



## Taxonomy

# *Afrocosmoderes* bark beetles (Curculionidae, Scolytinae): an ancient, but overlooked, species radiation of pygmy borers in Madagascar

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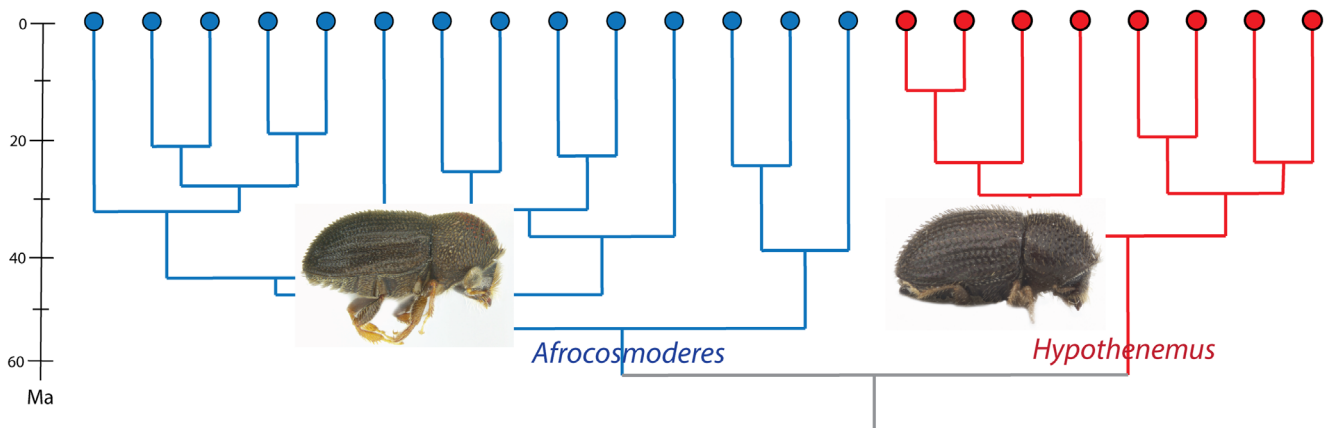
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The recently described genus *Afrocosmoderes* Johnson and Jordal, 2020 forms the sister group to *Hypothenemus* Westwood, 1836 that includes a range of worldwide tramp species such as the coffee berry borer *H. hampei* (Ferrari, 1867). *Afrocosmoderes* differs strongly from *Hypothenemus* in their distribution, being largely restricted to Madagascar and elsewhere found only in southeastern part of Africa. DNA data from multiple genes indicated an ancient origin in the early Cenozoic era. This is one of the oldest extant groups of bark beetles on Madagascar with a possible geographical origin from the Palearctic. Species in *Afrocosmoderes* are despite their ancient origin remarkably similar to each other morphologically and DNA data would be advisable in many cases to confirm species identity. Only a few characters, particularly those associated with the male genitalia, are indicative of relationships supported also by molecular data. Ecological features are therefore more promising in grouping species, such as host plant type, with only two possible origins of feeding in lianas. The genus is taxonomically revised with a total of 19 species included, in which 12 are described as new to science: *Afrocosmoderes asper*, **sp. nov.**, *Afrocosmoderes brevicostatus*, **sp. nov.**, *Afrocosmoderes carinatus*, **sp. nov.**, *Afrocosmoderes confertus*, **sp. nov.**, *Afrocosmoderes lenifrons*, **sp. nov.**, *Afrocosmoderes longisetus*, **sp. nov.**, *Afrocosmoderes longus*, **sp. nov.**, *Afrocosmoderes parvus*, **sp. nov.**, *Afrocosmoderes plenus*, **sp. nov.**, *Afrocosmoderes saetiger*, **sp. nov.**, *Afrocosmoderes seriatus*, **sp. nov.**, all from Madagascar, and *Afrocosmoderes zambesianus*, **sp. nov.** from Tanzania. *Afrocosmoderes africanus* (Schedl), **comb. nov.** is transferred from *Eidophelus* Eichhoff, 1875.

