Organisms Diversity & Evolution (2021) 21:245–278
https://doi.org/10.1007/s13127-021-00481-4

ORIGINAL ARTICLE

A phylogenetic and taxonomic assessment of Afrotropical Micracidini (Coleoptera, Scolytinae) reveals a strong diversifying role for Madagascar

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Received: 12 June 2020 / Accepted: 3 January 2021 / Published online: 10 February 2021

Abstract

Afrotropical bark beetle genera in the tribe Micracidini are revised and an identification key provided. The new classification is based on phylogenetic analyses of five molecular markers (COI, EF-1α, 28S, PABP1, CAD) in combination with morphological characters. Five new genera are erected and one genus synonymized, resulting in a total of 11 valid genera: *Lanurgus* Eggers, 1920, *Traglostus* Schedl, 1938, *Pseudomicracis* Eggers, 1920 (=*Saurotocis* Wood, 1984 **syn. nov.**), *Phloeocurus* Wood, 1984, *Afromicracis* Schedl, 1959, *Dendrochilus* Schedl, 1959, *Neomicracis* Jordal **gen. nov.**, *Leiomicracis* Jordal **gen. nov.**, *Diplotrichus* Jordal **gen. nov.**, *Pseudolanurgus* Jordal **gen. nov.**, *Microlanurgus* Jordal **gen. nov.** The following new species are described to be included in the new genera: *Leiomicracis aurea* Jordal **sp. nov.**, *Neomicracis squamigera* Jordal **sp. nov.**, both from Tanzania, and *Microlanurgus bicolor* Jordal **sp. nov.** and *Microlanurgus ater* Jordal **sp. nov.**, from Madagascar. The following new synonyms and new combinations are proposed: *Afromicracis dubius* (Schedl, 1950) (=*Afromicracis angolensis* Schedl, 1962 **syn. nov.**), *Afromicacis elongatulus* (Schedl, 1977) **comb. nov.,** *Afromicracis jasminiae* (Schedl 1957) **comb. nov.** (=*Dendrochilus mikaniae* Schedl 1957 **syn. nov.**), *Afromicracis robustus* (Schedl 1957) **comb. nov.** (=*Dendrochilus arundinarius* Schedl 1957 **syn. nov.**, =*Hypothenemus bambusae* Browne, 1970 **syn. nov.**, =*Dendrochilus filum* Schedl, 1977 **syn. nov.**) (all from *Dendrochilus*), *Afromicracis setifer* (Schedl 1957) **comb. nov.** (*Mimiocurus*), *Lanurgus longipilis* (Schedl, 1958) **comb. nov.**, *Lanurgus pubescens* (Schedl, 1961) **comb. nov.** (both from *Traglostus*), *Diplotrichus catenatus* (Schedl, 1953) **comb. nov.,** *Diplotrichus elongatus* (Schedl, 1950) **comb. nov.,** *Diplotrichus euphorbia* (Schedl, 1961) **comb. nov.,** *Diplotrichus gracilis* (Schedl, 1958) **comb. nov.,** *Diplotrichus minor* (Schedl, 1950) **comb. nov** (=*Lanurgus frontalis* Schedl, 1953 **syn. Nov.**), *Diplotrichus obesus* (Schedl, 1953) **comb. nov.**, *Diplotrichus pygmaeus* (Schedl, 1965) **comb. nov.**, *Diplotrichus rugosipes* (Schedl, 1961) **comb. nov.**, *Diplotrichus subdepressus* (Schedl, 1965) **comb. nov.**, *Diplotrichus widdringtoniae* (Schedl, 1962) **comb. nov.** (all from *Lanurgus*), *Diplotrichus ignotus* (Schedl, 1965) **comb. nov.** (*Pseudomicracis*), *Pseudolanurgus harunganae* (Schedl, 1961) **comb. nov.** (=*Lanurgus cribrellus* Schedl, 1965 **syn. nov.**), *Pseudolanurgus bugekeae* (Schedl, 1957) **comb. nov.** (both from *Pseudomicracis*), *Pseudolanurgus minutissimus* (Schedl, 1961) **comb. nov.** (*Lanurgus*), *Pseudomicracis dispar* (Schedl, 1961) **comb. nov.**, *Pseudomicracis tomicoides* (Schedl, 1961) **comb. nov.** (both from *Saurotocis*). The following taxa were transferred to genera in other tribes: *Acanthotomicus intermedius* (Schedl, 1977) **comb. nov.**, *Xylocleptes villiersi* (Lepesme, 1942) **comb. nov.** (both from *Dendrochilus*); *Eidophelus agnathus* (Schedl, 1942) **comb. nov.**, and *Eidophelus ciliatipennis* (Schedl, 1979) **comb. nov.** (all from *Miocryphalus*). The following five species were included in *Karlsenius* **gen. nov.** (Trypophloeini): *Karlsenius klainedoxae* (Schedl, 1957) **comb. nov.**, *Karlsenius nitidum* (Schedl, 1965) **comb. nov.**, *Karlsenius nigrinum* (Schedl, 1957) **comb. nov.**, and *Karlsenius attenuatus* (Eggers, 1935) **comb. nov.** (from *Miocryphalus*), and *Karlsenius ghanaensis* (Schedl, 1977) **comb. nov.** (from *Eidophelus*). A time-tree and biogeographical analysis suggested that Madagascar was colonized only once in Micracidini, from East Africa soon after the origin of the tribe in late Cretaceous. Multiple re-colonisations from Madagascar to the mainland have contributed to further diversification of a tribe which is otherwise highly restricted in geographical distribution.

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Keywords Afrotropical · Bark beetles · Biogeography · Madagascar · Micracidini · Molecular phylogeny · Scolytinae · Taxonomy

Introduction

Most bark beetles that live in dry, old twigs and branches are of little economic importance. Hiding away in their largely cryptic or forgotten habitats, these beetles are often overlooked in field collections. The diversity of tiny dry-adapted bark beetles is nevertheless high and numerous species have been described from these kinds of habitats, often based just on a single or a few collecting events. In Africa and Madagascar such habitats are typically occupied by species in the genera *Hypothenemus* Westwood and *Afrocosmoderes* Johnson and Jordal (Trypophloeini), *Glostatus* Schedl (Xyloctonini), and several genera in the tribe Micracidini. The taxonomy of tiny and obscure beetles is often in flux, or largely ignored, as one may find it difficult to diagnose species properly. This is mainly the case for Micracidini where recent phylogenetic work has pointed towards many errors in the classification, particularly in the Afrotropical fauna (Jordal and Kaidel 2017).

Members of Micracidini are found in the Neotropics and southern parts of the Nearctic, and in the Afrotropical region, including Madagascar. More than 160 species have been described from the first two regions, whereas Africa and Madagascar are much less explored with fewer species known. The Afrotropics is nevertheless expected to have a similar diversity of species if given more taxonomic attention. Such inventories are accumulating, but the circumscription of meaningful genera has been a challenge. Micracidini included previously 13 genera globally (Wood 1986), with recent additions of two new Neotropical genera (Bright 2010, 2019) and inclusion of two genera from other tribes (Jordal and Kaidel 2017). Five additional new genera are here defined by molecular and morphological characters, and one genus is synonymized, with a new total of 21 genera (Table 1).

The biology of many species in Micracidini is unusual and deviates from the more typical bark beetles in several aspects. They are often bigamous where two females pair up with a colonizing male. This is a rare mating system in nature; in bark beetles, it seems more common to establish harem polygamy if more than one female should be accepted (Kirkendall 1983; Kirkendall et al. 2015). Females in this tribe are often gracefully ornamented, with long golden setae in the forehead and on the antennal scapus which is often enlarged or extended into a spine (Fig. 1). They use these structures in tactile communication with the male to gain access to a tunnel entrance in the bark. After mating, the two females extend the engravings of two independent tunnels where they deposit eggs in individual egg niches. Secondary sexual characters in the head region are species specific and provide the most useful characters to distinguish closely related species. Males in some genera can be more elaborated on the elytral declivity, with tubercles and mucronate elytral apices. In *Cactopinus,* and occasional other micracidine species, the male rather than the female has a concave frons, with horn-like projections (Atkinson 2010; Jordal and Kaidel 2017).

Taxonomists have focussed mainly on sexually evolving characters as a mean to define species. As a potential consequence, the classification at higher taxonomic levels became poorly developed. There are now obvious mixtures of species in each genus that belong to different genera in Micracidini (Jordal and Kaidel 2017) or even from other tribes (Johnson et al. 2020). Taxonomic inconsistencies were likely fostered by a general lack of diagnostic characters at the genus level. These problems are perhaps connected to a very ancient origin of Micracidini, which is considered the oldest monophyletic tribe in Scolytinae (Jordal and Cognato 2012; Pistone et al. 2018; Jordal and Kaidel 2017).

Molecular data from five genes are included in this study to provide a robust phylogeny which enable assessment of morphological consistency in groups of similar evolutionary age. New diagnostic features are supported by phylogenetic analyses and incorporated in a new identification key to genera which will improve accurate identification. Molecular data also allow for testing biogeographical scenarios—more specifically the role of Madagascar in the diversification of Afrotropical micracidines. Are species in Madagascar monophyletic with respect to the mainland, with few, or even a single, very ancient origin? If not, are Malagasy taxa paraphyletic, and of more recent origin, with adventive African lineages on the island? Alternatively, multiple recolonizations of the mainland could have happened, which is more in accordance with historical geophysical conditions (Ali and Huber 2010).

Methods

Samples

Type material of the type species for each genus was examined in museum collections in Vienna (NHMW), Tervuren (RMCA), and Paris (MNHN). In the preparation of revisions of the Afrotropical genera, the main types for each species have been studied (holotype, holotype with allotype and/or paratypes, or Egger's 'type', except *Miocryphalus ciliatipennis* Schedl, 1979). Fresh material useful for DNA analyses (Table 2) was

Table 1 Classification of Micracidini genera

Wood 1986; Bright 2010, 2019	Current study; Jordal and Kaidel (2017)
Neotropical	
	Cactopinus Schwarz, 1899
Micracis LeConte, 1868	*Micracis* LeConte, 1868
Micrasicella Blackman, 1928	*Micrasicella* Blackman, 1928
Hylocurus Eichhoff, 1872	*Hylocurus* Eichhoff, 1872
Phloeocleptus Wood, 1956	*Phloeocleptus* Wood, 1956
Stenoclyptus Blackman, 1943	*Stenoclyptus* Blackman, 1943
Thysanoes LeConte, 1876	*Thysanoes* LeConte, 1876
Pseudothysanoes Blackman, 1920	*Pseudothysanoes* Blackman, 1920
Stevewoodia Bright, 2010	*Stevewoodia* Bright, 2010
Parathysanoes Bright, 2019	*Parathysanoes* Bright, 2019
Afrotropical	
Lanurgus Eggers, 1920	*Lanurgus* Eggers, 1920
Traglostus Schedl, 1938	*Traglostus* Schedl, 1938
Pseudomicracis Eggers, 1920	*Pseudomicracis* Eggers, 1920
Saurotocis Wood, 1984	–
Phloeocurus Wood, 1984,	*Phloeocurus* Wood, 1984,
Afromicracis Schedl, 1959	*Afromicracis* Schedl, 1959
	Dendrochilus Schedl 1957
	Neomicracis Jordal, **gen. nov.**
	Leiomicracis Jordal, **gen. nov.**
	Diplotrichus Jordal, **gen. nov.**
	Pseudolanurgus Jordal, **gen. nov.**
	Microlanurgus Jordal, **gen. nov.**

collected in several African countries between 1998 and 2015, after obtaining the necessary collecting and export permits as required at the time of field work.

Molecular data

Sequence data were obtained from five genes: Cytochrome Oxidase I (COI, 690 bp), Elongation Factor 1a (EF-1a, 822 bp), Carbamoyl-phosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase (CAD, 458 bp), Poly-A binding protein 1 (PABP1, 435 bp), and the large ribosomal subunit (28S, 720 aligned nucleotide positions). DNA extraction, PCR and sequencing followed Mugu et al. (2018). The ribosomal alignment was made in Muscle (Edgar 2004) given default settings and a portion of ambiguous alignment sites were pruned in GBlock (Castresana 2000) using the most liberal settings possible (allow smaller blocks, allow gaps, allow less strict flanking regions, allow contiguous non-conserved positions). GenBank accession numbers are listed in Table 2.

Morphological analyses

Morphology was studied in a Leica MZ16 stereoscope and photographs made in a Leica 205 C stereoscope with a Leica camera. Multiple photos were stacked and aligned in ZereneStacker. Internal structures were dissected from macerated specimens (Proteinase K, or KOH 8%) and mounted on slides in Euparal. Thirty-six morphological characters were selected for phylogenetic analysis, including flight wings, proventriculus, and male genitalia (Table 3; Figs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 15, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44).

Phylogenetic and biogeographical analyses

Nucleotide sequences from all five genes were concatenated and analysed in combination with the 36 morphological characters in MrBayes v 3.2.6 (Ronquist and Huelsenbeck 2003). Best models for each gene partition were selected in MrModelTest (Nylander 2004). Models for morphological characters were given a gamma-distribution based on empirical character variation. Stationarity in likelihoods was visualized in Tracer (Rambaut et al. 2014) and was reached before 3 million generations set as burn-in.

Approximate age for clades were estimated in Beast 1.10.4, with the xml file prepared in Beauti (Drummond and Rambaut 2007). Rates were calibrated with time estimates from a

Table 2 Sequence ID vouchers and their GenBank accession numbers

Voucher	Tribe	Species	Country	Locality	Leg.	CO1	EF-1a	28S	CAD	PABP1
IpIps03	Ipini	Ips duplicatus	Estonia	Mooste, Põlva	K. Voolma	JX263834	JX264122	JX263733	JX264050	–
XyPre01	Ipini	*Premnobius cavipennis*	South Africa	E. Cape Prov, Grahamstown	T. Ekrem	HQ883694	HQ883762	HQ883605	HQ883839	MF771718
MiMio02	Micracidini	Afromicracis congonus	Cameroon	Limbe, Ekonjo	B. Jordal	JX263839	–	JX263738	JX264053	–
IpDen01	Micracidini	Afromicracis robustus	Tanzania	Udzungwa NP	B. Jordal	KX100006	KY805874	KY805981	KX099993	MF771663
IpDen02	Micracidini	Afromicracis setifer	Tanzania	Uluguru Mts	V. Grebennikov	KX100007	KY805875	KX099970	KX099994	MF771664
MiMio07	Micracidini	Afromicracis sp. C	Tanzania	Udzungwa NP	B. Jordal	MW192035	–	MW192262	MW192678	MW192715
MiMio04	Micracidini	Afromicracis sp. G	Uganda	Kibale Forest, S. Fort Portal	B. Jordal	MW192033	–	MW192260	MW192676	MW192713
MiMio03	Micracidini	Afromicracis sp. H	Cameroon	Mt. Cameroon, Mann Spring	B. Jordal	JX263840	–	JX263739	JX264054	–
MiMio12	Micracidini	Afromicracis sp. I	South Africa	West Cape, Wildrness	B. Jordal	MW192039	MW192742	MW192266	MW192682	MW192719
MiMio01	Micracidini	Afromicracis sp. J	South Africa	East Cape, Hogsback	B. Jordal	JX263838	–	JX263737	–	–
MiMio05	Micracidini	Afromicracis sp. K	Tanzania	Udzungwa NP	B. Jordal	MW192034	MW192740	MW192261	MW192677	MW192714
CaCac03	Micracidini	Cactopinus nasutus	Mexico		T. Atkinson	–	–	KY805961	–	–
CaCac02	Micracidini	Cactopinus rhettbutleri	Mexico		T. Atkinson	KY805886	KY805858	KY805960	KX099992	–
CaCac01	Micracidini	*Cactopinus rhois*	USA, CA	Riverside Co., San Bernadino NF	A. Cognato	JX263783	JX264075	EU090343	–	–
MiMio10	Micracidini	Dendrochilus sp. A	Tanzania	Udzungwa NP	B. Jordal	MW192037	–	MW192264	MW192680	MW192717
MiMio08	Micracidini	Dendrochilus sp. E	Tanzania	Udzungwa NP	B. Jordal	MW192036	–	MW192263	MW192679	MW192716
MiLan16	Micracidini	Diplotrichus catenatus	Madagascar	Ankarafantsika NP	B. Fischer	MW192026	–	MW192253	MW192669	MW192706
MiLan19	Micracidini	Diplotrichus elongatus	Madagascar	Ankarafantsika NP	B. Jordal	MW192031	MW192738	MW192258	MW192674	MW192711
MiLan20	Micracidini	Diplotrichus elongatus	Madagascar	Ankarafantsika NP	B. Jordal	MW192032	MW192739	MW192259	MW192675	MW192712
MiLan06	Micracidini	Diplotrichus gracilis	South Africa	West Cape, 5 km N. Hoekville	B. Jordal	MW192016	MW192731	MW192243	MW192660	MW192696
MiLan18_1	Micracidini	Diplotrichus minor	Madagascar	Ankarafantsika NP	B. Jordal	MW192029	MW192736	MW192256	MW192672	MW192709
MiLan18_2	Micracidini	Diplotrichus minor	Madagascar	Ankarafantsika NP	B. Jordal	MW192030	MW192737	MW192257	MW192673	MW192710
MiLan17_1	Micracidini	Diplotrichus sp. 1	Madagascar	Ankarafantsika NP	B. Jordal	MW192027	MW192735	MW192254	MW192670	MW192707
MiLan17_2	Micracidini	Diplotrichus sp. 2	Madagascar	Ankarafantsika NP	B. Jordal	MW192028	–	MW192255	MW192671	MW192708
MiLan09	Micracidini	Diplotrichus sp. E	South Africa	West Cape, Knysna, Goudeveld	B. Jordal	MW192019	MW192733	MW192246	MW192663	MW192699
MiLan10	Micracidini	Diplotrichus sp. E	South Africa	East Cape, Tsitsikamma, Ratel walk	B. Jordal	MW192020	–	MW192247	MW192664	MW192700
MiLan02_2	Micracidini	Diplotrichus sp. G	South Africa	East Cape, Hogsback	B. Jordal	MW192012	–	MW192239	MW192657	MW192692
MiLan02	Micracidini	Diplotrichus sp. K	South Africa	West Cape, Nature's Valley	B. Jordal	JX263837	JX264125	–	–	–
MiLan11	Micracidini	Diplotrichus sp. K	South Africa	East Cape, Tsitsikamma, Platboos walk	B. Jordal	MW192021	–	MW192248	MW192665	MW192701
MiHyl01	Micracidini	*Hylocurus femineus*	USA	AZ, Madera Canyon, S. Tucson	B. Jordal	AF187108	AF186678	JX263736	JX264052	–

