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 diadematus* Eliassen & Jordal, sp. nov., *Xyleborinus laevipennis* Eliassen & Jordal, sp. nov., *Xyleborinus magnispinosus* Eliassen & Jordal, sp. nov., *Xyleborinus margo* Eliassen & Jordal, sp. nov., *Xyleborinus ntsoi* 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 fascipatus* (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...
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...
Beauti to construct the input file. Calibration of rates was made by anthropogenic activity have been ignored to reduce the maximum number of areas allowed in the analyses of historical distribution.

Phylogenetic trees 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 (Mazurk 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 fur 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.zerenesystems.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-118B6E0BEEE4

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
| Voucher name | Species | Collection code | Country | Location | Leg./Lab | COI | 28S | CAD |
|--------------|---------|-----------------|---------|----------|----------|-----|-----|-----|
| J0           | Taurodemus sharpi | 19784 | Belize | Las Cuevas | Johnson/Hulcr | MW617383 | MT895818 | MW656502 |
| J61          | Xyleborinus aduncus | 3x-5 | Madagascar | F. L., Homestead | Johnson/Hulcr | MW617442 | MT895941 | MW656562 |
| J48          | Xyleborinus aemulus | 18xi-3 | South Africa | Kologha Forest, Stutterheim (EC) | Jordal | MW617429 | MT895928 | MW656549 |
| J1           | Xyleborinus aemulus | 12xi-4 | South Africa | Tsisikamma, Goesa walk | Jordal | MW617384 | MT895882 | MW656503 |
| J13          | Xyleborinus andrewesii | 19754 | United States | FL, Homestead | Johnson/Hulcr | MW617395 | MT895893 | MW656514 |
| J14          | Xyleborinus artestriatus | 19753 | China | Fujian | Johnson/Hulcr | MW617396 | MT895894 | MW656515 |
| J23          | Xyleborinus attenuatus | 19vii-1 | South Africa | Kologha Forest, Stutterheim (EC) | Jordal | MW617405 | MT895903 | MW656524 |
| J17          | Xyleborinus bicorinatus | 18588 | Belize | Las Cuevas | Johnson/Hulcr | MW617399 | MT895897 | MW656518 |
| J29          | Xyleborinus castriformis | 11v-1 | Madagascar | daylight | Jordal | MW617411 | MT895909 | MW656530 |
| J53          | Xyleborinus castriformis | 26x-5 | Madagascar | Sundarbans, Marojejy National Park | Eliassen/Jordal | MW617434 | MT895933 | MW656554 |
| J40          | Xyleborinus clavus | Oct 2012 | Madagascar | Ranomafana National Park | Jordal | MW617422 | MT895920 | MW656541 |
| J28          | Xyleborinus concavus | 29x-16 | Madagascar | Ranomafana National Park | Jordal | MW617410 | MT895908 | MW656529 |
| J43          | Xyleborinus concavus | 4x-3 | Madagascar | Ranomafana National Park | Jordal | MW617424 | MT895923 | MW656544 |
| J41          | Xyleborinus coronatus | 9x-v | Madagascar | Ankarafantsika National Park | Eliassen/Jordal | MW617423 | MT895921 | MW656542 |
| J34          | Xyleborinus cupulatus | 30x-7 | Madagascar | Ranomafana National Park | Jordal | MW617416 | MT895914 | MW656535 |
| J31          | Xyleborinus cupulatus | 25x-E4 | Madagascar | Sundarbans, Marojejy National Park | Eliassen/Jordal | MW617432 | MT895931 | MW656552 |
| J38          | Xyleborinus dentellus | 31x-3 | Madagascar | Diana, Ankarana National Park | Eliassen/Jordal | MW617439 | MT895938 | MW656559 |
| J63          | Xyleborinus dentellus | 31x-3 | Madagascar | Diana, Ankarana National Park | Eliassen/Jordal | MW617444 | MT895943 | MW656564 |
| J21          | Xyleborinus diadematus | 28ix-6 | Madagascar | Ranomafana National Park | Jordal | MW617403 | MT895901 | MW656522 |
| J46          | Xyleborinus diapiformis | 6x-2D | Madagascar | Ranomafana National Park | Jordal | MW617427 | MT895926 | MW656547 |
| J3          | Xyleborinus diapiformis | 30x-10 | Madagascar | Ranomafana, Centre ValBio | Jordal | MW617386 | MT895884 | MW656505 |
