

From Eastern Arc Mountains to extreme sexual dimorphism: systematics of the enigmatic assassin bug genus *Xenocaucus* (Hemiptera: Reduviidae: Tribelocephalinae)

C. Weirauch¹  · M. Forthman^{1,2} · V. Grebennikov³ · P. Baňář⁴

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Abstract The Eastern Arc Mountains (EAM) have long been recognized as an area of extraordinary endemic biodiversity but have remained understudied compared to other biodiversity hotspots. The tribelocephaline assassin bug genus *Xenocaucus* China & Usinger, 1949, currently comprises two species known from the Uluguru Mountains of the EAM and Bioko Island in the Gulf of Guinea. Both species are based on single apterous and apparently eyeless female specimens. Based on collections resulting from extensive leaf litter sampling in Tanzania and Ethiopia, we here describe six new species, five based on females (*Xenocaucus chomensis*, n. sp., *Xenocaucus kimbozensis*, n. sp., *Xenocaucus nguru*, n. sp., *Xenocaucus rubeho*, n. sp., and *Xenocaucus uluguru*, n. sp.) and *Xenocaucus ethiopiensis*, n. sp., for which we discovered a macropterous male with well-developed eyes in addition to the apterous females. Molecular phylogenetic analyses indicate that *Xenocaucus ethiopiensis*, n. sp., is the sister taxon to the Tanzanian clade and support morphology-based species concepts. Divergence dating shows that diversification in the

Tanzanian clade started ~15 mya, with the youngest species-level split occurring ~8 mya. Three species occur across multiple mountain ranges in the EAM or occur also on Mt. Hanang, and biogeographic analyses suggest a complex history of *Xenocaucus* in East Africa.

Keywords Phylogeny · Biogeography · Divergence dating · Tropical montane forest · Biodiversity · Afrotropical region

Introduction

Although tropical rainforests of the Guineo-Congolian floristic region and of the mountain and coastal regions of East Africa are now separated by vast arid areas, they are thought to have covered a large part of Africa during the Eocene (Axelrod and Raven 1978), thus explaining the floristic and faunistic affinities between the two regions today (Couvreur et al. 2008). Details on the history of these areas of now disjunct tropical rainforests are under debate with competing hypotheses postulating one (Davis et al. 2002) or multiple fragmentation and reconnection events (Couvreur et al. 2008; Jacobs et al. 1999) since the Oligocene. Rising from low-elevation grasslands to more than 2600 m, the Eastern Arc Mountains (EAM) in Tanzania and Kenya are a chain of 13 isolated mountain ranges or blocks covered with a variety of vegetation types, including tropical montane rainforest and one of the most prominent areas of the East African montane rainforest remnants (Burgess et al. 2007). Combining high species diversity and endemism with high threat, the EAM are classified as part of the “Eastern Afrotropical Biodiversity Hotspot,” which is known to support the highest concentration of endemic plant and vertebrate species worldwide (Lovett et al. 2005; Myers et al. 2000). Both the EAM and the Coastal Forests of Eastern Africa Hotspot are

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✉ C. Weirauch
christiane.weirauch@ucr.edu

¹ Department of Entomology, University of California, Riverside, CA 92521, USA

² Entomology and Nematology Department, University of Florida, Gainesville, FL 32607, USA

³ Canadian Food Inspection Agency, 960 Carling Ave, Ottawa, ON K1A 0Y9, Canada

⁴ Department of Entomology, Moravian Museum, Hviezdoslavova 29a, 627 00 Bmo, Czech Republic

characterized by highly fragmented natural habitats, adding to the extinction threat of endemic species. Theories on why the EAM accommodate such startling biodiversity have invoked (1) a stable climate during the past 30 mya; (2) cycles of warm, wet and cool, dry periods; or (3) a combination of both (Lawson 2010; Loader et al. 2014; Lovett et al. 2005).

Perhaps even to a higher degree than the remaining African biodiversity hotspots, the EAM are severely understudied (Lovett and Wasser 2008; Yessoufou et al. 2012), and new species continue to be described (Bocák et al. 2014; Hemp et al. 2013, 2014; Loader et al. 2015; Marshall 2014; Štys and Baňar 2013). The EAM have been shown to function as centers of diversification (Blackburn and Measey 2009), and systematic studies focusing on EAM biota increasingly include biogeographic and divergence dating analyses that have the potential to reveal shared spatial and temporal patterns between taxonomic groups. The majority of phylogenetic, biogeographic, and phylogeographic studies has focused on plants (Couvreur et al. 2008; Dimitrov et al. 2012; Gizaw et al. 2016; Lovett and Wasser, 2008; Pócs 1998) and vertebrates, especially birds (Beresford et al. 2004; Bowie et al. 2004; Bowie et al. 2006; Fjeldså and Bowie 2008; Fjeldså 2010; Roy 1997), amphibians, and reptiles (e.g., Gravlund 2002; Blackburn and Measey 2009). Insect-focused studies are very scarce (Davis et al. 2001; Grebennikov 2015).

China and Usinger (1949) discovered and described a new genus and species of Reduviidae, the assassin bugs, from “Fernando Poo” (today known as Bioko Island in the Gulf of Guinea) that possessed several features that are otherwise rare or unknown in Reduviidae: the single female specimen is apterous, according to the authors lacks compound eyes, has a long and ventrally concave scape, hair fringes on various body parts, and one-segmented tarsi on all pairs of legs. Due to the absence of ocelli, the long first visible labial segment, and because other rather unique-looking genera of Tribelocephalinae had recently been described (e.g., Jeannel 1919), China and Usinger (1949) placed this new genus, *Xenocaucus* China and Usinger, and new species, *Xenocaucus mancinii* China and Usinger, 1949, in the Tribelocephalinae. Villiers (1960) subsequently described a second species in *Xenocaucus*, *X. schoutedeni* Villiers, 1960, based on two apterous and also apparently eyeless female specimens collected in the Uluguru Mountains of East Africa.

The Tribelocephalinae currently comprises 15 genera and more than 120 species that are restricted to the Old World tropics and subtropics (Ishikawa et al. 2015). Although potentially not monophyletic (Weirauch 2010), Tribelocephalinae are recognized in recent classifications and identification keys of Reduviidae and are diagnosed by the dense cover of setae with a bulbous base, absence of ocelli, only slightly protruding compound eyes, the long and fairly stout scape with the distal antennal segments being more slender and typically folded underneath the scape, and the reduced corium (Maldonado 1990;

Schuh and Slater 1995; Weirauch et al. 2014). Villiers (1943) classified Tribelocephalinae into the tribes Tribelocephalini and Opistoplatyini based on wing venation, but later left the wingless *Xenocaucus* unplaced (Villiers 1960). Maldonado (1996) utilized Villiers’ wing characters in his key to the tribes of Tribelocephalinae and created a new tribe, Xenocaucini, to accommodate the wingless *Xenocaucus*. He did not formally diagnose the new tribe, but diagnostic features can be deduced from the key: apterous, eyeless, all tarsi one-segmented, setal fringes on antenna, head, and pronotum, and the scape with ventral concavity.

Assassin bug specimens collected by one of us in the EAM, Mt. Hanang, and Mt. Kilimanjaro in Tanzania and the Bale Mountains in Ethiopia between 2010 and 2014 now shed new light on this enigmatic taxon. The majority of specimens from the EAM are apterous and seemingly eyeless females, but some of the immatures show wing pads indicating that some adult morphs have wings. This finding was followed by the discovery of a winged, male tribelocephaline specimen from the Bale Mountains in Ethiopia. This specimen did not fit the morphological concept of any of the described genera of Tribelocephalinae but was collected during the same collecting event as some female *Xenocaucus* specimens. We therefore suspected that *Xenocaucus* represents a highly sexually dimorphic taxon, much beyond the degree of sexual dimorphism typically observed in Reduviidae. Sexual dimorphism is ubiquitous in Reduviidae where it ranges from subtle morphological differences of overall body size, size of eyes and ocelli, or wing type to drastic dimorphism that involves wing reduction or loss in the female sometimes associated with modifications of the head, thorax, and legs (Forthman et al. 2016; Villiers 1948; Wygodzinsky 1966; Zhang and Weirauch 2011). Sexual dimorphism is common in Ectrichodiinae, the millipede assassin bugs that are close relatives of Tribelocephalinae (Hwang and Weirauch 2012; Weirauch 2008, 2010). The majority of species of Tribelocephalinae were described from only one sex, typically the male, and the abundance and extent of sexual dimorphism in this group is therefore poorly documented. Conspecific macropterous males and micropterous females, where females also possess smaller eyes and slightly different head and pronotal proportions, were recently described for species in the genus *Abelocephala* Maldonado (Ishikawa et al. 2015). The tribelocephaline *Enigmocephala deinorhyncha* Rédei, 2007, that combines a number of uncommon or unique morphological features, namely the very wide labium, apically bifurcating third visible labial segment, short and curved legs, and almost completely fused abdominal sternites was described from a single apterous female specimen with small eyes (Rédei 2007). The male of this species from Borneo remains unknown, but given the similarity in the structure of the labium and assuming that the male may be macropterous, it could well resemble species of the African genus *Afrodecius* Jeannel, 1919.

We here contribute to the documentation of the species-level diversity of this unusual group of assassin bugs, based

on the recently collected material from Tanzania and Ethiopia. Using molecular data, we show that the single known male specimen from the Bale Mountains in Ethiopia (macropterous, with eyes) is conspecific with a female specimen of *Xenocaucus* collected at the same locality. Taxonomic treatments for the six new species from the EAM and Bale Mts. are provided and include images of habitus and morphological details, measurements, and distribution maps. The generic description and diagnosis is revised to reflect the discovery of a congeneric male specimen. We further test the monophyly of *Xenocaucus*, investigate species-level relationships within the genus, and examine its systematic position within the Tribelocephalinae using molecular data and taxon sampling that includes representatives of the two remaining Tribelocephalinae tribes. Based on biogeographic and divergence dating analyses, we investigate the evolutionary history of this group in Eastern Africa, adding to a body of biogeographic literature on the EAM that has, so far, largely ignored arthropods and insects.

Material and methods

Material and specimen-based protocols A total of 74 specimens of East African *Xenocaucus* were sorted and organized by locality and putative species. The samples comprised 38 adult females, one adult male, four late instar immatures that we identified as males due to the developing wing pads, and 31 additional immatures that included late instar females and early instars for which the sex cannot be determined. The holotypes of *X. schoutedeni* and *X. mancinii* had previously been examined and imaged (PB and CW, respectively). For the molecular analyses, outgroups include species of three additional Tribelocephalinae genera and three Ectrichodiinae species derived from published Weirauch lab datasets (e.g., Forthman and Weirauch 2016; Hwang and Weirauch 2012).

Matrix-code labels with a specimen identifier consisting of a unique combination of an UCR_ENT prefix and an eight-digit number were associated with each specimen. UCR_ENT prefixes were removed in the “material examined” sections of descriptions to conserve space. Specimen data including species name, sex, locality and collection event information, and “RCW” numbers used for internal specimen tracking of molecular vouchers in the Weirauch lab were databased using the PBI’s Arthropod Easy Capture database served from the American Museum of Natural History (<https://research.amnh.org/pbi/locality/>). Holotypes of *X. mancinii* and *X. schoutedeni* were databased from the original publications and retroactively georeferenced using Google Earth. Distribution maps for species of *Xenocaucus* were generated in SimpleMappr <http://www.simplemappr.net/>.

For digital habitus imaging, specimens were temporarily fixed in a droplet of hand sanitizer in a watch glass and

subsequently emerged with 96% ethanol. A Leica DFC 450 C Microsystems setup with Planapo $\times 1.0$ and $\times 2.0$ objectives, the Leica Application Suite (LAS) V4.3., and Zerene Stacker were used to generate images and assemble composite images. One female each of *X. chomensis* (UCR_ENT 00020646) and *X. nguru* (UCR_ENT 00020634) were mounted on a stub using an adhesive carbon sticker, coated with a platinum-palladium mixture using a Cressington 108 auto sputter coater, and documented using a Hitachi S-4700 electron microscope at the Central Facility for Advanced Microscopy and Microanalysis at the University of California, Riverside (UCR). Images were edited in Photoshop CS4 or Corel Photo Paint X3 and photo plates assembled in Corel Draw X3.

Measurements (Table 1) were taken using the measure tool in LAS and used to calculate the ratios of various body parts used in the diagnoses and descriptions.

