Integrated taxonomic revision of Afrotropical *Xyleborinus* reveals an extraordinary recent radiation on Madagascar

Jonas Meland Eliassen

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Front page: *Xyleborinus quadrispinosus* (Eichhoff, 1878)

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Abstract

Collection efforts on Madagascar have previously revealed a high species diversity in the Scolytinae genus *Xyleborinus* Reitter, 1913 compared with the African mainland. This study has produced a well supported phylogeny based on gene fragments of COI, 28S and CAD revealing that the genus colonized Madagascar once as recently as 8.5-11.0 Ma, indicating an extraordinary recent radiation on the island that has given rise to at least 32 species. Two recolonization events back to the African mainland are also proven, with several more being indicated. A taxonomic re-evaluation of Afrotropical *Xyleborinus* has been conducted, resulting in a revision of the genus in the Afrotropic. Eleven species from Madagascar are described as new to science, six species names are synonymized, two species names are given new status and two species are removed from the genus. An updated species register of *Xyleborinus* in the Afrotropic based on morphology and molecular data, when available, is included. Register includes diagnostic characters and photographs of all 46 described species. The first identification key for the group is also included.

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Introduction

Understanding the diversity of life has been one of the longest running projects in biology. Taxonomy, the science of classifying groups of biological organisms on the basis of shared characteristics, has a long tradition and has retained its core principles since the 18th century (Ferraris and Eschmeyer, 2000). Carl Linnaeus' zoological nomenclature system is still used today and his 10th edition of *Systema Naturae* is considered the starting point of modern taxonomy (Ferraris and Eschmeyer, 2000). Linnaeus' main methods of defining species, by morphology and sexual interbreeding[1], are still widely used today (Ferraris and Eschmeyer, 2000).

Taxonomy was revolutionized by the field of phylogenetics, the study of the evolutionary history and relationships among organisms, and its use of genetic data to help define groups of organisms. Molecular data from different genes enable comparison between individuals on population and species level. If the genetical material matches enough to reach a pre-defined limit (e.g. 98% similarity) then one can assume the individuals to be part of the same species and the gene can be used as a barcode for the 'species' (Hebert *et al.*, 2004). When this relatedness has been assessed, it can also be easier to discover morphological differences if we know that the individuals belong to different species. Genetic information gives a whole new level of assessment for classifying organisms, and it is particularly useful in understanding their evolutionary history.

The use of various methods in assessing what constitutes a species is critical to minimize the shortcomings of both morphology and molecular data. For example, there are several cases of organisms that are morphologically very similar, but in fact show enough differences in behavior and genetics to be considered different species. Cryptic species complexes may arise in these cases (Hebert *et al.*, 2004). On the other hand, it is not uncommon that a species displays large morphological variation. Sexual dimorphism for example can be rather conspicuous. The males of many species of anglerfish only exist as small parasites of the

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[1] Species as a group of individuals that actually or potentially interbreed in nature.

much larger female (Pietsch, 1976). In such cases, phentic similarity alone cannot define a species.

With the advent of genetical methods for assessing species we are now better equipped to resolve the issues raised above. However, relying entirely on molecular data can be troubling. Pure analytical approaches, like using algorithms and statistics, may often fail to reflect known trends and variations that occur in nature. Knowledge on distribution of individuals and their morphology can quickly make relationships obvious when molecular data is not clear. Today, the importance of traditional taxonomic methods is recognized amongst modern researchers, and most taxonomists rely on both morphology and genetic data to assess relationships among organisms (Cognato *et al.*, 2020) [2].

At the start of the decade the number of described species was at around 1,9 million (Mora *et al.*, 2011). A relatively conservative estimate of total eukaryotic species on earth at about 8.7 million (±1.3 million SE) indicates that we have a long way to go before the biodiversity of earth has been fully understood (Mora *et al.*, 2011). Not only is the sheer number of species important to researchers, but also the evolutionary relationship between them. In other words, phylogeneticists seek to not only discover what exists, but also how it came to be.

As an addition to the continuing work of understanding and cataloging the diversity of life this study will look at the bark beetle genus *Xyleborinus* Reitter, 1913 in the Afrotropic*,* with a main focus on Madagascar. They are part of the order Coleoptera which contains about 20% of all described species (ca. 350 000), by far the largest order (Evans & Bellamy, 1997).

Xyleborinus

Xyleborinus is a genus within the tribe Xyleborini placed in the subfamily Scolytinae, often referred to as bark and ambrosia beetles (Smith and Hulcr, 2015). Bark and ambrosia beetles are placed within the family Curculionidae, commonly known as the "true weevils" (Kirkendall *et al.*, 2015). Scolytinae differ in morphology from most other subfamilies within Curculionidae as they lack the distinctive weevil long snout (Kirkendall *et al.*, 2015). Because

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[2] It is important to note that species categorization is mainly meant as a helping tool for humans to understand and communicate the biodiversity of Earth. Classification does not necessarily reflect the concept that all life is interconnected, as the act of placing individuals in fixed groups is at odds with the evolutionary theory that all life is changeable and often without sharp boundaries (Hey, 2001).

of this bark beetles were traditionally considered as a separate family, the Scolytidae (Hulcr *et al.*, 2015).

Xyleborinus as a monophyletic group has strong support (Cognato *et al.*, 2011, 2020) [3]. The genus can easily be distinguished from other Scolytinae by having a conical scutellum surrounded by setae rather than a triangular plate that flush with the elytra (Hulcr *et al.*, 2007). The tribe Xyleborini is, like several other lineages in Scolytinae, haplo-diploid and strictly inbreeding (Kirkendall *et al.*, 2015). Individuals usually always mate with siblings. The sex ratio is heavily female biased with one small male mating with many larger sisters (Kirkendall *et al.*, 2015; Smith and Hulcr, 2015). This makes collecting females significantly more common than collecting males. They live in small colonies with their siblings and like other ambrosia beetles in Scolytinae they gain their nutrients from ambrosia fungi whom they form a symbiotic relationship with (Smith and Hulcr, 2015). About one-third of species in Scolytinae cultivate fungal gardens inside of mostly dead wood and are therefore, together with the subfamily Platypodinae, referred to as ambrosia beetles (Hulcr *et al.*, 2015).

Scolytinae are adapted to a wood-boring lifestyle and as such they are quite limited in how they can evolve morphologically. When they are inside their tunnels only the head and the end of the abdomen, the declivity, are not in contact with the tight corridors. These are the only body parts that can be subject to great changes that does not interfere with their effectiveness in travelling through tunnels (Hulcr *et al*., 2015). In addition, inbreeding results in no sexual selection on morphological traits, one does not need to “sell” oneself to a

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[3] Modern classification of the genus *Xyleborinus*:

Kingdom: Animalia
Phylum: Arthropoda
Class: Insecta
Order: Coleoptera
Family: Curculionidae
Subfamily: Scolytinae
Tribe: Xyleborini
Genus: *Xyleborinus* Reitter, 1913

potential partner if your partner is predecided (Hulcr *et al.*, 2015). These biological traits coupled with a short evolutionary timespan (Jordal and Cognato, 2012) has led to many morphologically similar species. In the case of *Xyleborinus* the only major difference in morphology can be observed on the declivity, the lowest end of the elytra (Schedl, 1977).

Madagascar

Madagascar has long been of great interest for biologists. The island is known as a biodiversity hotspot and 90% of its described species are endemic to Madagascar (Wiig, 2008)[4]. Thorough research has been done on the vertebrate fauna of the island, especially on mammals (Garbutt, 2007) and birds (Warren *et al.*, 2013), where lemurs are probably the most famous and recognizable. However, there are still great uncertainties within several invertebrate groups. This is in large part because most invertebrates found on Madagascar have not been examined phylogenetically on a molecular level.

Madagascar split from the Indian sub-continent some 88 million years ago and has been an isolated island ever since. In effect, immigration after this event has been over the ocean (Ducousso *et al.*, 2004). Comprehensive studies on the vertebrate fauna's colonization history of Madagascar has been made, the most significant findings being how changes in ocean currents have played a major role in Madagascar colonization (Ali and Huber, 2010; Samonds *et al.*, 2012). During the Paleogene period, 66 to 23 mya, the ocean currents went from mainland Africa to Madagascar, ideal for "rafters" and swimmers. 15 to 20 mya the currents shifted and now flow from Madagascar to mainland Africa. The result is a serious drop in non-avian terrestrial and freshwater fauna colonizing Madagascar in the last 20 million years (Ali and Huber, 2010; Samonds *et al.*, 2012).

The importance of these ocean currents is not equally understood for terrestrial invertebrate colonization. Documented cases of both in- and out-of-Madagascar colonization events have been made (Bukontaite *et al.*, 2015). Though terrestrial arthropods may cross the ocean as "rafters", either on logs or floating islands, the importance of this type of transportation is uncertain. Many insects are great flyers and their light weight makes wind dispersal possible (Bukontaite *et al.*, 2015).

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[4] Island endemism is a common well documented phenomenon (Kier *et al.*, 2009).

Aim of study

The tribe Xyleborini, which *Xyleborinus* is part of, has in less than 20 million years experienced a very rapid species radiation (Jordal and Cognato, 2012). The tribe is by far the most species rich tribe of Scolytinae with 1200 described species (Cognato *et al.*, 2011; Gohli *et al.*, 2017), remarkable given the tribe's young age of ca. 20 million years. The fast radiation has caused the tribe, including *Xyleborinus,* to include a number of very morphologically similar species (Schedl, 1977). A reevaluation of the genus could help shed new light on the species and their relationship. It can also give a better understanding of the true genetic variation that is hiding within the genus.

Conducting molecular and new taxonomic research on the genus may also help in revealing new species or possible synonyms. Much of the genus, and indeed, the entire Xyleborini tribe has been described by Austrian taxonomist K.E Schedl, who erected many species and sub-species names, many of which have later been revealed as synonyms. Though detailed molecular analyzes have been conducted within the tribe Xyleborini as a whole (Cognato *et al.*, 2011), the phylogenetic relationships within the *Xyleborinus* genus and its species have yet to be understood.

The tribe Xyleborini first started to radiate 20 million years ago, over 60 million years after Madagascar broke away from the Indian sub-continent (Storey *et al.*, 1995). It would therefore seem most likely that the genus immigrated from the African mainland, perhaps multiple times. *Xyleborinus* have, after colonization, evolved into many unique morphs and species on Madagascar. This may indicate that the genus colonized the island early in its evolutionary history. Comparing species from the African mainland to the species found on Madagascar can help to discover the colonization history of the genus. This study will hopefully shed light on the biogeography of the genus and help us understand how species have radiated through geographic space and geological time.

This study uses three genes in phylogenetic analyzes of *Xyleborinus,* cytochrome oxidase I (COI), 28S rDNA and the nuclear protein coding gene carbamoylphosphate synthetase 2 (CAD).

The study aims to give a better understanding of the genetic composition, distribution and history of *Xyleborinus* on Madagascar, and thereby facilitate assessment of species boundaries and species richness in the genus. By comparing species inhabiting Madagascar to species on the African mainland we will increase our understanding of the colonization history of the genus, such as the number of colonizations of the island, or vice versa. Also, genetic data will provide sufficient data to discover species new to science. In addition, species descriptions and types from the entire Afrotropic will be revised and the first identification key to Afrotropical species is provided. The taxonomic revision aims to reveal potential synonyms and create a detailed and thorough overview of all species described so far in *Xyleborinus* in the Afrotropic.

Material and Methods

Phylogeny

The material used for phylogenetic analyzes was collected during three field trips to Madagascar in 2012, 2015 and 2019, the author of the thesis participated in the last trip. The 2019 trip included visits to Marojejy National Park, Ankarana National Park and Montagne d'Ambre National Park. Additional material provided by University of Florida, Gainesville, was also used (see **Appendix A** for full list of material).

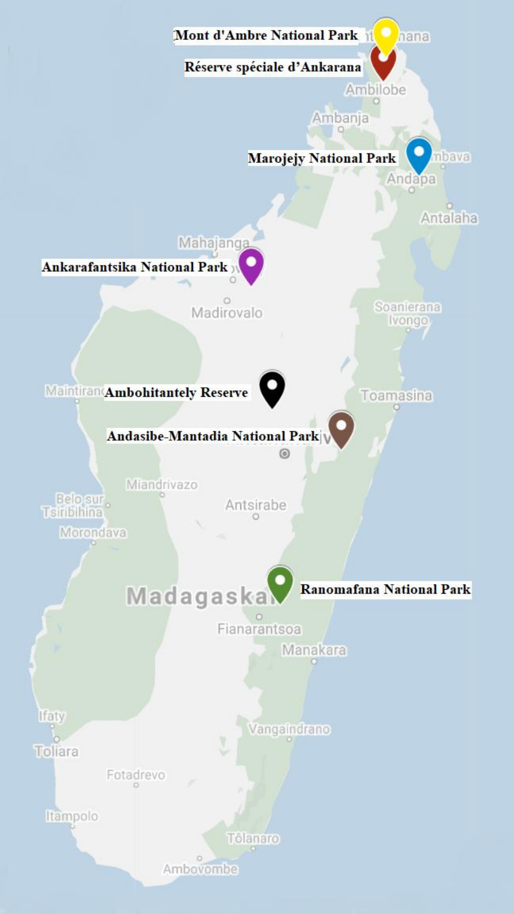

Figure 1.1. Collection sites on Madagascar. The author of the thesis participated in field work in Marojejy National Park, Réserve spéciale d'Ankarana and Mont d'Ambre National Park. Map made with https://www.google.com/maps/about/mymaps/.

DNA extraction was conducted on 67 individuals using the QIAGEN DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), following the manufacturers “full tissue” protocol. To increase DNA yield, an additional 100 µl Buffer AE was added and centrifuged as a final elution, after the instructed 200 µl.

DNA amplification of fragments from COI, 28S and CAD genes (primers in **Table 2**) was achieved with Qiagen Hot Star taq (**Table 1**). A polymerase chain reaction (PCR) was performed on a BioRad xxx thermocycler with settings listed in **Table 3**.

COI and 28S are common and well tested markers for phylogenetic analyzes in zoology and they complement each other well as they have different analytical strengths (Whiting *et al.*, 1997). CAD is not as common a marker, but is known to work quite well with Xyleborini species (Cognato *et al.*, 2020). Its lengthy introns may also give it an extra layer of information that would not be present if it just consisted of more conservative exons.

COI is a protein coding mitochondrial gene, often used to differentiate closely related species due to its fast mutation rate (Cognato *et al.*, 2020). COI is especially useful in delimiting species and has therefore become the most important marker for DNA barcoding (Hebert *et al.*, 2004). It is however less effective when trying to assess deeper phylogenetic relationships. When base differences between species exceed 10%-12% substitutions, patterns start to become muddled and relationships become difficult to assess (Cognato *et al.*, 2020).

28S DNA codes for structural ribosomal RNA that forms the large subunit in cytoplasmic ribosomes. The RNA has intramolecular base pairings, two regions of the same strand base-pairing to form a double helix that ends in an unpaired loop, called a stem-loop (Lodish *et al.*, 2013). This makes the mutation rate of some parts of 28S very slow, as base substitutions must occur simultaneously on two different bases for the RNA to not lose its structure[5]. This causes 28S to work best for assessing deeper phylogenetic relationships like species groups and older clades, but makes it a poor tool for delimiting species as 28S can be identical between two specimens exhibiting distinct morphologies.

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[5] This does not apply to bases forming the unpaired loop. Indeed, most of the genetic variation on 28S can be found in these bases.

The polyadenylate binding protein PABP1, or PyA, was initially chosen as the third genetic marker instead of CAD as it has previously been successfully used as a genetic marker for Scolytinae (Pistone *et al.,* 2016). However, it gave very poor results and was abandoned after several PCR amplification attempts on the first 28 specimens, which only resulted in ≈30% good quality sequences. After testing the more commonly used genes CAD and EF1α it was decided that CAD yielded the best quality sequences and became the new third marker. PABP1 was not considered further in this study.

Table 1. Ingredients of each sample run through a polymerase chain reaction

DNA extract	1,0 µl for COI and 28S	2,0 µl for CAD
Double distilled H_2O	16,35 µl for COI and 28S	15,35 µl for CAD
10X buffer containing dye	2,5 µl	
$MgCl_{12}$	1,0 µl	
dNTPs	2,0 µl	
Forward primer (10 µM)	1,0 µl	
Reverse primer (10 µM)	1,0 µl	
Qiagen Hot Star taq	0,15 µl	
Total	**25,0 µl**	

Table 2. Primers used in pre-PCR cocktail

Gene	Forward 5’-3’	Reverse 5’-3’
Cytochrome oxidase I (COI)	(S1718) GGAGGATTTGGAAATTGATTAGTTCC	(A2411) GCTAATCATCTAAAAACTTTAATTCCWGTWG (A2237) CCGAATGCTTCTTTTTTACCTCTTTCTTG
28S	(S3690) GAGAGTTMAASAGTACGTGAAAC	(A4394) TCGGAAGGAACCAGCTACTA
Carbamoylphosphate synthetase 2 (CAD)	(CAD forB2) GARAARGTNGCNCCNAGTATGGC (CAD for4) TGGAARGARGTBGARTACGARGTGGTYCG	(CAD rev1mod) GCCATYRCYTCBCCYACRCTYTTCAT

Table 3. Cycling protocols for PCR. The setup of the PCR machines depended on which gene was to be amplified. At the "Cycles" step the protocol returned to the "Denaturation" step X amount of times.

Gene	Lid preheating	Initial	Denaturation	Annealing	Extension	Cycles	Final extension	Resting temp.
COI	105C° (30 sec)	95C° (15 min)	94C° (30 sec)	46C° (45 sec)	72C° (1 min)	40	72C° (10 min)	6C° forever
28S	105C° (30 sec)	95C° (15 min)	94C° (30 sec)	55C° (45 sec)	72C° (1 min)	40	72C° (10 min)	6C° forever
CAD	105C° (30 sec)	95C° (5 min)	95C° (30 sec)	50C° (45 sec)	72C° (1 min)	40	72C° (10 min)	6C° forever

Amplicon (amplified DNA) concentration and quality assessment was performed through gel electrophoresis (85 volts for 20-30 minutes). The gel mix was made using 1X TAE buffer and 1% agarose, and stained with GelRed®.

Table 4. Gel mix (1X TAE buffer and 1% agarose) and GelRed® ratio used when making gel.

Small container	30 µl gel mix	1 µl gel red
Medium container	50 µl gel mix	3 µl gel red
Large container	100 µl gel mix	6 µl gel red

The agarose gel was run in a TAE buffer using a BioRad PowerPac™ Basic Power Supply. Gel was loaded with samples of 5 µl amplicon in individual wells. It was not necessary to add dye to the samples as the pre-PCR cocktail already contained dye present in the buffer (see **Table 1**). A 5 µl ladder (Thermofisher FastRule Low range DNA ladder) was also added to assess length and quality of amplified genes. The gel was then illuminated by UV-light and analyzed by a computer software.

Samples with strong DNA yield were prepared for sequencing by first undergoing a purification step using two hydrolytic enzymes, recombinant Shrimp Alkaline Phosphatase (SAP) and Exonuclease I (Exo I). The combination of these enzymes removes excess dNTPs and primers remaining from the PCR reaction (Bell, 2008). Each sample contained 0,1 µl EXO, 1,0 µl SAP and 0,9 µl dH_2O. In addition, samples with medium to weak amplicon yield contained 8,0 µl DNA mix (**Table 1**). Samples with high DNA yield contained 4,0 µl DNA mix and an additional 4,0 µl dH_2O. Finally, samples with very high DNA yield contained 1,0 µl DNA mix and an additional 7,0 µl dH_2O. Resulting in a total volume of 10,0 µl pr. purification reaction. The enzyme purification is temperature regulated and was carried out on thermocyclers (**Table 5**).

Table 5. Enzyme purification protocols

Lid preheating	Initial	Final	Resting temp.
105C° (30 sec)	37C° (30 min)	85C° (15 min)	8C° forever

PCR for Sanger sequencing was performed with BigDye on purified amplicons as specified in **Tables 6** and **7**. Sequencing from both the 5´- and 3´-ends where performed in COI and CAD using both forward and reverse sequencing primers. For 28S sequencing was performed from the 5´-end only.

Table 6. Cocktail for sequencing

Double distilled H_2O	6,0 µl
Primer (3,2 µM concentration)	1,0 µl
Sequencing buffer	1,0 µl
BigDye	1,0 µl
Enzyme washed DNA mix	1,0 µl
Total	**10,0 µl**

The BigDye contains a small percent of four dNTP specific fluorescent dyes that each, through polymerase, connect to its compliment nucleotide, terminating that specific fragments sequencing. In effect, after 24 cycles a sequencing reaction contains a multitude of fragments in various lengths, each fragment terminated with a fluorescently marked nucleotide revealing the nucleotide in that position (Rosenblum *et al.*, 1997). Finally, 10 µl of ddH_2O was added to each sample before they were sent to the sequencing facility for sequence reading, conducted on a capillary-based Applied Biosystem 3730XL Analyzer.

Table 7. Thermocycler protocol for DNA sequencing reactions. At the “Cycles” step the protocol returned to the “Denaturation” step X amount of times.

Lid preheating	Initial	Denaturation	Annealing	Extension	Cycles	Final extension	Resting temp.
105C° (30 sec)	96C° (5 min)	96C° (10 sec)	50C° (5 sec)	60C° (4 min)	24	72C° (5 min)	8C° forever

DNA extraction, PCR, enzyme purification and sequence reactions were conducted at the shared Institute for Biosciences and Bergen Museum DNA lab at the University of Bergen (UiB). The sequence reading was conducted at the Institute for Biosciences, UiB sequencing lab, located at “Høyteknologisenteret”.

The sequenced genes were processed and edited in the sequence editing and analysis tool Geneious Prime (Geneious Prime 2019: https://www.geneious.com). Genes from each specimen were aligned and ambiguities were resolved when possible. All genes were concatenated into a single Nexus file (See attachments). The partitions in the nexus file were COI, 28S, CAD exon and CAD intron (**Table 8**). The CAD intron was originally placed within the coding exon of the extracted CAD gene, but it was edited out and placed at the end for easier analyzes. Sequences from three outgroup species used in earlier studies (Cognato *et al.*, 2011, 2020), *Ambrosiodmus asperatus* (Blandford, 1895), *Xylosandrus germanus* (Blandford, 1894) and *Xyleborus xylographus* (Say, 1826), were obtained from Genbank (https://www.ncbi.nlm.nih.gov/genbank/). This was done to make the rooting of the tree more robust and in case *Taurodemus sharpi* (Blandford, 1898) is shown to be a poor outgroup candidate.

Table 8. **Nexus file partitions and models used in MrBayes and BEAST analyzes.** Models selected by MrModeltest2 based on Akaike Information Criterion (AIC) scores.

Gene and codon position	**Partition delineation**	**Model selected by MrModeltest2**	**Model used in Mr Bayes**	**Model used in BEAST**
COI-1st codon	2-692\3	GTR+I+G	GTR+I+G	GTR
COI-2nd codon	3-692\3	F81	F81	HKY
COI- 3rd codon	1-692\3	GTR+G	GTR+G	GTR
28S rRNA	693-1545	GTR+I+G	GTR+I+G	GTR
CAD exon-1st codon	1547-2221\3	GTR+G	GTR+G	GTR
CAD exon-2nd codon	1548-2221\3	F81	F81	HKY
CAD exon-3rd codon	1546-2221\3	HKY+G	HKY+G	HKY
CAD intron	2222-2450	GTR+G	GTR+G	GTR

Genetic distance matrixes for COI, 28S, and CAD were calculated in Geneious and edited in Excel. These were used to compare genetic divergence between specific specimens. Added as attachments.

Phylogenetic trees were reconstructed in a Bayesian framework in MrBayes 3.2.7 (Huelsenbeck and Ronquist, 2001). Models of molecular evolution for each partition were determined using MrModeltest2 (Nylander, 2004) based on Akaike Information Criterion scores. MrModeltest2 is specifically made for MrBayes. jModeltest tests 88 different models, but MrModeltest2 only tests 24. Mr. Bayes only uses 24 models so MrModeltest2 is the most efficient tool for this analyzes. For each of the protein coding genes COI and CAD, three separate models, for 1st, 2nd, and 3rd codon positions were calculated. Complete Nexus-file added to thesis as attachment. Two parallel unlinked model searches were run in MrBayes for 30 million generations with a sample frequency of 10 000, number of chains 4, burn in 100 and temperature 0.3.

Age of nodes was estimated in Beauti and BEAST (Suchard *et al.*, 2018). Age calibration was achieved with the age of the tribe, Xyleborini, which has been estimated to be 21-23 Ma, based on three amber fossils, two from the Cretaceous and one from the Paleogene (Jordal and Cognato, 2012). The root of the tree was dated at 22 (million) with a standard deviation of 2 (million). BEAST only uses four evolutionary models, so the models selected for analyzes were not identical to the ones used in MrBayes (**Table 8**). Tree search ran for 15 million generations with a sample frequency of 10 000. Partitions were unlinked, uncorrelated relaxed clock model was used and tree prior was set to Yule process (Gernhard T, 2008).

The biogeographic history of *Xyleborinus* was analyzed using RASP (Yu *et al.*, 2015; 2019). Time trees and a consensus time tree were retrieved from BEAST. The species included in the phylogeny were distributed among seven ranges: A=Madagascar, B=Afrotropic, C=Palearctic, D=Indomalaya, E=Australasia, F=Neotropics, G=Nearctic. Madagascar was separated from the rest of the Afrotropic to clearly illustrate the colonization history of Madagascar. Range dispersals caused by anthropogenic activity have been ignored as they only disturb the aim of the study. For example, *Xyleborinus attenuatus* (Blandford, 1894) and *Xyleborinus andrewesii* (Blandford, 1896) have recently been introduced to the USA, but are native to Eurasia and Australasia, respectively (Hoebeke and Rabaglia, 2007; Bateman *et al.*, 2015). These recent dispersals are irrelevant to understanding the evolutionary history of the genus.

The BioGeoBEARS package was used to determine the best fit model for RASP analyzes. The model tester has the option to test +j models, models that include an extra parameter that takes into consideration the possibility that daughter species have “jumped” to an area outside the ancestral range (as opposed to daughter ranges just being subsets to the ancestral range). These models have been criticized for undermining the importance of time-dependent processes, with papers discouraging their use (Ree and Sanmartín, 2018). However, this stance is not shared by all (Matzke, 2013). +j models remain controversial and were therefore not used in this study. S-DIVA was chosen as the best model with zero range constraints.