Table 2 (continued)

Voucher	Tribe	Species	Country	Locality	Leg.	CO1	EF-1a	28S	CAD	PABP1
MiHyl02	Micracidini	Hylocurus longstoni	USA		B. Jordal	KY805905	KY805876	KY805982	KX099995	MF771667
MiLan07	Micracidini	Lanurgus podocarpi	South Africa	East Cape, Bloukrans, Rugbos Forest	B. Jordal	MW192017	MW192732	MW192244	MW192661	MW192697
MiLan04	Micracidini	Lanurgus rhusi	South Africa	West Cape, Nature's Valley	B. Jordal	MW192013	MW192729	MW192240	–	MW192693
MiLan05	Micracidini	Lanurgus sp. SA3	South Africa	East Cape, Tsitsikamma, Ratel walk	B. Jordal	MW192014	MW192730	MW192241	MW192658	MW192694
MiLan05_2	Micracidini	Lanurgus sp. SA3	South Africa	West Cape, Knysna, Goudeveld	B. Jordal	MW192015	–	MW192242	MW192659	MW192695
MiLan08	Micracidini	Lanurgus sp. B	South Africa	East Cape, Stutterheim, Kologha forest	B. Jordal	MW192018	–	MW192245	MW192662	MW192698
MiLan12	Micracidini	Lanurgus sp. L	South Africa	East Cape, Tsitsikamma, Platboos walk	B. Jordal	MW192022	–	MW192249	MW192666	MW192702
MiLan13	Micracidini	Lanurgus subsulcatus	South Africa	East Cape, Alexandria forest	B. Jordal	MW192023	–	MW192250	MW192667	MW192703
MiTra01	Micracidini	Lanurgus subsulcatus	South Africa	West Cape, Nature's Valley	B. Jordal	JX263842	JX264127	JX263741	JX264055	–
MiLan01	Micracidini	Lanurgus xylographus	South Africa	East Cape, Stutterheim, Kologha forest	B. Jordal	EU191855	EU191887	KY805983	KY805930	MF771668
MiLan01_2	Micracidini	Lanurgus xylographus	South Africa	East Cape, Bloukrans, Rugbos Forest	B. Jordal	MW192011	–	MW192238	MW192656	MW192691
MiMio11	Micracidini	Leiomicracis aurea	Tanzania	Udzungwa NP	B. Jordal	MW192038	MW192741	MW192265	MW192681	MW192718
MiMic01	Micracidini	*Micracis carinulatus*	USA	AZ, Herb Martyr, S. Tucson	B. Jordal	AF187107	AF186677	AF375303	–	–
MiMic02	Micracidini	*Micracis swainei*	USA	Massachusetts	B. Jordal	KX100010	–	KY805984	KX099998	MF771669
MiMis01	Micracidini	Micracisella nanula	USA	Arizona	B. Jordal	KX100013	KY805878	KY805986	KX100001	–
CrEcl02	Micracidini	Microlanurgus ater	Madagascar	Mahafaly Plateau, 6.2 km 74° ENE Itampolo	Fischer et al	JX263799	JX264090	JX263692	–	MF771613
CrCh?04	Micracidini	Microlanurgus bicolor	Madagascar	Parc National de Tsimanampetsotsa, 21 km E Efoetse	Fischer et al	JX263793	JX264086	JX263686	–	MF771607
MiMio09	Micracidini	Neomicracis squamigera	Tanzania	Udzungwa NP	B. Jordal	KX100011	KY805877	KY805985	KX099999	–
MiPhl01	Micracidini	Phloeocleptus cristatus	Mexico		B. Jordal	KX100014	KY805879	KY805987	KX100002	MF771670
MiLan15	Micracidini	Pseudolanurgus harunganae	Madagascar	Ranomafana NP	B. Jordal	MW192025	MW192734	MW192252	–	MW192705
MiLan14	Micracidini	Pseudolanurgus sp. O	Tanzania	Udzungwa NP	B. Jordal	MW192024	–	MW192251	MW192668	MW192704
MiPsd05_1	Micracidini	Pseudomicracis dispar	Madagascar	Ranomafana NP	B. Jordal	–	MW192745	MW192271	MW192686	MW192723
MiPsd05_2	Micracidini	Pseudomicracis dispar	Madagascar	Ranomafana NP	B. Jordal	MW192041	–	MW192272	MW192687	MW192724
MiPsd02	Micracidini	Pseudomicracis sp. A	Madagascar	Ranomafana NP	B. Jordal	MW192040	–	MW192267	–	–
MiPsd03	Micracidini	Pseudomicracis sp. B	Madagascar	Ranomafana NP	B. Jordal	–	MW192743	MW192268	MW192683	MW192720
MiPsd04_1	Micracidini	Pseudomicracis sp. C	Madagascar	Ranomafana NP	B. Jordal	–	MW192744	MW192269	MW192684	MW192721
MiPsd04_2	Micracidini	Pseudomicracis sp. C	Madagascar	Ranomafana NP	D. Pistone	–	–	MW192270	MW192685	MW192722
MiPsd06_1	Micracidini	Pseudomicracis sp. E	Madagascar	Ranomafana NP	B. Jordal	MW192042	MW192746	MW192273	MW192688	MW192725
MiPsd06_2	Micracidini	Pseudomicracis sp. E	Madagascar	Ranomafana NP	B. Jordal	MW192043	–	MW192274	MW192689	MW192726
MiPsd07	Micracidini	Pseudomicracis sp. H	Madagascar	Ranomafana NP	B. Jordal	MW192044	MW192747	MW192275	–	MW192727

Table 2 (continued)

Voucher	Tribe	Species	Country	Locality	Leg.	CO1	EF-1a	28S	CAD	PABP1
MiPst01	Micracidini	*Pseudothysanoes leechi*	USA	California, Hastings Reserve	L. Kirkendall	JX263841	JX264126	JX263740	–	–
MiPst03	Micracidini	Pseudothysanoes yuccae	USA		B. Jordal	KX100017	KY805880	KX099981	–	MF771671
MiSte01	Micracidini	Stenoclyptus sulcatus	Mexico		T. Atkinson	MW192045	–	MW192276	MW192690	MW192728
MiThy01	Micracidini	*Thysanoes fimbricornis*	USA		B. Jordal	KX100018	KY805881	KY805988	KX100005	MF771672

previous analysis of Scolytinae based on 18 genes (Pistone et al. 2018) and therefore given a normal distribution with 5 standard deviations to accommodate for uncertainties in these estimates. Nodes matching the previous published phylogeny included the root which combined taxa from Ipini, Hypoborini and Micracidini at 88 Ma, Micracidini without *Leiomicracis* at 79 Ma, and the Neotropical clade at 65 Ma.

Biogeographical scenarios were tested using model selection in RASP (Yu et al. 2020) using the time tree estimated in the Beast analysis. Areas in Africa were defined using biogeographical regions proposed by Linder et al. (2012): Southern African, Zambesian (eastern Africa), and Congolian (western Africa) regions, in addition to Madagascar and the Neotropical/Nearctic regions. The best model was selected among DEC, DIVAlike and BayArea using BioGeoBEARS, with or without the extra parameter for jump dispersal (+j). Because of the uncertain foundation for testing +j models (Ree and Sanmartín 2018), it was presumed that jump dispersal was more realistically involved in overseas splits, while vicariance motivated models can be more relevant in the inference of widespread taxa on the African mainland. Analyses with or without jump dispersal integrated in the model were furthermore compared to a Bayesian Binary MCMC analysis in RASP (Yu et al. 2015), using default parameters.

Results

Phylogeny

Bayesian inference of 3226 nucleotides and 36 morphological characters resulted in a well-resolved tree topology with high posterior probability for most nodes (Fig. 45). The inclusion of morphological characters did not change the tree topology, but increased node support for three nodes. Micracidini were monophyletic, with the Neotropical genera forming the sister group to all but one of the Afrotropical species. The excepted species formed the sister group to all Micracidini and is here described as a new genus, *Leiomicracis*.

The remaining Afrotropical taxa were distributed on two main clades. One was composed mainly by species in *Afromicracis* and its sister group, *Dendrochilus*. These two genera combined were placed as sister to a single species which is here described in the new genus *Neomicracis*. The other main clade included the genera *Lanurgus* and *Pseudomicracis* and three additional lineages described as new genera. One such lineage consisted of two tiny species with spatulate setae on odd-numbered interstriae only. This new genus, *Microlanurgus*, is not closely related to any other taxa (Fig. 45). Some species which are currently placed in *Lanurgus* have bifid setae on the metaventrite (and abdominal ventrites I-II) and all these species formed a lineage described as a new genus, *Diplotrichus*. This

Table 3 Morphological variation and information potential in various character states as performed on the Bayesian tree topology

Head

1. Eye size: 0 long, 1 short, 2 long and sinuate. CI=1.0, RI=1.0. Micracidini is one of very few scolytine groups having a short, almost round eye, but somewhat longer in *Micracis* and *Micrasicella*.
2. Male frons: 0 convex, 1 concave. CI=0.33, RI=0.33. The frons is typically concave in males of all known *Cactopinus* species and in one undescribed species of *Afromicracis* (sp H), in both sexes of *Traglostus*, and in females of many *Lanurgus* and *Diplotrichus*.
3. Female scapus length: 0 longer than funiculus, 1 shorter than funiculus. CI=0.33, RI=0.88. In micracidine genera other than *Afromicracis*, *Dendrochilus*, *Pseudothysanoes*, *Thysanoes* and *Leiomicracis*, the scapus is shorter than the length of the funiculus and often shorter than the male scapus.
4. Female scapus: 0 flat, 1 inflated, 2 spine shaped. CI=0.18, RI=0.76. The dorsal side of the scapus has a normal elongated club-shape in *Cactopinus*, *Hylocurus*, *Afromicracis* and *Dendrochilus*. Females in most genera in Micracidini has a strongly inflated or subtriangular scapus, most extremely expressed as a long spine in *Neomicracis*, one *Diplotrichus*, some *Pseudomicracis*, all *Lanurgus* and *Micracis*.
5. Scapus setae, female: 0 small tuft, 1 broad tuft of short setae, 2 large tuft of long setae. CI=0.25, 0.82. Females in Micracidini has generally long and dense setae on the dorsal side of the scapus. While less developed in *Cactopinus* and *Afromicracis*, the largest tufts of long setae are seen in *Lanurgus*, in most species of *Pseudomicracis*, and in the Malagasy members of *Diplotrichus*.
6. Funiculus segments: 0 six, 1 five, 2 four. CI=0.40, RI=0.80. *Leiomicracis, Dendrochilus*, *Afromicracis* and *Cactopinus* have five segments, all other micracidines have six.
7. Club shape: 0 round, 1 much elongated. CI=1.0, RI=1.0. Among the species included here, only *Dendrochilus* has elongated antennal clubs, otherwise seen in a few species of *Pseudomicracis* (previously *Saurotocis*).
8. Club sutures, anterior face: 0 two transverse, 1 two procurved, 2 two bisinuate, 3 one transverse and one recurved, 4 two partial, 5 first partial and second transverse, 6 terminal only, 7 all pubescent, 8 entirely corneous. CI=0.62, RI=0.76. Most species have two procurved or transverse sutures marked by dense setae. A single suture near apex is typical for *Afromicracis*, two bisinuate sutures define *Pseudolanurgus*, a continuous corneous area over segments 1 and 2 with suture 1 partial defines *Neomicracis*, two slightly recurved sutures define *Microlanurgus*, and a suture-free and shiny club defines *Dendrochilus*.

Pronotum

9. Pronotal asperities on anterior half: 0 present, 1 absent on anterior fifth, 2 few and coarse. CI=1.0, RI=1.0. All except two genera have asperities rather evenly distributed on the anterior half of the pronotum. In *Microlanurgus* the asperities are few and coarse-grained and not fully reaching the front margin, while in *Leiomicracis* the anterior fifth is smooth without any asperities.
10. Pronotal setae: 0 hair-like, 1 bristle-like, 2 scale-like. CI=0.13, RI=0.58. Varies between bristle-like and hairlike within genera. Particularly broad setae are observed in *Neomicracis* and the *Diplotrichus catenatus* species group.

Elytra

11. Interstrial setae: 0 absent, 1 in regular rows, 2 confused, 3 on odd-numbered interstriae only. CI=0.33, RI=0.69. These setae are densely placed and confused at least on the posterior-lateral areas of the elytra, but more often on all interstriae, in *Lanurgus* and a few other species. *Microlanurgus* is unique in the tribe bearing spatulate setae only on odd-numbered interstriae.
12. Interstrial setae, shape: 0 hair-like, 1 bristle-like, 2 spatulate. CI=0.29, RI=0.58. Most genera have mainly spatulate setae, but occasionally hair-like or bristle-like shapes occur in some *Afromicracis* and in several of the Neotropical genera.
13. Strial setae: 0 absent, 1 tiny in rows, 2 broad and confused. CI=0.5, RI=0.86. These setae are broader, almost scale-like or plumose, in *Lanurgus* and a few *Pseudomicracis* males; apparently missing in most *Hylocurus*.
14. Elytral apex: 0 rounded, 1 mucronate, 2 slightly extended flange. CI=0.33, RI=0.73. Typically mucronate in *Micracis*, *Hylocurus*, *Micracisella*, and in *Pseudomicracis*. The apex is somewhat intermediate and bulging in *Pseudolanurgus*, *Neomicracis*, and *Ploeocleptus*, or acuminate in a few *Diplotrichus*.
15. Sutural locking mechanism: 0 simple groove, 1 row of nodules, 2 single large nodule. CI=1.0, RI=1.0. All Micracidini have a row of nodules as opposed to a simple groove in the outgroups chosen.

Abdomen

16. Posterior edge of ventrite 5: 0 rounded, 1 truncated. CI=0.50, RI=0.92. It is truncated or transversely compressed to a variable degree in *Pseudomicracis*, *Pseudolanurgus* and *Dendrochilus*. In the latter it takes the shape of a bottleneck.

