

Taxonomy

Integrated Taxonomic Revision of Afrotropical *Xyleborinus* (Curculionidae: Scolytinae) Reveals High Diversity After Recent Colonization of Madagascar

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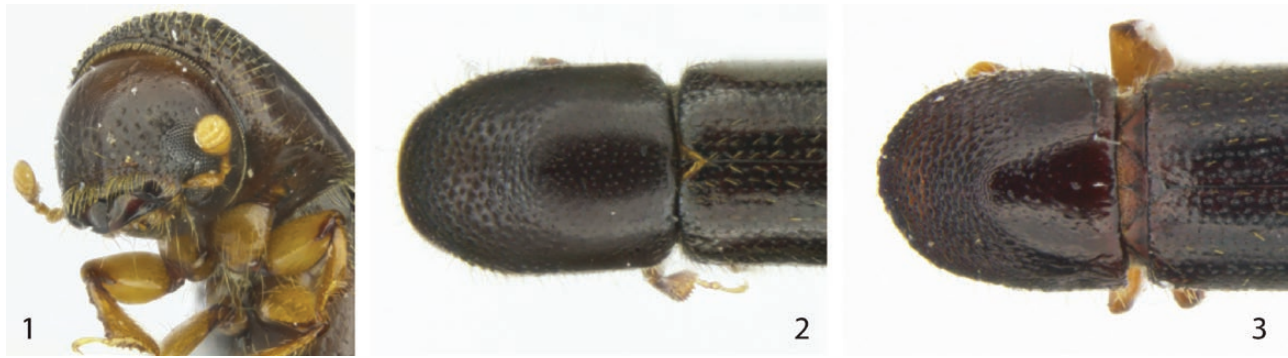
Abstract

The ambrosia beetle genus *Xyleborinus* Reitter, 1913 is particularly species rich in Madagascar where the genus exhibits extraordinary morphological variation not seen elsewhere. This study provides the first detailed molecular phylogeny of the genus based on COI, 28S, and CAD gene fragments. Biogeographical and taxonomic hypotheses were tested for the Afrotropical fauna with a particular focus on the Malagasy radiation. Analyses revealed a single colonization of Madagascar no earlier than 8.5–11.0 Ma, indicating an extraordinary recent radiation on the island which has given rise to at least 32 species. Two recolonization events of the African mainland were strongly supported by the molecular data, with several other intraspecific dispersals to the mainland inferred from species distributions. A taxonomic re-evaluation of all Afrotropical *Xyleborinus* resulted in several taxonomic changes. We found that morphological differences associated with COI divergence higher than 7% indicated different species. Twelve new species are described: *Xyleborinus castriformis* Eliassen & Jordal, sp. nov., *Xyleborinus clivus* Eliassen & Jordal, sp. nov., *Xyleborinus concavus* Eliassen & Jordal, sp. nov., *Xyleborinus coronatus* Eliassen & Jordal, sp. nov., *Xyleborinus diadematus* Eliassen & Jordal, sp. nov., *Xyleborinus laevipennis* Eliassen & Jordal, sp. nov., *Xyleborinus magnispinosus* Eliassen & Jordal, sp. nov., *Xyleborinus margo* Eliassen & Jordal, sp. nov., *Xyleborinus ntsoui* Eliassen & Jordal, sp. nov., *Xyleborinus singularis* Eliassen & Jordal, sp. nov., *Xyleborinus tuberculatus* Eliassen & Jordal, sp. nov., and *Xyleborinus turritus* Eliassen & Jordal, sp. nov., all from Madagascar. New synonyms are proposed for *Xyleborinus aemulus* (Wollaston, 1869) [= *Xyleborinus spinifer* (Eggers, 1920)], *Xyleborinus andrewesi* (Blandford, 1896) [= *Xyleborinus mimosae* (Schedl, 1957)], *Xyleborinus dentellus* (Schedl, 1953) [= *Xyleborinus forcipatus* (Schedl, 1957)], *Xyleborinus octospinosus* (Eggers, 1920) [= *Xyleborinus mitosomipennis* (Schedl, 1953)], and *Xyleborinus similans* (Eggers, 1940) [= *Xyleborinus sclerocaryae* (Schedl, 1962)]. Two species were given new status: *Xyleborinus profundus* (Schedl, 1961) is elevated from subspecies of *Xyleborinus aduncus* (Schedl, 1961), and *Xyleborinus mitosomus* (Schedl, 1965) is reinstated from its previous synonymy with *Xyleborinus spinosus* (Schaufuss, 1891). *Xyleborus gracilipennis* Schedl 1957 is reverted to its original genus, and a similar status is confirmed for *Xyleborus collarti* Eggers 1932. The number of taxonomically valid *Xyleborinus* species in the Afrotropical region is now 47, which includes 3 adventive species. Revised diagnoses for all species and a key for species identification are provided.

Key words: Afrotropics, molecular phylogeny, biogeography, taxonomy

Xyleborinus Reitter, 1913 is a characteristic genus of ambrosia beetles easily recognized by a conical scutellum (Figs. 1 and 2) and wood-boring lifestyle. They live deep inside wood, often in large logs

and branches of dead trees, where they cultivate ambrosia fungi as the sole food for their larvae (Kirkendall et al. 2015). This is one of many groups of fungus-farming beetles independently derived



Figs. 1–3. Head and dorsal side of (1, 2) *Xyleborinus* and (3) *Xyleborus*. Note the characteristic conical scutellum in *Xyleborinus*.

from bark beetle ancestors (Jordal and Cognato 2012, Johnson et al. 2018, Pistone et al. 2018). Ambrosia beetle is, therefore, a largely ecological term, not directly connected to the classification of the group. The ambrosial habit is of particular interest to forest entomologist as some species carry unwanted fungi which are potentially pathogenic when introduced to new trees on new continents (Hulcr and Dunn 2011). Taxonomic knowledge and ecological understanding of ambrosia beetles are, therefore, of substantial importance in nature management.

Xyleborini, with its name bearing mega genus *Xyleborus* Eichhoff, 1864 and 40 other genera (Cognato et al. 2020a), make up a large proportion of the ambrosia beetles, and more than one-fifth of all known bark and ambrosia beetle species in the world (Hulcr et al. 2015). *Xyleborinus* and most other xyleborines are found in warmer parts of the world, primarily in tropical forests, although a few species also extend into the boreal zone. The genus is likely of Indo-Malayan or Australasian origin which is the centre of diversification of Xyleborini (Hulcr et al. 2015, Cognato et al. 2018, Smith et al. 2020). Most species have a relatively restricted distribution (Wood and Bright 1992). About 16 species are found in Asian and Australian regions, while 18 are known from the Neotropics, 5 in the Holarctic, and 36 are reported from the Afrotropical region, including Madagascar. Only two of these species are widely pantropical and another three species are found on at least two continents.

Madagascar seems particularly diverse with respect to the limited area of the island, and a great many special elytral shapes characterize these species (Schedl 1977). The island is known for its endemism and many species radiations dominate the fauna and flora (Yoder and Nowak 2006). Separated from the African mainland by the Mozambique channel for more than 80 myr (Samonds et al. 2012, Toussaint et al. 2016), isolation has been sufficient to accumulate great endemic diversity on the island. The distance across the open ocean seems perhaps modest but oceanic currents and wind systems move toward the mainland and have done so since the early Miocene. The result is a serious drop in nonavian terrestrial and freshwater fauna colonizing Madagascar in the last 20 myr (Ali and Huber 2010, Samonds et al. 2012). The importance of these oceanic currents is not equally understood for terrestrial invertebrate colonization and convincing cases of both into and out of Madagascar colonization events have been made (Bukontaite et al. 2015). Even though terrestrial arthropods may cross the ocean as rafters, either on logs or floating debris, 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). A central question in this work is to use a group of wood-boring beetles to test the direction and frequency of range expansion across the ocean separating Africa and Madagascar.

Bark and ambrosia beetles are often not particularly easy to identify by morphological differences and *Xyleborinus* is no exception. Living their entire life cycle concealed in wood tunnels, morphologies tend to be uniform with few strikingly extravagant body features. Simple body shapes are even more typical for permanent inbreeders which lack sexual selection for mate choice (Kirkendall et al. 2015). In species like *Xyleborinus*, broods are strongly female biased, and a single or few males mate with their many more sisters. Taxonomic decisions are difficult in such species and molecular data have become an indispensable tool in defining species which has this type of mating system (Kambestad et al. 2017, Stouthamer et al. 2017, Cognato et al. 2018, Cognato et al. 2019, Jordal and Tischer 2020). It is therefore crucial to learn more about what minor morphological differences can inform us in separating evolutionary lineages that may equal different species. Taxonomic boundaries are often further complicated by high level of long-distance gene flow in many permanent inbreeders (Gohli et al. 2016). As such, geographical affinities may be less indicative of taxon relations as inbreeders establish easier in new places compared to outbreeders (Jordal et al. 2001). One may therefore observe low genetic variation across geographical sites, although it is not always expected.

The current study provides for the first time a detailed phylogenetic study of *Xyleborinus*. As a genus of permanently inbreeding species, we wish to test species boundaries in the most objective way feasible as a guidance for future studies, especially if molecular data are not available. This study will also provide a biogeographical test of the origin and frequency of island colonization and how geographical distance may influence intraspecific divergence. Based on the combined evaluation of morphological differences and molecular divergence, we revise the taxonomy of all Afrotropical species and provide the first identification key for this genus in the Afrotropical region. *Xyleborinus* has many of the key characteristics describing invasive species and our integrated approach will enable the early detection of invasive and potentially harmful species.

Materials and Methods

Phylogeny

Material used for molecular phylogenetic analyses was collected during three field trips to Madagascar in 2012, 2015, and 2019, to South Africa in 2006, Tanzania in 2010, Sierra Leone in 2010, Cameroon in 2007, and Gabon in 2016. Additional material from Southeast (SE) Asia and Neotropics was provided by the Hulcr lab at University of Florida, Gainesville (Table 1).

DNA was extracted from 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 was PCR amplified with Qiagen Hot Star taq and primers (Table 2) on a BioRad thermocycler with cycle parameters as described in Mugu et al. (2018). Single-banded PCR products were purified using two hydrolytic enzymes, recombinant Shrimp Alkaline Phosphatase (SAP) and Exonuclease I (Exo I). Sanger sequencing of COI and CAD amplicons was made in both directions, while 28S was sequenced using only forward primer.

DNA sequences were edited in the software Geneious Prime v. 10.0 (<https://www.geneious.com>). Sequences from different genes were concatenated into a single Nexus file. The partitions in the nexus file were COI, 28S, CAD exon, and CAD intron (Table 3). Sequences from four outgroup species were obtained to root the phylogenetic tree; *Taurodemus sharpi* (Blandford, 1898) by PCR and sequencing, while *Ambrosiodmus asperatus* (Blandford, 1895), *Xylosandrus germanus* (Blandford, 1894), and *Xyleborus xylographus* (Say, 1826) sequences were obtained from GenBank.

Genetic distance matrices for COI, 28S, and CAD were calculated in Geneious. Phylogenetic trees were reconstructed in a Bayesian framework in MrBayes 3.2.7 (Ronquist and Huelsenbeck 2003). Models of molecular evolution for each partition were determined using MrModeltest2 (Nylander 2004) based on the Akaike information criterion (AIC). For each of the protein coding genes COI and CAD, separate models were calculated for first, second, and third codon positions. Two parallel unlinked searches were run in MrBayes for 30 million generations with a sample frequency of 10,000, using three heated chains and one cold chain of temperature 0.3. Stationarity in likelihoods was confirmed after a burn-in of the first 1,000 trees, and low SD of split frequencies and a potential scale reduction factor (PSRF) value approaching 1.0 assured exhaustive searches.

Biogeography

Age of nodes was estimated in BEAST (Bouckaert et al. 2019) using Beauti to construct the input file. Calibration of rates was made with previously published age of the tribe Xyleborini, which has been estimated to be 21–23 Ma (Jordal and Cognato 2012, Pistone et al. 2018). This is a very reliable age estimate supported by similar ages for closely related lineages, but also the fact that Neotropical xyleborines are absent from Miocene Dominican ambers (Bright and Poinar 1994). BEAST implements fewer evolutionary models compared to MrBayes and was adapted to the most similar possible. Tree search ran for 15 million generations with a sample frequency of every 10,000 trees. Partitions were unlinked, each using an uncorrelated relaxed clock model with Yule branching priors adapted to species-level rates (Gernhard 2008). The type of branching prior is presumed to have little influence on time estimates for recent and compact clades (Condamine et al. 2015).

The biogeographic history of *Xyleborinus* was reconstructed in Reconstruct Ancestral State in Phylogenies (RASP) (Yu et al. 2015, 2020), based on the BEAST time tree. The species included in the phylogeny were distributed among five areas: A = Madagascar, B = Afrotropics, C = Palearctic, D = Indomalaya, E = Neotropics (including recent dispersal to the Nearctic). Madagascar is central in the evolution of the genus and was in these analyses treated separately from the rest of the Afrotropics to illuminate historical changes into and out of this island. Recent range expansions caused by anthropogenic activity have been ignored to reduce the maximum number of areas allowed in the analyses of historical distribution.

The BioGeoBEARS package in RASP was used to determine the best-fit model for RASP analyses, in which the DIVA-like was chosen as the best model with zero range constraints based on the corrected AIC (AICc) criterion. The model may include the +j parameter, which 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 which discourage their use (Ree and Sanmartin 2018), although not broadly supported (Matzke 2014). We included +j models in additional analyses to compare to the Bayesian analysis of ancestral areas applying the Bayesian Binary MCMC (BBM) method.

Taxonomy

Holotypes or equivalent material (e.g., lectotype or Eggers 'type') were studied for all except two species, mainly located in the Natural History Collections in Vienna, Paris, London, and Tervuren. The NHMW collection is nearly complete and contains paratypes of almost all species where the holotype is found elsewhere. Materials examined are deposited in the following collections:

NHMUK: British Museum of Natural History in London
 RBINS: Institut royal des Sciences naturelles de Belgique, Brussels
 ZMHB: Museum für Naturkunde, Berlin
 MNHN: Muséum National d'Histoire Naturelle in Paris
 RMCA: Musée Royal du Congo Belge in Tervuren
 NHMW: Museum of Natural History of Vienna
 TMSA: Ditsong National Museum of Natural History in Pretoria
 USNM: Smithsonian National Museum of Natural History in Washington D.C.
 ZMUB: University Museum of Bergen

All species were photographed from the dorsal, lateral, and declivital side using a Leica M205C camera with software LAS V4.13 (<https://www.leica-microsystems.com>) and multiple photos were stacked and aligned in the software Zerene Stacker (<https://www.zerene.com>). The type, or specimens directly compared to poorly preserved holotypes were photographed, whereas all available material was used for measurements.

We used congruence between morphological and genetic data to learn how much variation could be acceptable for a valid species. Species diagnoses are based on female specimens. Important anatomical features are shown in Figs. 1–21, focusing largely on the structure of the elytral declivity, and occasionally the shape of the tibiae. Most other body parts such as head and pronotum are near identical and we could not find any diagnostic differences between species and therefore not included in the descriptions.

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: zoobank.org/pub:448143DC-B507-472F-8CAE-118B6E0BEE4

Results

Bayesian analysis in MrBayes resulted in a nearly monophyletic *Xyleborinus*, only including the Neotropical outgroup species *T. sharpi* (Blandford, 1898) which was nested within a clade of all Neotropical *Xyleborinus* species (Fig. 22). Nodes were generally

Table 1. Specimens extracted for DNA and sequenced with sequence voucher name, collection details, and GenBank accession numbers

Voucher name	Species	Collection code	Country	Location	Leg./Lab	COI	28S	CAD
J0	<i>Taurodemus sharpi</i>	19784	Belize	Las Cuevas	Johnson/Hulcr	MW617383	MT895881	MW656502
J61	<i>Xyleborinus aduncus</i>	3xi-5	Madagascar	Diana, Montagne d'Ambre	Eliassen/Jordal	MW617442	MT895941	MW656562
J48	<i>Xyleborinus aemulus</i>	18xi-3	South Africa	Kologha Forest, Stutterheim (EC)	Jordal	MW617429	MT895928	MW656549
J1	<i>Xyleborinus aemulus</i>	12xi-4	South Africa	Tsitsikamma, Goesa walk	Jordal	MW617384	MT895882	MW656503
J13	<i>Xyleborinus andrewesii</i>	19754	United States	FL, Homestead	Johnson/Hulcr	MW617395	MT895893	MW656514
J14	<i>Xyleborinus artestriatus</i>	19753	China	Fujian	Johnson/Hulcr	MW617396	MT895894	MW656515
J23	<i>Xyleborinus attenuatus</i>	19vii-1	Russia	Anisimovka	Jordal	MW617405	MT895903	MW656524
J17	<i>Xyleborinus bicornatulus</i>	18588	Belize	Las Cuevas	Johnson/Hulcr	MW617399	MT895897	MW656518
J29	<i>Xyleborinus castriformis</i>	11v-1	Madagascar	Ambohitantely special reserve	Jordal	MW617411	MT895909	MW656530
J53	<i>Xyleborinus castriformis</i>	26x-5	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617434	MT895933	MW656554
J40	<i>Xyleborinus clivus</i>	Oct 2012	Madagascar	Ranomafana National Park	Jordal	MW617422	MT895920	MW656541
J28	<i>Xyleborinus concavus</i>	29ix-16	Madagascar	Ranomafana National Park	Jordal	MW617410	MT895908	MW656529
J43	<i>Xyleborinus concavus</i>	4x-3	Madagascar	Ranomafana National Park, Vato trail	Jordal	MW617424	MT895923	MW656544
J41	<i>Xyleborinus coronatus</i>	9x-v	Madagascar	Ankarafantsika National Park	Eliassen/Jordal	MW617423	MT895921	MW656542
J34	<i>Xyleborinus cupulatus</i>	30ix-7	Madagascar	Ranomafana National Park	Jordal	MW617416	MT895914	MW656535
J51	<i>Xyleborinus cupulatus</i>	25x-E4	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617432	MT895931	MW656552
J58	<i>Xyleborinus dentellus</i>	31x-3	Madagascar	Diana, Ankarana National Park	Eliassen/Jordal	MW617439	MT895938	MW656559
J63	<i>Xyleborinus dentellus</i>	31x-3	Madagascar	Diana, Ankarana National Park	Eliassen/Jordal	MW617444	MT895943	MW656564
J21	<i>Xyleborinus diadematus</i>	28ix-6	Madagascar	Ranomafana National Park	Jordal	MW617403	MT895901	MW656522
J46	<i>Xyleborinus diapiformis</i>	6x-2D	Madagascar	Ranomafana National Park, Vato trail	Jordal	MW617427	MT895926	MW656547
J3	<i>Xyleborinus diapiformis</i>	30ix-10	Madagascar	Ranomafana, Centre ValBio	Jordal	MW617386	MT895884	MW656505
J30	<i>Xyleborinus exiguus</i>	etoh-trap	Cameroon	Limbe, Ekonjo	Jordal	MW617412	MT895910	MW656531
J8	<i>Xyleborinus exiguus</i>	27	Gabon	Ivindo National Park, Ipassa, 5km w Makokou	Mally/Jordal	MW617391	MT895889	MW656510
J4	<i>Xyleborinus forficuloides</i>	11v-8	Madagascar	Ambohitantely special reserve	Jordal	MW617387	MT895885	MW656506
J44	<i>Xyleborinus forficuloides</i>	4x-3	Madagascar	Ranomafana National Park, Vato trail	Jordal	MW617425	MT895924	MW656545
J7	<i>Xyleborinus forficuloides</i>	1x-1	Madagascar	Ranomafana, Centre ValBio	Jordal	MW617390	MT895888	MW656509
J54	<i>Xyleborinus forficuloides</i>	26x-5	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617435	MT895934	MW656555
J16	<i>Xyleborinus gracilis</i>	19751	Mexico	Chiapas	Johnson/Hulcr	MW617398	MT895896	MW656517
J15	<i>Xyleborinus gracilis</i>	19752	United States	FL, Gainesville	Johnson/Hulcr	MW617397	MT895895	MW656516
J24	<i>Xyleborinus heveae</i>	2ii-3	Sierra Leone	Tiwai Island	Jordal	MW617406	MT895904	MW656525
J49	<i>Xyleborinus indet.</i>	25x-2	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617430	MT895929	MW656550
J12	<i>Xyleborinus insulosus</i>	19755	Puerto Rico	El Yunque	Johnson/Hulcr	MW617394	MT895892	MW656513
J18	<i>Xyleborinus intersetosus</i>	18588	Belize	Las Cuevas	Johnson/Hulcr	MW617400	MT895898	MW656519
J11	<i>Xyleborinus intersetosus</i>	19782	Honduras	Atlantida	Storer/Hulcr	MW617393	MT895891	MW656512

