



Genetic and taxonomic assessment of the widespread Afrotropical ambrosia beetle *Xyleborus principalis* (Coleoptera, Scolytinae)

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Abstract

The taxonomy of the widespread Afrotropical ambrosia beetle *Xyleborus principalis* Eichhoff, 1878 is reviewed based on morphological and molecular data. The species is both morphologically and genetically variable but without any structure corresponding to geography, or between genes and morphology. Examination of type material and other specimens collected across Africa and Madagascar documented the existence of a single species. New synonymies are proposed for *Xyleborus principalis* (= *X. alluaudi* Schauffuss, 1897, = *X. camerunus* Hagedorn, 1910, = *X. consobrinus* Eggers, 1932, = *X. discrepans* Schedl, 1950, = *X. annectens* Schedl, 1957, = *X. peramploides* Schedl, 1957).

Keywords *Xyleborus principalis* · *Xyleborus alluaudi* · Afrotropics · Madagascar · COI · 28S · EF-1 α · PABP1

Introduction

Xyleborus Eichhoff, 1864 is a species rich genus of ambrosia beetles found in humid tropical rain forests around the globe. Species in this genus are frequently collected in dead wood or ethanol baited traps and largely dominate wood decomposing beetle guilds in such places (Beaver and Loytyniemi 1991; Beeson 1961; Schedl 1956; Schedl 1959; Schedl 1977; Thunes 1998). Some of them have very broad distributions and are known to have extended their current circumtropical ranges independently from human transportation (Gohli et al. 2016). *Xyleborus* species are in principle well adapted to colonize new areas and new introductions to Europe and America are therefore frequently reported (Haack 2001; Haack and Rabaglia 2013; Kirkendall and Faccoli 2010). Global colonization success and subsequent regional expansion is best understood by a peculiar form of reproduction in which siblings

mate and assures insemination before dispersal. Permanent inbreeding over evolutionary time scales also makes new colonists resistant to the negative genetic effects of small founding populations (Jordal et al. 2001; Kirkendall et al. 2014).

As one of the more devastating groups of beetles in the timber industry, rapid and accurate identification is important to differentiate serious pest species from less harmful ones, albeit not a trivial task. Many species are indeed very similar to each other, which is a logical consequence of inbreeding without selection for secondary sexual characters often used in species identification. In Africa and Madagascar, one of the most commonly collected species is *Xyleborus principalis* Eichhoff, 1878, or *X. alluaudi* Schauffuss, 1897 (Figs. 1–6). These two names have been used about each other by various authors, apparently also by the same author. Less frequently used is the name *Xyleborus annectens* Schedl, 1957, but is – together with a handful of rarely reported taxa – part of the same group. The first two species have been reported repeatedly throughout the Afrotropical region from Gambia to Ethiopia and south to South Africa and Madagascar. If one compares collections identified by prominent taxonomists such as Eggers, Schedl, Nunberg, and Browne, it is clear that species diagnoses are weak. A taxonomic revision of the complex is therefore needed where molecular data from multiple genes enable assessment of variation within and between species.

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Table 1 Samples included from Africa and Madagascar

