenetics and Evolution* 20(1): 136-148.

Reitter, E. 1913. Bestimmungs-tabelle der Borkenkäfer (Scolytidae) aus Europa und den angrenzenden Ländern. *Wiener Entomologische Zeitung* 32(Beiheft): 1-116.

Rokas, A. and S. B. Carroll. 2005. More genes or more taxa? The relative contribution of gene number and taxon number to phylogenetic accuracy. *Molecular Biology and Evolution* 22: 1337-1344.

Rubino, D. 2006. DNA barcoding evolves into the familiar. *Conservation Biology* 25(5): 1548-1549.

Saha, N., P. K. Maiti, and S. Chakraborti. 1992. On some species of *Xylosandrus* Reitter (Scolytidae: Coleoptera) from the Sub-Himalayan West Bengal with description of a new species. *Record of the Zoological Survey of India* 91(1): 9-27.

Sampson, F. W. 1911. On two new woodboring beetles (Ipidae). *Annals and Magazine of Natural History* 8(8): 381-383.

Sampson, F. W. 1912. Some new species of Ipidae and Platypodidae in the British Museum. *Annals and Magazine of Natural History* 8(10): 245-250.

Sampson, F. W. 1914. Coleoptera: Platypodidae and Ipsidae from the Seychelles Islands. *Linnean Society of London, Transactions, Ser. 2 Zoology* 16: 379-391.

Sampson, F. W. 1921. Further notes on Platypodidae and Scolytidae collected by Mr. G. E. Bryant and others. *Annals and Magazine of Natural History* 7(9): 25-37.

Sankoff, D., Cedergren, R.J. 1983. Simultaneous comparison of three or more sequences related by a tree. In: Sankoff, D., Kruskal, J.B., (Eds.), *Time Warps, String Edits, and Macromolecules: The Theory and Practice of Sequence Comparison*. Addison-Wesley, Reading, Massachusetts, pp. 253-263.

- Schedl, K. E. 1934.** Neue Indomalayische Scolytidae. II. Beitrag. Entomologische Berichten 9: 84-92.
- Schedl, K. E. 1935.** New bark-beetles and ambrosia-beetles (Col.). Stylops 4(2): 270-276.
- Schedl, K. E. 1936.** Some new Scolytidae and Platypodidae from the Malay Peninsula. Journal of the Federated Malay States Museums 18(1): 19-35.
- Schedl, K. E. 1938.** Scolytidae and Platypodidae. Contribution, 49. New species from Australia and the Fijii Islands with some revisional notes. Royal Society of South Australia, Transactions 62: 34-52.
- Schedl, K. E. 1939.** Scolytidae and Platypodidae. 47 Beitrag. Tijdschrift voor Entomologie 82: 30-53.
- Schedl, K. E. 1942a.** Forschungberichte zur Scolytoiden-Fauna der Malayischen Halbinsel, V. 80 Betrag. Kolonialforstliche Mitteilungen 5(2-3): 169-218.
- Schedl, K. E. 1942b.** Neue Scolytidae aus Java. 76 Beitrag. Tijdschrift voor Entomologie 85: 1-49.
- Schedl, K. E. 1951.** Fauna Indomalayaensis, I. Tijdschrift voor Entomologie 93: 41-98.
- Schedl, K. E. 1952.** Formosan Scolytoidea, I. III Contribution. Philippine Journal of Science 81(1): 61-65.
- Schedl, K. E. 1953.** New Scolytoidea. Queensland Museum Memoirs 13: 80-83.
- Schedl, K. E. 1954.** Fauna Indomalayensis, IV. 141 Beitrag. Philippine Journal of Science 83(2): 137-159.
- Schedl, K. E. 1955.** Borken- und Ambrosiakafer aus den Pazifischen Raum. 150 Beitrag. Entomologischen Arbeit aus dem Museum G. Frey 6: 277-310.
- Schedl, K. E. 1957.** Scolytoidea nouveaux du Congo Belge, II. Mission R. Mayne -- K. E. Schedl 1952. Annales du Musee Royale du Congo Belge Tervuren (Belgique), Ser. 8. Sciences Zoologiques 56: 1-1162.
- Schedl, K. E. 1958.** Zur Synonymie der Borkenkafer, II. 159 Beitrag. Tijdschrift voor Entomologie 101(3-4): 141-155.
- Schedl, K. E. 1959.** A check list of the Scolytidae and Platypodidae (Coleoptera) of Ceylon with descriptions of new species and biological notes. Royal Entomological Society of London, Transactions 111(15): 469-534.