| J30          | Xyleborinus exigus | etoh-trap | Cameron | Limbe, Ekonjo | Mally/Jordal | MW617412 | MT895910 | MW656531 |
| J8           | Xyleborinus exigus | 27 | Gabon | Ivindo National Park, Ipassa, 5km w Makokou | Mally/Jordal | MW617391 | MT895889 | MW656510 |
| J4           | Xyleborinus forficuloides | 11v-8 | Gabon | Ambositra, Marojejy National Park | Jordal | MW617387 | MT895885 | MW656506 |
| J44          | Xyleborinus forficuloides | 4x-3 | Madagascar | Ranomafana National Park, Vato trail | Jordal | MW617425 | MT895924 | MW656545 |
| J7           | Xyleborinus forficuloides | 1x-1 | Madagascar | Ranomafana, Centre ValBio | Jordal | MW617390 | MT895888 | MW656509 |
| J54          | Xyleborinus forficuloides | 26x-5 | Madagascar | Sundarbans, Marojejy National Park | Eliassen/Jordal | MW617435 | MT895934 | MW656555 |
| J16          | Xyleborinus gracilis | 19751 | Mexico | Chiapas | Johnson/Hulcr | MW617398 | MT895896 | MW656517 |
| J15          | Xyleborinus gracilis | 19752 | United States | FL, Gainesville | Johnson/Hulcr | MW617397 | MT895895 | MW656516 |
| J24          | Xyleborinus hawaiiensis | 2ii-3 | Sierra Leone | Tiwai Island | Jordal | MW617406 | MT895904 | MW656525 |
| J49          | Xyleborinus indicus | 25x-2 | Madagascar | Sundarbans, Marojejy National Park | Eliassen/Jordal | MW617430 | MT895929 | MW656550 |
| J12          | Xyleborinus insulosus | 19755 | Puerto Rico | El Yunque | Johnson/Hulcr | MW617394 | MT895892 | MW656513 |
| J18          | Xyleborinus intersetosus | 18588 | Belize | Las Cuevas | Johnson/Hulcr | MW617400 | MT895898 | MW656519 |
| J11          | Xyleborinus intersetosus | 19782 | Honduras | Atlantida | Storer/Hulcr | MW617393 | MT895891 | MW656512 |
| Voucher name | Species | Collection code | Country | Location | Leg./Lab | COI | 28S | CAD |
|--------------|---------|----------------|---------|----------|----------|-----|-----|-----|
| J45          | Xyleborinus laevipennis | 4x-3 | Madagascar | Ranomafana National Park, Vato trail | Jordal | MW617426 | MT895925 | MW656546 |
| J5           | Xyleborinus laevipennis | 4x-5 | Madagascar | Ranomafana, Centre ValBio | Jordal | MW617388 | MT895886 | MW656507 |
| J37          | Xyleborinus magnispinosus | 1x-1D | Madagascar | Ranomafana National Park | Jordal | MW617419 | MT895917 | MW656538 |
| J31          | Xyleborinus margo | 14v-7 | Madagascar | Andasibe, Perinet Ranomafana National Park | Jordal | MW617413 | MT895911 | MW656532 |
| J42          | Xyleborinus margo | S-trap | Madagascar | Ranomafana National Park | Jordal | – | MT895922 | MW656543 |
| J55          | Xyleborinus margo | 24-27x | Madagascar | Sambava, Marojejy National Park | Eliassen/Jordal | MW617436 | MT895935 | MW656556 |
| J59          | Xyleborinus mitosomipennis | 2xi-3 | Madagascar | Diana, Montagne d’Ambre | Eliassen/Jordal | MW617440 | MT895939 | MW656560 |
| J62          | Xyleborinus mitosomipennis | 2xi-9 | Madagascar | Diana, Montagne d’Ambre | Eliassen/Jordal | MW617443 | MT895942 | MW656563 |
| J22          | Xyleborinus ntsoui | 28ix-6 | Madagascar | Ranomafana National Park | Jordal | MW617404 | MT895902 | MW656523 |
| J27          | Xyleborinus octospinosus | 11xi-3 | Tanzania | Udzungwa, 3-rivers camp | Jordal | MW617409 | MT895907 | MW656528 |
| J10          | Xyleborinus perexiguus | 19783 | Papua New Guinea | Ohu | Hulcr | MW617392 | MT895890 | MW656511 |
| J57          | Xyleborinus profundus | 27x-4 | Madagascar | Sambava, Marojejy National Park | Eliassen/Jordal | MW617438 | MT895937 | MW656558 |
| J39          | Xyleborinus quadriradiatus | Oct 2012 | Madagascar | Ranomafana National Park | Jordal | MW617421 | MT895919 | MW656540 |
| J56          | Xyleborinus quadriradiatus | 24-27x | Madagascar | Sambava, Marojejy National Park | Eliassen/Jordal | MW617437 | MT895936 | MW656557 |