Table 1. Continued

Voucher name	Species	Collection code	Country	Location	Leg./Lab	COI	28S	CAD
J45	<i>Xyleborinus laevipennis</i>	4x-3	Madagascar	Ranomafana National Park, Vato trail	Jordal	MW617426	MT895925	MW656546
J5	<i>Xyleborinus laevipennis</i>	4x-5	Madagascar	Ranomafana, Centre ValBio	Jordal	MW617388	MT895886	MW656507
J37	<i>Xyleborinus magnispinosus</i>	1x-1D	Madagascar	Ranomafana National Park	Jordal	MW617419	MT895917	MW656538
J31	<i>Xyleborinus margo</i>	14v-7	Madagascar	Andasibe, Perinet	Jordal	MW617413	MT895911	MW656532
J42	<i>Xyleborinus margo</i>	S-trap	Madagascar	Ranomafana National Park	Jordal	–	MT895922	MW656543
J55	<i>Xyleborinus margo</i>	24-27x	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617436	MT895935	MW656556
J59	<i>Xyleborinus mitosomipennis</i>	2xi-3	Madagascar	Diana, Montagne d'Ambre	Eliassen/Jordal	MW617440	MT895939	MW656560
J62	<i>Xyleborinus mitosomipennis</i>	2xi-9	Madagascar	Diana, Montagne d'Ambre	Eliassen/Jordal	MW617443	MT895942	MW656563
J22	<i>Xyleborinus ntsoui</i>	28ix-6	Madagascar	Ranomafana National Park	Jordal	MW617404	MT895902	MW656523
J27	<i>Xyleborinus octospinosus</i>	11xi-3	Tanzania	Udzungwa, 3-rivers camp	Jordal	MW617409	MT895907	MW656528
J10	<i>Xyleborinus perexiguus</i>	19783	Papua New Guinea	Ohu	Hulcr	MW617392	MT895890	MW656511
J57	<i>Xyleborinus profundus</i>	27x-4	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617438	MT895937	MW656558
J39	<i>Xyleborinus quadrispinosus</i>	Oct 2012	Madagascar	Ranomafana National Park	Jordal	MW617421	MT895919	MW656540
J56	<i>Xyleborinus quadrispinosus</i>	24-27x	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617437	MT895936	MW656557
J26	<i>Xyleborinus sharpae</i>	23xi-3	Cameroon	Bimbria	Jordal	MW617408	MT895906	MW656527
J25	<i>Xyleborinus sharpae</i>	2ii-3	Sierra Leone	Tiwai Island	Jordal	MW617407	MT895905	MW656526
J38	<i>Xyleborinus signatipennis</i>	8x-CVB	Madagascar	Ranomafana National Park	Jordal	MW617420	MT895918	MW656539
J6	<i>Xyleborinus signatipennis</i>	4x-5	Madagascar	Ranomafana, Centre ValBio	Jordal	MW617389	MT895887	MW656508
J52	<i>Xyleborinus singularis</i>	26x-4	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617433	MT895932	MW656553
J19	<i>Xyleborinus speciosus</i>	2713	Thailand	Doi Pui	Johnson/Hulcr	MW617401	MT895899	MW656520
J20	<i>Xyleborinus speciosus</i>	2669	Thailand	Doi Pui	Johnson/Hulcr	MW617402	MT895900	MW656521
J60	<i>Xyleborinus spiculatulus</i>	2xi-E4	Madagascar	Diana, Montagne d'Ambre	Eliassen/Jordal	MW617441	MT895940	MW656561
J65	<i>Xyleborinus spiculatulus</i>	1xi-5	Madagascar	Diana, Montagne d'Ambre	Eliassen/Jordal	MW617445	MT895944	MW656565
J66	<i>Xyleborinus spiculatulus</i>	3xi-E4	Madagascar	Diana, Montagne d'Ambre	Eliassen/Jordal	MW617446	MT895945	MW656566
J67	<i>Xyleborinus spiculatulus</i>	5xi-5	Madagascar	Diana, Montagne d'Ambre	Eliassen/Jordal	MW617447	MT895946	MW656567
J50	<i>Xyleborinus spiculatulus</i>	25x-4	Madagascar	Sambava, Marojejy National Park	Eliassen/Jordal	MW617431	MT895930	MW656551
J32	<i>Xyleborinus spiculatus</i>	3x-4	Madagascar	Ranomafana National Park	Jordal	MW617414	MT895912	MW656533
J35	<i>Xyleborinus spiculatus</i>	5x-14	Madagascar	Ranomafana National Park	Jordal	MW617417	MT895915	MW656536
J2	<i>Xyleborinus spiculatus</i>	30ix-7	Madagascar	Ranomafana, Centre ValBio	Jordal	MW617385	MT895883	MW656504
J33	<i>Xyleborinus spinosus</i>	27ix-1D	Madagascar	Ranomafana National Park	Jordal	MW617415	MT895913	MW656534
J36	<i>Xyleborinus turritus</i>	6x-1S	Madagascar	Ranomafana National Park	Jordal	MW617418	MT895916	MW656537
J47	<i>Xyleborinus turritus</i>	FIT	Madagascar	Ranomafana National Park, Telytakeli trail	Jordal	MW617428	MT895927	MW656548

Table 2. PCR primers and optimal annealing temperature used for PCR reactions

Gene	Forward 5'-3'	Reverse 5'-3'
Cytochrome oxidase I (COI) 46°	(S1718) GGAGGATTTGGAAATTGATTAGTTC	(A2411) GCTAATCATCTAAAACTTTAATTCCW GTWG (A2237) CCGAATGCTTCTTTTACCTCTTTCTTG (A4394)
28S, 55°	(S3690) GAGAGTTMAASAGTACGTGAAAC	TCGGAAGGAACCAGCTACTA
Carbamoylphosphate synthetase II (CAD), 52°	(CAD forB2) GARAARGTNGCNCNAGTATGGC (CAD for4) TGGAARGARTBGARTACGARGTGGTYCG	(CAD rev1mod) GCCATYRCYTCBCCYACRCTYTTTCAT

Table 3. Nexus file partitions and models used in MrBayes and BEAST analyzes

Gene and codon position	Partition delineation	MrModel-test2	MrBayes	BEAST
COI—first codon	2-692\3	GTR+I+G	GTR+I+G	GTR+I+G
COI—second codon	3-692\3	F81	F81	HKY
COI—third codon	1-692\3	GTR+G	GTR+G	GTR+G
28S rRNA	693-1545	GTR+I+G	GTR+I+G	GTR+I+G
CAD exon—first codon	1547-2221\3	GTR+G	GTR+G	GTR+G
CAD exon—second codon	1548-2221\3	F81	F81	HKY
CAD exon—third codon	1546-2221\3	HKY+G	HKY+G	HKY+G
CAD intron	2222-2450	GTR+G	GTR+G	GTR+G

Models selected by MrModel-test2 were based on the AIC.

well supported with posterior probabilities higher than 0.95 and only six nodes obtained probabilities lower than 0.90. Weakest support was observed in four of the earliest nodes separating SE Asian species in a grade of successively nested clades. The African mainland species *Xyleborinus sharpae* (Hopkins, 1915) and *Xyleborinus heveae* (Schedl, 1957) formed a polytomy with the Neotropical clade and together made potential sister groups to the Malagasy clade.

All Malagasy species comprised a distinct nested clade in *Xyleborinus*, with *Xyleborinus aemulus* (Wollaston, 1869) as the single African representative that may not be found on Madagascar (one record). We identified 12 species from Madagascar as new to science as these did not fit morphologically to any type specimens of described species. Differences in morphology were supported by genetic differences and all species represented by multiple specimens formed monophyletic groups in the phylogenetic analysis. At least 9 of the 11 new species with genetic data were maximally supported as part of a known species complex from that island. Several subclades containing multiple species groups obtained high node support, but there was no particular pattern in morphological evolution at this level.

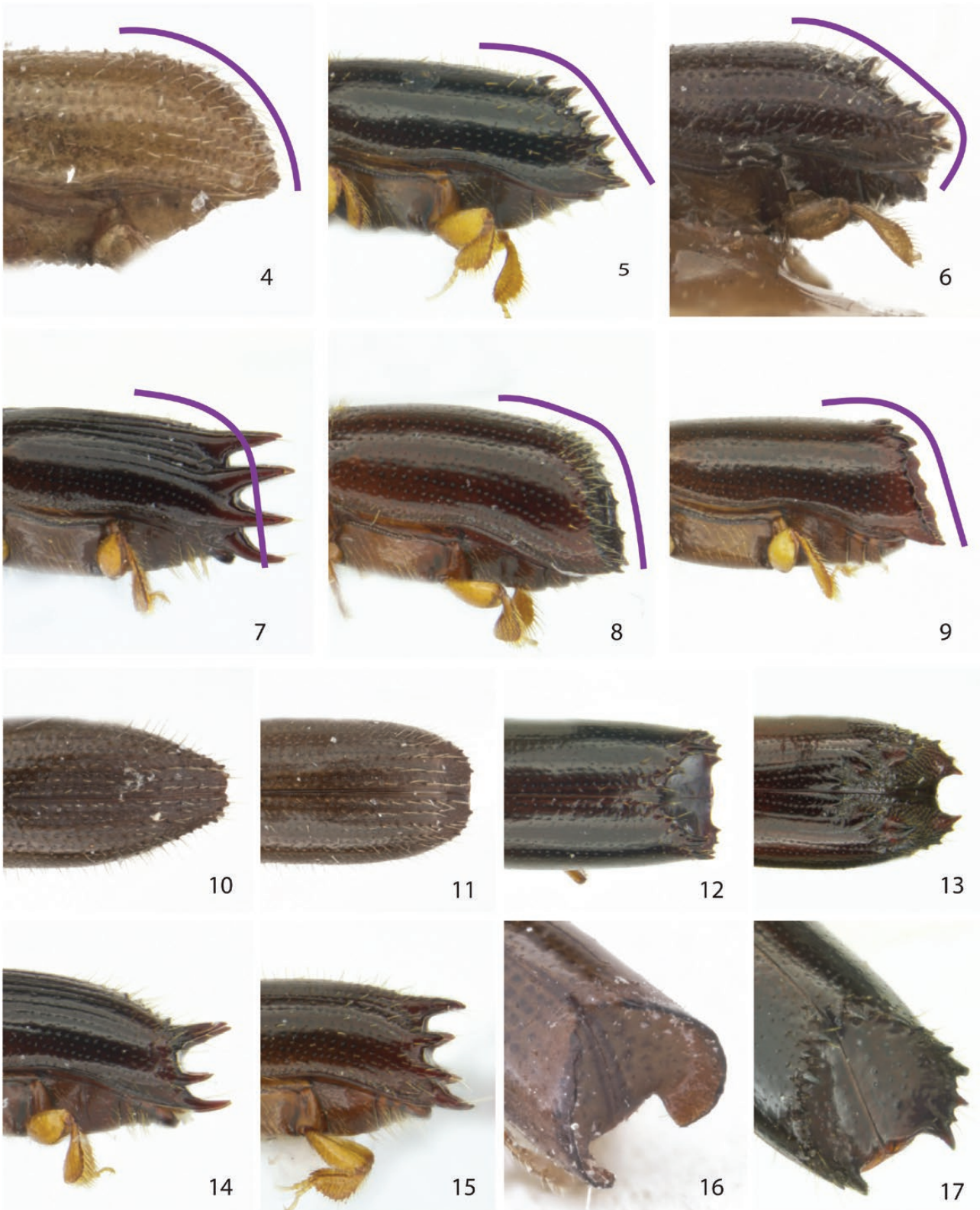
All genetically analyzed specimens were morphologically very similar when COI differences were less than 6%. Conversely, morphological differences were almost always obvious when COI differences were larger than 8%. Intraspecific variation was observed in both morphology and genes within *Xyleborinus margo*, sp. nov., *Xyleborinus forficuloides* (Schedl, 1951), *Xyleborinus quadrispinosus* (Eichhoff, 1878), and *Xyleborinus cupulatus* (Schedl, 1961) (Table 4; Fig. 22). Variation between individuals in the most variable species, *X. forficuloides*, was less than 6% in COI and morphological differences were evident, but slight. The molecular data placed specimens of the morphologically near-identical *Xyleborinus spiculatus*

(Schaufuss, 1891) and *Xyleborinus spiculatus* (Schedl, 1965) in two distinct genetic groups (Fig. 22; Table 4). The same or lower level of genetic divergence was observed between other species pairs, such as *Xyleborinus aduncus* (Schedl, 1961) and various members of the *aduncus* group such as *X. cupulatus*, or *Xyleborinus octospinosus* (Eggers, 1920) and *Xyleborinus laevipennis*, sp. nov., but these were morphologically clearly different. In most other cases, a moderate-to-low genetic variation corresponded to minimal morphological variation. *Xyleborinus octospinosus* was the only species sampled on both mainland and Madagascar, with less than 5.7% divergence in COI, and identical 28S sequences.

Biogeographical Analysis

The BioGeoBears selected DIVA-like as the best model in reconstructing ancestral areas. This analysis was nearly identical to the Bayesian estimation of ancestral areas in the BBM analysis (Fig. 23). Irrespective of analysis, SE Asia was the ancestral area for the genus *Xyleborinus*, which at least dates back to 13.6 Ma (crown age). Dispersal with vicariance of a combined Afro-tropical and Neotropical clade occurred no earlier than 12.2 Ma, with a single colonization of the Neotropics from Africa around 10 Ma. Madagascar was colonized only once, between 11 and 8.5 Ma. Reversed colonization of the mainland occurred in several species that are still present on Madagascar, including *X. octospinosus*, *X. quadrispinosus*, and *Xyleborinus dentellus* (Schedl, 1953), which were all likely recent events. In the case of *X. octospinosus*, the split between Africa and Madagascar was estimated to 1 Ma. A much older back colonization event occurred in the South African endemic *X. aemulus* (Wollaston, 1869) around 6.2 Ma.

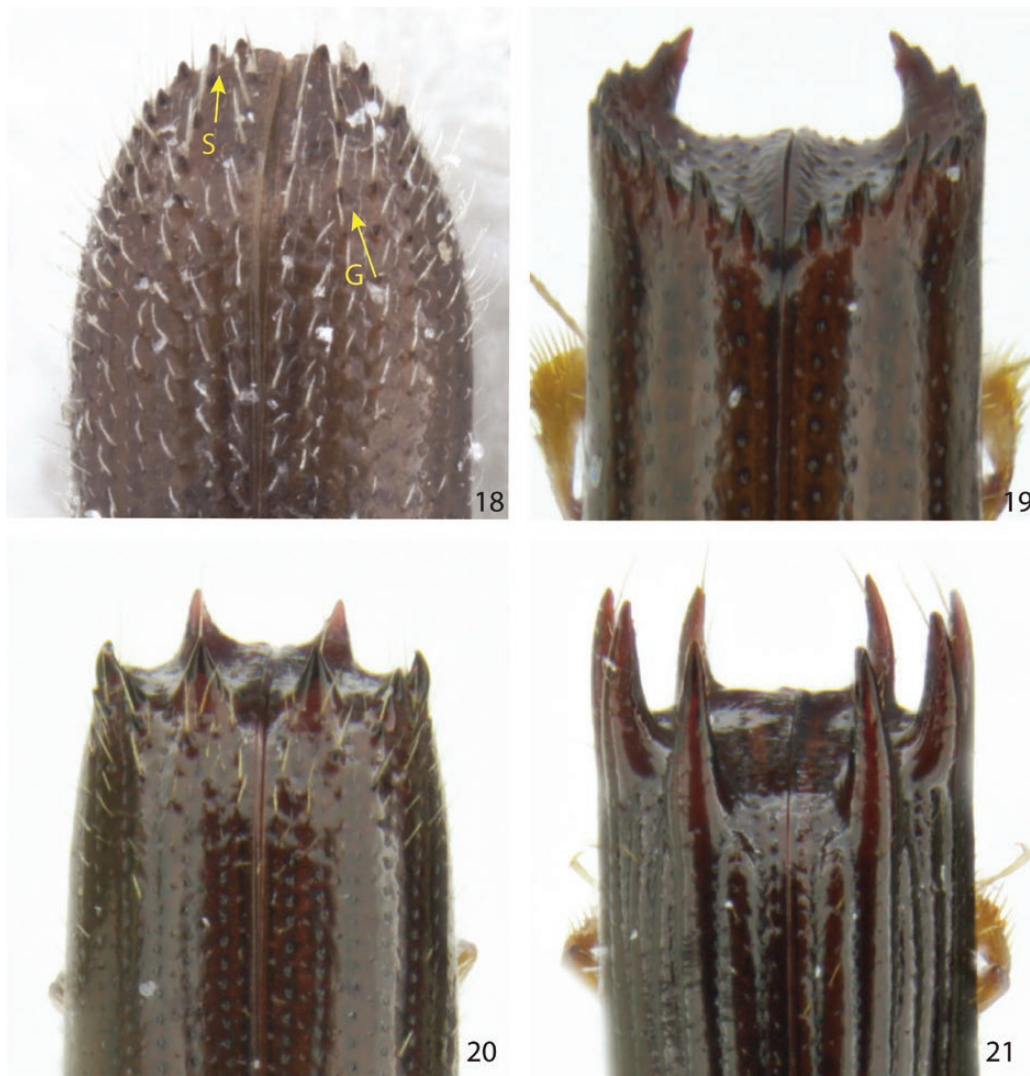
Species radiation is young and continuous in Madagascar. The *aduncus*, *spiculatus*, *octospinosus*, and *bicinctus* groups experienced



Figs. 4–17. Declivital variations in *Xyleborinus*. (4–9) Curvature variations. (10) Elongated, (11) rounded, (12, 17) wreathed, (13) *bicinctus* group, (14, 15) crowned, and (16) flanged declivity.