Taxonomy

Type material was studied in the Natural History Collections in Vienna in February 2020 to aid in the taxonomic revision of *Xyleborinus* in the Afrotropic. NHMW houses the largest collection and a near complete type repository of *Xyleborinus*. Holotypes were preferred, but lectotypes, paratypes, and sometimes non-type material was studied if the holotype was not available. At least one specimen, preferably type material, of almost every described species was taken to Bergen to be photographed and further studied, with the exception being if the holotype or a paratype was identical to specimens already in the Bergen collection. In this case the holotype or paratype was noted and left in Vienna.

All species new to science collected during the three trips to Madagascar have been formally described. A holotype was designated, remaining specimens in presentable condition were designated as paratypes.

All species were photographed from the dorsal, lateral and declivital side using a Leica M205 C camera with software LAS V4.13 and multiple photos were stacked and aligned in the software Zerene Stacker (by Zerene Systems). The frons was initially photographed, but minute differences in morphology made these photographs obsolete.

Synonymizing species names, erection of sub-species to species level, and removal of species from the genus was conducted when supported by morphological analyzes and genetic data when available. Species were then placed into groups based on morphology and genetics. Finally, diagnostic traits were established for every species and a binary identification key was constructed.

All morphological work has been conducted on female specimens. They are more common and are better to work with because of their larger size and more distinguishing characteristics (Jordal *et al.*, 2002).

Museum codes:

- ZMBN - Entomological Collections in Bergen
- NHMW - Museum of Natural History of Vienna
- MNHN - Muséum National d'Histoire Naturelle in Paris
- BMNH - British Museum of Natural History in London
- USNM - Smithsonian National Museum of Natural History in Washington D.C.
- MRCB - Musée Royal du Congo Belge in Tervuren
- IRNSB - Royal Belgian Institute of Natural Sciences in Brussel
- TMP - Ditsong National Museum of Natural History in Pretoria
- NICP - National Collection of Insects of the Republic of South Africa in Pretoria

Terms used to describe morphology are explained with illustrated examples below:

Figure 1.2. Examples of very steep (**A, B, C, D**), vertical (**E, F, G**) or near-vertical declivities (**H, I**). Declivital surface is usually flattened. Notice the often sharp contrast between declivity and elytral disc.

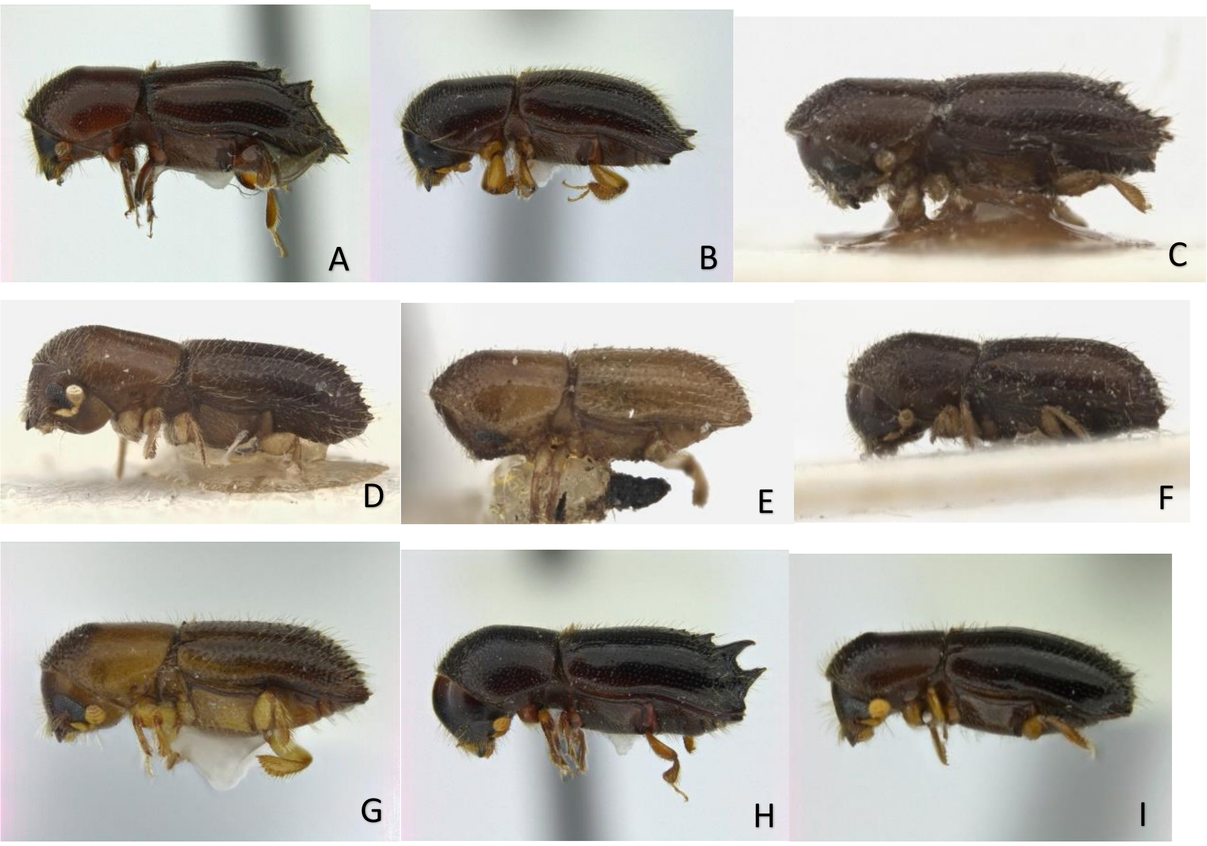

Figure 1.3. Examples of declivities that are sloped (**A, B, C, D**), evenly curved (**E, F, G, H**) or sharply curved halfway down the declivity (**I**). Declivity may be excavated.

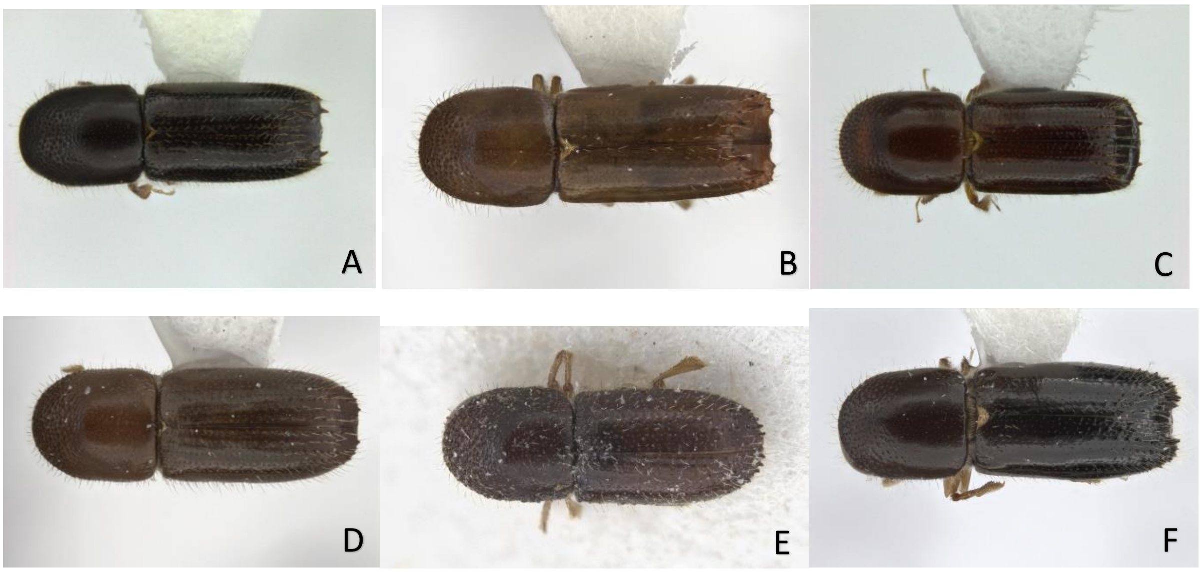

Figure 1.4. What is considered a very steep or vertical declivity may be ambiguous in a few species, but the distinction may be noticed in dorsal view. Very steep and vertical declivities appear truncated posteriorly (**A, B, C**) while other declivities appear more rounded (**D, E**) or sometimes excavated (**F**).

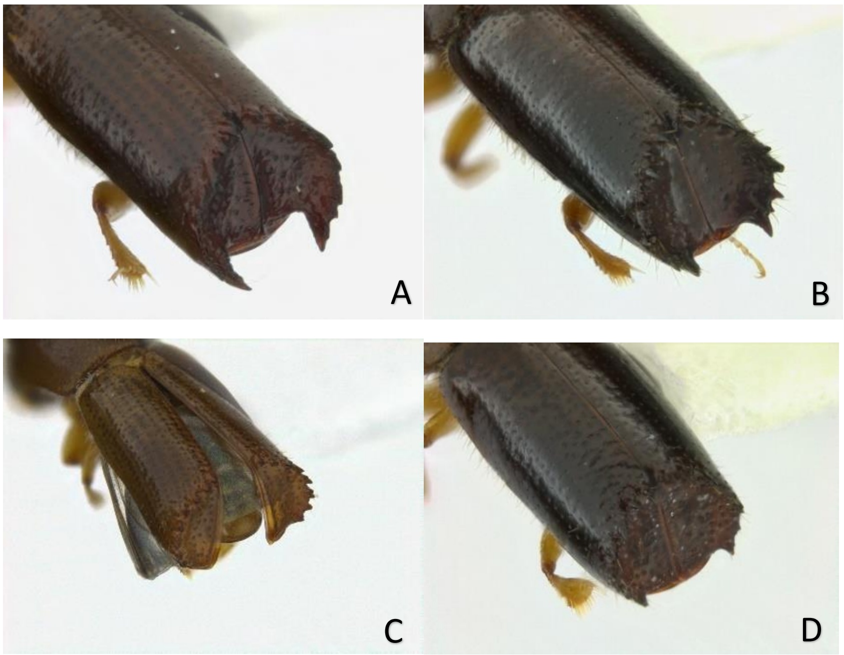

Figure 1.5. Examples of declivities encircled by a flange (**A**) or wreath (**B, C, D**). Wreaths are characterized as a rim with spines attached.

Figure 1.6. Examples of crown shaped declivities.

Figure 1.7. Variation gradient with examples of different spine sizes. Very small and miniscule spines may be named sharp tubercles and sharp granules respectively (Vega and Hofstetter, 2015. Pg. 66, Figure 2.8) (**A**). Small spines about the length of funicles and pedicel combined to length of fourth ventrite (**B**). Medium sized spines about the length of third ventrite (**C, D**). Large spines about the length of second ventrite to length of second and third ventrite combined (**E**). Very large spines about the length of first and second ventrite combined (**F**).

Results

Genetics and phylogeny

High quality sequences from all amplified genes were obtained from all specimens except COI in specimen J42. CAD sequences obtained from J39, J40, J41 and J42 were shorter than other CAD sequences due to a different primer being used, and therefore, did not include the CAD intron placed close to the 5’ end. All J64 sequences were contaminated with genetic material from a parasitic wasp (Apocrita) and were therefore removed from the analyzes.

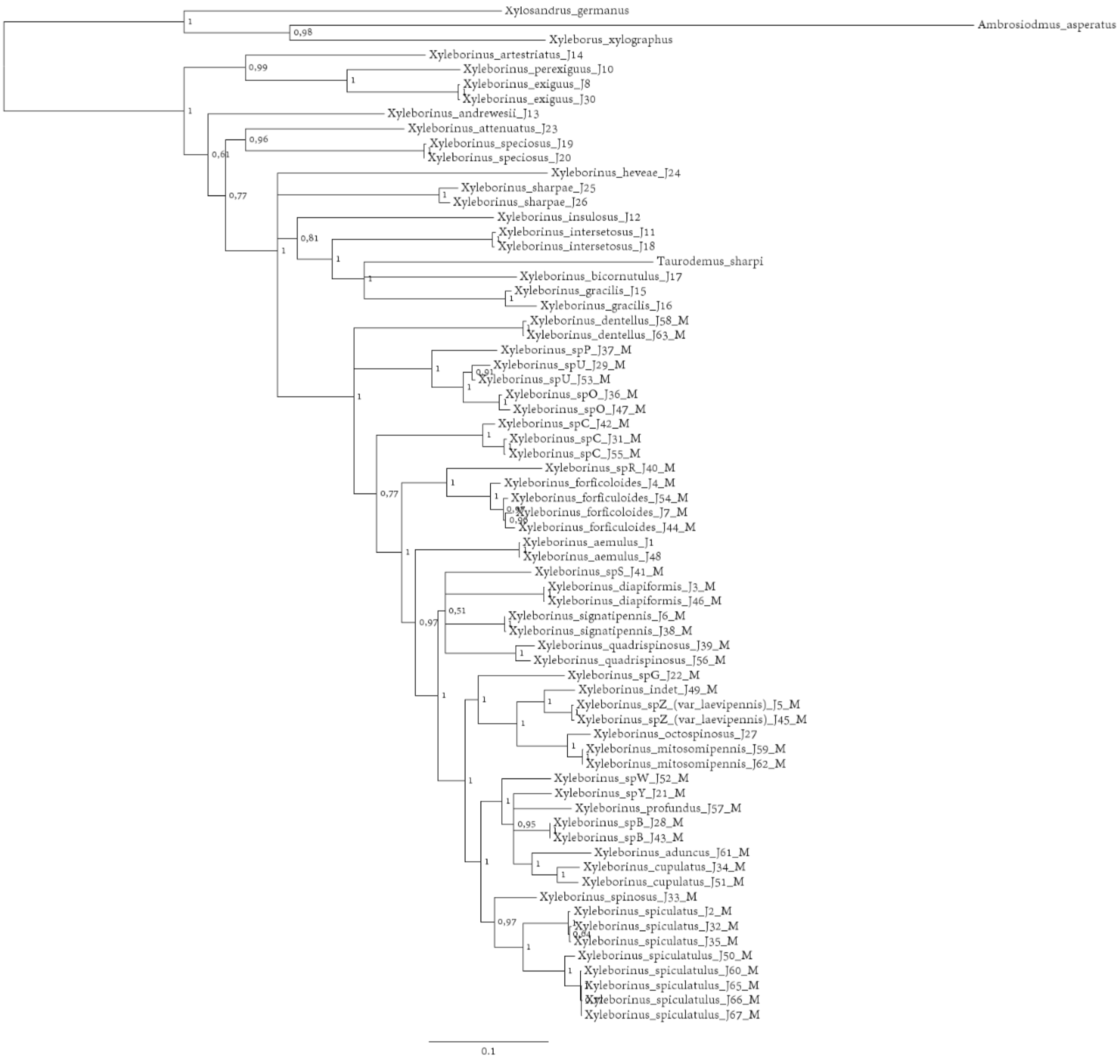

Figure 2.1. Molecular phylogeny results obtained from MrBayes. Node values represent posterior probabilities. Topology based on Bayesian analysis of 2,450 nucleotides from three unlinked gene fragments, using eight unlinked data partitions (COI positions 1, 2, and 3, CAD protein encoding gene positions 1, 2, and 3, 28S and CAD intron). Individuals collected from Madagascar are marked with an M. Species in tree identified by comparing morphology to type material, illustrations or original descriptions. Specimens not matching any described Afrotropical species morphologically or genetically are considered new and are indicated with capital letters (e.g. spB).

The standard deviation for split frequencies in the MrBayes run was 0.0 at the end of the run. The PSRF was close to 1 on all parameters (e.g. 9.998950e-001 or 1.001098e+000). Indicating very good support for the resulting phylogeny. Full list of result statistics are added as supplementary material.

Nodes were generally well supported with most having support over 95% and only five having support under 90%. Weak support in two of the most basal nodes. The placement of

Xyleborinus insulosus Bright & Torres, 2006 was somewhat uncertain. The clade that includes *Xyleborinus quadrispinosus* (Eichhoff, 1878) had weak support. Within the well supported Madagascar clade the relationship between the three most basal lineages was not clear.

Outgroup *Taurodemus sharpi* (Blandford, 1898) was placed within a clade of South American *Xyleborinus* making the genus paraphyletic. Its placement is deliberated further in the discussion.

Table 9. Genetic variation within species that show the highest variation. Interspecific variation between *X.*[6] spU *&* *X.* spO and *X.* spB & *X.* spY are added to demonstrate the lowest genetic differences observed between two species. Max patristic distances observed based on analyzes of COI, 28S and CAD combined. A patristic distance is the sum of the lengths of the branches that link two nodes in a tree. COI and CAD variation are shown as the percent of bases that are different between individuals. 28S has very small genetic differences and is therefore shown as number of bases that are different between individuals.

Species	**Max patristic distances observed**	**Max COI variation**	**Max 28S base differences**	**Max CAD variation**
X. spC	0.03	Missing data	2	0.6 %
X. *forficuloides*	0.03	4.3 %	1	0.7 %
X. quadrispinosus	0.03	5.6 %	0	0.8 %
X. mitosomipennis & X. octospinosus	0.03	5.7 %	0	1.0 %
X. gracilis	0.03	5.8 %	0	0.4 %
X. cupulatus	0.04	5.9 %	0	1.4 %
X. spU & X. spO	0.06	7.4 %	0	1.0 %
X. spB & X. spY	0.06	8.2 %	1	1.6 %

Table 10. Morphologically very similar species that show high genetical variation between individuals. *X. mitosomipennis* (Schedl, 1953) & X. spZ (classified as *X. mitosomipennis* var. *laevipennis*) were previously recognized as the same species (Schedl, 1961). *X. aduncus* & *X. profundus* were previously described as sub-species of *X. aduncus* (Schedl, 1961). Max patristic distance observed within species names is based on analyzes of COI, 28S and CAD.

Species	**Max patristic distances observed**	**Max COI variation**	**Max 28S base differences**	**Max CAD variation**
X. spiculatus & X. spiculatulus	0.09	11.6 %	3	2.9 %
X. mitosomipennis & X. spZ	0.10	10.8 %	5	1.8 %
X. aduncus & X. profundus	0.11	11.7 %	0	1.6 %

All genetically analyzed specimens showed great morphological and phylogenetic similarities when COI differences were less than 6%. Conversely, morphological differences were almost always obvious within Madagascar *Xyleborinus* when COI differences were larger than 8%. COI was therefore deemed the best genetic marker for delimiting species.

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[6] The abbreviation *"X."* always stands for *Xyleborinus* in this study

Intraspecific variation was observed in morphology and revealed in genes within *Xyleborinus* spC, X. *forficuloides* (Schedl, 1951)*, X. quadrispinosus, X. gracilis* (Eichhoff, 1868) and *X. cupulatus* (Schedl, 1961) (**Table 9**). Schedl noticed this variation in *X. forficuloides* and described three subspecies based on morphology (see **Figure 4.26**). However, the variation between individuals in the mentioned species was less than 6% in COI and morphological differences were evident, but slight. This did not make a strong case for splitting the species[7].

The molecular data placed the morphologically near identical *X. spiculatus* (Schaufuss, 1891) and *X. spiculatulus* (Schedl, 1965) specimens in two distinct groups separated by significant molecular differences, enough to categorize the two groups as individual species (**Table 10**). Refraining from doing so would have made the results inconsistent, as the same level of genetic divergence was observed between species, such as *X. aduncus* and *X. cupulatus*, that were clearly morphologically different.

Xyleborinus mitosomipennis (Schedl, 1953) (J5, J45, J59 and J62) did not form a monophyletic clade and had significant genetic variation (**Table 10**). Genetically analyzed specimens morphologically matching the lectotype of *X. mitosomipennis* showed considerable genetic divergence from genetically analyzed specimens matching the "lectotype" of an infrasubspecific taxon named *X. mitosomipennis* var. *leavipennis* (Schedl, 1961) (see **Figure 2.1**) [8]. This evidence supports that morphological differences previously noted by Schedl were not mere variation within a species, but constitute two different species. A new species, *X.* spZ, with the same morph as var. *leavipennis* was therefore described as new to science as infrasubspecific taxa have no status according to the ICZN (Article 1.3.4.).

The two *X.* spZ specimens (J5, J45) were genetically very close to a singleton collected from Marojejy that was missing the declivity (J49). The COI difference was only 6.5% making it ambiguous if this was a variation of *X.* spZ or a different species. Regardless, with the declivity missing it was impossible to formally describe the Marojejy specimen.

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[7] Perhaps obvious, infraspecific genetic variation was more common if a species was distributed across multiple regions on Madagascar.

[8] This fits neatly with the biogeography of the species. Specimens matching the lectotype of *X. mitosomipennis* are, like the lectotype, from Mont d'Ambre. Specimens matching the var. *leavipennis* are from Ranomafana and Andasibe, both in east-central Madagascar.

Two specimens of *X. mitosomipennis* (J59, J62) formed a sister group to *X. octospinosus* (Eggers, 1920) from Tanzania, with a high genetic similarity. The COI variation was only 5.7%, comparable to variation observed within species such as *X. quadrispinosus* and *X. gracilis* (**Table 9**). There were no differences in 28S. They had morphological differences, though they were slight (see **Figure 4.17**). The evidence called for synonymizing of the species names *X. mitosomipennis* and *X. octospinosus.*

Xyleborinus aduncus (Schedl, 1961) (J61, J57 and J21) was not monophyletic. It formed a clade with the species *X. cupulatus, X.* spW and *X.* spB. The exact phylogeny of the species in the clade was not clear from the molecular analyzes (**Figure 2.1**). *X. aduncus* has previously been described as three sub-species, *X. aduncus aduncus* (Shedl, 1961)*, X. aduncus profundus* (Shedl, 1961) and *X. aduncus adunculus* (Shedl, 1961). The specimen (J61) that formed a sister group with *X. cupulatus* matched two paratypes of *X. aduncus aduncus.* Another genetically analyzed *aduncus* specimen (J57) closely resembled the lectotype of *X. aduncus profundus* (see **Figure 4.3**). J21 morphologically resembled, but was not identical to any sub-species of *X. aduncus* (see **Figure 3.13**). Also, its COI sequence differed considerably from J61 at 12.3%. J21 was therefore treated as a species new to science, *X.* spY. No specimens matching a paratype of *X. aduncus adunculus* were found and genetically analyzed. Therefore, its genetic relationship with other *aduncus* remains unknown.

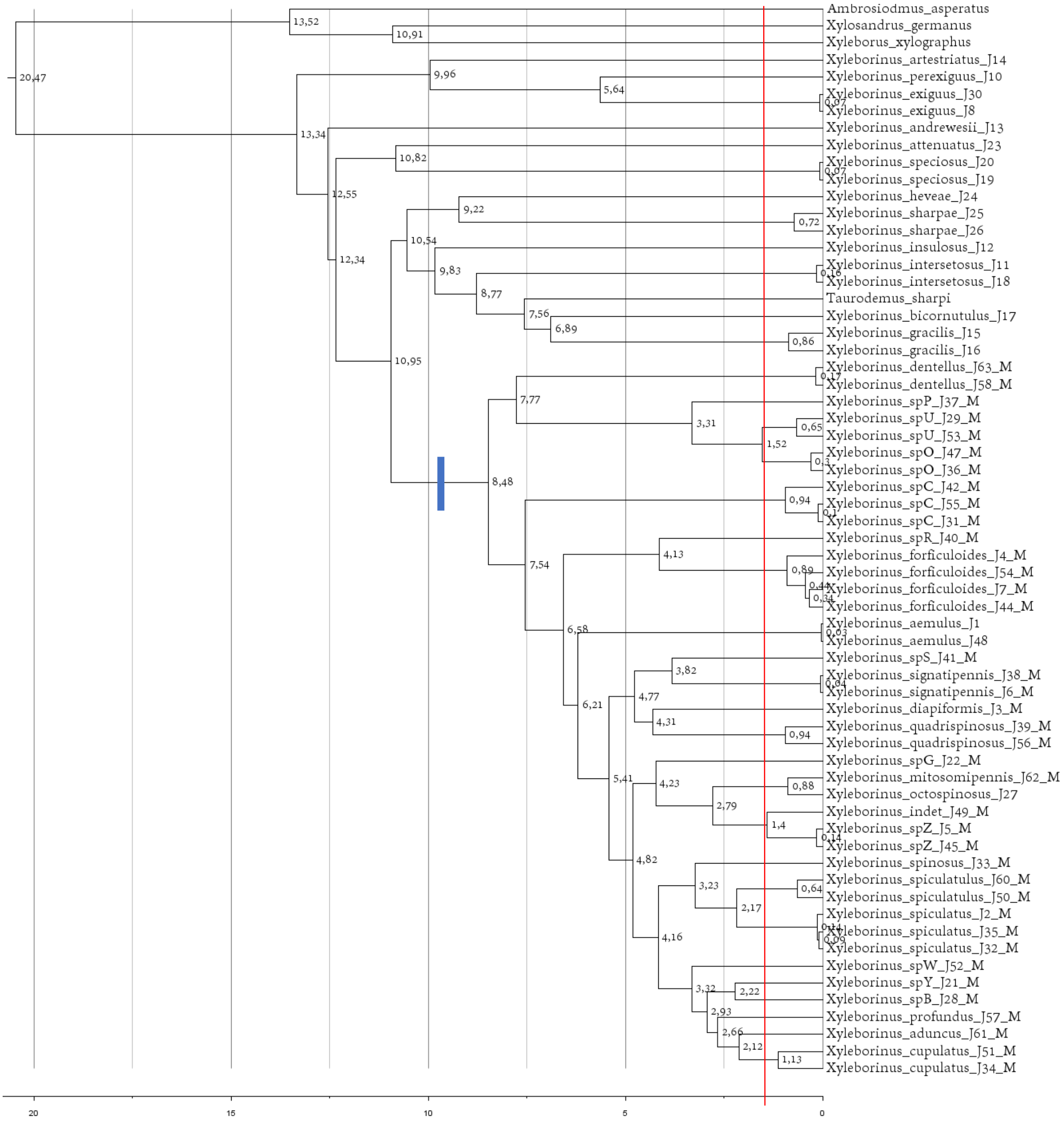

Figure 2.2. Cladogram with dated nodes obtained from BEAST. Tree shows dates of cladogenetic events in Ma starting from present. Root of tree age calibrated to 22 (Ma), standard deviation 2 (Ma). Blue line shows Madagascar colonization event between 8.5 Ma (crown age) and 11 Ma (stem age). Red line shows time of most recent split that has given rise to two different species (1.5 Ma), effectively making it a species delimitation line. Individuals collected from Madagascar are marked with an M. The tree is a forced binary tree to avoid polytomies. Six specimens that were genetically identical with other specimens in the tree have been removed.