| J26          | Xyleborinus sharpae | 23xi-3 | Cameroon | Bimbia | Jordal | MW617408 | MT895906 | MW656527 |
| J25          | Xyleborinus sharpe | 2ii-3 | Sierra Leone | Tiwai Island | Jordal | MW617407 | MT895905 | MW656526 |
| J38          | Xyleborinus signatipennis | 8x-CVB | Madagascar | Ranomafana National Park | Jordal | MW617420 | MT895918 | MW656539 |
| J6           | Xyleborinus signatipennis | 4x-5 | Madagascar | Ranomafana, Centre ValBio | Jordal | MW617389 | MT895887 | MW656508 |
| J52          | Xyleborinus singularis | 26x-4 | Madagascar | Sambava, Marojejy National Park | Eliassen/Jordal | MW617433 | MT895932 | MW656553 |
| J19          | Xyleborinus spicosus | 2713 | Thailand | Doi Pui | Johnson/Hulcr | MW617401 | MT895899 | MW656520 |
| J20          | Xyleborinus spicosus | 2669 | Thailand | Doi Pui | Johnson/Hulcr | MW617402 | MT895900 | MW656521 |
| J60          | Xyleborinus spiculatus | 2xi-E4 | Madagascar | Diana, Montagne d’Ambre | Eliassen/Jordal | MW617441 | MT895940 | MW656561 |
| J65          | Xyleborinus spiculatus | 1xi-5 | Madagascar | Diana, Montagne d’Ambre | Eliassen/Jordal | MW617445 | MT895944 | MW656565 |
| J66          | Xyleborinus spiculatus | 3xi-E4 | Madagascar | Diana, Montagne d’Ambre | Eliassen/Jordal | MW617446 | MT895945 | MW656566 |
| J67          | Xyleborinus spiculatus | 5xi-5 | Madagascar | Diana, Montagne d’Ambre | Eliassen/Jordal | MW617447 | MT895946 | MW656567 |
| J30          | Xyleborinus spiculatus | 25x-4 | Madagascar | Sambava, Marojejy National Park | Eliassen/Jordal | MW617431 | MT895930 | MW656551 |
| J32          | Xyleborinus spiculatus | 3x-4 | Madagascar | Ranomafana National Park | Jordal | MW617414 | MT895912 | MW656533 |
| J35          | Xyleborinus spiculatus | 5x-14 | Madagascar | Ranomafana National Park | Jordal | MW617417 | MT895915 | MW656536 |
| J2           | Xyleborinus spiculatus | 30x-7 | Madagascar | Ranomafana, Centre ValBio | Jordal | MW617385 | MT895883 | MW656504 |
| J33          | Xyleborinus spinosus | 27x-1D | Madagascar | Ranomafana National Park | Jordal | MW617415 | MT895913 | MW656534 |
| J36          | Xyleborinus turritus | 6x-15 | Madagascar | Ranomafana National Park | Jordal | MW617418 | MT895916 | MW656537 |
| J47          | Xyleborinus turritus | FIT | Madagascar | Ranomafana National Park, Telytakeli trail | Jordal | MW617428 | MT895927 | MW656548 |
Species radiation is young and continuous in Madagascar. The aduncus, spiculatus, octospinosus, and bicinctus groups experienced 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 Afrotropical species *Xylophagus sharpei* (Hopkins, 1915) and *Xylophagus 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 *Xylophagus*, with *Xylophagus aemulus* (Wollaston, 1869) as the single Afrotropical 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 *Xylophagus margo*, *X. octospinosus* (Schedl, 1953), and *X. sharpae* (Eggers, 1920), and *Xylophagus octospinosus* (Eichhoff, 1878), and *Xylophagus cupulatus* (Schedl, 1965) (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 *Xylophagus spiculatus* (Schauffuss, 1891) and *Xylophagus octospinus* (Schedl, 1957) 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 *Xylophagus aduncus* (Schedl, 1961) and various members of the *aduncus* group such as *X. cupulatus*, or *Xylophagus octospinosus* (Eggers, 1920) and *Xylophagus laevispina*, sp. nov., but these were morphologically clearly different. In most other cases, a moderate-to-low genetic variation corresponded to minimal morphological variation. *Xylophagus 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 *Xylophagus*, which at least dates back to 13.6 Ma (crown age). Dispersal with vicariance of a combined Afrotropical 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. quadsirpinosus*, and *Xylophagus 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
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.
Taxonomy