11 species lineage splits in less than 3.5 myr, and additional 8 splits in the same and additional groups between 3.5 and 6 Ma. For eight species sampled from multiple locations, a clear genetic divergence

was seen in all cases (Fig. 22), with a tendency for the south location in Ranomafana, and the northern location in Mt d’Ambre, to be the more deviant sites genetically.



Figs. 18–21. Spines and shapes of the elytral declivity in *Xyleborinus*. (18) Declivital spines and granules, (19) declivital flange, and (20, 21) 'crowned' declivities.

Taxonomy

Xyleborinus Reitter, 1913

Type species: *Bostrichus saxesenii* Ratzeburg, 1837.

Diagnosis, Female. Eyes elongated, oval shaped, emarginated, indentation $0.3\times-0.5\times$ as deep as the width of the eye. Frons with scattered deep punctures, with few long setae which are more densely set and shorter on the epistoma. Antennal funiculus five-segmented; club obliquely truncated, type 2, occasionally type 1 (Hulcr et al. 2007). Pronotum of type 7 or 8 (Hulcr et al. 2007), posterior half with tiny punctures spaced by $2-4\times$ their diameter, anterior half with small transverse asperities. Scutellum conical, surrounded by a tuft of setae. Elytral declivity with spines, sharp tubercles, or flanges, rarely nearly smooth. Vestiture consisting of erect interstitial setae, and much shorter, fine strial setae. Protibiae and metatibiae laterally gently curved with four to eight socketed teeth on its edge. **Male** smaller, features less pronounced, less sclerotized; wingless.

Remarks. *Xyleborinus* is readily recognized and distinguished from all other scolytine beetles by the conical scutellum.

Afrotropical *Xyleborinus*

All currently valid species occurring in Africa and Madagascar are listed in Table 5.

The *aduncus* Species Group

Species with a flange along the declivital margin, with or without small spines or incisions on the edge.

Xyleborinus aduncus (Schedl, 1961)

Xyleborus aduncus Schedl, 1961, orig. spelling

Xyleborus aduncus adunculus Schedl, 1961 (syn. by Wood and Bright 1992)

(Figs. 24–26)

Material Examined. Holotype, female: MADAGASCAR, Montagne d'Ambre (MNHN). Paratypes (females): MADAGASCAR, Mont d'Ambre, 5.XII.1952, K. E. Schedl (1); 4.XII.1952, K. E. Schedl (1). Paratype of subspecies *X. a. adunculus*: MADAGASCAR, Morafenobe, forêt Mahajebly, May 1952, K. E. Schedl (1). Other material: Supp Table S1 (online only).

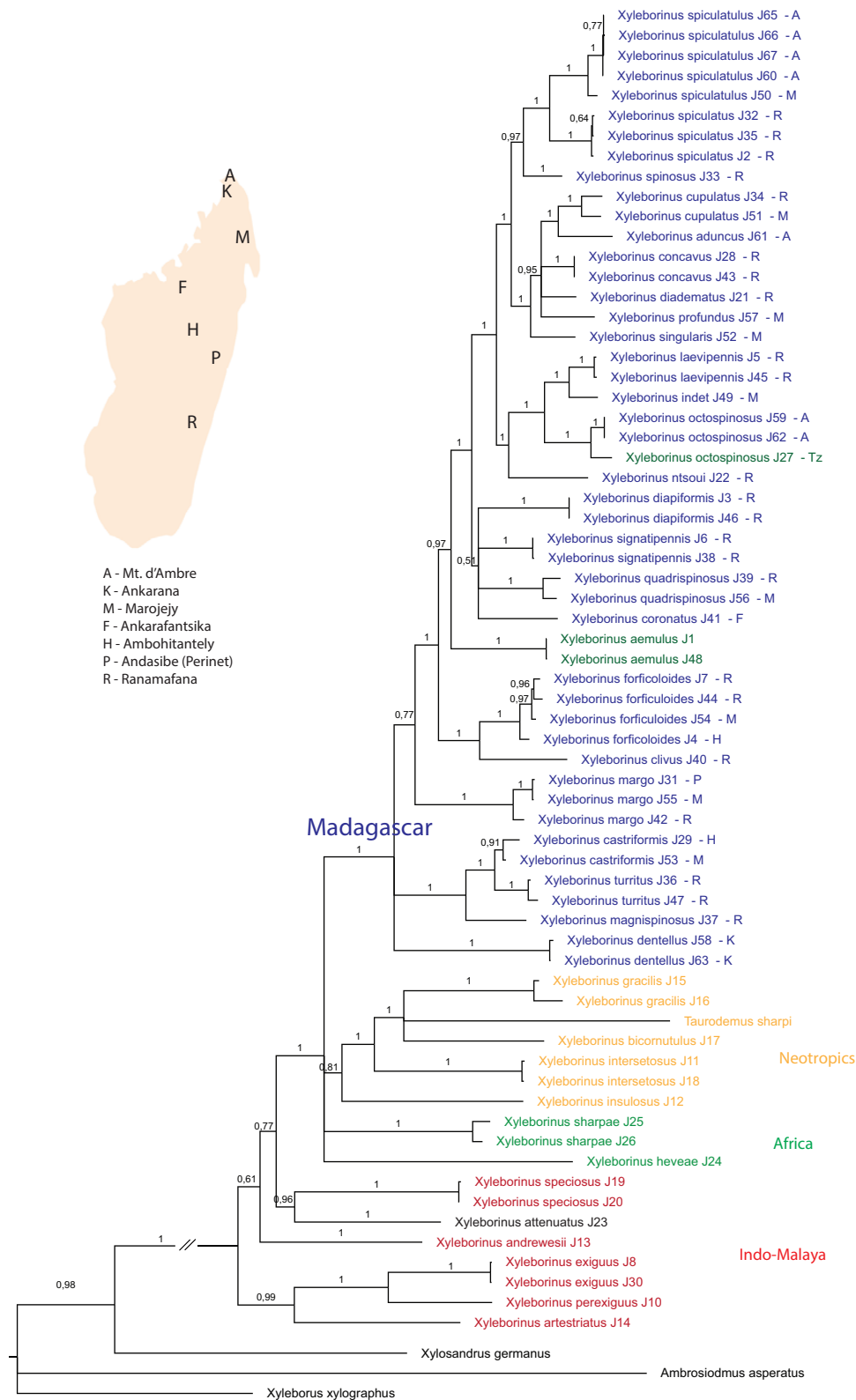


Fig. 22. Phylogenetic tree topology resulting from the Bayesian analysis of five gene fragments. The SD for split frequencies was 0.001, and PSRF close to 1 on all parameters. Posterior probabilities are shown above each branch leading to the evaluated node.

Diagnosis. A vertical declivity encircled by a lightly serrated flange from interstriae 5 to 9, ending in a pair of broad, triangularly acute flanks pointing inwards. Upper declivital margin

on each elytron with three small spines on interstriae 1, 2, and 3/4 that precede the lower flange. The inside of apical flanks smooth.

Table 4. Genetic variation within and between closely related species of *Xyleborinus*

Species	All data	COI	CAD	28S
	Patristic distance	Max p-distance	Max p-distance	Base substitutions
A				
<i>X. margo</i>	0.03	0.9	0.6	1
<i>X. forficuloides</i>	0.03	4.3	0.7	1
<i>X. quadrispinosus</i>	0.03	5.6	0.8	0
<i>X. octospinosus</i>	0.03	5.7	1.0	0
<i>X. gracilis</i>	0.03	5.8	0.4	0
<i>X. cupulatus</i>	0.04	5.9	1.4	0
B				
<i>X. turritus</i> and <i>X. castriformis</i>	0.06	7.4	1.0	0
<i>X. concavus</i> and <i>X. diadematus</i>	0.06	8.2	1.6	1
C				
<i>X. spiculatus</i> and <i>X. spiculatulus</i>	0.09	11.6	2.9	3
<i>X. octospinosus</i> and <i>X. laevipennis</i>	0.10	10.8	1.8	5
<i>X. aduncus</i> and <i>X. profundus</i>	0.11	11.7	1.6	0

28S has very small genetic differences and is therefore shown as number of bases. A: The genetically most variable species observed. B: Interspecific variation for morphological distinct species pairs with limited genetic differences. C: Morphologically very similar species with high interspecific genetic variation. *Xyleborinus octospinosus* (as *X. mitosipennis*) and *X. laevipennis* were previously treated as the same species (Schedl, 1961). *Xyleborinus profundus* was previously described as subspecies of *X. aduncus*.

Distribution. Madagascar.

Comments. The subspecies *adunculus* is fairly similar to subspecies *aduncus*. Although no exact match was found to sequenced specimens, the status of *adunculus* is retained as a synonym of *aduncus*.

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

Zoobank LSID: zoobank.org/act:FE548C60-B729-4810-9AD1-0D748DF55726
(Figs. 27–29)

Type Material. Holotype, female: MADAGASCAR, Ranomafana National Park, Centre ValBio, 2012: 28ix-6, B. Jordal, ex *Oncostemum* log [GIS: -21.25, 47.42] alt. 950 m. Paratypes (2): Same data as holotype. Holotype and one paratype in ZMUB, one paratype in NHMW.

Diagnosis. Declivity steep, encircled by a wavy flange from interstriae 4 to 9; each flange continues into narrow and slightly serrated flanks, pointing obliquely inwards, terminating in a distinct spine. Upper declivity with three small spines on interstriae 1, 2, and 3; first and second spine same length as third ventrite, third spine slightly thicker and longer than third ventrite. Inside of apical flanks smooth.

Female. Length 2.0–2.2 mm, 3.1–3.3× as long as wide; color brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–3× their diameter; interstriae smooth, shiny, punctures as large as striae punctures, spaced by 5–7× their diameter. Declivity steep, encircled by a continuous flange on declivital margin from interstriae 4 to 9; flange wavy and increasingly serrated toward the narrow spine-like and inwards pointing apical flank, these flanks as long as length of second and third ventrite combined; space between flank tips as long or slightly longer than length of metatibiae; margin on upper declivity with three small spines on interstriae 1, 2, and 3;

first and second spine as long as third ventrite, third spine slightly thicker and longer than length of third ventrite. Inside of bottom flanks smooth. Vestiture almost completely absent, declivity glabrous. **Legs.** Lateral edge of protibiae pointed, appearing triangular, with seven socketed teeth on apical three-fifth, larger gap between proximal teeth 1 and 2. Metatibiae broadened and gently curved laterally on apical 2/3, with at least five very small, socketed teeth on apical three-fourth, biggest gap between proximal teeth 1 and 2.

Male. Not known.

Distribution and Biology. Madagascar. Only known from Ranomafana National Park, where it was dissected from wood tunnels in an *Oncostemum* tree log.

Etymology. The Latin name *diadematus* is a masculine adjective, meaning adorned with a diadem (a type of crown), referring to the shape of the declivity resembling a diadem.

Comment. Specimens of this species were originally thought to be *X. aduncus*. However, molecular analyses revealed significant genetic differences (Fig. 22) and subsequent morphological studies show clear differences in the shape of the declivital flanks (Figs. 26 and 29).

***Xyleborinus profundus* (Schedl, 1961), stat. nov.**

Xyleborus aduncus profundus Schedl, 1961, orig. spelling.
(Figs. 30–32)

Material Examined. Lectotype, female: MADAGASCAR, Ambodivoangy, J. Vadon (MNHN). Other material: [Supp Table S1](#) (online only).

Diagnosis. A vertical declivity encircled on its lower two-thirds by an almost completely smooth flange from interstriae 5 to 9, ending

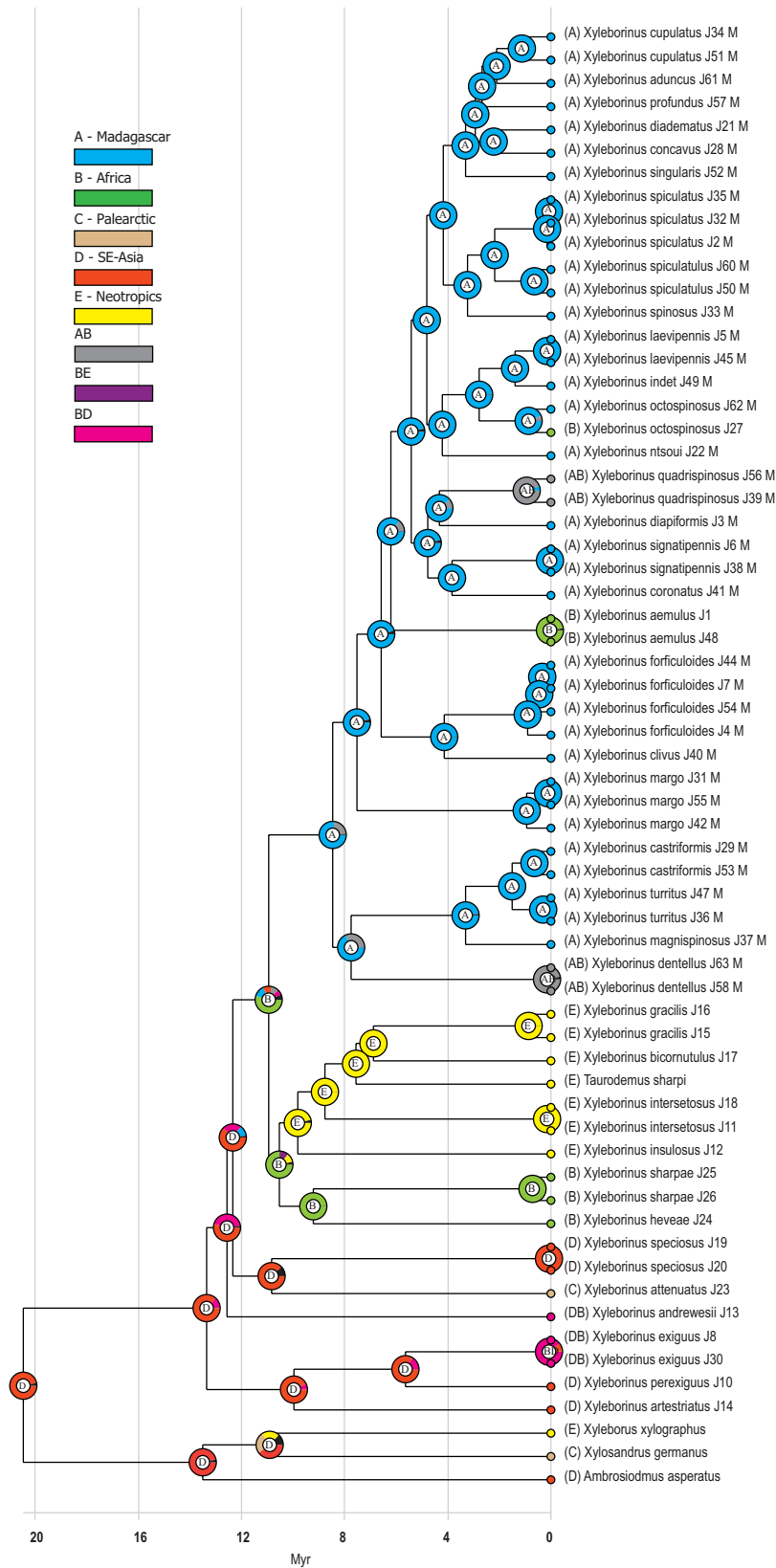


Fig. 23. Reconstruction of ancestral areas in RASP based on the BBM method, using the Beast consensus topology as input tree. Scale indicates time (myr).

Table 5. Currently valid Afrotropical *Xyleborinus* species with synonyms and distribution

Genus	Species	Author	Year	Synonyms	Distribution
<i>Xyleborinus</i>	<i>aduncus</i>	Schedl	1961		Madagascar
<i>Xyleborinus</i>	<i>aemulus</i>	Wollaston	1869	<i>Xyleborus spinifer</i> Eggers, 1920, syn. nov.	Angola, Namibia, Botswana, South Africa, St. Helena, Madagascar
<i>Xyleborinus</i>	<i>alienus</i>	Schedl	1977		South Africa
<i>Xyleborinus</i>	<i>armatus</i>	Schaufuss	1896		Madagascar
<i>Xyleborinus</i>	<i>bicinctus</i>	Schedl	1965		Madagascar
<i>Xyleborinus</i>	<i>castriformis</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>clivus</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>concauus</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>coronatus</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>cuneidentis</i>	Schedl	1961		Madagascar
<i>Xyleborinus</i>	<i>cupulatus</i>	Schedl	1961		Madagascar
<i>Xyleborinus</i>	<i>dentellus</i>	Schedl	1953	<i>Xyleborus forcipatus</i> Schedl, 1957, syn. nov.	Madagascar, Congo
<i>Xyleborinus</i>	<i>diadematus</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>diapiformis</i>	Schedl	1961		Madagascar
<i>Xyleborinus</i>	<i>forciculoides</i>	Schedl	1951		Madagascar
<i>Xyleborinus</i>	<i>forciculus</i>	Eggers	1922		Angola, Kenya, South Africa
<i>Xyleborinus</i>	<i>heveae</i>	Schedl	1957		Congo, Sierra Leone
<i>Xyleborinus</i>	<i>laevipennis</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>magnispinosus</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>marcidus</i>	Schedl	1965		Madagascar
<i>Xyleborinus</i>	<i>margo</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>mitosomiformis</i>	Schedl	1953		Madagascar
<i>Xyleborinus</i>	<i>mitosomus</i>	Schedl	1965		Madagascar
<i>Xyleborinus</i>	<i>namibiae</i>	Schedl	1982		Namibia
<i>Xyleborinus</i>	<i>ntsoui</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>octospinosus</i>	Eggers	1920	<i>Xyleborus mitosomipennis</i> Schedl, 1953, syn. nov.	Madagascar, Tanzania
<i>Xyleborinus</i>	<i>pilosellus</i>	Schedl	1957		Congo
<i>Xyleborinus</i>	<i>polyalthiae</i>	Schedl	1952		Congo
<i>Xyleborinus</i>	<i>profundus</i>	Schedl	1961		Madagascar
<i>Xyleborinus</i>	<i>pseudopityogenes</i>	Eggers	1943		Congo, Namibiae, Mozambique, South Africa
<i>Xyleborinus</i>	<i>quadrispinis</i>	Schedl	1953		Madagascar
<i>Xyleborinus</i>	<i>quadrispinosus</i>	Eichhoff	1878		South Africa, Madagascar
<i>Xyleborinus</i>	<i>sharpae</i>	Hopkins	1915	<i>Xyleborus schreineri</i> Eggers, 1920 (syn. by Wood, 1962)	Liberia, Tanzania, Sierra Leone, Cameroon
<i>Xyleborinus</i>	<i>signatipennis</i>	Schedl	1961		Madagascar
<i>Xyleborinus</i>	<i>similans</i>	Eggers	1940	<i>Xyleborus sclerocaryae</i> Schedl, 1962, syn. nov.	Angola, Bioko, Ivory Coast, Ghana, Congo, Rep. Congo, Somalia, South Africa
<i>Xyleborinus</i>	<i>singularis</i>	Eliassen & Jordal	sp. nov.		Madagascar
<i>Xyleborinus</i>	<i>spiculatulus</i>	Schedl	1965		Grand Comore, Madagascar
<i>Xyleborinus</i>	<i>spiculatus</i>	Schaufuss	1891		Madagascar
<i>Xyleborinus</i>	<i>spinipes</i>	Schedl	1957		Congo
<i>Xyleborinus</i>	<i>spinosus</i>	Schaufuss	1891		Madagascar
<i>Xyleborinus</i>	<i>subsulcatus</i>	Eggers	1927		Congo, Zambia
<i>Xyleborinus</i>	<i>syzygii</i>	Schedl	1959		Tanzania
<i>Xyleborinus</i>	<i>turritus</i>	Eliassen & Jordal	sp. nov.		Madagascar
Adventive species					
<i>Xyleborinus</i>	<i>andrewesii</i>	Blandford	1896	See manuscript	Worldwide
<i>Xyleborinus</i>	<i>exiguus</i>	Walker	1859	See manuscript	Worldwide
<i>Xyleborinus</i>	<i>saxeseni</i>	Ratzeburg	1837	See manuscript	Worldwide



Figs. 24–35. *aduncus* group. Dorsal, lateral, and declivital view of (24–26) *Xyleborinus aduncus* paratype; (27–29) *Xyleborinus diadematus* holotype; (30–32) *Xyleborinus profundus* paratype (labeled lectotype); (33–35) *Xyleborinus cupulatus* paratype.

in a pair of broad, triangular flanks, inner margin perpendicular to body axis. A small swelling or additional tooth present on the inside of the two flanks. Upper declivity with three small spines on interstriae 1, 2, and 3, preceding the flange, spine 3 partly fused with flange.