**Keywords:** Afrotropics, bark beetles, Scolytinae, taxonomy, time tree

## Graphical abstract



## Introduction

Many forest entomologists are familiar with a group of tiny wood-boring beetles called pygmy borers, particularly those in the genus *Hypothenemus* Westwood, 1836 and related genera in the tribe Trypophloeini Nüßlin, 1911. Regardless of their small body size, they are found everywhere in warmer climates around the globe and contribute a large proportion of the wood-boring fauna. Some species can be highly destructive pests, especially the coffee berry borer, which damage coffee berries in coffee-producing countries. Whereas these small species are a relatively well-known and ubiquitous group in tropical forests (Schedl 1956, Beeson 1961, Browne 1961), their origin and closest relatives have until recently been largely unknown. From a group of species formerly scattered among several poorly characterized genera, Johnson et al. (2020b) erected a new genus named *Afrocosmoderes* Johnson and Jordal, 2020 for the sister clade to *Hypothenemus* (see also Pistone et al. 2018). Their common ancestry with the sib-mating species in *Hypothenemus* makes *Afrocosmoderes* an interesting group which can provide clues about the evolution of permanent inbreeding (Kirkendall 1993) and paternal genome elimination (Brun et al. 1995).

*Afrocosmoderes* is a strictly south-eastern Afrotropical genus mainly found on Madagascar (Johnson et al. 2020b). These species are rarely collected and therefore little is known about their distribution and biology. As for many groups of small beetles, typically just a little longer than one millimeter, they are less frequently reported than larger species (Stork et al. 2024). However, careful hand collecting during recent field expeditions in Africa and Madagascar has resulted in the discovery of many new species of *Afrocosmoderes*. Some of these species can be collected repeatedly in a restricted area by an experienced collector and some of the apparent rarity might be due to ignorance rather than low abundance.

With the recent field expeditions, it has become evident that *Afrocosmoderes*, to some extent, prefer lianas as the breeding substrate and thereby provide a test system on the evolution of host plant growth forms. *Hypothenemus* and all other genera in the tribe are largely twig and small branch phloem feeders, which indicate that feeding in small branches and twigs is the ancestral state for *Afrocosmoderes*. With the many new species described here, including detailed observations on their breeding biology, the implementation of molecular methods in reconstructing a reliable phylogeny provides a first step in evaluating this hypothesis and in reconstructing the biogeographical history for *Afrocosmoderes* and near relatives.

Among the seven currently known species in *Afrocosmoderes* (Johnson et al. 2020b), five are endemic to Madagascar, and two are known only from southern Africa. The genus therefore has a transoceanic distribution which requires historical dispersal across the Mozambique channel (Yoder and Nowak 2006). One may expect, if their ancestor was Afrotropical, that the Malagasy species originated before the strong trade winds began to dominate during the early Miocene and onwards (Ali and Huber 2010, Samonds et al. 2012). These winds have, since that time, blown in an almost entirely westerly direction. Mainland species, on the other hand, may have descended from a Malagasy lineage in the Miocene or later, although colonization towards the mainland is extremely rarely reported (except diving beetles, see Bukontaite et al. 2015). Alternatively, the mainland lineage is older than Miocene and perhaps forms the oldest lineage as sister to, or a grade leading to, the Malagasy lineage. Patterns in other bark beetle genera are quite mixed (eg Eliassen and Jordal 2021, Jordal 2021a,b, 2023), however, the hypotheses raised are therefore somewhat tentative rather than an absolute hypothesis.

Morphological variation between species, including the many new discoveries reported here, is extremely limited and species have been notoriously difficult to differentiate based on



external morphological features. In perspective of a likely early origin as the sister group to *Hypothenemus* about 50 Ma (Pistone et al. 2018), one may speculate if similar morphologies reflect a recent radiation on Madagascar, with few old lineages and the majority of diversity being rather young. If not, one may infer morphological stasis for these beetles. Morphological characters are therefore coded (eg Figs 1 to 25) and analyzed phylogenetically to visualize the level of phylogenetic congruence with molecular data and thereby guide the use of morphological variation in taxonomy and identification when molecular data are not available.

Altogether, 12 new species are described in this article (Table 1). A key to all species is provided to enable species identification and is supported by DNA barcode data for many of these. Descriptions and the identification key are illustrated with photos of all species.

## Materials and Methods

Type material and other material studied are deposited in the following collections:

CAS—California Academy of Science, San Francisco, USA  
 MNHN—Muséum National d'Histoire Naturelle, Paris, France  
 NHMW—Naturhistorisches Museum, Vienna, Austria  
 ZMUB—University Museum of Bergen, Norway

Beetles were studied in a Leica MZ16 stereoscope (7.1× to 115×). Measurements of body length included the range from the anteriormost point of the pronotum to the apical margin of the elytra, and width was measured at the broadest point; all measures were made in perpendicular angles to the beetle. An eventual gap between elytra and pronotum was subtracted from the total length. Photographs were taken in a Leica M205C; multiple z-stacked photos were aligned and combined in Zerene Stacker (<https://zerenestacker.com>).