*Xyleborinus* Reitter, 1913

Type species: *Bostrichus saxesenii* Ratzeburg, 1837.

*Diagnosis, Female.* Eyes elongated, oval shaped, emarginated, indentation 0.3×–0.5× 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× 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 declivative 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, fôret Mahajeby, May 1952, K. E. Schedl (1). Other material: Supp Table S1 (online only).
**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       |            |     |     |     |
| X. margo | 0.03      | 0.9 | 0.6 | 1   |
| X. forciculoides | 0.03 | 4.3 | 0.7 | 1   |
| X. quadrispinosus | 0.03 | 5.6 | 0.8 | 0   |
| X. octospinosus | 0.03 | 5.7 | 1.0 | 0   |
| X. gracilis | 0.03 | 5.8 | 0.4 | 0   |
| X. cupulatus | 0.04 | 5.9 | 1.4 | 0   |
| B       |            |     |     |     |
| X. turritus and X. castriformis | 0.06 | 7.4 | 1.0 | 0   |
| X. concavus and X. diadematus | 0.06 | 8.2 | 1.6 | 1   |
| C       |            |     |     |     |
| X. spiculatus and X. spiculatulus | 0.09 | 11.6 | 2.9 | 3   |
| X. octospinosus and X. laevipennis | 0.10 | 10.8 | 1.8 | 5   |
| X. aduncus and X. profundus | 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. mitosomipennis) 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-B729-4810-9AD1-0D748DE55726 (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 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 declival 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, Ambodivoary, J. Vardon (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).
| Genus       | Species    | Author         | Year | Synonyms                                                                 | Distribution                                                                 |
|-------------|------------|----------------|------|--------------------------------------------------------------------------|------------------------------------------------------------------------------|
| Xyleborinus | aduncus    | Schedl         | 1961 |                                                                          | Madagascar                                                                   |
| Xyleborinus | aemulus    | Wollaston      | 1869 | Xyleborus spinifex Eggers, 1920, syn. nov.                                | Angola, Namibia, Botswana, South Africa, St. Helena, Madagascar              |
| Xyleborinus | alienus    | Schedl         | 1977 |                                                                          | South Africa                                                                |
| Xyleborinus | armatus    | Schaufuss      | 1896 |                                                                          | Madagascar                                                                   |
| Xyleborinus | bicinctus  | Schedl         | 1965 |                                                                          | Madagascar                                                                   |
| Xyleborinus | castriformis | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | clivus     | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | concavus   | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | coronatus  | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | caneidentis| Schedl         | 1961 |                                                                          | Madagascar                                                                   |
| Xyleborinus | capulatus  | Schedl         | 1961 |                                                                          | Madagascar                                                                   |
| Xyleborinus | dentellus  | Schedl         | 1953 | Xyleborus forcipatus Schedl, 1957, syn. nov.                             | Madagascar, Congo                                                           |
| Xyleborinus | diadematus | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | datiformis | Schedl         | 1961 |                                                                          | Madagascar                                                                   |
| Xyleborinus | forficuloides | Schedl | 1951 |                                                                          | Madagascar                                                                   |
| Xyleborinus | forficulus | Eggers        | 1922 |                                                                          | Angola, Kenya, South Africa                                                 |
| Xyleborinus | heueae     | Schedl         | 1957 |                                                                          | Congo, Sierra Leone                                                         |
| Xyleborinus | laevipennis| Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | magnispinosus | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | marcidus   | Schedl         | 1965 |                                                                          | Madagascar                                                                   |
| Xyleborinus | margo      | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | mitosomiformis | Schedl | 1953 |                                                                          | Madagascar                                                                   |
| Xyleborinus | mitosonus  | Schedl         | 1965 |                                                                          | Madagascar                                                                   |
| Xyleborinus | namibiae   | Schedl         | 1982 |                                                                          | Namibia                                                                     |
| Xyleborinus | ntsoui     | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | octospinosus | Eggers       | 1920 | Xyleborus mitosomipennis Schedl, 1953, syn. nov.                         | Madagascar, Tanzania                                                        |
| Xyleborinus | pilosellus | Schedl         | 1957 |                                                                          | Congo                                                                        |
| Xyleborinus | polyalthiae| Schedl         | 1952 |                                                                          | Congo                                                                        |
| Xyleborinus | profundus  | Schedl         | 1961 |                                                                          | Congo                                                                        |
| Xyleborinus | pseudopityogenes | Eggers | 1943 |                                                                          | Congo, Namibia, Mozambique, South Africa                                    |
| Xyleborinus | quadrispinis | Schedl       | 1953 |                                                                          | Madagascar                                                                   |
| Xyleborinus | quadrispinosus | Eichhoff | 1878 |                                                                          | South Africa, Madagascar                                                   |
| Xyleborinus | sharpae    | Hopkins        | 1915 | Xyleborus schreineri Eggers, 1920 (syn. by Wood, 1962)                  | Liberia, Tanzania, Sierra Leone, Cameroon                                    |
| Xyleborinus | signatipennis | Schedl        | 1961 |                                                                          | Madagascar                                                                   |
| Xyleborinus | similans   | Eggers        | 1940 | Xyleborus sclerocarvae Schedl, 1962, syn. nov.                           | Angola, Bioko, Ivory Coast, Ghana, Congo, Rep. Congo, Somalia, South Africa |
| Xyleborinus | singularis | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Xyleborinus | spiculatus | Schedl         | 1965 |                                                                          | Madagascar                                                                   |
| Xyleborinus | spiculatus | Schaufuss      | 1891 |                                                                          | Madagascar                                                                   |
| Xyleborinus | spinipes   | Schedl         | 1957 |                                                                          | Congo                                                                        |
| Xyleborinus | spinosus   | Schaufuss      | 1891 |                                                                          | Congo                                                                        |
| Xyleborinus | subsulcatus | Eggers        | 1927 |                                                                          | Congo, Zambia                                                               |
| Xyleborinus | szygyi     | Schedl         | 1959 |                                                                          | Tanzania                                                                     |
| Xyleborinus | turritus   | Eliassen & Jordal | sp. nov. |                                                                          | Madagascar                                                                   |
| Adventive species | andrewesii | Blandford    | 1896 |                                                                          | See manuscript                                                              | Worldwide                                                                    |
| Adventive species | exiguus | Walker       | 1859 |                                                                          | See manuscript                                                              | Worldwide                                                                    |
| Adventive species | saxeseni | Ratzeburg    | 1837 |                                                                          | See manuscript                                                              | Worldwide                                                                    |