Distribution. Madagascar.

Comments. *Xyleborinus aduncus profundus* is here elevated to species status based on molecular evidence (Table 4). It has a unique small swelling or tooth on the inside of the apical flanks which runs more in parallel with the body axis.

***Xyleborinus cupulatus* (Schedl, 1961)**

Xyleborus cupulatus Schedl, 1961, orig. spelling (Figs. 33–35)

Material Examined. Holotype, female: MADAGASCAR, Perinet (MNHN). Paratype (1): MADAGASCAR, Ambila, Nr. M.119, 28.XI.1952, K. E. Schedl (NHMW). Other material: Supp Table S1 (online only).

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

Distribution. Madagascar. New locations: Andasibe-Mantadia National Park, Ranomafana National Park, Marojejy National Park.

Comments. Distinguished from all close relatives by the smooth edge of the flange.

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

Zoobank LSID: zoobank.org/act:37C54F6B-E6A0-498F-AF25-C4FFA8E5EDF6 (Figs. 36–38)

Type Material. Holotype, female: MADAGASCAR, Marojejy National Park, 2019: 26x-4, B. Jordal, *Cussonia* (Voantsilana) log, [GIS: -14.44, 49.76] alt. 1,000 m. Paratype (1): MADAGASCAR, Andranomalaza, X-57. Holotype deposited in ZMUB, paratype in NHMW.

Diagnosis. Declivity truncated, steep, encircled on declivital margin by eight pairs of evenly spaced, small and partly jagged spines of approximately equal size forming a wreath, except none present on the transverse elytral apex. Declivital surface slightly convex.

Female. Length 1.9 mm, 3.0× as long as wide; color light brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–2× their diameter; interstriae smooth, shiny, punctures as large as striae punctures, spaced by 4–5× their diameter. Declivity truncated, steep, encircled on declivital margin by eight pairs of evenly spaced, small, jagged spines from interstriae 1 to 9 forming a wreath, except none present on transverse elytral apex; declivital surface slightly convex, with approximately 50 punctures, each associated with a tiny granule. Vestiture consisting of short, scant, erect interstitial setae, glabrous on declivity except microscopic setae. **Legs.** Lateral edge of protibiae evenly curved with seven socketed teeth on apical 2/3, gap between proximal teeth 1 and 2 larger than others. Metatibiae gently curved laterally, with nine socketed teeth on apical three-fourth.

Male. Not known.

Distribution and Biology. Madagascar. Known from Marojejy National Park, and Andranomalaza near Antananarivo. Dissected from a wood tunnel in *Cussonia* (Voantsilana).

Etymology. The Latin name *singularis* is a masculine/feminine adjective, meaning unique or unmatched, referring to an undescribed singleton of this species labeled with this name in NHMW.

Comment. This species forms the sister group to all other members of the *aduncus* group (Fig. 22). An undescribed singleton labeled '*Xyleborus singularis*' was found in NHMW and matches a recently collected specimen in better condition; hence, the latter was chosen as the holotype.

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

Zoobank LSID: zoobank.org/act:F1545518-AF8A-4858-8D8F-822BEF5917F3 (Figs. 39–44)

Type Material. Holotype, female: MADAGASCAR, Ranomafana, Vato trail, 2012: 5x-12, B. Jordal, ex unknown log, [GIS: -21.29, 47.42] alt. 1,100 m. Allotype: MADAGASCAR, Ranomafana Centre ValBio, 2012: 27ix-1, B. Jordal, ex *Cryptocarya* branch, [GIS: -21.25, 47.42] alt. 950 m. Paratypes (18): All from MADAGASCAR, Ranomafana, coll. B. Jordal, 2012: same data as allotype (3); Centre ValBio, 29ix-16, Unknown log, [GIS: -21.25, 47.42] alt. 950 m (6); Vato trail, 4x-3, ex *Harungana madagascariensis*, [GIS: -21.29, 47.42] alt. 1,100 m (3); Centre ValBio, 28ix-6, ex *Oncostemum* log, [GIS: -21.25, 47.42] alt. 950 m (1); Centre ValBio, 30ix-7, ex *Polyscias*, [GIS: -21.25, 47.42] alt. 950 m (1); Vato trail, 4x-5,

Unknown log, [GIS: -21.29, 47.42] alt. 1,100 m (1); Centre ValBio, 1x-2, *Mussaenda* log, [GIS: -21.25, 47.42] alt. 950 m (1); Village E. ValBio, 10x-3, ex *Oncostemum* stump, [GIS: -21.24, 47.42] alt. 900 m (1); Centre ValBio, 30ix-7, ex *Polyscias* branch, [GIS: -21.25, 47.42] alt. 950 m (1). Holotype, allotype, and 16 paratypes deposited in ZMUB, 2 paratypes in NHMW.

Diagnosis, Female. Declivity vertical, truncated, encircled on declivital margin by a wreath consisting of seven to eight irregularly sized, small spines and tubercles on each side positioned between interstriae 1 and 9; third and lowermost spines (interstriae 4 and 9) longest, but shorter than length of fourth ventrite. Bottom pair appear more pronounced than others in dorsal view. Declivital surface concave.

Female. Length 1.8–2.0 mm, 2.8–3.0× as long as wide; color brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–2× their diameter. Interstriae smooth, shiny, punctures as large as striae punctures, spaced by 3–5× their diameter. Declivity vertical, truncated, encircled on declivital margin by wreath with seven to eight small spines and tubercles on each side on interstriae 1–9. Spine and tubercle pairs may be unsymmetrical or jagged, third and lowermost spine (interstriae 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 interstitial setae, mainly on posterior fourth on disc. Declivity glabrous, except microscopic striae setae. **Legs.** Lateral edge of protibiae angularly curved, appearing triangular, with seven socketed teeth from apical two-thirds to apical one-fourth. Large gap between proximal tooth 1 and 2. Metatibiae with lateral edge gently curved, eight socketed teeth on apical three-fourth, deep gap between proximal tooth 1 and 2.

Male. Length 1.5–1.7 mm, 2.5–2.7× as long as wide; color yellow. Elytral striae on disc not impressed, punctures shallow, spaced by 3–4× their diameter; interstriae variably smooth and rugose, shiny, punctures as large as striae punctures, spaced by 8–10× their diameter. Declivity vertical, truncated, encircled by granules on declivital margin on interstriae 1–9, one pair of larger tubercles on interstriae 4. Vestiture consisting of fine erect interstitial setae, declivity glabrous. **Legs.** Similar to female except socketed teeth on apical three-fifth of protibiae, on apical two-third of metatibiae.

Distribution and Biology. Madagascar. Only known from Ranomafana National Park, where it was frequently dissected from wood tunnels in *Cryptocarya*, *Harungana madagascariensis*, *Oncostemum*, *Polyscias*, and *Mussaenda* logs or branches.

Etymology. The Latin name *concavus* is a masculine adjective, meaning concave, referring to the concave surface of this species' declivity.

The *spiculatus* Group

Species with densely set sharp, short spines along the entire declivital margin. This group shares with the *aduncus* group a tendency for an extended flange on the declivital margin containing small spines.

***Xyleborinus spiculatus* (Schedl, 1965)**

Xyleborus spiculatus Schedl, 1965, orig. spelling (Figs. 45–47)



Figs. 36–44. *aduncus* group, cont. Dorsal, lateral, and declivital view of (36–38) *Xyleborinus singularis* holotype; (39–41) *Xyleborinus concavus* female holotype; (42–44) *Xyleborinus concavus* male allotype.

Material Examined. Holotype, female: Comoros, Grande Comore, K. E. Schedl (NHMW). MADAGASCAR, Mont d'Ambre, 12. XII. 1952, K. E. Schedl (two females); same data, one female labeled *Xyleborus dentipennis* (NHMW). Other material: see [Supp Table S1](#) (online only).

Diagnosis. A vertical to steeply sloping declivity encircled on declivital margin by a wreath with six to eight spines on each side. Spine on interstriae 4 and 8 longest, of approximately equal length, longer than length of third ventrite, spines on interstriae 5 and 6 very slightly shorter. Wreath very irregular, the number and length of spines may be asymmetrical between the two elytra.

Distribution. Grande Comoro Island, Madagascar. New locations: Marojejy National Park (Madagascar).

Comments. The spines nearest suture on top of declivity are slightly more upward compared to *X. spiculatus* (Schaufuss, 1891), as the declivity is slightly less steep.

***Xyleborinus spiculatus* (Schaufuss, 1891)**
Xyleborus spiculatus Schaufuss, 1891, orig. spelling
 (Figs. 48–50)

Material Examined. See [Supp Table S1](#) (online only). Holotype not examined, lost (Hamburg); Madagascar.

Diagnosis. A vertical declivity encircled on declivital margin by a wreath with six to eight spines on each side. Spine on interstriae 4 and 8 longest, of approximately equal length, longer than length of third ventrite, spines on interstriae 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.

Distribution. Madagascar. New locations: Ranomafana National Park, Andasibe-Mantadia National Park.

Comments. This species is almost indistinguishable from *X. spiculatus* by morphology and is better identified by molecular data. The upper spines near the elytral suture are slightly less upward compared to *X. spiculatus*, as the declivity is slightly steeper (Figs. 46 and 49).

The holotype of *X. spiculatus* was lost during WWII and the written description is the only account we have of its morphology (Schaufuss, 1891). 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 the elytra in the same specimen. Thus, only some specimens match the description of *X. spiculatus* completely. However, given that this study has revealed two genetically distinct groups (see [Fig. 22](#); [Table 4](#)), it is here proposed that each genetic group should be given one of the two names. The group with specimens most closely resembling the holotype of *X. spiculatus* was given that name and the other group was given the name of *X. spiculatus*.

Xyleborinus spinosus (Schaufuss, 1891)

Xyleborus spinosus Schaufuss, 1891, orig. spelling (Figs. 51–53)

Material Examined. MADAGASCAR, Mont d’Ambre, K. E. Schedl [labeled ‘Paratype *X. mitosomus*’]. Other material: see [Supp. Table S1](#) (online only). Holotype not examined: Madagascar (lost, Hamburg).

Diagnosis. A vertical declivity encircled on declivital margin by an irregular wreath consisting of 7–10 mixed spines and sharp tubercles on each side; longest spine on interstria 4, longer than length of third ventrite, second longest spine on interstria 2 slightly shorter. The last three spines on interstriae 5–8 very small, less than half the length of longest spine.

Distribution. Madagascar. New locations: Ranomafana National Park.

The *quadrispinosus* Group

Species with three to four very long spines along each side of the declivital margin. Most species have impressed striae on most of the elytral disc.

Xyleborinus diapiformis (Schedl, 1961)

Xyleborus diapiformis Schedl, 1961, orig. spelling (Figs. 54–56)

Material Examined. Holotype, female: MADAGASCAR, Perinet (MNHN). Other material. See [Supp Table S1](#) (online only).

Diagnosis. A vertical declivity encircled on declivital margin by one very short and four long spines on each side positioned on interstriae 3, 4, 7, 9, and 10, 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 one-third the length or less. Striae distinctly impressed, most apparent on posterior half of elytral disc.

Distribution. Madagascar. New locations: Ranomafana National Park.

Xyleborinus quadrispinis (Schedl, 1953)

Xyleborus quadrispinis Schedl, 1953, orig. spelling (Figs. 57–59)



Figs. 45–53. *spiculatus* group. Dorsal, lateral, and declivital view of (45–47) *Xyleborinus spiculatus* directly compared to holotype; (48–50) *Xyleborinus spiculatus* compared to original description; (51–53) *Xyleborinus spinosus* compared to original description.

Material Examined. Lectotype, female: MADAGASCAR, Mont Tsaratanana: alt. 1,500, X-49, RP (NHMW).

Diagnosis. A vertical declivity encircled by four pairs of spines on interstriae 3, 6, 7, and 9 in a crowned pattern, with additional small, sharp tubercles along the same margin on interstriae 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 one-third the length of first spine; spine 3 is intermediate of spine 2 and 4.

Distribution. Madagascar.

Xyleborinus quadrispinosus (Eichhoff, 1878)

Xyleborus quadrispinosus Eichhoff, 1878, orig. spelling (Figs. 60–62)

Material Examined. MADAGASCAR, det. K. E. Schedl (NHMW). Other material: see [Supp Table S1](#) (online only). Syntypes females: Africa meridional (RBINS), not examined.

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, and 9. Striae noticeably impressed on posterior two-thirds of elytral disc.

Distribution. Madagascar, South Africa. New locations (Madagascar): Ranomafana National Park, Andasibe-Mantadia National Park, Marojeje National Park.

Comments. The description of the species matches exactly Schedl identified material in Vienna.

Xyleborinus armatus (Schaufuss, 1891)

Xyleborus armatus Schaufuss, 1891, orig. spelling

Material Examined: None. Holotype: Madagascar; lost (Hamburg).

Diagnosis (Inferred From Description). Length 2.5 mm. A vertical declivity encircled by four pairs of spines. The first three spines originate on interstriae 3, 6, and 7 at the declivital margin; lowermost pair of spines thinner than other spines and more widely spaced than the uppermost pair. Striae impressed.

Distribution. Madagascar.

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

Xyleborinus signatipennis (Schedl, 1961)

Xyleborus signatipennis Schedl, 1961, orig. spelling (Figs. 63–65)

Material Examined. Holotype, female: MADAGASCAR, Perinet (MNHN).

Diagnosis. A vertical declivity encircled by three pairs of long, thin spines on interstriae 4, 8, and 9, and one small pair of spines on

interstriae 6, all positioned in a crowned pattern. First and last pair of spines longest, which are longer than the combined length of second and third ventrite; the second pair of long spines are about half the length of the first pair. Several sharp tubercles present close to upper declivital margin. Striae distinctly impressed on most of the elytral disc.

Distribution. Madagascar. New locations: Ranomafana National Park.

Xyleborinus coronatus Eliassen & Jordal, sp. nov.

Zoobank LSID: [zoobank.org:act:3B1FE5C9-8CB2-4FCC-87C4-3C377C9E9440](https://zoobank.org/act:3B1FE5C9-8CB2-4FCC-87C4-3C377C9E9440) (Figs. 66–68)

Type Material. Holotype, female: MADAGASCAR, Ankarafantsika National Park, 2015: 9v-x, B. Jordal, Multilure trap, [GIS: -16.264, 46.828] alt. 200 m. Paratype (1): same data as holotype. Holotype deposited in ZMUB, one 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, and 9; upper and lowermost pairs longest, as long as length of ventrite 2 and 3 combined; the two pairs in the middle shorter, slightly shorter than the length of the second ventrite.

Female. Length 2.0–2.1 mm, 2.9–3.1× as long as wide; color brown. Elytral striae on disc slightly impressed, punctures shallow, spaced by 1× their diameter; interstriae shiny, punctures slightly smaller than striae 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, and 9; pair 1 and 4 longest, as long as length of ventrite 2 and 3 combined; air 2 and 3 shorter, slightly shorter than length of second ventrite. Vestiture consisting of fine erect interstitial and tiny striae setae, declivity glabrous, long setae near tips of spines. Legs. Protibiae with lateral edge curved with six socketed teeth on apical two-thirds, distinct gap between proximal teeth 1 and 2. Metatibiae with lateral edge curved with seven evenly spaced socketed teeth on apical two-thirds. Apical third broader than proximal third.

Male. Not known.

Distribution and Biology. Madagascar. Only known from Ankarafantsika National Park, taken in a multilure trap.

Etymology. The Latin name *coronatus* is a masculine participle, meaning crowned, referring to the crown-like declivity.

The *octospinosus* Group

Species in this group have two pronounced spines near elytral apex.

Xyleborinus octospinosus (Eggers, 1920)

Xyleborus octospinosus Eggers, 1920, orig. spelling
Xyleborus mitosomipennis Schedl, 1953, syn. nov. (Figs. 69–71)

Material Examined. Lectotype, female: TANZANIA, Derema bei Amani, 11.VII.1911, Hagedorn (NHMW). Lectotype, female, of *X. mitosomipennis*: MADAGASCAR, Mont d'Ambre, 1950, det. K. E. Schedl (NHMW).



Figs. 54–68. *quadrispinosus* group. Dorsal, lateral, and declivital view of (54–56) *Xyleborinus diapiformis* directly compared to paratype; (57–59) *Xyleborinus quadrispinis* holotype; (60–62) *Xyleborinus quadrispinosus* compared to original description; (63–65) *Xyleborinus signatipennis* directly compared to paratype; (66–68) *Xyleborinus coronatus* holotype.

Diagnosis. Declivity nearly vertical, steep, encircled by four pairs of spines on interstriae 2/3, 4, 6, and 9 (in line with interstria 2 at the 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, occasionally with two tips, pointing more upward than first and third spine; additional tubercles present just below the third pair of spines, and near upper margin of declivity.

Distribution. Tanzania, Madagascar. New locations: Udzungwa foothills, Mang'ula (Tanzania).

Comments. Because *X. octospinosus* is nested within a series of clades endemic to Madagascar, this species must have colonized the African mainland rather recently (see Fig. 23) and has possibly remained isolated from its Malagasy relatives ever since. However, morphological and molecular differences have not yet developed and *X. mitosomipennis* must therefore be treated as a synonym of *X. octospinosus*.