Specimens are deposited in the following collections:

AMNH—American Museum of Natural History, NY, USA

BMNH—Natural History Museum, London, UK

CNC—Canadian National Collection, Ottawa, Canada

MMBC—Moravian Museum, Brno, Czech Republic

MNHN—Muséum national d’Histoire naturelle, Paris, France

MSNG—Museo Civico di Storia Naturale, Genova, Italy

UCR—University of California, Riverside, USA

USNM—National Museum of Natural History, Washington, DC, USA

Molecular protocols, phylogenetic, divergence dating, and biogeographic analyses Fourteen specimens of *Xenocaucus* representing seven species were sequenced. New sequences or sequences previously generated by us and downloaded from GenBank for seven species of Tribelocephalinae representing the genera *Abelocephala* Maldonado, *Opistoplatys* Westwood, and *Tribelocephala* Stål, and three species of Ectrichodiinae served as outgroups. GenBank accession numbers are provided along with USIs and RCW as Table 2. Protocols for DNA extraction, PCR, PCR cleaning, Sanger sequencing, sequence assembly and sequence editing follow recently published protocols in the Weirauch lab (e.g., Forthman and Weirauch 2016; Gordon and Weirauch 2016; Zhang et al. 2015) using one hind leg for extraction. We sampled one mitochondrial (16S rDNA) and three nuclear gene regions (28S rDNA D2 and D3–D5, 18S rDNA) using primer sequences from (Forero et al. 2013; Weirauch and Munro 2009). Gene regions were aligned separately in MAFFT (Kato and Standley 2013) using the E-INS-i algorithm. We used Sequence-Matrix v1.7.8 (Vaidya et al. 2011) to concatenate gene regions, exporting sequences with external gaps coded as question marks. This aligned concatenated matrix

Table 1 (continued)

	LenL3	LenForefem	LenForetib	LenFortars	WidHead	WidPro/AntProno	WidMeso/meta/ PostProno	WidAbdom	WidMedioTerg
<i>Xenocaucis ethiopiensis</i>	0.09	1.04	0.86	0.39	0.77	1.02	1.31	1.99	1.25
M (N = 1)	0.06	1.01	0.99	0.35	0.59	0.51	1.21	1.26	0.91
F (N = 3)	0.1	0.96	0.89	0.33	0.56	0.8	0.9	1.72	0.99
	0.02	0.01	0.04	0.02	0.01	0.03	0.03	0.03	0.04
	0.03	0.02	0.07	0.04	0.02	0.06	0.05	0.05	0.08
	0.08	0.95	0.85	0.31	0.55	0.87	0.87	1.69	0.96
	0.12	0.97	0.93	0.35	0.58	0.84	0.93	1.74	1.04
<i>Xenocaucis kimbozensis</i>									
F (N = 3)	0.18	0.55	0.39	0.19	0.39	0.59	0.63	1.17	0.63
	0.21	0.01	0.02	0.01	0.02	0.04	0.06	0.02	0
	0.36	0.02	0.04	0.03	0.03	0.08	0.12	0.05	0.01
	0.06	0.54	0.36	0.18	0.38	0.54	0.56	1.15	0.63
	0.42	0.57	0.41	0.21	0.41	0.62	0.68	1.19	0.64
<i>Xenocaucis nguru</i>									
F (N = 3)	0.09	0.69	0.51	0.27	0.47	0.7	0.72	1.28	0.76
	0.02	0.03	0.02	0.04	0.04	0.05	0.01	0.03	0.01
	0.02	0.06	0.04	0.08	0.07	0.09	0.03	0.06	0.02
	0.08	0.67	0.49	0.23	0.42	0.65	0.71	1.26	0.76
	0.1	0.73	0.53	0.3	0.49	0.74	0.73	1.32	0.78
<i>Xenocaucis rubeho</i>									
F (N = 1)	0.08	0.84	0.68	0.27	0.66	0.89	1.05	1.78	1.13
<i>Xenocaucis schoutedeni</i>									
F (N = 2)	0.09	0.54	0.55	0.24	0.47	0.61	0.68	1.28	0.78
	0.02	0.2	0	0.02	0.02	0.01	0.01	0.01	0
	0.02	0.28	0	0.03	0.02	0.02	0.02	0.02	0
	0.08	0.4	0.55	0.23	0.46	0.61	0.67	1.27	0.78
	0.11	0.69	0.56	0.26	0.48	0.62	0.69	1.29	0.78
<i>Xenocaucis uluguru</i>									
F (N = 1)	0.09	0.75	0.63	0.27	0.51	0.71	0.79	1.57	0.94

Total Leng total length, *LenHead d* length of head in dorsal view, *LenPro (female)/AntProno (male)* length of pronotum in the female and length of anterior pronotal lobe in the male, *Len Meso/metano (female) PostProno (male)* length of meso-and metanotum in the female and posterior pronotal lobe in the male, *LenAbd* length of abdomen, *LenScapus* length of scapus, *LenHead l* length of head in lateral view, *LenL1* length of visible labial segment 1, *LenL2* length of visible labial segment 1, *LenL3* length of visible labial segment 3, *LenForefem* length of forefemur, *LenForetib* length of foretibia, *LenFortars* length of foretarsus, *WidHead* width of head, *WidPro/AntProno* width of pronotum (female) or anterior pronotal lobe (male), *WidMeso/meta/PostProno* width of meso-and metanotum (female) or posterior pronotal lobe (male), *WidAbdom* greatest width of abdomen, *WidMedioTerg* greatest width of mediotergites

Table 2 Voucher information for the molecular component of this study, including GenBank, USI, and RCW numbers

Subfamily	Taxon	USI	RCW	Dep.	GenBank accession no.			
					16S	18S	28S D2	28S D3–D5
Ectrichodiinae	<i>Brontostoma colossus</i>	UCR_ENT 00119017	3049	UCR	KU764538	KT221911 ^a	KT221940 ^a	KT221969 ^a
	<i>Ectrichodia lucida</i>	AMNH_PBI 00218769	13	UCR	FJ230387 ^a	FJ230461 ^a	FJ230542 ^a	FJ230620 ^a , FJ230699 ^a
	<i>Ectrychotes</i> sp.	UCR_ENT 00119028	571	UCR	KU764546	KT221920 ^a	KT221947 ^a	KT221978 ^a
Tribelocephalinae	<i>Abelocephala</i> sp.	UCR_ENT 00106432	3308	UCR	KU764536	KU764567	KU764572	KU764588
	<i>Abelocephala</i> sp.2	UCR_ENT 00107032	3963	UCR		KU764566	KU764571	KU764587
	<i>Opistoplatys</i> sp.	UCR_ENT 00119024	3056	UCR		KT221926 ^a		KT221984 ^a
	<i>Opistoplatys</i> sp.	UCR_ENT 00052187	1592	UCR	JQ897851 ^a	JQ897612 ^a	JQ897682 ^a	JQ897767 ^a
	<i>Opistoplatys</i> sp.	UCR_ENT 00121753	3017	UCR	KX365207	KX365215	KX365225	KX298733
	<i>Tribelocephala peyrrierasi</i>	AMNH_PBI 00219033	287	CAS	FJ230440 ^a	FJ230521 ^a	FJ230601 ^a	
	<i>Tribelocephala</i> sp.	UCR_ENT 00119023	3048	UCR	KU764562		KT221965 ^a	KT221994 ^a
	<i>Xenocaucus chomensis</i>	UCR_ENT 00020645	3905	CNC		KX365220	KX365232	KX298739
	<i>Xenocaucus chomensis</i>	UCR_ENT 00020648	3908	CNC		KX365221	KX365233	KX298740
	<i>Xenocaucus ethiopiensis</i>	UCR_ENT 00117765	4694	CNC	KX365208		KX365226	
	<i>Xenocaucus ethiopiensis</i>	UCR_ENT 00020656	4707	CNC	KU764563		KU764584	KU764599
	<i>Xenocaucus kimbozensis</i>	UCR_ENT 00020640	3915	CNC	KX365211	KX365217	KX365228	KX298736
	<i>Xenocaucus kimbozensis</i>	UCR_ENT 00020639	3912	CNC	KX365210	KX365216	KX365227	KX298735
	<i>Xenocaucus kimbozensis</i>	UCR_ENT 00020651	3974	CNC	KX365214		KX365231	
	<i>Xenocaucus nguru</i>	UCR_ENT 00020629	3860	CNC	KX365212	KX365218	KX365229	KX298737
	<i>Xenocaucus nguru</i>	UCR_ENT 00020637	3934	CNC	KX365213	KX365219	KX365230	KX298738
	<i>Xenocaucus nguru</i>	UCR_ENT 00117774	3973	CNC	KX365209			KX298734
	<i>Xenocaucus rubeho</i>	UCR_ENT 00020650	3840	CNC		KX365222	KX365234	KX298741
	<i>Xenocaucus schoutedeni</i>	UCR_ENT 00020641	3833	CNC		KX365223	KX365236	KX298742
	<i>Xenocaucus schoutedeni</i>	UCR_ENT 00020642	3903	CNC		KX365224	KX365237	KX298743
<i>Xenocaucus uluguru</i>	UCR_ENT 00117767	3971	CNC			KX365235		

^a Previously published sequences obtained from GenBank

is deposited at TreeBASE and can be accessed using <http://purl.org/phylo/treebase/phyloids/study/TB2:S19519?x-access-code=17ae9ae9de4c221c1cd89274f93429&format=html>.

Phylogenetic analyses of the partitioned (by gene region) molecular dataset were performed using RAxML-HPC2 on XSEDE v8.0.24 (Stamatakis 2014) at CIPRES (http://www.phylo.org/sub_sections/portal/). Topologies were rooted on the ectrichodiine taxon *Brontostoma colossus* (Distant). We conducted rapid bootstrapping (1000 iterations) and searched for the best-scoring maximum likelihood tree in one run (–f a option). All other parameters were kept at default. The resulting phylogeny and bootstrap values are provided in Fig. 1. This phylogeny was subsequently used for divergence dating and biogeographic analyses.

The divergence dating analysis was performed using BEAST2 on XSEDE at CIPRES (Bouckaert et al. 2014). We assigned a linked clock model to 28S D2 and 28S D3–D5 since they are part of the same gene, but an unlinked clock model to 16S rDNA and 18S rDNA. Each gene region was assigned an HKY model, with the gamma category count set

to four and the substitution rate and gamma shape parameters estimated; all other parameters were kept at the default. Unlinked relaxed lognormal clock models were assigned for each gene region, keeping all parameters as default. To improve ESS values, the default Jeffrey’s prior was replaced with a uniform prior for the mutation rates. We secondarily calibrated the *Opistoplatys* + *Tribelocephala* node assigning a normal distribution (M = 47.68, S = 9.32; see Forthman and Weirauch (2016) for details). The root was calibrated using an undescribed *Ectrichodiella* species from Dominican amber and log normal distribution with “mean in real space” selected (M = 53.2, S = 0.16, offset = 15.0); all other priors and parameters were kept as default. Four Markov Chain Monte Carlo (MCMC) chains were ran for 300 million generations, with parameters and trees logged every 30,000 generations. Each chain was assessed for convergence in Tracer and combined after discarding 10% burn-in. Combined ESS values for each parameter were >200. Trees were combined in LogCombiner v2.1.3 with 10% of trees discarded as burn-in. We used TreeAnnotator v2.1.2 to annotate median heights. Median node ages are provided in Fig. 2 and the estimated

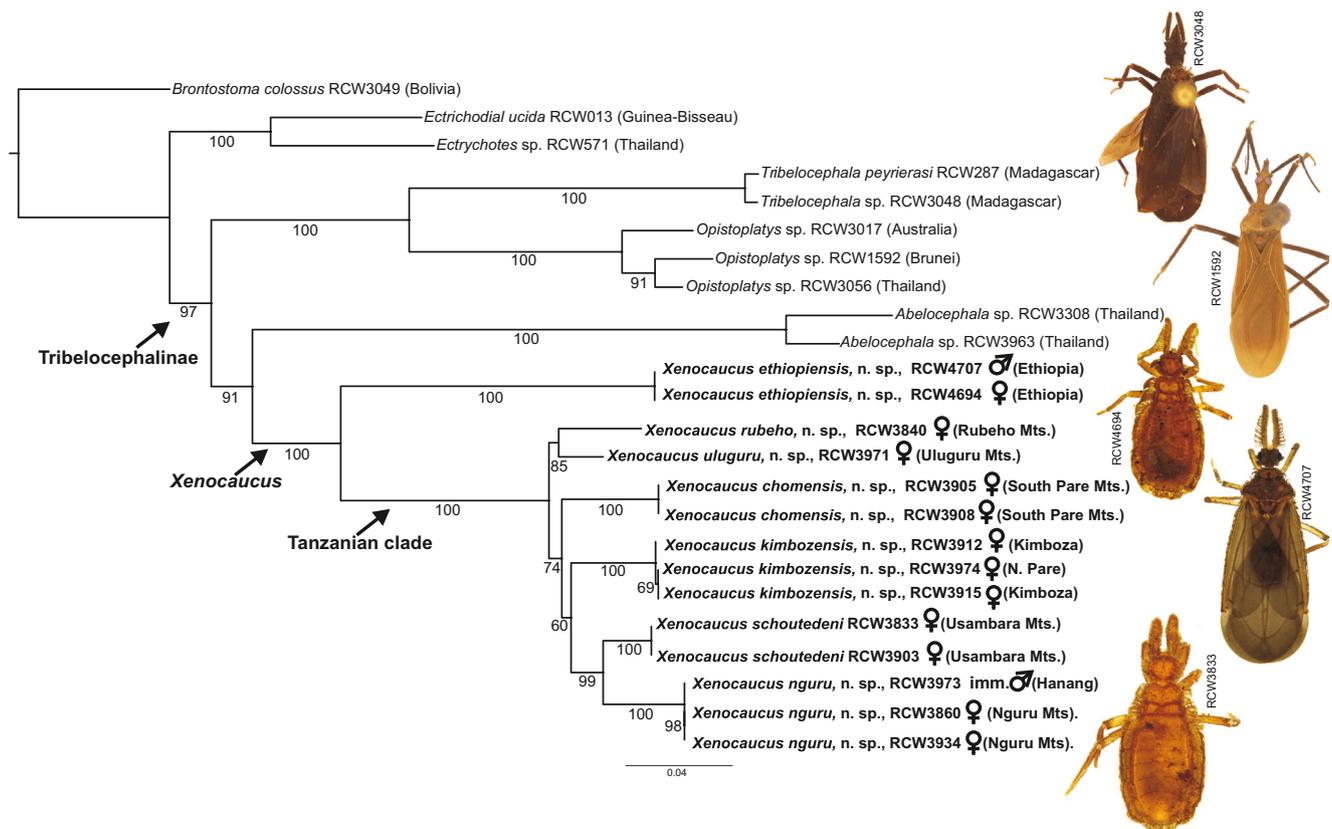


Fig. 1 Best maximum likelihood tree based on three gene regions (16S, 18S, 28S D2 and 28S D3–5; 3060 bp alignment) and 14 ingroup terminals representing the seven currently known East African species of *Xenocaucus* and ten outgroup taxa; *Xenocaucus* is recovered as

monophyletic, with *X. ethiopiensis* as the sister group to the Tanzanian clade that includes species from the Eastern Arc Mountains and Mt. Hanang

95% highest posterior density (HPD) credibility interval as Online Resource 2.