Schedl, K. E. 1961a. Fauna of the Philippines, IX. 193 Contribution. Philippine Journal of Science 90(1): 147-168.

Schedl, K. E. 1961b. Fauna Madagascariensis, IV. 188 Contribution. Institut Scientifique de Madagascar, Memoires, Ser. E 12: 127-170.

Schedl, Karl Eduard, 1962. Scolytidae und Platypodidae Afrikas. Band 3. Familie Platypodidae. Revista de Entomologia de Mocambique 5(1): 1-594.

Schedl, K. E. 1963. Neotropische Scolytoidea, VII. 211 Beitrag. Reichenbachia 1(27): 209-234.

Schedl, K. E. 1964. Zur Synonymie der Borkenkäfer, XIV. 223 Beitrag. Reichenbachia, Dresden 2: 209-223.

Schedl, K. E. 1967. Zur Synonymie der Borkenkäfer, XVI. 242 Beitrag. Entomologisk Tidskrift 88(3/4): 146-163.

Schedl, K. E. 1971. Indomalayan bark and timber beetles. 276 Contribution. Oriental Insects 5(3): 361-399.

Schedl, K. E. 1972. Neotropische Scolytoidea, XI. 293 Beitrag. Koleopterologische Rundschau 50: 37-86.

Schedl, K. E. 1979a. Die Typen der Sammlung Schedl Familie Scolytidae (Coleoptera). 3(2): 286 pp.

Schedl, K. E. 1979b. New Scolytidae and Platypodidae from Papua New Guinea (V) (Coleoptera). 311 Contribution. Faunistische Abhandlungen 7: 95-120.

Scheffer, S. J. and M. L. Lewis. 2001. Two nuclear genes confirm mitochondrial evidence of cryptic species within *Liriomyza huidobrensis* (Diptera: Agromyzidae). Annals of the Entomological Society of America 94: 648-653.

Schultz J. W. and J. C. Regier. 2000a. Phylogenetic analysis of arthropods using two nuclear protein-encoding genes supports a crustacean + hexapod clade. Proceedings of the Royal Society of London, B 267:1011-1019.

Schultz, J. W. and J. C. Regier. 2000b. Phylogenetic analysis of Myriapoda (Arthropoda) using two nuclear protein-encoding genes. Zoological Journal of the Linnean Society 132: 469-486.

Simon, C, F. Frati, A. Beckenback, B. Crespi, H. Liu, and P. Flook. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the Entomological Society of America 87: 651-701.

Simon, U., M. Grossner, and K. E. Linsenmair. 2003. Distribution of ants and bark-beetles in crowns of tropical oaks, pp. 59-68. *In* Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching (eds.), *Arthropods of tropical forests*. Cambridge University Press, Cambridge, United Kingdom.

Song, H., J. E. Buhay, M. F. Whiting, and K. A. Crandall. 2008. Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. *Proceedings of the National Academy of Sciences of the United States of America* 105(36): 13486-13491.

Sorensen, M.D. 1996. Treerot. University of Michigan, Ann Arbor, MI.

Southwood, T. R. E. 1961. The Number of Species of Insects Associated with Various Trees. *The Journal of Animal Ecology* 30(1): 1-8.