Table 5. Currently valid Afrotropical Xyleborinus species with synonyms and distribution
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, Cassonia (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, 3.0x as long as wide; color light brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–2x their diameter; interstriae smooth, shiny, punctures as large as striaal punctures, spaced by 4–5x 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 interstrial setae, glabrous on declivity except microscopical 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 Cassonia (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-Xyleborinus concavus Eliassen & Jordal, sp. nov. (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: 27x-1, B. Jordal, ex Cryptocarya branch, [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, 28x-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, 28x-6, ex Oncostenum log, [GIS: −21.25, 47.42] alt. 950 m (1); Centre ValBio, 30x-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, Musaenda log, [GIS: −21.25, 47.42] alt. 950 m (1); Village E. ValBio, 10x-3, ex Oncostenum 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, 2.8–3.0x as long as wide; color brown. Elytral striae on disc not impressed, punctures shallow, spaced by 1–2x their diameter. Interstriae smooth, shiny, punctures as large as striaal punctures, spaced by 3–5x 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 interstrial setae, mainly on posterior fourth on disc. Declivital glabrous, except microscopic interstrial 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, 2.5–2.7x as long as wide; color yellow. Elytral striae on disc not impressed, punctures shallow, spaced by 3–4x their diameter; interstriae variably smooth and rugose, shiny, punctures as large as striaal punctures, spaced by 8–10x 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 interstrial 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, Oncostenum, Polyscias, and Musaenda 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.

Xyleborus spiculatus (Schedl, 1965)

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

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

Material Examined. See Supp Table S1 (online only). Holotype not examined, lost (Hamburg): Madagascar.

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*. 

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

Material Examined. MADAGASCAR, Mont d’Ambre, K. E. Schell
[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 ir-
regular 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 Tsaratana: 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 in 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, Marojejy National Park.

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

Xyleborinus armatus (Schauffuss, 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; lowest 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 (Schauffuss, 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 (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 strial punctures, spaced by 3–5× their diameter. Declivity vertical, truncated, encircled on declivital margin by four pairs of large spines in a crowned pattern on interstriae 3, 5/6, 7, 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 interstrial and tiny strial 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).
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

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, Harungana 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 large as axial punctures, spaced by 4–5× their diameter. Declivity steep, encircled by four pairs of spines on interstriae 2/3, 4, 6, 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 interstrial setae mainly on posterior fourth of elytral disc; declivity glabrous, except microscopic 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 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 of 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 ntsoui Eliassen & Jordal, sp. nov.