Internal morphological characters (Figs 15 to 25) included examination of the inner face of the proventriculus (Nobuchi 1969), and the male genitalia (see eg Jordal 1998). These parts, and antennae and mouthparts were mounted from specimens already macerated by proteinase K in the DNA extraction procedure. Selected slide preparations were photographed in a Leica microscope with integrated Leica LAS stacking and alignment software.

DNA from four gene fragments were amplified (Mugu et al. 2018) and Sanger sequenced: 690 bp of Cytochrome Oxidase I (COI), 561 bp of Elongation Factor 1 $\alpha$  (EF-1 $\alpha$ ), 435 bp of the Poly(A)-binding protein 1 (PABP1), and 677 aligned positions of the large ribosomal subunit (28S). Sequences were submitted to GenBank with accession numbers listed in Table 2. The 28S sequences were aligned by the software Muscle (Edgar 2004) using default settings. Taxon sampling included all recently collected *Afrocosmoderes* species, eight species of the sister group *Hypothenemus* representing all major morphological forms of that genus, and a broad selection of other outgroup species in Trypophloeini, Ernoporini, and Hypoborini (Table 2).

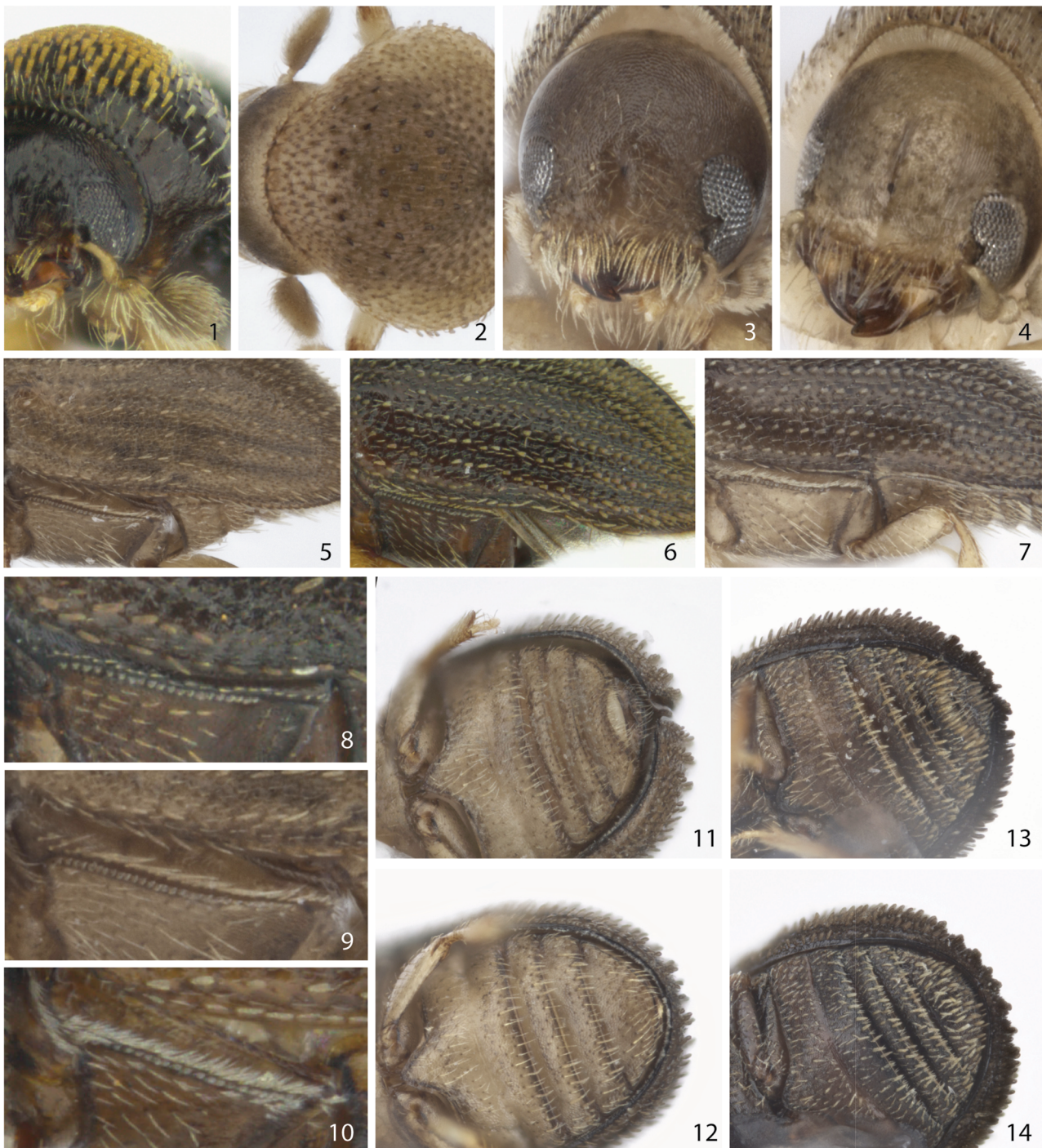
Morphological and ecological characters were analyzed by parsimony using implied reweighting in PAUP (Swofford