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

Xyleborus mitosomipennis var. *laevipennis* Schedl, 1961, unavailable name

Zoobank LSID: zoobank.org/act:46F89AAF-17FC-4811-826E-2B8171CA607E (Figs. 72–74)

Type Material. Holotype, female: MADAGASCAR, Ranomafana Centre ValBio, 2012: 1x-6, B. Jordal, *Albizia* log, [GIS: -21.25, 47.42] alt. 950 m. Paratypes (10): MADAGASCAR, Ranomafana: Vato trail, 2012: 3x-8, B. Jordal, *Croton* log, [GIS: -21.29, 47.42] alt. 1,100 m (2); Vato trail, 2012: 2x-5, B. Jordal, *Sloanea* log, [GIS: -21.29, 47.42] alt. 1,100 m (1); Vato trail, 2012: 2x-6, B. Jordal, *Cryptocarya* log, [GIS: -21.29, 47.42] alt. 1,100 m (1); Vato trail, 2012: 4x-3, B. Jordal, *Harunga madagascariensis*, [GIS: -21.29, 47.42] alt. 1,100 m (1); Vato trail, 2012: 4x-5, B. Jordal, unknown log, [GIS: -21.29, 47.42] alt. 1,100 m (2); Vato trail, 2012: 6x-15, B. Jordal, *Croton* branch, [GIS: -21.31, 47.43] alt. 1,100 m (1); Teletakely trail, 2012: 8x-D3, D. Pistone, unknown log, [GIS: -21.26, 47.41] alt. 950 m (1); Village E. ValBio, 2012: 10x-11, B. Jordal, *Trema* log, [GIS: -21.24, 47.42] alt. 900 m (1). Holotype and eight paratypes deposited in ZMUB, two paratypes in NHMW.

Additional Material. MADAGASCAR, Perinet, M. 6811, 21.XI.1952, K. E. Schedl, 'Lectotype *Xyleborus mitosomipennis* var. *laevipennis*'.

Diagnosis. Declivity steep, encircled by four pairs of spines on interstriae 2/3, 4, 6, and 9 (in line with interstria 3 near elytral apex), appearing crown-like; upper three spines evenly separated, approximately of the same length, about as long as third ventrite; last pair of spines more prominent, slightly larger.

Female. Length 2.8–2.9 mm, 3.2–3.3× as long as wide; color dark brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1× their diameter; interstriae smooth, shiny, punctures as large as striae punctures, spaced by 4–5× their diameter. Declivity steep, encircled by four pairs of spines on interstriae 2/3, 4, 6, and 9 (in line with interstria 3 near elytral apex), appearing crown-like; spines approximately of the same length, no longer than length of third ventrite; first three pairs very similar in shape, evenly separated, lower pair more prominent; additional tubercles just below the third pair of spines, and on top of declivity. Vestiture consisting of fine erect interstitial setae mainly on posterior fourth of elytral disc; declivity glabrous, except microscopic setae. **Legs.** Protibiae with lateral edge evenly curved with seven socketed teeth on apical two-third, distinct gap between proximal tooth 1 and 2, tiny gaps between distal tooth 1, 2, and 3. Metatibiae with lateral edge curved with eight to nine socketed teeth on apical two-third, gap present between proximal tooth 1 and 2.

Male. Not known.

Distribution and Biology. Madagascar. Known from Andasibe and Ranomafana, dissected from wood tunnels in *Albizia*, *Croton*, *Sloanea*, *Cryptocarya*, *Trema*, and *Harungana madagascariensis*, primarily in large logs and thick branches.

Etymology. The word *laevipennis* is composed by the stem of the Latin masculine adjective *laevis*, meaning smooth, and the plural dative form of noun *penna*, meaning wing. The original proposal of the word (Schedl, 1961) likely referred to the glossy and smooth declivity of the elytra.

Comment. Morphologically similar individuals from Perinet, Madagascar, deposited in NHMW, were previously described as an infrasubspecific taxon with the name *Xyleborus mitosomipennis* var. *laevipennis* (Schedl, 1961). This name has no status and therefore not available according to ICZN article 1.3.4. We now make this name available at the species level.

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

Zoobank LSID: zoobank.org/act:A4DD3786-8F8E-4B76-8855-5E756781C392 (Figs. 75–77)

Type Material. Holotype, female: MADAGASCAR, Ranomafana Centre ValBio, 2012: 28ix-6, B. Jordal, *Oncostemum* log, [GIS: -21.25, 47.42] alt. 950 m. Paratypes (2): same data as holotype. Holotype and one paratype in ZMUB, one paratype in NHMW.

Diagnosis. Elytral declivity sloped on upper half, steeply curved on lower half, with first and third interstriae flat, smooth, interstria 2 slightly raised to a sharp, curved carinae. Interstriae 1–3 on posterior part of elytral disk and upper declivity with irregular row of granules and small spines, impressed, interstriae 4–6 with granules and spines also on lower declivity which is strongly inflated.

Female. Length 2.1–2.4 mm, 2.7–3.0× as long as wide; color dark brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–2× their diameter. Interstriae on disc smooth, shiny, with punctures as large as striae punctures spaced by 2–4× their diameter. Upper half of declivity sloped, lower half steeply curved, with first and third interstriae impressed and smooth, interstria 2 lightly raised carinae; appearing as excavated cleft, with two swollen lateral areas with more than 10 spines and tubercles each; largest spine on interstria 3 on the middle of declivity, as long as length of third ventrite, other spines under half its size. Vestiture consisting on elytral disc of regular rows of erect interstitial setae and short semirecumbent striae setae, and on declivity denser and longer, erect striae and interstitial setae. **Legs.** Protibiae with lateral edge gently curved with 8–11 socketed teeth on apical three-fourth, a big gap between proximal tooth 1 and 2. Metatibiae with lateral edge curved, with 10 socketed teeth on apical three-fourth, big gap between proximal tooth 1 and 2.

Male. Not known.

Distribution and Biology. Madagascar. Known only from Ranomafana National Park where it was dissected from wood tunnels in an *Oncostemum* log.



Figs. 69–77. *octospinosus* group. Dorsal, lateral, and declivital view of (69–71) *Xyleborinus octospinosus* directly compared to lectotype; (72–74) *Xyleborinus laevipennis* holotype; (75–77) *Xyleborinus ntsoui* holotype.

Etymology. The name *ntsoui* is a masculine noun in the genitive case composed of the stem Ntsou, which is the given name of the student Ntsou Rasolobera, who worked as assistant field guide on one of our excursions to Madagascar.

The *mitosomiformis* Group

Species with near vertical declivity, encircled by a very faint rim with one to five pairs of small tubercles or very small spines along the declivital margin; declivity smooth and shiny, occasionally with small granules on interstria 1.

Xyleborinus mitosomiformis (Schedl, 1953)

Xyleborus mitosomiformis Schedl, 1953, orig. spelling (Figs. 78–80)

Material Examined. Lectotype, female: MADAGASCAR, Mont Tsaratanana, alt. 1,500 m, X-49, RP (NHMW).

Diagnosis. Declivity nearly vertical, encircled on declivital margin by a sharp granule on each interstria 1–3 and at least five small spines on each side from interstria 4 and below, last pair near apex on interstria 3. All spines fairly similar in size, shorter than length of third ventrite;

interstria 1 on declivity with a row of three to four very small spines or sharp granules.

Distribution. Madagascar.

Xyleborinus mitosomus (Schedl, 1965), stat. res.

Xyleborus mitosomus Schedl, 1965, orig. spelling (Figs. 81–83)

Material Examined. Holotype, female: MADAGASCAR, Ankaratra, K. E. Schedl (NHMW).

Diagnosis. Declivity near vertical, encircled by a tiny rim on declivital margin on interstriae 6–9; three small tubercles present along the rim located on interstriae 6, 8, and near elytral apex in line with interstria 3; additional tiny sharp granules may be present.

Distribution. Madagascar.

Comment. This species was synonymized with *Xyleborinus spinosus* (Schaufuss, 1891) by Schedl in 1977. However, the holotype of *X. mitosomus* is clearly different from its paratypes which are *X. spinosus*. The holotype of *X. spinosus* is lost, but the paratypes

of *X. mitosomus* match the original description of *X. spinosus*. The species name *X. mitosomus* is, therefore, reinstated.

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

Zoobank LSID: [zoobank.org:act:659EB046-6D99-4190-8651-04325FA610BC](https://zoobank.org/act:659EB046-6D99-4190-8651-04325FA610BC)

(Figs. 84–86)

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

Diagnosis. Declivity vertical, steep, encircled by small rim on declivital margin, with tiny tubercles from interstriae 4 or 5, with a pair of slightly larger tubercles near elytral apex on interstria 3; interstria 1 on declivity with two to four pairs of sharp tubercles decreasing in size toward apex.

Female. Length 2.0–2.2 mm, 3.0× as long as wide; color dark brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–2× their diameter; interstriae smooth, shiny, punctures as large as striae punctures, spaced by 2–3× their diameter. Declivity vertical, steep, encircled by small rim on declivital margin, with tiny tubercles appearing from interstriae 4 or 5. Rim ends near elytral apex with a pair of slightly larger tubercles, about the length of the pedicel. Two to four pairs of sharp tubercles run down declivity on interstria 1. Vestiture consisting of fine erect interstitial setae primarily near and just on to declivity which has long setae on interstria 1; striae setae microscopic. Legs. Protibiae with lateral edge gently curved on proximal half, then abruptly broadening, subtriangular, with six socketed teeth on apical three-fifth, distinct gap between proximal tooth 1 and 2. Metatibiae with lateral edge curved, with six to seven socketed teeth on apical two-thirds, larger gap between proximal tooth 1 and 2.

Male. Not known.

Distribution and Biology. Madagascar. Known from Ranomafana National Park, Marojejy National Park and Andasibe, and was dissected from wood tunnels in *Cryptocarya* and *Trema* logs.

Etymology. The Latin name *margo* is a masculine/feminine noun, meaning margin or edge, referring to the small rim encircling the declivity of this species.

***Xyleborinus syzygii* (Schedl, 1959)**

Xyleborus syzygii Schedl, 1959, orig. spelling
(Figs. 87–89)

Material Examined. Paratype, female: TANZANIA, North Province, 19.X.1956, J.C.M. Gardner (NHMUK).

Diagnosis. Declivity steep; upper declivital margin has few and barely visible granules on interstriae 1–3; from interstriae 6 to 9 with

three to four sharp tubercles along the margin, the last pair near apex located on interstria 3. Declivity smooth elsewhere.

Distribution. Tanzania.

***Xyleborinus tuberculatus* Eliassen and Jordal, sp. nov.**

Zoobank LSID: [zoobank.org:act:B6208FEF-16A0-4068-8193-8EDB421E8C35](https://zoobank.org/act:B6208FEF-16A0-4068-8193-8EDB421E8C35)

(Figs. 90–92)

Type Material. Holotype, female: MADAGASCAR, Centre-Sud, 1901 Alluaud [leg]. '87'.

Holotype deposited in NHMW.

Diagnosis. Declivity nearly vertical, steep. Several tubercles or granules on upper declivital margin between interstriae 1 and 4; on margin below interstria 5 with small spines and sharp tubercles, last pair near apex located on interstria 2; declivity otherwise smooth.

Female. Length 2.4 mm, 2.9× as long as wide; color dark brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–2× their diameter; interstriae smooth, shiny, punctures slightly smaller than striae punctures, spaced by 4–5× their diameter. Declivity nearly vertical, steep, declivital margin marked on lower two thirds by a very faint rim, upper declivity with one or two sharp tubercles on each of interstriae 1–4, with slightly larger small spines along margin on interstriae 5, 7, 8, and 9 (in line with interstria 2). Vestiture consisting of fine erect interstitial setae primarily near and just on to declivity, and along lateral margins; striae setae microscopic. Legs not visible, covered by glue.

Male. Not known.

Distribution and Biology. Madagascar, central area. The label does not specify the location and host plant.

Etymology. The Latin name *tuberculatus* is a masculine nominative adjective, meaning having tubercles, referring to the small tubercles along the declivital margin of the elytra.

Comment. The description is based on a single specimen in NHMW labeled '*Xyleborus margino-tuberculatus*' by Schedl, but it was never published. The specimen is most similar to *X. mitosomus*, both of which have a distinct tubercle near apex on interstria 2, while the other three species in this group has the last pair of tubercles on interstria 3. It is distinguished from *X. mitosomus* primarily by the larger spines along the declivital margin which is also more coarsely granulated and tuberculate.

The *forficuloides* Group

Species with gradually sloped declivity and two pairs of moderately long spines on lower half of declivital margin, lower ones longer than those above.

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

Xyleborus forficuloides Schedl, 1951, orig. spelling

Xyleborus forficuloides forficuloides Schedl, 1951, subspecies (implicit)

Xyleborus forficuloides dentibarbis Schedl, 1961

Xyleborus forficuloides pinguis Schedl, 1961

(Figs. 93–101)



Figs. 78–92. *mitosomiformis* group. Dorsal, lateral, and declivital view of (78–80) *Xyleborinus mitosomiformis* lectotype; (81–83) *Xyleborinus mitosomus* holotype; (84–86) *Xyleborinus margo* paratype; (87–89) *Xyleborinus syzygii* paratype; (90–92) *Xyleborinus tuberculatus*, sp. nov. holotype.

Material Examined. Lectotype female: MADAGASCAR, tsimbazaza, 21.vi.1949, ex. *Mangifera indica*, R. Paulian [NHMW]. Paratype of ssp *dentibarbis*, female: Mont d’Ambre: no. g.89, 26.v–vi.50, R. Paulian [NHMW]. Paratype of ssp *pinguis*, female: Perinet, m. 103, 24.xi.1952, K. E. Schedl [NHMW].

Diagnosis. Elytral declivity gently curved, median area lightly impressed, furrowed, at lower posterolateral margin with two pairs of spines on interstriae 5 and 8, occasionally (ssp *dentibarbis*) with one additional 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, and they vary in the distance and angle within pairs.

Distribution. Madagascar. **New locations:** Ranomafana National Park, Andasibe-Mantadia National Park, Ambohitantely Nature Reserve, Marojejy National Park.

Comments. Three subspecies of this species were described by Schedl: *X. forficuloides forficuloides* (Schedl, 1951), *X. forficuloides pinguis* (Schedl, 1961), and *X. forficuloides dentibarbis* (Schedl, 1961). The first subspecies has a smaller distance between spines across the declivity, pointing slightly more inwards, and the upper declivital margin appears slightly more granulated. Genetic data were not obtained from *X. forficuloides dentibarbis*, and therefore we cannot test its taxonomic status. However, based on the limited genetic variation between the subspecies *forficuloides* and *pinguis*, it seems prudent to keep all three subspecies under the valid species *forficuloides* as currently treated (Wood and Bright 1992).

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

Zoobank LSID: zoobank.org/act:6BE28E5F-E170-4B04-805F-3C96F230E4E3 (Figs. 105–107)

Type Material. Holotype, female: MADAGASCAR, Ranomafana Teletakely trail, Cedar tree oil FIT, [GIS: -21.26, 47.42] alt. 950 m, October 2012, B. Jordal. Paratypes: same as holotype (1); same data as holotype except Ipsenol FIT, Centre ValBio (1). Holotype and one paratype deposited in ZMUB, one paratype in NHMW.

Diagnosis. Elytral declivity abruptly curved, lower half nearly vertical, surface smooth, shiny. Two pairs of spines of equal size located on interstria 3 near middle of declivity and interstria 9 along declivital apical margin, length of these spines slightly shorter than fourth ventrite; two pairs of sharp tubercles located on interstriae 6 and 7 along the declivital margin.

Female. Length 2.4 mm, 3.0× as long as wide; color dark brown. Elytral striae not impressed, punctures shallow, spaced by 1–3× their diameter. Interstriae shiny, punctures as large as striae punctures, spaced by 3–4× their diameter. Declivity sharply curved, nearly vertical on lower half. Two pairs of spines of equal size present on declivity, on interstria 3 near middle of declivity and near apex on interstria 9, each spine slightly shorter than length of fourth ventrite; two pairs of sharp tubercles present on declivital margin on interstriae 6 and 7. Vestiture consisting of long erect interstitial setae and fine, very short striae setae in single rows from elytral base to declivital margin, declivity with fine striae setae. Legs. Protibiae with lateral edge gently curved and seven to nine socketed teeth on apical three-fifth, and two tiny granules on proximal two-fifth, and a distinct gap between proximal tooth 1 and 2. Metatibiae with lateral edge curved and 10 socketed teeth on apical two-thirds, gaps between proximal teeth 1–3 slightly larger than others.

Male. Not known.

Distribution and Biology. Madagascar. Only known from the type locality in Ranomafana National Park, collected from flight intercept traps baited with either Cedar tree oil or Ipsenol lures.

Etymology. The Latin name *clivus* is a masculine noun, meaning slope or cliff, referring to the sharply curved declivity of this species resembling a steep slope or cliff.

Comments. This species has a quite different declivity from the other species in this group. It is steeper, and the lower pair of spines short and only marginally longer than the upper pair. The molecular data nevertheless place this species close to *X. forficuloides*, with maximum support on a short separating node.

The *bicinctus* Group

Very large species with sloped and lightly concave declivity, elytral apex extended and emarginated.

***Xyleborinus bicinctus* (Schedl, 1965)**

Xyleborus bicinctus Schedl, 1965, orig. spelling (Figs. 108–110)

Material Examined. Holotype, female: MADAGASCAR, Mont d'Ambre, Nr. M. 192a, 10.XII.1952, K.E. Schedl (NHMW).

Diagnosis. Elytral declivity excavated, occupying about three-seventh of elytra length, obliquely sloped; declivity encircled by spines on interstriae 1–4 along the declivital margin, largest spine on interstria 3; four sharp tubercles from interstriae 5 to 8. On interstria 8 close to elytral apex with extended spine-like flanks which are longer than length of second ventrite; inner flanks straight, form a 90 degree angle to the elytral apex.

Distribution. Madagascar.

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

Zoobank LSID: zoobank.org/act:B8E30E89-3DAB-4FB0-8DFA-A014675B3381 (Figs. 111–113)

Type Material. Holotype, female: MADAGASCAR, Ranomafana Village E. ValBio, 2012: 10x-11, *Trema* log, [GIS: -21.24, 47.42] alt. 900 m, B. Jordal. Paratypes (4): same data as holotype (1); Ranomafana, Valo area, 2012: 6x-S2, S. Roth, *Cryptocarya* branch, [GIS: -21.29, 47.42] alt. 1,100 m (1); 6x-S1, S. Roth, *Garcinia* standing tree (1); Teletakely trail, 2012: B. Jordal, Cedar tree oil FIT, [GIS: -21.26, 47.42] alt. 950 m (1). The holotype and two paratypes are deposited in ZMUB, two paratypes in NHMW.