Type Material. Holotype, female: MADAGASCAR, Ranomafana Centre ValBio, 2012: 28ix-6, B. Jordal, Oncostemum log, [GIS: −21.25, 47.41] 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 axial 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 interstrial setae and short semicircular elytral setae, and on declivity denser and longer, erect stria and interstrial 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.
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

(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: −18.94, 48.42] 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.

**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 declival 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 declival 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 declival margin, lower ones longer than those above.

**Xyleborinus forficuloides** Schedl, 1951

**Zoobank LSID**: 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 declival 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 strial punctures, spaced by 4–5× their diameter. Declivity nearly vertical, steep, declival 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; strial 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 margino-tuberculatus is a masculine nominative adjective, meaning having tubercles, referring to the small tubercles along the declival 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 declival 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 declival margin, lower ones longer than those above.

**Xyleborinus forficuloides** Schedl, 1951

**Zoobank LSID**: zoobank.org:act:B6208FEF-16A0-4068-8193-8EDB421E8C35

(Figs. 93–101)
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

Figs. 78–92. mitosomiformis group. Dorsal, lateral, and declival 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.
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, Ambolohitany National 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 declival apical margin, length of these spines slightly shorter than fourth ventrite; two pairs of sharp tubercles located on interstriae 6 and 7 along the declival 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 strial 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 declival margin on interstriae 6 and 7. Vestiture consisting of long erect interstrial setae and fine, very short interstrial setae in single rows from elytral base to declival margin, declivity with fine strial 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.

**Diagnosis.** 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, Tremoa 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 declival 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 strial punctures, spaced by 3–4× their diameter. Declivity obliquely sloped, occupying three-seventh of the elytra, excavated, slightly bisulcated, encircled by spines on declival margin. Three spines on interstriae 1, 3, and 4 as thick as long; third spine longest of the three, as
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.

Figs. 93–107. forficuloides group. Dorsal, lateral, and declivital view of (93–95) Xyleborinus forficuloides forficuloides directly compared to lectotype; (96–98) Xyleborinus forficuloides pinguis directly compared to lectotype; (99–101) Xyleborinus forficuloides dentibaris paratype; (102–104) Xyleborinus forficulus directly compared to syntype; (105–107) Xyleborinus clivus holotype.
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, Ambositra, 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 strial 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 interstrial setae, mainly on posterior third on disc and lateral sides. Declivity with almost microscopic strial 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 Ambohonitantly forest reserve, dissected from wood tunnels in branches of *Weinmannia* and *Solanum aphanathum* 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/ Ambohonitantly) populations, but more geographical sampling is needed to conclude.

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

ZOObank. LSID: zoobank.org:act:8C72DD44-9DD2-4CCB-A07E-DD39108R24B8 (Figs. 117–119)

Type Material. Holotype, female: MADAGASCAR, Marojejy National Park and Ambohitantely forest reserve, dissected from wood tunnels in branches of *Weinmannia* and *Solanum aphanathum* trees.

Diagnosis. Elytral declivity has two long and tall posterio-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*.

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

Distribution. Madagascar.

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 to two long and tall posterior 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*.

The cuneidentis Group

*Xyleborinus cuneidentis* (Schedl, 1961)

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

Material Examined. Paratype, female: MADAGASCAR, Amboboavoany, 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 declival 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 declival 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:** Ankaran (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 Chembra, 1929, P. Lesne (NHMW). Other specimens: ANGOLA, Lungo, Vila Arriaga, 7–9.IX.1956, G. Rudebeck (one, NHMW, labeled *X. spinifer*). NAMIBIA, Grootofontein, Farm Mariabronn, 28.1.1973, H. Roer (one, NHMW, labeled *X. spinifer*).

**Diagnosis.** Declivity sloped, encircled by four to five pairs of small spines and sharp tubercles on declival margin from interstriae 3 to 9, declivity otherwise smooth. Longest spine on interstria 67, 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 forcipatus** (Eggers, 1922)

*Xyleborus forcipatus* Eggers, 1922, orig. spelling (Figs. 102–104)

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

**Diagnosis.** Declivity sloped, surface lightly rugose, encircled on or just inside declival 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.