2002). Potentially parsimony informative characters included the following character states:

1. Eye shape, anterior margin: 0, entire (Fig. 1); 1, emarginated (Figs 3, 4).
2. Funicular segments: number of segments (3, 4, or 5), see Figs 19 and 20.
3. Male frons: 0, smooth (Fig. 1); 1, carinate (Fig. 4); 2, grooved (Fig. 3).
4. Anterior margin of the male pronotum: 0, rounded (Fig. 27); 1, protruding (Fig. 2).
5. Male pronotal setae: 0, hair-like; 1, broad and spatulate (Fig. 1).
6. Elytral main setae on lateral interstriae: 0, mixed bristles and broader scale-like setae (Fig. 5); 1, scale-like setae only (Figs 6, 7).
7. Pattern of interstitial main setae posterolaterally on the elytra: 0, regular (Fig. 7); 1, irregular (Fig. 6).
8. Elytral ground vestiture: 0, absent (Fig. 76); 1, hair-like (Fig. 7); 2, scale-like (Figs 5, 6).
9. Metanepisternal setae: 0, simple (Fig. 8, 9); 1, split (Fig. 10).
10. Length of metanepisternal setae: 0, short (Fig. 8); 1, long (Figs 9, 10).
11. Main setae on abdominal ventrites: 0, thin bristles (Figs 11, 12); 1, spatulate scales (Figs 13, 14).
12. Shortest setae on ventrites: 0, hair-like (Figs 11, 12); 1, trifold (Figs 13, 14).
13. Number of socketed denticles along the lateral margin of protibia: 0, 4 to 6 (Figs 94, 95); 1, 7 to 10 (Figs 53, 55).
14. Number of socketed denticles along the lateral and apical margin of metatibia: 0, 3 to 4; 1, 5 to 6.
15. Anterior plate of the proventriculus: 0, most of its surface smooth except sutural teeth (left part of Fig. 16, 17); 1, asperate or finely toothed (Fig. 15).
16. Apex of aedeagus: 0, rounded (Figs 23, 24); 1, constricted and extended into an apical tongue (Figs 21, 22).
17. Aedeagus, major basal sclerites: 0, rounded pieces (Fig. 21); 1, forming a continuous elongated loop (Figs 22 to 24); 2, base V-shaped and apically open ended (Fig. 25).
18. Aedeagus, basal sclerites with lateral tooth: 0, absent (Figs 24, 25); 1, present (Figs 21, 22).
19. Feeding and breeding in: 0, tree branches; 1, lianas.
20. Geographical distribution: 0, Palearctic; 1, Southern Africa; 2, Madagascar.

Morphological data were also analyzed in a Bayesian framework using MrBayes (Ronquist and Huelsenbeck 2003), with independent character rates (rates = gamma, ratepr = variable). Five million generations were run using two parallel sets of one cold (temp = 0.3) and three heated chains in the Markov Chain Monte Carlo search.

Combined molecular data were analyzed using separate models for each codon position and for the ribosomal data, running for 10 million generations. These data were also analyzed in Beast where first and second positions were combined to reduce unnecessary complexity in stabilizing the search. The time tree was calibrated using a minimum age of 100 myrs for



**Figs. 1 to 14.** Details of important morphological characters in *Afrocosmoderes*. 1) Golden setae on the pronotum and entire eye of male *A. plenus*; 2) narrowly prolonged pronotum in male *A. carinatus*; 3) groove in female frons of *A. longus*; 4) longitudinal carina in male frons of *A. carinatus*; 5) long bristle-like setae on the lateral elytral interstriae of *A. longisetus*; 6) confused scale-like setae on posterolateral interstriae, and coarse scale-like ground vestiture, of *A. confertus*; 7) hair-like ground vestiture and mainly regular rows of interstitial setae of *A. pellitus*; 8) short, simple (unifid) setae on metanepisternum of *A. lenifrons*; 9) long, simple setae on the metanepisternum of *A. longisetus*; 10) long split setae on the metanepisternum of *A. seriatus*; 11) abdominal ventrites of male and 12) female *A. pellitus*; 13) ventrites of male and 14) female *A. asper*. Note the reception of the last tergite reaching a procurved last abdominal ventrite in the males.

the split between Scolytinae and other weevils and 90 myrs for the scolytine taxa included here (st. dev. = 10). Due to the thorough estimate in a previous study (Pistone et al. 2018), a normal distribution was used for these node ages.