Legs

17. Lateral edge of protibia: 0 straight, 1 twisted. CI_0.20, RI=0.60. Most scolytines and some micracidines have their protibia flattened with denticles on its lateral edge. In most micracidines the inner mucro is large and the lateral edge is twisted and rotated posteriorly towards the mucro, but is not twisted in *Hylocurus*, *Micracis*, *Micracisella*, *Cactopinus*, *Thysanoes* and *Phloeocurus*.
18. Protibial denticles: 0 along the edge only, 1 mainly on posterior side. CI=0.25, RI=0.40. Placed along the edge in outgroups, *Cactopinus*, one *Afromicracis*, and at least partly so in *Micracisella*.
19. Protibial transverse denticles: 0 none, 1 one, 2 two, 3 three, 4 four+. CI=0.31, RI=0.70. The number of denticles that deflects from the lateral edge towards the inner mucro varies within the tribe, but nearly all species have at least one. The common state in Afrotropical species is two denticles, with typically three in *Lanurgus* and *Dendrochilus*, and a single denticle in *Leiomicracis*, and one posterior and one lateral in *Microlanurgus*.
20. Protibial groove for reception of tarsus: 0 absent, 1 present. CI=1.0, RI=1.0. A groove is not present in Micracidini or Hypoborini.
21. Metatibial denticle position: 0 both apically and laterally, 1 apically only in transverse row. CI=0.17, RI=0.71. A transverse apical margin with 2–4 denticles is present in *Stenoclyptes* and *Cactopinus rhois*, *Hylocurus*, *Lanurgus*, *Neomicracis*, *Leiomicracis*, and *Dendrochilus*.
22. Metatibial mucro: 0 short, 1 long spur. CI=1.0, RI=1.0. This feature is difficult to define but is typically thinner and longer in all *Afromicracis*, *Dendrochilus* and *Neomicracis*.

Sclerites

23. Setae on metasternum and ventrite I: 0 simple, 1 bifid, 2 plumose. CI=1.0, RI=1.0. The bifid condition is unique to *Diplotrichus* in Micracidini.
24. Pleural suture: 0 zigzag-shaped, 1 straightened. CI=1.0, RI=1.0. The suture is straightened out in many other tribes, but generally zig-zag shaped in all Micracidini.

Hind wings

25. Precostal setae: 0 zero, 1 one, 2 two, 3 three. CI=0.50, RI=0.87. The normal condition in Micracidini is three closely set setae near the junction of subcosta and costa. *Afromicracis*, *Dendrochilus*, *Neomicracis*, and possibly *Microlanurgus*, have only a single seta.
26. Setae on radial cell (pterostigma): 0 none, 1 one, 2 two, 3 three. CI=0.43, RI=0.71. All Micracidini have one, two, or three setae on the apical portion of the radial cell, most commonly two setae, but frequently three setae in Pseudomicracis.

Male aedeagus

27. Apophyses length: 0 1–2 times as long as aedeagal body, 1 extremely elongated, 2 shorter than aedeagal body. CI=0.33, RI=0.80. Shorter than aedeagal body in Thysanoes, no more than twice as long in *Neomicracis*, *Lanurgus*, *Microlanurgus*, *Micracis*, *Hylocurus* and *Micracisella*; extremely elongated in all others.
28. Tegmen: 0 ring, 1 Y-shaped, 2 tube-shaped, 3 absent. CI=1.0, RI=1.0. The normal condition is a closed tegmen forming a ring, with or without a manubrium (median struts). This feature is extremely difficult to assess in many taxa, and is apparently absent in *Diplotrichus*, *Pseudolanurgus* and *Pseudomicracis*; it is prolonged as a tube in *Cactopinus*, *Stenoclyptus* and *Phloeocleptus*, and variably reduced to a small Y-shaped piece in *Dendrochilus* and *Afromicracis*.
29. Manubrium (median struts): 0 absent, 1 no longer than tegmen thickness, 2 several times longer than tegmen thickness. CI=0.4, RI=0.8. For those with a normal tegmen, the manubrium is long and thin in the Neotropical genera, and in *Neomicracis*.

Table 3 (continued)

30. Flagellum: 0 absent, 1 sac-like, 2 long, thin and coiled, 3 extremely enlarged. CI = 0.60, RI = 0.95. The flagellum is unusually long and enlarged in *Pseudomicracis*, *Pseudolanurgus* and *Diplotrichus*, much thinner in *Neomicracis*, *Dendrochilus* and *Afromicracis*, in the latter very long and coiled. In *Micracis*, *Hylocurus* and *Micracisella* the inner sac is inflated, which may or may not be a homologous structure.
31. Spiculum gastrale: 0 simple rod, 1 rod with apical fork, 2 absent. CI = 0.67, RI = 0.97. Missing in *Pseudomicracis*, *Pseudolanurgus* and *Diplotrichus*. The speculum contains an apical fork in all Neotropical genera except *Thysanoes*, and simple rod elsewhere.
Proventriculus
32. Proventriculus with median suture: 0 tight, 1 wide open. CI = 0.20, RI = 0.50. All Micracidini has a longitudinally divided apical plate, but the median suture is occasionally rather narrow as in some *Lanurgus* and *Cactopinus*.
33. Apical plate with: 0 sharp teeth, 1 rows of tubercles, 2 smooth. CI = 0.50, RI = 0.50. In most species the teeth on the apical plate are very sharp and placed in lines. Occasionally they are less sharp and more granulate as in *Cactopinus*, and nearly so in *Leiomicracis* and *Microlanurgus*.
34. Closing teeth: 0 finely plumose, 1 serrated. Most micracidines have plumose or weakly dentated closing teeth. In *Dendrochilus* the closing teeth are not spreading but compact in a serrated pattern.
35. Crop spines: 0 absent, 1 tiny and dispersed, 2 bundle of long spines, 3 few spines on a tubercle per plate, 4 one or two spines per plate. CI = 0.36, RI = 0.74. Micracidini species typically has bundles of enlarged spines in the crop, pointing posteriorly towards the lumen of the proventriculus. These spines are small and dispersed in *Cactopinus*, *Stenoclyptus*, *Micracisella*, *Neomicracis* and *Leiomicracis*. In *Dendrochilus* and *Afromicracis* these spines are shorter and placed on a tubercle, in *Dendrochilus* with only one or two such spines.
36. Termination of lateral teeth: 0 gradual, 1 U-shaped and strongly enforced. CI = 1.0, RI = 1.0. Lateral teeth on the apical plate are usually faint but form an enforced and sharp U-shaped ridge in *Lanurgus*.

genus was more closely related to *Pseudomicracis* and a lineage erected as a new genus, *Pseudolanurgus,* which has a less mucronate elytral apex compared to *Pseudomicracis*. These three genera together were defined as a group by having a greatly enlarged and prolonged flagellum in the male aedeagus with the loss of tegmen and spiculum gastrale. *Saurotocis*, here represented by the type species *S. dispar* (Schedl, 1961), was furthermore nested within *Pseudomicracis* with maximum support.

A separate parsimony analysis of 36 morphological characters resulted in 68,947 trees. Nearly all genera as supported by molecular data were monophyletic, with two genera forming polytomies not contradicting monophyly (*Afromicracis* and *Diplotrichus*). Most characters performed well in terms of high retention indices, with 28 characters obtaining a retention index above 0.6 irrespective of optimization on the Bayes combined analysis topology or one of the parsimony tree topologies. Characters with the lowest performance had RI between 0.4 and 0.6 and these less optimal characters included features of the male frons (character 2), shape of pronotal and interstrial setae (10, 12), shape of the lateral edge of the protibiae (17) and the position of its denticles (18), the shape of the suture and teeth on the apical plate of the proventriculus (32, 33) and its closing teeth (34).

Biogeography

Model selection based on the AIC criterion in RASP using the Beast tree suggested DIVAlike (with or without the additional parameter for jump dispersal) as the best model for biogeographical analysis. The BBM reconstruction (Fig. 46) was similar to the DIVAlike+j analysis. Both of these differed from the DIVAlike analysis primarily by the simultaneously dispersal and vicariance events in accordance with jump dispersal theory, while DIVAlike always estimated dispersal one node before the inferred vicariance event, suggesting expansion of the ancestral area with subsequent vicariant splits in geographical isolation.

BBM estimated an origin of the tribe in Eastern Africa, which occurred about 78.5 Ma (Table 4), and several subsequent range expansions took place from this area. Colonization of the Neotropics occurred in a single event not long after the origin of the tribe, around 69.3 Ma. Madagascar was colonized around 59.6 Ma, from eastern Africa, and thereafter colonized Southern Africa from Madagascar twice (*Lanurgus* 58 Ma, *Diplotrichus* subclade 29.5 Ma) and Eastern Africa once (*Pseudolanurgus* 31.5 Ma). The *Afromicracis* clade likely originated in Eastern Africa and expanded its ranges towards the west 47.4 Ma and more recently moved several times between various African regions. This clade never expanded its range outside the African mainland.

Taxonomy

Micracidini LeConte 1876
Type genus – *Micracis* LeConte 1876.

Diagnosis. Eyes entire, short (longer in *Micracis* and *Micracisella*), female scapus usually with a small to large tuft of golden setae, funiculus 5- or 6-segmented, club moderately to strongly flattened, usually with two sutures, occasionally without; labial palps long, basal segment obliquely triangular and thereby separating diverging palps, segment 3 narrow, twice as long as segment 2. Pronotum weakly to strongly dome-shaped, asperate on anterior half. Elytra usually with rows of scale-like setae (hair-like in *Cactopinus*, some *Hylocurus* and some *Afromicracis*). Protibiae either parallel-sided or twisted, with one or more denticles apically on posterior side. Hindwings with either 1 or 3 setae on precosta, 2–9 on costa, and usually 2 (1–3) on distant margin of the radial cell (pterostigma). Scutoscutellar suture parallel to the scutellar grove for most of its length. Pleural suture zigzag shaped. Postnotum separated from metanotum by a membrane.

Figs. 1–7 Various parts of the beetle body important for classification and identification of Micracidini genera. **1** *Micracis carinulata* head with antennae showing long dorsal horns on the scapus with tuft of setae, and a club with two procurved sutures. **2** Posterior view of declivity and the truncated shape of the last ventrite in *Pseudolanurgus harunganae* and **3** *Dendrochilus* sp. **4** Lateral view of elytron and ventrites in *Lanurgus podocarpi* and **5** *Diplotrichus gracilis*. **6** Dorsal view of elytra in *Lanurgus oleae* and **7** *Diplotrichus subdepressus*

Anterior plate of the proventriculus longitudinally divided and broadly separated (tight suture in some *Lanurgus* and most *Cactopinus*), transversely set by sharp teeth, or ridges (*Cactopinus*), closing teeth plumose or serrated, sometimes compacted. Male genitalia usually strongly elongated by very long apophyses, tegmen y- or ring-shaped, or absent; if

Figs. 8–17 Antennae of female Micracidini: **8** *Leiomicracis aurea*; **9** *Afromicracis setifer*; **10** *Dendrochilus* sp.; **11** *Neomicracis squamigera*; **12** *Phloeocurus africanus*; **13** *Lanurgus rhusi*; **14** *Diplotrichus* sp.; **15** *Pseudolanurgus* sp.; **16** *Pseudomicracis* sp.; **17** *Microlanurgus bicolor*

Figs. 18–27 Legs of selected species in Micracidini. Protibiae of **18** *Micracis carinulata*; **19** *Pseudolanurgus* sp.; **20** *Lanurgus podocarpi*; **21** *Dendrochilus* sp.; **22** *Leiomicracis aurea*. Metatibiae of **23** *Micracis carinulata*; **24** *Lanurgus* sp.; **25** *Pseudolanurgus* sp.; **26** *Leiomicracis aurea*; **27** *Dendrochilus* sp.

present the median struts (manubrium) usually very long (short to absent in *Lanurgus, Microlanurgus*, *Thysanoes*).

***Leiomicracis* Jordal, gen. nov**

urn:lsid:zoobank.org:act:4876A2E7-5058-49C8-ADB3-B0DE245EC2A9

Type species. *Leiomicracis aureus* Jordal, sp. nov., monotypic.

Etymology. From Greek *Leios*, meaning smooth, referring to the lack of asperities on the anterior part of the pronotum, and the Greek genus name *Micracis*. Gender feminine as explained for *Micracis* by Alonso-Zarazaga and Lyal (2009).

Diagnosis. Typical micracidine by the twisted lateral edge of the protibiae with only a single socketed denticle present on the posterior face; inner mucro large, curved posteriorly. Female scapus longer than funiculus, with a triangular tuft of setae on its dorsal side. Antennal funicle 5-segmented; club setose, without sutures. Pronotum asperate in middle, smooth on posterior half, lateral thirds and anterior sixth. Interstriae with a single row of scale-like setae. Setae on ventrites simple, unifid. Hindwing precosta with a single seta, radial cell with two setae. Proventriculus with anterior plate much longer than posterior plate, longitudinally, broadly divided, with bundles of strong, long crop teeth; apical teeth enforced, forming U-shaped structure.

Distribution. Tanzania.

Remarks. *Leiomicracis* is phylogenetically isolated as the sister group to all other Micracidini. The basal position in Micracidini was also confirmed by adding DNA sequences to the previously published 182 Scolytinae taxa dataset of Pistone et al. (2018). The new genus is distinguished from all other genera in the tribe by the smooth anterior sixth of the pronotum and by the scattered long setae forming a triangular tuft on the scapus.

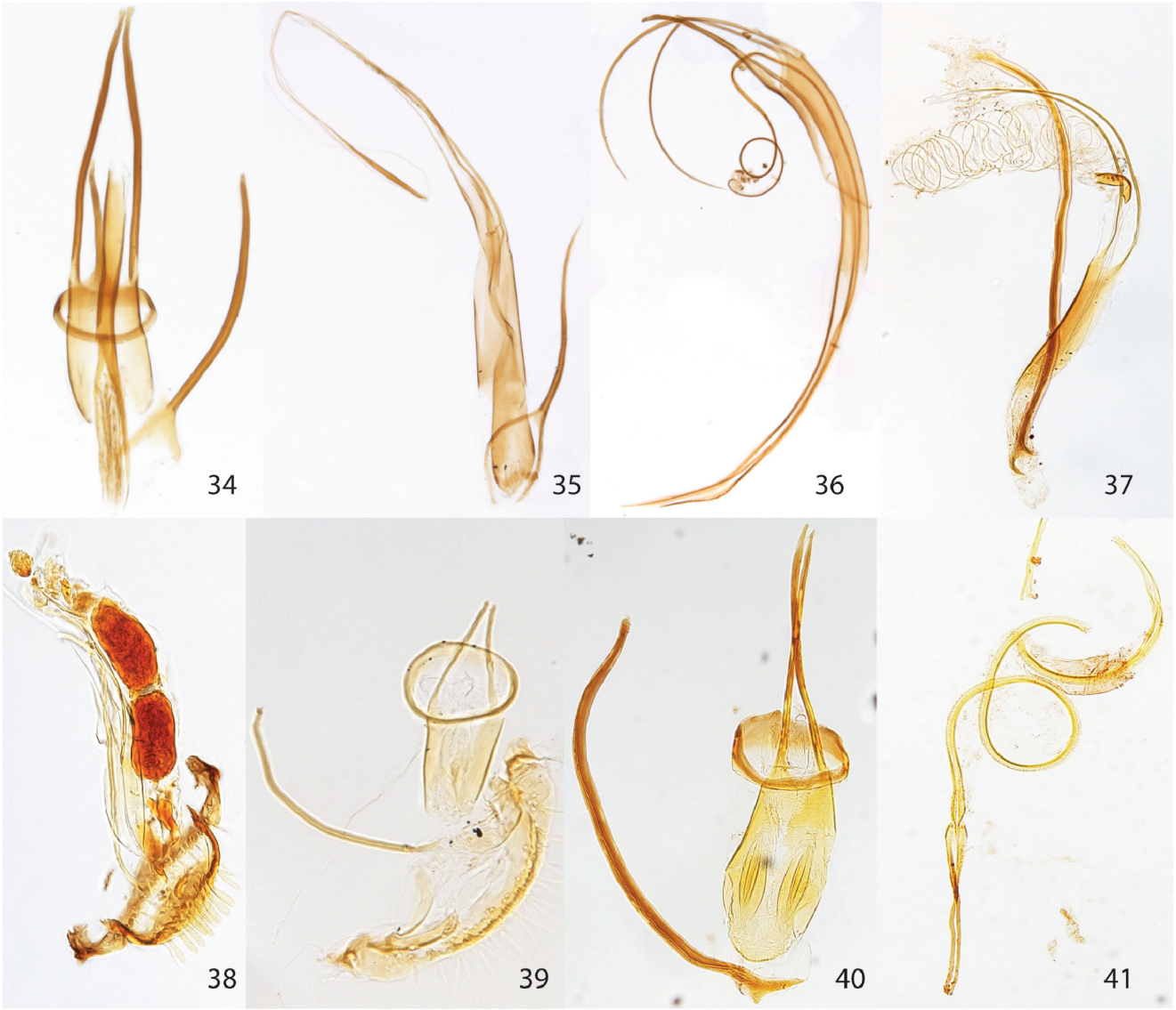
Figs. 28–33 Digestive systems in Micracidini. **28** Maxillae and labium of *Lanurgus podocarpi*, dorsal view. **29** Proventriculus of *Lanurgus podocarpi*; **30** *Leiomicracis aurea*; **31** *Neomicracis squamigera*; **32** *Dendrochilus* sp.; **33** *Afromicracis* sp.