Species	Author	Country	Locality	GIS
<i>Xyleborus madagascariensis</i>	Schaufuss, 1891	Madagascar	Ranomafana NP	-21.253, 47.421
<i>Xyleborus sakalava</i>	Schedl, 1953	Madagascar	Ranomafana NP	-21.253, 47.421
<i>Xyleborus ambasiusculus</i>	Eggers, 1920	Cameroon	Limbe, Ekenjo	4.081, 9.172
<i>Xyleborus comparabilis</i>	Schedl, 1957	Cameroon	Mt. Cameroon	4.129, 9.134
<i>Xyleborus conradti</i>	Hagedorn, 1910	Cameroon	Bakingili, N. Limbe	4.068, 9.040
<i>Xyleborus rothkirchi</i>	Eggers, 1920	Cameroon	Limbe, Ekenjo	4.081, 9.172
<i>Xyleborus</i> sp. O		Cameroon	Mt. Cameroon, S. slope	4.143, 9.186
<i>Xyleborus principalis</i> - 01	Eichhoff, 1878	Sierra Leone	Tiwai Island	7.554, -11.353
<i>Xyleborus principalis</i> - 02	Eichhoff, 1878	Cameroon	Limbe, Ekenjo	4.081, 9.172
<i>Xyleborus principalis</i> - 03	Eichhoff, 1878	Cameroon	Bakingili, N. Limbe	4.068, 9.040
<i>Xyleborus principalis</i> - 04	Eichhoff, 1878	Uganda	Kibale forest	0.562, 30.358
<i>Xyleborus principalis</i> - 05	Eichhoff, 1878	Tanzania	Sanje, Udzungwa	-7.725, 36.872
<i>Xyleborus principalis</i> - 06	Eichhoff, 1878	Tanzania	3-rivers, Udzungwa	-7.868, 36.844
<i>Xyleborus principalis</i> - 07	Eichhoff, 1878	Madagascar	Andasibe	-18.861, 48.447
<i>Xyleborus principalis</i> - 08	Eichhoff, 1878	Madagascar	Ranomafana	-21.253, 47.421
<i>Xyleborus principalis</i> - 09	Eichhoff, 1878	Uganda	Kibale forest	0.562, 30.358
<i>Xyleborus principalis</i> - 10	Eichhoff, 1878	Gabon	Ivindo NP	0.512, 12.802
<i>Xyleborus principalis</i> - 11	Eichhoff, 1878	Cameroon	Limbe, Ekenjo	4.081, 9.172
<i>Xyleborus principalis</i> - 12	Eichhoff, 1878	Cameroon	Mt. Cameroon, S. slope	4.143, 9.186
<i>Xyleborus principalis</i> - 13	Eichhoff, 1878	Tanzania	3-rivers, Udzungwa	-7.868, 36.844
<i>Xyleborus principalis</i> - 14	Eichhoff, 1878	Tanzania	Sanje, Udzungwa	-7.725, 36.872
<i>Xyleborus principalis</i> - 15	Eichhoff, 1878	Madagascar	Ranomafana NP	-21.253, 47.421
<i>Xyleborus principalis</i> - 16	Eichhoff, 1878	Madagascar	Ranomafana NP	-21.253, 47.421

Table 2 GenBank accession numbers for nucleotide sequences generated for this study

Species	COI	28S	PABP1	EF-1 α
<i>Xyleborus madagascariensis</i>	MN893807	MN894602	MN894625	MN894648
<i>Xyleborus sakalava</i>	MN893808	MN894603	MN894626	MN894649
<i>Xyleborus ambasiusculus</i>	MN893809	MN894604	MN894627	MN894650
<i>Xyleborus comparabilis</i>	MN893810	MN894605	MN894628	MN894651
<i>Xyleborus conradti</i>	MN893811	MN894606	MN894629	MN894652
<i>Xyleborus rothkirchi</i>	MN893812	MN894623	MN894646	MN894668
<i>Xyleborus</i> sp. O	-	MN894624	MN894647	MN894669
<i>Xyleborus principalis</i> - 01	MN893813	MN894607	MN894630	MN894653
<i>Xyleborus principalis</i> - 02	MN893814	MN894608	MN894631	MN894654
<i>Xyleborus principalis</i> - 03	MN893815	MN894609	MN894632	-
<i>Xyleborus principalis</i> - 04	MN893816	MN894610	MN894633	MN894655
<i>Xyleborus principalis</i> - 05	MN893817	MN894611	MN894634	MN894656
<i>Xyleborus principalis</i> - 06	MN893818	MN894612	MN894635	MN894657
<i>Xyleborus principalis</i> - 07	MN893819	MN894613	MN894636	MN894658
<i>Xyleborus principalis</i> - 08	MN893820	MN894614	MN894637	MN894659
<i>Xyleborus principalis</i> - 09	MN893821	MN894615	MN894638	MN894660
<i>Xyleborus principalis</i> - 10	MN893822	MN894616	MN894639	MN894661
<i>Xyleborus principalis</i> - 11	MN893823	MN894617	MN894640	MN894662
<i>Xyleborus principalis</i> - 12	MN893824	MN894618	MN894641	MN894663
<i>Xyleborus principalis</i> - 13	MN893825	MN894619	MN894642	MN894664
<i>Xyleborus principalis</i> - 14	MN893826	MN894620	MN894643	MN894665
<i>Xyleborus principalis</i> - 15	MN893827	MN894621	MN894644	MN894666
<i>Xyleborus principalis</i> - 16	MN893828	MN894622	MN894645	MN894667