We reconstructed ancestral distribution ranges using dispersal-variance analysis (DIVA) in RASP v3.02 (Ronquist 1997; Yu et al. 2015) and BAYAREALIKE, DEC, and DIVALIKE models implemented in the BioGeoBEARS v0.2.1 package (Matzke 2014). For the latter, we analyzed the dataset with and without the parameter *j* that models for founder-effect speciation, conducted likelihood ratio tests (LTRs), and examined AIC and AICc values outputted by the program. All models were constrained to a maximum area of four. Given that three species have distribution ranges that extend beyond one mountain block, we used two area of endemism partitioning schemes. The first scheme treated individual mountain blocks in the EAM as areas of endemism (“mountains partitioning scheme”), with the exception that the lower elevation forest fragment of Kimboza Forest was combined with the nearby Uluguru Mts., resulting in eight areas (Ethiopia [Bale Mts.], Hanang, Uluguru/Kimboza, Nguru, North Pare, South Pare, Rubeho, and Usambara). A second partitioning scheme combined mountain blocks and forest fragments into four broader regions (“regions partitioning scheme”) that we treated as areas of endemism, namely Ethiopia, the northern EAM ranges (North Pare, South Pare, and Usambara), the

central EAM ranges and Mt. Hanang (Hanang, Kimboza, Uluguru, and Nguru), and the southernmost ranges represented by Rubeho.

For analyses using distance-constrained dispersal we follow Loader et al. (2014) for the determination of dispersal rates. For the mountain partitioning scheme, we assigned a rate of 1.0 to the diagonal of the matrix (i.e., same area), with 0.75 and 0.5 for areas separated by <200 and 200–400 km, respectively. In contrast to Loader et al. (2014), who assigned a rate of 0.001 between areas separated by more than 1000 km, we assigned a rate of 0.1 to apply to any EAM locality relative to the Bale Mts. For the region partitioning scheme, we assigned a rate of 1.0 to the diagonal of the matrix, with 0.75 for neighboring and 0.5 for non-neighboring areas, respectively; a rate of 0.1 was assigned between EAM localities and the Bale Mts. These dispersal probability values were assigned to periods during which dispersal can be expected to be more likely due to more extensive forest coverage; for the classification of periods as either wet or arid, we used Trauth et al. (2009). For periods of aridification, dispersal probabilities were reduced equally by a factor of 10 (except for matrix diagonal), to simulate the reduced probability of dispersal during those times.

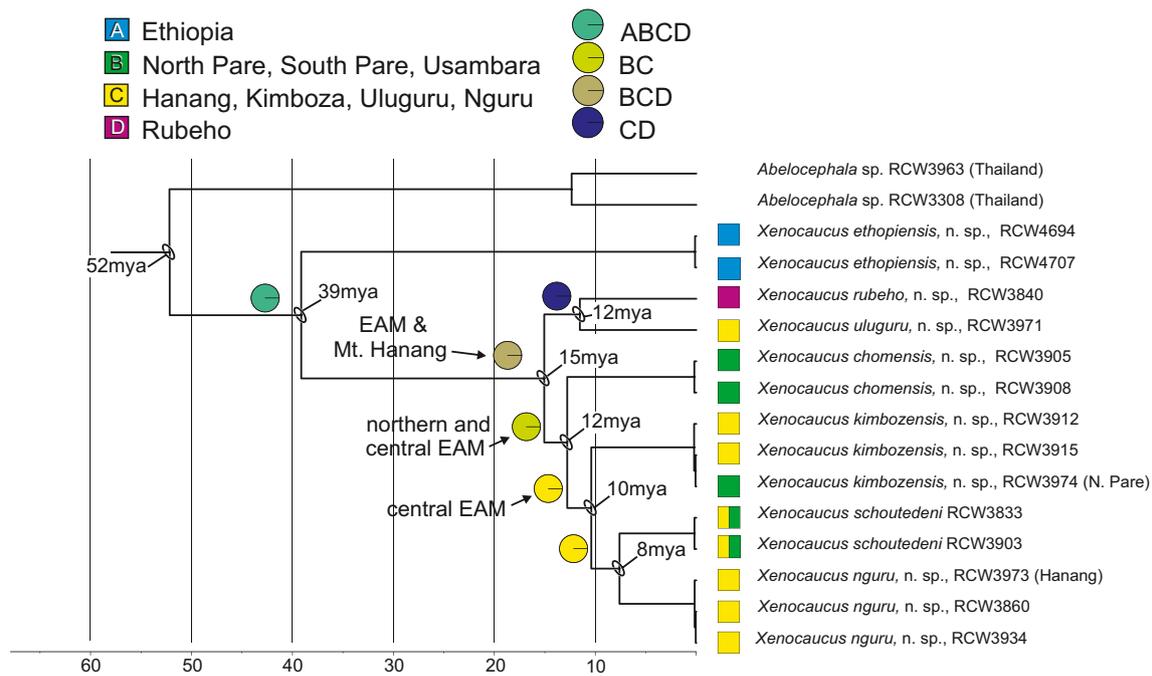


Fig. 2 Biogeographic (DIVA RASP; areas of endemism are regions) and divergence dating (BEAST; timescale mya) hypotheses dating the split between *X. ethiopiensis* and the Tanzanian clade to about 39 mya, with species level divergences within the Tanzanian clade occurring between about 12 and 8 mya; the ancestral area for the East African *Xenocaucus* is

broadly reconstructed to East Africa and the Tanzanian clade to the Eastern Arc Mountains plus Mt. Hanang; see Online Resource 3 for summary of results for the BioGeoBEAR analyses and the DIVA RASP analysis using mountain blocks as areas of endemism

Results

Taxonomy

Xenocaucus China and Usinger.

Figures 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10.

Type species: *Xenocaucus mancinii* China and Usinger, 1949

Revised diagnosis *Male* (based on *X. ethiopiensis*, n. sp.): recognized among Tribelocephalinae by the relatively small size (total length with wings ~5 mm), head wider than long in dorsal view (Fig. 3), reniform eyes strongly expanded ventrally (Figs. 6 and 7), third visible labial segment short and triangular (Fig. 7), scape long and slender and ventrally excavated and with distinctive fringes of setae, antennal flagellum four-segmented (Fig. 7), cell formed by Cu and Pcu large and club-shaped with narrow “handle” basally (Figs. 3 and 8), and two-segmented tarsi (Fig. 8). Male most similar to the Oriental *Abelocephala* in size, head shape, and two-segmented tarsi, but clearly separated by the four-segmented flagellum, eyes extending ventrally, and distinctive wing venation. *Female*: unique among Tribelocephalinae by the small size (2.2–3.75 mm), apterous (Fig. 4), reduction of compound eyes to only two or three ommatidia (Fig. 7), and the characteristic arrangement of fringes of setae on head, thorax, and abdomen.

Re-description *Male* (based on *X. ethiopiensis*, n. sp.): total length, 3.46 mm (5.21 to apex of wings), ratio of total length and greatest abdominal width 4.1; macropterous, with dense vestiture consisting of fairly long and slender setae arranged in rows on scape, laterally on head, lateral margin of pronotum, lateral margin of scutellum, costal wing margin to apex of corium, lateral margin of dorsal laterotergites; body, scape and legs with patches and rows of bulbous trichomes. *Coloration*: brown with antenna, labium, anterior pronotal lobe, scutellum, meso- and metapleuron and -sternum, legs, and base of hemelytron yellowish. *Structure*: Head: wider than long in dorsal view, almost globular in lateral view, anteocular area (gena, maxillary and mandibular plates, clypeus) very small, vertex with glabrous area circular, longitudinal sulcus extending about 1/2 of glabrous area, lateral “tuft” on head distinct, lateral fringes longer laterally than around posterior half of head, row of bulbous trichomes lateral to labium in ventral view forming a “rostral groove”; reniform compound eye consisting of numerous large ommatidia, reaching ventral head margin and almost reaching dorsal margin in lateral view, diameter in dorsal view about 1/5 of head width, in ventral view almost reaching lateral margin of labium. Antenna: pedicel and flagellomeres folded underneath scape at rest, scape slender, basal 3/4 straight, apical 1/4 slightly curved, with ventral longitudinal groove, dorsally with sparse short setae and bulbous trichomes, posterolateral margin with row of long setae, longest basally, with length

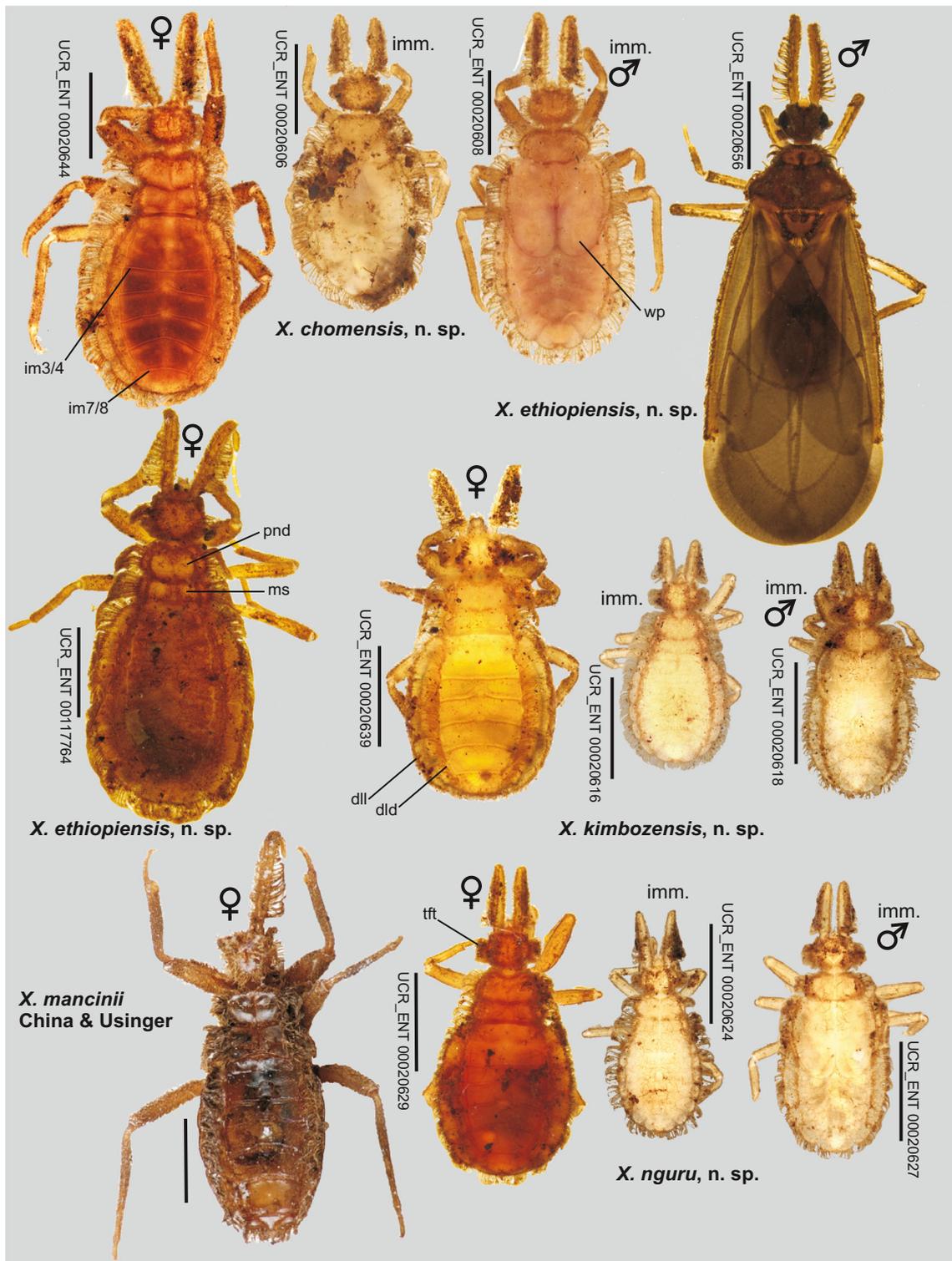


Fig. 3 Dorsal habitus of *X. chomensis*, n. sp., (female, unsexed immature, and male immature), *X. ethiopiensis*, n. sp., (male holotype and female), *X. kimbozensis*, n. sp., (female, unsexed immature, and male immature), the female holotype of *X. mancini*, and *X. nguru*, n. sp., (female, unsexed immature, and male immature). *dld* setae dorsally

on dorsal laterotergites, *dll* setae laterally on dorsal laterotergite, *im3/4* intersegmental membrane between tergites 3 and 4, *im7/8* intersegmental membrane between tergites 7 and 8, *pnd* pronotal disk, *ms* mesonotum, *tft* tuft of setae laterally on head, *wp* wing pad in male immatures; *scale bars*, 1 mm

decreasing towards apex, ventral surface glabrous, scape length: head length 2.8; pedicel about 1/4 length of scape,

slender; flagellum short, very slender, subdivided into four flagellomeres. Labium: long first visible segment, with shorter