Node support was generally weaker in the BEAST tree than in MrBayes, but the resulting typology is identical to the one obtained from MrBayes (except for the fact that the tree in BEAST is a forced binary). Results statistics file for the BEAST run is attached to the thesis.

The clade including X. aduncus, X. spY, X. cupulatus and X. spB has experienced a rapid radiation where five species appear to have evolved in the last 3 to 3.2 million years (this estimate excludes X. spW). These species exhibit a maximum of 1 base pair difference at the 28S gene, but they are morphologically distinct and COI differ at least 8.2% between species.

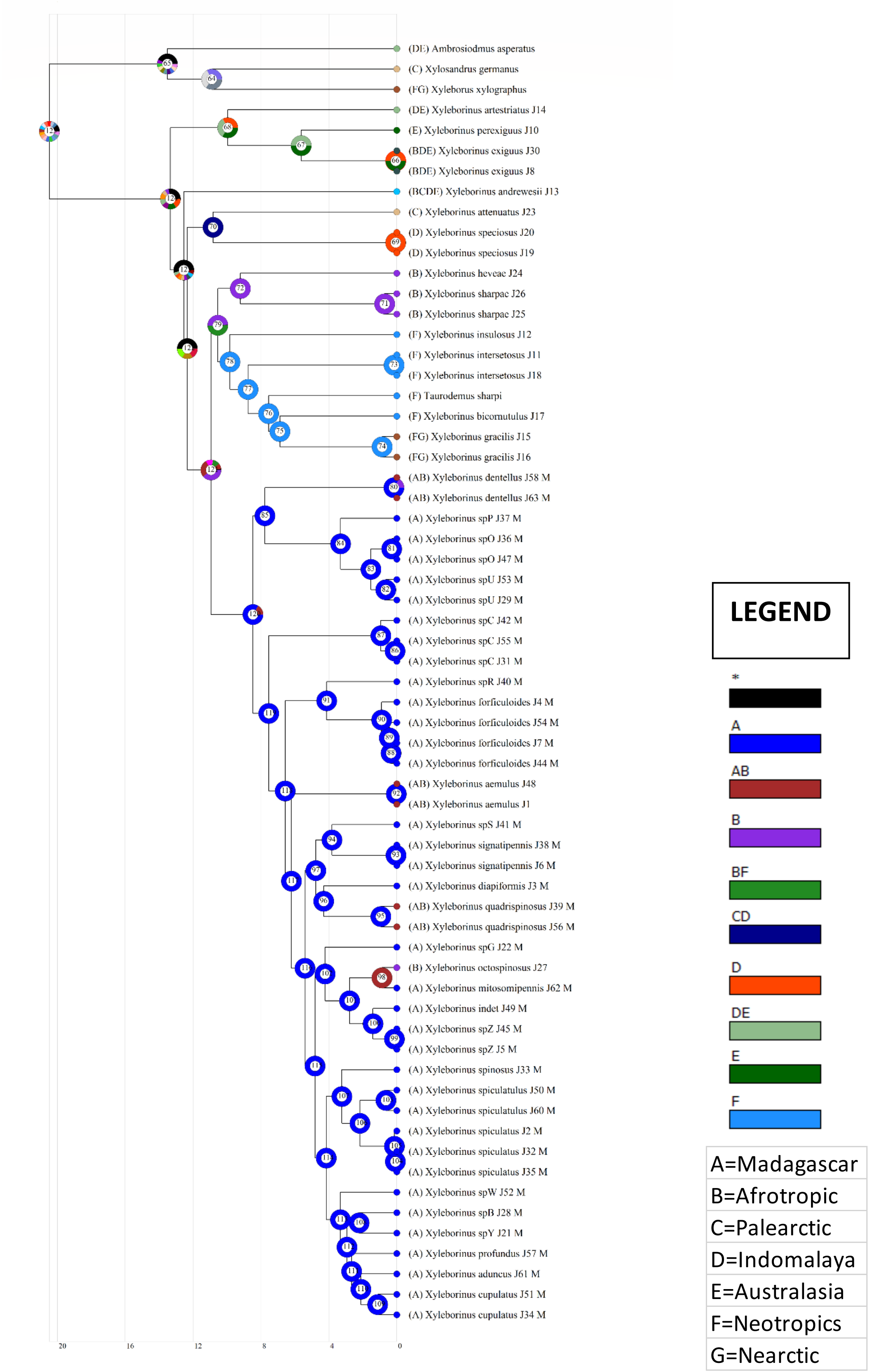

Figure 2.3. Biogeographic tree obtained from RASP using an S-DIVA test with zero range constraints. Time trees used for analyzes obtained from BEAST. Nodes show probable distribution ranges of common ancestors.

All genetically analyzed *Xyleborinus* species from Madagascar are contained in a single clade (**Figure 2.3**, marked in dark blue). The BEAST and RASP tree strongly indicate a single colonization event to Madagascar that happened between 8.5 Ma (crown age) and 11 Ma (stem age) which gave rise to all Malagasy *Xyleborinus* species. Included in the clade are two mainland African species, *Xyleborinus aemulus* (Wollaston, 1869) and *Xyleborinus octospinosus.* There are also reports of *X. quadrispinosus* on the mainland, but it is mainly found on Madagascar. In the case of *X. octospinosus*, *X. aemulus* and *X. quadrispinosus* a recolonization from Madagascar to the African mainland appears to have taken place. During the last 1 million years for *X. octospinosus*, at any point during the last 6.2 million years for *X. aemulus* and very recently in the case of *X. quadrispinosus.*

Taxonomy

Order Curculionidae

Family Scolytinae

***Xyleborinus* Reitter, 1913**

Diagnosis. *Xyleborinus* differ from other Scolytinae by having a conical scutellum surrounded by setae rather than a triangular plate that flush with elytra.

Description female. *Head.* Eyes elongated, oval shaped, emarginated, indention 0.3x-0.5x as deep as width of eye. Frons surface punctured, with sparse, long setae. Usually densely set course setae on epistoma. Antennal funiculus 5-segmented, club obliquely truncated, type 2, occasionally type 1 (Hulcr *et al.*, 2007) ***Pronotum*** Type 7 or 8 (Hulcr *et al.*, 2007). Posterior half with tiny punctures spaced by 2–4 × their diameter; anterior half with small transverse aserities laterally spaced by half their length or less. ***Elytra*** Declivity with spines, tubercles or flange (except; *X. pilosellus* (Schedl, 1957)). **Vestiture** unifid. Interstrial setae longer than strial setae. **Legs.** Protibiae and metatibiae curved with socketed denticles on lateral side.

Figure 3.1. *Xyleborinus* frons has very little variation between species. *X. octospinosus* (**A**)*, X.* spG (**B**) and *X. diapiformis* (Schedl, 1961) (**C**).

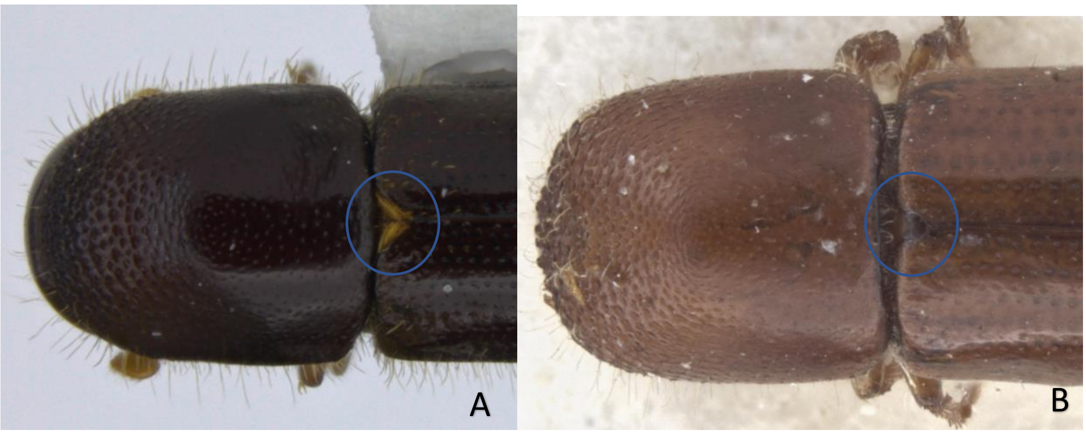

Figure 3.2. Comparing conical scutellum surrounded by setae on *Xyleborinus aemulus* and triangular plate on *Xyleborus curtidentis* Schedl, 1961. The triangular plate is a trait *Xyleborus* shares with all other Scolytinae except *Xyleborinus*.

Descriptions of species new to science

Note. New species are not given proper names. This is done to avoid making the master thesis the official source for the species descriptions. An article with the proper names will be published at a later time. All specimens are females except when noted. Length of ventrites are measured laterally, not ventrally.

Xyleborinus spB Eliassen & Jordal, sp. nov.

http://zoobank.org

(**Figures 3.3, 3.4**)

Type material. Holotype, female: Madagascar, Ranomafana Vato trail, 2012: 5x-12, B. Jordal, Unknown log, [-21.29, 47.42] alt. 1100m **Allotype:** Madagascar, Ranomafana Centre ValBio, 2012: 27ix-1, B. Jordal, ?Cryptocarya branch, [-21.25, 47.42] alt. 950m **Paratypes (18):** All from Madagascar, Ranomafana, collected by B. Jordal in 2012: Same as allotype (3); Centre ValBio, 29ix-16, Unknown log, [-21.25, 47.42] alt. 950m (6); Vato trail, 4x-3, *Harunga madagascariensis*, [-21.29, 47.42] alt. 1100m (3); Centre ValBio, 28ix-6, Oncostemum log, [-21.25, 47.42] alt. 950m (1); Centre ValBio, 30ix-7, Polyscias, [-21.25, 47.42] alt. 950m (1); Vato trail, 4x-5, Unknown log, [-21.29, 47.42] alt. 1100m (1); Centre ValBio, 1x-2, Mussaenda log, [-21.25, 47.42] alt. 950m (1); Village E. ValBio, 10x-3, Oncostemum stump, [-21.24, 47.42] alt. 900m (1); Centre ValBio, 30ix-7, Polyscias branch, [-21.25, 47.42] alt. 950m (1) **Deposited:** Holotype, allotype and 16 paratypes in ZMBN, 2 paratypes in NHMW.

Diagnosis female. Declivity vertical, truncated, encircled on declivital margin by wreath with 7-8 small spines and tubercles on each side on interstriae 1 to 9. Spine and tubercle pairs may be unsymmetrical. Some spines or tubercles may have two tips on some specimens. Spines barely longer than tubercles, third and last spine (interstria 4 and 9) longest, but shorter than length of fourth ventrite. Bottom pair appear more pronounced than others in dorsal view. Declivital surface concave.

Description female. Length 1.8-2.0 mm, 2.8-3.0 × as long as wide; color brown ***Elytra.*** Striae on disc not impressed, punctures shallow, spaced by 1-2× their diameter. Interstriae smooth, shiny, punctures as large as strial punctures, spaced by 3-5× their diameter. Declivity vertical, truncated, encircled on declivital margin by wreath with 7-8 small spines and tubercles on each side on interstriae 1 to 9. Spine and tubercle pairs may be unsymmetrical. Some spines or tubercles may have two tips on some specimens. Spines barely longer than tubercles, third and last spine (interstria 4 and 9) longest, but shorter than length of fourth ventrite. Bottom pair appear more pronounced than others in dorsal view. Declivital surface concave. More than 50 granules associated with punctures on the declivity. Vestiture consisting of fine erect interstrial setae, mainly on posterior fourth on disc. Declivity glabrous, except microscopic strial setae. ***Legs.*** Protibiae: lateral edge curved with 7 socketed denticles from apical 2/3 to apical ¼ that make protibiae appear triangular. Large gap between proximal denticle 1 and 2. Metatibiae: lateral edge gently curved with 8 socketed denticles on apical ¾, pronounced deep gap between proximal denticle 1 and 2. Apical third broader than proximal third.

Description male. Length 1.5-1.7 mm, 2.5-2.7 × as long as wide; color yellow ***Elytra.*** Striae on disc not impressed, punctures shallow, spaced by 3-4× their diameter. Interstriae creased, shiny, punctures as large as strial punctures, spaced by 8-10× their diameter. Declivity vertical, truncated, encircled by granules on declivital margin on interstria 1 to 9, one pair of tubercles on interstriae 4. Vestiture consisting of fine erect interstrial setae, declivity glabrous. ***Legs.*** Protibiae: same as female except socketed denticles on apical 3/5. Metatibiae: same as female except socketed denticles on apical 2/3.

Distribution and biology. Madagascar. Known from Ranomafana National Park, dissected from wood tunnels in *Cryptocarya, Harunga madagascariensis, Oncostemum, Polyscias, Mussaenda.*

Figure 3.3. Holotype of *X.* spB in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Figure 3.4. Allotype of *X.* spB in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus **spC Eliassen & Jordal, sp. nov.**

http://zoobank.org
(**Figure 3.5**)

Type material. Holotype, female: Madagascar, Ranomafana Centre ValBio, 2012: 28ix-1c, B. Jordal, Cryptocarya log, [-21.25, 47.42] alt. 950m **Paratypes (8):** All from Madagascar: Ranomafana Village E. ValBio, 2012: 10x-11, B. Jordal, Trema log, [-21.24, 47.42] alt. 900m (1); Ranomafana Centre ValBio, 2012: B. Jordal, Cubeb oil S-trap, [-21.26, 47.42] alt. 950m (2); Andasibe Analamazaotra res., 2015: 14v-7, B. Jordal, Unknown standing tree, [-18.941, 48.426] alt. 800m (4); Marojejy National Park, 2019: 24-27x, B. Jordal, Boswellia-baited FIT, [-14.44, 49.76] alt. 700m (1). **Deposit:** Holotype and 6 paratypes in ZMBN, 2 paratypes in NHMW.

Diagnosis. Declivity vertical, steep, encircled by small rim on declivital margin, with fused tubercles, appearing from interstria 4 or 5. Rim ends near elytral apex with a pair of slightly larger tubercles, about the length of the pedicel. 2-4 pairs of tubercles and/or sharp granules run down declivity on interstriae 1.

Description female. Length 2.0-2.2 mm, 3.0 × as long as wide; color dark brown ***Elytra.*** Striae on disc not impressed, punctures shallow, spaced by 1-2× their diameter. Interstriae smooth, shiny, punctures as large as strial punctures, spaced by 2-3× their diameter. Declivity vertical, steep, encircled by small rim on declivital margin, with fused tubercles, appearing from interstria 4 or 5. Rim ends near elytral apex with a pair of slightly larger tubercles, about the length of the pedicel. 2-4 pairs of tubercles and/or sharp granules run down declivity on interstriae 1. Fine erect interstrial setae. Declivity has setae on interstria 1, rest glabrous (except microscopic setae) ***Legs.*** Protibiae: lateral edge with a slight curve, abruptly broadening on apical half, with 6 socketed denticles on apical 3/5, gap between proximal denticle 1 and 2. Metatibiae: lateral edge curved with 6-7 socketed denticles on apical 2/3, gap between proximal denticle 1 and 2. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Ranomafana National Park, Marjojey National Park and Analamazaotra Reserve, dissected from wood tunnels in *Cryptocarya* and *Trema*.

Figure 3.5. Paratype of *X.* spC in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spG Eliassen & Jordal, sp. nov.

http://zoobank.org
(**Figure 3.6**)

Type material. Holotype, female: Madagascar, Ranomafana Centre ValBio, 2012: 28ix-6, B. Jordal, Oncostemum log, [-21.25, 47.42] alt. 950m **Paratypes (2):** Same as holotype **Deposit:** Holotype and 1 paratype in ZMBN, 1 paratype in NHMW.

Diagnosis. First half of declivity sloped, second half steeply curved, impressed first and second interstria, appearing as excavated cleft. Cleft; first and second interstria smooth; first stria only has sharp granules. Interstria 3 and beyond all have spines and/or tubercles. Gives appearance of two swollen areas with more than 10 spines and tubercles each, separated by cleft. Interstria 3 has the largest spine, situated halfway down declivity, as long as length of third ventrite, other spines under half its size. Vestiture dense on declivity.

Description female. Length 2.1-2.4 mm, 2.7-3.0 × as long as wide; color dark brown. ***Elytra*** Striae on disc not impressed, punctures shallow, spaced by 1-2× their diameter. Interstriae smooth, shiny, punctures as large as strial punctures, spaced by 2-4× their diameter. First half of declivity sloped, second half steeply curved, impressed first and second interstria, appearing as excavated cleft. Cleft; first and second interstria smooth; first stria only has sharp granules. Interstria 3 and beyond all have spines and/or tubercles. Gives appearance of two swollen areas with more than 10 spines and tubercles each, separated by cleft. Interstria 3 has the largest spine, situated halfway down declivity, as long as length of third ventrite, other spines under half its size. Vestiture dense, consisting of fine erect strial and interstrial setae, mainly on posterior fourth including declivity. ***Legs.*** Protibiae: lateral edge evenly curved with 8-11 socketed denticles on apical ¾, big gap between proximal denticle 1 and 2. Metatibiae: lateral edge curved, rounded with 10 socketed denticles on apical ¾, big gap between proximal denticle 1 and 2. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Ranomafana National Park, dissected from wood tunnels of *Oncostemum*.

Figure 3.6. Holotype of *X.* spG in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spO Eliassen & Jordal, sp. nov.

http://zoobank.org
(**Figure 3.7**)

Type material. Holotype, female: Madagascar, Ranomafana Village E. ValBio, 2012: 10x-11, B. Jordal, Trema log, [-21.24, 47.42] alt. 900m **Paratypes (4):** All from Madagascar, Ranomafana: Same as holotype (1); Valo area, 2012: 6x-S2, S. Roth, Cryptocarya branch, [-21.29, 47.42] alt. 1100m (1); Valo area, 2012: 6x-S1, S. Roth, Garcinia standing tree, [-21.29, 47.42] alt. 1100m (1); Teletakely trail, 2012: B. Jordal, Cedar tree oil FIT, [-21.26, 47.42] alt. 950m (1). **Deposit:** Holotype and 2 paratypes in ZMBN, 2 paratypes in NHMW.

Diagnosis. Declivity coarse, excavated, occupying 3/7 of the elytra, encircled by spines on declivital margin. Three spines on interstria 1, 3, 4 as thick as long; third spine longest of the three, as long as length of ventrite three and four combined, first spine under half that size, second spine is an intermediate. Spine-like flanks on interstriae 8, close to elytral apex, almost as thick and long as length of second ventrite; margin between elytral apex and tip of bottom flanks curved, makes the space between bottom flanks look like a half circle in dorsal view.

Description female. Length 3.4-3.5 mm, 2.7-2.8 × as long as wide; color dark brown ***Elytra.*** Striae on disc slightly impressed, punctures shallow, spaced by 1-2× their diameter. Interstriae smooth, shiny, punctures slightly smaller than strial punctures, spaced by 3-4× their diameter. Declivity coarse, excavated, occupying 3/7 of the elytra, encircled by spines on declivital margin. Three spines on interstria 1, 3, 4 as thick as long; third spine longest of the three, as long as length of ventrite three and four combined, first spine under half that size, second spine is an intermediate. Spine-like flanks on interstriae 8, close to elytral apex, almost as thick and long as length of second ventrite; margin between elytral apex and tip of bottom flanks curved, makes the space between bottom flanks look like a half circle in dorsal view. Small spines on interstria 5, 7, 8; shorter and considerably thinner than other spines, barely longer than length of fourth ventrite. Vestiture consisting mainly of dense, very small strial setae on declivity. ***Legs.*** Protibiae: lateral edge evenly curved with 8-10 socketed denticles on apical 2/3 and 2-3 granules on proximal third, gap between every denticle.

Metatibiae: lateral edge gently curved, with 11 evenly separated socketed denticles on apical 2/3. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Ranomafana National Park, dissected from wood tunnels in *Trema, Cryptocarya, Garcinia.*

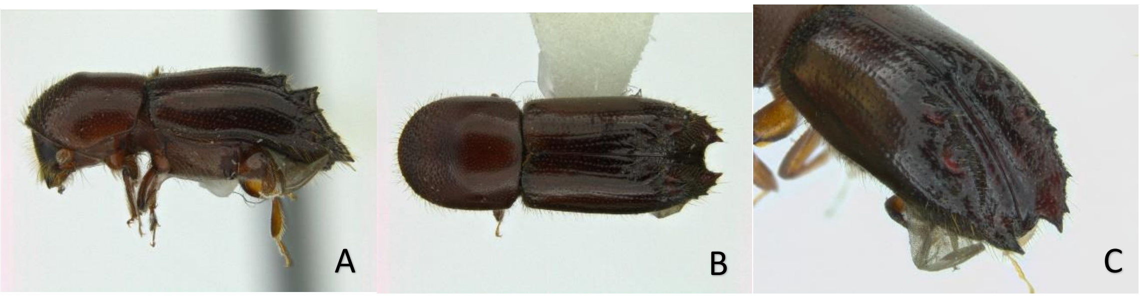

Figure 3.7. Paratype of *X.* spO in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spP Eliassen & Jordal, sp. nov.

http://zoobank.org

(**Figure 3.8**)

Type material. Holotype, female: Madagascar, Ranomafana Centre ValBio, 2012: 1x-D1, D. Pistone, Cryptocarya branch, [-21.25, 47.42] alt. 950m **Paratypes (2):** Same as holotype. **Deposited:** Holotype and 1 paratype in ZMBN, 1 paratype in NHMW.

Diagnosis. Declivity coarse, impressed, appearing excavated with three pairs of spines on interstriae 3, 4, 7&8. Pair two and three on declivital margin, of very large size, third pair is about the same length as second ventrite, second pair is even longer. First pair is slightly longer than length of third ventrite. Sharp tubercles present on top of declivity.

Description female. Length 3.3 mm, 2.7-2.8 × as long as wide; color dark brown, almost black. ***Elytra*** Striae on disc faintly impressed, punctures shallow, spaced by 1× their diameter. Interstriae shiny, punctures as large as strial punctures, spaced by 2-4× their diameter. Declivity coarse, impressed, appearing excavated with three pairs of spines on interstriae 3, 4, 7&8. Pair two and three on declivital margin, of very large size, third pair is about the same length as second ventrite, second pair is even longer. First pair is slightly longer than length of third ventrite. Sharp tubercles present on top of declivity. Vestiture consisting of fine erect interstrial setae, mainly on posterior third on disc. Declivity with very small strial setae. ***Legs.*** Protibiae: lateral edge evenly curved with 8 evenly separated socketed denticles on apical 2/3. Metatibiae: lateral edge curved with 10 evenly separated socketed denticles on apical 3/5. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Ranomafana National Park, dissected from wood tunnels in *Cryptocarya*.

Figure 3.8. Holotype of *X.* spP in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus **spR Eliassen & Jordal, sp. nov.**

http://zoobank.org
(**Figure 3.9**)

Type material. Holotype, female: Madagascar, Ranomafana Teletakely trail, October 2012: B. Jordal, Cedar tree oil FIT, [-21.26, 47.42] alt. 950m **Paratypes (2):** Same as holotype (1); Same as holotype expect collected in Ipsenol FIT at Centre ValBio (1) **Deposited:** Holotype and 1 paratype in ZMBN, 1 paratype in NHMW.

Diagnosis. Declivity sharply curved. Two pairs of spines, on interstriae 3 and 9 of equal size, slightly shorter than length of fourth ventrite; first pair of spines located almost halfway down declivity, second pair at bottom. Two pairs of tubercles, on interstriae 6 and 7.

Description female: Length 2.4 mm, 3.0 × as long as wide; color dark brown ***Elytra.*** Striae on disc not impressed, punctures shallow, spaced by 1-3× their diameter. Interstriae shiny, punctures as large as strial punctures, spaced by 3-4× their diameter**.** Declivity sharply curved. Two pairs of spines, on interstria 3 and 9 of equal size, slightly shorter than length of fourth ventrite; first pair of spines located almost halfway down declivity, second pair at bottom. Two pairs of tubercles, on interstriae 6 and 7. Spines and tubercles on interstria 6 to 8 encircle declivity on declivital margin, spine on interstria 3 on declivity. Vestiture consisting of fine erect strial and interstrial setae on every puncture on disc. Declivity has strial setae and setae on interstria 3. ***Legs.*** Protibiae: lateral edge curved with 7-9 socketed denticles on apical 3/5 and 2 granules on proximal 2/5, gap between proximal denticle 1 and 2 slightly bigger than others. Metatibiae: lateral edge curved with 10 socketed denticles on apical 2/3, gap between proximal denticles 1-3 slightly bigger than others. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Ranomafana National Park, collected from *Cedar* tree oil and Ipsenol FIT.

Figure 3.9. Holotype of *X.* spR in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus **spS Eliassen & Jordal, sp. nov.**

http://zoobank.org

(**Figure 3.10**)

Type material. Holotype, female: Madagascar, Ankarafantsika National Park, 2015: 9v-x, B. Jordal, Multilure trap, [-16.264, 46.828] alt. 200m **Paratypes (1):** Same as holotype **Deposited:** Holotype in ZMBN, 1 paratype in NHMW.

Diagnosis. Declivity vertical, truncated, encircled on declivital margin by four pairs of large spines in a crowned pattern on interstriae 3, 5&6, 7, 9 (last close to elytral apex). Pair one and four longest, as long as length of ventrite two and three combined. Pair two and three shorter, slightly shorter than length of second ventrite.