***Leiomicracis aurea* Jordal, sp. nov**

urn:lsid:zoobank.org:act:67223A57-D607-43D7-83DA-3754CB428B1C

(Figs. 47, 50, 53)

Type material. Holotype female: Tanzania, Udzungwa, Megombera forest, NE Mang'ula, GIS: −7.817, 36.980, ex. old twig, 15 Nov. 2009, 15xi-2, B. Jordal leg. Paratypes: same data as holotype (3). Holotype and two paratypes types deposited in ZMBN, one paratype in NHMW.



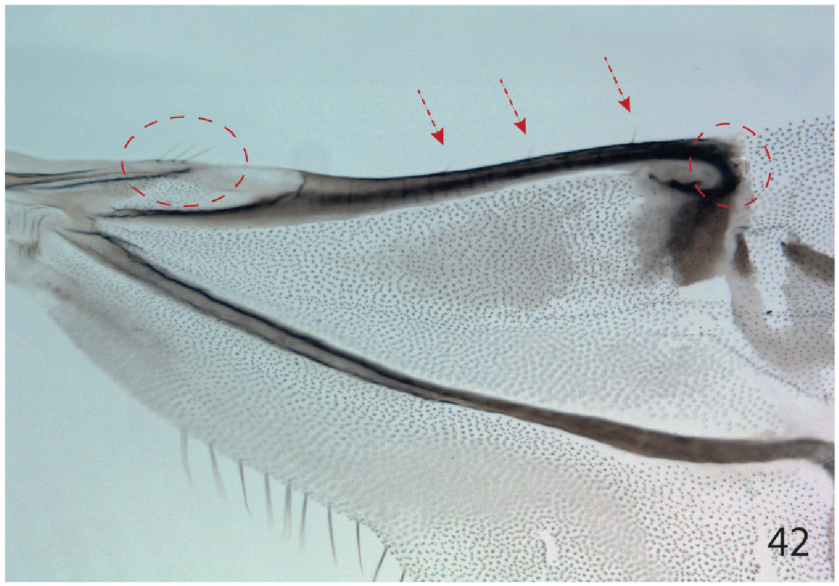
Figs. 34–41 Male genitalia in selected Micracidini. **34** *Micracisella nanula*; **35** *Cactopinus rhois*; **36** *Phloeocleptes cristatus*; **37** *Afromicracis* sp.; **38** *Neomicracis squamigera* (with last two sternites and gut remains); **39** *Microlanurgus bicolor*; **40** *Lanurgus podocarpi*; **41** *Diplotrichus gracilis*

Etymology. Latin adjective *aurea* meaning golden or splendid, referring to the golden-brown colour of the most mature specimens, and the elegant golden setae on the female scapus.

Diagnosis. Female scapus with long golden setae on its dorsal side increasing in length towards its distal end, tuft appearing triangular. Pronotum with asperities in middle, reaching only to anterior sixth. Protibiae with a single denticle on its posterio-lateral side. Proventriculus with closing teeth compacted and coarsely serrated.

Description, female. Length 1.1–1.3 mm long, 2.4–2.5 × as long as wide. **Colour** light golden or bronze brown (possibly young individuals). **Frons** flat to weakly impressed, surface reticulate, obscurely punctured; scattered fine setae, slightly thicker and denser on epistoma. Antennal scapus longer than funiculus, dilated apically, with a tuft of increasingly long golden setae on its dorsal side; funiculus 5-segmented, pediculus about as long as segment 2 and 3 combined; club flat, 1.6 × as long as wide, pubescent, with a faint trace of one procurved suture. **Pronotum** distinctly humpbacked, on median half from summit to anterior sixth with sharp asperities, on posterior half, laterally, and anterior sixth smooth, with

Figs. 42–44 Hind wings of Micracidini species with stippled circles around precostal setae patch and radial cell setae, and arrows pointing at costal setae. **42** *Phloeocleptus cristatus* (3 precostal setae, 3 costal setae, and 1 radial cell seta); **43** *Lanurgus podocarpi* (4 costal setae, 3 radial cell setae); **44** *Neomicracis squamigera* (1 precostal seta, 2 costal setae, 2 radial cell setae) ▶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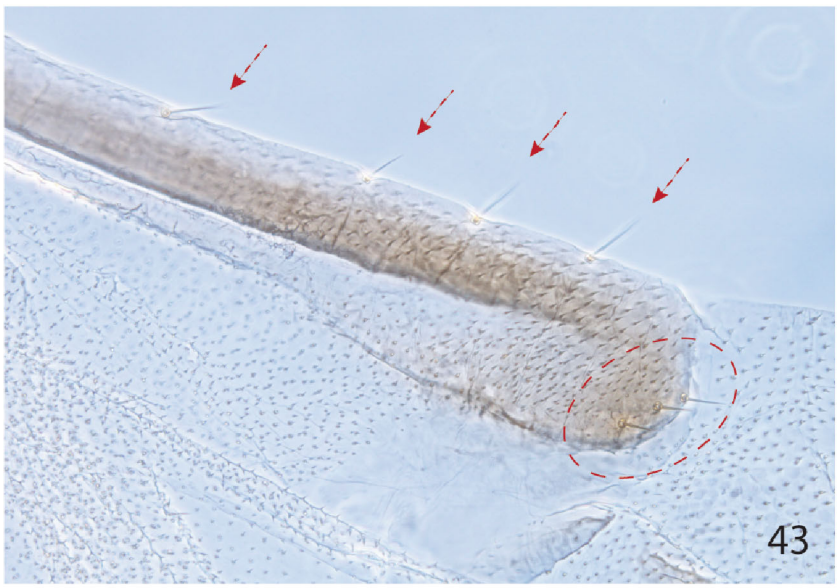
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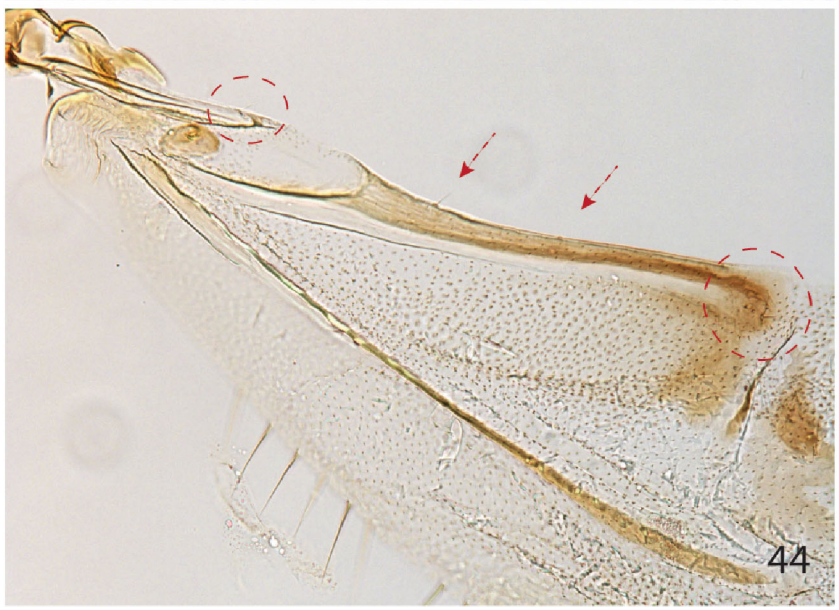
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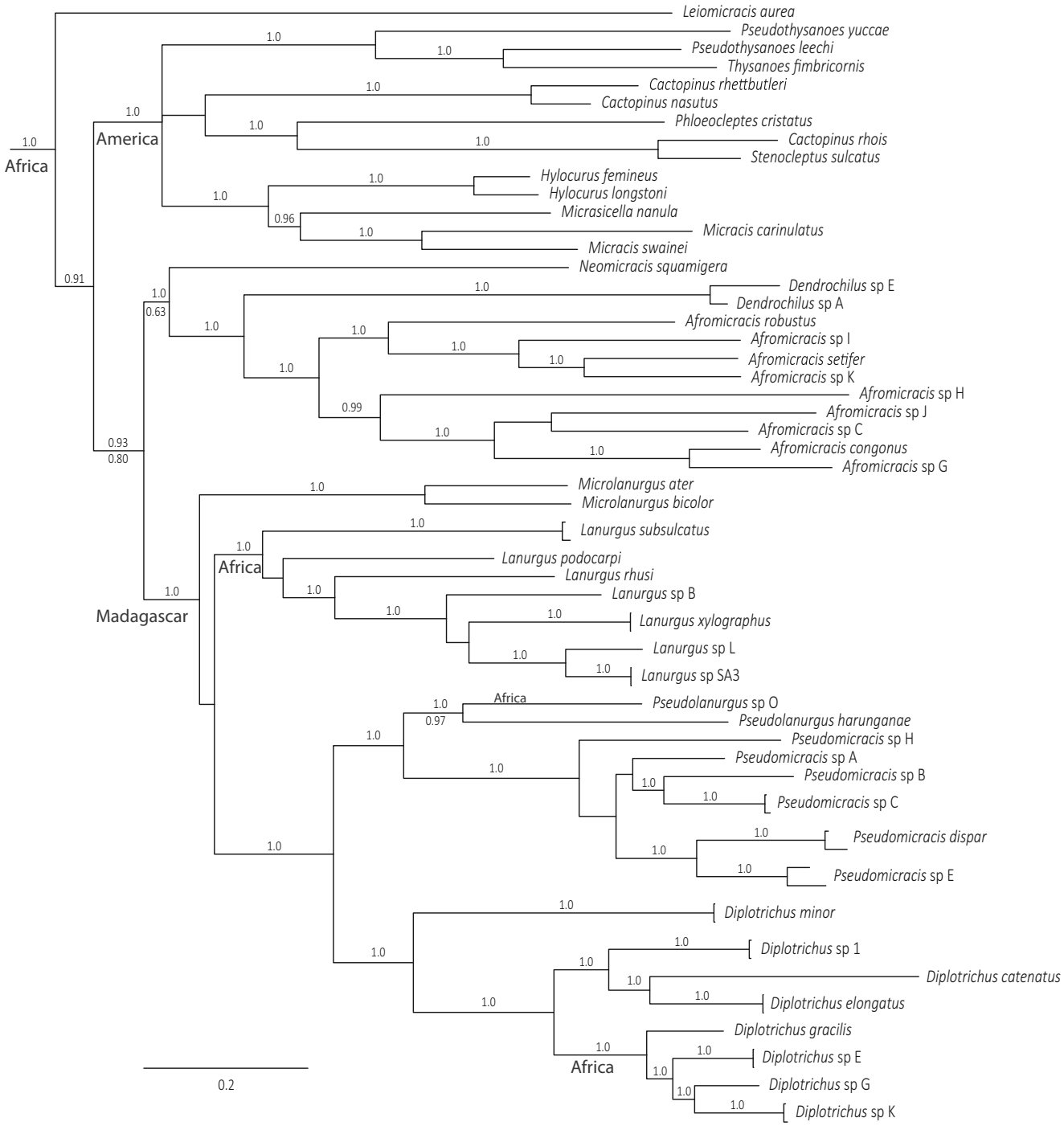


Fig. 45 Bayesian tree resulting from the combined analysis of four molecular markers and 36 morphological characters. Standard deviation of split frequencies 0.005, potential scale reduction factor 0.002. The tree topology was identical when morphological data were excluded. Posterior probabilities are shown above branches, and below if probability differed in the separate molecular analysis

obscure punctures. Basal and lateral margin rounded. Vestiture consisting of fine, semi-erect setae. **Scutellum** wider than long, posterior margin U-shaped. **Elytra** finely rugose, shiny, with irregular rows of very small interstrial and strial punctures. Vestiture consisting of regular interstrial rows of erect, narrowly spatulate setae, and fine, short semi-recumbent

Fig. 46 Reconstruction of ancestral areas for Micracidini using Bayesian binary MCMC optimisations (similar to DIVAlike+j). Pie diagrams on nodes indicate the relative probability for of each area. Larger circles are all inferred simultaneous dispersal and vicariance events. In the DIVA-like analysis without the extra jump dispersal parameter, each dispersal event occurred one node earlier than the vicariant event

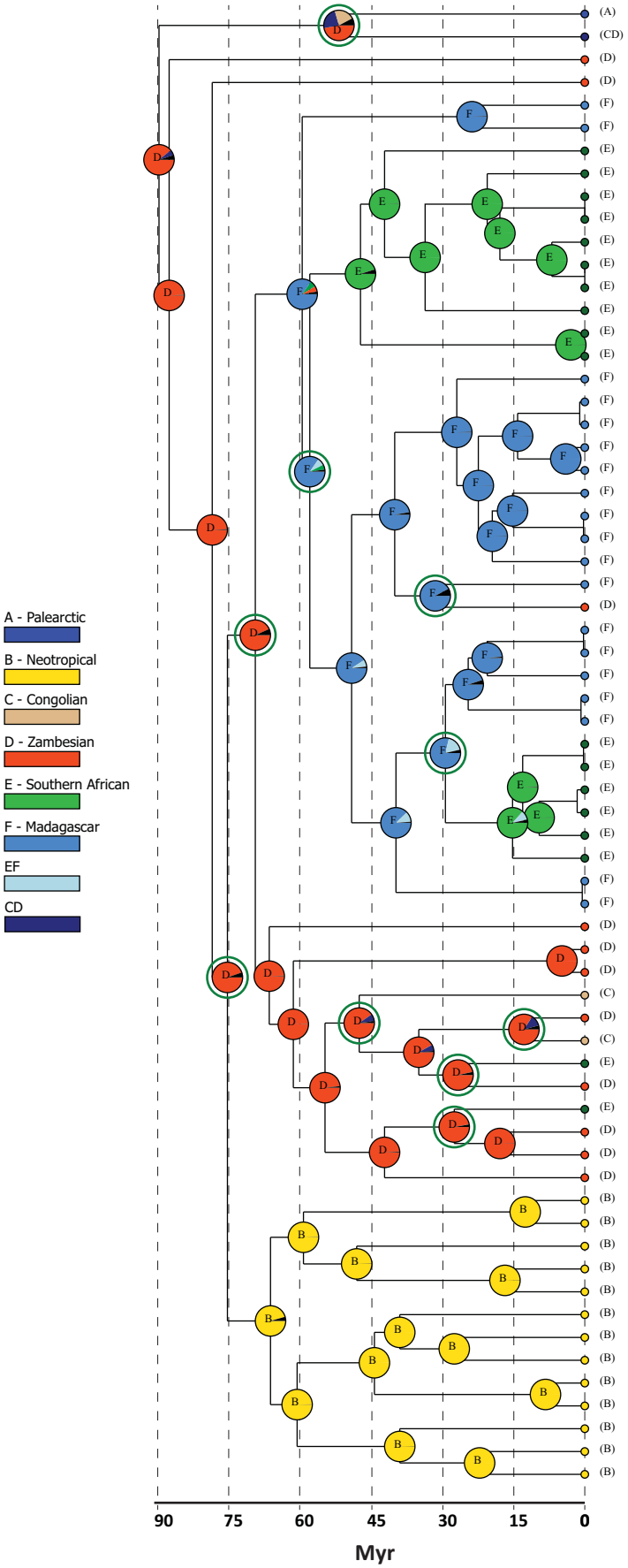

A - Palearctic
B - Neotropical
C - Congolian
D - Zambesian
E - Southern African
F - Madagascar
EF
CD
90
75
60
45
30
15
0
Myr

Table 4 Summary of key biogeographical events in Micracidini. Age of dispersal event was estimated in Beast, with median age given, and 95% highest posterior density in brackets

Clade	Age (95%hpd)	Ancestral origin	Expansion to
Micracidini	78.5 (73–84)	East Africa	–
Neotropical clade	66.2 (71–85)	East Africa	Neotropics
Microlanurgus	59.6 (57–72)	East Africa	Madagascar
Lanurgus	58.0 (55–69)	Madagascar	South Africa
Afromicracis	47.4 (41–55)	East Africa	West Africa
Pseudolanurgus	31.5 (22–40)	Madagascar	East Africa
Diplotrichus	29.5 (25–34)	Madagascar	South Africa

strial setae. Ventral vestiture of fine, rather long setae. **Legs.** Protibiae evenly rounded on lateral and inner sides, ending in an apical central mucro which is rather strong, curved posteriorly; one additional tiny socketed denticle on posterior side close to tarsal insertion. Metatibiae narrow, sides parallel, with distinct, fine, long inner mucro, and three transversely set apical denticles. **Proventriculus.** Apical plate 2.5 × as long as posterior plate, with regular transverse rows of sharp triangular or obovate teeth. Apical teeth connected in an U-shaped formation with 2–4 longer, sharp teeth. Closing teeth short, rather smooth.