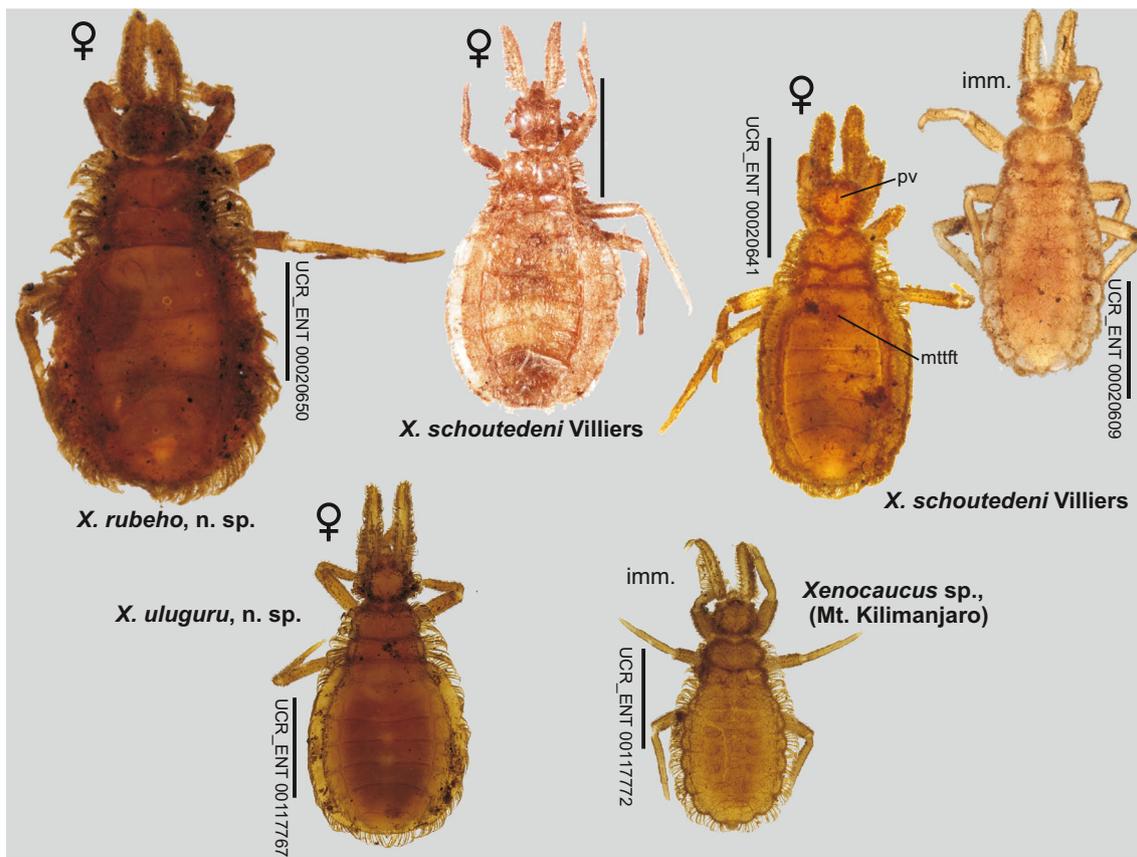


Fig. 4 Dorsal habitus of *X. rubeho*, n. sp., (female), the female holotype as well as one female and one unsexed immature (both from Uluguru) of *X. schoutedeni*, *X. uluguru*, n. sp., (female), and one immature (unsexed)

from Mt. Kilimanjaro that has remained unassociated with the female-based species. *mtfft* tuft of setae on mediotergite 1/2 and 3, *pv* longitudinal pit on vertex; *scale bars*, 1 mm

and slightly bulbous second segment and short triangular third segment, first segment ventrally excavated basally. Thorax: pronotum trapezoidal, with anterior pronotal lobe narrow, posterior lobe wide and with rounded humeral angles, anterior pronotal lobe much shorter than posterior pronotal lobe, pronotal length: mesonotal length 0.4, greatest pronotal width: pronotal length 1.5, metasternum with large bilobed process. Legs: slender, with fore- and midfemora and -tibiae stouter than those of hindleg, tarsi two-segmented with basal tarsomere very short, foretrochanter without ventral process, forefemur length: body length 0.2, forefemur very slender, tibiae slightly curved. Hemelytron: corium restricted to subcostal margin, with cell enclosed by Sc and proximal part of M+Cu narrow and elongate, Cu + Pcu cell large and club-shaped with narrow “handle” basally, M+Cu cell large and trapezoid, claval furrow indistinct, Pcu short. Abdomen: distinctly longer than wide, length: width of abdomen 1.5. *Genitalia*: pygophore in ventral view semicircular, with slender parameres slightly protruding (not dissected).

Female Total length ranging from 2.2–3.75 mm, total length: greatest abdominal width 1.9–2.1; apterous; general vestiture with dense vestiture consisting of long and slender setae

arranged in rows or patches on scape, laterally on head, dorsolaterally on all pleura, on lateral margin and dorsally on dorsal laterotergites, in addition to shorter vestiture in between rows, and on labium and legs. *Coloration*: uniformly yellowish brown to reddish brown or light brown to yellowish. *Structure*: head: about as long as wide or very slightly longer than wide in dorsal view, almost globular in lateral view; anteocular area deflected and very small or slightly elongated; vertex with glabrous area circular, elongate or indistinct; longitudinal sulcus indistinct, pitlike and very short, or extending about 2/3 or 1/2 of glabrous area; lateral setal fringes of similar length around posterior half of head or shaped into distinct “tufts” of setae; row of setae laterad of labium forming a “rostral groove” in ventral view; compound eye represented by two or three ommatidia, either adjacent or separated by as much as width of ommatidium. Antenna: pedicel and flagellomeres folded underneath scape at rest, scape length: head length 1.3–1.8; scape moderately slender or slender and slightly curved in lateral view, with longitudinal groove ventrally, dorsally with dense cover of setae of similar length, posterolateral margin with row of long setae, longest basally, with length decreasing towards apex, ventral surface glabrous; pedicel about 1/5 length of scape, slender; flagellum

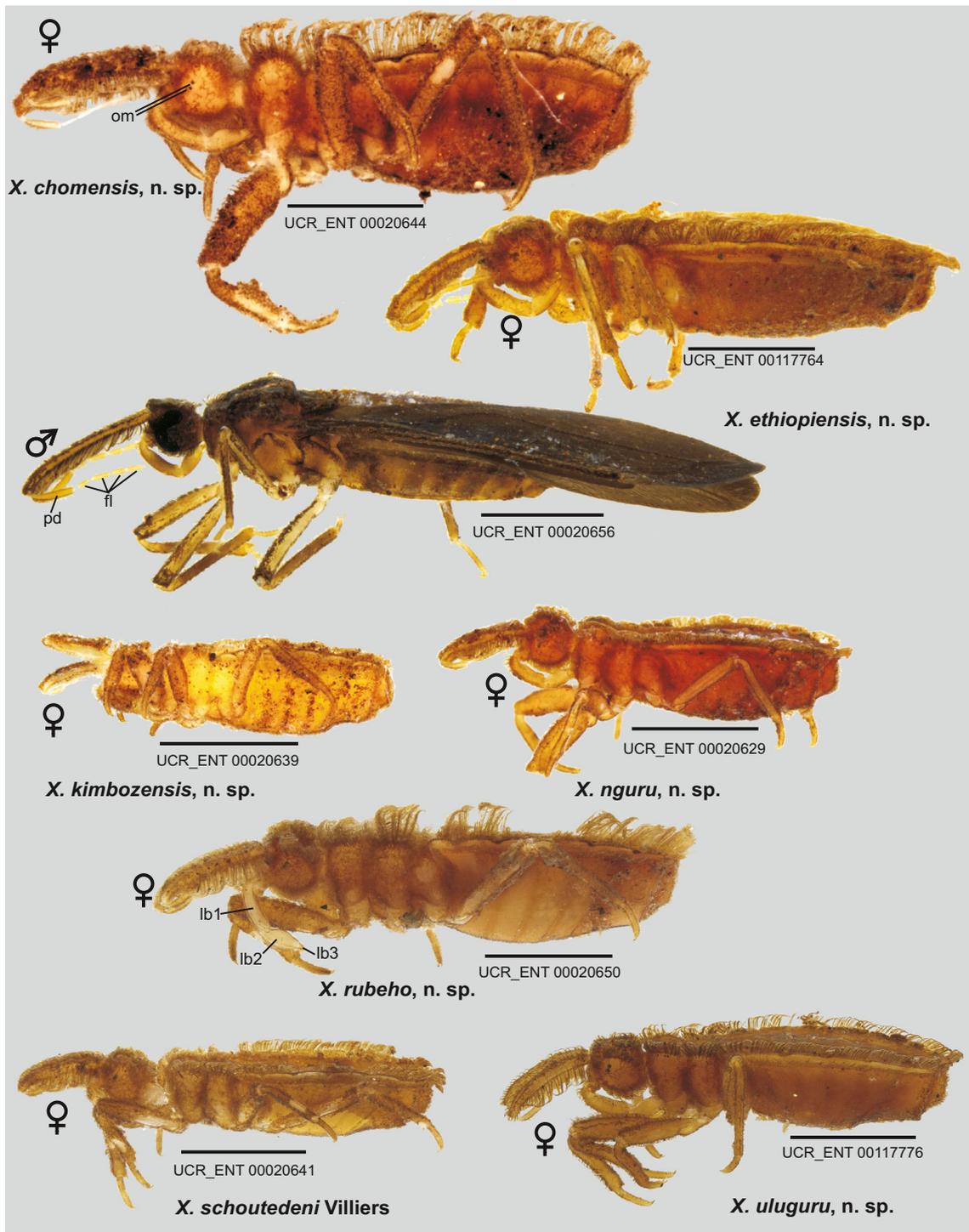


Fig. 5 Lateral habitus of females of the seven East African species of *Xenococcus* and the male of *X. ethiopiensis*. *fl* flagellomeres, *lb1–3* first, second, and third visible labia segments, *om* ommatidium, *pd* pedicel; *scale bars*, 1 mm

short, very slender, subdivided into four flagellomeres. Labium: long first visible segment, bulbous second segment shorter, and short triangular third segment, first segment with base ventrally excavated, first segment: head length 0.7–0.9. Thorax: transverse suture between pronotum and mesonotum distinct or indistinct, pronotum not divided into anterior and

posterior pronotal lobes, pronotum without raised disk, rectangular or with circular or heart-shaped raised disk, or with slightly raised transversally elongate disk, pronotum about as long as mesonotum or longer, in *X. mancinii* with separate posterolateral triangular sclerites that may represent metanotum, pronotal length: mesonotal length 0.9–1.7,

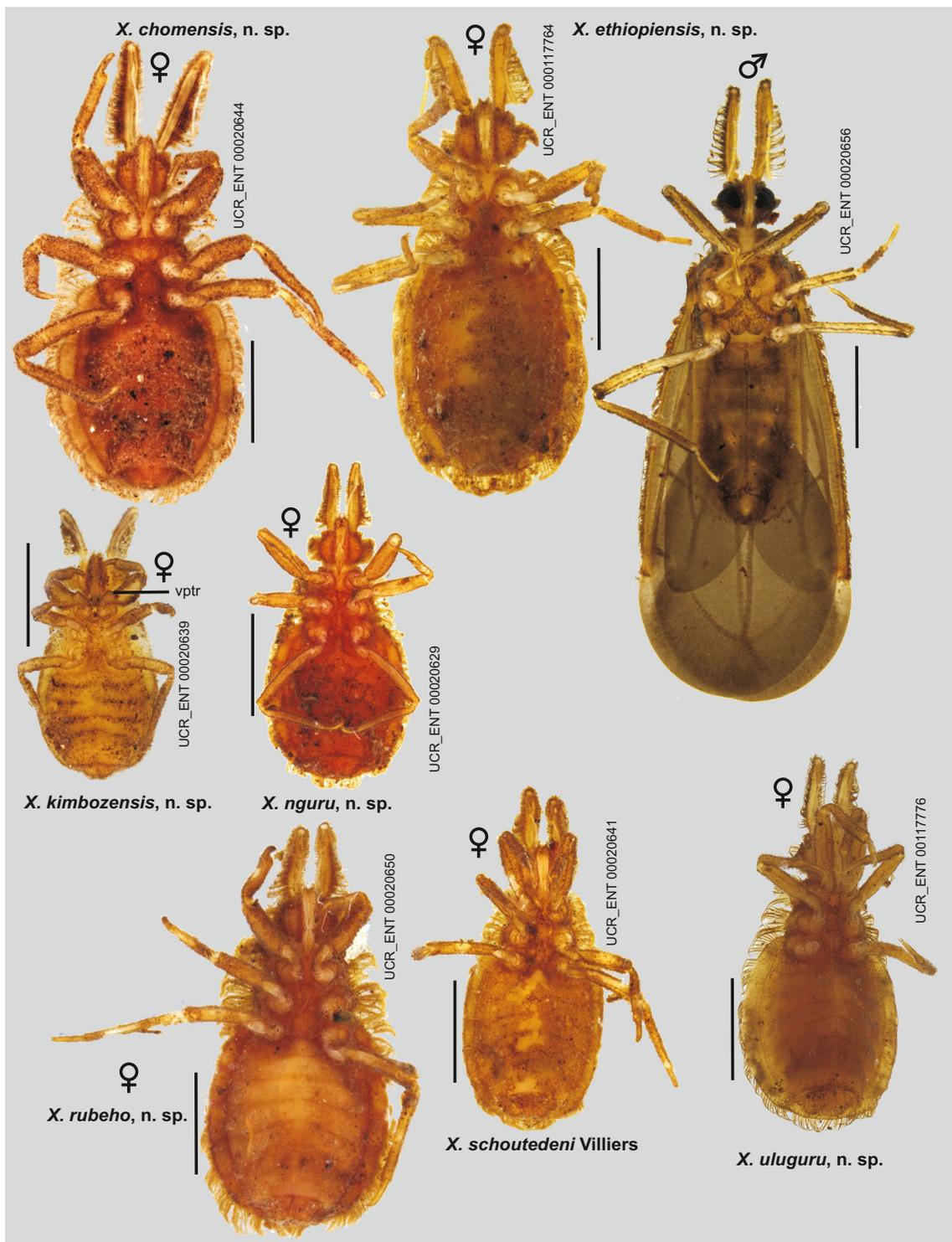


Fig. 6 Ventral habitus of the seven East African species of *Xenocaucus* and the male of *X. ethiopiensis*; abbreviation: vptr, ventral process on trochanter

greatest pronotal width: pronotal length 1.2–1.5, mesosternum without process. Legs: moderately stout, with fore- and midfemora and -tibiae stouter than those of hindleg, tarsi one-segmented, foretrochanter with or without ventral process, forefemur length: body length 0.2–0.3, forefemur fairly slender to stout, tibiae slightly curved. Abdomen: slightly to

distinctly longer than wide, abdominal length: width 1.1–1.5, mediotergites 1–3 fused, glabrous or with sparse setae or tuft of setae, with faint lateral lines possibly indicating intersegmental membrane, dorsal synlaterotergite 1/2 and laterotergite 3 separated, setae dorsally and on lateral margin of dorsal laterotergites ranging from short to long in different species,