Ancestral geographical ranges were estimated in RASP (Reconstructing Ancestral State in Phylogeny) using the Bayesian Binary Markov chain Monte Carlo algorithm (Yu et al. 2020). A maximum of two ancestral areas and a model of



**Table 1.** Currently valid species in *Afrocosmoderes**Afrocosmoderes africanus* (Schedl), comb. nov.

*Afrocosmoderes asper* Jordal, sp. nov.  
*Afrocosmoderes brevicostatus* Jordal, sp. nov.  
*Afrocosmoderes carinatus* Jordal, sp. nov.  
*Afrocosmoderes confertus* Jordal, sp. nov.  
*Afrocosmoderes grobleri* (Schedl, 1961)  
*Afrocosmoderes lenifrons* Jordal, sp. nov.  
*Afrocosmoderes longisetus* Jordal, sp. nov.  
*Afrocosmoderes longus* Jordal, sp. nov.  
*Afrocosmoderes madagascariensis* (Schedl, 1961)  
*Afrocosmoderes niger* (Schedl, 1961)  
*Afrocosmoderes parvus* Jordal, sp. nov.  
*Afrocosmoderes pellitus* (Schedl, 1953)  
*Afrocosmoderes pennatus* (Schedl, 1953)  
*Afrocosmoderes plenus* Jordal, sp. nov.  
*Afrocosmoderes saetiger* Jordal, sp. nov.  
*Afrocosmoderes schedli* Johnson, 2020  
*Afrocosmoderes seriatus* Jordal, sp. nov.  
*Afrocosmoderes zambesianus* Jordal, sp. nov.

variable area frequencies (F81) were used in searches based on a Bayesian consensus time tree. Areas included relevant regions in the Afrotropical realm based on Linder et al.'s statistically defined subareas (Linder et al. 2012).

**Results****Molecular Phylogeny**

Beast analysis of the combined molecular data resulted in a well resolved tree topology for the ingroup with all except four nodes receiving support higher than 0.95 (Fig. 26). Four species groups were strongly supported, here indicated as clades A, B, C, and A. *plenus* as the only solitary lineage. All eight species of *Hypothenemus* formed a maximally supported sister clade to *Afrocosmoderes*.

Bayesian mcmc searches in MrBayes resulted in standard deviation of split frequencies below 0.01, with PDFR equal 1.0. The consensus tree was well resolved and largely congruent with the Beast analysis, with some additional nodes moderately