**Comment.** 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 declival 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, Acox 2487, July 1970, D. B. Scott (NHMUK). Holotype of *X. spinifer*: Südafrika, Sogosse, 20.XI.[19]06, von Seiner gesammelt (ZMH).

**Diagnosis.** Declivity nearly vertical. Two pairs of small spines about the length of third ventrite, located on interstriae 3 and near the declival 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).
**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.
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)

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

**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. polysulcatus* may be conspecific but the types show differences in the size and spacing of apical spines, and by the degree of smoothness on declival interstria 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 interstrial setae dense. More than five small spines and sharp tubercles on first interstria between top of declivity and elytral apex. Three pairs of small spines on posterior margin of elytra are of equal size and evenly spaced, longer than thick, 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, Lohitin, 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
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 *sharpeae* group and forms a basal grade of species related to the combined Neotropical–Afrotropical clade.

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**Figs. 147–161.** *sharpeae* 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 sharpeae* directly compared to holotype.
Xyleborinus saxesenii (Ratzeburg, 1837)
Bostrichus saxesenii Ratzeburg, 1837, orig. spelling
Tomicus dobrni Wollaston 1854 (syn. by Ferrari, 1867)
Tomicus 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 subspinuosus Eggers 1930 (syn. by Wood, 1989)
Xyleborinus libocedri Swaine 1934 (syn. by Wood, 1957)
Xyleborinus tsugae Swaine 1934 (syn. by Wood, 1957)
Xyleborus pseudogracilis 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 opimus Schedl 1976 (syn. by Wood, 2007)
Xyleborus cinctipennis Schedl 1980 (syn. by Wood, 1989)

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 exiguis (Walker, 1859)
Bostrichus exiguis 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 interstrial 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.

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Figs. 162–167. sharpeae 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 exigus compared to holotype; (174–176) Xyleborinus diversus lectotype (synonym of X. exigus); (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. exigus*. The holotype bear some resemblance to *X. similans*, but we follow here the recent suggestion by Smith et al. (2020).

*Xyleborinus andrewesi* (Blandford, 1896)  
*Xyleborinus andrewesi* Blandford, 1896, orig. spelling

*Xyleborinus mimosae* Schedl, 1957, syn. nov

*Xyleborinus persphenos* Schedl, 1970 (Syn. by Schedl 1975)

*Xyleborinus insolitus* Bright, 1972 (Syn. by Bright 1985)

*Cryptoxyloborus 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.** *Xyleborinus 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, 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 declival 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 declival margin .....................................................5
   - Rim on the declival 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 declival flange is completely smooth from interstriae 1 or spines completely absent (Fig. 16) ..........................................................5
   - More than one pair of spines on declival margin ..........6

6. Spines on declival margin fairly similar in length, short, as long as broad, no spines longer than length of fourth ventrite ..............................................................7
   - Declivity has at least one pair of spines longer than length of fourth ventrite; this includes spine-like flanks near elytral apex ..............................................................8

7. Declivitl spines on interstria 3 and 9 1.5–2x longer than other small spines; those on upper declival margin irregularly shaped, very small. Declival surface concave ......*Xyleborinus concavus*, sp. nov.
   - Declival spines of equal length, as long as broad, some bifid at the tip. Declival surface slightly convex .................................
   - *Xyleborinus singularis*, sp. nov. ..................................

8. Declivity has three short spines along the upper declival margin on interstria 1, 2, and 3(4); a continuous flange from runs interstriae 4–5 towards a spine-like flank at interstriae 9 ...........................................9
   - Declivity has a spiny wraath containing 6–10 pairs of irregularly sized spines. The number and length of spines are often asymmetrical between elytra in the same individual ......11

9. A small swelling or elevation present on the inside of the two flanks at the bottom of the declival flange .............................
   - The inside of the two flanks on the bottom of the declival flange smooth ..............................................................10

10. From interstria 5 the flange along the declival 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 declival 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........................
   - Spine on interstria 4 and 8 longest, of approximately equal length, longer than length of third ventrite. Spines on interstria 5 and 6 may be as long or slightly shorter ......12