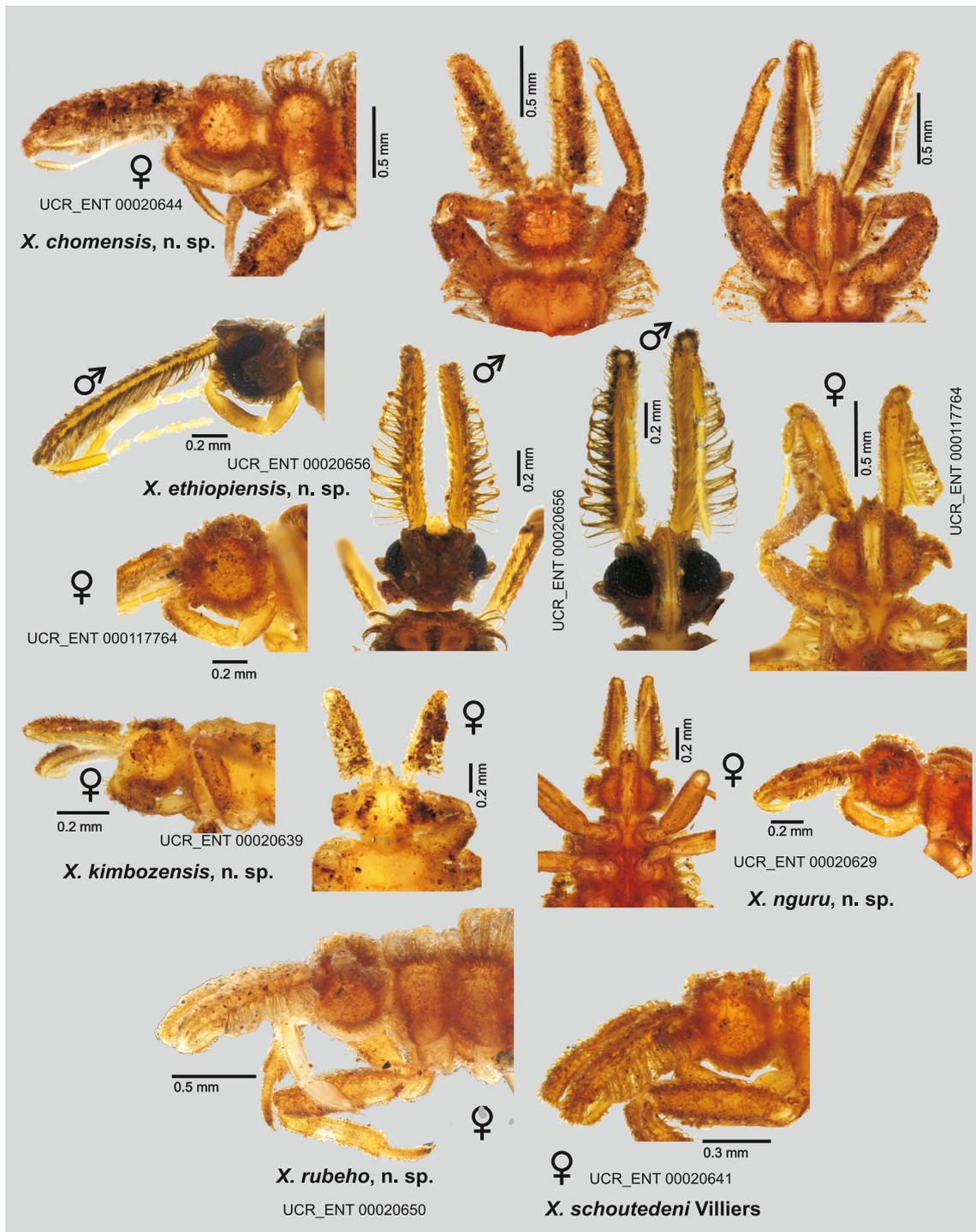


Fig. 7 Details of the head (dorsal, lateral, and/or ventral view) of selected species of *Xenocaucus*

intersegmental membrane between tergites 3 and 4 straight or slightly curved caudad, intersegmental membrane between tergites 6 and 7 slightly or distinctly curved anteriad, intersegmental membrane between tergites 7 and 8 straight or curved, intersegmental membrane more strongly notched at position of dorsal abdominal gland (DAG) between tergites 5 and 6 than between tergites 6 and 7, pores of DAG 3 slightly more

widely separated than those of DAG 2. *Genitalia*: external genitalia with valvifer 8 short triangular, tergites 9 and 10 indistinct.

Notes: collecting method, distribution range, and altitude All specimens, including the macropterous male specimen of *X. ethiopiensis*, n. sp., were collected by sifting leaf litter from

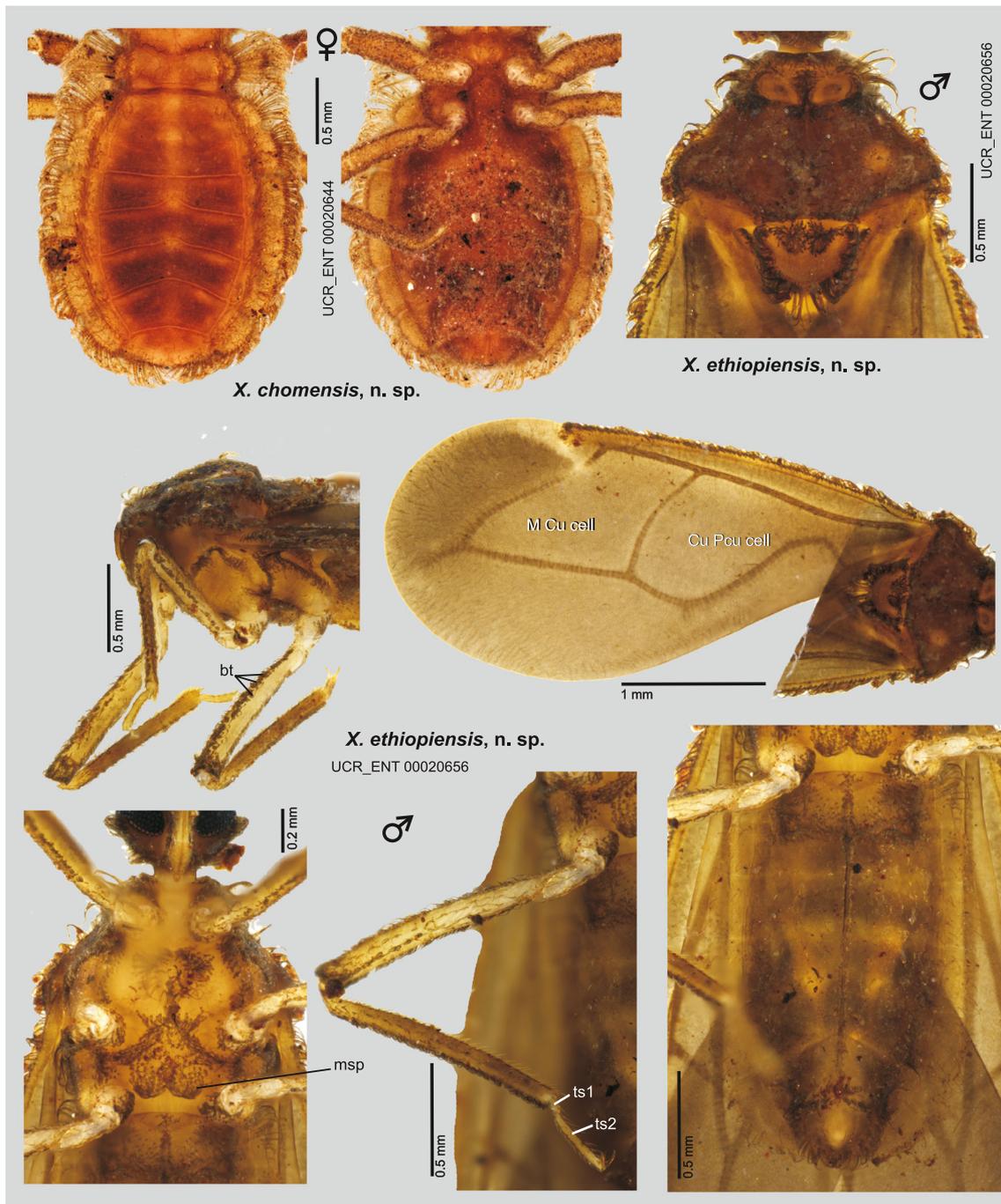


Fig. 8 Details of thorax and abdomen of a female of *X. chomensis* and the male holotype of *X. ethiopiensis*. *bt* bulbous trichome, *msp* bilobed process on metasternum, *ts1,2* tarsomere 1 and 2

forests floors with subsequent specimen extraction using Winkler funnels. Unlike the *Xenocaucus* females and immatures found in the Winkler's receptacle together with numerous other litter arthropods, the single *Xenocaucus* male was accidentally observed actively running on the rim of the Winkler funnel ready to escape, and was captured individually by hand. The known distribution of *Xenocaucus* is disjunct between West African lowland rainforests and montane and lowland rainforest of East Africa. The single West African

species, *X. mancinii*, is only known from the female holotype collected in Bioko Sur, at an elevation of about 500 m. Increased leaf litter sorting and new collecting efforts from rainforests on mainland West Africa will likely reveal additional specimens and potentially undescribed West African species. The number of collection events for the seven East African species is small, but based on currently available records, six of these species are montane: *X. chomensis*, n. sp., was collected between 1629 and 2239 m, the single locality of

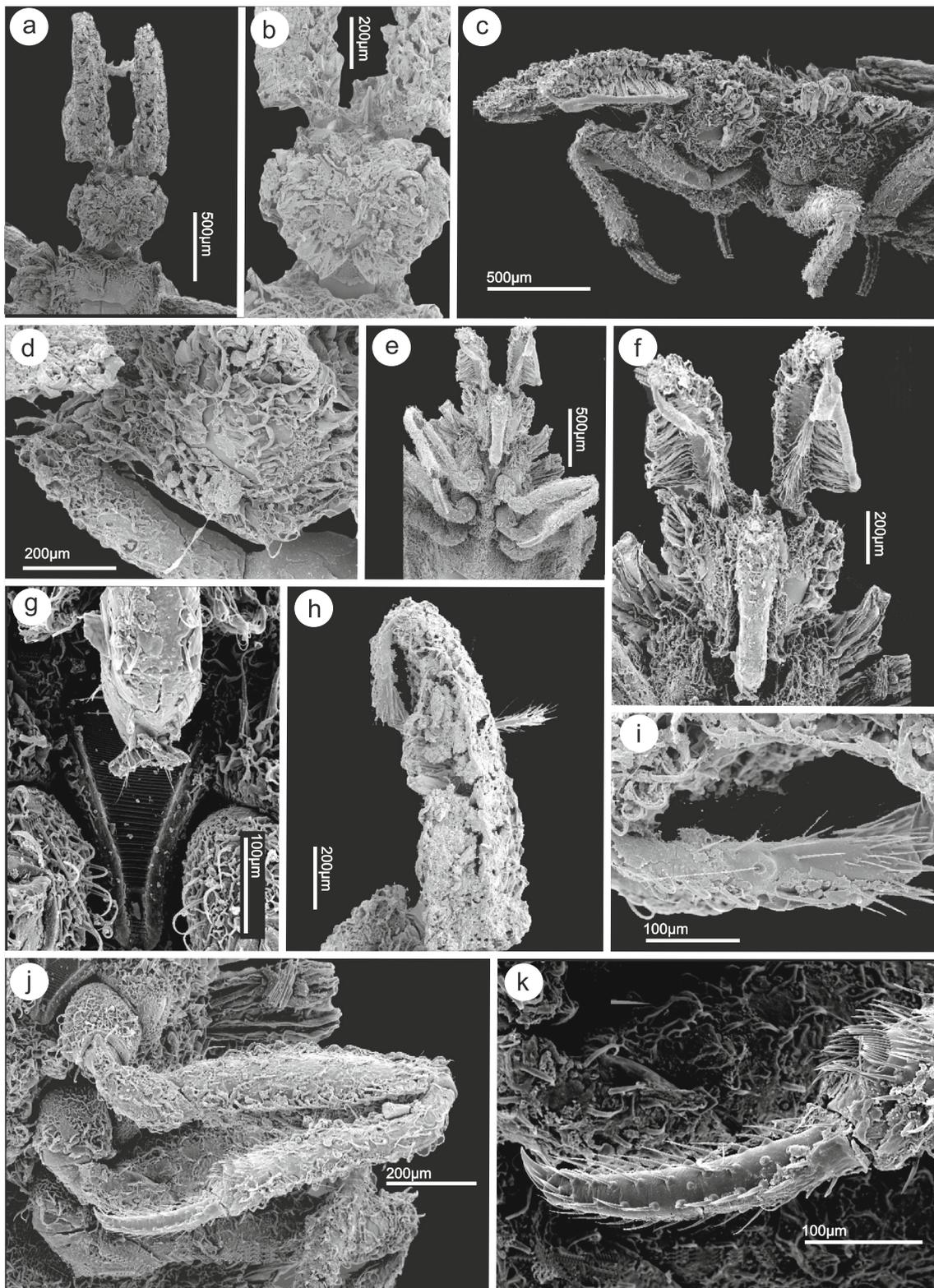


Fig. 9 Scanning electron micrographs of females of *X. chomensis* (UCR_ENT 00020646; **a**, **b**, **d**, **h**, **i**) and *X. nguru* (UCR_ENT 00020634; **c**, **e**, **f**, **g**, **j**, **k**). **a** Head, dorsal view; **b** head closeup, dorsal view; **c** head and thorax, lateral view; **d** head, lateral view; **e** head and

thorax, ventral view; **f** head, ventral view; **g** apex of labium and prosternal stridulatory sulcus, ventral view; **h** antenna, lateral view; **i** pedicel with proximal trichobothrium, lateral view; **j** leg, anterior view; **k** one-segmented tarsus of foreleg and protibial comb, anterior view