Fig. 1–6 Dorsal, lateral and posterior view of two different *Xyleborus principalis* morphs. **1–3** narrow morph with less steep declivity and larger spines on interstriae 1 and 3 only, corresponding closely with the *X. principalis* holotype from Madagascar. **4–6** broader morph with steeper declivity and smaller interstitial granules on interstriae 1–3, corresponding to the holotype of *X. annectens* from Congo



Materials and methods

Type material and other material identified by Schedl, Eggers and Browne were examined in the natural history entomology collections in Vienna (NHMW), Tervuren (MRCB), Paris (MNHN), London (BMNH), Berlin (MNB) and Muncheberg (DEI). Field collections were made by the first author in Uganda (1998), Sierra Leone (2010), Cameroon (2008), Tanzania (2009–2010), and Madagascar (2012, 2015).

We tested species boundaries by comparing nucleotide sequences from multiple genes (Tables 1 and 2). DNA was

extracted with the Qiagen DNEasy kit, and PCR was made with primers targeting the mitochondrial gene cytochrome oxidase I (COI), the large subunit ribosomal RNA (28S), elongation factor 1- α (EF-1 α), and poly-A binding protein 1 (PABP1). We used primers and PCR-cycles described in Mugu et al. (2018). Sequences from four gene fragments were analysed by maximum parsimony both separately and in combination. Because very few substitutions separated nuclear genome sequences in the *principalis* group and the closest outgroups, we preferred a simple type of analysis as a means to visualize substitutions separating clades and

Table 3 Score of morphological characters on the elytral declivity

Species	Country	striae 2	puncture	interstriae 1 micropunctures	strial setae	spines interstriae 1 & 3	granules interstria 2	strial punctures	interstitial setae	declivity shape
<i>X. sakalava</i>	Madagascar	straight	round	absent	absent	small	absent	separate	long&pointed	impressed
<i>X. ambasiusculus</i>	Cameroon	straight	round	present	long	small	present	separate	thick	impressed
<i>X. comparabilis</i>	Cameroon	straight	round	absent	absent	small	absent	separate	long&pointed	impressed
<i>X. conradti</i>	Cameroon	straight	round	present	absent	small	absent	contiguous	thick	impressed
<i>X. rothkirchi</i>	Cameroon	straight	round	absent	short	small	present	separate	thick	rounded
<i>X. sp. O</i>	Cameroon	straight	round	absent	absent	small	absent	separate	thick	rounded
<i>X. principalis</i> - 01	Sierra Leone	curved	flat	present	short	small	present	contiguous	thick	rounded
<i>X. principalis</i> - 02	Cameroon	curved	flat	present	short	large	absent	separate	thick	impressed
<i>X. principalis</i> - 03	Cameroon	curved	flat	present	short	small	present	separate	thick	rounded
<i>X. principalis</i> - 04	Uganda	curved	flat	present	short	small	absent	separate	thick	rounded
<i>X. principalis</i> - 05	Tanzania	curved	flat	present	short	small	absent	separate	long&pointed	impressed
<i>X. principalis</i> - 06	Tanzania	curved	flat	present	short	small	present	separate	long&pointed	rounded
<i>X. principalis</i> - 07	Madagascar	curved	flat	present	short	small	absent	contiguous	long&pointed	impressed
<i>X. principalis</i> - 08	Madagascar	curved	flat	present	short	large	absent	separate	long&pointed	impressed
<i>X. principalis</i> - 09	Uganda	curved	flat	present	short	small	present	separate	long&pointed	rounded
<i>X. principalis</i> - 10	Gabon	curved	flat	present	short	small	present	contiguous	thick	rounded
<i>X. principalis</i> - 11	Cameroon	curved	flat	present	short	small	present	separate	thick	rounded
<i>X. principalis</i> - 12	Cameroon	curved	flat	present	short	small	present	separate	thick	rounded
<i>X. principalis</i> - 13	Tanzania	curved	flat	present	short	small	present	separate	long&pointed	rounded
<i>X. principalis</i> - 14	Tanzania	curved	flat	present	short	small	present	contiguous	long&pointed	rounded
<i>X. principalis</i> - 15	Madagascar	curved	flat	present	short	large	absent	separate	long&pointed	impressed
<i>X. principalis</i> - 16	Madagascar	curved	flat	present	short	large	absent	separate	long&pointed	impressed