Diagnosis. Declivity obliquely sloped, excavated, occupying three-seventh of elytra length, encircled by spines on declivital margin; spines on interstriae 1, 3, and 4 much larger, as thick as long, the third spine (on interstria 4) longest, as long as length of ventrite 3 and 4 combined; interstria 8 near elytral apex with spine-like flanks which are almost as long as the length of second ventrite; inner side of flanks curved, space between them semicircular.

Female. Length 3.4–3.5 mm, 2.7–2.8× as long as wide; color dark brown. Elytral striae on disc slightly impressed, punctures shallow, spaced by 1–2× their diameter. Interstriae smooth, shiny, punctures slightly smaller than striae punctures, spaced by 3–4× their diameter. Declivity obliquely sloped, occupying three-seventh of the elytra, excavated, slightly bisulcated, encircled by spines on declivital margin. Three spines on interstriae 1, 3, and 4 as thick as long; third spine longest of the three, as



Figs. 93–107. *forciculooides* group. Dorsal, lateral, and declivital view of (93–95) *Xyleborinus forciculooides forciculooides* directly compared to lectotype; (96–98) *Xyleborinus forciculooides pinguis* directly compared to lectotype; (99–101) *Xyleborinus forciculooides dentibarbis* paratype; (102–104) *Xyleborinus forcifulus* directly compared to syntype; (105–107) *Xyleborinus clivus* holotype.

long as length of ventrites 3 and 4 combined, first spine under half that size, second spine intermediate; spine-like flanks extend on interstria 8 near elytral apex, almost as thick and long as length of second ventrite; inner sides of flanks curved, semicircular; additional small spines located on interstriae 5, 7, and 8, barely longer than length of ventrite 4. Elytral

vestiture consisting mainly of dense, very small strial setae on declivity. **Legs.** Protibiae with lateral edge evenly curved, with 8–10 socketed teeth on apical two-thirds and two to three granules on proximal third, a distinct gap between every tooth. Metatibiae with lateral edge gently curved, with 11 equally separated socketed teeth on apical two-thirds.

Male. Not known.

Distribution and Biology. Madagascar. Known only from Ranomafana National Park where it was dissected from wood tunnels in logs of *Trema*, *Cryptocarya*, and *Garcinia* trees.

Etymology. The Latin name *turritus* is a masculine adjective, meaning towered or towering, referring to the tower-like spines on the declivity together with the large size of this species.

Xyleborinus castriformis Eliassen & Jordal, sp. nov.

Zoobank LSID: zoobank.org/act:CC98DC60-195B-4471-BEC5-6B1E4C60D06C
(Figs. 114–116)

Type Material. Holotype, female: MADAGASCAR, Marojejy National Park, 2019: 26x-5, B. Jordal, *Weinmannia* standing tree, [GIS: -14.44, 49.76] alt. 800–1,000 m. Paratype: MADAGASCAR, Ambohitantely reserve, 2015: 11v-1, B. Jordal, *Solanum aphanathum* branch, [GIS: -18.189, 47.292] alt. 1,500 m. Holotype deposited in ZMUB, one paratype in NHMW.

Diagnosis. Elytral declivity obliquely sloped, excavated, occupying three-seventh of the elytra, encircled on declivital margin by spines on interstriae 1, 2, and 3 which are as thick as long, third spine longer than other two; additional spine on interstria 4 just inside declivital margin, as long as third spine, but considerably thinner. Spine-like flanks on interstria 8 near elytral apex, almost as thick and long as length of second ventrite; inner side of each flank curved, semicircular in dorsal view.



Figs. 108–119. *bicinctus* group. Dorsal, lateral, and declivital view of (108–110) *Xyleborinus bicinctus* holotype; (111–113) *Xyleborinus turritus* paratype; (114–116) *Xyleborinus castriformis* holotype; (117–119) *Xyleborinus magnispinosus* holotype.

Female. Length 3.2–3.3 mm, 2.7–2.8× as long as wide; color dark brown. Elytral striae on disc slightly impressed, punctures shallow, spaced by 1× their diameter. Interstriae smooth, shiny, punctures slightly smaller than striae punctures, spaced by 3–5× their diameter. Declivity excavated, occupying three-seventh of elytra length, encircled by spines on interstriae 1, 2, and 3 along declivital margin, each as thick as long, third spine twice as large as the other two. Spine on interstria 4 as long as third spine, but considerably thinner. Spine-like flanks on interstria 8 near elytral apex, almost as thick and long as length of second ventrite; inner side of flanks curved, semicircular in dorsal view; four to five additional sharp tubercles on interstriae 4–8, barely longer than length of pedicel. Vestiture consisting of scattered erect interstitial setae, mainly on posterior third on disc and lateral sides. Declivity with almost microscopic striae setae. **Legs.** Protibiae with lateral edge evenly curved with eight to nine evenly spaced socketed teeth on apical two-thirds and two to three additional granules on proximal third. Metatibiae missing from specimen.

Male. Not known.

Distribution and Biology. Madagascar. Known from Marojejy National Park and Ambohitantely forest reserve, dissected from wood tunnels in branches of *Weinmannia* and *Solanum aphananthum* trees.

Etymology. The Latin name *castriformis* is composed of the stem of the Latin noun *castrum*, meaning castle or fort, the connecting vowel –i, and the noun *forma*, meaning shape or form. The name refers to the fort-like spines of the species' declivity.

Comments. This species is very closely related to *X. turritus* but is distinguished mainly by the shorter declivital spines and genetic differences. Differences may be due to geographical divergence between southern (Ranomafana) and northern/middle (Marojejy/Ambohitantely) populations, but more geographical sampling is needed to conclude.

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

Zoobank LSID: [zoobank.org:act:8C72DD44-9DD2-4CCB-A07E-DD39108B24B8](https://zoobank.org/act:8C72DD44-9DD2-4CCB-A07E-DD39108B24B8) (Figs. 117–119)

Type Material. Holotype, female: MADAGASCAR, Ranomafana Centre ValBio, 2012: 1x-D1, D. Pistone, *Cryptocarya* branch, [GIS: –21.25, 47.42] alt. 950 m. Paratypes (2): same data as holotype. Holotype and one paratype deposited in ZMUB, one paratype in NHMW.

Diagnosis. Elytral declivity rough, lateral profile gently rounded, excavated with three pairs of spines along declivital margin on interstriae 3, 4, and 7/8. Pair 2 and 3 on declivital margin, of very large size, third pair is about the same length as second ventrite, second pair slightly longer. First pair is shorter, slightly longer than length of third ventrite. Additional sharp tubercles are present on the upper margin of the declivity.

Female. Length 3.3 mm, 2.7–2.8× as long as wide; color dark brown, almost black. Elytral striae on disc weakly impressed, punctures shallow, spaced by 1× their diameter. Interstriae shiny, punctures as

large as striae punctures, spaced by 2–4× their diameter. Declivity coarse, impressed, with three pairs of spines on interstriae 3, 4, and 7/8. Pair 2 and 3 on declivital margin, of very large size, third pair is about the same length as second ventrite, second pair slightly longer. First pair is shorter, slightly longer than length of third ventrite; additional sharp tubercles present on upper declivity. Vestiture consisting of sparse, fine, erect interstitial setae, mainly on posterior third on disc and lateral areas; declivity with very fine, short striae setae. Legs. Protibiae with lateral edge evenly curved with eight equally separated socketed teeth on apical two-thirds. Metatibiae with lateral edge curved with 10 evenly separated socketed teeth on apical three-fifth.

Male. Not known.

Distribution and Biology. Madagascar. Known only from the type locality in Ranomafana National Park, where it was dissected from wood tunnels in a *Cryptocarya* tree branch.

Etymology. The Latin name *magnispinosus* is composed of the stem of the Latin adjective *magnus*, meaning large or great, a linking vowel –i, and the Latin adjective *spinosus*, meaning spiny or thorny. The name refers to the unusually large spines on the elytral declivity.

Comments. This species deviates from all other species in this group by the shorter and gradually rounded declivity, and by having more pronounced lower spines rather than extended flanks on interstria 8. Morphological differences are clearly reflected in equally divergent genetic sequences (Fig. 22).

The *marcidus* Group

***Xyleborinus marcidus* (Schedl, 1965)**

Xyleborus marcidus Schedl, 1965, orig. spelling (Figs. 120–122)

Material Examined. Holotype, female: MADAGASCAR, Mont d'Ambre, alt. 1,000 m, 12.XII.1952, K. E. Schedl (NHMW).

Diagnosis. Elytral declivity has two long and tall postero-lateral flanges which gives the entire declivity a flat U-shape form in dorsal view. Three blunt spines are present on the dorsal edge of each flange. This shape is unique within *Xyleborinus*.

Distribution. Madagascar.

The *cuneidentis* Group

***Xyleborinus cuneidentis* (Schedl, 1961)**

Xyleborus cuneidentis Schedl, 1961, orig. spelling (Figs. 123–125)

Material Examined. Paratype, female: MADAGASCAR, Ambodivoangy, J. Vadon (MNHN).

Diagnosis. Declivity gently curved. Four pairs of spines located on interstriae 6, 7, and 9 along the declivital margin, and on interstria 3 on the middle of declivity, together forming a small circle on lower half of declivity. Spines on interstria 3 longest, slightly longer than length of third ventrite. Additional sharp tubercles present on interstriae 1–3 on upper half of declivity.

Distribution. Madagascar.

The *dentellus* Group

Species with obliquely sloping declivity, lightly impressed declivity with one to two small spines along declivital margin on upper third, and two to three very slightly longer spines on lower third, and declivity abruptly vertical on lower one-fifth.

Xyleborinus dentellus (Schedl, 1953)

Xyleborus dentellus Schedl, 1953, orig. spelling

Xyleborus forcipatus Schedl, 1957, **syn. nov.**

(Figs. 126–131)

Material Examined. Lectotype, female: MADAGASCAR, Mont d'Ambre, K. E. Schedl (NHMW). MADAGASCAR, Ambila, Nr. M. 113, 28.XI.1952, K. E. Schedl (1, NHMW). Paratype of *X. forcipatus*: Congo, Mulungu, 624, 11.VIII.1952, K. E. Schedl (1, NHMW).

Diagnosis. Declivity obliquely sloped, encircled on declivital margin by five to six pairs of spines on each side from interstriae 3 to 9, declivity otherwise smooth. Longest spine on interstria 7, about the length of or slightly longer than third ventrite, followed in length by spines on interstriae 3 and 9. Lower two pairs of spines fang-like in dorsal view.

Distribution. Madagascar, Congo. **New locations:** Ankarana (Madagascar).

Comment. *Xyleborus forcipatus* (Schedl, 1957) is synonymized with *X. dentellus* based on comparisons between the *X. dentellus* holotype and a *X. forcipatus* paratype from the holotype locality in Congo, both deposited in NHMW, Wien.

Xyleborinus pseudopityogenes (Eggers, 1943)

Xyleborus pseudopityogenes Eggers, 1943, orig. spelling

(Figs. 132–134)

Material Examined. Holotype, female: MOZAMBIQUE, Zambezi river, Nova Choupanga near Chemba, 1929, P. Lesne (NHMW). Other specimens: ANGOLA, Lungo, Vila Ariaga, 7-9.IX.1956, G. Rudebeck (one, NHMW, labeled *X. spinifer*). NAMIBIA, Grootfontein, Farm Mariabronn, 28.1.1975, H. Roer (one, NHMW, labeled *X. spinifer*).

Diagnosis. Declivity sloped, encircled by four to five pairs of small 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 interstriae 3 and 9. Two sharp tubercles on interstriae 4 and 5.

Distribution. Congo, Namibia, Mozambique, South Africa. **New country:** Angola (Lungo, Vila Arriaga, 9.IX.1956, coll. G. Rudebeck (NHMW)).

Comment. Some specimens of *X. pseudopityogenes* in the NHMW collection are wrongly labeled *X. spinifer*. The latter species is a synonym of *X. aemulus* which is a very different species. *Xyleborinus pseudopityogenes* is distinguished from the much closer relative *X. dentellus* by fewer and much shorter spines on the declivity. Differences are small and genetic data are needed to confirm validity of both species.

Xyleborinus forficulus (Eggers, 1922)

Xyleborus forficulus Eggers, 1922, orig. spelling

(Figs. 102–104)

Material Examined. Syntype, female: TANZANIA, Makonde Plateau (Methner Collection, ZMHB). Other material (1): ANGOLA, Alto Chicapa r., Gungo, 4219, 27.VI.1954, Machado (NHMW).

Diagnosis. Declivity sloped, surface lightly rugose, encircled on or just inside declivital margin by four spines on each side located on interstriae 3, 4, 5/6, and 7/8, with smaller spines or sharp tubercles variably present above some of the major spines; the lowermost pair of spines the longest, longer than length of second ventrite, hooked inwards with tips facing each other.

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

Comments. This species bears some resemblance with the *forficuloides* group but a tentative placement in the *dentellus* group is based on the multiple pairs of spines along the entire declivital margin, lacking in *X. forficuloides*.

The *aemulus* Group

Species with a gradually rounded upper part of declivity to a near vertical lower declivity, with two pairs of short spines.

Xyleborinus aemulus (Wollaston, 1869)

Tomicus aemulus Wollaston, 1869, orig. spelling

Xyleborus spinifer Eggers, 1920, **syn. nov.**

(Figs. 135–137)

Material Examined. Holotype, female: UNITED KINGDOM, St. Helena, Blandford [leg.] (NHMUK). SOUTH AFRICA, Humansdorp, Acx 2487, July 1970, D. B. Scott (NHMUK). Holotype of *X. spinifer*: Südafrika, Sogosse, 20.XI.[19]06, von Seiner gesammelt (ZMHB).

Diagnosis. Declivity nearly vertical. Two pairs of small spines about the length of third ventrite, located on interstria 3 and near the declivital margin at interstria 8; two to three sharp tubercles from interstriae 4 to 7 and at least one small tubercle pair on top of declivity at interstriae 1–2.

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

Comment. *Xyleborus spinifer* is synonymized with *X. aemulus* based on comparison of morphologically near-identical holotypes. Based on its nested position in the Malagasy clade, and one record from Madagascar (not confirmed), there is a yet untested possibility that the broadly distributed southern African populations originated from that island.

Xyleborinus alienus (Schedl, 1977)

Xyleborus alienus Schedl, 1977, orig. spelling

(Figs. 138–140)

Material Examined. Holotype, female: SOUTH AFRICA, Humansdorp, July 1970, D. B. Scott (NHMW).



Figs. 120–134. *marcidus*, *cuneidentis*, and *dentellus* groups. Dorsal, lateral, and declivital view of (120–122) *Xyleborinus marcidus* holotype; (123–125) *Xyleborinus cuneidentis* paratype; (126–128) *Xyleborinus dentellus* lectotype; (129–131) *Xyleborinus forcipatus* paratype (syn. nov. of *Xyleborinus dentellus*); (132–134) *Xyleborinus pseudopyyogenes* holotype.

Diagnosis. Elytral disk sloping toward a low and abruptly curved declivity, near vertical on lower two-thirds; declivity with three pairs of spines on interstriae 3, 4, and 7/8, none longer than length of antennal club; first spine very short, in horizontal line with the second spine along upper declivital margin, a faint trace of rim along margin to interstriae 7/8 with largest spine broad, incised.

Distribution. South Africa.

Comments. The unique holotype is reminiscent of males in *Xyleborinus* as indicated by the relatively large pronotum compared to a small and sloping elytral disc. It could therefore be a male of *X. aemulus* showing identical position of the two main pairs of spines on declivity. This hypothesis cannot be tested until more specimens becomes available.



Figs. 135–146. *aemulus* and *sharpae* groups. Dorsal, lateral, and declivital view of (135–137) *Xyleborinus aemulus* directly compared to holotype; (138–140) *Xyleborinus alienus* holotype. *sharpae* group. Dorsal, lateral, and declivital view of (141–143) *Xyleborinus pilosellus* paratype; (144–146) *Xyleborinus spinipes* unspecified type.

The *sharpae* Group

Species without long spines and flanks on the elytral declivity, typically with rows of small sharp granules or rounded tubercles, rarely with very short spines (one species). The declivity appears rounded without posterolateral extensions and swellings. All species are found on the African mainland and are morphologically very similar. However, the molecular data reveals that very similar species are not necessarily closely related albeit in one clade (see Fig. 22). Identification relies on unusually small morphological details in the presence and absence and the shape of spines and tubercles on declivital interstriae 1–5, particularly along the apical margin.

Xyleborinus pilosellus (Schedl, 1957)

Xyleborus pilosellus Schedl, 1957, orig. spelling (Figs. 141–143)

Material Examined. Paratype, female: DR Congo, Yangambi, Nr. 850, 12.IX.1952, K. E. Schedl (RMCA).

Diagnosis. Declivity gently curved on posterior half of elytra, completely without spines and sharp granules.

Distribution. Congo.

Comments. This species is unique for the genus having a smooth declivity without any spines or sharp granules. The overall habitus nevertheless indicate affiliation with the other members of the *sharpae* group based on the rounded shape of the declivity.

Xyleborinus spinipes (Schedl, 1957)

Xyleborus spinipes Schedl, 1957, orig. spelling (Figs. 144–146)

Material Examined. Type, female: DR CONGO, Yangambi, 258, 28.VI.1952, K. E. Schedl (RMCA).

Diagnosis. Declivity gently sloped on posterior half of elytra, with rows of sharp tubercles present on interstria 3 and fewer sharp tubercles present from interstriae 4 to 9, longest spines found along the posterior elytral margin, including a pair of outwardly curved short spines on interstria 2; tiny additional granules present on declivital interstria 1, surface smooth on interstria 2 and lower half of interstria 4.

Distribution. Congo.

Xyleborinus polyalthiae (Schedl, 1952)

Xyleborus polyalthiae Schedl, 1952, orig. spelling (Figs. 147–149)

Material Examined. Paratype, female: DR CONGO, Yangambi, Z. 873, R. 2388, 1957, R. Mayne (RMCA).

Diagnosis. Declivity sloped, interstriae 1 and 2, and lower part of 3 and 4 smooth and glabrous (a few setae on upper part), other interstriae have rows of sharp tubercles or granules and setae present on declivity. Three pairs of spines on posterior margin of elytra located at interstriae 3–4 of equally small size and evenly spaced.

Distribution. Congo.

Xyleborinus subsulcatus (Eggers, 1927)

Xyleborus subsulcatus Eggers, 1927, orig. spelling (Figs. 150–152)

Material Examined. Type, female: DR Congo, Yangambi, Z. 541, R. 2366, 1951, R. Mayne (RMCA); one female with no status: same data as holotype (NHMW).

Diagnosis. Declivity sloped, interstriae 1 and 2 smooth and glabrous (a few setae on upper part), other interstriae have rows of sharp tubercles or granules and setae present on declivity. Four pairs of sharp tubercles on posterior margin of elytra located on interstriae 2–5 irregularly spaced and differ in size.

Distribution. Congo, Zambia.

Comments. The previous species *X. polyalthiae* may be conspecific but the types show differences in the size and spacing of apical spines, and by the degree of smoothness on declivital interstriae 3 and 4. Until more specimens are collected, both species are treated as valid.