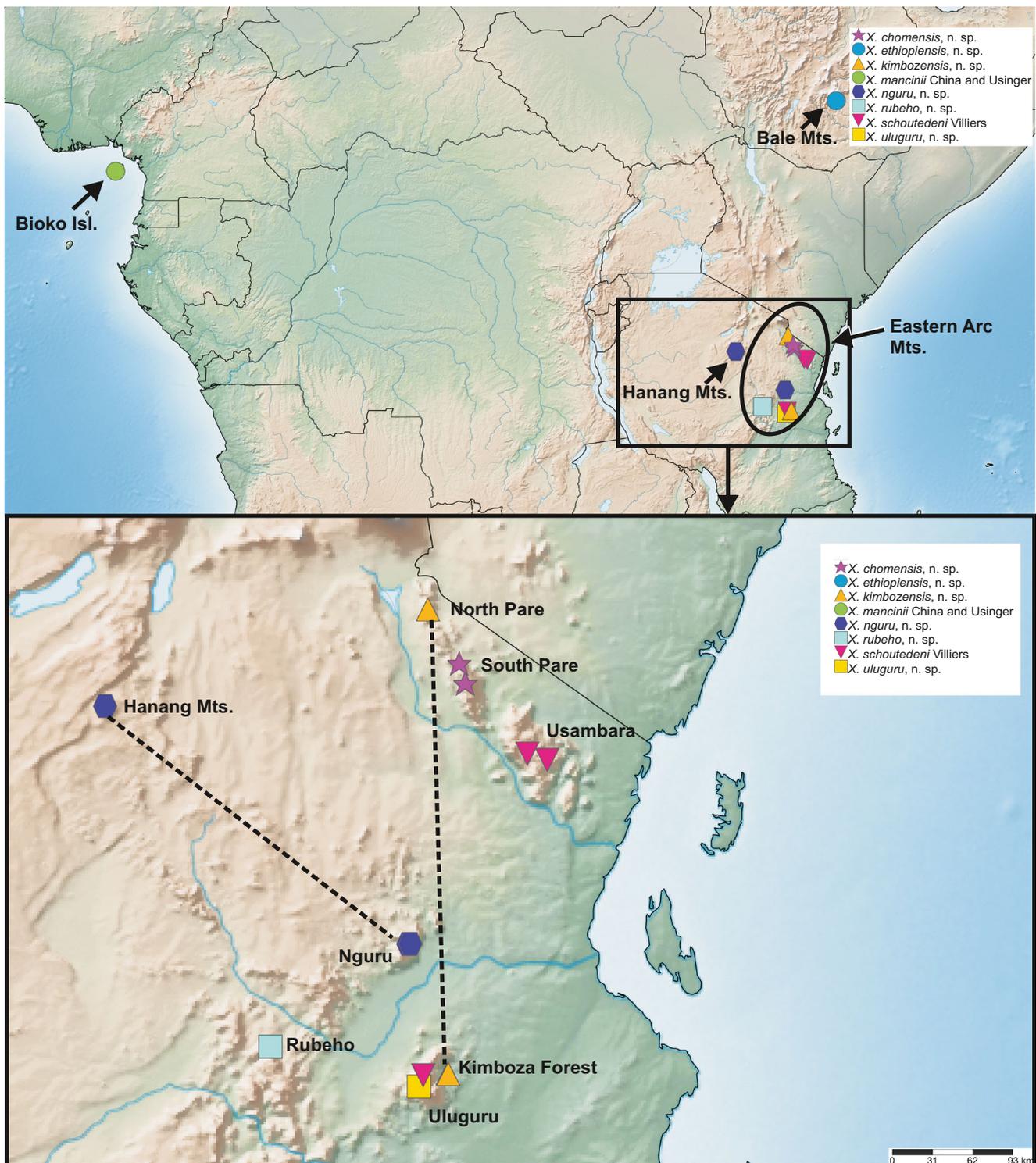


Fig. 10 Distribution of East and West African species of *Xenocaucus* (top) with a close-up of collecting localities of the species occurring in Tanzania (bottom). The stippled lines indicate disjunct collecting localities for *X. kimbozensis*, n. sp., and *X. nguru*, n. sp.

X. ethiopiensis, n. sp., is at 1576 m, *X. nguru*, n. sp., was collected between 967 and 2275 m, *X. rubeho*, n. sp., from a single locality at 1993 m, *X. schoutedeni* between 1300 and 1618 m, and *X. uluguru*, n. sp., from a single locality at 2258 m. In contrast, *X. kimbozensis*, n. sp., is known from

three localities between 217 and 1281 m. Four of the East African species may be restricted to a given mountain block: *X. ethiopiensis*, n. sp., *X. rubeho*, n. sp., and *X. uluguru*, n. sp., are known from single collection events in the Bale, Rubeho, and Uluguru Mountains, respectively. *Xenocaucus*

chomensis is known from three collection events, all in the South Pare Mountains. In contrast, two of the montane species, *X. nguru*, n. sp. and *X. uluguru*, n. sp., are known from two mountain blocks, the Nguru Mountains and Mount Hanang and Uluguru Mountains and the East Usambara Mountains, respectively. The Uluguru Mountains are currently known to harbor two species of *Xenocaucus* (*X. schoutedeni* and *X. uluguru*, n. sp.), whereas only one species has been documented from other mountain blocks. The low elevation species *X. kimbozensis*, n. sp., shows a similar wide distribution range, with specimens known from Kimboza Forest close to the Uluguru Mountains and a mid-elevation site in the North Pare Mountains.

Immatures Immatures for selected species are documented in Figs. 3 and 4. They were associated with female-based species based on collection event, except the single immature collected at Mt. Kilimanjaro (Fig. 4) that remains unassociated (attempts to obtain sequence data failed). We were unable to identify the instar number for early instars and immatures that we assume to represent later instar immature females (e.g., Fig. 3: *X. chomensis*, n. sp.); we therefore do not provide formal descriptions for immatures. For three species (Fig. 3: *X. chomensis*, n. sp., *X. kimbozensis*, n. sp., and *X. nguru*, n. sp.), we discovered immatures with large wing pads, which indicated that some morphs of EAM *Xenocaucus* species are winged even prior to the discovery of the macropterous male from Ethiopia. The discovery of the strongly sexually dimorphic *X. ethiopiensis*, n. sp., now strongly suggests that these immatures with wing pads will molt into macropterous males. Additional collecting efforts in the EAM using leaf litter sifting, Malaise traps or light traps are therefore likely to reveal additional *Xenocaucus* males.

Compound eye in females China and Usinger (1949) and Villiers (1960) diagnosed *Xenocaucus* by the absence of eyes. All specimens collected by us, including specimens that we treat as conspecific with *X. schoutedeni* (Fig. 7), feature two or three more or less widely separated ommatidia. They appear to vary slightly in size between species (e.g., small and widely separated in the specimen of *X. chomensis* shown in Fig. 7, larger and adjacent in *X. ethiopiensis*, n. sp.), but since some variations also occur within species and the exact size and position of ommatidia is sometimes difficult to determine due to adhered debris particles, we refrain from using this feature in species diagnoses. Setae and debris particles obscure the lateral surface of the head in the holotype of *X. mancinii*, and we were therefore unable to confirm the presence of ommatidia; given how easily these structures are overlooked, we assume that they are also present in *X. mancinii*.

Female-based key to species of *Xenocaucus*

- 1- Small, total length about 2.2 mm, head slightly longer than wide, appearing elongate with pointed apex in dorsal view (Fig. 3), lateral tufts of setae on head pronounced (Fig. 7), foretrochanter with ventral process (Fig. 6), forefemur stout (Fig. 6), setae on lateral margin of dorsal laterotergites short (Fig. 3) *X. kimbozensis*, n. sp.
- 1'- Larger, total length 2.5–3.8 mm, head about as long as wide (Fig. 3), apex not appearing pointed in dorsal view, lateral tufts of setae on head distinct or absent (Fig. 7), foretrochanter without ventral process (Fig. 6), forefemur fairly slender or fairly stout (Fig. 6), setae on lateral margin of dorsal laterotergites short or long (Figs. 3 and 4) 2
- 2- Body length ≤ 3 mm 3
- 2'- Body length distinctly >3 mm (3.4 to 3.8 mm) 5
- 3- Lateral setal tuft on head absent, lateral fringes of similar length around posterior half of head (Fig. 4), pronotum with raised disk lobed or heart-shaped, pronotum distinctly longer than mesonotum (Fig. 4), pronotal length: mesonotal length 1.9, intersegmental membrane between tergites 7 and 8 curved (Fig. 4), mediotergites 1/2 and 3 with tuft of setae (Fig. 4) *X. schoutedeni* Villiers
- 3'- Lateral setal tuft on head distinct, fringes around posterior half of head shorter (Figs. 3 and 4, *X. nguru*, *X. uluguru*), pronotum with slightly raised transversally elongate disk, pronotum longer than mesonotum (Figs. 3 and 4), pronotal length: mesonotal length 1.3–1.5, intersegmental membrane between tergites 7 and 8 straight (Figs. 3 and 4), mediotergites 1/2 and 3 glabrous (Figs. 3 and 4) 4
- 4- Body size about 2.5 mm, ratio of first visible labial segment: head length 0.7, intersegmental membrane between tergites 3 and 4 straight (Fig. 3) *X. nguru*, n. sp.
- 4'- Body size about 2.9 mm, ratio of first visible labial segment: head length 0.9, intersegmental membrane between tergites 3 and 4 slightly curved caudad (Fig. 4) *X. uluguru*, n. sp.
- 5- Longitudinal sulcus on vertex extending about 2/3 of glabrous area, only known from West Africa (Bioko Island) *X. mancinii* China and Usinger
- 5'- Longitudinal sulcus on vertex very short or indistinct (Figs. 3, 4, and 7, *X. chomensis*, *X. ethiopiensis*, *X. rubeho*), only known from East Africa 6
- 6- Pronotum with slightly raised transversally elongate disk (Fig. 4), pronotum about as long as mesonotum (ratio 0.9), intersegmental membrane between tergites 3 and 4 slightly curved caudad (Fig. 4), dorsal setae on dorsal laterotergites long (Fig. 4), total length about 3.4 mm *X. rubeho*, n. sp.
- 6'- Pronotum with raised circular or heart-shaped disk (Fig. 3, *X. chomensis* and *X. ethiopiensis*), pronotum longer than mesonotum (ratio 1.4), intersegmental membrane

- between tergites 3 and 4 straight (Fig. 3), dorsal setae on dorsal laterotergites short (Fig. 3), total length about 3.7 mm. 7
- 7- Abdomen slightly longer than wide (ratio 1.2), intersegmental membrane between tergites 7 and 8 curved (Fig. 3, *X. chomensis*), only known from the Eastern Arc Mountains *X. chomensis*, n. sp.
- 7'- Abdomen distinctly longer than wide (ratio 1.4), intersegmental membrane between tergites 7 and 8 straight (Fig. 3, *X. ethiopiensis*), only known from the Bale Mts. in Ethiopia *X. ethiopiensis*, n. sp.

Xenocaucus chomensis, n. sp.

Figures 3, 5, 6, 7, 8, 9, and 10.

Diagnosis Female: recognized by the large size (>3 mm), the very short pit on vertex, the pronotal disk raised and heart-shaped, the intersegmental membranes between tergites 3 and 4 straight (Fig. 3) and between tergites 7 and 8 curved (Fig. 3), and the setae on lateral margin of dorsal laterotergites very long and those dorsally short (Fig. 3).

Description Female: total length, 3.67 mm; total length: greatest abdominal width 1.9; wing condition and general vestiture as in generic description. **Coloration:** uniformly brown to reddish brown. **Structure:** head: about as long as wide in dorsal view, with very small genal and maxillary plate areas, glabrous area on vertex circular, pit very short, tuft absent, lateral fringes of similar length around posterior half of head. Antenna: scape length: head length 1.8, scape slender. Labium: first visible segment: head length 0.8. Thorax: transverse suture between pronotum and mesonotum distinct, pronotal disk raised with lobed, heart-shaped appearance, pronotum longer than mesonotum (ratio 1.4), greatest pronotal width: pronotal length 1.5. Legs: foretrochanter without ventral process, fore femur length: body length 0.3, forefemur fairly stout. Abdomen: slightly longer than wide, length: width 1.2, intersegmental membrane between tergites 3 and 4 straight, intersegmental membrane between tergites 6 and 7 distinctly curved anteriorly, intersegmental membrane between tergites 7 and 8 curved, mediotergites 1/2 and 3 glabrous, setae on lateral margin of dorsal laterotergites very long, setae dorsally on dorsal laterotergites short. **Genitalia:** as in generic description.

Male: unknown. Immatures with wing pads suggest that males are macropterous.

Immatures: as in Fig. 3.

Etymology Named for the collecting locality of the paratypes, Chome Forest in the South Pare Mountains.