Description female. Length 2.0-2.1 mm, 2.9-3.1 × as long as wide; color brown ***Elytra.*** Striae on disc slightly impressed, punctures shallow, spaced by 1× their diameter. Interstriae shiny, punctures slightly smaller than strial punctures, spaced by 3-5× their diameter***.*** Declivity vertical, truncated, encircled on declivital margin by four pairs of large spines in a crowned pattern on interstriae 3, 5&6, 7, 9 (last close to elytral apex). Pair one and four longest, as long as length of ventrite two and three combined. Pair two and three shorter, slightly shorter than length of second ventrite. Vestiture consisting of fine erect interstrial and tiny strial setae, declivity glabrous, long setae near tips of spines. ***Legs.*** Protibiae: lateral edge curved with 6 socketed denticles on apical 2/3, gap between proximal denticle 1 and 2. Metatibiae: lateral edge curved with 7 evenly spaced socketed denticles on apical 2/3. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Ankarafantsika National Park, collected from Multilure trap.

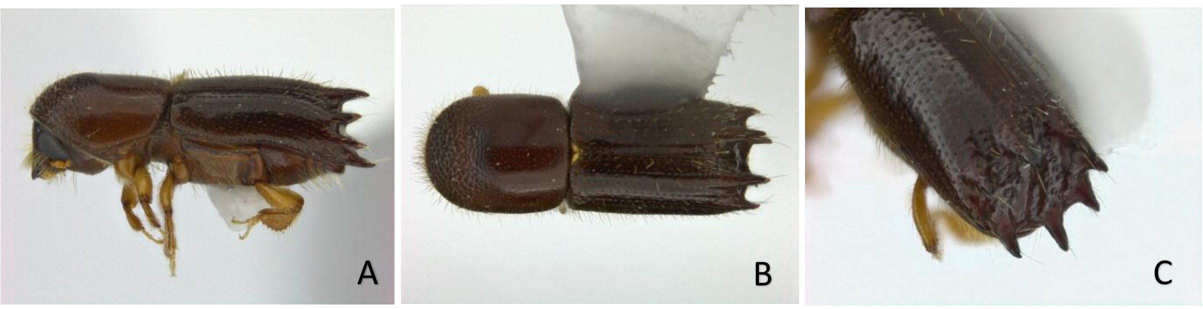

Figure 3.10. Holotype of *X.* spS in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spU Eliassen & Jordal, sp. nov.

http://zoobank.org
(**Figure 3.11**)

Type material. Holotype, female: Madagascar, Marojejy National Park, 2019: 26x-5, B. Jordal, *Weinmannia* standing tree, [-14.44, 49.76] alt. 800-1000m **Paratypes (1):** Madagascar, Ambohitantely reserve, 2015: 11v-1, B. Jordal, *Solanum aphanathum* branch, [-18.189, 47.292] alt. 1500m **Deposited:** Holotype in ZMBN, 1 paratype in NHMW.

Diagnosis. Declivity appear excavated, occupying 3/7 of the elytra, encircled by spines and tubercles on declivital margin. Three spines on interstria 1, 2, 3 as thick as long; third spine double the size of the other two, as long as length of pedicel and funicles combined. Spine on interstria 4 as long as third pair, but considerably thinner. Spine-like flanks on interstria 8, close to elytral apex, almost as thick and long as length of second ventrite; margin between elytral apex and tip of bottom flanks curved, makes the space between bottom flanks look like a half circle in dorsal view.

Description female: Length 3.2-3.3 mm, 2.7-2.8 × as long as wide; color dark brown ***Elytra.*** Striae on disc slightly impressed, punctures shallow, spaced by 1× their diameter. Interstriae smooth, shiny, punctures slightly smaller than strial punctures, spaced by 3-5× their diameter. Declivity appear excavated, occupying 3/7 of the elytra, encircled by spines and tubercles on declivital margin. Three spines on interstria 1, 2, 3 as thick as long; third spine double the size of the other two, as long as length of pedicel and funicles combined. Spine on interstria 4 as long as third pair, but considerably thinner. Spine-like flanks on interstria 8, close to elytral apex, almost as thick and long as length of second ventrite; margin between elytral apex and tip of bottom flanks curved, makes the space between bottom flanks look like a half circle in dorsal view. 4-5 sharp tubercles on interstria 4 to 8, barely longer than length of pedicel. Vestiture consisting of erect interstrial setae, mainly on posterior third on disc. Declivity with almost microscopic strial setae. ***Legs.*** Protibiae: lateral edge evenly curved with 8-9 evenly spaced socketed denticles on apical 2/3 and 2-3 granules on proximal third. Metatibiae: unknown, missing.

Male. Not known.

Distribution and biology. Madagascar. Known from Marojejy National Park and Ambohitantley Reserve, dissected from wood tunnels in *Weinmannia* and *Solanum aphanathum.*

Figure 3.11. Holotype of *X.* spU in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus **spW Eliassen & Jordal, sp. nov.**

http://zoobank.org
(**Figure 3.12**)

Type material. Holotype, female: Madagascar, Marojejy National Park, 2019: 26x-4, B. Jordal, Cussonia (Voantsilana) log, [-14.44, 49.76] alt. 1000m **Paratypes (1):** Madagascar, Andranomalaza, X-57 **Deposit:** Holotype in ZMBN, 1 paratype in NHMW.

Diagnosis. Declivity truncated, steep, encircled on declivital margin by eight pairs of evenly spaced, small spines of approximately equal size forming a wreath; some spines may have two tips on some specimens, none present on or close to the elytral apex. Declivital surface slightly convex.

Description female. Length 1.9 mm, 3.0 × as long as wide; color light brown. ***Elytra*** Striae on disc not impressed, punctures shallow, spaced by 1-2× their diameter. Interstriae smooth, shiny, punctures as large as strial punctures, spaced by 4-5× their diameter. Declivity truncated, steep, encircled on declivital margin by eight pairs of evenly spaced, slightly fused small spines from interstriae 1 to 9 forming a wreath; some spines may have two tips on some specimens, none present on or close to the elytral apex. All spines are approximately of the same size and length, about the length of the funicles and pedicel combined. More than 50 granules associated with punctures on the declivity. Declivital surface slightly convex. Vestiture consisting of short, scruffy erect interstrial setae. Declivity glabrous, except microscopic setae ***Legs.*** Protibiae: lateral edge evenly curved with 7 socketed denticles on apical 2/3, gap between proximal denticle 1 and 2. Metatibiae: lateral edge gently curved, rounded with 9 socketed denticles on apical ¾, gap between proximal denticles 1-4. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Marjojey National Park and Andranomalaza, dissected from wood tunnels in *Cussonia* (Voantsilana).

Comment. An undescribed singleton labeled "*Xyleborus singularis*" was found in the Wien collections that morphologically matches the holotype of *X.* spW. Someone in the museum probably realized they had found a new species, but never got around to describe it formally. It has been designated as paratype.

Figure 3.12. Holotype of *X.* spW in lateral (**A**), dorsal (**B**) and declivital view (**C**).

Xyleborinus spY Eliassen & Jordal, sp. nov.

http://zoobank.org
(**Figure 3.13 A, B, C**)

Type material. Holotype, female: Madagascar, Ranomafana Centre ValBio, 2012: 28ix-6, B. Jordal, Oncostemum log, [-21.25, 47.42] alt. 950m **Paratype (2):** Same as holotype (2) **Deposit:** Holotype and 1 paratype in ZMBN, 1 paratype in NHMW.

Diagnosis. Declivity steep, encircled by flange on declivital margin from interstria 4 to 9; flange continuous but has an uneven, crested, almost serrated edge, ends with pronounced spine-like flanks, flanks as long as length of second and third ventrite combined; space between flank tips as long or slightly longer than length of metatibiae. Three small spines precede flange on interstria 1, 2, 3; first and second spine same length as third ventrite, third spine slightly longer and thicker than length of third ventrite. Inside of bottom flanks smooth.

Description female. Length 2.0-2.2 mm, 3.1-3.3 × as long as wide; color brown ***Elytra.*** Striae on disc not impressed, punctures shallow, spaced by 1-3× their diameter. Interstriae smooth, shiny, punctures as large as strial punctures, spaced by 5-7× their diameter. Declivity steep, encircled by flange on declivital margin from interstria 4 to 9; flange continuous but has an uneven, crested, almost serrated edge, ends with pronounced spine-like flanks, flanks as long as length of second and third ventrite combined; space between flank tips as long or slightly longer than length of metatibiae. Three small spines precede flange on interstria 1, 2, 3; first and second spine same length as third ventrite, third spine slightly longer and thicker than length of third ventrite. Inside of bottom flanks smooth. Vestiture almost completely absent, declivity glabrous. ***Legs.*** Protibiae: lateral edge pointed making protibiae triangular, has 7 socketed denticles on apical 3/5, big gap between proximal denticle 1 and 2. Metatibiae: lateral edge broadened and curved on apical 2/3, at least 5 very small socketed denticles on apical ¾, big gap between proximal denticle 1 and 2. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Ranomafana National Park, dissected from wood tunnels in *Oncostemum.*

Comment. *X.* spY was originally thought to be *X. aduncus* (Schedl, 1961). However, molecular analyzes reveal significant genetic differences (see **Figure 2.1**) and morphological comparison shows it is not identical to *X. aduncus* paratypes (**Figure 3.13**).

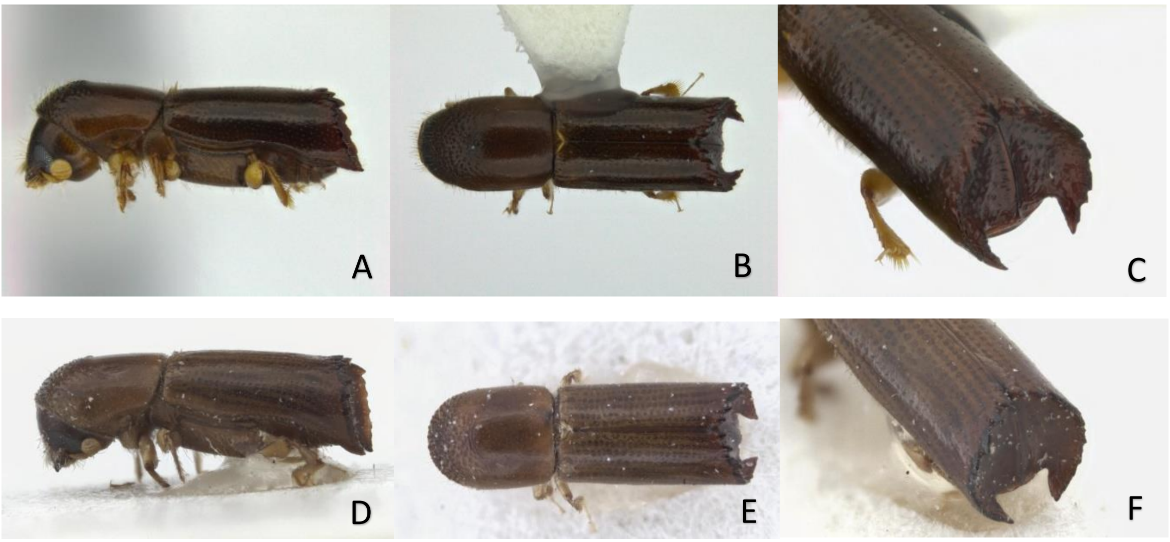

Figure 3.13. Comparing holotype of *X.* spY in lateral (**A**), dorsal (**B**) and declivital view (**C**) and paratype of *X. aduncus* in lateral (**D**), dorsal (**E**) and declivital view (**F**). Notice the flanges of the former being more rugged and the bottom flanks being thinner and slightly shorter.

Xyleborinus **spZ Eliassen & Jordal, sp. nov.**

http://zoobank.org

(**Figure 3.14 A, B, C**)

Xyleborus mitosomipennis var. *laevipennis* – Schedl, 1961

Type material. Holotype, female: Madagascar, Ranomafana Centre ValBio, 2012: 1x-6, B. Jordal, Albizia log, [-21.25, 47.42] alt. 950m **Paratypes (10):** All from Madagascar, Ranomafana: Vato trail, 2012: 3x-8, B. Jordal, Croton log, [-21.29, 47.42] alt. 1100m (2); Vato trail, 2012: 2x-5, B. Jordal, Sloanea log, [-21.29, 47.42] alt. 1100m (1); Vato trail, 2012: 2x-6, B. Jordal, Cryptocarya log, [-21.29, 47.42] alt. 1100m (1); Vato trail, 2012: 4x-3, B. Jordal, *Harunga madagascariensis*, [-21.29, 47.42] alt. 1100m (1); Vato trail, 2012: 4x-5, B. Jordal, Unknown log, [-21.29, 47.42] alt. 1100m (2); Vato trail, 2012: 6x-15, B. Jordal, Croton branch, [-21.31, 47.43] alt. 1100m (1); Teletakely trail, 2012: 8x-D3, D. Pistone, Unknown log, [-21.26, 47.41] alt. 950m (1); Village E. ValBio, 2012: 10x-11, B. Jordal, Trema log, [-21.24, 47.42] alt. 900m (1) **Deposit:** Holotype and 8 paratypes deposited in ZMBN, 2 paratypes in NHMW.

Diagnosis. Declivity steep, encircled by four pairs of spines on interstriae 2&3, 4, 6 and 9 (or 3) near elytral apex, appearing crown-like; spines approximately of the same length, no longer than length of third ventrite. First three pairs of spines very similar in shape, evenly separated.

Description female. Length 2.8-2.9 mm, 3.2-3.3 × as long as wide; color dark brown. ***Elytra*** Striae on disc not impressed, punctures shallow, spaced by 1× their diameter. Interstriae smooth, shiny, punctures as large as strial punctures, spaced by 4-5× their diameter. Declivity steep, encircled by four pairs of spines on interstriae 2&3, 4, 6 and 9 (or 3) near elytral apex, appearing crown-like; spines approximately of the same length, no longer than length of third ventrite. First three pairs of spines very similar in shape, evenly separated. Tubercles under the third pair of spines, and several tubercles and granules on top of declivity. Vestiture consisting of fine erect interstrial setae mainly on posterior fourth on disc. Declivity glabrous, except microscopic setae. ***Legs.*** Protibiae: lateral edge evenly curved with 7 socketed denticles on apical 2/3, gap between proximal denticle 1 and 2, tiny gap between distal denticle 1, 2 and 3. Metatibiae: lateral edge curved with 8-9 socketed denticles on apical 2/3, gap between proximal denticle 1 and 2. Apical third broader than proximal third.

Male. Not known.

Distribution and biology. Madagascar. Known from Andasibe and Ranomafana National Park, dissected from wood tunnels in *Albizia, Croton, Sloanea, Cryptocarya, Trema* and *Harungana madagascariensis.*

Comment: Morphologically similar individuals from Perinet, Madagascar, were previously described as an infrasubspecific taxon with the name *Xyleborus mitosomipennis* var. *laevipennis* (Schedl, 1961). This name has no status but is not available according to ICZN article 1.3.4.

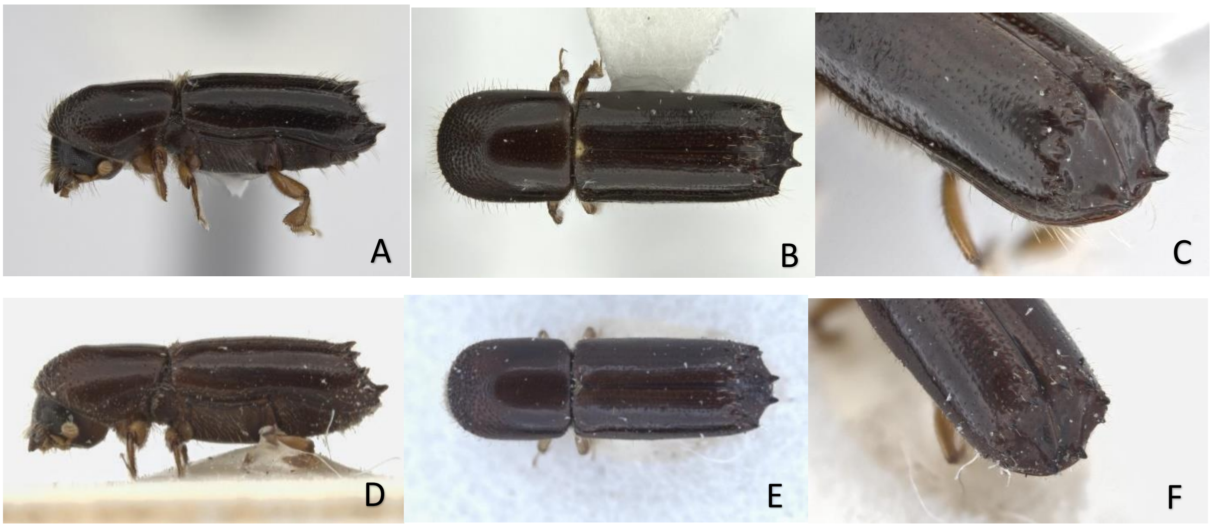

Figure 3.14. Holotype of *X.* spZ in lateral (**A**), dorsal (**B**) and declivital view (**C**) compared with specimen labeled "lectotype *Xyleborus mitosomipennis* var. *laevipennis"* (no status) in lateral (**D**), dorsal (**E**) and declivital view (**F**).

Register of described *Xyleborinus* species in the Afrotropic (including species described in this study)

Note: Species are sorted in groups. **Table 11** is a summary index**.** Includes location of holotype or lectotype, diagnosis, distribution, comments and pictures. Every diagnosis is based on female specimens. Length of ventrites are measured laterally, not ventrally. *X. gracilipennis* (Schedl, 1957) and *X. collarti* (Eggers, 1932) have been removed from the genus as they are both missing the conical scutellum that is common to all *Xyleborinus* (see **Figure 3.2**). The exclusion of *X. collarti* from the genus has been noted earlier (Hulcr *et al.*, 2007).

Table 11. List of Afrotropical *Xyleborinus* sorted in groups based on morphology and molecular data (COI, 28S, CAD) when available. Distribution and defining characteristics are included. Author and year are not included in list, but are included in the ensuing register.

Species names	Previously described?	Molecular data	Distribution	Declivity characteristics	Vertical/steep declivity	Declivital wreath or flange	Declivital crown
Xyleborinus aduncus	yes	yes	Madagascar	Declivity encircled by a flange or wreath	x	x	
Xyleborinus cupulatus	yes	yes	Madagascar		x	x	
Xyleborinus profundus	yes (described as sub-species)	yes	Madagascar		x	x	
Xyleborinus spB	no	yes	Madagascar		x	x	
Xyleborinus spW	no	yes	Madagascar		x	x	
Xyleborinus spY	no	yes	Madagascar		x	x	
Xyleborinus spiculatulus	yes	yes	Grand Comore, Madagascar	Spiky, uneven wreath. Elytras often unsymmetrical	x	x	
Xyleborinus spiculatus	yes	yes	Madagascar		x	x	
Xyleborinus spinosus	yes	yes	Madagascar		x	x	
Xyleborinus armatus	yes	no	Madagascar	Declivity is vertical and crown shaped	x		x
Xyleborinus diapiformis	yes	yes	Madagascar		x		x
Xyleborinus quadrispinis	yes	no	Madagascar		x		x
Xyleborinus quadrispinosus	yes	yes	Madagascar, Safr		x		x
Xyleborinus signatipennis	yes	yes	Madagascar		x		x
Xyleborinus spS	no	yes	Madagascar		x		x
Xyleborinus octospinosus	yes	yes	Madagascar, Tanzania	Three pairs of equally spaced out spines at top half of declivity, one pair at bottom	x		
Xyleborinus spZ	no (named aberration of *X. mitosomipennis* (Schedl, 1961))	yes	Madagascar		x		
Xyleborinus spG	no	yes	Madagascar	Cleft seperating two swollen spiny areas			
Xyleborinus mitosomiformis	yes	no	Madagascar	Steep declivity encircled by small spines or tubercles	x		
Xyleborinus mitosomus	yes	no	Madagascar		x		
Xyleborinus spC	no	yes	Madagascar		x		
Xyleborinus syzygii	yes	no	Tanzania		x		
Undescribed *[Xyleborinus margino-tuberculatus]*	no	no	Madagascar		x		
Xyleborinus forficuloides	yes	yes	Madagascar	Two (or three) pairs of spines posterior laterally			
Xyleborinus forficulus	yes	no	Angola - Kenya - SAfr	Bottom spines hooked inwards			
Xyleborinus spR	no	yes	Madagascar	Vertical with two pairs of small spines, one in middle and one on bottom	x		
Xyleborinus aemulus	yes	yes	Angola, Namibia, Botswana, South Africa, St. Helena, Madagascar	Vertical declivity with two (or three) pairs of small spines, one (or two) pair on top, one on bottom	x		
Xyleborinus alienus	yes	no	SAfr		x		
Xyleborinus bicinctus	yes	no	Madagascar	Excevated declivities extending far up the elytra. Large species, over 3.0 mm in length			
Xyleborinus spO	no	yes	Madagascar				
Xyleborinus spU	no	yes	Madagascar				
Xyleborinus spP	no	yes	Madagascar				
Xyleborinus cuneidentis	yes	no	Madagascar	Four pairs of small spines form a small circle on lower half			
Xyleborinus marcidus	yes	no	Madagascar	Large posterior lateral flanges flanks declivity			
Xyleborinus dentellus	yes	yes	Madagascar, Congo	Sloped declivity encircled by spines. Pair on top as large as two pairs on bottom			
Xyleborinus pseudopityogenes	yes	no	Congo, Namibiae, Mozambique, SAfr				
Xyleborinus andrewesii	yes	yes (non-African specimen)	Worldwide	Elongated declivity, extended apically			
Xyleborinus pilosellus	yes	no	Congo	Spines, tubercles and granules absent			
Xyleborinus spinipes	yes	no	Congo	Bottom spines hooked outward from each other			
Xyleborinus polyalthiae	yes	no	Congo	Sloped declivity, first and second interstriae smooth and glabrous			
Xyleborinus subsulcatus	yes	no	Congo, Zambia				
Xyleborinus exiguus	yes	yes	Worldwide	Rounded with rows of spines, tubercles or granules present on interstriae, except interstriae 2			
Xyleborinus heveae	yes	yes	Congo, Sierra Leone				
Xyleborinus namibiae	yes	no	Namibia				
Xyleborinus saxesenii	yes	yes (non-African specimen)	Worldwide				
Xyleborinus sharpae	yes	yes	Liberia, Tanzania, Sierra Leone, Cameroon				
Xyleborinus similans	yes	no	Angola, Bioko, Ivory Coast, Ghana, Congo, Rep. Congo, Somalia, Safr				

Xyleborinus aduncus (Schedl, 1961)

Holotype: MNHN – Paris

Diagnosis. A vertical declivity encircled by a very smooth flange on the declivital margin from interstriae 5 to 9, ending in a pair of spine-like flanks. Three small spines precede flange on interstria 1, 2 and 3&4, the third partly fused with flange. The inside of the two flanks on the bottom of the declivital flange smooth.

Distribution. Madagascar

Figure 4.1. Paratype of *X. aduncus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus cupulatus (Schedl, 1961)

Holotype: MNHN – Paris

Diagnosis. A vertical declivity encircled by an entirely smooth flange on the declivital margin from interstriae 1 or 2 to 9. A pair of small spines may be present on interstriae 1.

Distribution. Madagascar

Figure 4.2. Paratype of *X. cupulatus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

***Xyleborinus profundus* (Schedl, 1961)**

Holotype: IRSM – Madagascar

Diagnosis. A vertical declivity encircled by an almost completely smooth flange on the declivital margin from interstriae 5 to 9, ending in a pair of spine-like flanks. Three small spines precede flange on interstria 1, 2 and 3&4, the third partly fused with flange. A small swelling or elevation present on the inside of the two flanks on the bottom of the declivital flange.

Distribution. Madagascar

Comments. The subspecies *X. aduncus aduncus* (Schedl, 1961) and *X. aduncus profundus* (Schedl, 1961) have been reclassified as two different species based on molecular evidence (See **Table 10**). The small swelling morphologically separating the species from *X. aduncus* found on the inside of the declivity's bottom flanks are to a larger extent physically separated from the flanks in the genetically analyzed specimen J57 compared to paratype (**Figure 4.3**). However, as the genetically analyzed specimen was a singleton this slight variation has been ignored.

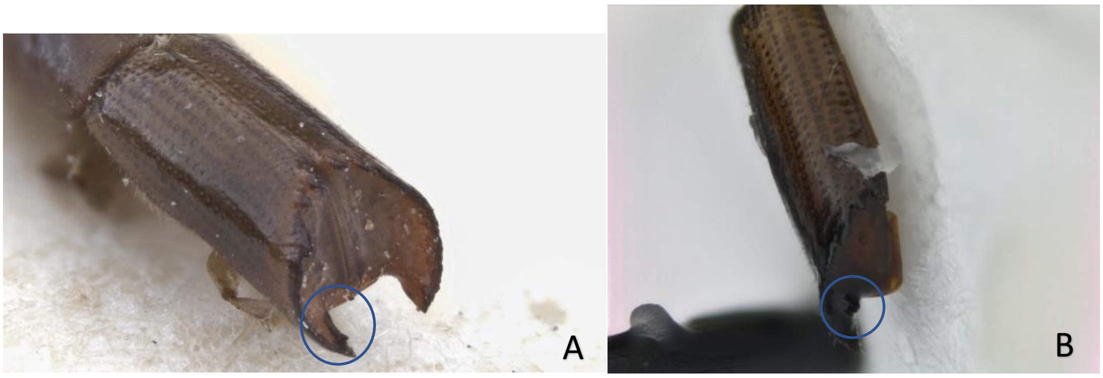

Figure 4.3. Comparing paratype *X. aduncus profundus* (**A**) and J57 specimen (**B**). Notice the slight difference in placement of swelling on the inside of bottom flanks.

Figure 4.4. Paratype (labeled lectotype) of *X. profundus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spB Eliassen & Jordal, sp. nov.

Holotype: ZMBN – Bergen

Diagnosis. Declivity vertical, truncated, encircled on declivital margin by wreath with 7-8 small spines and tubercles on each side on interstriae 1 to 9. Spine and tubercle pairs may be unsymmetrical. Some spines or tubercles may have two tips on some specimens. Spines barely longer than tubercles, third and last spine (interstria 4 and 9) longest, but shorter than length of fourth ventrite. Bottom pair appear more pronounced than others in dorsal view. Declivital surface concave.

Distribution. Madagascar

Figure 4.5. Holotype of *X.* spB in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spW Eliassen & Jordal, sp. nov.