Xyleborinus heveae (Schedl, 1957)

Xyleborus heveae Schedl, 1957, orig. spelling (Figs. 153–155)

Material Examined. Paratype, female: DR CONGO, Yangambi, S. 402.14, 14.VII.1952, K. E. Schedl (NHMW). Other material: see [Supp Table S1](#) (online only).

Diagnosis. Declivity gently curved, nearly a straight slope in middle; interstria 2 and lower third of interstriae 1 and 3 smooth and glabrous (except few setae on top of declivity), other interstriae have rows of small sharp tubercles and setae. Apical margin of elytra with

granule on interstriae 2 and 4–6. Striae distinctly impressed on posterior two-thirds of elytra, also on the declivity. Length 2.0 mm.

Distribution. Congo, Sierra Leone (new country).

Xyleborinus namibiae (Schedl, 1982)

Xyleborus namibiae Schedl, 1982, orig. spelling (Figs. 156–158)

Material Examined. Paratype, female, NAMIBIA, Klein Spitzkoppe, 15.5.1972, L & O Prozesky (NHMW).

Diagnosis. Elytral declivity curved, steep on lower half; interstria 2 smooth, other interstriae with rows of tubercles and setae; no more than five tubercles on interstria 1 between upper declivity and elytral apex. Three pairs of sharp tubercles on posterior margin of elytra are of equal size and evenly spaced, longer than thick, located on interstriae 2, 3, and 4, and smaller tubercles on apical margin of interstriae 5 and 6. About 2.1 mm in length.

Distribution. Namibia.

Xyleborinus sharpae (Hopkins, 1915)

Xyleborus sharpae Hopkins, 1915, orig. spelling
Xyleborus schreineri Eggers, 1920 (syn. by Wood, 1962) (Figs. 159–161)

Material Examined. Holotype, female: LIBERIA, Mount Coffee, type no. 7648, 1896, Mrs. Sharp (USNM). One female, DR CONGO, 25.VII(L?) 1952, K. E. Schedl (NHMW). Other material: see [Supp Table S1](#) (online only).

Diagnosis. Smaller than other African species, length 1.4–1.5 mm. Elytral declivity curved, with interstria 2 and posterior two-thirds of interstria 4 smooth and often glabrous, other interstriae have rows of densely set, small, sharp spines, and long erect setae. The many small spines, which may be twice as long as thick, makes declivity appear rugged. Fine erect, long interstitial 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, located on interstriae 2–4, and two additional shorter spines on margin of interstriae 5 and 6.

Distribution. Angola, Cameroon, Congo, Equatorial Guinea, Ghana, Guinea, Ivory Coast, Liberia, Tanzania, Sierra Leone (new country), Gabon (new country).

Xyleborinus similans (Eggers, 1940)

Xyleborus similans Eggers, 1940, orig. spelling
Xyleborus sclerocaryae Schedl, 1962, syn. nov (Figs. 162–167)

Material Examined. Holotype, female: DR CONGO, Kasamvu, 30.IX.25, A. Collart (NHMW). Paratype, female of *X. sclerocaryae*: SOUTH AFRICA, Transvaal, Lothion, 16.10.1959, J. H. Grobler (NHMW). Lectotype, female of *X. diversus*: Gold Coast [GHANA], Sunyani, T.23, 1945, G. H. Thompson (NHMW).

Diagnosis. Elytral declivity gradually curved, with interstria 2 smooth and glabrous, other interstriae with rows of sharp tubercles



Figs. 147–161. *sharpae* group, cont. Dorsal, lateral and declivital view of (147–149) *Xyleborinus polyalthiae* paratype; (150–152) *Xyleborinus subsulcatus* directly compared to type; (153–155) *Xyleborinus heveae* paratype; (156–158) *Xyleborinus namibiae* paratype; (159–161) *Xyleborinus sharpae* directly compared to holotype.

or granules and setae. Posterior margin of elytra with only small granules, one each on interstriae 2–6. Length 1.8–2.0 mm.

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

Comments. *Xyleborinus sclerocaryae* is synonymized with *X. similans* based on near-identical types. These types vary only

slightly in color which likely reflects different stages of maturation, and marginally in the size of declivital granules.

Recently Established Asian Species

Three species which are broadly distributed in Asia are also found in Africa. They are fairly similar to the *sharpae* group and forms a basal grade of species related to the combined Neotropical–Afrotropical clade.

***Xyleborinus saxesenii* (Ratzeburg, 1837)**

Bostrichus saxesenii Ratzeburg, 1837, orig. spelling
Tomiscus dohrni Wollaston 1854 (syn. by Ferrari, 1867)
Tomiscus decolor Boieldieu 1859 (syn. by Ferrari, 1867)
Xyleborus angustatus Eichhoff 1866 (syn. by Schedl, 1964)
Xyleborus aesculi Ferrari 1867 (syn. by Eichhoff, 1878)
Xyleborus sobrinus Eichhoff 1875 (syn. by Schedl, 1964)
Xyleborus subdepressus Rey 1883 (syn. by Bedel, 1888)
Xyleborus frigidus Blackburn 1885 (syn. by Samuelson, 1981)
Xyleborus arbuti Hopkins 1915 (syn. by Wood, 1957)
Xyleborus floridensis Hopkins 1915 (syn. by Wood, 1962)
Xyleborus pecanus Hopkins 1915 (syn. by Wood, 1962)
Xyleborus quercus Hopkins 1915 (syn. by Wood, 1962)
Xyleborus subspinosus Eggers 1930 (syn. by Wood, 1989)
Xyleborinus libocedri Swaine 1934 (syn. by Wood, 1957)
Xyleborinus tsugae Swaine 1934 (syn. by Wood, 1957)
Xyleborus pseudoagracilus Schedl 1937 (syn. by Wood, 1989)
Xyleborus retrusus Schedl 1940 (syn. by Wood, 1989)
Xyleborus peregrinus Eggers 1944 (syn. by Schedl, 1980)
Xyleborus pseudoangustatus Schedl 1948 (syn. by Schedl, 1964)
Xyleborus paraguayensis Schedl 1949 (syn. by Wood, 1989)
Xyleborus opimulus Schedl 1976 (syn. by Wood, 2007)
Xyleborus cinctipennis Schedl 1980 (syn. by Wood, 1989)
 (Figs. 168–170)

Material Examined. Holotype *X. floridensis*: United States, type no. 7646, Hubbard & Schwarz (USNM). Syntypes collected in Southern Germany were not located in museums and are presumably lost.

Diagnosis. Elytral declivity steeply curved, nearly vertical on lower half; interstria 2 (and lower third of interstria 1) smooth, other interstriae with rows of tiny tubercles and erect setae; posterior margin of elytra with three pairs of sharp tubercles in decreasing size located on interstriae 2–4, minute granules on 5 and 6. Length 2.0–2.2 mm.

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

Comments. Although morphological rather homogeneous worldwide, we note that South African specimens deviates from the Holarctic populations of this species (Jordal and Kambestad 2014) and therefore needs some further studies to clarify its taxonomic status.

***Xyleborinus exiguus* (Walker, 1859)**

Bostrichus exiguus Walker, 1859, orig. spelling
Xyleborus muriceus Eichhoff 1878 (syn. by Eggers, 1925)
Xyleborus diversus Schedl, 1954 (syn. by Smith et al. 2020)
Xyleborus perexiguus Schedl, 1971 (syn. by Hulcr and Cognato, 2013)
Xyleborus ankius Schedl, 1975 (syn. by Hulcr and Cognato, 2013)
 (Figs. 171–176)

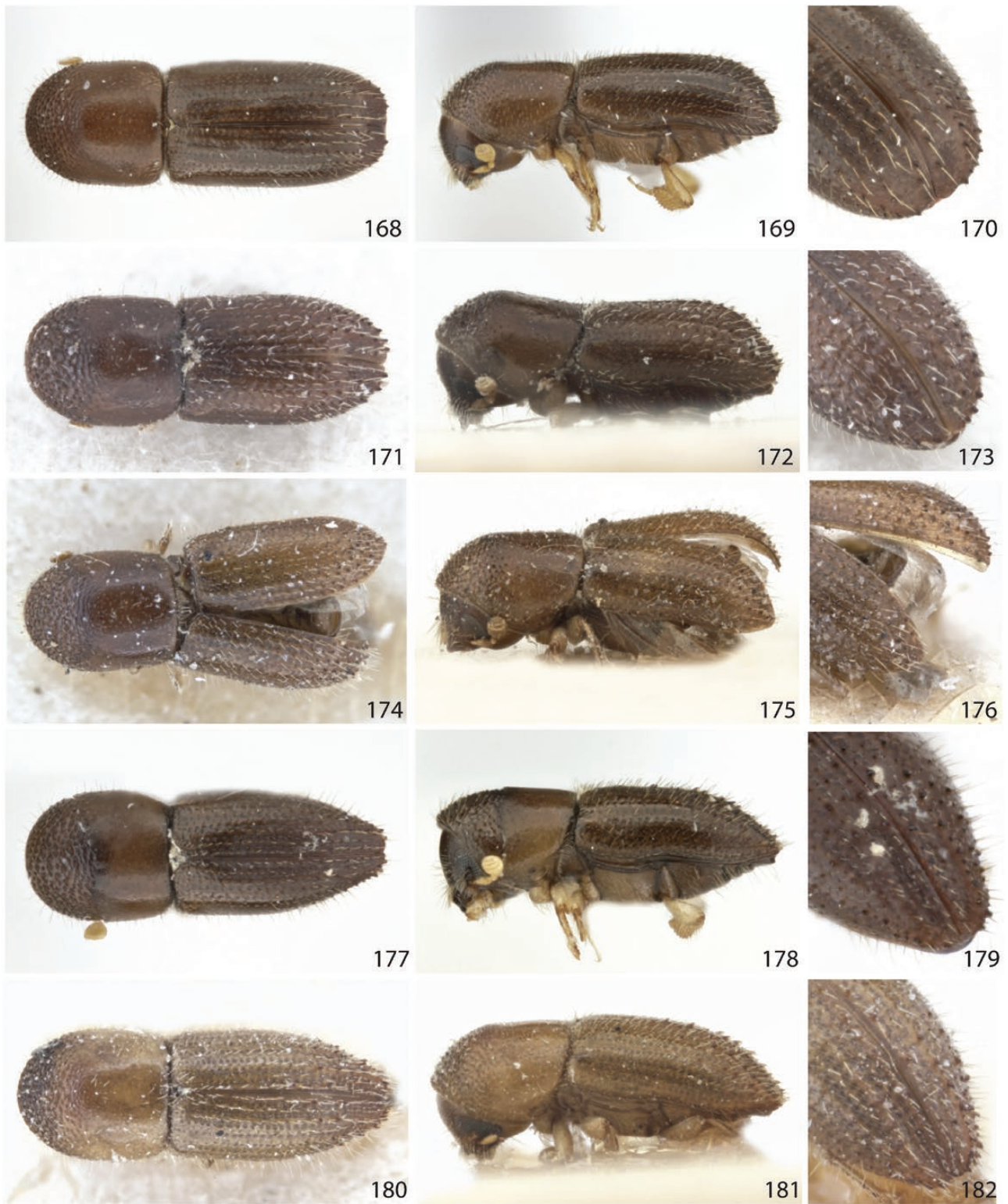
Material Examined. Holotype, female: Sri Lanka (NHMUK). Other specimens (female): Sri Lanka, Sabargamuva, Millavitiya Est, 24.–31.VII.1956, E. Judenko (NHMUK). Myanmar, Tenasserim, Sukli 75 km E. of Mouimeia, alt. 600 m, 27.–31.X.34, Malaise trap (NHMW). **Supp Table S1** (online only): Gabon and Cameroon.

Diagnosis. Elytral declivity curved on upper part, then obliquely sloped to lower one-sixth, then abruptly recurved, making a sharp angular transition from apex to lower margin of elytra. Interstria 2 are mainly smooth and glabrous, other interstriae with rows of small spines, sharp tubercles and long interstitial setae; spines may be longer than they are thick; interstria 1 on declivity with five or fewer small spines and/or sharp tubercles; posterior margin of elytra with three pairs of equally small spines evenly spaced, longer than they are thick, located on interstriae 2–4, additional smaller spines irregularly spaced on interstriae 5 and 6. About 1.6–1.8 mm in length.

Distribution. Introduced worldwide, native area Asia. **New locations:** Gabon, Cameroon.



Figs. 162–167. *sharpae* group, cont. Dorsal, lateral, and declivital view of (162–164) *Xyleborinus similans* holotype; (165–167) *Xyleborinus sclerocaryae* paratype (syn. nov. of *Xyleborinus similans*).



Figs. 168–182. Recently established Asian species. Dorsal, lateral, and declivital view of (168–170) *Xyleborinus saxesenii* directly compared to *Xyleborus floridensis* holotype (synonym); (171–173) *Xyleborinus exiguus* compared to holotype; (174–176) *Xyleborinus diversus* lectotype (synonym of *X. exiguus*); (177–179) *Xyleborinus andrewesi* compared to holotype; (180–182) *Xyleborinus mimosae* paratype (**syn. nov.** of *Xyleborinus andrewesi*).

Comments. *Xyleborinus diversus* was synonymized recently in *X. exiguus*. The holotype bear some resemblance to *X. similans*, but we follow here the recent suggestion by Smith et al. (2020).

Xyleborinus andrewesi (Blandford, 1896)

Xyleborus andrewesi Blandford, 1896, orig. spelling

Xyleborus mimosae Schedl, 1957, syn. nov

Xyleborus persphenos Schedl, 1970 (Syn. by Schedl 1975)

Xyleborus insolitus Bright, 1972 (Syn. by Bright 1985)

Cryptoxyleborus gracilior Browne, 1984 (Syn. by Beaver 1995)

(Figs. 177–182)

Material Examined. Holotype, female: INDIA, Belgaum (NHMUK). Paratype of *X. mimosae*: ‘Côte d’Afrique or. angl. Tiwi’ [unknown area], November 1911, Alluaud & Jeannel (NHMW).

Diagnosis. 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; striae 1 and 2 lightly impressed.

Distribution. Introduced worldwide. In the Afrotropics: Congo, Tanzania, Kenya, Zambia, Seychelles

Comments. *Xyleborus mimosae* (Schedl, 1957) is here synonymized with *X. andrewesi*. This species has a documented huge variation in the length and degree of tapering of the elytral apex (Hulcr and Cognato 2013). The morphology of *X. mimosae* is clearly within the variation seen in *X. andrewesi*.

Excluded Species

Xyleborus collarti Eggers, 1932, (comb. res. by Hulcr et al. 2007)

Xyleborus gracilipennis Schedl, 1957 comb. res.

Both species have a flat scutellum that flush with the elytral disc and are therefore confirmed and transferred to their original genus.

Key to Afrotropical *Xyleborinus*

- 1 Elytral declivity with a series of longer spines or flanks, or with marked rim or flange, or swollen areas (Figs. 19–21)2
 - Declivity gradually rounded, with at most very short spines and sharp granules (Figs. 18, 151)36
- 2 Declivity with two long, straight, posterolateral flanges with three blunt dorsal spines, in dorsal view declivity is broadly U-shaped (Fig. 120)*Xyleborinus marcidus* (Schedl, 1965)
 - Declivity either without flanks, or flanks are without dorsal spines, or flank is apically spine-like and curved inwards ..3
- 3 Declivity very steep, vertical or nearly vertical. There is a sharp contrast between the elytral disc and the declivity or at least sharply curved at upper declivital margin (Figs. 5, 7–9)4
 - The declivity is gradually descending or obliquely sloped (Fig. 6)27
- 4 The declivity has a wreath (Fig. 17) or flange (Fig. 16) encircling the entire declivital margin5
 - Rim on the declivital margin is either very small, or replaced by sharp tubercles, or completely absent; declivity may be encircled by spines in a crowned fashion (Figs. 20–21) or spines more scattered (Fig. 13)13

- 5 The declivital flange is completely smooth from interstriae 2. Either one pair of small spines on interstria 1 or spines completely absent (Fig. 16)*Xyleborinus cupulatus* (Schedl, 1961)
 - More than one pair of spines on declivital margin6
- 6 Spines on declivital margin fairly similar in length, short, as long as broad, no spines longer than length of fourth ventrite7
 - Declivity has at least one pair of spines longer than length of fourth ventrite; this includes spine-like flanks near elytral apex8
- 7 Declivital spines on interstria 3 and 9 1.5–2× longer than other small spines; those on upper declivital margin irregularly shaped, very small. Declivital surface concave*Xyleborinus concavus*, sp. nov.
 - Declivital spines of equal length, as long as broad, some bifid at the tip. Declivital surface slightly convex*Xyleborinus singularis*, sp. nov.
- 8 Declivity has three short spines along the upper declivital margin on interstria 1, 2, and 3(4); a continuous flange from runs interstriae 4–5 towards a spine-like flank at interstriae 99
 - Declivity has a spiny wreath containing 6–10 pairs of irregularly sized spines. The number and length of spines are often asymmetrical between elytra in the same individual11
- 9 A small swelling or elevation present on the inside of the two flanks at the bottom of the declivital flange*Xyleborinus profundus* (Schedl, 1961)
 - The inside of the two flanks on the bottom of the declivital flange smooth10
- 10 From interstria 5 the flange along the declivital margin is continuous and has a smooth edge, terminating at a broadly triangular flank*Xyleborinus aduncus* (Schedl, 1961)
 - From interstria 4 the flange is continuous, but it has an uneven, almost serrated, edge, terminates in a narrow spine*Xyleborinus diadematus*, sp. nov.
- 11 The spine on interstria 4 on declivital margin is the longest, longer than length of the 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 longest, of approximately equal length, longer than length of third ventrite. Spines on interstria 5 and 6 may be as long or slightly shorter12
- 12 Spines on the declivity rise about 45° compared to elytral disc.*Xyleborinus spiculatulus* (Schedl, 1965)
 - Spines on the declivity rise about 30° compared to elytral disc*Xyleborinus spiculatus* (Schaufuss, 1891)
- 13 At least two pairs 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 Figs. 7, 14, 15, 21)14