Male. Unknown.

Biology and distribution. Only known from the lowland type locality near the Udzungwa mountains in Tanzania. Six young female specimens were taken from a small twig of an unknown host plant.

***Neomicracis* Jordal, gen. nov.**

urn:lsid:zoobank.org:act:F44DE0EF-DCD7-4285-BFAC-8AA30D30BEF3

Type species. *Neomicracis squamigera* Jordal, sp. nov., monotypic.

Etymology. The Greek prefix *Neo-*, new, reflects the designation of a new genus in Micracidini. Gender feminine (Alonso-Zarazaga and Lyal 2009).

Diagnosis. Typical micracidine with twisted protibia which has apical denticles on its posterior side, and a long tuft of setae on a dorsally strongly elongated female scapus. Antennal funicle 6-segmented; club with first suture absent on median 3/4 and the second suture complete, transverse, surface of segment 1 and 2 fused, corneous. Elytral apex slightly inflated. Setae on pronotum in both sexes and on ventrites III-V in the males broad and scale-like. Apical margin of metatibia transverse. Precosta in hind wings bearing a single seta, radial cell with two setae. Proventriculus with fine, dispersed crop spines; apical plate shorter than posterior plate. Male genitalia with tegmen Y-shaped, manubrium long; spiculum gastrale a simple rod.

Distribution. Tanzania.

Remarks. This genus is superficially similar to the new genera *Pseudolanurgus* and *Diplotrichus* described below, having an inflated elytral apex, but differ from those genera by the elongated horn on the scapus. *Neomicracis* is unique in the tribe by having corneous first two segments of the antennal club (first suture interrupted), and by the broad scale-like setae on ventrites III-V in the males. It differs further from the sister group, which consists of *Dendrochilus* and *Afromicracis*, by the 6-segmented funiculus.

***Neomicracis squamigera* Jordal, sp. nov.**

urn:lsid:zoobank.org:act:8D5258B2-AC48-4EF2-8C22-607F50C2F3D5

(Figs. 48, 51, 54)

Type material. Female holotype: Tanzania, Udzungwa National Park, GIS -7.868, 36.844, ex small twig, 11xi-7, B. Jordal, leg. Allotype male and paratypes: same data as holotype (5). Holotype, allotype and two paratypes in ZMBN, two paratypes in NHMW.

Etymology. Latin adjective composed by *squama*, meaning scale, and *-ger*, meaning bearing, referring to the broad scale-like setae associated particularly with asperities on the pronotum.

Diagnosis, female. Pronotum with very broad scale-like setae. Scapus short, bearing dorsally an elongated spine with long setae pointing inwards; funiculus 6-segmented; frons smooth and slightly impressed on central third; scutellum with four short setae in a transverse row. **Male** similar to female except scapus elongated, frons flat, reticulated, and ventrites III-V with very broad and long scale-like setae.

Description, female. Length 1.1–1.2 mm long, 2.4–2.6 × as long as wide. **Colour** brown. **Frons** flat, weakly impressed and impunctate on central one-third, coarsely reticulated elsewhere; scattered fine setae present around impressed area, slightly thicker and much longer, dense setae on epistoma. Antennal scapus shorter than funiculus, strongly elongated on its dorsal side into a long triangular horn, with a tuft of long forwardly pointing setae; funiculus 6-segmented, pediculus about as long as segment 2–4 combined; club flat, as long as wide, with suture 2 transverse, suture 1 absent in median three quarter, segments 1 and 2 fused, corneous, shiny. **Pronotum** short, much wider than long, summit slightly elevated, anterior slope short, steep; anterior half with

Figs. 47–55 Dorsal, lateral and front view of the female holotypes of **47, 50, 53** *Leiomicracis aurea*; **48, 51, 54** *Neomicracis squamigera*; **49, 52, 55** female(?) holotype of *Dendrochilus strombosiopsis*

sharp, almost quadrated asperities, each associated on its posterior side with a broad scale-like setae; on posterior half generally smooth, reticulated, in median posterior area slightly granulated; vestiture consisting of fine, semi-erect setae. Basal and lateral margin rounded. **Scutellum** U-shaped, wider than long, with 3–4 short setae. **Elytra** finely rugose, finely granulated, on declivity granules sharper; punctures faint, confused. Vestiture consisting of regular interstrial rows of slightly curved, pointed or slightly spatulate setae, and fine, short semi-erect strial setae. Ventral vestiture of fine, rather long setae. **Legs.** Protibiae with lateral edges evenly rounded towards a large, posterio-laterally curved terminal mucro, appearing slightly twisted; one lateral socketed denticle and one additional denticle on posterior side close to tarsal insertion. Metatibiae narrow, sides parallel, with a distinct, fine, long inner mucro, and two transversely set apical denticles. **Proventriculus.** Apical plate slightly shorter than posterior plate, with regular transverse rows of sharp triangular. Apical teeth not apparent. Closing teeth smooth, long; femoral teeth sharp, connected to base of closing teeth.

Male. Similar to female except length 1.0–1.1 mm, 2.2–2.5 × as long as wide; frons rugose, lightly impressed on lower half; upper margin of impressed area marked by two small tubercles; antennal scapus short, rounded; setae on abdominal ventrites III–V very broad and long, one transverse row on each ventrite, pointing posteriorly. Genitalia elongated, apophyses as long as penis body, tegmen open dorsally, Y-shaped, with long manubrium; spiculum gastrale a simple rod, as long as penis.

Biology and distribution. Only known from the type locality in the Udzungwa mountains in Tanzania. It was taken from a 1 cm thick twig of an unknown host plant where it was excavating longitudinal but irregular egg tunnels.

The *Afromicracis* clade

This group consist of two genera defined by a long, narrow scapus with scant setae in both sexes, and a 5-segmented funiculus. The precosta on the hind wing has only a single seta, the inner mucro of the metatibiae is long and thin, and in males the tegmen is minute and Y-shaped, and a very long, thin and often coiled flagellum runs through the aedeagus.

Dendrochilus Schedl, 1957
Type species. *Dendrochilus strombosiopsis* Schedl, 1957. (Figs. 49, 52, 55)

Diagnosis. Small, elongated species. Funiculus 5-segmented, scapus at least as long as the funiculus in both sexes, in females with a fine tuft of setae on its dorsal side; antennal club elongated, corneous on both sides, shiny and suture-free. Last ventrite elongated, bottle-shaped and truncated. Proventriculus with closing teeth compact and serrated.

Included species:
Dendrochilus strombosiopsis Schedl 1957.

Excluded species: D*endrochilus arundinarius* Schedl, 1957, *Dendrochilus elongatulus* Schedl, 1977, *Dendrochilus filum* Schedl, 1977, *Dendrochilus jasminae* Schedl, 1957, *Dendrochilus mikaniae* Schedl, 1957 *Dendrochilus robustus* Schedl, 1957, all to *Afromicracis*; *Thamnurgus villersi* Lepesme, 1942 to *Xylocleptes* Ferrari, and *Dendrochilus intermedius* Schedl, 1977, to *Acanthotomicus* Blandford.

Distribution. Congo, Tanzania.

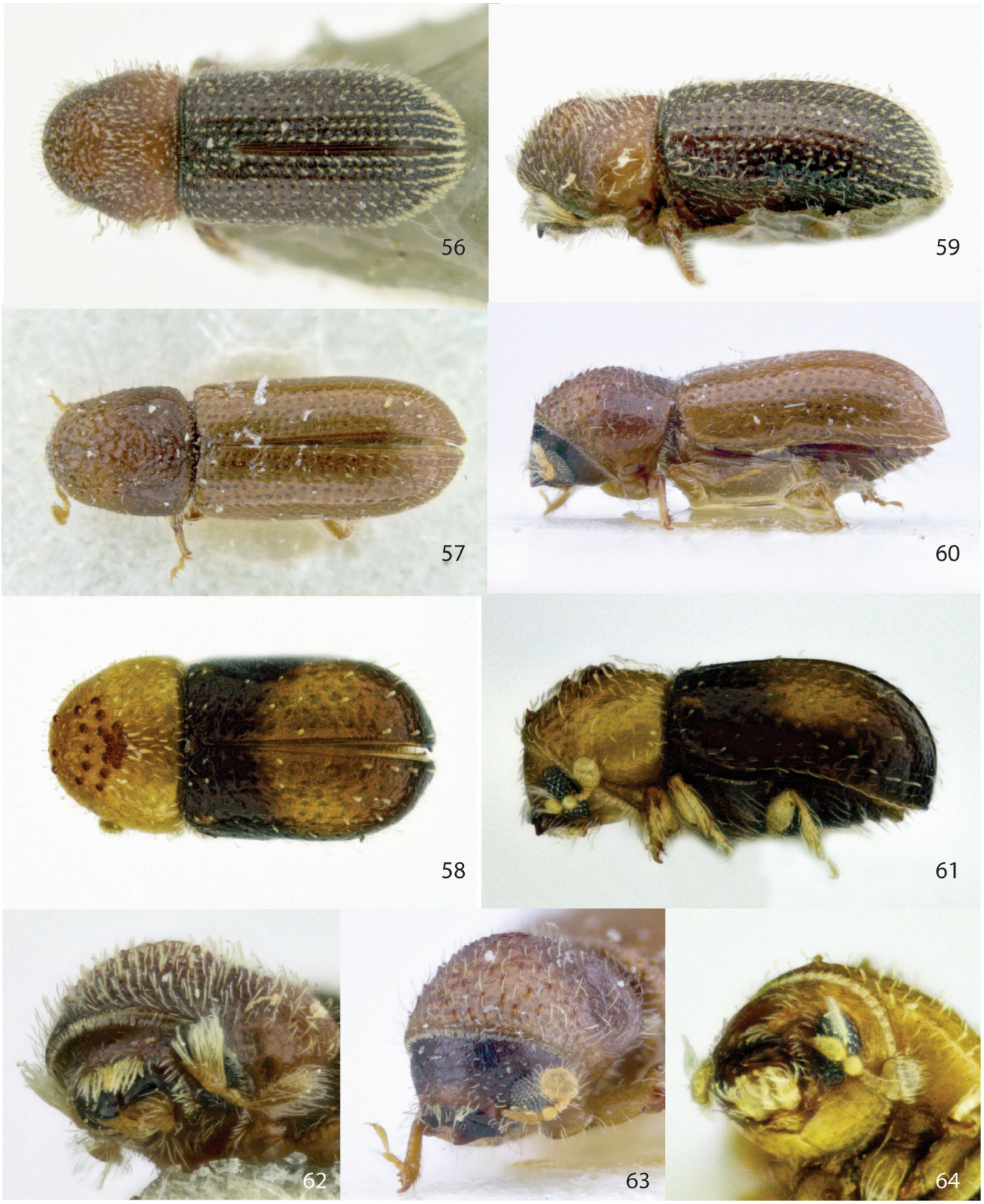
Remarks. The type species differs from other species previously included in this genus by the elongate, shiny and suture-free antennal club, and by the peculiar bottleneck-shaped apical part of the last ventrite. Two very similar, but undescribed, species grouped as the sister to *Afromicracis* by maximum support. Both genera share the presence of a long scapus in both sexes, 5-segmented funicle, and a reduced Y-shaped tegmen. Most species assigned to *Dendrochilus* by Schedl belong to *Afromicracis* (see below).

Afromicracis Schedl, 1959.
=*Miocryphalus* Schedl, 1939, synonym by Alonso-Zarazaga and Lyal (2009), name unavailable

Type species. *Afromicracis kenyaensis* Schedl, 1959. (Figs. 56, 59, 62)

Diagnosis. Antennal scapus in both sexes straight, longer than funiculus, slightly dilated but not strongly inflated; in females with a fine tuft of scant long setae; funiculus 5-segmented; club on anterior face usually with one procurved suture close to apex. Elytra with scale-like or hair-like setae, always in single rows. Protibiae twisted, with 2 or 3 denticles on latero-posterior side near apex. Ventral setae always simple, never bifid or plumose. Proventriculus with cluster of few crop spines attached to a tubercle base. Male genitalia with a long flagellum, sometimes shorter and broad, sometimes very long and coiled; tegmen reduced to absent, apophyses more than twice as long as aedeagal body.

Included species:
Afromicracis congonus (Eggers, 1940) (original genus *Miocryphalus*)
Afromicracis convexus Schedl, 1962
Afromicracis dubius (Schedl, 1950) (*Miocryphalus*)
=*Afromicracis angolensis* Schedl, 1962 **syn. nov.**
Afromicacis elongatulus (Schedl, 1977) **comb. nov.** (*Dendrochilus*)



Figs. 56–64 Dorsal, lateral and front view of the female holotype of **56, 59, 62** *Afromicracis kenyaensis*; **57, 60, 63** *Afromicracis jasminiae*; **58, 61, 64** *Microlanurgus bicolor*

Figs. 65–73 Dorsal, lateral and front view of the female holotype of **65, 68, 71** *Microlanurgus ater*; **66, 69, 72** female paratype of *Traglostus exornatus*; **67, 70, 73** male holotype of *Traglostus exornatus*

Figs. 74–82 Dorsal, lateral and front view of females directly compared to the holotype of **74, 77, 80** *Lanurgus barbatus*; **75, 78, 81** *Diplotrichus gracilis*; **76, 79, 82** *Pseudolanurgus harunganae*

Afromicracis jasminiae (Schedl, 1957) **comb. nov.** (*Dendrochilus*)

=*Dendrochilus mikaniae* Schedl, 1957 **syn. nov.**

Afromicracis kenyaensis Schedl, 1962

Afromicracis longus (Nunberg, 1964) (*Miocryphalus*)

Afromicracis natalensis (Eggers, 1936) (*Stephanoderes*)

Afromicracis robustus (Schedl, 1957), **comb. nov.** (*Dendrochilus*) (Figs. 57, 60, 63)

=*Dendrochilus arundinarius* Schedl, 1957 **syn. nov.**

=*Hypothenemus bambusae* Browne, 1970 **syn. nov.**

=*Dendrochilus filum* Schedl, 1977 **syn. nov.**

Afromicracis setifer (Schedl, 1957) **comb. nov.** (*Mimips*, via *Mimiocurus*)

Excluded species. The following species have entire eyes and large suture-free antennal clubs and are therefore placed in *Eidophelus* Eichhoff: *Afromicracis agnathus* (Schedl, 1942), *Afromicracis ciliatipennis* (Schedl, 1979), and *Afromicracis klainedoxae* (Schedl, 1957). *Afromicracis nitidus* (Schedl, 1965) was originally described in *Eidophelus* but has emarginated eyes and a general habitus as in *Hypothenemus* and transferred to that genus (see below). *Afromicracis nigrinus* (Schedl, 1957) has emarginated eyes and is placed in a new genus *Karlsenius* near *Afrocosmoderes* (described below). Six species previously placed in *Afromicracis* were transferred to *Macrocryphalus* Nobuchi, *Afrocosmoderes*, *Hypothenemus* and *Eidophelus* by Johnson et al. (2020). One of these, *H. attenuatus* (Eggers, 1935) is very similar to *A. nigrinus* and is here placed in the same genus, closely related to *Afrocosmoderes* and *Hypothenemus* (see below).