Holotype: ZMBN – Bergen

Diagnosis. Declivity truncated, steep, encircled on declivital margin by eight pairs of evenly spaced, slightly fused small spines from interstriae 1 to 9 forming a wreath; some spines may have two tips on some specimens, none present on or close to the elytral apex. All spines are approximately of the same size and length, about the length of the funicles and pedicel combined. Declivital surface slightly convex.

Distribution. Madagascar

Figure 4.6. Holotype of *X.* spW in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spY Eliassen & Jordal, sp. nov.

Holotype: ZMBN - Bergen

Diagnosis. Declivity steep, encircled by flange on declivital margin from interstria 4 to 9; flange continuous but has an uneven, crested, almost serrated edge, ends with pronounced spine-like flanks. Three small spines precede flange on interstria 1, 2, 3; first and second spine same length as third ventrite, third spine slightly longer and thicker. Inside of bottom flanks smooth.

Distribution. Madagascar

Figure 4.7. Holotype of *X.* spY in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spiculatulus (Schedl, 1965)

Holotype: NHMW - Wien

Diagnosis. A vertical declivity encircled on declivital margin by a wreath with 6-8 spines on each side. Spine on interstria 4 and 8 longest, of approximately equal length, longer than length of third ventrite, spines on interstria 5 and 6 may be as long or slightly shorter. Wreath very irregular, number and length of spines may be asymmetrical between the two elytra. The spines of the declivity gape very slightly more upward in *X. spiculatulus* compared with *X. spiculatus* (Schaufuss, 1891), probably caused by the declivity being slightly less steep.

Distribution. Grand Comore, Madagascar

Figure 4.8. Specimen directly compared with holotype of *X. spiculatulus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spiculatus (Schaufuss, 1891)

Holotype: Lost (Hamburg)

Diagnosis. A vertical declivity encircled on declivital margin by a wreath with 6-8 spines on each side. Spine on interstria 4 and 8 longest, of approximately equal length, longer than length of third ventrite, spines on interstria 5 and 6 may be as long or slightly shorter. Wreath very irregular, number and length of spines may be asymmetrical between the two elytra. The spines of the declivity gape very slightly less upward in *X. spiculatus* compared with *X. spiculatulus* (Schedl, 1965), probably caused by the declivity being slightly steeper.

Distribution. Madagascar

Figure 4.9. Specimen of *X. spiculatus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Comments to *X. spiculatulus* and *X. spiculatus.* *X. spiculatus* and *X. spiculatulus* are similar not only in name but in morphology. The holotype of *X. spiculatus* is lost and the written description is the only account we have of its morphology (Schaufuss, 1891). This description is however not enough to make an obvious distinction between the two species. The distinction becomes even more difficult by the fact that the size and number of spines on the declivity varies between genetically similar individuals and sometimes even between elytra of the same individual. This makes it so that only some specimens match the description of *X. spiculatus* completely.

However, given that this study has revealed two genetically distinct groups (see **Figure 2.1**) that both can be classified as either *X. spiculatus* or *X. spiculatulus* it has been decided that each group should be given one of the two names. The group most closely resembling the holotype of *X. spiculatulus* was given that name and the other group was given the name of *X. spiculatus.* The two groups have very slight morphological differences, to the point that you would never categorize them as individual species on morphology alone.

Figure 4.10. Holotype of *X. spiculatulus* (Schedl, 1965) (**A**) from Grande Comore. Specimen designated *X. spiculatulus* (**B**) from Marojejy in northern Madagascar. Specimen designated as *X. spiculatus* (Schaufuss, 1891) (**C**) (based on high genetic difference and slight morphological difference from *X. spiculatulus*) from Ranomafana south-central Madagascar. Slightly more upwards pointing spines on the first two individuals (**A, B**), most noticeable on the uppermost spine, probably caused by the declivity being slightly less steep than on *X. spiculatus* (**C**).

Xyleborinus spinosus (Schaufuss, 1891)

Holotype: Lost (Hamburg)

Dagnosis. A vertical declivity encircled on declivital margin by a wreath with 7-10 spines and sharp tubercles on each side. Spine on interstria 4 is the longest, longer than length of third ventrite, spine on interstria 2 as long or slightly shorter. The last spines on interstria 5 to 8 are small, half the length of longest spine or shorter. Wreath very irregular, number and length of spines often asymmetrical between the two elytra.

Distribution. Madagascar

Figure 4.11. Specimen compared with original description of *X. spinosus* (Schaufuss, 1891) in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus armatus (Schaufuss, 1891)

Holotype: Lost (Berlin)

Diagnosis. A vertical declivity encircled by four pairs of spines. The first three spines on interstria 3, 6 and 7. Spines on bottom are thinner than others. Last pair spaced further away from each other than first pair. Striae impressed. 2.5 mm in length.

Distribution. Madagascar

Comment. The holotype of *X. armatus* is lost and no material matching the original description is available. It has been included in the species lists and diagnoses based only on the original written German description (Schaufuss, 1891). However, its lack of information on length of spines makes it impractical to add to the identification key.

Xyleborinus diapiformis (Schedl, 1961)

Holotype: MNHN - Paris

Diagnosis. A vertical declivity encircled on declivital margin by five spines on each side on interstriae 3, 4 or 5, 6, 8, 9 in a crowned pattern. First spine longest, longer than the combined length of first and second ventrite, fourth and fifth pair almost as long, second and third pair 1/3 the length or less. Striae noticeably impressed, most apparent on posterior half of elytra (excluding the declivity), gives the elytra a grooved pattern.

Distribution. Madagascar

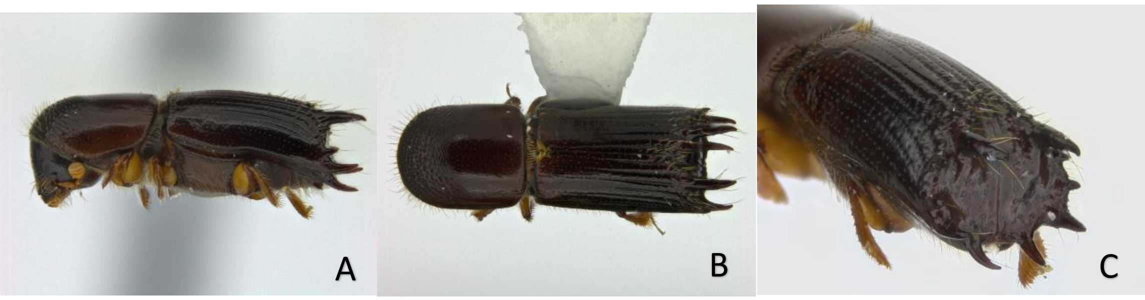

Figure 4.12. Specimen directly compared with paratype of *X. diapiformis* in lateral (**A**), dorsal (**B**) and declivital view (**C**).

Xyleborinus quadrispinis (Schedl, 1953)

Holotype: NHMW - Wien

Diagnosis. A vertical declivity encircled by four pairs of spines on interstria 3, 6, 7, 9 in a crowned pattern. Sharp tubercles on interstria 4 and 5. First spine longest, longer than the combined length of third and fourth ventrite. Last spine almost as long as first. Second spine is 1/3 the length of first spine. Spine three is an intermediate of spine two and four.

Distribution. Madagascar

Figure 4.13. Holotype of *X. quadrispinis* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus quadrispinosus **(Eichhoff, 1878)**

Syntypes: IRSNB - Brussel

Diagnosis. A vertical declivity encircled on declivital margin by four very large spines on each side in a crowned pattern. All spines are of similar length, as long as or longer than the combined length of first and second ventrite, on interstriae 3, 5&6, 7&8, 9. Striae noticeably impressed, most apparent on posterior half of elytra (excluding the declivity), gives the elytra a grooved pattern.

Distribution. Madagascar, South Africa

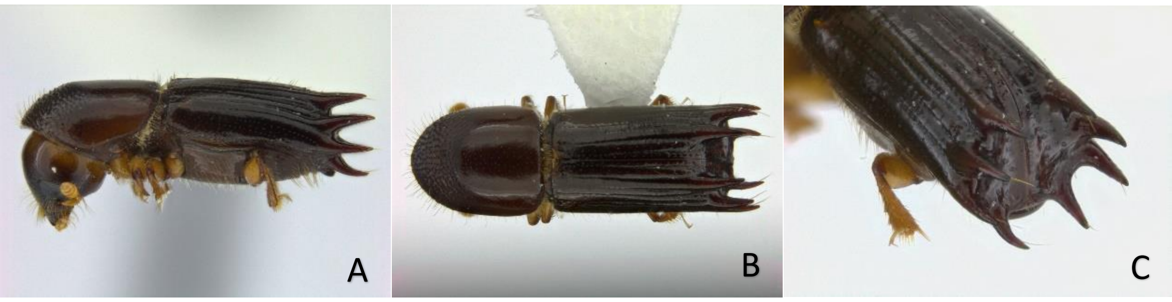

Figure 4.14. Specimen of *X. quadrispinosus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus signatipennis **(Schedl, 1961)**

Holotype: MNHN - Paris

Diagnosis. A vertical declivity encircled by three long, but thin, pair of spines on interstriae 4, 8, 9 and one small pair of spines on interstriae 6 in a crowned pattern. First and last pair of spines are the longest, longer than the combined length of second and third ventrite, second pair of long spines are about half the length of the first pair. Several sharp tubercles on top of declivity. Striae noticeably impressed, gives the elytra a grooved pattern.

Distribution. Madagascar

Figure 4.15. Specimen directly compared with paratype of *X. signatipennis* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spS Eliassen & Jordal, sp. nov.

Holotype: ZMBN - Bergen

Diagnosis. Declivity vertical, truncated, encircled on declivital margin by four pairs of large spines in a crowned pattern on interstriae 3, 5&6, 7, 9 (last close to elytral apex). Pair one and four longest, as long as length of ventrite two and three combined. Pair two and three shorter, slightly shorter than length of second ventrite. Striae slightly impressed.

Distribution. Madagascar

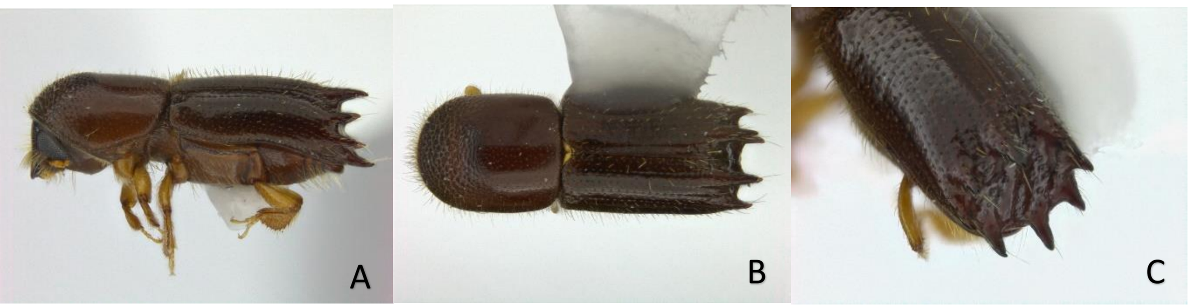

Figure 4.16. Holotype of *X.* spS in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus octospinosus (Eggers, 1920)

Lectotype: NHMW - Wien

Diagnosis. Declivity nearly vertical, steep, encircled by four pairs of spines on interstriae 2&3, 4, 6 and 9 (or interstriae 2 on bottom of declivity), appearing crown-like. First, third and fourth spine approximately of the same length, no longer than length of third ventrite. Second spine slightly shorter and points upward more than first and third spine, second spine may have two tips on some specimens. Tubercles under third pair of spines, and several tubercles and granules on top of declivity.

Distribution. Tanzania, Madagascar

Comments. *X. octospinosus* colonized Tanzania coming from Madagascar less than 1 Ma (see **Figure 2.2**) and has remained isolated from its Malagasy relatives ever since. However, not enough time has passed for it to radiate into a completely separate species from individuals on Madagascar described as *X. mitosomipennis* (Schedl, 1953). It appears that *X. octospinosus* represents a mainland branch of *X. mitosomipennis* which is found on Madagascar. *X. mitosomipennis* is therefore synonymized with *X. octospinosus* based on molecular data and comparisons between lectotypes of *X. octospinosus* and *X. mitosomipennis*, both deposited in NHMW – Wien.

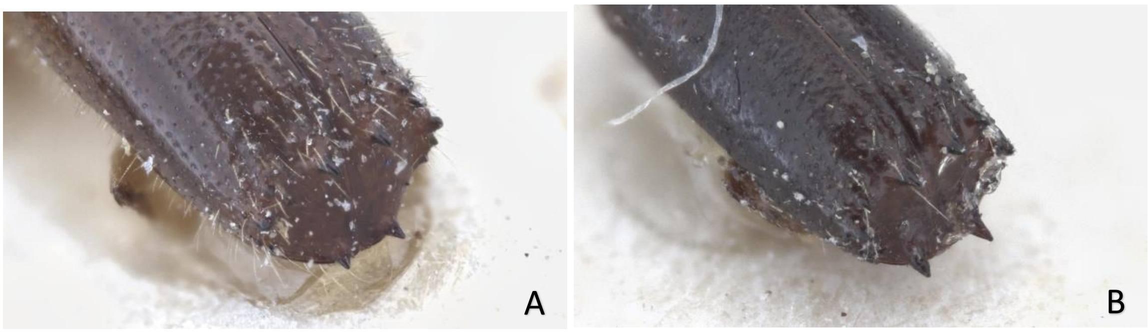

Figure 4.17. Comparing lectotypes of *X. mitosomipennis* (**A**) and *X. octospinosus* (**B**)*;* very similar, but note somewhat larger bottom spines in the latter specimen.

Figure 4.18. Specimen directly compared with lectotype of *X. octospinosus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spZ Eliassen & Jordal, sp. nov.

Holotype: ZMBN - Bergen

Diagnosis. Declivity steep, encircled by four pairs of spines on interstriae 2&3, 4, 6 and 9 (or interstriae 3 near elytral apex), appearing crown-like; spines approximately of the same length, no longer than length of third ventrite. First three pairs of spines very similar in shape, evenly separated. Tubercles under the third pair of spines, and several tubercles and granules on top of declivity.

Distribution. Madagascar

Figure 4.19. Holotype of *X.* spZ in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spG Eliassen & Jordal, sp. nov.

Holotype: ZMBN - Bergen

Diagnosis. First half of declivity sloped, second half steeply curved, impressed first and second interstria, appearing as excavated cleft. Cleft; first and second interstria smooth; first stria only has sharp granules. Interstria 3 and beyond all have spines and/or tubercles. Gives appearance of two swollen areas with more than 10 spines and tubercles each, separated by cleft. Interstria 3 has the largest spine, situated halfway down declivity, as long as length of third ventrite, other spines under half its size. Vestiture dense on declivity.

Distribution. Madagascar

Figure 4.20. Holotype of *X.* spG in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus mitosomiformis (Schedl, 1953)

Lectotype: NHMW - Wien

Diagnosis. Declivity near vertical, steep, encircled on declivital margin by at least 5 small spines on each side from interstriae 4 and beyond. The spines do not differ greatly in size, all shorter than length of third ventrite. The first interstria has a row of three very small spines present on declivity.

Distribution. Madagascar

Figure 4.21. Lectotype of *X. mitosomiformis* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus mitosomus (Schedl, 1965)

Holotype: NHMW - Wien

Diagnosis. Declivity near vertical, steep, encircled by a tiny rim on declivital margin on interstria 6 to 9. The most pronounced structures on the rim are three tubercles on interstria 6, 8 and 3 near elytral apex. Tubercle on interstria 4 may also be present.

Distribution. Madagascar

Comment. *X. spinosus* (Schaufuss, 1891) and *X. mitosomus* were synonymized in 1977 by Schedl. However, inspection of types in the Wien collection reveals this synonymizing is an error. The holotype of *X. mitosomus* is clearly different from its paratypes. The holotype of *X. spinosus* is lost, but the paratypes of *X. mitosomus* match the original description of *X. spinosus* by Schaufuss (see **Figure 4.11** for reference). The species name *X. mitosomus* is therefore reinstated.

Figure 4.22. Holotype of *X. mitosomus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

***Xyleborinus* spC Eliassen & Jordal, sp. nov.**

Holotype: ZMBN - Bergen

Diagnosis. Declivity vertical, steep, encircled by small rim on declivital margin, with fused tubercles, appearing from interstria 4 or 5. Rim ends near elytral apex with a pair of slightly larger tubercles, about the length of the pedicel. 2-4 pairs of tubercles and/or sharp granules run down the declivity on interstriae 1.

Distribution. Madagascar

Figure 4.23. Paratype of *X.* spC in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus syzygii (Schedl, 1959)

Holotype: BMNH - London

Diagnosis. Declivity sharply curved, vertical. Top of declivity only has a couple of barely visible granules from interstria 1 to 3. 3-4 sharp tubercles on declivital margin from interstria 6 to 9. Declivity otherwise smooth.

Distribution. Tanzania

Figure 4.24. Paratype of *X. syzygii* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Undescribed *[Xyleborinus margino-tuberculatus]*

Holotype: None, undescribed

Diagnosis. Declivity near vertical, steep. Several tubercles or granules present from interstria 1 to 4 on top of declivity. 5 small spines and sharp tubercles on each side encircle the declivity on declivital margin from interstria 5 and down. Declivity otherwise smooth.

Distribution. Madagascar

Comment. This entry is based on a singleton labeled *"Xyleborus margino-tuberculatus"* that was found in the Wien collections. The specimen does not resemble any known species. Its labels have little information and it is therefore not given a formal description. It is included for future reference.

Figure 4.25. Undescribed singleton in lateral (**A**), dorsal (**B**) and declivital view (**C**)

***Xyleborinus forficuloides* (Schedl, 1951)**

Lectotype: NHMW - Wien

Diagnosis. Curved declivity only has two pairs of spines present posterior laterally near bottom of declivity on interstriae 3-5 (placement may be difficult to assess) and 8. *X. forficuloides dentibarbis* (Schedl, 1961) has an extra smaller spine on interstria 3. Spines vary in size from slightly longer than length of third ventrite to as long as length of second ventrite.

Distribution. Madagascar

Comments. Three sub-species are described, *X. forficuloides forficuloides* (Schedl, 1951)*, X. forficuloides pinguis* (Schedl, 1961) and *X. forficuloides dentibarbis* (Schedl, 1961). Genetic data was obtained from the first two sub-species, but not from *X. forficuloides dentibarbis.* Its genetic relationship with the other two sub-species is therefore not known, it may perhaps represent a different species.

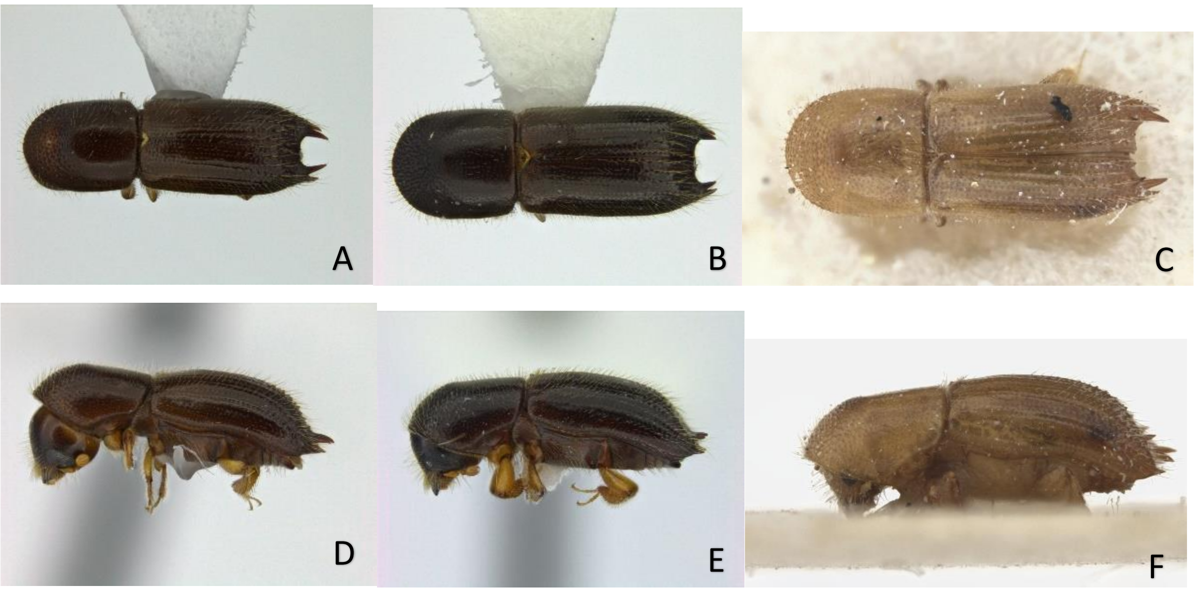

Figure 4.26. Morphological variation in X. *forficuloides forficuloides* (**A, D**) (specimen directly compared with lectotype), *X. forficuloides pinguis* (**B, E**) (specimen directly compared with paratype) and X. *forficuloides dentibarbis* (**C, F**) (paratype).

Xyleborinus forficulus (Eggers, 1922)

Syntypes: Methner Collection and USNM, Washington

Diagnosis. Declivity sloped, encircled on declivital margin by four spines on each side on interstriae 3, 4, 5&6, 7&8 (small spines or sharp tubercles may be present above some spines). Lowermost pair longest, longer than length of second ventrite, hooked inwards with tips facing each other.

Distribution. Angola, Kenya, Mozambique, South Africa, Tanzania, Zaire, Zimbabwe and Zambia

Figure 4.27. Specimen of *X. forficulus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spR Eliassen & Jordal, sp. nov.

Holotype: ZMBN - Bergen

Diagnosis. Declivity sharply curved. Two pairs of spines, on interstriae 3 and 9 of equal size, slightly shorter than length of fourth ventrite; first pair of spines located almost halfway down declivity, second pair at bottom. Two pairs of tubercles, on interstriae 6 and 7.

Distribution. Madagascar

Figure 4.28. Holotype of *X.* spR in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus aemulus (Wollaston, 1869)

Holotype: BMNH - London

Diagnosis. Declivity vertical, steep. Two pairs of spines, on interstriae 3 and 8 of equal size, about the length of third ventrite. First spine close to top of declivity, second spine on declivital margin near bottom of declivity. More than two sharp tubercles from interstria 4 to 7 and at least one small tubercle pair on top of declivity.

Distribution. Angola, Namibia, Botswana, South Africa, St. Helena, Madagascar

Comment. *X. spinifer* (Eggers, 1920) is synonymized with *X. aemulus* based on comparisons between holotypes (deposited in MNB - Berlin and BMNH - London respectively) done by Bjarte Jordal.

Figure 4.29. Specimen of *X. aemulus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus alienus (Schedl, 1977)

Holotype: NHMW - Wien

Diagnosis. Declivity is very gently sloped on first half, followed by a very sharp curve making the second half nearly vertical. Declivity has three spines on interstria 3, 4, 7 or 8, none longer than length of antennal club. First and second spine placed right next to each other, parallelly, on top of declivital cliff. Body is unusually stocky for *Xyleborinus.*

Distribution. South Africa

Figure 4.30. Holotype of *X. alienus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus bicinctus (Schedl, 1965)

Holotype: NHMW - Wien

Diagnosis. Excavated declivity occupying 3/7 of the elytra encircled by spines on declivital margin. Spines on interstria 1 to 4 thick, spine on interstria 3 thickest. Spine-like flanks on interstriae 8, close to elytral apex, longer than length of second ventrite. The margin between the elytral apex and tip of bottom flanks has a 90° angle. This makes the space between bottom flanks look rectangular, like the bottom half of a bottle, in dorsal view. Four sharp tubercles from interstria 5 to 8.

Distribution. Madagascar

Figure 4.31. Holotype of *X. bicinctus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spO Eliassen & Jordal, sp. nov.

Holotype: ZMBN - Bergen

Diagnosis. Declivity coarse, excavated, occupying 3/7 of the elytra, encircled by spines on declivital margin. Three spines on interstria 1, 3, 4 as thick as long; third spine longest of the three, as long as length of ventrite three and four combined, first spine under half that size, second spine is an intermediate. Spine-like flanks on interstriae 8, close to elytral apex, almost as thick and long as length of second ventrite; margin between elytral apex and tip of bottom flanks curved, makes the space between bottom flanks look like a half circle in dorsal view. Small spines on interstria 5, 7, 8; shorter and considerably thinner than other spines, barely longer than length of fourth ventrite.

Distribution. Madagascar

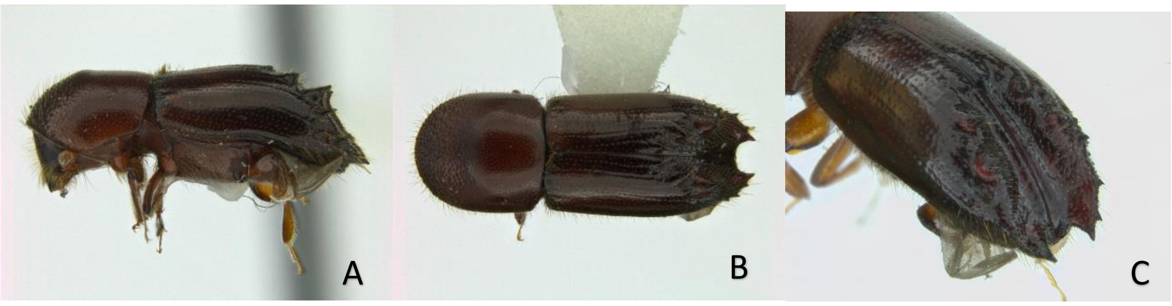

Figure 4.32. Paratype of *X.* spO in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus **spU Eliassen & Jordal, sp. nov.**

Holotype: ZMBN - Bergen

Diagnosis. Declivity appear excavated, occupying 3/7 of the elytra, encircled by spines and tubercles on declivital margin. Three spines on interstria 1, 2, 3 as thick as long; third spine double the size of the other two, as long as length of pedicel and funicles combined. Spine on interstria 4 as long as third pair, but considerably thinner. Spine-like flanks on interstria 8, close to elytral apex, almost as thick and long as length of second ventrite; margin between elytral apex and tip of bottom flanks curved, makes the space between bottom flanks look like a half circle in dorsal view. 4-5 sharp tubercles on interstria 4 to 8, barely longer than length of pedicel.