- All spines on declivity are shorter than the combined length of third and fourth ventrite.....18
- 14 Striae distinctly impressed, most apparent on posterior half of elytral disc, appearing grooved15
- Striae only slightly (if at all) impressed near declivity only ...17
- 15 Elytral 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, and 9
..... *Xyleborinus quadrispinosus* (Eichhoff, 1878)
- Declivity with three pairs of long spines, and one or two pairs of much shorter spines16
- 16 Declivity has three pairs of long spines along the declivital margin on interstriae 3, 8, 9 and two pairs of short spines on interstriae 4 and 6. First pair is longest, fourth and fifth pair almost as long, second and third pair one-third the length of the first pair or less *Xyleborinus diapiformis* (Schedl, 1961)
- Declivity with three long spines on interstria 4, 8, 9; first and third pair twice as long as the length of second pair. There is a small additional spine on interstria 6. Several sharp tubercles on upper part of declivity.....
..... *Xyleborinus signatipennis* (Schedl, 1961)
- 17 Declivity has four spines along its margin on interstria 3, 6, 7, and 9. Spine one and four longest, these as long as the length of ventrite 2 and 3 combined. Spine two and three slightly shorter
.....*Xyleborinus coronatus*, sp. nov.
- Declivity has four spines on interstria 3, 6, 7, and 9. Two additional sharp tubercles on interstriae 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, and slightly longer than spine four.....
.....*Xyleborinus quadrispinis* (Schedl, 1953)
- 18 Four pairs spines along declivital margin on interstria 2, 4, 5, and 9 (on declivital interstriae 2 or 3 near elytral apex), upper and lower pair of spine slightly longer than other spines, as long or longer than ventrite 319
- All declivital spines shorter than ventrite 3, differ in number and placement20
- 19 First, third and fourth spine along declivital margin of equal size. The second pair is slightly shorter and points more upward than first and third spine, and may have two tips in some specimens. Lower pair of spines in line with declivital interstriae 3. Tubercles present on top of declivity.....
..... *Xyleborinus octospinosus* (Eggers, 1920)
- All four spines on declivital margin of approximately the same size. First three spines similar in shape and angle. Lower pair of spines in line with declivital interstriae 2.....
.....*Xyleborinus laevipennis*, sp. nov.
- 20 Two pairs of spines are equally long, short, but distinctly longer than other very small spines and tubercles on declivity, located on interstriae 3 and near apical margin on interstriae 8, lateral margin of declivity rounded, without rim21
- All spines on declivity of fairly similar size, or only one pair near elytral apex larger; lateral declivital margin sharp, often with a fine rim23
- 21 Upper pair of spines on interstriae 3 near middle of declivity; second pair of spines at apical margin on interstriae 8 (declivital interstriae 4) *Xyleborinus clivus*, sp. nov.
- Upper pair of spines on interstriae 3 near upper margin, second pair of spines at apical margin on interstriae 9 (declivital interstriae 3).....22
- 22 Elytral disc flat before the steeply descending declivity. Two or three additional sharp tubercles located between the two main spines and at least one small tubercle pair on top of declivity
.....*Xyleborinus aemulus* (Wollaston, 1869)
- Elytral disc and first half of declivity gently sloped, second (lower) half of declivity nearly vertical. Additional small tubercles barely visible (possibly a male of *X. aemulus*)
..... *Xyleborinus alienus* (Schedl, 1977)
- 23 Interstriae 1 on declivity with row of 3–4 sharp tubercles24
- Interstriae 1 smooth (occasional granules near upper margin)25
- 24 Declivital margin with fine tubercles on a tiny rim. A single pair of longer tubercles or spines more pronounced than other tubercles, in line with interstriae 3; declivital face has a rounded outline *Xyleborinus margo*, sp. nov.
- At least 5 pairs of small spines on declivital margin between interstriae 4 and 9; declivital face has a pentagonal outline
.....*Xyleborinus mitosomiformis* (Schedl, 1953)
- 25 A tiny rim on declivital margin from interstria 5 to 9 with three tubercles on interstria 6, 8, and 9 (near elytral apex at declivital interstriae 3) *Xyleborinus mitosomus* (Schedl, 1965)
- Declivital margin with obscure rim, densely set with 6–10 sharp tubercles26
- 26 Declivity steep but gradually descending; upper declivital margin with few and barely visible granules on interstria 1 to 3, additional small sharp granules on interstriae 4–5, and 3–4 sharp tubercles from interstria 6 to 9, the last tubercle in line with declivital interstriae 3
.....*Xyleborinus syzygii* (Schedl, 1959)
- Declivity abruptly descending; 8–10 small tubercles and granules present along upper declivital margin on interstria 1 to 4, and 5 pairs of very small spines along margin on interstriae 5 to 9, last one in line with declivital interstriae 2
.....*Xyleborinus tuberculatus*, sp. nov.
- 27 Large species, longer than 3.0 mm, with 2–3 very coarse spines along the upper half of each declivital margin, each spine at their base broader than antennal club; posterolateral area of declivity extended into a long spine-like flank or coarse spine28
- Smaller species, shorter than 2.5 mm, spines along declivital margin smaller, thinner than width of antennal club, posterolateral flanks may not be present or less developed31
- 28 On declivital margin one pair of small-sized spines on interstriae 3 are followed by two very large pairs of spines on interstriae 4 and 7. Last two pairs of spines at least as long as length of second ventrite, the lower spine forms a flank on lower half of declivity, directed obliquely upwards
.....*Xyleborinus magnispinosus*, sp. nov.

- Three pairs of thick spines along declivital margin from interstria 1–4, each shorter than length of second ventrite. At the bottom of the declivity a pair of very pronounced spine-like flanks directed posteriorly29
- 29 The angle between the elytral apex and inside of posterolateral flanks 90°, gap appears rectangular; flanks directed straight posteriorly *Xyleborinus bicinctus* (Schedl, 1965)
 - The transition between the elytral apex and inner side of flanks curved, appearing U-shaped; flanks pointed slightly downwards.....30
- 30 Two pairs of larger declivital spines fairly similar in size, upper spine as long as ventrite 3, slightly longer than lower spine; smaller spine on interstria 1 as small as spine on interstriae 2 *Xyleborinus castriformis*, sp. nov.
 - Three pairs of large declivital spines increasing in length from interstriae 1 to 4; spine on interstriae 4 very large, as long and thick as length of ventrites 3 and 4 combined, spine on interstriae 1 larger than spine on interstriae 2, smaller than spine on interstriae 3 *Xyleborinus turritus*, sp. nov.
- 31 Elytral declivity with posterolateral areas broadly swollen, each with more than 10 short spines and tubercles slightly longer than tibial teeth; interstriae 3 with one pair of spines halfway down declivity slightly longer than other spines, as long as length of third ventrite; lower parts of interstriae 1 and 3 smooth, interstriae 2 forms a low, sharp keel *Xyleborinus ntsoui*, sp. nov.
 - Elytral declivity not broadly swollen, but may have acute flanks; declivity with at least two pairs of spines longer than third ventrite32
- 32 Elytral declivity without extensions in posterolateral areas, on lower half of declivity with four small straight spines on each side located in a semi-circular fashion, altogether eight spines forming a circle; upper spines located on interstriae 3 are slightly longer than those below and longer than length of third ventrite; additional sharp tubercles present on interstriae 1 to 3 near upper margin of declivity *Xyleborinus cuneidentis* (Schedl, 1961)
 - Elytral declivity with posterolateral areas prolonged; spines on declivity not forming a circle, all spines located along declivital margin; terminal pair of spines slightly to strongly fang-shaped33
- 33 Declivity has only two pairs of spines present on posterolaterally area of declivity, located close to each other on or near apical part of interstria 4 and 8, occasionally with an extra smaller spine or tubercle on interstriae 3 close to the other spines; length of spines varies from slightly longer than length of third ventrite to as long as length of second ventrite; upper two-thirds of declivity asperate, without spines *Xyleborinus forficuloides* (Schedl, 1951)
 - Elytral declivity with 3–5 spines along the entire length of the declivital margin; upper declivity smooth34
- 34 Elytral declivity encircled by four spines on each lateral margin, located on interstria 3, 4, 6, and 8; additional minute spines or sharp tubercles may be present just above some of the larger spines; lower apical pair of spines longest, hooked inwards with tips facing each other *Xyleborinus forficulus* (Eggers, 1922)
 - Elytral declivity encircled by 5–6 pairs of spines or small tubercles on declivital margin from interstria 3 to 9. Longest spine located on interstria 6 or 7, about as long or slightly longer than length of third ventrite, followed in length by spines on interstria 3 and 9. Three spines set in a half star-like formation on an abruptly descending last one-fifth of the declivital margin35
- 35 In lateral view, three spines more clearly marked along the declivital margin, with 2–3 very small additional tubercles *Xyleborinus pseudopityogenes* (Eggers, 1943)
 - In lateral view, five spines are clearly marked..... *Xyleborinus dentellus* (Schedl, 1953)
- 36 Declivity is completely without spines, tubercles or sharp granules; pronotum with anterior margin raised and serrated *Xyleborinus pilosellus* (Schedl, 1957)
 - Short spines, tubercles or sharp granules are present on declivity; pronotal margin not raised or deeply serrated.....37
- 37 The declivity is elongated, extended apically, giving the appearance of a flattened cone in dorsal view *Xyleborinus andrewesi* (Blandford, 1896)
 - The posterior margin of declivity is gently curved giving a rounded appearance in dorsal view.....38
- 38 Elytral apex with a pair of short spines, in dorsal view curved outward..... *Xyleborinus spinipes* (Schedl, 1957)
 - Pair of spine at elytral apex pointing posteriorly, or absent ..39
- 39 The first and second interstriae on declivity smooth and glabrous; other interstriae have rows of small spines or sharp tubercles and setae present on declivity.....40
 - Interstriae 1 have rows of spines, tubercles or granules and setae present on at least part of the declivity, interstriae 2 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 smooth in central area *Xyleborinus polyalthiae* (Schedl, 1952)
 - Four pairs of small spines and sharp tubercles on posterior margin of elytra irregularly placed and clearly differ in size. Declivital surface slightly shrivelled in central area *Xyleborinus subsulcatus* (Eggers, 1927)
- 41 Interstriae 1 and 3 are smooth and glabrous on posterior third of declivity except apex42
 - Spines, tubercles or granules and setae run down the entire first and third interstriae on declivity.....43
- 42 Declivity steeply curved on lower half, nearly vertical *Xyleborinus saxesenii* (Ratzeburg, 1837)
 - Declivity gently curved, almost sloped *Xyleborinus heveae* (Schedl, 1957)
- 43 Entire declivity except interstriae 2 densely set 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 interstriae on declivity. About 1.5 mm in length *Xyleborinus sharpae* (Hopkins, 1915)
- Most spines on declivity are no larger than a tubercle. Five or fewer small spines and sharp tubercles present on interstriae 1 between upper declivital margin and elytral apex44
- 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
- 46 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 few, shorter or just as long as thick. About 1.8–2.0 mm in length
..... *Xyleborinus similans* (Eggers, 1940)

Discussion

The phylogenetic analyses of *Xyleborinus* revealed three clear patterns about its evolution. A grade of Indo-Malayan and Australasian species clearly reflects the presumed Asian origin of the genus. Asia and neighboring areas are also the most diverse for xyleborines in general, with the highest number of genera and species (Smith et al. 2020). Colonization of other continents occurred in fewer genera and took place some time after the origin of the tribe, with *Xyleborinus* as one of the early expanding genera in the tribe (Gohli et al. 2017).

Secondly, the Neotropical species are monophyletic for region and also included the Neotropical representative of the genus *Taurodemus*. This is not an entirely new hypothesis as other studies have placed *Taurodemus* species approximately near or within the *Xyleborinus* clade (Cognato et al. 2020b). The nested placement could be a case of long branch attraction, given the relatively long branches at the base of the topology which may attract outgroups (Bergsten 2005). More genetic material from *Taurodemus* could possibly resolve this issue. Regardless, the Neotropical taxa forms a potential sister group to the African species (Fig. 23) or a polytomy with the African and Malagasy clades, altogether clearly distinguished from the Asian and Holarctic grade of species. The connection between the Afrotropics and the Neotropics is a familiar biogeographical relationship seen in several other wood-boring beetle groups (Jordal 2015, Peris et al. 2015, Jordal 2021).

Third, all Malagasy species were placed in one clade with maximum support, with a few African species or populations nested within. The highest number of species and the majority of morphological variation for the entire genus are found in Madagascar. Thus, we must look closer at the evolution of Malagasy species to understand patterns of diversity in the Afrotropical region.

Phylogenetics and Species Delimitation in Taxonomically Challenging Taxa

Most strongly supported nodes in the Malagasy clade contained groups of morphologically similar species and illustrate to a certain degree that morphology reflects evolution. However, many species tend to be morphologically variable, and have limited genetic variation, illustrating that evolution is a recent and possibly ongoing process on the island. Morphological variation both within and between closely related species is mainly restricted to the shape of the declivity, particularly in the pattern of spines and tubercles.

The purpose of declivital spines is not known, although it is clear from their inbreeding mating system that they have no purpose in mate recognition (Kirkendall et al. 2015). One theory suggests that the spines may have a defence function against intruders who are trying to enter their nest, another that they are used for shovelling wood dust. However, these theories do not explain why they show such great variation between species and cannot explain why this is largely a Malagasy phenomenon. In the absence of sexual selection, it seems more plausible that differences evolve largely by random genetic processes such as genetic drift.

Most African mainland species are on the contrary very uniform morphologically, but they are nevertheless genetically more diverged than species in the Malagasy clade. Such observations emphasize the importance of molecular data in making phylogenetically based classifications. Molecular data are also particularly important in assessing boundaries between permanently inbreeding taxa like those of Xyleborini. Morphological differences between species are expectedly small in the absence of sexual selection for mate preferences. Their evolutionary adaptation to permanent inbreeding by sibling mating makes gene flow within a population rare, even though outbreeding may occasionally happen (Gottlieb et al. 2009, Holzman et al. 2009). Consequently, the concept of species as natural interbreeding populations does not apply to this kind of organisms, as each offspring represents a new distinct lineage that will (almost) never again mix with a larger gene pool. As a form of ‘quasiclinal’ reproduction, it shares many similarities to parthenogenetic or unicellular organisms (Andersen et al. 2012). Defining the boundaries between species is therefore largely dependent on molecular data for consistent species delimitation. The best way to define species in these organisms is to find a logical ‘cut-off’ point comparing morphological variation with molecular data. This creates species delimitation that is consistent and facilitates a clear understanding of the genetic and morphological variation that exists within this 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 had obvious morphological differences when COI p-distances exceeded 7%. It was therefore decided for consistency that COI differences above 7% constituted different species. The combined patristic distances observed for COI, 28S, and CAD worked even better, with maximum distances above 0.04 indicating species divergence (see Table 4). Morphological differences were in a few cases very small when COI divergence exceeded 7% but nevertheless sufficient to separate species unambiguously, except *X. spiculatus* and *X. spiculatulus*. It is also noteworthy that *X. forficuloides* contains distinct morphs despite minimal genetic variation. These two exceptions demonstrate quite clearly the irregular nature of species boundaries, and also emphasize that subjective aspects in the evaluation of taxonomy are unavoidable. A species delimitation threshold is therefore not applied equally to different genera (Cognato 2006, Cognato et al. 2020b). For *Xyleborinus*, we find that divergences in the last 1.2 myr (see Fig. 23) have not resulted in sufficient morphological and genetic divergence for separate species status.

The Madagascar Radiation

With an origin in the Indo-Malayan and Australasian regions nearly 20 Ma (Gohli et al. 2017), the expansion of *Xyleborinus* into Africa and the Neotropics occurred considerably later, around 12–10 Ma (mid-Miocene). This was far too late for dispersal through the

boreo-tropical corridor that was available only during the thermal maximum ending in the Eocene (Zachos et al. 2001, Morley 2003). Due to the wide oceanic divides present in the mid-Miocene, it is clear that ancestral *Xyleborinus* must have drifted along oceanic currents or blown over oceans by storms. Historical connections between Africa or Madagascar and the Neotropics are well documented (Yoder and Nowak 2006, Jordal 2015, Peris et al. 2015). Many Caribbean genera of bark and ambrosia beetles are present in Africa (Wood 1986), and Platypodinae indicate a close relationship between Africa and the Neotropics, but also between Madagascar and the Neotropics (Jordal 2015). This connection is largely explained for Miocene processes by drifting along the Benguelan or South Equatorial currents (reviewed in Peris et al. 2015).

At more or less the same time as reaching the Neotropics, Madagascar was colonized by *Xyleborinus* from the African mainland. The long internal branch leading to the Malagasy clade provides strong evidence for a single colonization of the island, whereas multiple back-colonizations to the mainland occurred much more recently (see Fig. 23). More complete taxon sampling will likely not change this hypothesis because missing taxa are fairly similar to the genetically analyzed species, or have spines and flanks not seen in any African mainland species. The only possible candidate for a second colonization of Madagascar is *X. dentellus* which is placed as sister to all other Malagasy species. This species is also found on the mainland, and has a near-identical sister species, *X. pseudopityogenes*, found only on the mainland. Furthermore, *X. dentellus* is related to *X. forficulus*, a species found only on the mainland, but genetic data are not available to infer their relationship. However, lending support from morphological data we note that spines are not observed in any other African mainland species, and it seems therefore more likely that the *dentellus* group is of Malagasy origin, and that *X. pseudopityogenes* and *X. forficulus* evolved from a recolonizing ancestor in the *dentellus* group.

The colonization of Madagascar occurred after the ocean currents started travelling from Madagascar to the African mainland (Ali and Huber 2010), which at least partly explains why there was only a single colonization of the island. Rare instances of Miocene counter-current colonization of Madagascar is documented for other non-marine, nonavian animals, but colonization of the mainland following the currents are much more common (Nobre et al. 2010, Samonds et al. 2012, Bukontaite et al. 2015). We can infer additional recolonizations in *Xyleborinus* judged by morphological similarities between African and Malagasy species as seen in *X. syzygii* (vs. *X. tuberculatus*), *X. forficulus* and *X. pseudopityogenes* (vs. *X. dentellus*), and the obvious recent occurrence on the mainland of the Malagasy species *X. quadrispinosus* and *X. octospinosus*, perhaps also *X. aemulus* if its anecdotal report from Madagascar (Schedl 1977) can be confirmed.

Madagascar stands out as the most diverse area for Afrotropical *Xyleborinus*. Since the origin of the Malagasy lineage less than 9 Ma, 32 species are known to the island, and many more expected to be found based on the high number of recently discovered species. The difference in number of continental and insular species described, with only 18 species known from the African mainland, is not the result of higher sampling efforts in Madagascar. Especially Ghana, Nigeria, South Africa, Zambia, and Congo have been thoroughly researched (Schedl 1956, 1959; Roberts 1961), including extensive recent field work by one of the authors in mainland Africa. The Malagasy clade must therefore be recognized as a rapid radiation where many unique morphs and species evolved in a short period of time.

It is tempting to explain high morphological variation in Madagascar using the theory of adaptive radiation which is commonly observed on islands (MacArthur and Wilson 1967). When a

species colonizes an island there may be several unoccupied niches that were not available in the ancestral area. This may cause rapid speciation as the colonizing ancestor can fill new niches. However, we are not yet able to define how adaptation materialize in this particular lineage as the function of the morphological variable ‘elytral declivity’ is not well understood. It is clear that intraspecific genetic variation is substantial and seems to vary with geography (see Fig. 22). Even though geography could play a vital role in shaping species diversity in Madagascar, we do not see similar covariation in morphological traits.

Research on the ecology of Malagasy *Xyleborinus* will hopefully provide more accurate indications on which ecological factors that may foster morphological variation in elytral declivities, or which genetic factors that let such a minor part of the body evolve into such fascinating patterns. Whatever the reason, *Xyleborinus* is yet another example of how important Madagascar is for Afrotropical diversification processes: isolated, but still sufficiently exposed to immigrants to spur new lineage diversification.

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Author Contributions

JE: Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing—original draft; Writing—review & editing. BHJ: Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Supervision; Visualization; Validation; Writing—review & editing.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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