specimens. Node support was estimated by bootstrapping 200 replicates with 100 heuristic searches each, keeping a maximum of 1000 trees to enable searches on matrices with few variable characters.

Variation in morphology between *X. principalis* populations and outgroups are described in Table 3. Characters were restricted to the declivity of the elytra (Figs. 3, 6) which is the only location on the body that varies within the *X. principalis* complex. Morphology was studied in a Leica M16 stereoscope. Multiple photographs were taken with a Leica camera on a Leica M205 C stereomicroscope and aligned and stacked using Zerene Stacker (ZereneSystems.com).

Results

Phylogenetic analysis of morphological characters resulted in a monophyletic *X. principalis*, with limited support (Fig. 7). This taxon is mainly defined by the curved striae 1 and 2 on

declivity, the large-sized strial punctures with a flat bottom, the presence of small and confused punctures on interstriae 1 on declivity, and the short, recumbent strial setae which are no longer than the size of a puncture. Variation within *X. principalis* was found mainly in five morphological characters (Table 3). There was no geographical pattern in these data, and none of the nodes within *X. principalis* were strongly supported. Specimens examined varied from having slightly narrower elytra with elevated interstriae on declivity, often with a transverse impression on lower third of declivity, a few large conical granules or spines in interstriae 1 and 3, but with no granules present on interstriae 2 (Figs. 1–3), to the morph which is not impressed on lower third of declivity, has small granules on all interstriae 1–3 on declivity, and is slightly wider and more broadly rounded at elytral apex (Figs. 4–6).

Phylogenetic analyses of nucleotide sequences from four gene fragments resulted in a different tree topology for each gene (Figs. 8–9). The analysis of all molecular data combined resulted in a tree topology identical to the COI topology for