**Table 2.** DNA accession numbers for samples included in the molecular phylogenetic analyses

Code	Tribe	Species	Country	Leg.	CO1	EF-1a	28S	PABP1
CLar01	Lixini	<i>Larinus</i> sp.	Russia	B. Jordal	HQ883622	HQ883707	HQ883541	KX160752
MoPor01	Amorphocerini	<i>Porthethes hispidus</i>	South Africa	R. Oberprieler	HQ883666	HQ883737	HQ883577	KX160765
CrCry02	Cryphalini	<i>Cryphalus asperatus</i>	Sweden	B. Jordal	JX263795	-	JX263688	MF771610
CrCry04	Cryphalini	<i>Cryphalus longus</i>	Russia	B. Jordal	JX263796	JX264088	JX263689	MF771611
CrPti01	Ernoporini	<i>Eidophelus</i> sp. 1	Papua New Guinea	A. Sequeira	-	JX264095	JX263698	MF771622
CrErn04	Ernoporini	<i>Eidophelus spessivtzevi</i>	Russia	B. Jordal	JX263800	JX264091	JX263694	MF771616
CrErn03	Ernoporini	<i>Ernopus tiliae</i>	Czech Republic	K. Novakova	EU191841	EU191873	JX263693	MF771615
CrPro01	Ernoporini	<i>Procryphalus mucronatus</i>	USA	B. Jordal	JX263804	JX264094	JX263697	MF771621
HyDac01	Hypoborini	<i>Dacryostactus kolbei</i>	Angola	S. Roth	KY805902	KY805872	KY805979	MF771658
HyLip02	Hypoborini	<i>Liparthrum nigrescens</i>	Spain	K. Harkestad	AY377032	AY377096	AF308370	MF771661
CrAfr01	Trypophloeini	<i>Afrocosmoderes asper</i>	Madagascar	B. Jordal	PX056634	PX068273	PX059509	PX068282
CrAfr02	Trypophloeini	<i>Afrocosmoderes brevicostatus</i>	Madagascar	B. Jordal	PX056635	PX068274	PX059510	PX068283
CrAfr11	Trypophloeini	<i>Afrocosmoderes carinatus</i>	Madagascar	B. Jordal	PX056643	PX068278	PX059518	PX068290
CrAfr06	Trypophloeini	<i>Afrocosmoderes grobleri</i>	South Africa	B. Jordal	PX056639	-	PX059514	PX068286
CrAfr07	Trypophloeini	<i>Afrocosmoderes lenifrons</i>	Madagascar	B. Jordal	PX056640	-	PX059515	PX068287
CrCor01	Trypophloeini	<i>Afrocosmoderes longisetus</i>	Madagascar	B. Jordal	KY805892	-	KY805966	MF771608
CrAfr04	Trypophloeini	<i>Afrocosmoderes longus</i>	Madagascar	B. Jordal	PX056637	PX068276	PX059512	PX068285
CrAfr03	Trypophloeini	<i>Afrocosmoderes parvus</i>	Madagascar	B. Jordal	PX056636	PX068275	PX059511	PX068284
CrAfr08	Trypophloeini	<i>Afrocosmoderes pellitus</i>	Madagascar	B. Jordal	PX056641	-	PX059516	PX068288
CrAfr13	Trypophloeini	<i>Afrocosmoderes pennatus</i>	Madagascar	J. Eliassen	PX056645	PX068280	PX059520	PX068291
CrAfr05	Trypophloeini	<i>Afrocosmoderes plenus</i>	Madagascar	B. Jordal	PX056638	PX068277	PX059513	—
CrAfr12	Trypophloeini	<i>Afrocosmoderes schedli</i>	Madagascar	B. Jordal	PX056644	PX068279	PX059519	—
CrAfr10	Trypophloeini	<i>Afrocosmoderes seriatus</i>	Madagascar	B. Jordal	PX056642	—	PX059517	PX068289
CrGen01	Trypophloeini	<i>Afrocosmoderes zambesianus</i>	Tanzania	B. Jordal	KY805895	KY805863	KY805969	MF771617
CrAll01	Trypophloeini	<i>Cosmoderes euonymi</i>	Russia	B. Jordal	—	JX264084	JX263685	MF771605
CrHyp04	Trypophloeini	<i>Hypothenemus abruptus</i>	Madagascar	B. Jordal	—	—	PX059522	PX068293
CrHyp01	Trypophloeini	<i>Hypothenemus aff. eruditus</i>	USA	B. Jordal	JX263802	JX264092	JX263695	MF771619
CrHyp06	Trypophloeini	<i>Hypothenemus aff. melanarius</i>	Tanzania	B. Jordal	PX056647	—	PX059524	PX068295
CrHyp02	Trypophloeini	<i>Hypothenemus birmanus</i>	Thailand	K. Harkestad	JX263803	JX264093	JX263696	MF771620
CrHyp07	Trypophloeini	<i>Hypothenemus biseriatus</i>	Tanzania	B. Jordal	—	—	PX059525	PX068296
CrHyp05	Trypophloeini	<i>Hypothenemus carbonarius</i>	Tanzania	B. Jordal	—	—	PX059523	PX068294
CrHyp03	Trypophloeini	<i>Hypothenemus criticus</i>	Gabon	R. Mally	PX056646	—	PX059521	PX068292
CrHyp08	Trypophloeini	<i>Hypothenemus</i> sp G	Madagascar	B. Jordal	PX056648	—	PX059526	PX068297
CrTry05	Trypophloeini	<i>Trypophloeus granulatus grothi</i>	Norway	O. Hansen	KU144915	KY805865	OQ685088	MF771625
CrTry03	Trypophloeini	<i>Trypophloeus populi</i>	USA	L. Kirkendall	KC845441	OQ694479	OQ685087	MF771624
CrScg01	Tribe?	Genus et species indet	Tanzania	B. Jordal	PX056649	PX068281	PX059527	PX068298



**Figs. 15 to 25.** Slide preparations of internal and cryptic external features of *Afrocosmoderes* species. The inner face of proventricular blades in 15) *A. asper*, 16) *A. pennatus*, 17) *A. plenus*; 18) inner face of the labium and maxillae of *A. longisetus*; 19) antennal club with 3-segmented funicle in *A. seriatus*; 20) 5-segmented funicle in *A. plenus*; dorsal view of the male genitalia in 21) *A. asper*, 22) *A. pennatus*, 23) *A. longisetus*, 24) *A. grobleri*, 25) *A. seriatus*.

supported. Poorly resolved nodes included the position of *A. plenus*, and the arrangement of taxa in clade B (*A. parvus*, *A. grobleri*, *A. zambesianus*, *A. pellitus*, and *A. longisetus*). The sister group *Hypothenemus* was nearly unresolved for its internal relationships.