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 declival margin by at least three pairs of long spines making the declivity appear crowned (see Figs. 7, 14, 15, 21) ..........14
14 Striae distinctly impressed, most apparent on posterior half of elytral disc, appearing grooved ........................................ 15
- 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 spines ......................16
16 Declivity has three pairs of long spines along the declival 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 interstriae 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 interstriae 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 declival margin on interstria 2, 4, 5, and 9 (on declival interstriae 2 or 3 near elytral apex), upper and lower pair of spine slightly longer than other spines, as long or longer than ventrite 3 .........................19
- All declival spines shorter than ventrite 3, differ in number and placement ..................................................20
19 First, third and fourth spine along declival 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 declival interstriae 3. Tubercles present on top of declivity..................... Xyleborinus octospinosus (Eggers, 1920)
- All four spines on declival margin of approximately the same size. First three spines similar in shape and angle. Lower pair of spines in line with declival 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 rim ................21
- All spines on declivity of fairly similar size, or only one pair near elytral apex larger; lateral declival margin sharp, often with a fine rim ..................23
21 Upper pair of spines on interstriae 3 near middle of declivity; second pair of spines at apical margin on interstriae 8 (declival interstriae 4) .................... Xyleborinus citius, sp. nov.
- Upper pair of spines on interstriae 3 near upper margin, second pair of spines at apical margin on interstriae 9 (declival interstriae 3) .....................22
22 Elytral disc flat before the steeply descending declivity. Two or three additional sharp tubercules 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 tubercules barely visible (possibly a male of X. aemulus) ......
- Xyleborinus alienus (Schedl, 1977)
23 Interstriae 1 on declivity with row of 3–4 sharp tubercles ......24
- Interstriae 1 smooth (occasional granules near upper margin) .................................................................25
24 Declival margin with fine tubercles on a tiny rim. A single pair of longer tubercles or spines more pronounced than other tubercles, in line with interstria 3; declival face has a rounded outline ....................... Xyleborinus margo, sp. nov.
- At least 5 pairs of small spines on declival margin between interstriae 4 and 9; declival face has a pentagonal outline ..........................................................26
25 A tiny rim on declival margin from interstria 5 to 9 with three tubercles on interstria 6, 8, and 9 (near elytral apex at declival interstriae 3) .... Xyleborinus mitosomiformis (Schedl, 1953)
- Declival margin with obscure rim, densely set with 6–10 sharp tubercles ...........................................26
26 Declivity steep but gradually descending; upper declival 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 declival interstriae 3 .................
- Xyleborinus syzygii (Schedl, 1959)
- Declivity abruptly descending; 8–10 small tubercles and granules present along upper declival 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 declival 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 declival margin, each spine at their base broader than antennal club; posterolateral area of declivity extended into a long spine-like flank or coarse spine ..................28
- Smaller species, shorter than 2.5 mm, spines along declival margin smaller, thinner than width of antennal club, posterolateral flanks may not be present or less developed .................31
28 On declival 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 posteriorly ........................................29

29 The angle between the elytral apex and inside of posteralateral flanks 90°, gap appears rectangular; flanks directed straight posteriorly ....................... Xyleborinus biczicinctus (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 interstria 2 ............................................. Xyleborinus castreformis, sp. nov.

- Three pairs of large declivital spines increasing in length from interstria 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 posteralateral 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 tsotsii, sp. nov.

- Elytral declivity not broadly swollen, but may have acute flanks; declivity with at least two pairs of spines longer than third ventrite ........................................32

32 Elytral declivity without extensions in posteralateral 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 posteralateral areas prolonged; spines on declivity not forming a circle, all spines located along declivital margin; terminal pair of spines slightly to strongly fang-shaped ........................................ Xyleborinus forficuloides (Schedl, 1951)

33 Declivity has only two pairs of spines present on posteralaterally 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 smooth ........................................34

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 forficuloides (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 margin ..............................................35

35 In lateral view, three spines more clearly marked along the declivital margin, with 2–3 very small additional tubercles ...... Xyleborinus pseudodiptyogenes (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 apex ........................................42

- 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 saxensii (Ratzeburg, 1837)

- Declivity gently curved, almost sloped Xyleborinus leveae (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
- 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 apex

- Declivity curved on top and bottom, middle half sloped. About 1.7 mm in length
- Declivity has an even, or close to even, curve from top of declivity to elytral apex

- Sharp tubercles on posterior margin of elytra are longer than they are thick. About 2.1 mm in length
- Sharp tubercles on posterior margin of elytra few, shorter or just as long as thick. About 1.8–2.0 mm in length

**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 *Taurodema*. This is not an entirely new hypothesis as other studies have placed *Taurodema* 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 *Taurodema* 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 adaption 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 ‘quasicalonal’ 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 nearly 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 p-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 Benganual 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, Bukontante et al. 2015). We can infer additional recolonizations in Xyleborinus judged by morphological similarities between African and Malagasy species as seen in X. syzygi (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. BJH: 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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