Morphology

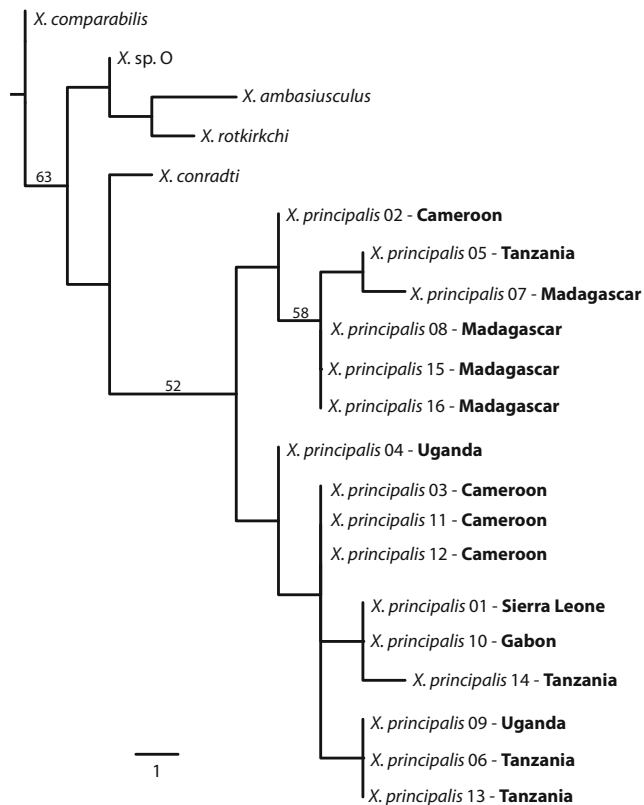


Fig. 7 One of 745 shortest trees found in the parsimony analysis of nine morphological characters ($L = 20$ steps, $RC = 0.36$). The strict consensus tree resulted in a monophyletic *X. principalis*, but with complete polytomy within. Numbers above branches indicate bootstrap support

X. principalis, and nearly so for the outgroups, with the same nodes supported by near identical bootstrap support. *Xyleborus principalis* was monophyletic in all analyses, but without any consistent pattern within this species. The only consistent result was the grouping of four Malagasy specimens in the same clade, but these were mixed with different specimens from the African mainland in the four different gene fragment analyses.

Mitochondrial genetic variation was much higher than for the nuclear genes, with a maximum of 14.2% divergence between individuals of *X. principalis* (Table 4). These same specimens differed only by a single substitution at the 28S gene, and four in total for the three genes combined (see Fig. 9).

Examination of type material and other specimens identified as *X. principalis*, *X. alluaudi*, and *X. annectens* by Schedl, Nunberg, Browne and Eggers revealed no consistent differences (Figs. 1–6). Additionally, the holotypes of *X. peramploides*, *X. consobrinus*, and *X. discrepans* were

found to be within the same range of variation. Illustrations of *X. alluaudi* by Schedl (1977) and Nunberg (1978) correspond to the first and second morphotype, respectively, while Nunberg's illustration of *X. principalis* fits the first morphotype. The same author illustrates *X. annectens* in very much the same way as for *X. principalis*. All three illustrations by Nunberg has a scale indicating exactly 3.0 mm length for all three taxa.

Discussion

Based on the great similarity in morphological characters in six named Afrotropical species of *Xyleborus*, we conclude that only one species exists – *X. principalis*. Genetic data indicate high mitochondrial variation within this species, but there is no correlation between morphology and genetic variation. Neither is there a consistent pattern in the variation across genes, and there is no geographical pattern in the genetic or morphological data. Although more than 10% divergence was observed for COI between several subgroups of *X. principalis*, such high intraspecific variation in the mitochondrial genome is quite normal for permanently inbreeding species (Andersen et al. 2012; Cognato et al. 2019; Gohli et al. 2016; Kambestad et al. 2017). At the same time there is very limited variation in nuclear genes for this species, most notably no more than two substitutions in the 28S gene. Several species in the *Hypothenemus eruditus* Westwood, 1836 complex, but also in related *Xyleborus* species such as *X. ferrugineus* (Fabricius, 1801), harbour higher genetic variation than in *X. principalis*. It is therefore likely that *X. principalis* has maintained large genetic variation over time in the same manner as for other permanently inbreeding species, and is reflected in morphological polymorphism.

Karl Schedl had a rather unfortunate habit of describing new species based on tiny differences from the holotype of a known species (Wood and Bright 1992). Many of these erroneous taxa are now synonymized, particularly in Neotropical and Oriental species which have been studied in more detail. We would therefore not be surprised if many new synonyms are proposed as the revision of the African fauna proceeds.