Distribution. Madagascar

Figure 4.33. Holotype of *X.* spU in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus **spP Eliassen & Jordal, sp. nov.**

Holotype: ZMBN - Bergen

Diagnosis. Declivity coarse, impressed, appearing excavated with three pairs of spines on interstriae 3, 4, 7&8. Pair two and three on declivital margin, of very large size, third pair is about the same length as second ventrite, second pair is even longer. First pair is slightly longer than length of third ventrite. Sharp tubercles present on top of declivity.

Distribution. Madagascar

Figure 4.34. Holotype of *X.* spP in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus cuneidentis **(Schedl, 1961)**

Holotype: MNHN - Paris

Diagnosis. Declivity evenly curved. Four pairs of spines on interstriae 3, 6, 7, 9 form a small circle on bottom half of declivity. Spine on interstria 3 longest, longer than length of third ventrite, but not length of third and second ventrite combined. Sharp tubercles present on interstriae 1 to 3 on top half of declivity.

Distribution. Madagascar

Figure 4.35. Paratype of *X. cuneidentis* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus marcidus **(Schedl, 1965)**

Holotype: NHMW – Wien

Diagnosis. Declivity has two long posterior lateral flanges. Gives the entire declivity a U-shape in dorsal view. Three spines present dorsally on each flange. A highly unique shape for Afrotropical *Xyleborinus.*

Distribution. Madagascar

Figure 4.36. Holotype of *X. marcidus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus dentellus **(Schedl, 1953)**

Lectotype: NHMW - Wien

Diagnosis. Declivity sloped, encircled on declivital margin by 5-6 pairs of spines on each side from interstriae 3 to 9, declivity otherwise smooth. Longest spine on interstria 6-7, about the length of or slightly longer than third ventrite, followed in length by spines on interstria 3 and 9. Bottom two spines on interstria 6-7 and 9 placed posterior laterally. 2-3 small spines on interstria 4 to 6, may reach length of fourth ventrite.

Distribution. Madagascar, Congo

Comment. *X. forcipatus* (Schedl, 1957) is synonymized with *X. dentellus* based on comparisons between *X. dentellus* holotype and *X. forcipatus* paratype, both deposited in NHMW – Wien.

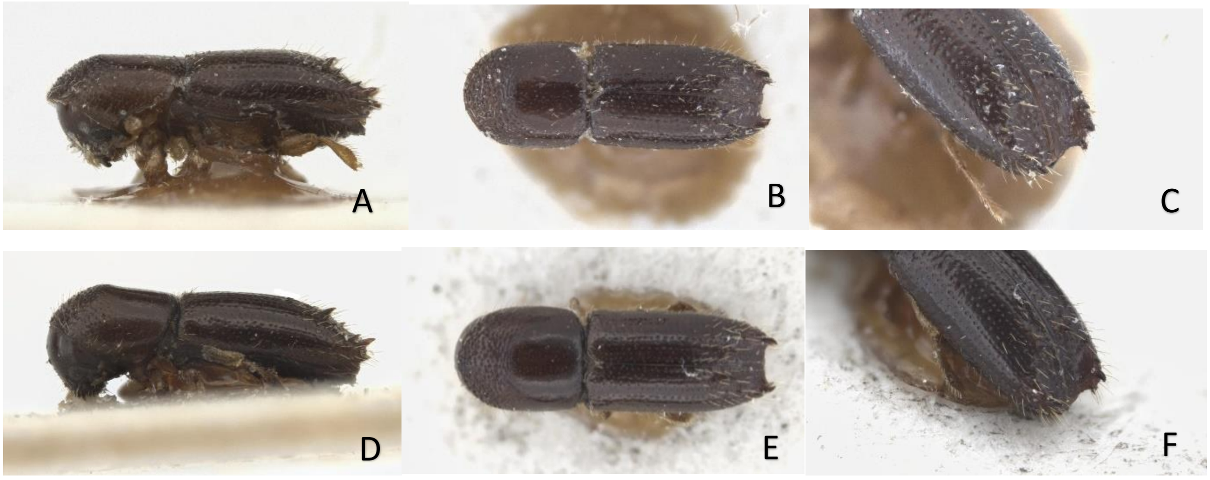

Figure 4.37. Comparing lectotype of *X. dentellus* in lateral (**A**), dorsal (**B**) and declivital view (**C**) and paratype of *X. forcipatus* in lateral (**D**), dorsal (**E**) and declivital view (**F**)

Xyleborinus pseudopityogenes (Eggers, 1943)

Holotype: NHMW - Wien

Diagnosis. Declivity sloped, encircled by 5 pairs of spines and sharp tubercles on declivital margin from interstriae 3 to 9, declivity otherwise smooth. Longest spine on interstria 6-7, about the length of or slightly longer than third ventrite, followed in length by spines on interstria 3 and 9. Bottom two spines on interstria 6-7 and 9 placed posterior laterally. Two sharp tubercles on interstria 4 and 5.

Distribution. Congo, Namibia, Mozambique, South Africa

Comment. NHMW has some *X. pseudopitygenes* specimens wrongly labeled *X. spinifer.*

Figure 4.38. Holotype of *X. pseudopityogenes* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus andrewesi (Blandford, 1896)

Holotype: BMNH - London

Diagnosis. Declivity elongated, extended apically. Elytral apex produced, tapering, giving declivity the appearance of a flattened cone in dorsal view. Rows of sharp tubercles present on each interstria on declivity.

Distribution. Worldwide. In the Afrotropic: Congo, Tanzania, Kenya, Zambia, Seychelles

Comments. *X. mimosae* (Schedl, 1957) is synonymized with *X. andrewesii* based on *X. mimosae* paratype, and descriptions and several specimens of the morphologically diverse and wordwide *X. andrewesii* (Hulcr and Cognato, 2013). The apically extended declivity of *X. andrewesii* is not present in any other Afrotropical species, making it less likely that the trait appeared in a species endemic to the Afrotropic.

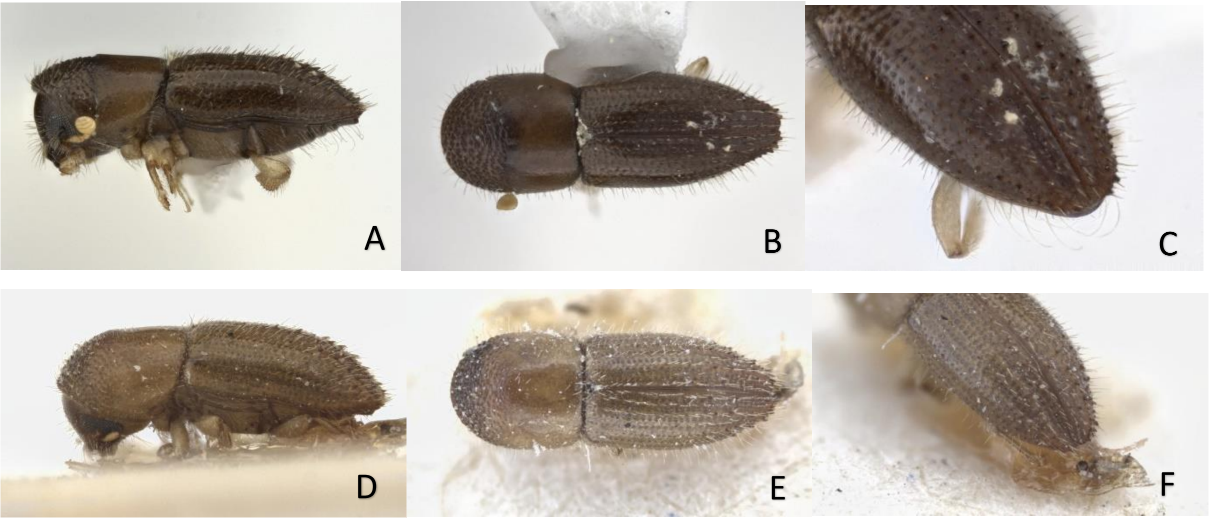

Figure 4.39. Comparing specimen of *X. andrewesii* in lateral (**A**), dorsal (**B**) and declivital view (**C**) and paratype of *X. mimosae* in lateral (**D**), dorsal (**E**) and declivital view (**F**)

Xyleborinus pilosellus (Schedl, 1957)

Holotype: MRCB - Tervuren

Diagnosis. Declivity evenly curved, completely without spines, tubercles or sharp granules. Declivity has no distinguishing traits, unique for Afrotropical *Xyleborinus.*

Distribution. Congo

Figure 4.40. Paratype of *X. pilosellus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus spinipes (Schedl, 1957)

Holotype: MRCB - Tervuren

Diagnosis. Declivity sloped, rows of sharp tubercles present on interstriae 3 and several sharp tubercles present from interstriae 4 and beyond, including on posterior elytral margin. Granules on interstriae 1, interstriae 2 smooth. Hooked short pair of spines on the elytral apex point outward from each other in dorsal view.

Distribution. Congo

Figure 4.41. Unspecified type of *X. spinipes* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus polyalthiae (Schedl, 1952)

Holotype: MRCB - Tervuren

Diagnosis. Declivity sloped, first and second interstriae are smooth and glabrous (except on top of declivity), other interstriae have rows of sharp tubercles or granules and setae present on declivity. Third interstriae have 1-2 tubercles, may vary between elytra on the same specimen. Three pairs of spines on posterior margin of elytra are of equal small size and evenly spaced. Declivital surface (ignoring spines) smooth.

Distribution. Congo

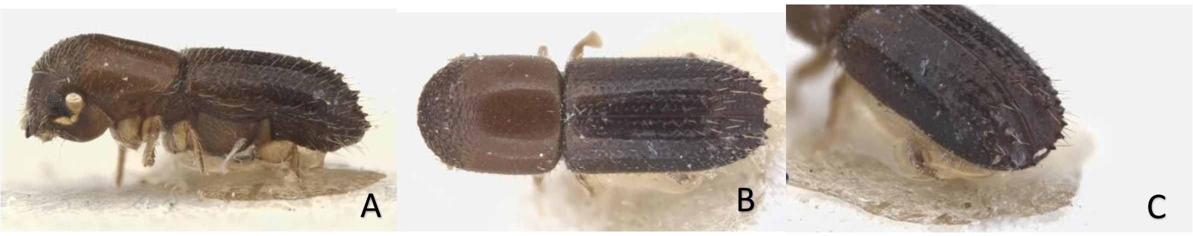

Figure 4.42. Paratype of *X. polyalthiae* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus subsulcatus (Eggers, 1927)

Holotype: MRCB - Tervuren

Diagnosis. Declivity sloped, first and second interstriae are smooth and glabrous (except on top of declivity), other interstriae have rows of sharp tubercles or granules and setae present on declivity. Third interstriae have 1-2 tubercles, may vary between elytra on the same specimen. Four pairs of sharp tubercles on posterior margin of elytra irregular and clearly differ in size. Declivital surface (ignoring spines) somewhat rugged.

Distribution. Congo, Zambia

Figure 4.43. Specimen of *X. subsulcatus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus exiguus (Walker, 1859)

Holotype: BMNH, London

Diagnosis. Declivity curved on top and bottom, middle half is sloped. Second interstriae are smooth and glabrous (except on top of declivity), other interstriae have rows of small spines, sharp tubercles and long interstrial setae present on declivity. Spines may be longer than they are thick. Five or less small spines and/or sharp tubercles on first interstria between top of declivity and elytral apex. Three pairs of small spines or sharp tubercles on posterior margin of elytra are of equal size and evenly spaced, longer than they are thick. About 1.6-1.8mm in length.

Distribution. Worldwide. In the Afrotropic: Gabon, Cameroon (first record)

Figure 4.44. Specimen of *X. exiguus* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus heveae (Schedl, 1957)

Holotype: MRCB – Tervuren

Diagnosis. Declivity gently curved, almost sloped, second interstriae are smooth and glabrous (except on top of declivity), other interstriae have rows of sharp tubercles and setae. Interstriae 1 and 3 are smooth and glabrous on posterior third of declivity. Stria are impressed on posterior 2/3 of elytra, including the declivity. 2.0mm in length.

Distribution. Congo, Sierra Leone (first record)

Figure 4.45. Paratype of *X. heveae* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus namibiae (Schedl, 1982)

Holotype: TMP - Pretoria

Diagnosis. Declivity curved, quite steep on lower half. Second interstriae are smooth, other interstriae have rows of tubercles and setae present on declivity. Less than five tubercles on first interstria between top of declivity and elytral apex. Three pairs of sharp tubercles on posterior margin of elytra are of equal size and evenly spaced, longer than thick. About 2.1 mm in length.

Distribution. Namibia

Figure 4.46. Specimen of *X. namibiae* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus saxeseni (Ratzeburg, 1837)

Holotype. Unknown

Diagnosis. Declivity curves steeply, making it vertical on second half. Second interstriae are smooth (except on top of declivity), other interstriae have rows of tubercles and setae present on declivity. Interstria 1 is smooth and glabrous on posterior 1/3 of declivity, less than five tubercles on first interstria between top of declivity and elytral apex. Three pairs of sharp tubercles on posterior margin of elytra. About 2.0-2.2 mm in length.

Distribution. Worldwide. In the Afrotropic: Cameroon, South Africa

Figure 4.47. Specimen of *X. saxeseni* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus sharpae (Hopkins, 1915)

Holotype: USNM - Smithsonian

Diagnosis. Declivity curved, second interstria and posterior 2/3 of fourth interstria smooth and often glabrous, other interstriae have rows of small spines, sharp tubercles and setae present on declivity. Many small spines, may be twice as long as thick, makes declivity appear rugged. Fine erect, long interstrial setae dense. More than five small spines and sharp tubercles on first interstria between top of declivity and elytral apex. Three pairs of small spines on posterior margin of elytra are of equal size and evenly spaced, longer than thick. 1.4-1.5mm in length.

Distribution. Liberia, Tanzania, Sierra Leone (first record), Cameroon (first record)

Figure 4.48. Specimen of *X. sharpae* in lateral (**A**), dorsal (**B**) and declivital view (**C**)

Xyleborinus similans **(Eggers, 1940)**

Holotype: NHMW - Wien

Diagnosis. Declivital curve forms an almost perfect quadrant from declivital top to elytral apex, second interstriae are smooth and glabrous (except on top of declivity), other interstriae have rows of sharp tubercles or granules and setae present on declivity, spines not present. May have granules or tubercles on posterior margin of elytra. Color light brown. About 1.8-2.0mm in length.

Distribution. Angola, Bioko, Ivory Coast, Ghana, Congo, Rep. Congo, Somalia, South Africa

Comments. *Xyleborinus diversus* (Schedl, 1954) and *Xyleborinus sclerocaryae* (Schedl, 1962) are synonymized with *X. similans* based on comparisons between *X. similans* holotype, *X. diversus* lectotype and *X. sclerocaryae* paratype, all deposited in NHMW – Wien. The Wien collections have some specimens that are incorrectly labeled *X. similans.*

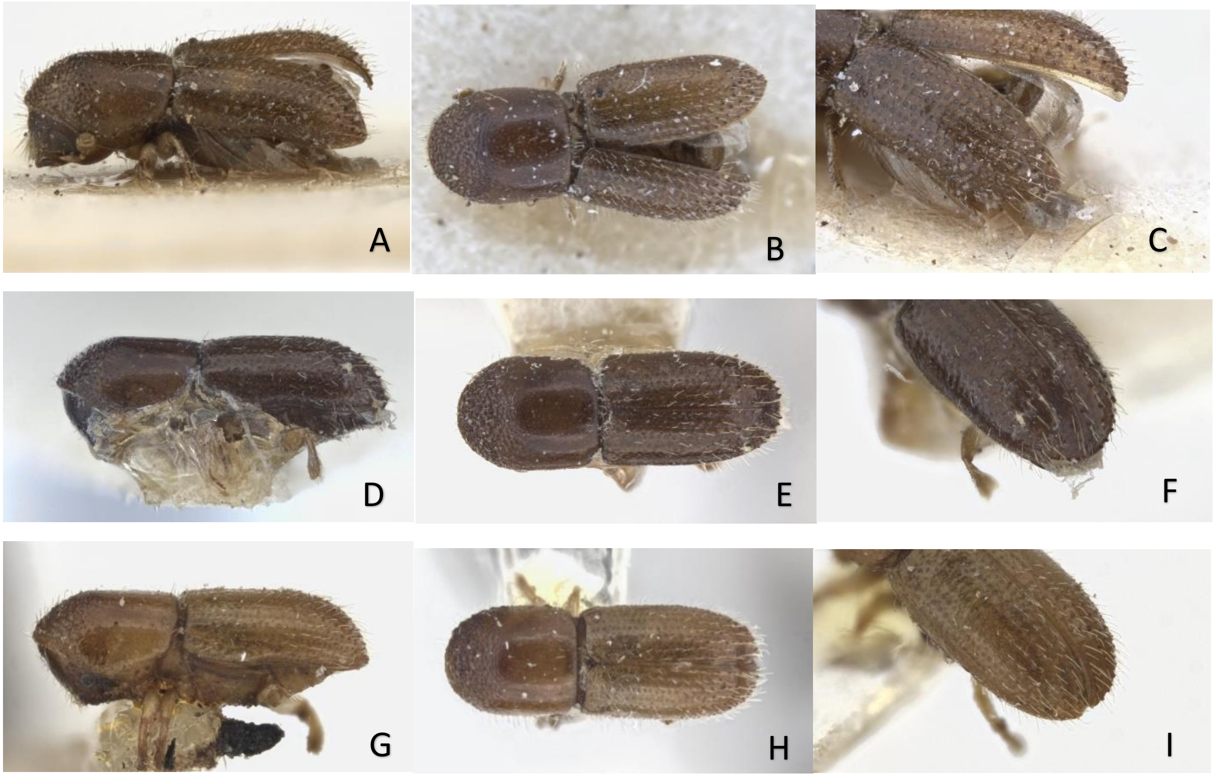

Figure 4.49. Comparing holotype of *X. similans* (**A, B, C**), lectotype of *X. diversus* (**D, E, F**) and paratype of *X. sclerocaryae* (**G, H, I**) in lateral, dorsal and declivital view.

Comment to *X. exiguus, X. heveae, X. namibiae, X. saxesenii, X. sharpae* and *X. similans:* These species are morphologically very similar. However, the molecular data reveals that these species are not necessarily closely related (see **Figure 2.1**) making accurate distinctions between the species important. Careful inspection of multiple specimens was conducted and with the aid of supervisor Bjarte Jordal some small differences were found between each species.

Complete taxonomic revision of Afrotropical *Xyleborinus* summary

Table 12. List of previously described Afrotropical *Xyleborinus* with author, year, distribution and new synonyms. *Xyleborinus gracilipennis* (Schedl, 1957) and *Xyleborinus collarti* (Eggers, 1932) are removed from the genus as they do not have the conical scutellum that defines *Xyleborinus.* They have been placed in the genus they were originally described in, *Xyleborus* Eichhoff, 1864.

Previously described species					**New synonym?**
Genus	**Species**	**Author**	**Year**	**Distribution**	
Xyleborinus	*aduncus*	Schedl	1961	Madagascar	
Xyleborinus	*aemulus*	Wollaston	1869	Angola, Namibia, Botswana, SAfr, St. Helena, Madagascar	*Xyleborinus spinifer* Eggers, 1920
Xyleborinus	*alienus*	Schedl	1977	SAfr	
Xyleborinus	*andrewesii*	Blandford	1896	Worldwide	*Xyleborinus mimosae* Schedl, 1957
Xyleborinus	*armatus*	Schaufuss	1896	Madagascar	
Xyleborinus	*bicinctus*	Schedl	1965	Madagascar	
Xyleborinus	*cuneidentis*	Schedl	1961	Madagascar	
Xyleborinus	*cupulatus*	Schedl	1961	Madagascar	
Xyleborinus	*dentellus*	Schedl	1953	Madagascar, Congo	*Xyleborinus forcipatus* Schedl, 1957
Xyleborinus	*diapiformis*	Schedl	1961	Madagascar	
Xyleborinus	*exiguus*	Walker	1859	Worldwide	
Xyleborinus	*forficuloides*	Schedl	1951	Madagascar	
Xyleborinus	*forficulus*	Eggers	1922	Angola - Kenya - SAfr	
Xyleborinus	*heveae*	Schedl	1957	Congo, Sierra Leone	
Xyleborinus	*marcidus*	Schedl	1965	Madagascar	
Xyleborinus	*mitosomiformis*	Schedl	1953	Madagascar	
Xyleborinus	*namibiae*	Schedl	1982	Namibia	
Xyleborinus	*octospinosus*	Eggers	1920	Madagascar, Tanzania	*Xyleborinus mitosomipennis* Schedl, 1953
Xyleborinus	*pilosellus*	Schedl	1957	Congo	
Xyleborinus	*polyalthiae*	Schedl	1952	Congo	
Xyleborinus	*pseudopityogenes*	Eggers	1943	Congo, Namibiae, Mozambique, SAfr	
Xyleborinus	*quadrispinis*	Schedl	1953	Madagascar	
Xyleborinus	*quadrispinosus*	Eichhoff	1878	SAfr, Madagascar	
Xyleborinus	*saxeseni*	Ratzeburg	1837	Worldwide	
Xyleborinus	*sharpae*	Hopkins	1915	Liberia, Tanzania, Sierra Leone, Cameroon	
Xyleborinus	*signatipennis*	Schedl	1961	Madagascar	
Xyleborinus	*similans*	Eggers	1940	Angola, Bioko, Ivory Coast, Ghana, Congo, Rep. Congo, Somalia, Safr	*Xyleborinus diversus* Schedl, 1954 & *Xyleborinus sclerocaryae* Schedl, 1962
Xyleborinus	*spiculatulus*	Schedl	1965	Grand Comore, Madagascar	
Xyleborinus	*spiculatus*	Schaufuss	1891	Madagascar	
Xyleborinus	*spinipes*	Schedl	1957	Congo	
Xyleborinus	*spinosus*	Schaufuss	1891	Madagascar	
Xyleborinus	*subsulcatus*	Eggers	1927	Congo, Zambia	
Xyleborinus	*syzygii*	Schedl	1959	Tanzania	

Species removed from the genus					**New genus**
Genus	**Species**	**Author**	**Year**	**Distribution**	
Xyleborinus	*gracilipennis*	Schedl	1957	Ghana, Congo	*Xyleborus* Eichhoff, 1864
Xyleborinus	*collarti*	Eggers	1932	Ghana, Cameroon, Congo, Angola, Tanzania	*Xyleborus* Eichhoff, 1865

Table 13. List of species names given new status and new species described in this study.