Distribution. Tropical Africa.

Remarks. *Afromicracis* was removed from synonymy under *Miocryphalus* by Alonzo-Zarazaga and Lyal (2009), with the latter taxon deemed *nomen nudum*. Many species were erroneously assigned to *Afromicracis* (see Wood and Bright, 1992) and are now placed in many different genera in different tribes. Although species are small in size, they do have sufficient characters for reliable classification as noted in the diagnosis.

***Microlanurgus* Jordal, gen. nov.**

urn:lsid:zoobank.org:act:8 AD67315-6B08-43D4-9FF1-296B37B06702

Type species. *Microlanurgus bicolor* Jordal, sp. nov.

Etymology. Adding the Greek prefix *Micro-*, meaning very small, to the genus name *Lanurgus* (masculine), referring to the size of species which are shorter than 0.8 mm.

Diagnosis. This genus consists of very small and stout species (<0.8 mm), with the typical twisted shape of micracidine protibiae which have only one lateral denticle and a single additional denticle on its posterior face. The scapus is much shorter than the 6-segmented funiculus, in females with a little tuft of setae on its dorsal side. The antennal club has two sutures where suture 1 is transverse and suture 2 slightly recurved, appearing ring-like. Unique features include a pronotum which is strongly dome-shaped, with few but large asperities which are not fully reaching the anterior margin; basal and lateral margins rounded. Elytra have scattered, erect, spatulate setae on odd-numbered interstriae only. Scutellum triangular, as wide as long. Male genitalia have tegmen shaped as a complete ring without manubrium, and the apophyses are not longer than the aedeagal body. Proventriculus with apical plate longitudinally divided, much shorter than posterior plate, with few sharp triangular teeth. Lateral, apical and femoral teeth absent; closing teeth lightly serrated, masticatory brush appears spiny.

Distribution. Madagascar (southern parts).

Remarks. This is the only micracidine genus with erect elytral setae only on odd-numbered interstriae. The proventriculus and protibiae are typical micracidine and molecular data firmly placed the two included species in the tribe (Pistone et al. 2018). There are no obvious close relatives based on morphological comparison or by phylogenetic analyses, but one may note that the male genitalia is quite similar to species in *Lanurgus*.

Included species:

***Microlanurgus bicolor* Jordal, sp. nov.**

urn:lsid:zoobank.org:act:65D3E941-661E-41A5-B287-998CC3052A62

(Figs. 58, 61, 64)

Type material. Holotype, female: Madagascar, Parc National de Tsimanampetsotsa, Forêt de Bemanateza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, B. Fischer et al., leg. BLF6254, EH11 sifted litter (leaf mould, rotten wood) [GIS: 23° 59′ 32” S, 043° 52′ 50″ E]. Paratypes: same data as holotype (8); Parc National d’Andohahela, Manantalinjo, 33.6 km ENE Amboasary [24° 49′ 01” S, 046° 36′ 36″ E], ex sifted litter. BLF4810, B. Fischer, leg. (1). Holotype and 4 paratypes in CAS, 2 paratypes each in ZMBN and NHMW.

Etymology. The Latin adjective *bicolor*, meaning two-coloured, refers to the light yellow and black colours of the elytra.

Diagnosis. Pronotum with about 20 coarse asperities, 2 or 3 of these near the anterior margin. Elytra bicolored, spatulate

setae present on odd-numbered interstriae only, each separated by 2–3 times the length of a seta.

Description, female. Length 0.6–0.7 mm long, 2.0–2.2 × as long as wide. **Colour** yellow and black; primarily yellow on pronotum and posterior part of elytra, venter, and anterior part of elytra black. **Frons** flat, shiny and impunctate on central half from epistoma to upper level of eyes, reticulate elsewhere; scattered, short, fine setae present around glabrous central area. Antennal scapus much shorter than funiculus, rounded, with a scant tuft of long setae on its dorsal side; funiculus 6-segmented, pediculus about as long as segment 2 and 3 combined; club flat, slightly longer than wide, suture 1 transverse, suture 2 recurved, appears ring-like in dorso-lateral view. Eyes separated by 2.7–2.9 × their width. **Pronotum** strongly dome-shaped, on anterior two-thirds with large, rounded asperities, only 2–3 of these reaching near anterior margin. Vestiture consisting of mixed spatulate and fine setae, longest setae near pronotal summit. **Elytra** smooth, shiny, stria not impressed, punctures shallow, large compared to body size, interstrial punctures obscure. Vestiture consisting of rows of erect, spatulate setae on odd-numbered interstriae, and scattered, fine and very short strial setae. Ventral vestiture of fine, rather long setae. **Legs.** Protibiae with lateral edges subparallel, inner mucro strong, curved posteriorly; two tiny socketed denticle transversely set apically on posterior side close to tarsal insertion. Metatibiae broader apically, with a distinct, fine, long inner mucro, and one apical and two laterally placed thin denticles.

Male near identical to female, except fewer and shorter seta on scapus.

Biology and distribution. Many specimens were sifted from leaf mould and rotten wood. It is only known from two localities in in southern Madagascar characterized by dry vegetation types.

***Microlanurgus ater* Jordal, sp. nov.**

urn:lsid:zoobank.org:act:DA34F050-3BDE-4688-BB28-68202E8841F5

(Figs. 65, 68, 71)

Type material. Holotype, female: Madagascar, Mahafaly Plateau, 6.2 km 74° ENE Itampolo, B. Fischer, leg. BLF5758, EH11 sifted litter (leaf mould, rotten wood) [GIS: 24°39′13″S, 043°59′48″E]. Paratypes: same data as holotype (6). Holotype and 1 paratype in CAS, 2 paratypes each in ZMBN and NHMW.

Etymology. The Latin adjective *ater* means black, referring to the colour of the species.

Diagnosis. Frons impressed below upper level of eyes. Pronotum with about 15–20 coarse asperities, 4–5 of these near the anterior margin. Elytra and pronotum black, legs yellow; spatulate setae present on odd-numbered interstriae only, each separated by 2–3 times the length of a seta.

Description, female. Length 0.7–0.8 mm long, 2.0–2.1 × as long as wide. **Colour** black, legs yellow. **Frons** rounded from vertex to just below upper level of eyes, then impressed from a faint transverse rim to epistoma; impressed area glabrous, smooth and impunctate, striate and rugose elsewhere, with fine, short scattered setae. Antennal scapus much shorter than funiculus, rounded, with a scant tuft of long setae on its dorsal side; funiculus 6-segmented, pediculus about as long as segment 2 and 3 combined; club flat, slightly longer than wide, suture 1 transverse, suture 2 recurved, appears ring-like in dorso-lateral view. Eyes separated by 2.4–2.5 × their width. **Pronotum** strongly dome-shaped, on anterior two-thirds with large, rounded asperities, only 4 or 5 of these reaching near anterior margin; posterior third lightly rugose. Vestiture consisting of mixed spatulate and fine setae, longest setae near pronotal summit. **Elytra** smooth, shiny, stria not impressed, punctures shallow, separated by 2–3 × their diameter, interstrial punctures absent. Vestiture consisting of rows of erect, lightly curved, spatulate setae on odd-numbered interstriae, and scattered, fine and very short strial setae. Ventral vestiture of fine, rather long setae. **Legs.** Protibiae with lateral edges subparallel, inner mucro strong, curved posteriorly; two tiny socketed denticle transversely set apically on posterior side close to tarsal insertion. Metatibiae broader apically, with a distinct, fine, long inner mucro, and one apical and two laterally placed thin denticles.

Male near identical to female, except fewer and shorter seta on scapus.

Biology and distribution. Only known from the type locality in dry thorny shrub vegetation in south-western Madagascar where it was sifted from leaf mould and rotten wood. Habitat occupation is similar to the close relative *M. bicolor*, both were collected in large numbers on two occasions, and localities were less than 300 km apart.

***Traglostus* Schedl, 1938**

Type species. *Traglostus exornatus* Schedl, 1938.

(Figs. 66, 67, 69, 70, 72, 73)

Diagnosis. Antennal scapus short, funicle 6-segmented, club finely pubescent without sutures. Female mandibles with a pair of sharp spines directed upwards, frons concave in both sexes, female frons with two long tufts of setae curved up and forward. Elytra with confused rows of bristle-like setae of variable length and thickness, male elytra with a pair of spines at base of declivity.

Included species:
Traglostus exornatus Schedl, 1938

Excluded species: *Traglostus longipilus* Schedl, 1958; *Traglostus pubescens* Schedl, 1941, to *Lanurgus*. *Traglostus brevisetosus* Schedl, 1957 and *T. spathulatus* Schedl, 1982 were transferred to *Lanurgus* by Beaver (2011), as synonyms of other *Lanurgus* species.

Distribution. Africa (Kenya).

Remarks. Pronotum and elytra are very much as in *Lanurgus*, but female *Traglostus* differs particularly by the two peculiar long spines on the mandibles directed dorsally. Until DNA data become available it seems prudent to treat this taxon as a valid genus. Four previous members of the genus are now in *Lanurgus*, two of which are synonymized under other species in that genus (Beaver 2011).

***Lanurgus* Eggers, 1920**
Type species. *Lanurgus barbatus* Eggers, 1920.
(Figs. 74, 77, 80)

Diagnosis. Antennal club with two procurved sutures; scapus short, with dorsal spine. Interstrial setae scale- or bristle-like, often in multiple confused rows; strial setae broad, confused. Ventral setae simple and hair-like. Protibiae with 3–6 lateral and apical denticles; metatibiae transverse near apex. Male genitalia with apophyses as long as the aedeagal body, tegmen a simple ring. Apical plate of the proventriculus only narrowly separated by a longitudinal suture, lateral teeth reinforced medially.

Included species:
Lanurgus barbatus Eggers, 1920
Lanurgus capensis Schedl, 1965
Lanurgus longipilis (Schedl, 1958) **comb. nov.** (*Traglostus*)
Lanurgus oleae Schedl, 1955
Lanurgus podocarpi Schedl, 1955
=*Traglostus brevisetosus* Schedl, 1957 (syn. Beaver, 2011)
=*Lanurgus bicolor* Schedl, 1961 (syn. Beaver, 2011)
=*Pseudohylocurus caplandicus* Nunberg, 1961 (syn. Schedl, 1962)
Lanurgus pubescens (Schedl, 1961) **comb. nov.** (*Traglostus*)
Lanurgus rhusi Schedl, 1962
=*Traglostus spatulatus* Schedl, 1982 (syn. Beaver, 2011)
Lanurgus spathulatus Schedl, 1948
Lanurgus subsulcatus Browne, 1970
Lanurgus xanthophloeae Schedl, 1957
Lanurgus xylographus Schedl, 1963
=*Lanurgus oleaeformis* Schedl, 1970 (syn. Beaver, 2011)
Excluded species: *Lanurgus cribrellus* Schedl, 1965 and *Lanurgus minutissimus* Schedl, 1961 to *Pseudolanurgus*, *Micraciops catenatus* Schedl, 1953, *Landolphianus elongatus* Schedl, 1950, *Lanurgus euphorbiae* Schedl, 1961, *Lanurgus frontalis* Schedl, 1953, *Lanurgus gracilis* Schedl, 1958, *Landolphianus minor* Schedl, 1950, *Micraciops obesus* Schedl, 1953, *Lanurgus pygmaeus* Schedl, 1965, *Lanurgus rugosipes* Schedl, 1961, *Lanurgus subdepressus* Sched, 1965, *Lanurgus widdringtoniae* Schedl, 1962, all to *Diplotrichus*.

Distribution. South Africa, Namibia, Tanzania, Kenya.

Remarks. *Traglostus pubescens* share all typical features with *Lanurgus* and is transferred to that genus. *Traglostus longipilus* is more atypical by the transverse sutures on the antennal club, very long vestiture, and two hornlike projections on the epistoma. However, it is more similar to other *Lanurgus* species than the type species of *T. exornatus*.

The 'flagellum' clade

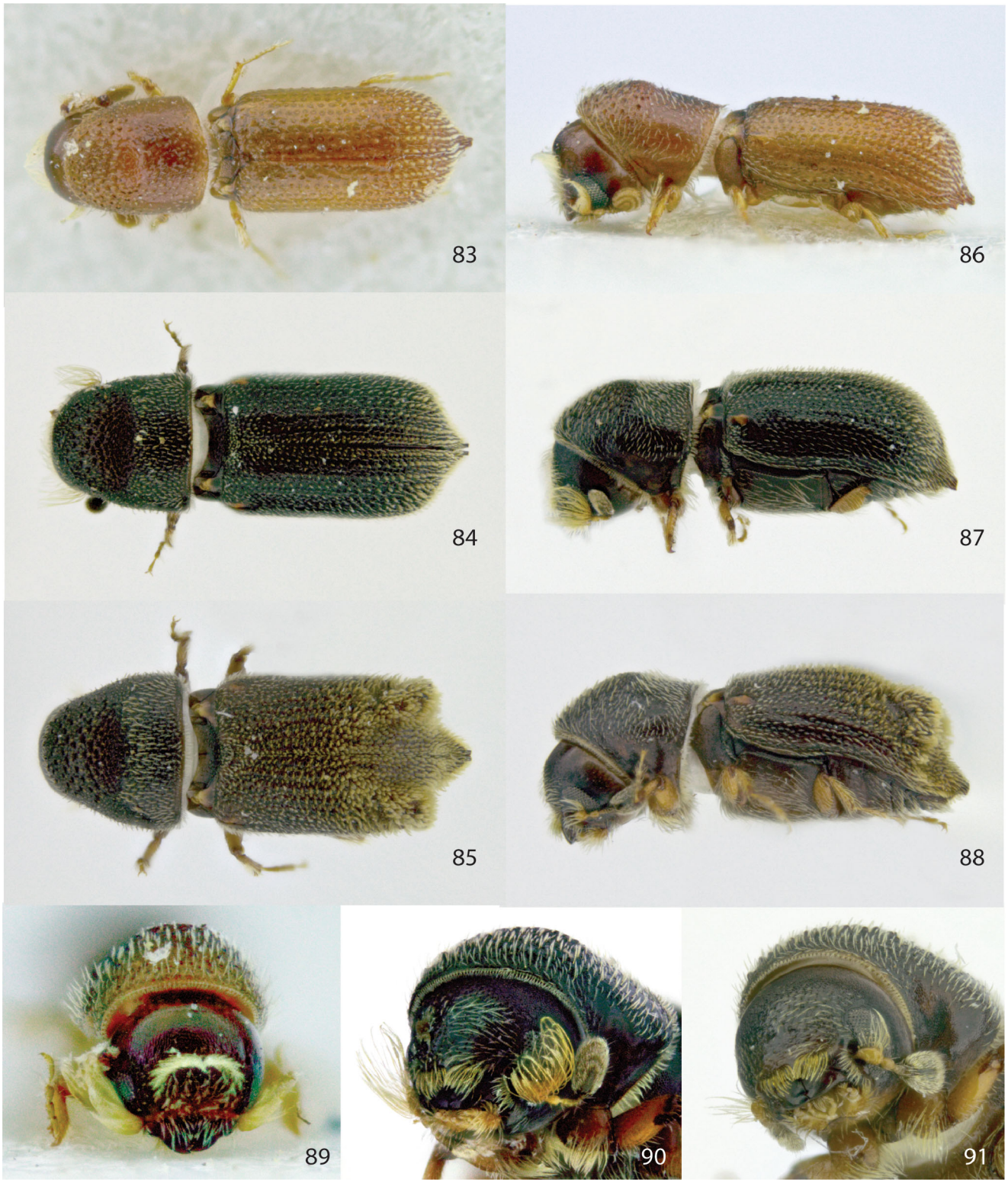
Three genera are defined by an enormously expanded and prolonged flagellum in the male aedeagus, where the tegmen and spiculum gastrale are missing. The last ventrite is slightly to strongly compressed or truncated. Most species are found in Madagascar, the remaining in south to south-eastern parts of Africa.