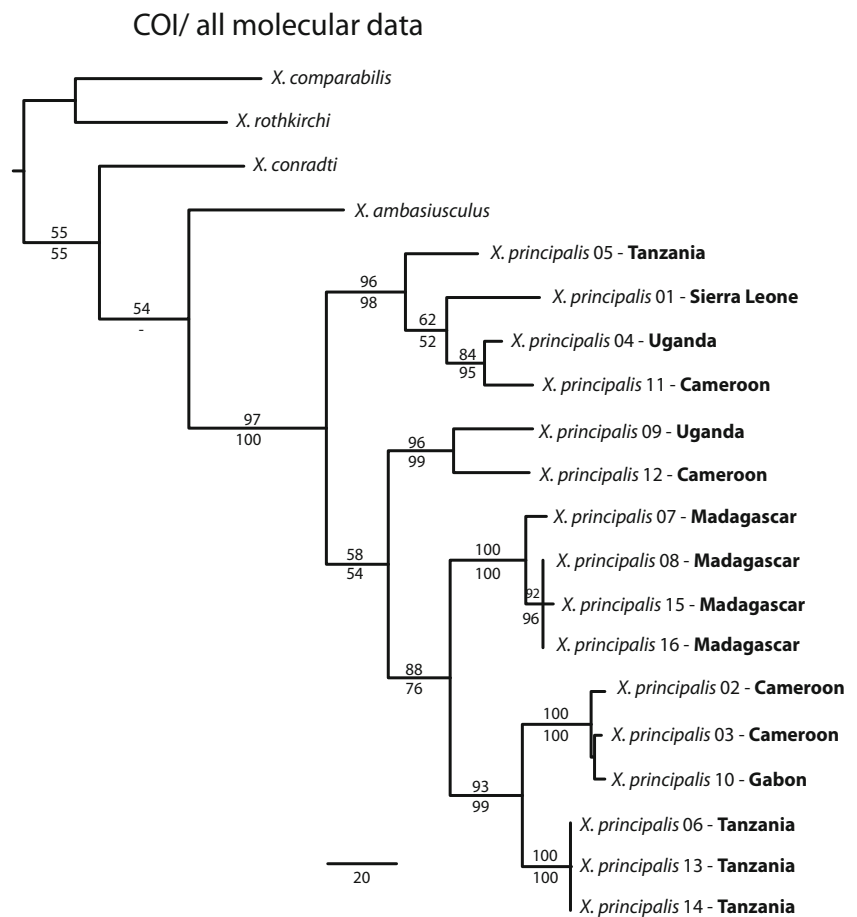
Taxonomy

Xyleborus principalis Eichhoff, 1878

Xyleborus alluaudi Schauffuss, 1897, **n. syn.**

Xyleborus camerunus Hagedorn, 1910, synonymy of *X. alluaudi* by Schedl 1957.

Fig. 8 Tree topologies resulting from the parsimony analysis of COI (6 trees, L = 752, RC = 0.32). The analysis of all molecular data combined resulted in identical topology except for the sister relationship between *X. ambasiusculus* and *X. conradti* (2 trees, L = 942, RC = 0.38). Numbers on branches indicate bootstrap support: COI above, all molecular data below. Outgroups *X. sakalava* and *X. madagascariensis* were pruned from the trees due to long connecting branches



Xyleborus consobrinus Eggers, 1932, **n. syn.**
Xyleborus discrepans Schedl, 1950, **n. syn.**
Xyleborus annectens Schedl, 1957, **n. syn.**
Xyleborus peramploides Schedl, 1957, **n. syn.**

Type material examined: holotypes of *X. camerunus* (MNB), *X. consobrinus* (MRCB), *X. discrepans* (NHMW), *X. annectens* (MRCB), and *X. peramploides* (NHMW), and syntypes of *X. principalis* (NHMW) and *X. alluaudi* (NHMW).

Revised diagnosis

Length 2.9–3.6 mm, 2.4–2.8 × as long as wide, colour reddish brown. **Pronotum** smooth and shiny on posterior half, abruptly declivitous and strongly asperate on anterior half. **Elytra** with striae in regular rows on disc, on declivity punctures larger and more irregularly

placed, bottom of puncture flat with margins clearly marked, punctures sometimes contiguous, or well separated, striae 1, 2 and sometimes 3 usually curved laterally; interstriae on disc smooth, on declivity with granules, sometimes missing on interstriae 2, sometimes two or more granules on interstriae 1 and 3 larger than the average size of a granule; punctures in interstriae much smaller than in striae, variable in size, on interstriae 1 small and strongly confused. Vestiture consisting of long and thin interstitial setae, intermixed with, or entirely replaced by, thicker setae; strial setae fine, recumbent, barely longer than diameter of a strial puncture. Elytral apex broadly to more narrowly rounded, sometimes with a distinct transverse impression on lower third, sometimes terminal interstriae 1–2 slightly elevated to make apex more pointed. **Protibiae** with 6 lateral socketed teeth, metatibiae with 8–10 lateral teeth on distal two-thirds.