New status					
Genus	**Species**	**Author**	**Year**	**Distribution**	**Old status**
Xyleborinus	*profundus*	Schedl	1961	Madagascar	*Xyleborinus aduncus profundus Schedl, 1961*
Xyleborinus	*mitosomus* (reinstated)	Schedl	1965	Madagascar	Synonym of *Xyleborinus spinosus* Schaufuss, 1891
New species					
Genus	**Placeholder name**			**Distribution**	
Xyleborinus	spB			Madagascar	
Xyleborinus	spC			Madagascar	
Xyleborinus	spG			Madagascar	
Xyleborinus	spO			Madagascar	
Xyleborinus	spP			Madagascar	
Xyleborinus	spR			Madagascar	
Xyleborinus	spS			Madagascar	
Xyleborinus	spU			Madagascar	
Xyleborinus	spW			Madagascar	
Xyleborinus	spY			Madagascar	
Xyleborinus	spZ			Madagascar	

Key to Afrotropical *Xyleborinus*:

1 Declivity has two long posterior lateral flanges. Gives the entire declivity a U-shape in dorsal view. Three spines present dorsally on each flange ……………………………………………………………………………………………***Xyleborinus marcidus* (*S*chedl, 1965)**

- Not as above……**2**

2 Declivity is very gently sloped on first half, followed by a very sharp curve making the second half nearly vertical. Declivity has three spines on interstria 3, 4, 7 or 8, none longer than length of antennal club. First and second spine placed right next to each other, parallelly, on top of declivital cliff.……………………………………………………***Xyleborinus alienus* (Schedl, 1977)**

- Not as above……**3**

3 Close to the entire declivity is very steep, vertical or nearly vertical. There is a sharp contrast between the declivity and the elytral disc or the declivity is sharply curved at the top (see **Figure 1.2** and **1.4**). Declivity often encircled by spines, rim or flange.…………………………………**4**

- The declivity is sloped, evenly curved, rounded, or may be sharply curved on the second half of declivity (see **Figure 1.3**)……………………………………………………………………………………………**26**

4 The declivity has a wreath or flange encircling the declivital margin (see **Figure 1.5**). Wreaths are characterized as a rim with spines attached, flanges are without spines ……………………………**5**

- Rim on the declivital margin is very small, may only have sharp tubercles attached, or rim is completely absent. Declivity may be encircled by spines, not fused together, in a crowned shape (see **Figure 1.6**)……………………………………………………………………………………………………**13**

5 The declivital flange is completely smooth. Either one pair of small spines on interstria 1 or spines completely absent……**…………………………………. *Xyleborinus cupulatus* (Schedl, 1961)**

- More than one pair of spines on declivity………………………………………………………………………**6**

6 Spines on declivity do not differ much in length. No spines longer than length of fourth ventrite (ventrite length always measured laterally)……………………………………………………………**7**

- Declivity has at least one pair of spines longer than length of fourth ventrite. This includes spine-like flanks on bottom of declivity………………………………………………………………………………**8**

7 Declivital spines on interstria 3 and 9 are the longest. Declivital surface concave. Some spines may have two tips ………………………………………………………… ***Xyleborinus* spB Eliassen & Jordal**

- No spines on declivity stand out. Declivital surface slightly convex. Some spines may have two tips…………………………………………………………………….……………… ***Xyleborinus* spW Eliassen & Jordal**

8 Declivity has three short spines on interstria 1, 2, 3 (third spine sometimes extends to interstria 4). From interstriae 4-5 and beyond a continuous flange, ends with spine-like flanks……………………………………………..…………………………………………………………………….**9**

- Declivity has a spiny wreath. 6-10 pairs of spines that clearly vary in size makes the wreath very irregular. The number and length of spines are often asymmetrical between elytra on the same individual………………………………………………………………………………………………….**11**

9 A small swelling or elevation present on the inside of the two flanks on the bottom of the declivital flange…………..……………………………………………… ***Xyleborinus profundus* (Schedl, 1961)**

\- The inside of the two flanks on the bottom of the declivital flange is smooth…………………….**10**

10 From interstria 5 the flange is continuous and has a very smooth edge. Very similar to *X.* spY, (see **Figure 3.13**)……………………………………………………..***Xyleborinus aduncus* (Schedl, 1961)**

- From interstria 4 the flange is continuous, but it has an uneven, crested, almost serrated edge. Very similar to *X. aduncus* (see **Figure 3.13**)……………. ***Xyleborinus* spY Eliassen & Jordal**

11 The spine on interstria 4 is the longest, longer than length of third ventrite, spine on interstria 2 as long or slightly shorter. The last spines on interstria 5 to 8 are small, half the length of longest spine or shorter………………………………***Xyleborinus spinosus* (Schaufuss, 1891)**

- Spine on interstria 4 and 8 are longest, of approximately equal length, longer than length of third ventrite. Spines on interstria 5 and 6 may be as long or slightly shorter……………………**12**

12 Spines on the declivity gape very slightly more upward than in *X. spiculatus*, probably caused by the declivity being slightly less vertical.………….…… ***Xyleborinus spiculatulus* (Schedl, 1965)**

- Spines on the declivity gape very slightly less upward than in *X. spiculatulus*, probably caused by the declivity being slightly more vertical. The difference is cryptic (see **Figure 4.10**) ………………………………………………………………………… ***Xyleborinus spiculatus* (Schaufuss, 1891)**

13 At least on pair of spines on declivity longer than the combined length of third and fourth ventrite. Declivity encircled on declivital margin by at least three pairs of long spines making the declivity appear crowned (see **Figure 1.6**)……………….………………………………………..………**14**

- All spines on declivity are shorter than the combined length of third and fourth ventrite……**18**

14 Striae noticeably impressed, most apparent on posterior half of elytra (excluding the declivity). Gives the elytra a grooved pattern…………………………………………………………..…………**15**

- Striae only slightly impressed…………………………………………..……………………………..………………..**17**

15 Declivity has four pairs of very long spines of similar length, as long as or longer than the combined length of first and second ventrite, on interstriae 3, 5&6, 7&8, 9 ……………………………………………………………………………***. Xyleborinus quadrispinosus* (Eichhoff, 1878)**

- The longest spines on declivity are twice the length or longer than the smallest spines ….….**16**

16 Declivity has five pairs of spines on interstriae 3, 4 or 5, 6, 8, 9. First pair is longest, fourth and fifth pair almost as long, second and third pair 1/3 the length of first pair or less ………...…......................................***Xyleborinus diapiformis* (Schedl, 1961)**

- Declivity with three long, but thin, spines on interstria 4, 8, 9. First and third pair double the length of second pair. There is a small spine on interstria 6. Several sharp tubercles on top of declivity.……………………………….…………………………… ***Xyleborinus signatipennis* (Schedl, 1961)**

17 Declivity has four spines on interstria 3, 5&6, 7, 9. Spine one and four longest, as long as length of ventrite two and three combined. Spine two and three somewhat shorter ……………………………………………………………………………………………***Xyleborinus* spS Eliassen & Jordal**

- Declivity has four spines on interstria 3, 6, 7, 9. Two sharp tubercles on insterstria 4 and 5. Spine one and four longest, each about the length of third and fourth ventrite combined. Spine one is three times longer than spine two…………***Xyleborinus quadrispinis* (Schedl, 1953)**

18 Four spines on interstria 2 or 3, 4 or 5, 6, 9 (last spine may be on interstria 3 on elytral apex). First spine on the topmost part of the declivity, other spines on declivital margin.……………**19**

- Not as above………………………………………………………………….…………………………………………….**20**

19 Declivity has four spines on interstria 3, 4 or 5, 6, 9(3) where the first, third and fourth are of equal size. The second pair is slightly shorter and points more upward than first and third spine, second spine may have two tips on some specimens. Tubercles present on top of declivity…………………………………………………..……………… ***Xyleborinus octospinosus* (Eggers, 1920)**

- The declivity has four spines on interstria 2&3, 4, 6, 9(3) of approximately the same size. First three spines very similar in shape and angle.……………………***Xyleborinus* spZ Eliassen & Jordal**

20 Two spines on interstria 3, 8 or 9 are larger than other spines and tubercles on declivity……**21**

\- Two pairs of spines are not noticeably larger than other spines and tubercles on declivity….**22**

21 First spine pair is not on top, but halfway down the declivity. Second spine pair on interstriae 9. Two sharp tubercles on interstria 6 and 7……..………………***Xyleborinus* spR Eliassen & Jordal**

- First spine pair close to the top of declivity. Second spine pair on interstriae 8. More than two sharp tubercles from interstria 4 to 7 and at least one small tubercle pair on top of declivity ……………………………………………………………………………***Xyleborinus aemulus* (Wollaston, 1869)**

22 First interstria has a row of 2-4 sharp tubercles present on declivity……………………………...**23**

- A row of tubercles not present on first interstria on declivity. Tubercles may be present on first interstria on top of declivity……………………………………………………………………………………..**24**

23 Tiny rim with tubercles on declivital margin. The bottom pair of spines on declivity are very small, but more pronounced than other spines/tubercles ………………………………………………………………………………………***…Xyleborinus* spC Eliassen & Jordal**

- At least 5 pairs of small spines encircle the declivity on declivital margin from interstriae 4 and beyond. Spines do not differ greatly in size…..***Xyleborinus mitosomiformis* (Schedl, 1953)**

24 A tiny rim on declivital margin from interstria 6 to 9. The most pronounced structures on the rim are three tubercles on interstria 6, 8 and 3 near elytral apex. Tubercle on interstria 4 may also be present…………………………………………………………… ***Xyleborinus mitosomus* (Schedl, 1965)**

- The declivital margin does not have a tiny rim………………………………………………………………..**25**

25 Only a couple of barely visible granules present on top of sharply curved declivity on interstria 1 to 3. 3-4 sharp tubercles on declivital margin from interstria 6 to 9 ……………………………………………………………………………………..***Xyleborinus syzygii* (Schedl, 1959)**

\- Several tubercles and granules present on interstria 1 to 4 on top of steep declivity. 5 small pairs of spines and sharp tubercles encircle the declivity on the declivital margin from interstriae 5 and down.…………………..………. **Undescribed *Xyleborinus [margino-tuberculatus]***

26 Declivity is completely without spines, tubercles or sharp granules ……………………………………………………………………………………..***Xyleborinus pilosellus* (Schedl, 1957)**

- Spines, tubercles and/or sharp granules are present on declivity…………………………………………**27**

27 Declivity only has two pairs of spines present posterior laterally near bottom of declivity on interstria 3-5 (placement may be difficult to assess) and 8, may have an extra smaller spine or tubercle on interstria 3. Spines vary in size from slightly longer than length of third ventrite to as long as length of second ventrite……………………….***Xyleborinus forficuloides* (Schedl, 1951)**

- Not as above……**28**

28 At least one pair of spines on declivity as long as length of second ventrite or longer. This includes spine-like flanks on bottom of declivity…………………………………………………………...**29**

- All spines on declivity are shorter than length of second ventrite……………………………………**33**

29 Under 3.0 mm in length. Declivity encircled by four spines on declivital margin on interstria 3, 4, 5&6, 7&8 (small spines or sharp tubercles may be present above some spines). Lowermost pair longest, hooked inwards with tips facing each other ……………………………………………………………………………***Xyleborinus forficulus* (Eggers, 1922)**

- Over 3.0 mm in length………………………………………………………………………………………….**30**

30 On declivity one pair of medium sized spines on interstriae 3 are followed by two very large pairs of spines on interstriae 4 and 7&8 on declivital margin. Last two pairs of spines at least as long as length of second ventrite………………………………… ***Xyleborinus* spP Eliassen & Jordal**

- An excavated declivity occupying 3/7 of the elytra. Spines on declivital margin from interstria 1 to 3 or 4 thick. At the bottom of the declivity a pair of very pronounced spine-like flanks…**31**

31 The margin between the elytral apex and tip of the bottom flanks has a 90° angle. This makes the space between the bottom flanks look rectangular, like the bottom half of a bottle, in dorsal view…………………………………………………………………***Xyleborinus bicinctus* (Schedl, 1965)**

- The margin between the elytral apex and tip of the bottom flanks is curved. This makes the space between the bottom flanks look like a half circle in dorsal view…………………………………**32**

32 Spine on interstria 4 as long as length of pedicel and funicles combined, smaller than spine on interstria 3……………………………………………………………………….. ***Xyleborinus* spU Eliassen & Jordal**

- Spine on interstria 4 is very large, as long and thick as length of ventrite three and four combined, bigger than spine on interstria 3……………………… ***Xyleborinus* spO Eliassen & Jordal**

33 Declivity sloped, encircled by 5-6 pairs of spines or tubercles on declivital margin from interstria 3 to 9, declivity otherwise smooth. Longest spine on interstria 6-7 about the length of or slightly longer than length of third ventrite, followed in length by spines on interstria 3 and 9. Bottom two spines on interstria 6-7 and 9 placed posterior laterally……………………….**34**

- Spines or sharp tubercles present on declivity, not only on declivital margin………..……………**35**

34 Spines on interstria 4 and 5 are very short, no longer than a tubercle. Spines generally shorter than on *X. dentellus*………………………………..…….. ***Xyleborinus pseudopityogenes* (Eggers, 1943)**

- Spines on interstria 4 and 5 may reach length of fourth ventrite. Spines generally longer than on *X. pseudopityogenes*…………………………….……………… ***Xyleborinus dentellus* (Schedl, 1953)**

35 Four pairs of spines on interstriae 3, 6, 7, 9 form a small circle on bottom half of declivity. Spine on interstria 3 largest, longer than length of third ventrite, but not third and second ventrite combined. Sharp tubercles present on interstria 1 to 3 on the top half of declivity ……………………………………….…………………………….……… ***Xyleborinus cuneidentis* (Schedl, 1961)**

- Not as above……………………….……………………………………………………………………………….**36**

36 Declivity has two swollen areas each with more than 10 spines and tubercles separated by a cleft on interstriae 1 and 2. One pair of spines halfway down declivity on interstriae 3 is as long as length of third ventrite, longer than all other spines …………………………………………………………………………………….***Xyleborinus* spG Eliassen & Jordal**

- A single pair of spines is not significantly longer than all other spines present on declivity….**37**

37 The declivity is elongated, extended apically. Elytral apex produced, giving the appearance of a flattened cone in dorsal view……………………………. ***Xyleborinus andrewesi* (Blandford, 1896)**

- The posterior margin of declivity is curved giving a rounded appearance in dorsal view………**38**

38 Hooked short pair of spines on the elytral apex point outward from each other in dorsal view ….………………………………………………………………………. ***Xyleborinus spinipes* (Schedl, 1957)**

- Spine pair (if present) on the elytral apex point posteriorly…………………….…………………...**39**

39 The first and second interstriae stand out by being smooth and glabrous on the declivity. Other interstriae have rows of small spines or sharp tubercles and setae present on declivity………………………………………………………………….…………………………………….**40**

- The first interstriae have rows of spines, tubercles or granules and setae present on declivity, the second interstriae are (mostly) smooth and glabrous……….……………………………..**41**

40 Three pairs of spines on posterior margin of elytra are of equal small size and evenly spaced. Declivital surface (ignoring spines) smooth…………………***Xyleborinus polyalthiae* (Schedl, 1952)**

- Four pairs of small spines and sharp tubercles on posterior margin of elytra irregular and clearly differ in size. Declivital surface (ignoring spines) somewhat rugged ………………………………………………………………………………………***Xyleborinus subsulcatus* (Eggers, 1927)**

41 Interstriae 1 and 3 are smooth and glabrous on posterior third of declivity (except sharp tubercles on bottom). About 2.0-2.2mm in length……………………………………………………………….**42**

- Spines, tubercles or granules and setae run down the entire first and/or third interstria on declivity……**43**

42 Declivity curves steeply on second half, making bottom half vertical ……………………………………………………………………………………… ***Xyleborinus saxeseni* (Ratzeburg, 1837)**

- Declivity gently curved, almost sloped …………………………… ***Xyleborinus heveae* (Schedl, 1957)**

43 Entire declivity (except interstria 2) is filled with small spines that may be twice as long as thick, making declivity appear rugged; vestiture dense. More than five small spines and sharp tubercles on first interstria between top of declivity and elytral apex. About 1.5 mm in length ………………………………………………………………………………………… ***Xyleborinus sharpae* (Hopkins, 1915)**

\- Most spines on declivity are no larger than a tubercle (**Figure 1.7 A**). Five or less small spines and sharp tubercles on first interstria between top of declivity and elytral apex…………………**44**

44 Declivity curved on top and bottom, middle half sloped. About 1.7 mm in length ……………………………………………………………………………………………..***Xyleborinus exiguus* (Walker, 1859)**

- Declivity has an even, or close to even, curve from top of declivity to elytral apex………………**45**

45 Sharp tubercles on posterior margin of elytra are longer than they are thick. About 2.1 mm in length……………………………………………………………………………… ***Xyleborinus namibiae* (Schedl, 1982)**

- Sharp tubercles on posterior margin of elytra (if present) are shorter or as long as they are thick. About 1.8-2.0mm in length……………………………………***Xyleborinus similans* (Eggers, 1940)**

Discussion

Phylogenetic analyzes

Trees started to stabilize very quickly in the MrBayes analyzes. The standard deviation between the two unlinked runs was very small after less than 50 000 generations, with tree likelihoods remaining stable for the rest of the analyzes. This indicates that running 30 million generations in each run was unnecessary. Furthermore, it indicates that the quite complicated models chosen by MrModeltest2 may not have been necessary. Strong results could probably have been achieved with fewer generations and simpler models.

Taurodemus sharpi is placed within a clade of South American *Xyleborinus* (see **Figure 2.1**). There is no strong support for *Taurodemus* Wood, 1980 and *Xyleborinus* forming a monophyletic clade, though other phylogenies have placed single *Taurodemus* species within the *Xyleborinus* clade before (Cognato *et al.*, 2020). In this study, *Taurodemus sharpi* differs significantly in morphology from *Xyleborinus,* but genetically it is more similar to *Xyleborinus* then the other outgroups. Its placement within *Xyleborinus* may be a case of long branch attraction given the relatively long branches between non-Madagascar species, the slightest dissimilarity with the outgroups will almost randomly place a taxa within the ingroup (Bergsten, 2005). More genetic material from *Taurodemus*, aiding in a monophyly, could possibly resolve the issue.

X. spS, *X. signatipennis, X. quadrispinosus* and *X. diapiformis* form a clade in the phylogenetic tree obtained from MrBayes, but it has weak support (see **Figure 2.1**). However, their morphological structure is very similar as they all have a vertical crown-shaped declivity with long spines (see **Figure 1.6**). This trait is unique for these species (including *X. quadrispinis*) which gives very strong morphological support for grouping these species together.

Time tree

There are uncertainties with the calibration of the time tree. The dating of the root node used in this study is based on the stem/crown age of the tribe Xyleborini (Jordal and Cognato, 2012). However, this study only includes four genera from the tribe, and it is uncertain which genus is placed basally in the tribe (Cognato *et al.*, 2011, 2020). The placement of *Xyleborinus* for example is not clear with some studies placing it basally (Cognato *et al.*, 2011) while others place it deeper within the tree (Cognato *et al.*, 2020). The point being, including too few genera can lead to unprecise estimates. If none of the four genera in this study are basal in Xyleborini, then their common ancestor is younger than the maximum age of Xyleborini. This will cause the node ages in the BEAST tree to be unprecise and skew the age of the Malagasy origin.

At what point is a species a species?

Using molecular data to assess species boundaries is especially useful in a tribe like Xyleborini. Their evolutionary adaption to regular inbreeding makes gene flow within a population a rare occurrence (though outbreeding does occasionally happen (Gottlieb *et al.*, 2009; Holzman *et al.*, 2009)). Consequently, the concept of species as natural interbreeding populations does not apply for inbreeding Scolytinae, as each offspring represents a new distinct lineage that will (almost) never again mix with a larger gene pool. As a form of "quasiclonal" reproduction, it shares many similarities to the reproduction of unicellular organisms. Defining the boundaries between species in such organisms is therefore somewhat arbitrary. The best way to delimit species in these organisms is to find a logical "cut-off" point using morphological variation and molecular data. This creates species delimitation that is consistent and facilitates a clear understanding of the genetic and morphological variation that exists within the organism group.

In the present study the interspecific variation in COI correlated quite neatly with species delimitation based on morphology. Morphological differences were always small when COI p-distances were less than 6% between specimens. Most specimens started exhibiting obvious morphological differences and some clades became less well defined when COI p-distances exceeded 7%. It was therefore decided for consistency that COI differences above

7% constituted different species[9]. Some specimens revealed COI divergence over 7% but were quite similar morphologically. Nevertheless, these differences were considered obvious enough to make the separations between similar species unambiguous (the only exception is *X. spiculatus* and *X. spiculatulus*). It is important to note that the specific species delimitation used in this study for Xyleborinus does not necessarily apply to other genera (Cognato et al., 2020). Coupling the BEAST time tree with our species delimitation criteria we find that evolutionary tree splits in the last 1.2 million years have not resulted in morphological and genetic divergence great enough to give rise to new species (see **Figure 2.2**).

In *Xyleborinus,* only the declivity and its spines exhibit great variation between species. The purpose of the declivital spines is not known (Kirkendall *et al.*, 2015). One theory suggests that the spines may be a defense mechanism against intruders who are trying to enter their nest, another that they are used for shoveling wood dust. However, these theories do not explain why they show such great variation between species. As Xyleborini are inbreeding they are not affected by sexual selection, as such the variation may simply be the effect of genetic drift.

Biogeography

The molecular data reveal a monophyletic clade that contains all genetically analyzed species from Madagascar. The clade is surprisingly isolated from other species, giving a strong indication that the genus only colonized Madagascar once. Though already well supported, genetically analyzing the remaining Madagascar species would solidify the hypothesis of a single Madagascar colonization event. Also included in the clade are two specimens from the African mainland, *X. aemulus* and *X. octospinosus*. Based on the unambiguous genetic data, these lineages represent recent back-colonizations from Madagascar to the African mainland.

Only *X. dentellus* gives some doubt to the single colonization hypothesis. *X. dentellus* has no close relatives in the phylogenetic tree, stands out morphologically from other Madagascar species and is placed basally in the Madagascar clade (see **Figure 2.1**). It may perhaps

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[9] The same was true for max patristic distances observed for COI, 28S and CAD combined. Max patristic distances observed under 0.04 correlated with COI differences under 6% (see **Table 9**).

represent a colonization of Madagascar independent from the rest of the Madagascar clade, perhaps more recently, that has retained the morphological structure of its mainland ancestor that is shares with mainland species *X. pseudopityogenes*. It is also possible that *X. pseudopityogenes* and *X. dentellus* recolonized the mainland from Madagascar. Genetic material from mainland specimens of *X. dentellus* and *X. pseudopityogenes* will hopefully shed light on the evolution and colonization history of this group.

The vertical/steep declivity (see **Figure 1.2**) is almost exclusively found in Malagasy species (see **Table 11**). It is characterized as a steep (near) vertical declivity, often with spines, flange or wreath encircling the declivital margin. Its shape creates an obvious contrast between the declivity and elytral disc. The only species not found on Madagascar with the trait are *X. aemulus*[10], *X. syzygii* and *X. alienus.* Genetic data includes *X. aemulus* in the Madagascar clade, so there is reason to believe that the Tanzanian *X. syzygii* and South African *X. alienus* may also be part of the clade. They may represent additional recolonization events from Madagascar to the African mainland. If this is true, then the trait has evolved on Madagascar and is therefore unique to the Madagascar clade[11]. The only species on Madagascar not exhibiting the trait are *X.* spG, *X. forficuloides, X. cuneidentis, X. marcidus, X. dentellus,* and the group containing *X. bicinctus* (**Table 11**). *X. dentellus* and the *X. bicinctus* group are placed basally in the Madagascar clade, indicating that the trait may not yet have evolved in their common ancestor.

The time tree obtained from BEAST indicates that Madagascar was colonized only once by *Xyleborinus* between 8.5 to 11 Ma[12], making the Madagascar clade quite young. This suggests that the clade has experienced a very rapid radiation that has given rise to many unique morphs and species in a relatively short time.

The timing places the colonization event after the ocean currents started travelling from Madagascar to the African mainland (Ali and Huber, 2010). If the colonization happened by "log-rafting", then the genus traveled against the ocean currents when it colonized Madagascar. Though somewhat uncommon, there are other documented cases of non-

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[10] The synonym *X. spinifer* has reported sightings on Madagascar, so *X. aemulus* may be present on the island.

[11] This does of course not exclude the possibility that the trait has evolved independently in *Xyleborinus* in other parts of the world.

[12] The crown age of the Madagascar clade is 8.48 Ma, the stem age is 10.95 Ma.

marine, non-avian animals colonizing Madagascar in the last 20 million years (Nobre *et al.*, 2010; Samonds *et al.*, 2012; Bukontaite *et al.*, 2015)[13]. The currents also help to explain why the genus only colonized Madagascar once, but has recolonized the African mainland at least twice. Possibly it has occurred more often as judged by morphological similarities to Malagasy species as seen in African *X. quadrispinosus, X. syzygii* and *X. alienus*. Wind currents usually follow the same patterns as ocean currents, but they are not as consistent (Ali and Huber, 2010). The timing is still significant, but not as critical if *Xyleborinus* colonized Madagascar by wind rather than by sea.

It is clear from the phylogenetic and dating analyses that the diversification of *Xyleborinus* is much higher on Madagascar compared to the African mainland, it is possibly the highest in the world. This is noteworthy given the geographic size difference between the mainland and Madagascar and the short evolutionary history of the Madagascar clade. The difference in number of species described, 30 on Madagascar vs. 18 on the African mainland, is not the result of higher collection efforts on Madagascar compared to the mainland. Especially Ghana, Nigeria, South Africa, Zambia and Congo have been thoroughly researched and supervisor Bjarte Jordal has spent twice the amount of time on mainland Africa compared to Madagascar (Jordal, 2020). Also, this means that the consistently varied and striking declivities Madagascar species often exhibit compared to the quite plain declivities on the mainland is quite certainly not an effect of sampling bias.

It is tempting to explain the high morphological variation observed on Madagascar using the theory of adaptive radiation that is commonly observed on islands (MacArthur and Wilson, 2001). When a species colonizes an island there may be several unoccupied niches that were previously not available for the species. This causes rapid speciation as the original species fills several niches. This may have happened with *Xyleborinus* on Madagascar with their common ancestor quickly starting to radiate when it started to colonize wood of several tree species on the entire island with little competition from other ambrosia beetles. However, it is difficult to explain why this radiation has caused so many distinct declivities as their effect

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[13] The endemic large-bodied diving beetle species on Madagascar in the 2015 study did not form a monophyletic clade, suggesting multiple either in- or out-of-Madagascar colonization events. Because of the currents, it was suggested that the beetles may have had an easier time colonizing out of Madagascar than in (Bukontaite *et al.*, 2015).

on survival is not obvious. If the declivital variation is caused only by genetic drift, why does species on mainland Africa not exhibit this variation also? Perhaps less competition and empty niches caused *Xyleborinus* to adapt to live in many types of plants and form symbiotic relationships with many types of ambrosia fungi, and the variation in declivities is just a random byproduct of this radiation. Research on the ecology of Malagasy *Xyleborinus* may give support to this hypothesis.

The phylogenetic trees give insight into the colonization history of the entire genus, not only to Madagascar. In the RASP tree, the two most basal lineages of *Xyleborinus* only include Indomalayan, Australasian and species found worldwide. They are all found in Australasia, indicating that the genus originated there. The third most basal clade contains *X. speciosus*, indicating that the genus subsequently colonized the Palearctic. The rest of the tree consists of a clade that only contains species that are endemic either to the Afrotropic or the Neotropic/Nearctic. Neotropical and Nearctic *Xyleborinus* form a monophyletic clade within the larger clade it shares with Afrotropical species. This indicates that the genus colonized the Americas from the Afrotropic once. It also gives support to the notion that the most likely origin of the Madagascar clade is mainland Africa. This exact colonization pattern, from Asia to the Afrotropic and then America, has previously been observed in Platypodinae (Jordal, 2015). More data from outside Madagascar can potentially clarify the exact colonization history of *Xyleborinus*.

Concluding remarks

The study has given clarity to the phylogeny and diversity of *Xyleborinus* in the Afrotropic, especially on Madagascar. Though there are still some questions left unanswered, the strong results will hopefully entice other researchers to closely study other genera of Xyleborini so that the entire tribe can be accurately understood. Also, understanding the colonization history of a wide range of organisms on Madagascar will help to increase our knowledge on the ecological history of the island. This study once again demonstrates that the biology of the island is highly unique and strengthens arguments for conservation of Madagascar.