Material examined holotype: Tanzania South Pare Mts., Kwizu For., 4.12924° S, 37.88445° E, 1629 m, 7 Jan. 2013,

V. Grebennikov, 1;female (00020644) (CNC). Paratypes: TANZANIA: South Pare Mts., Chome For., 4.27064° S, 37.92595° E, 2159 m, 3 Jan. 2013, V. Grebennikov, 1;female (00020643) (CNC). South Pare Mts., Chome For., 4.26945° S, 37.92814° E, 2239 m, 3 Jan. 2013, V. Grebennikov, 2;female (00020645, 00020646) (CNC), 2;female (00020647, 00020648) (AMNH). Other specimens examined: Tanzania: South Pare Mts., Chome For., 4.26945° S, 37.92814° E, 2239 m, 3 Jan. 2013, V. Grebennikov, 2;juvenile male (00020606, 00020607) (CNC). South Pare Mts., Kwizu For., 4.12924° S, 37.88445° E, 1629 m, 7 Jan. 2013, V. Grebennikov, 1;juvenile male, (00020608) (CNC).

Xenocaucus ethiopiensis, n. sp.

Figures 3, 5, 6, 7, 8, and 10.

Diagnosis Male: as in generic description. **Female:** recognized by the large size (>3 mm), the very short or indistinct pit on vertex, the pronotal disk raised and slightly transversely circular, the intersegmental membranes between tergites 3 and 4 and between tergites 7 and 8 straight (Fig. 3), setae on the lateral margin of the dorsal laterotergites very long and those dorsally short (Fig. 3).

Description Male: as in generic description. **Female:** total length 3.69 mm, total length: greatest abdominal width 2.1; wing condition and general vestiture as in generic description. **Coloration:** uniformly yellowish brown to reddish brown. **Structure:** head: about as long as wide in dorsal view, with very small anteocular area, glabrous area on vertex circular, longitudinal sulcus or pit indistinct, tuft distinct, lateral fringes longer laterally than around posterior half of head; Antenna: scape length: head length 1.7, slender. Labium: first visible segment: head length 0.8. Thorax: transverse suture between pronotum and mesonotum distinct, pronotum with slightly transverse, almost circular raised disk, pronotum longer than mesonotum (ratio 1.4), greatest pronotal width: pronotal length 1.2. Legs: foretrochanter without ventral process, forefemur length: body length 0.3, forefemur fairly slender. Abdomen: longer than wide, length: width 1.4, intersegmental membrane between tergites 3 and 4 straight, intersegmental membrane between tergites 6 and 7 distinctly curved anteriorly, intersegmental membrane between tergites 7 and 8 straight, mediotergites 1/2 and 3 with sparse setae, setae on lateral margin of dorsal laterotergites long, setae dorsally on dorsal laterotergites short. **Genitalia:** as in generic description.

Etymology: named for the holotype's country of origin.

Material examined holotype: Ethiopia Oromia Region Co.: Bale Mts, 6.5141° N, 39.7434° E, 1576 m, 4 Nov. 2014, V. Grebennikov, 1;male (00020656) (CNC). Paratypes: Ethiopia: Oromia Region Co.: Bale Mts, 6.5141° N, 39.7434° E, 1576 m, 4 Nov. 2014, V. Grebennikov, 2;female (00117764, 00117765) (BMNH), 7;female (00117769, 00020657–

00020662) (CNC). Other specimens examined: Ethiopia: Oromia Region Co.: Bale Mts, 6.5141° N, 39.7434° E, 1576 m, 4 Nov. 2014, V. Grebennikov, 4;juvenile (00020663–00020666) (CNC).

Xenocaucus kimbozensis, n. sp.
Figures 3, 5, 6, 7, and 10.

Diagnosis Female: recognized by the small body length (~2.2 mm), the head slightly longer than wide, appearing elongate with pointed apex in dorsal view (Fig. 3), the pronounced lateral tufts of setae on the head (Fig. 7), the foretrochanter with a stout ventral process (Fig. 6), the stout forefemur (Fig. 6), and the short setae on the lateral margin of the dorsal laterotergites (Fig. 3).

Description Female: total length: 2.19 mm, total length: greatest abdominal width 1.9; wing condition and general vestiture as in generic description. *Coloration:* uniformly light brown to yellowish. *Structure:* head: slightly longer than wide in dorsal view, with slightly elongated anteocular area, glabrous area on vertex elongate, longitudinal sulcus extending about 2/3 of glabrous area, tuft distinct, lateral fringes longer laterally than around posterior half of head. Antenna: scape length: head length 1.3, slender. Labium: first visible segment: head length 0.7. Thorax: transverse suture between pronotum and mesonotum indistinct, pronotal disk flat and rectangular, pronotum distinctly longer than mesonotum (ratio 1.7), greatest pronotal width: pronotal length 1.5. Legs: foretrochanter with ventral process, forefemur length: body length 0.3, forefemur stout. Abdomen: about as long as wide, length: width 1.14, intersegmental membrane between tergites 3 and 4 straight, intersegmental membrane between tergites 6 and 7 slightly curved anteriorly, intersegmental membrane between tergites 7 and 8 straight, mediotergites 1/2 and 3 glabrous, setae on lateral margin of dorsal laterotergites short, setae dorsally on dorsal laterotergites long. *Genitalia:* as in generic description.

Male: unknown. Immatures with wing pads suggest that males are macropterous.

Immatures: as in Fig. 3.

Etymology: named for the holotype locality, Kimboza Forest in Tanzania.

Material examined: holotype: Tanzania Morogoro: Kimboza Forest, 7.02417° S, 37.80806° E, 217 m, 9 Jan. 2012, V. Grebennikov, 1;female (00020639) (CNC). Paratypes: Tanzania: Morogoro: Kimboza Forest, 7.0218° S, 37.8035° E, 295 m, 16 Oct. 2014, V. Grebennikov, 1;female (00117773) (CNC). Kimboza Forest, 7.02417° S, 37.80806° E, 217 m, 9 Jan. 2012, V. Grebennikov, 1;female (00020640) (CNC). North Pare Mts, 3.75° S, 37.66667° E, 1281 m, 9 Jan. 2012, V. Grebennikov, 4;female (00020651–00020654) (CNC). Other specimens examined: Tanzania: Kimboza

Forest, 7.02417° S, 37.80806° E, 217 m, 9 Jan. 2012, V. Grebennikov, 11;juvenile (00020610–00020620) (CNC). North Pare Mts, 3.75° S, 37.66667° E, 1281 m, 09 Jan. 2012, V. Grebennikov, 1;juvenile male, (00020655) (CNC).

Xenocaucus mancinii China and Usinger.
Figure 3.

Diagnosis Female: recognized by the large size (>3 mm) and the long longitudinal sulcus on the vertex that extends about 2/3 of the glabrous area.

Re-description Female: total length 3.75 mm (according China and Usinger). *Coloration:* uniformly yellowish brown. *Structure:* head: about as long as wide in dorsal view, glabrous area on vertex circular, longitudinal sulcus extending about 2/3 of glabrous area, lateral setal fringes on head of similar length around posterior half of head. Antenna: pedicel about 1/5 length of scape, slender, flagellomeres missing. Labium: obscured in digital habitus images. Thorax: transverse suture between pronotum and mesonotum distinct, raised pronotal disk circular, pronotum about as long as mesonotum, with separate posterolateral triangular sclerites that may represent metanotum. Legs: femur fairly slender. Abdomen: distinctly longer than wide, intersegmental membrane between tergites 3 and 4 straight, intersegmental membrane between tergites 6 and 7 slightly curved anteriorly, intersegmental membrane between tergites 7 and 8 straight, mediotergites 1/2 and 3 glabrous, setae on lateral margin of dorsal laterotergites long, setae dorsally on dorsal laterotergites indistinct. *Genitalia:* not observed.

Male: unknown.

Material examined: holotype: equatorial guinea Bioko Sur: Musola, 3.44448° N, 8.61782° E, 500 m, 1 Mar. 1902, L. Fea, 1;female (MSNG).

Notes: Given this holotype is old, matted with debris, fragile, and glued onto cardboard, we were only able to observe a subset of the characters examined and documented for the remaining *Xenocaucus* species. The very short diagnosis and description of this species will need to be revised, should additional specimens and species be discovered in West Africa.

Xenocaucus nguru, n. sp.
Figures 3, 5, 6, 7, 9, 10.

Diagnosis Female: recognized by the small medium size (~2.5 mm), the distinct lateral setal tufts on head (Figs. 3 and 6), the slightly raised and transversally elongate pronotal disk, the pronotum longer than the mesonotum (Fig. 3; ratio 1.5), the intersegmental membrane between tergites 7 and 8 straight (Fig. 3), and mediotergites 1/2 and 3 glabrous (Fig. 3).

Description Female: total length: 2.48 mm, total length: greatest abdominal width 1.9; wing condition and general vestiture as in generic description. *Coloration:* uniformly yellowish brown to reddish brown. *Structure:* head: about as long as wide in dorsal view, with very small anteocular area, glabrous area on vertex circular, longitudinal sulcus extending about 1/2 of glabrous area, tuft distinct, lateral fringes longer laterally than around posterior half of head. Antenna: scape length: head length 1.6, moderately slender. Labium: first visible segment: head length 0.7. Thorax: transverse suture between pronotum and mesonotum distinct, pronotal disk slightly raised and transversally elongate, pronotum longer than mesonotum (ratio 1.5), greatest pronotal width: pronotal length 1.4. Legs: foretrochanter without ventral process, forefemur length: body length 0.3, forefemur fairly slender. Abdomen: slightly longer than wide, length: width 1.2, intersegmental membrane between tergites 3 and 4 straight, intersegmental membrane between tergites 6 and 7 slightly curved anteriorly, intersegmental membrane between tergites 7 and 8 straight, mediotergites 1/2 and 3 glabrous, setae on lateral margin of dorsal laterotergites short, setae dorsally on dorsal laterotergites short. *Genitalia:* as in generic description.

Male: unknown. Immatures with wing pads suggest that males are macropterous.

Immatures: as in Fig. 3.

Etymology: named for the holotype locality, Nguru Mts. in Tanzania.

Material examined: holotype: Tanzania Nguru Mts. at Mhonda, 6.10611° S, 37.54389° E, 967 m, 4 Jan. 2012, V. Grebennikov, 1;female (00020629) (CNC). Paratypes: Tanzania: Morogoro: Nguru Mts. at Turiani, 6.10667° S, 37.53° E, 1236 m, 5 Nov. 2010, V. Grebennikov, 1;female (00117766) (CNC). Nguru Mts. at Mhonda, 6.10611° S, 37.54389° E, 967 m, 4 Jan. 2012, V. Grebennikov, 2;female (00020631, 00020632) (CNC), 2;female (00020633, 00020634) (MMBC), 2;female (00020635, 00020636) (UCR), 2;female (00020637, 00020638) (USNM). Other specimens examined: Tanzania: Manyara: Mt. Hanang, NE slope, 4.43058° S, 35.41616° E, 2275 m, 16 Dec. 2012, V. Grebennikov, 1;juvenile male, (00117774) (CNC). Nguru Mts. at Mhonda, 6.10611° S, 37.54389° E, 967 m, 4 Jan. 2012, V. Grebennikov, 9;juvenile (00020621–00020628, 00020630) (CNC).

Notes This species is morphologically similar to *X. schoutedeni* and recovered as its sister species in the molecular phylogeny. It is clearly divergent from that species in the molecular phylogram (Fig. 1) and is morphologically distinguished by the head setation, shape of the pronotal disk, ratio of the

pronotum to mesonotum, the shape of the intersegmental membrane 7 and 8, and the setation of mediotergites 1/2 and 3.

Xenocaucus rubeho, n. sp.

Figures 4, 5, 6, 7, and 10.

Diagnosis Female: recognized by the relatively large body size (~3.4 mm), the slight raised and transversally elongate pronotal disk (Fig. 4), the pronotum about as long as the mesonotum (ratio 0.9), the intersegmental membrane between tergites 3 and 4 slightly curved caudad (Fig. 4), and setae dorsally on the dorsal laterotergites long (Fig. 4).

Description Female: total length 3.37 mm, total length: greatest abdominal width 1.9; wing condition and general vestiture as in generic description. *Coloration:* uniformly yellowish brown to reddish brown. *Structure:* head: about as long as wide in dorsal view, with very small anteocular area, glabrous area on vertex indistinct, longitudinal sulcus or pit indistinct, tuft distinct, lateral fringes longer laterally than around posterior half of head. Antenna: scape length: head length 0.7, moderately slender. Labium: first visible segment: head length 0.8. Thorax: transverse suture between pronotum and mesonotum distinct, pronotal disk slightly raised and transversally elongate, pronotum about as long as mesonotum (ratio 0.9), greatest pronotal width: pronotal length 1.4. Legs: foretrochanter without ventral process, forefemur length: body length 0.3, forefemur fairly slender. Abdomen: slightly longer than wide, length: width 1.2, intersegmental membrane between tergites 3 and 4 slightly curved caudad, intersegmental membrane between tergites 6 and 7 distinctly curved anteriorly, intersegmental membrane between tergites 7 and 8 slightly curved, mediotergites 1/2 and 3 glabrous, setae on lateral margin of dorsal laterotergites long, setae dorsally on dorsal laterotergites long. *Genitalia:* as in generic description.

Male: unknown.

Etymology: named for the holotype locality of the holotype, Rubeho Mts. in Tanzania.

Material examined: holotype: Tanzania Rubeho Mts. at Ipondelo Vil., 6.83056° S, 36.56889° E, 1993 m, 20 Dec. 2011, V. Grebennikov, 1;female (00020650) (CNC).

Notes This species was recovered as sister species to *X. uluguru*, from which it differs by the larger body size and other character given in the key and diagnosis.

Xenocaucus schoutedeni Villiers.

Figures 4, 5, 6, 7, and 10.

Diagnosis Female: recognized by the medium-sized body length (~2.7 mm), the head with setal fringes of similar length laterally and posteriorly (Fig. 4), the raised, heart-shaped

pronotal disk, the pronotum distinctly longer than the mesonotum (Fig. 4; ratio 1.9), the intersegmental membrane between tergites 7 and 8 curved (Fig. 4), and the mediotergites 1/2 and 3 with a tuft of setae (Fig. 4).