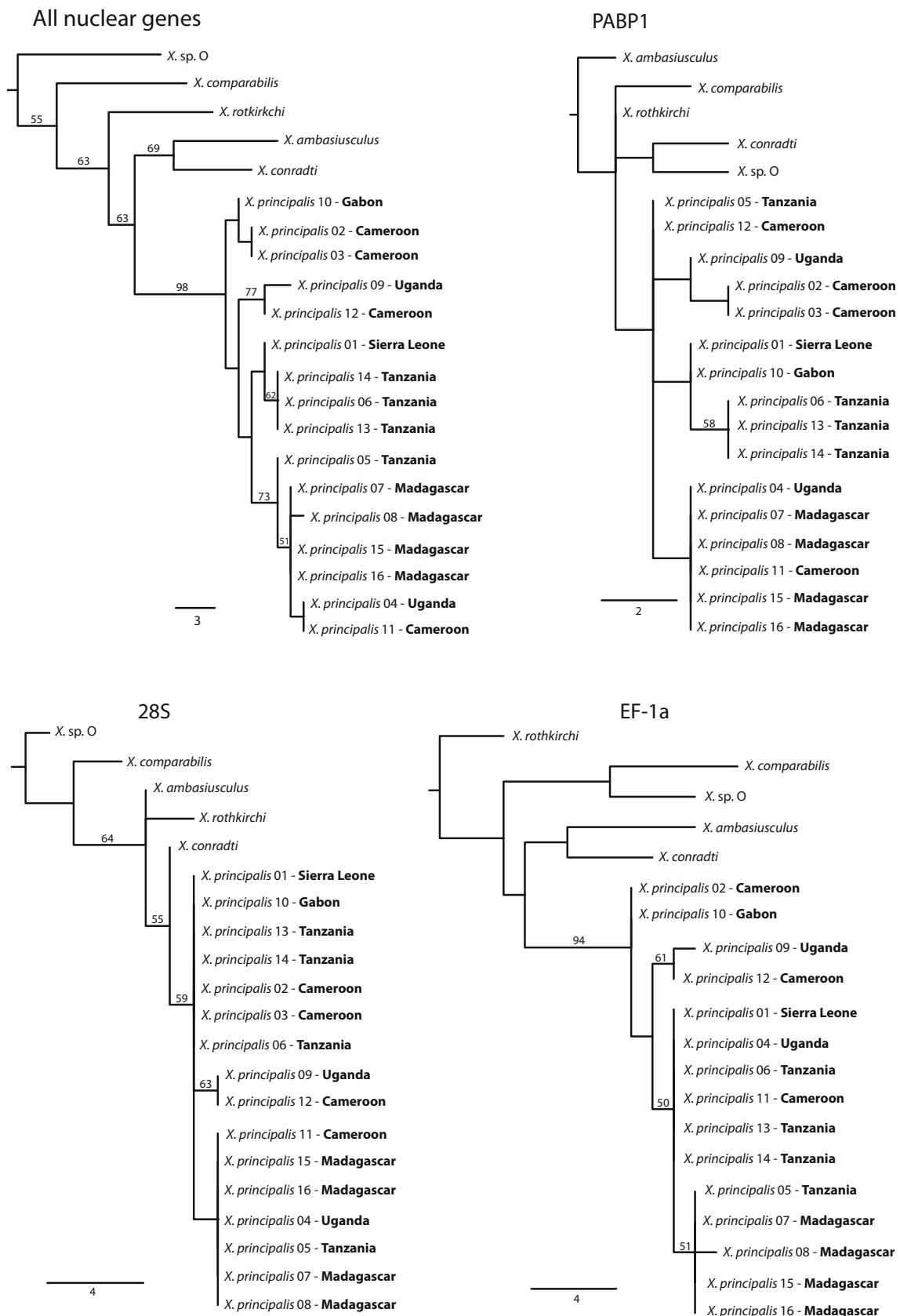


Fig. 9 Tree topologies resulting from the parsimony analyses of all nuclear genes combined (11 trees, L = 217, RC = 0.76), 28S (2 trees, L = 93, RC = 0.94), PABP1 (36 trees, L = 38, RC = 0.80) and EF-1 α

(20 trees, L = 85, RC = 0.85). Outgroups were pruned from the trees due to long connecting branches

Table 4 Genetic p-distances at the mitochondrial Cytochrome Oxidase I locus (656 base pairs)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 <i>X. ambasiusculus</i>	-																			
2 <i>X. comparabilis</i>	0.167	-																		
3 <i>X. conradi</i>	0.164	0.174	-																	
4 <i>X. rothkirchi</i>	0.174	0.149	0.159	-																
5 <i>X. principalis</i> - 01	0.176	0.162	0.179	0.182	-															
6 <i>X. principalis</i> - 02	0.171	0.175	0.183	0.184	0.130	-														
7 <i>X. principalis</i> - 03	0.171	0.175	0.186	0.186	0.131	0.011	-													
8 <i>X. principalis</i> - 04	0.174	0.159	0.162	0.177	0.064	0.125	0.127	-												
9 <i>X. principalis</i> - 05	0.173	0.163	0.182	0.182	0.090	0.125	0.128	0.073	-											
10 <i>X. principalis</i> - 06	0.170	0.163	0.169	0.178	0.128	0.058	0.056	0.120	0.142	-										
11 <i>X. principalis</i> - 07	0.182	0.169	0.169	0.167	0.125	0.106	0.106	0.123	0.135	0.095	-									