***Diplotrichus* Jordal, gen. nov.**
urn:lsid:zoobank.org:act:3A8EE90B-38FC-4D0E-93A8-F988F76EB5DE
=*Landolphianus* Schedl, 1950, syn. – type not designated (Alonso-Zarazaga and Lyal 2009)
=*Micraciops* Schedl, 1953, syn. – type species not designated (Alonso-Zarazaga and Lyal 2009)

Type species. *Lanurgus gracilis* Schedl, 1958.
(Figs. 75, 78, 81)

Etymology. From Greek *Diplo-*, meaning double, and *thrix*, meaning hair, referring to the split setae on ventral sclerites.

Diagnosis. Antennal scapus inflated, in females rarely with a dorsal spine, funiculus 6-segmented, antennal club with two procurved sutures. All interstriae with a single row of setae (except *catenatus* group), strial setae very fine, in rows. Protibiae with 3–4 lateral and apical denticles: metatibiae rounded near apex. Ventrites 1 and 2 and part of the metaventrite with bifid setae. Male genitalia with long apophyses, exceedingly long and enlarged flagellum, tegmen and spiculum gastrale missing.



Figs. 83–91 Dorsal, lateral and front view of **83, 86, 89** female holotype of *Pseudomicracis madagascariensis*; **84, 87, 90** female specimen (compared to the female holotype) of *Pseudomicracis dispar*; **85, 88, 91** male specimen (compared to allotype) of *Pseudomicracis dispar*

Included species:

Diplotrichus catenatus (Schedl, 1953) **comb. nov.** (*Micraciops*)

Diplotrichus elongatus (Schedl, 1950) **comb. nov.** (*Landolphianus*)

Diplotrichus euphorbia (Schedl, 1961) **comb. nov.** (*Lanurgus*)
Diplotrichus gracilis (Schedl, 1958) **comb. nov.** (*Lanurgus*)
Diplotrichus ignotus (Schedl, 1965) **comb. nov.** (*Pseudomicracis*)
Diplotrichus minor (Schedl, 1950) **comb. nov.** (*Landolphianus*)
=*Lanurgus frontalis* Schedl, 1953 **syn. nov**
Diplotrichus obesus (Schedl, 1953) **comb. nov.** (*Lanurgus*)
Diplotrichus pygmaeus (Schedl, 1965) **comb. nov.** (*Lanurgus*)
Diplotrichus rugosipes (Schedl, 1961) **comb. nov.** (*Lanurgus*)
Diplotrichus subdepressus (Schedl, 1965) **comb. nov.** (*Lanurgus*)
Diplotrichus widdringtoniae (Schedl, 1962) **comb. nov.** (*Lanurgus*)
=*Glostatus perplexus* Schedl, 1982 (syn. Beaver 2011)

Distribution. South Africa, Madagascar.

Remarks. The bifid condition of ventral setae is unique among Afrotropical micracidines and is the most reliable character matching the molecular data. Some species related to *D. ignotus* has an extended flange on the elytral apex, but they all have bifid setae and are therefore not *Pseudolanurgus*. The South African clade of species consist of the type species and one more known species, and several very similar undescribed species, suggesting a recent recolonization of the mainland (see Fig. 46).

***Pseudolanurgus* Jordal, gen. nov.**
urn:lsid:zoobank.org:act:204E9AE5-A4BF-4995-8367-F97EF1CDB9D5.

Type species. *Micracis harunganae* Schedl, 1961.
(Figs. 76, 79, 82)

Etymology. From Greek, *Pseudo,* meaning false, referring to the superficial similarity to the genus *Lanurgus*.

Diagnosis. Antennal scapus short, inflated, in females with a small tuft of setae; club with two moderately procurved and slightly bisinuate sutures, funiculus 6-segmented. Interstrial setae scale-like, in single rows; elytral apex extended, but not sharply mucronate; ventrite 5 truncated, setae on ventrites simple. Male genitalia with long apophyses, an exceedingly long and enlarged flagellum; tegmen and spiculum gastrale absent.

Included species:
Pseudolanurgus bugekeae (Schedl, 1957) **comb. nov.** (*Hylocurus*).
Pseudolanurgus harunganae (Schedl, 1961) **comb. nov.** (*Pseudomicracis*).
=*Lanurgus cribrellus* Schedl, 1965 **syn. nov.**
Pseudolanurgus minutissimus (Schedl, 1961) **comb. nov.** (*Lanurgus*)

Distribution. Afrotropical (Tanzania, Madagascar).

Remarks. This genus can be distinguished from the closely related *Pseudomicracis* Eggers, 1920 by the less procurved and slightly bisinuate sutures on the antennal club and by the slightly extended, but not mucronate, apex of the elytra. It is further distinguished from *Diplotrichus* by the simple hair-like setae on ventrites, and from *Lanurgus* by the very different male genitalia. The shared distribution between Madagascar and Tanzania is known for several scolytine genera where more recent colonisations of the mainland have taken place (e.g. Johnson et al. 2020; Jordal 2013).

***Pseudomicracis* Eggers, 1920**
(Figs. 83, 86, 89).
=*Saurotocis* Wood, 1984 **syn. nov.**
(Figs. 84, 85, 87, 88, 90, 91)

Type species. *Pseudomicracis elsae*, Eggers, 1920.

Diagnosis. Antennal scapus short, inflated, in females with a long tuft of golden setae; funiculus 6-segmented, club usually with two strongly procurved sutures, suture along first segment reaching basal and not lateral margin, corneous part usually longer than broad. Apex of elytra strongly mucronate; ventrite 5 truncated or impressed. Setae on ventral sclerites never split.

Included species:
Pseudomicracis camerunus (Hagedorn, 1909) (*Araptus*)
Pseudomicracis difficilis (Schedl, 1965) (*Micracis*)
Pseudomicracis dispar (Schedl, 1961) **comb. nov.** (*Saurotocis*)
Pseudomicracis elsae Eggers, 1920
Pseudomicracis madagascariensis (Schedl, 1961) (*Micracis*)
Pseudomicracis pennatus (Schedl, 1965) (*Micracis*)
Pseudomicracis tomicoides (Schedl, 1961) **comb. nov.** (*Saurotocis*)

Excluded species: *Pseudomicracis harunganae* (Schedl, 1961) and *Pseudomicracis bugekeae* (Schedl, 1957)

Figs. 92–95 Dorsal, lateral and front view of specimens compared to the holotype of *Phloeocurus africanus*; **92–94** female; **95** male frons

(*Hylocurus*) to *Pseudolanurgus*; *Pseudomicracis ignotus* (Schedl, 1965) to *Diplotrichus*.

Distribution. Afrotropical, mainly Madagascar.

Remarks. This genus is distinguished from all Afrotropical genera, except *Phloeocurus*, by the strongly mucronate elytral apex, and from the latter genus and the mucronate American genera by the round and twisted lateral margin of the protibiae which has only few apical teeth. Some undescribed species of *Diplotrichus* have an extended (but not mucronate) elytral apex, and a narrow and elongated corneous first segment on the antennal club, but these species have split setae on the ventral sclerites as in all other *Diplotrichus*.

The type specimens of the type species *P. elsae* were lost during the world war attack on Hamburg and no other specimens are known from collections. The description states that the apex of the elytra is prolonged and mucronate. The antennal club of the type species has possibly only weakly procurved sutures and may reach the lateral instead of basal margin. The type of *P. camerunus* is also lost. The description of *P. camerunus* is in Latin and the diagnostic characters are ambiguous, except body length is 3.5 mm. it will likely remain as a ghost taxon. With the possibility, albeit less likely, that African *Pseudomicracis* might be *Pseudolanurgus*, we seek a solution requiring the fewest possible taxonomic changes and thereby nomenclatural stability.

Both molecular and morphological data supported the synonymy of *Saurotocis* (Fig. 45). The two *Saurotocis* species transferred here, and *Pseudomicracis pennatus*, are generally similar in that males have rather deviating shapes of the elytra with excessive tubercles and confused, broad interstrial and strial setae (Fig. 85). The females of these three species (Fig. 84) are more similar to other species of *Pseudomicracis* in this respect.

***Phloeocurus* Wood, 1984**

Type species. *Hylocurus africanus* Schedl, 1957. Monotypic.

(Figs. 92–95)

Diagnosis. Antennal scapus short, inflated, with a dense tuft of setae; funiculus 6-segmented, club with two weakly procurved sutures at middle and near apex. Frons convex in both sexes. Body elongated, elytral apex mucronate, surface of elytra asperate with short spines or sharp granules on declivity, interstrial setae scale-like, in rows, intermixed with confused smaller setae. Protibiae broad, squared and flattened, with transverse row of denticles at apex; inner mucro much enlarged, curved posteriorly.

Distribution. Ethiopia to South Africa.

Remarks. This monotypic genus is unique among the Afrotropical members of Micracidini by having a broadly flattened, squared protibiae with apical, transversely set denticles, and a mucronate elytral apex similar to *Micracis*. Molecular data was not available but based on the strict Neotropical-Afrotropical split between genera, irrespective of morphological similarities, it is hypothesised that the similarity to Neotropical micracidines is not reflecting a close evolutionary relationship.

Key to the Afrotropical genera of Micracidini

Includes species which have protibiae with one or more apical denticles placed on the posterior face of the protibiae, rough asperities on most of the anterior half of the pronotum, entire eyes, and a small to large tuft of setae on the female scapus.

1. Scapus much longer than broad, as long or longer than funiculus; funiculus 5-segmented. 2

– Scapus shorter than funiculus, inflated, or extended into dorsal horns, funiculus 6-segmented. 4

2. Anterior sixth and lateral thirds of pronotum smooth, asperate between middle and anterior sixth; female scapus with a long triangular tuft of golden setae (Tanzania). .. ..***Leiomicracis***

– Anterior half of pronotum with distinct asperities reaching anterior margin and near lateral margins; female scapus with scant, long setae. 3

3. Antennal club elongated, glabrous and shiny on both sides, apex of ventrite 5 bottleneck-shaped (Tanzania and Congo). .. ..***Dendrochilus***

– Antennal club as long as broad, on anterior face with one procurved suture marked by setae near anterior margin, ventrite 5 broadly rounded (Africa). .. ..***Afromicracis***

4. Protibiae very broad, parallel-sided, with a transverse row of apical denticles on its posterior side (Kenya). .. ..***Phloeocurus***

– Protibiae not parallel-sided, twisted, with 1 or 2 lateral denticles and 1–5 denticles on the posterior side near apex. 5

5. Pronotum in both sexes with broad scale-like setae, in males ventrites IV and V with transverse row of caudally pointed broad setae; antennal club with suture 1 absent on median three quarter, segment 1 and 2 fused, corneous and shiny (Tanzania). .. .. ***Neomicracis***

– Pronotum with hair-like or bristle-like setae; antennal club with two complete sutures (or rarely not visible), at least segment 2 and 3 pubescent. 6

6. Elytra with erect spatulate setae on odd-numbered interstriae only; pronotum strongly dome-shaped, 10–20 large asperities on anterior half, very few near anterior margin; tiny species, 0.6–0.8 mm; aedeagal tegmen a simple ring (Madagascar). .. .. M***icrolanurgus***

– Elytra with erect setae on all interstriae, asperities on pronotum more numerous, smaller, evenly distributed; body size more variable; tegmen with median struts. 7

7. Frons in both sexes concave; each mandible in females with a long hornlike structure pointed dorsally; antennal club pubescent, without sutures. .. ..***Traglostus***

– Frons in at least the male, or in both sexes, convex; mandibles without horns; antennal club with two complete sutures (exceptions in some *Pseudomicracis*). 8

8. Elytra with confused rows of bristle-like setae on at least some interstriae; ventral setae simple; male genitalia with complete tegmen and median struts, spiculum gastrale, and apophyses only slightly longer than aedeagal body (mainly South Africa). .. .. ***Lanurgus***

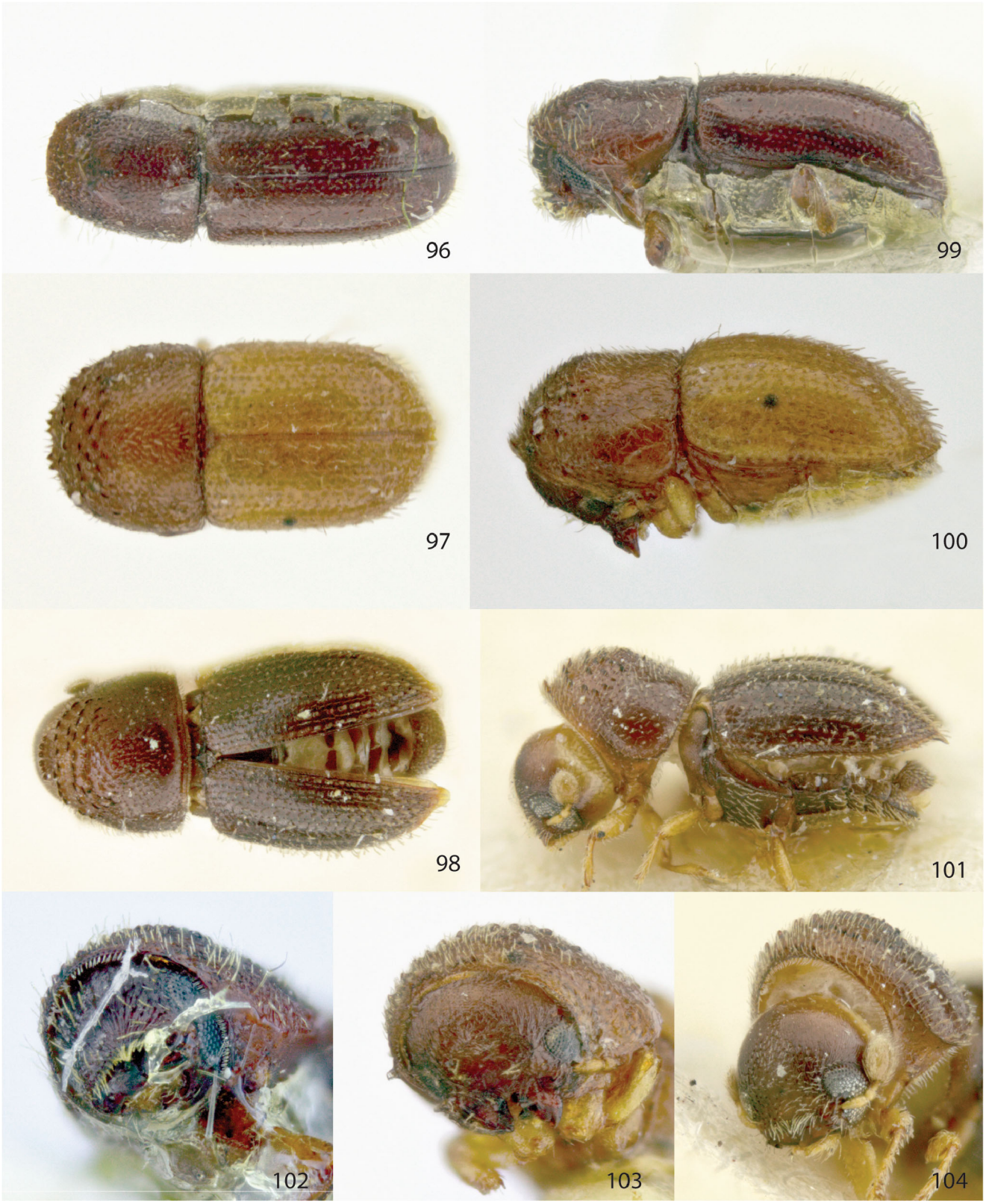
– Elytra usually with single rows of spatulate or bristle-like setae (if confused then ventral setae bifid); ventral setae simple or bifid; male genitalia with enlarged and very long flagellum, apophyses very long, spiculum gastrale and tegmen missing (‘flagellum group’). 9

9. Ventrites I, II and metaventrite with bifid setae; elytral declivity gently rounded, rarely slightly mucronate, last ventrite apically rounded (Madagascar and South Africa). .. ..***Diplotrichus***