Re-description Female: total length 2.75 mm (according to Villiers 1960) (2.68 mm; specimens measured here), total length: greatest abdominal width 2.1; wing condition and general vestiture as in generic description. *Coloration:* uniformly yellowish brown to reddish brown. *Structure:* head: about as long as wide in dorsal view, with very small anteocular area, glabrous area on vertex circular, longitudinal sulcus extending about 1/2 of glabrous area, tuft absent, lateral fringes of similar length around posterior half of head. Antenna: scape length: head length 1.4, moderately slender. Labium: first visible segment: head length 0.7. Thorax: transverse suture between pronotum and mesonotum distinct, pronotal disk raised, lobed, and heart-shaped, pronotum distinctly longer than mesonotum (ratio 1.9), ratio of greatest pronotal width : pronotal length 1.2. Legs: foretrochanter without ventral process, forefemur length: body length 0.2, forefemur fairly stout. Abdomen: slightly longer than wide, length: width 1.3, intersegmental membrane between tergites 3 and 4 straight, intersegmental membrane between tergites 6 and 7 slightly curved anteriorly, intersegmental membrane between tergites 7 and 8 curved, mediotergites 1/2 and 3 with tuft of setae, setae on lateral margin of dorsal laterotergites short, setae dorsally on dorsal laterotergites short. *Genitalia:* as in generic description.

Male: unknown.

Immatures: as in Fig. 4.

Material examined: holotype: Tanzania Bunduki, Uluguru Mts., moy Mgeta, 7.03333° S, 37.63333° E, 1300 m, 2 May 1957, Unknown, 1;female (MNHN). Other specimens examined: Tanzania: W. Usambara Mts., Mazumbai Forest, 4.81054° S, 38.49858° E, 1618 m, 11 Jan. 2013, V. Grebennikov, 2;female (00020641, 00020642) (CNC). W. Usambara Mts., Mkusu For., 4.76585° S, 38.36022° E, 1576 m, 14 Jan. 2013, V. Grebennikov, 1;juvenile (00020609) (CNC).

Notes Based on examination and documentation of the holotype of *X. schoutedeni* from the Uluguru Mountains and specimens collected by one of us in the Usambara Mountains (Fig. 4), we assume these specimens to be conspecific. They agree in size and other characters listed in the key and diagnosis. The species re-description is largely based on the fresh specimens from the Usambara Mountains since certain features were difficult to see in the poorly preserved holotype.

Xenocaucus uluguru, n. sp.

Figures 4, 5, 6, and 10.

Diagnosis Female: recognized by the medium size (~2.9 mm), the distinct lateral setal tufts on the head (Figs. 3 and 6), the slightly raised and transversally elongate pronotal disk, the pronotum longer than the mesonotum (Fig. 3; ratio 1.5), the intersegmental membranes between tergites 3 and 4 slightly curved caudad and between segments 7 and 8 straight (Fig. 3), and mediotergites 1/2 and 3 glabrous (Fig. 3).

Description Female: total length 2.95 mm, total length: greatest abdominal width 1.9; wing condition and general vestiture as in generic description. *Coloration:* uniformly yellowish brown to reddish brown. *Structure:* head: about as long as wide in dorsal view, with very small anteocular area, glabrous area on vertex circular, longitudinal sulcus extending about 1/2 of glabrous area, tuft distinct, lateral fringes longer laterally than around posterior half of head. Antenna: scape length: head length ratio 1.5, moderately slender. Labium: first visible segment: head length 0.9. Thorax: transverse suture between pronotum and mesonotum distinct, pronotal disk slightly raised and transversally elongate, pronotum longer than mesonotum (ratio 1.3), greatest pronotal width: pronotal length 1.3. Legs: foretrochanter without ventral process, forefemur length: body length 0.3, forefemur fairly slender. Abdomen: slightly longer than wide, length: width 1.2, intersegmental membrane between tergites 3 and 4 slightly curved caudad, intersegmental membrane between tergites 6 and 7 slightly curved anteriorly, intersegmental membrane between tergites 7 and 8 straight, mediotergites 1/2 and 3 with sparse setae, setae on lateral margin of dorsal laterotergites moderately long, setae dorsally on dorsal laterotergites short. *Genitalia:* as in generic description.

Male: unknown.

Etymology: named for the holotype locality, Uluguru Mts. in Tanzania.

Material examined: holotype: Tanzania Uluguru Mts. at Tchenzema vil., 7.11222° S, 37.60444° E, 2258 m, 13 Nov 2010, V. Grebennikov, 1;female (00117767) (CNC). Other specimens examined: Tanzania: Uluguru Mts. at Tchenzema vil., 7.11222° S, 37.60444° E, 2258 m, 13 Nov. 2010, V. Grebennikov, 1;juvenile (00117763) (CNC).

Notes The molecular phylogeny recovered this species as sister to *X. rubeho*, from which it is clearly separated by the size and other features outlined in the key and diagnosis.

Discovery of male *Xenocaucus*

Together with nine female and four juvenile specimens of an undescribed *Xenocaucus* species, one male tribelocephaline specimen was recovered from one leaf litter sift in the Bale

Mts. in Ethiopia. Molecular data unambiguously grouped the single female specimen that we sequenced with this male (Fig. 1; see Online Resource 1 for 28S rDNA uncorrected pairwise distances), and we here describe this species as *X. ethiopiensis*, n. sp., making it the first species of *Xenocaucus* that is known from both male and female specimens. The female specimens show the typical *Xenocaucus* habitus (i.e., seemingly eyeless, wingless, etc.), but the male is macropterous and has large eyes. The male specimen features bulbous setae, lacks ocelli, has fairly flat eyes and an elongate scape in which the pedicel and the four flagellomeres are folded, and a very reduced corium with the membrane taking up most of the hemelytron, all diagnostic features of Tribelocephalinae (Weirauch et al. 2014). Villiers (1943) classified Tribelocephalinae into the tribes Opisthoplatyini and Tribelocephalini, diagnosed by the presence or absence, respectively, of a m-cu cross vein at what he called the “base of the inner discal cell” (Weirauch et al. 2014). This cross vein is lacking in the male of *X. ethiopiensis*, providing an argument for its inclusion in the tribe Tribelocephalini as currently recognized. However, we refrain from synonymizing the two tribes because a comprehensive combined morphological and molecular phylogeny of Ectrichodiinae and Tribelocephalinae is in preparation that will propose a new classification for the entire clade (Forthman and Weirauch, unpublished data).

Phylogeny

The monophyly of *Xenocaucus* is supported with 100% bootstrap support (BS) in the best ML tree (Fig. 1). Tribelocephalini are represented by two species each of *Tribelocephala* and *Abelocephala*, with *Tribelocephala* recovered as sister to *Opisthoplatys* (three species) and *Abelocephala* as sister to *Xenocaucus* (91% BS), rendering Tribelocephalini paraphyletic with respect to Opisthoplatyini and Xenocaucini. Within *Xenocaucus*, *X. ethiopiensis* (represented by one female paratype and the male holotype) is the sister taxon to a clade that comprises the six described *Xenocaucus* species from the EAM and Mt. Hanang that we refer to as the Tanzanian clade. *Xenocaucus rubeho* and *X. uluguru* are represented by single specimens, recovered as sister species (85% BS), and form the sister group to the remaining Tanzanian *Xenocaucus* species (74% BS). Relationships within that clade are (*X. chomensis* + (*X. kimbozensis* + (*X. schoutedeni* + *X. nguru*))) with BS ranging between 60 and 99% BS.

Divergence dating and biogeography

Xenocaucus is here estimated to have diverged from the Oriental *Abelocephala* around 52 mya (95% HPD 39–67 mya), with *X. ethiopiensis* splitting from the Tanzanian clade that is

restricted to the EAM and Mt. Hanang, around 39 mya (95% HPD 27–52 mya; Fig. 2; see Online Resources 2 for dates with 95% HPD bars). Based on our sampling that does not include the West African *X. mancinii* and may be incomplete for the East African lineages, diversification within the Tanzanian clade started around 15 mya and all species recognized by us diverged between 12 and 8 mya. Two species represented in the molecular dataset have been collected from more than one mountain region or forest fragment, *X. kimbozensis* (samples from lowland Kimboza and North Pare; about 350 km apart) and *X. nguru* (samples from Nguru and Mt. Hanang; about 400 km apart). In both cases, the intraspecific divergence between different mountain blocks or forest fragments is estimated to be very young (i.e., less than 1 mya). This result is somewhat puzzling, assuming that the apterous and leaf-litter dwelling females of *Xenocaucus* are poor active dispersers. More comprehensive geographic and genetic sampling is now required to further test our findings.

Biogeographic reconstructions using either mountain blocks or broader regions as areas of endemism and employing different algorithms in BioGeoBEARS (BAYAREALIKE, DEC, DIVALIKE; both with and without *j*) and RASP DIVA resulted in a range of scenarios for areas occupied by the respective most recent common ancestors (MRCA). The following comparison between analyses focuses on the reconstructed ancestral areas for the MRCA of East African *Xenocaucus*, the Tanzanian clade, and the ancestor of *X. schoutedeni* + *X. nguru* that represents the youngest species-level divergence in our dataset (Fig. 2; see also Online Resources 3). When using mountain blocks (combined with the lowland forest fragment of Kimboza in the case of Uluguru) as areas of endemism, AIC and AICc values indicate that BAYAREALIKE+J is the best model compare to all other models. The most likely ancestral area for the MRCA of East African *Xenocaucus* is reconstructed as Ethiopia/Uluguru/Usambara, for the Tanzanian clade as Uluguru, and of *X. schoutedeni* + *X. nguru* as Uluguru/Usambara. BAYAREALIKE+J is also the best-fitting model in the analysis using four larger regions as areas of endemism, i.e. Ethiopia, the northern EAM ranges (North Pare, South Pare, Usambara), the central ranges and Mt. Hanang (Hanang, Kimboza, Uluguru, Nguru), and the southern range represented by Rubeho. Ethiopia was reconstructed as the ancestral range for the East African *Xenocaucus*, and the central ranges are the ancestral areas for both the Tanzanian clade and *X. schoutedeni* + *X. nguru*. The RASP DIVA analyses (also separated into analyses using regions and mountain blocks as areas of endemism) are similar in treating Ethiopia, Rubeho, Uluguru, and South Pare (mountains) or all of East African (regions) as ancestral area for the East African *Xenocaucus*; Rubeho, Uluguru, and South Pare (mountains) and EAM plus Mt. Hanang (regions) for the Tanzanian clade; and Uluguru, Hanang, Nguru (mountains) and Hanang, Kimboza, Uluguru, Nguru (regions) for *X. schoutedeni* + *X. nguru*.

Discussion

Xenocaucus is well supported as a clade, as are several of the species-level relationships within the genus. *Xenocaucus ethiopiensis* that is currently only known from the Bale Mts. in Ethiopia is recovered as the sister to all remaining described species of *Xenocaucus* except *X. mancinii* for which sequence data remain unavailable. The holotype of *X. mancinii* is in poor condition, was not measured by us, and ventral and lateral morphological features were not examined, making it difficult to speculate on its putative phylogenetic position. It shares the relatively large size with *X. ethiopiensis*, *X. rubeho*, and *X. chomensis*, three species that diverged relatively early and the large size may therefore be a plesiomorphic feature given it is also seen in *Abelocephala* spp. Based on divergence dates between the Ethiopian species and the Tanzanian clade (39 mya) and patterns of arid and wet climates (break up of pan-African tropical rain forest started between 35 to 30 mya), *X. mancinii* could either be the sister species to the entire East African clade, or sister to the Tanzanian clade, especially if there were indeed multiple fragmentation and reconnection events as postulated by Couvreur et al. (2008). Leaf litter sifting in West African forest could not only reveal DNA-quality specimens of *X. mancinii*, but also has the potential to discover as yet undescribed species.

Lineage divergences coincided with times of both wet and arid climates: the divergence of *Xenocaucus* from the Oriental *Abelocephala* (52 mya) has likely occurred during a period characterized by an unbroken pan-African rainforest extending across Africa, while the split between *X. ethiopiensis* and the Tanzanian clade falls during the later part of this period (39 mya), but likely before increased aridification started to impact East Africa between 23.0–33.9 mya. Our analyses suggest that lineage diversification within the Tanzanian clade started around 15 mya and therefore at the end of the wet and warm Miocene climatic optimum (15–18 mya). All species of *Xenocaucus* restricted to the EAM and Mt. Hanang diverged from their sister species between 12 and 8 mya, during a time characterized by aridification and forest fragmentation. Cycles of relatively brief periods of wet and arid climates occurred in the Pliocene and one of these recent wet periods may explain the young (i.e., less than 1 mya) intraspecific divergences of *X. kimbozensis* from lowland Kimboza and North Pare and *X. nguru* from Nguru and Mt. Hanang. The fairly old diversification ages that we here report for *Xenocaucus* are consistent with the hypothesis of a pre-Pleistocene origin of many lineages that are endemic to East African rainforest, e.g., the African violet genus *Saintpaulia*, where species-level divergences date to in-between 22 and 5 mya (Dimitrov et al. 2012). *Xenocaucus* resembles that plant genus in comprising a mixture of species with distributions that appear to be restricted to one mountain block and species that have broader distribution ranges, a pattern that is in contrast to the well-defined northern and southern clades observed in

certain bird and amphibian species (Beresford et al. 2004; Blackburn and Measey 2009; Bowie et al. 2004). Roy (1997) found that in a genus of forest dwelling birds, some of which are strictly montane, some widespread lowland species, the strictly montane species form a clade. This pattern is not found either in our dataset, where *X. kimbozensis* the single species that has so far also been collected at low elevations (217 m) is nested among a clade of species that seem to be restricted to mid- to high-elevation forest (900 to 2000 m). Additional sampling efforts across the EAM and more in depth molecular analyses have the potential to test and further reveal the evolutionary history of *Xenocaucus* and to contribute to our understanding of how biodiversity was shaped in this biodiversity hotspot.

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