Stebbing, E. P. 1908. On some undescribed Scolytidae of economic importance from the Indian Region. I. *Indian Forest Memoirs, Forest Zoology Series* 5, 1(1): 1-12.

Strohmeyer, H. 1910. Uber Kaffeeschadlinge auf der Insel Java. *Entomologische Blatter* 6: 186-187.

Swofford, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Thunes, K. H. 1998. Bark and ambrosia beetles (Coleoptera: Curculionidae, Scolytinae and Platypodinae) in a neotropical rain forest. Comparing occurrence and distribution between different forest habitats within a continuous reserve in Costa Rica. Doctoral Dissertation. Institute of Zoology. Bergen, University of Bergen.

Varón, A., L. S. Vinh, I. Bomash, W. C. Wheeler. 2008. POY 4.0.2881. New York, American Museum of Natural History.

Vogler, A. P. and M. T. Monaghan. 2006. Recent advances in DNA taxonomy. *Journal of Zoological Systematics and Evolutionary Research* 45(1): 1-10.

Wheeler, W.C. 1996. Optimization alignment: The end of multiple sequence alignment in phylogenetics? *Cladistics* 12: 1-9.

Wiegmann, B. M., C. Miller, J. C. Regier, T. P. Friedlander, D. M. Wagner, and E. S. Nielsen. 2000. Nuclear genes resolve Mesozoic-aged divergences in the insect order Lepidoptera. *Molecular Phylogenetics and Evolution* 15(2): 242-259.

Wild, A. L. and D. R. Maddison. 2008. Evaluating nuclear protein-coding genes for phylogenetic utility in beetles. *Molecular Phylogenetics and Evolution* 48: 877-891.

- Wood, S. L. 1962.** Miscellaneous taxonomic notes on Scolytidae (Coleoptera). Great Basin Naturalist 21: 87-107.
- Wood, S. L. 1969.** New synonymy and records of Platypodidae and Scolytidae (Coleoptera). Great Basin Naturalist 29: 113-128.
- Wood, S. L. 1973.** New synonymy in American bark beetles (Scolytidae: Coleoptera). Part III. Great Basin Naturalist 33(3): 169-188.
- Wood, S. L. 1974.** New synonymy and records of American bark beetles (Coleoptera: Scolytidae). Great Basin Naturalist 34: 277-290.
- Wood, S. L. 1977.** New synonymy and new species of American bark beetles (Coleoptera: Scolytidae). Part IV. Great Basin Naturalist 37(2): 207-220.
- Wood, S. L. 1980.** New genera and new generic synonymy in Scolytidae (Coleoptera). Great Basin Naturalist 40: 89-97.
- Wood, S. L. 1982.** The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist, Memoirs 6. 1359 pp.
- Wood, S. L. 1984.** New generic synonymy and new genera of Scolytidae (Coleoptera). Great Basin Naturalist 44(2): 223-230.
- Wood, S. L. 1986.** A reclassification of the genera of Scolytidae (Coleoptera). Great Basin Naturalist Memoirs 10: 126.
- Wood, S. L. 1989.** Nomenclatural changes and new species of Scolytidae (Coleoptera), part IV. Great Basin Naturalist 49: 167-185.
- Wood, S. L. 2007.** Bark and Ambrosia Beetles (Coleoptera: Scolytidae) of South America: a taxonomic monograph. Monte Bean Life Sciences Museum, Brigham Young University, Provo, United States. 900pp. + 230 plates.
- Wood, S. L. and D. E. Bright. 1992.** A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic Index. Great Basin Naturalist Memoirs, No. 13(A). Brigham Young University, Provo. 1553 pp.
- Wurth, T. 1908.** De boeboek (Xyleborus coffeae n. sp.) op Coffea robusta. Salatiga Cultuurgids (2e gedeelte) 10: 63-78.
- Yoder, M.J., K. Dole, K. Seltsmann, and A. Deans. 2006-Present.** MX, a collaborative web based content management for biological systematists.