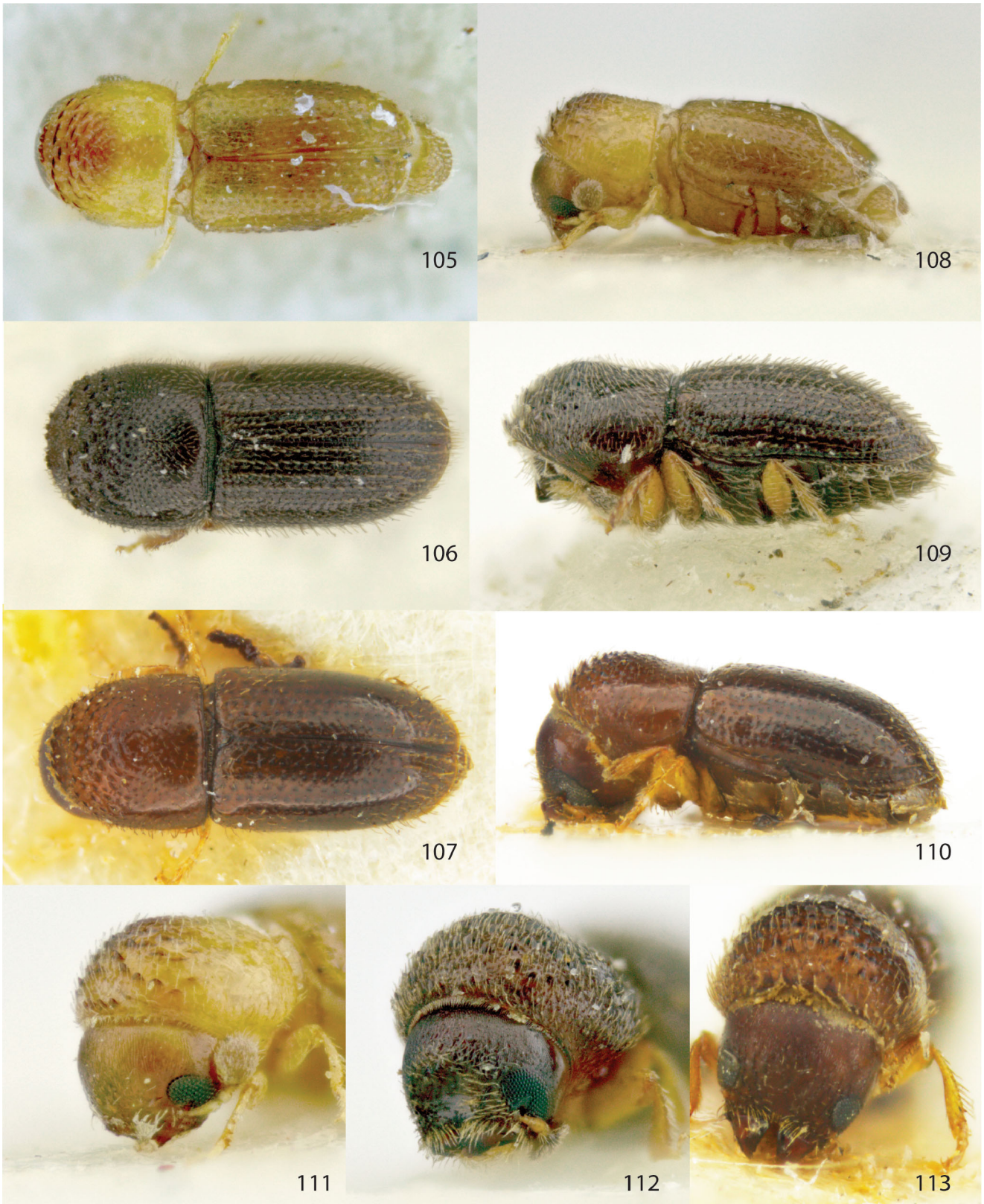
– Ventral setae simple; elytral apex slightly extended or inflated to strongly mucronate; last ventrite apically slightly to strongly truncated. 10

10. Elytral apex strongly mucronate; antennal club with first suture usually strongly procurved, beginning at basal margin (Madagascar and Tanzania). .. .. ***Pseudomicracis***

– Elytral apex slightly extended and inflated, sutures on antennal club procurved, originating at lateral margins, slightly bisinuate (Madagascar and Tanzania). .. ..***Pseudolanurgus***



Figs. 96–104 Dorsal, lateral and front view of the holotype of **96, 99, 102** *Acanthotomicus intermedius*; **97, 100, 103** *Eidophelus agnathus*; **98, 101, 104** *Karlsenius attenuatum*



Figs. 105–113 Dorsal, lateral and front view of the holotype of **105, 108, 111** *Karlsenius klainedoxae*. **106, 109, 112** *Karlsenius nigrinum*; **107, 110, 113** *Karlsenius nitidum*

Taxa removed from Micracidini

Several taxa are not members of Micracidini and transferred to their appropriate genus.

IPINI

Acanthotomicus intermedius (Schedl, 1977) **comb. nov.** (*Dendrochilus*)
(Figs. 96, 99, 102)

The type of this species is partly embedded in glue. The frons is visible and aciculate as in many Afrotropical *Acanthotomicus*, and the eyes are large and broadly emarginate as in most Ipini. Together with the characteristic humpbacked pronotum typical for *Acanthotomicus*, this species is transferred to that genus.

DRYOCOETINI

Xylocleptes villiersi (Lepesme, 1942) **comb. nov.** (*Thamnurgus*, via *Dendrochilus*)

For some unjustified reason, this species was transferred to *Dendrochilus* by Schedl (1957). It is a typical species of *Xylocleptes* which seems largely mixed with *Thamnurgus* Eichhoff and *Cyrtogenius* Strohmeyer as currently classified. A revision of Afrotropical Dryocoetini is therefore much needed.

ERNOPORINI

Eidophelus agnathus (Schedl, 1942) **comb. nov.** (*Miocryphalus*)
(Figs. 97, 100, 103)
Eidophelus ciliatipennis (Schedl, 1979) **comb. nov.** (*Miocryphalus*)

Species in *Eidopheles* were recently revised by Johnson et al. (2020). Two species which currently resides in *Afromicracis* are *Eidophelus* as recognized by the flattened protibiae with lateral denticles, entire eyes, and antennal clubs without sutures. These species are not Afrotropical (*E. agnathus*, Australia; *E. ciliatipennis*, Fiji), which further exclude relationship to the Afrotropical genus *Afrocosmoderes*.

TRYPOPHLOEINI

***Karlsenius* Jordal, gen. nov.**
urn:lsid:zoobank.org:act:
Type species. *Miocryphalus nigrinus* Schedl 1957

Etymology. Named after Karl Schedl—a senior Austrian taxonomist—in gratitude for all the mess he made in bark beetle taxonomy which made younger apprentices busy for years in revising dodgy classifications. The Latin suffix -*senius* is a neuter nominal adjective, meaning senior.

Diagnosis. Frons sexually dimorphic in at least one species, cuticle on vertex and behind eyes finely strigose. Eyes weakly to distinctly emarginated. Antennal scapus elongated with scattered setae, funiculus 4-segmented, club flat and pilose without sutures. Pronotum declivitous and strongly asperate on anterior half, anterior margin elevated, with 4–6 recurved small teeth; posterior half of pronotum shiny, finely punctured, basal margin with a fine, sharp rim which continues laterally; vestiture consisting of fine hair-like setae. Scutellum triangular, flush with elytra. Elytra with striae not impressed, punctures minute. Interstriae smooth, shiny. Vestiture consisting of single rows of rectangular or spatulate interstrial setae and fine hair-like strial setae. Protibiae variable, narrow to broad, with 4–7 lateral socketed teeth. Mesocoxae moderately separated by little more than the width of scapus.

Included species
Karlsenius attenuatum (Eggers, 1935) **comb. nov.** (*Stephanoderes*, via *Miocryphalus*)
(Figs. 98, 101, 104)
Karlsenius ghanaensis (Schedl, 1977) **comb. nov.** (*Cryphalomorphus*, via *Eidophelus*)
Karlsenius klainedoxae (Schedl, 1957) **comb. nov.** (*Miocryphalus*)
(Figs. 105, 108, 111)
Karlsenius nigrinum (Schedl 1957) **comb. nov.** (*Miocryphalus*)
(Figs. 106, 109, 112)
Karlsenius nitidum (Schedl, 1965) **comb. nov.** (*Eidophelus*, via *Miocryphalus*)
(Figs. 107, 110, 113)

Distribution
Tropical Africa, Madagascar

New record. *Karlsenius nigrinum*: Madagascar, Sakalava beach, MA-01-04B-05, Malaise trap, B. Fischer, leg, 2001. **New country.**

Remarks
Species in this genus have nearly all the salient characters of *Afrocosmoderes*, except for the fine hair-like setae (vs. scale-like) on a flat, shiny and finely punctate pronotal disc (vs. gradually rounded, granulated), and which becomes abruptly declivitous on anterior third (vs. gradually curved). In these aspects the new genus relates to *Hypothenemus* but is distinguished by the very different antennal club. One may note, however, that at least one species of *Hypothenemus* is

known to have a rounded club without sutures (Johnson et al. 2016). It seems problematic to place all *Karlsenius* species in *Hypothenemus*, particularly because *K. nigrinum* is dimorphic in the frons, which indicate normal outbreeding. As *Afrocosmoderes* and *Hypothenemus* are sister genera (Johnson et al. 2020; Pistone et al. 2018), it seems equally possible that *Karlsenius* is the closest relative to one or the other.

Karlsenius nitidum has no antennae available on the holotype but otherwise exhibits the general body shape of *Hypothenemus* and *Karlsenius*. Because this species is near identical *to K. klainedoxae*, it is tentatively placed in the same genus. Even though this paper relates to species previously placed in Micracidini, it is worth noting that *Eidophelus ghanaensis* (Schedl, 1977) (see Johnson et al. 2020) is fairly similar to the type species of *Karlsenius* and therefore transferred to this genus.

Note added in press: a 28S partial sequence place *Karlsenius klainedoxae* in Trypophloeini, but clearly separate from both *Hypothenemus* and *Afrocosmoderes*.

Discussion

Previous phylogenetic studies have indicated a very early origin of Micracidini which is likely the oldest tribe within the subfamily, dating back to the Cretaceous (Jordal and Cognato 2012; Jordal et al. 2008; Pistone et al. 2018). The time estimates provided here may be slightly exaggerated, as some studies have indicated a younger age for the subfamily, around 90–70 Ma (McKenna et al. 2009; Shin et al. 2017). However, irrespective of the root age, Micracidini will not be as young as tertiary in age in any of the proposed scenarios because the tribe is almost as old as the subfamily. Earlier mistakes in the classification can therefore be explained in part by slow morphological evolution, confounded by an ancient origin and subsequent radiations within the tribe. One may note that genera such as *Afromicracis*, *Lanurgus* and *Diplotrichus* could need further splitting into multiple genera, but no consistent morphological differences have yet been found to justify erection of further genera.

Many new morphological characters were discovered and were helpful in diagnosing genera and groups thereof. It is quite unusual that the shape of setae is diagnostic for a genus, as documented by the split setae on ventrites in the new genus *Diplotrichus*. This feature is nevertheless the most consistent and is the only reliable external character distinguishing *Diplotrichus* from *Lanurgus* and *Pseudolanurgus*. One may also note that parts of the antennae are very informative. Not necessarily the presence or absence of an elongated horn on the scapus, but rather the length of the scapus compared to the funiculus. Furthermore, the number of funicular segments accurately diagnose clades in Micracidini; we know this feature may vary within some genera (Jordal 1998; Jordal et al. 2004), or even within a species (Johnson et al. 2020). Similarly, the sutures in the antennal club also reflect evolution quite accurately, while past taxonomic work on this tribe never took this information into account.

Despite the recognition of many new diagnostic characters, Afrotropical micracidines are still a challenge to identify correctly. In view of their considerable old age, the limited differentiation of external morphological characters is puzzling, although by no means exceptional among beetles, or other animals. The limited variation in external characters has therefore motivated investigation of internal morphological characters, which has previously proven a rich source of taxonomically informative characters in Scolytinae (Johnson et al. 2020; Jordal 2009; Jordal and Kaidel 2017). Male genitalia differ substantially between externally similar species in the genera *Lanurgus* and *Diplotrichus* and reflect more accurately than external characters the ancient split between these two lineages. While aedeagal apophyses are of normal length in *Lanurgus* and *Microlanurgus*, and the tegmen and spiculum gastrale are present, the apophyses are extremely elongated and the tegmen and spiculum gastrale absent or not recognizable in the 'flagellum' group where *Diplotrichus* belong. Another internal structure, the proventriculus, is easily characterized for the tribe, but *Lanurgus* differ from most other genera by the narrow suture and enforced lateral to apical teeth in the anterior plate. The two genera *Afromicracis* and *Dendrochilus* have multiple crop spines attached on a tubercle base as another example of easily recognized shared characters. They also have many species with a coiled, thin flagellum in the male genitalia, and together with *Neomicracis* have only a single seta on the hindwing precosta. All these examples demonstrate the great utility of internal anatomical structures in assessing relationships and placing new taxa in the correct genus, or group of genera. In the molecular era, the application of morphological character is therefore by no means in vain. Rather the contrary, taxonomically informative characters are immediately apparent once a solid phylogeny is established based on broadly sampled molecular and morphological data. This is of great value when molecular data are not possible to obtain.

The Malagasy–African faunal interchange

Madagascar and the Zambesian region of the African mainland stand out as the historically most important drivers of Afrotropical diversity in Micracidini. The Zambesian region is the most likely ancestral area for the tribe, given the endemic distribution of several basal taxa. Subsequent radiations, for instance of the largely Zambesian dominated *Afromicracis* clade into the Congolian and Southern African regions, further support this view. These are the most widely distributed micracidine genera, but nevertheless restricted to the African continent.

Two particularly important range expansions out of the Zambesian region resulted in markedly increased diversification. The first significant event involved the colonization of

the Neotropics (66.2 Ma), which occurred just after the origin of the tribe near the Cretaceous-Tertiary boundary. The diversity of Neotropical (and Nearctic) micracidines is now the largest in the tribe (Wood and Bright 1992). The second significant event was the colonization of Madagascar, which possibly only happened once, in the Palaeocene (59.6 Ma). Both Madagascar and the South American continent had then already been separated from Africa by oceans for a long time and therefore the ancestors of these two lineages must have dispersed over open waters. Broad oceanic barriers have therefore been significant restrictions to further dispersal in Micracidini. The same pattern was found in the wood-boring weevil subfamily Platypodinae which dispersed from Africa into the Neotropics only three times during the Palaeocene to Oligocene, and to Madagascar only once, in the Eocene (Jordal 2015).

Madagascar is particularly diverse in micracidines, with several clades endemic to this island. In addition to the species poor *Microlanurgus*, the island is likely the ancestral source of *Lanurgus*, *Diplotrichus*, *Pseudolanurgus* and *Pseudomicracis*. African origin of Malagasy lineages is the most common pattern inferred across plants and animals (Yoder and Nowak 2006) and these data fit nicely with the general biogeographical pattern (see also Jordal 2013). It is also commonly inferred that colonization of Madagascar is a rare event, and that dispersal towards the African mainland occurred more frequently, especially during Miocene and later (Bukontaite et al. 2015; Jordal 2013), consistent with changes in oceanic and wind currents after the Oligocene period (Ali and Huber 2010). In at least three cases micracidines recolonized the African mainland, which has further contributed to increased diversity of the tribe. Only the oldest of these events (*Lanurgus*) resulted in a rather broad south- to eastern African distribution, with the other two much more restricted. In all its simplicity, it may be taken as yet another evidence for limited dispersal capacity in micracidine beetles.

Acknowledgements I thank the curators in the natural history museum in Vienna (H. Schillhammer), Paris (H. Perrin), and Tervuren (S. Hanot), for facilitating visits and loans from those institutions. Museum visits was funded by the EU Synthesys programme. I would also like to thank L. Lindblom and S. Mugu for assistance with DNA sequencing.

Funding Open Access funding provided by University of Bergen (incl Haukeland University Hospital).

Data availability The molecular genetic datasets generated during the current study and referred to in Table 2 are available in GenBank, [https://www.ncbi.nlm.nih.gov/genbank/].

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