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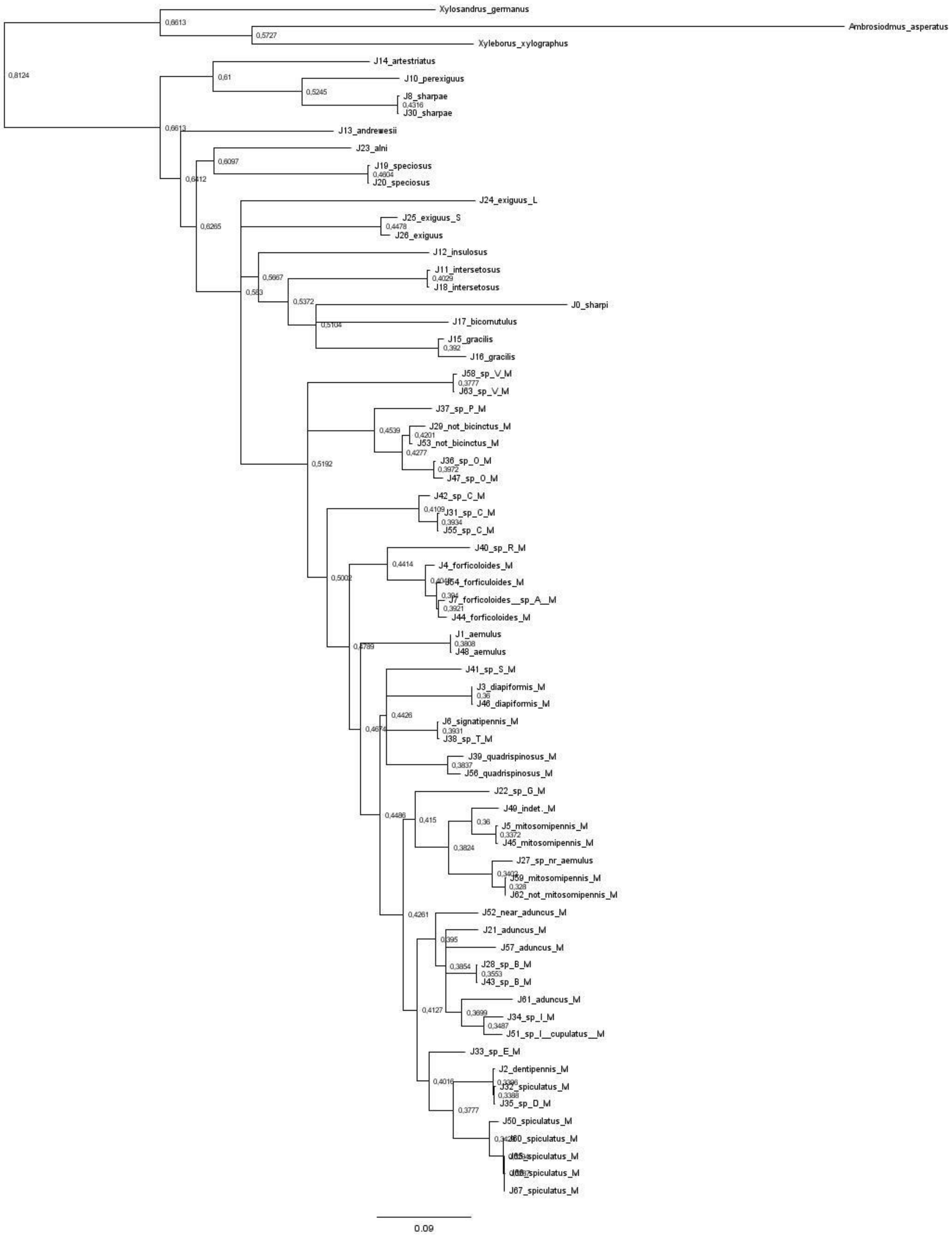
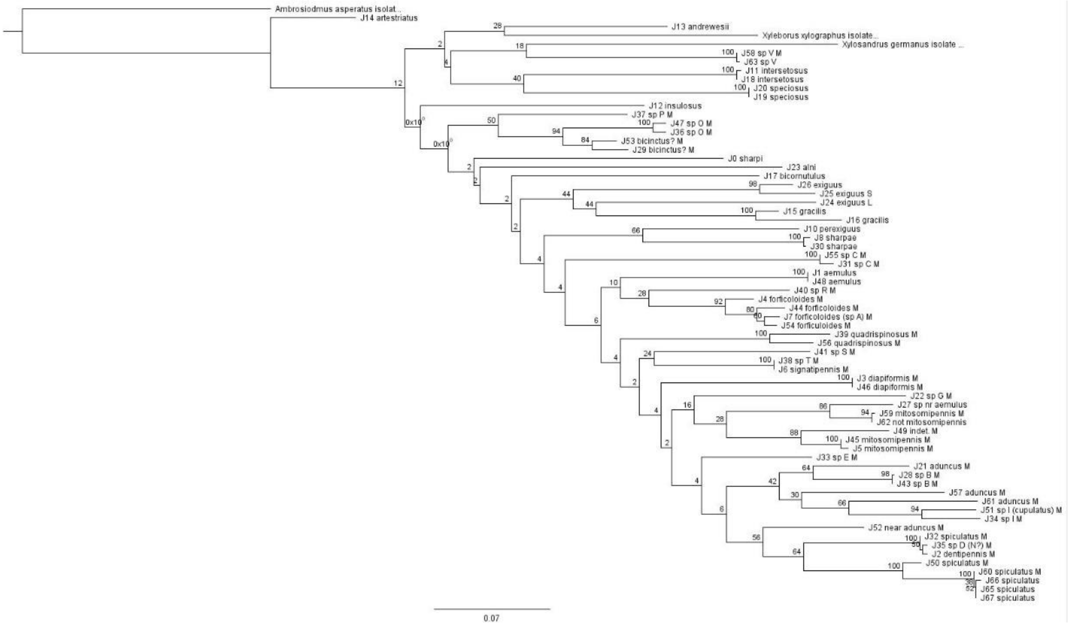
Appendices

Appendix A: List of every sequenced specimen with sequence name, date of preparation, species name, collection code, and collection site.

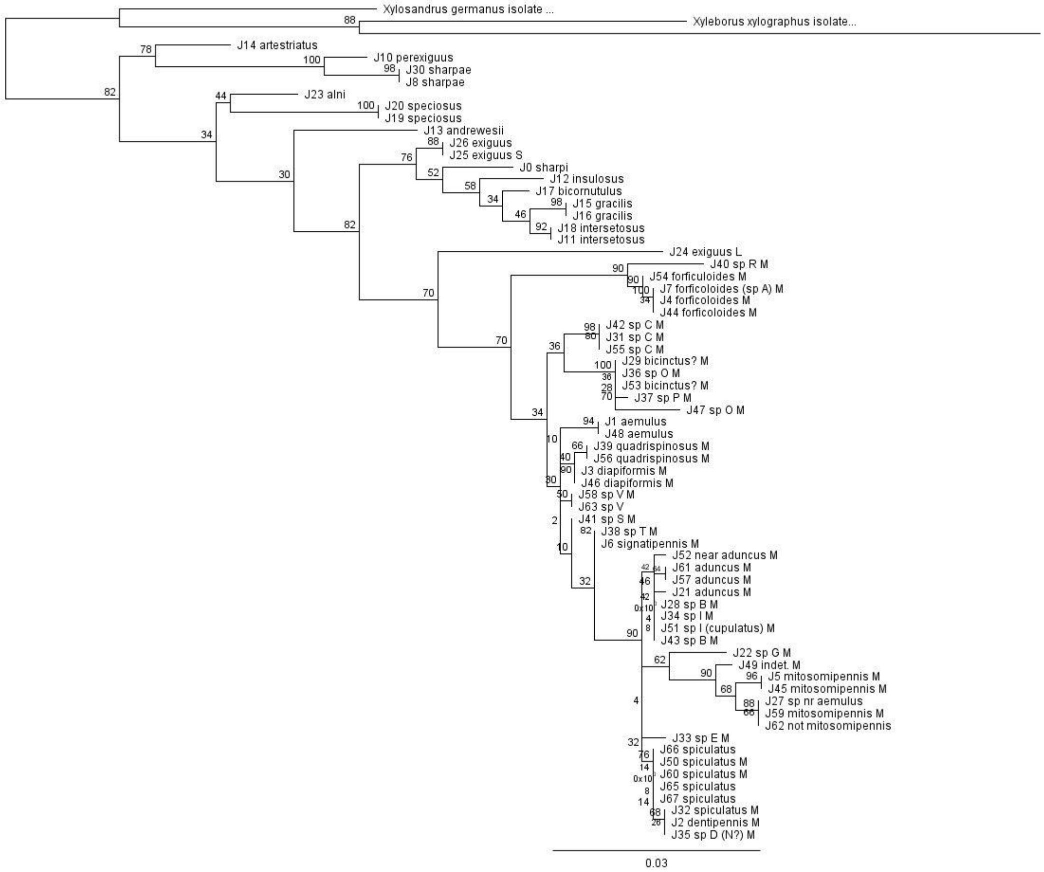
Sequence name	Date of preperation	Tribe	Species	Collection code	Location	
J1	9.5.19	Xyleborini	*Xyleborinus aemulus*	12xi-4	South Africa	Tsitsikamma, Goesa walk
J2	9.5.19	Xyleborini	*Xyleborinus spiculatus*	30ix-7	Madagascar	Ranomafana, Centre ValBio
J3	9.5.19	Xyleborini	*Xyleborinus diapiformis*	30ix-10	Madagascar	Ranomafana, Centre ValBio
J4	9.5.19	Xyleborini	*Xyleborinus forficuloides*	11v-8	Madagascar	Ambohitantely special reserve
J5	9.5.19	Xyleborini	*Xyleborinus spZ*	4x-5	Madagascar	Ranomafana, Centre ValBio
J6	9.5.19	Xyleborini	*Xyleborinus signatipennis*	4x-5	Madagascar	Ranomafana, Centre ValBio
J7	9.5.19	Xyleborini	*Xyleborinus forficuloides*	1x-1	Madagascar	Ranomafana, Centre ValBio
J8	9.5.19	Xyleborini	*Xyleborinus exiguus*	27	Gabon	Ivindo NP, Ipassa, 5km w Makokou
J9	7.6.19	Xyleborini	*Taurodemus sharpi*	19784	Belize	Las Cuevas
J10	7.6.19	Xyleborini	*Xyleborinus perexiguus*	19783	PNG	Ohu
J11	7.6.19	Xyleborini	*Xyleborinus intersetosus*	19782	Honduras	Atlantida
J12	7.6.19	Xyleborini	*Xyleborinus insulosus*	19755	Puerto Rico	El Yunque
J13	7.6.19	Xyleborini	*Xyleborinus andrewesii*	19754	USA	FL, Homestead
J14	7.6.19	Xyleborini	*Xyleborinus artestriatus*	19753	China	Fujian
J15	7.6.19	Xyleborini	*Xyleborinus gracilis*	19752	USA	FL, Gainsvile
J16	7.6.19	Xyleborini	*Xyleborinus gracilis*	19751	Mexico	Chiapas
J17	7.6.19	Xyleborini	*Xyleborinus bicornutulus*	18588	Belize	Las Cuevas
J18	7.6.19	Xyleborini	*Xyleborinus intersetosus*	18588	Belize	Las Cuevas
J19	7.6.19	Xyleborini	*Xyleborinus speciosus*	2713	Thailand	Doi Pui
J20	7.6.19	Xyleborini	*Xyleborinus speciosus*	2669	Thailand	Doi Pui
J21	7.6.19	Xyleborini	*Xyleborinus spY*	28ix-6	Madagascar	Ranamafana
J22	7.6.19	Xyleborini	*Xyleborinus spG*	28ix-6	Madagascar	Ranamafana
J23	7.6.19	Xyleborini	*Xyleborinus attenuatus*	19vii-1	Russia	Anisimovka
J24	7.6.19	Xyleborini	*Xyleborinus heveae*	2ii-3	Sierra Leone	Tiwai Island
J25	7.6.19	Xyleborini	*Xyleborinus sharpae*	2ii-3	Sierra Leone	Tiwai Island
J26	7.6.19	Xyleborini	*Xyleborinus sharpae*	23xi-3	Cameroon	Bimbia
J27	7.6.19	Xyleborini	*Xyleborinus octospinosus*	11xi-3	Tanzania	Udzungwa, 3-rivers camp
J28	7.6.19	Xyleborini	*Xyleborinus sp B*	29ix-16	Madagascar	Ranamafana
J29	28.8.19	Xyleborini	*Xyleborinus spU*	11v-1	Madagascar	Ambohitantely special reserve
J30	28.8.19	Xyleborini	*Xyleborinus exiguus*	etoh-trap	Cameroon	Limbe, Ekonjo
J31	28.8.19	Xyleborini	*Xyleborinus sp C*	14v-7	Madagascar	Andasibe, Perinet
J32	28.8.19	Xyleborini	*Xyleborinus spiculatus*	3x-4	Madagascar	Ranomafana NP
J33	28.8.19	Xyleborini	*Xyleborinus spinosus*	27ix-1D	Madagascar	Ranomafana NP
J34	28.8.19	Xyleborini	*Xyleborinus cupulatus*	30ix-7	Madagascar	Ranomafana NP
J35	28.8.19	Xyleborini	*Xyleborinus spiculatus*	5x-14	Madagascar	Ranomafana NP
J36	28.8.19	Xyleborini	*Xyleborinus sp O*	6x-1S	Madagascar	Ranomafana NP
J37	28.8.19	Xyleborini	*Xyleborinus sp P*	1x-1D	Madagascar	Ranomafana NP
J38	28.8.19	Xyleborini	*Xyleborinus signatipennis*	8x-CVB	Madagascar	Ranomafana NP
J39	28.8.19	Xyleborini	*Xyleborinus quadrispinosus*	Oct 2012	Madagascar	Ranomafana NP
J40	28.8.19	Xyleborini	*Xyleborinus sp R*	Oct 2012	Madagascar	Ranomafana NP
J41	28.8.19	Xyleborini	*Xyleborinus sp S*	9x-v	Madagascar	Ankarafantsika NP
J42	10.10.19	Xyleborini	*Xyleborinus sp C*	S-trap	Madagascar	Ranomafana NP
J43	10.10.19	Xyleborini	*Xyleborinus sp B*	4x-3	Madagascar	Ranomafana NP, Vato trail
J44	10.10.19	Xyleborini	*Xyleborinus forficuloides*	4x-3	Madagascar	Ranomafana NP, Vato trail
J45	10.10.19	Xyleborini	*Xyleborinus spZ*	4x-3	Madagascar	Ranomafana NP, Vato trail
J46	10.10.19	Xyleborini	*Xyleborinus diapiformis*	6x-2D	Madagascar	Ranomafana NP, Vato trail
J47	10.10.19	Xyleborini	*Xyleborinus sp O*	FIT	Madagascar	Ranomafana NP, Telytakeli trail
J48	10.10.19	Xyleborini	*Xyleborinus aemulus*	18xi-3	South Africa	Kologha Forest, Stutterheim (EC)
J49	14.11.2019	Xyleborini	*Xyleborinus indet.*	25x-2	Madagascar	Sambava, Marojejy Nat. Park
J50	14.11.2019	Xyleborini	*Xyleborinus spiculatulus*	25x-4	Madagascar	Sambava, Marojejy Nat. Park
J51	14.11.2019	Xyleborini	*Xyleborinus cupulatus*	25x-E4	Madagascar	Sambava, Marojejy Nat. Park
J52	14.11.2019	Xyleborini	*Xyleborinus spW (singularis)*	26x-4	Madagascar	Sambava, Marojejy Nat. Park
J53	14.11.2019	Xyleborini	*Xyleborinus spU*	26x-5	Madagascar	Sambava, Marojejy Nat. Park
J54	14.11.2019	Xyleborini	*Xyleborinus forficuloides*	26x-5	Madagascar	Sambava, Marojejy Nat. Park
J55	14.11.2019	Xyleborini	*Xyleborinus sp C*	24-27x	Madagascar	Sambava, Marojejy Nat. Park
J56	14.11.2019	Xyleborini	*Xyleborinus quadrispinosus*	24-27x	Madagascar	Sambava, Marojejy Nat. Park
J57	14.11.2019	Xyleborini	*Xyleborinus profundus*	27x-4	Madagascar	Sambava, Marojejy Nat. Park
J58	14.11.2019	Xyleborini	*Xyleborinus dentellus*	31x-3	Madagascar	Diana, Ankarana Nat. Park
J59	14.11.2019	Xyleborini	*Xyleborinus mitosomipennis*	2xi-3	Madagascar	Diana, Montagne d'Ambre
J60	14.11.2019	Xyleborini	*Xyleborinus spiculatulus*	2xi-E4	Madagascar	Diana, Montagne d'Ambre
J61	14.11.2019	Xyleborini	*Xyleborinus aduncus*	3xi-5	Madagascar	Diana, Montagne d'Ambre
J62	20.01.2020	Xyleborini	*Xyleborinus mitosomipennis*	2xi-9	Madagascar	Diana, Montagne d'Ambre
J63	20.01.2020	Xyleborini	*Xyleborinus dentellus*	31x-3	Madagascar	Diana, Ankarana Nat. Park
J64	20.01.2020	Xyleborini	*Xyleborinus aduncus*	4xi-5	Madagascar	Diana, Montagne d'Ambre
J65	20.01.2020	Xyleborini	*Xyleborinus spiculatulus*	1xi-5	Madagascar	Diana, Montagne d'Ambre
J66	20.01.2020	Xyleborini	*Xyleborinus spiculatulus*	3xi-E4	Madagascar	Diana, Montagne d'Ambre
J67	20.01.2020	Xyleborini	*Xyleborinus spiculatulus*	5xi-5	Madagascar	Diana, Montagne d'Ambre



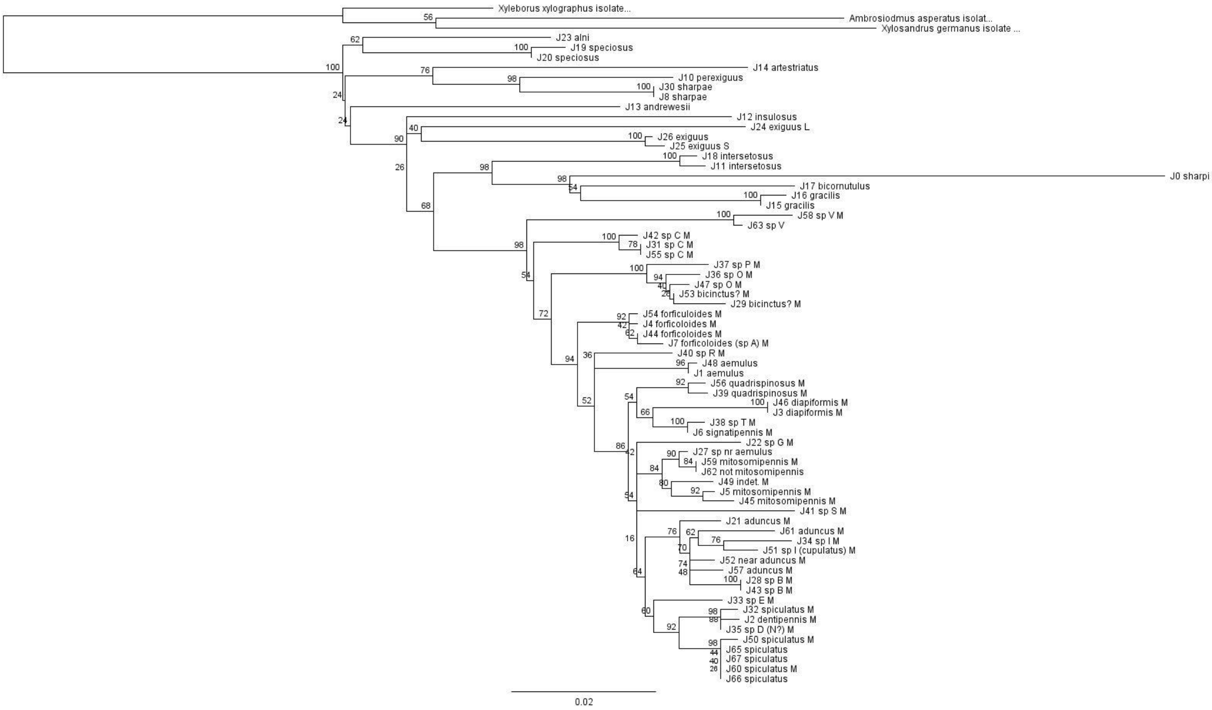
Appendix B: Molecular phylogeny results obtained from MrBayes with preliminary names used before thorough taxonomic work was conducted. This shows how much the taxonomic work changed the perceived content of the tree.



Appendix C. PHYML (Guindon *et al.,* 2010) tree on COI using HKY85 model and 50 bootstraps. Notice the long branches near the tips of the tree and how support declines markedly towards the older nodes. The gene works best for species delimitation. Only meant as an illustrated example as the results are very weak.



Appendix D. PHYML (Guindon *et al.,* 2010) tree on 28S using HKY85 model and 50 bootstraps. Notice how species make distinct groups, but no distinction is made between closely related species. The gene is most effective when working on older phylogenetic relationships. Only meant as an illustrated example as the results are very weak.



Appendix F. PHYML (Guindon *et al.,* 2010) tree on CAD using HKY85 model and 50 bootstraps. The gene works well for delimiting species and understanding older relationships when working on a genus, perhaps caused by the fragment containing both exons and introns. A good starting point for a phylogenetic analyzes. Only meant as an illustrated example as the results are quite weak.

Appendix G: All *Xyleborinus* specimens collected during field work on Madagascar 2019.

COUNTRY	LOC	GIS	ALT	CODE	DATE	HOST	HOST-FAM.	HABITAT	DIAM	TISSUE	SUBFAM	TRIBE	SPECIES	AUCTOR	# specimens
Madagascar	Sambava, Marojejy Nat. Park		800	25x-2	25.10.2019	"Tafonana"		wood	30	wood	Scolytinae	Xyleborini	Xyleborinus indet.		1
Madagascar	Sambava, Marojejy Nat. Park		800	25x-4	25.10.2019	Mania lunga "Vongo"		wood	50	wood	Scolytinae	Xyleborini	Xyleborinus spiculatus		2
Madagascar	Sambava, Marojejy Nat. Park		800	25x-E4	25.10.2019	unknown		wood	6	wood	Scolytinae	Xyleborini	Xyleborinus sp I (cupulatus)		2
Madagascar	Sambava, Marojejy Nat. Park		1000	26x-4	26.10.2019	"Voantsilana"		log	20	wood	Scolytinae	Xyleborini	Xyleborinus sp I (cupulatus)		1
Madagascar	Sambava, Marojejy Nat. Park		1000	26x-4	26.10.2019	"Voantsilana"		log	20	wood	Scolytinae	Xyleborini	Xyleborinus near aduncus		2
Madagascar	Sambava, Marojejy Nat. Park		1000	26x-5	26.10.2019	Weinmannia		standing tree	15	wood	Scolytinae	Xyleborini	Xyleborinus bicinctus?		1
Madagascar	Sambava, Marojejy Nat. Park		1000	26x-5	26.10.2019	Weinmannia		standing tree	15	wood	Scolytinae	Xyleborini	Xyleborinus forficuloides		3
Madagascar	Sambava, Marojejy Nat. Park		700	24-27x	26.10.2019	FIT		Boswellia			Scolytinae	Xyleborini	Xyleborinus sp C		1
Madagascar	Sambava, Marojejy Nat. Park		700	24-27x	26.10.2019	EtOH trap		EtOH			Scolytinae	Xyleborini	Xyleborinus quadrispinosus		1
Madagascar	Sambava, Marojejy Nat. Park		500	27x-4	27.10.2019	unknown		liana	7	bark	Scolytinae	Xyleborini	Xyleborinus aduncus (near?)		1
Madagascar	Diana, Ankarana Nat. Park		50	31x-1	31.10.2019	etoh trap		etoh			Scolytinae	Xyleborini	Xyleborinus sp. V		1
Madagascar	Diana, Ankarana Nat. Park		50	31x-3	31.10.2019	Boswellia trap		Boswellia			Scolytinae	Xyleborini	Xyleborinus sp. V		4
Madagascar	Diana, Montagne d'Ambre		1000	1xi-3	01.11.2019	unknown		log	30	wood	Scolytinae	Xyleborini	Xyleborinus mitosomipennis		3
Madagascar	Diana, Montagne d'Ambre		1000	1xi-3	01.11.2019	unknown		log	30	wood	Scolytinae	Xyleborini	Xyleborinus spiculatus		2
Madagascar	Diana, Montagne d'Ambre		1000	1xi-5	01.11.2019	Ocotea?		log	40	wood	Scolytinae	Xyleborini	Xyleborinus spiculatus		5
Madagascar	Diana, Montagne d'Ambre		1000	1xi-5	01.11.2019	Ocotea?		log	40	wood	Scolytinae	Xyleborini	Xyleborinus spiculatus		1 (+6 larvae)
Madagascar	Diana, Montagne d'Ambre		1000	2xi-3	02.11.2019	"Umbara"		log	50	wood	Scolytinae	Xyleborini	Xyleborinus mitosomipennis		3
Madagascar	Diana, Montagne d'Ambre		1000	2xi-5	02.11.2019	"Titata"		log	40	wood	Scolytinae	Xyleborini	Xyleborinus spiculatus		3
Madagascar	Diana, Montagne d'Ambre		1000	2xi-E4	02.11.2019	unknown		log	40	wood	Scolytinae	Xyleborini	Xyleborinus spiculatus		11
Madagascar	Diana, Montagne d'Ambre		1000	3xi-5	03.11.2019	Ficus		branch	7	wood	Scolytinae	Xyleborini	Xyleborinus spiculatus		2
Madagascar	Diana, Montagne d'Ambre		1000	3xi-5	03.11.2019	Ficus		branch	7	wood	Scolytinae	Xyleborini	Xyleborinus aduncus		2
Madagascar	Diana, Montagne d'Ambre		1000	3xi-E4	03.11.2019	Ficus		??	??	??	Scolytinae	Xyleborini	Xyleborinus spiculatus		4
Madagascar	Diana, Montagne d'Ambre		1000	4xi-4	04.11.2019	Ficus		log	20	wood	Scolytinae	Xyleborini	Xyleborinus mitosomipennis		1
Madagascar	Diana, Montagne d'Ambre		1000	4xi-5	04.11.2019	unknown		log	15	wood	Scolytinae	Xyleborini	Xyleborinus mitosomipennis		1
Madagascar	Diana, Montagne d'Ambre		1000	4xi-5	04.11.2019	unknown		log	15	wood	Scolytinae	Xyleborini	Xyleborinus aduncus		1
Madagascar	Diana, Montagne d'Ambre		1000	5xi-5	05.11.2019	Ficus		log		bark	Scolytinae	Xyleborini	Xyleborinus spiculatus		2
Madagascar	Diana, Montagne d'Ambre		1000	2xi-9	02.11.2019	unknown		??		??	Scolytinae	Xyleborini	Xyleborinus not mitosomipennis		1

Supplementary material added as attachments:

- Nexus file used in phylogenetic analyzes
- MrBayes consensus tree
- MrBayes results statistics files (vstat and tstat)
- BEAST consensus tree
- BEAST log
- RASP results
- Excel files of COI, 28S and CAD distance matrixes
- Sequencing list Excel file
- Excel file containing **Table 8-13**