12 <i>X. principalis</i> - 08	0.179	0.166	0.177	0.166	0.114	0.101	0.104	0.113	0.122	0.093	0.017	-								
13 <i>X. principalis</i> - 09	0.173	0.165	0.183	0.160	0.131	0.108	0.113	0.122	0.128	0.117	0.124	0.119	-							
14 <i>X. principalis</i> - 10	0.171	0.172	0.186	0.181	0.124	0.012	0.008	0.119	0.125	0.055	0.101	0.096	0.108	-						
15 <i>X. principalis</i> - 11	0.178	0.167	0.161	0.181	0.077	0.130	0.132	0.029	0.072	0.130	0.124	0.112	0.126	0.124	-					
16 <i>X. principalis</i> - 12	0.184	0.172	0.195	0.175	0.131	0.122	0.122	0.130	0.119	0.125	0.112	0.107	0.069	0.116	0.132	-				
17 <i>X. principalis</i> - 13	0.170	0.163	0.169	0.178	0.128	0.058	0.056	0.120	0.142	0.000	0.095	0.093	0.117	0.055	0.130	0.125	-			
18 <i>X. principalis</i> - 14	0.170	0.163	0.169	0.178	0.128	0.058	0.056	0.120	0.142	0.000	0.095	0.093	0.117	0.055	0.130	0.125	0.000	-		
19 <i>X. principalis</i> - 15	0.184	0.171	0.178	0.168	0.119	0.105	0.108	0.117	0.124	0.098	0.021	0.005	0.120	0.101	0.113	0.108	0.098	0.098	-	
20 <i>X. principalis</i> - 16	0.179	0.166	0.177	0.166	0.114	0.101	0.104	0.113	0.122	0.093	0.017	0.000	0.119	0.096	0.112	0.107	0.093	0.093	0.005	-

Intraspecific variation for *X. principalis* is emphasized in bold font

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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