### Morphology

Bayesian and parsimony analysis of 18 morphological and 2 ecological characters resulted in a completely unresolved tree topology except for a clade with *A. carinatus* and *A. brevicostatus*. Successive reweighting produced a single most parsimonious tree of length 63. This tree supported clades A and C, with the remaining taxa in clade B scattered and incongruent with molecular data. Species without molecular data grouped in clade A (*A. saetiger*), clade C (*A. madagascariensis*), and with *A. plenus* (*A. africanus*).

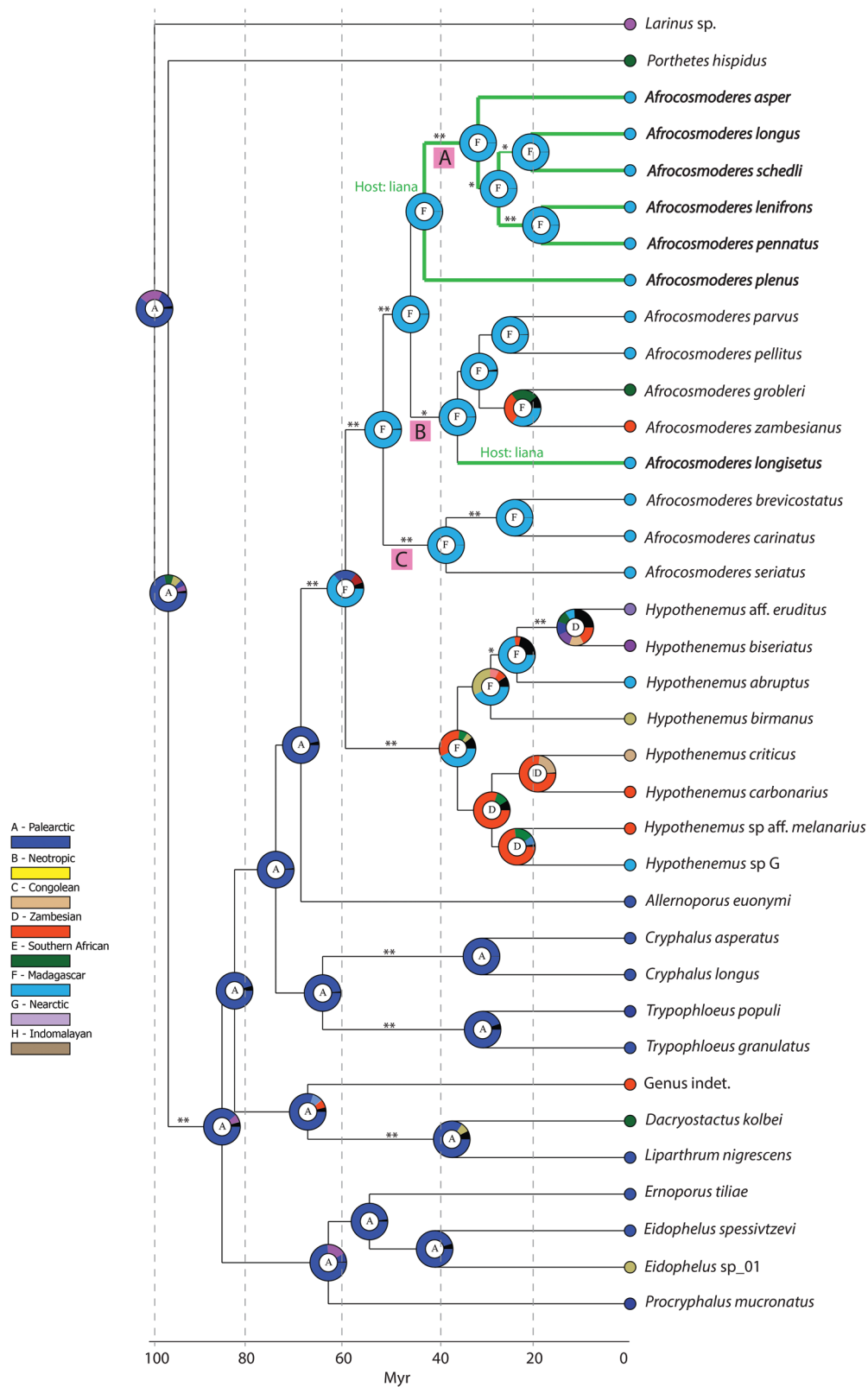
Very few morphological characters were indicative of relationships, and these were mainly restricted to the shape of basal

sclerites in the male genitalia (Table 3). When optimized on the morphological data topology, there was only slightly higher congruence, including features of the eyes (entire vs. emarginated), the male frons (smooth, grooved or carinated), and the elytral ground vestiture (hair-like vs. scale-like). For identification purposes, the number of denticles on the lateral edge of the protibiae proved useful for sorting larger groups, whereas the number of funicle segments, which is an accurate specific trait, varies much between closely related species (3 to 5 segments). Whereas the number of denticles on tibiae were only slightly affected by body size, entire eyes and absent ground vestiture were observed in the three smallest species (*A. parvus*, *A. plenus* and *A. africanus*), indicative of reductions due to small size.

### Biogeography

Reconstruction of ancestral geographical ranges based on the BBM method in RASP indicated a single origin of





**Fig. 26.** Reconstruction of ancestral geographical ranges based on the BBM method in RASP, using a time calibrated Beast tree. Node support is given above nodes based on Bayesian posterior probability estimated in Mr Bayes (\*\* $P=1$ ; \* $P>0.95$ ). Posterior probabilities in the Beast search were generally higher.





**Figs. 27 to 38.** Dorsal, lateral, and front view of (27, 31, 35) *Afrocosmoderes asper* male and (28, 32, 36) *A. asper* female; (29, 33, 37) *Afrocosmoderes saetiger* male and (30, 34, 38) *A. saetiger* female.

Malagasy *Afrocosmoderes* (Fig. 1). The genus diverged from a common ancestor with *Hypothenemus* around 59 Ma. Diversification on Madagascar occurred soon after this event, with a crown age of 52 Ma for the genus. *Hypothenemus*, which was sampled across most of the major morphs known in the genus, diversified later, with a crown age of 36 Ma.

*Afrocosmoderes* colonized the African mainland from Madagascar at least once. The Beast analysis indicated a single origin on the mainland around 32 Ma, whereas the MrBayes Bayesian analysis indicated two independent origins at approximately the same time. Given the low phylogenetic signal in morphological characters, it was not possible in the absence of DNA data to infer the origin of the South African *A. africanus*.





**Figs. 39 to 47.** Dorsal, lateral, and front view of (39, 42, 45) *Afrocosmoderes longus* male and (40, 43, 46) *A. longus* female; (41, 44, 47) *Afrocosmoderes schedli* male.

### Host Plants and Reproductive Biology

*Afrocosmoderes* appears specific to the type of breeding material they prefer. Only one species (*A. pennatus*) was collected from 2 unrelated plant families, but always from lianas (Table 4). All collected species were either found either in lianas or under bark of tree branches. Lianas were all in the range of 1 to 3 cm thick rope type of hanging lignified vines with well developed bark. The switch to lianas was derived from branch feeding

and only occurred twice, or alternatively, only once if a single reversal to branch feeding occurred (Fig. 1).

Males rarely stayed with the female for very long, and usually left their offspring at early larval stage or before eggs were hatching. The female usually stayed much longer. Broods were generally small, with no more than 15 eggs laid by any female, in any substrate (Table 4). In thin lianas, the number could be as few as 1 to 3 eggs. The structure of egg tunnels differed





**Figs. 48 to 56.** Dorsal, lateral, and front view of (48, 51, 54) *Afrocosmoderes lenifrons* female; (49, 52, 55) *Afrocosmoderes pennatus* male; (50, 53, 56) *A. pennatus* female.

considerably, from straight or spiral-shaped tunnels along the longitudinal axis, to tube- or cave-like. In the first two types, eggs were deposited in niches along the tunnel, whereas in the cave type, eggs were deposited in a cluster, with larvae feeding away from the cave in star formation.

## Taxonomy

### *Afrocosmoderes* Johnson and Jordal, 2020

Type of genus: *Miocryphalus pennatus* Schedl, 1953: 79, designated by Johnson et al., 2020.





**Figs. 57 to 65.** Dorsal, lateral, and front view of (57, 60, 63) *Afrocosmoderes confertus* female; (58, 61, 64) *Afrocosmoderes longisetus* female; (59, 62, 65) *A. longisetus* male.

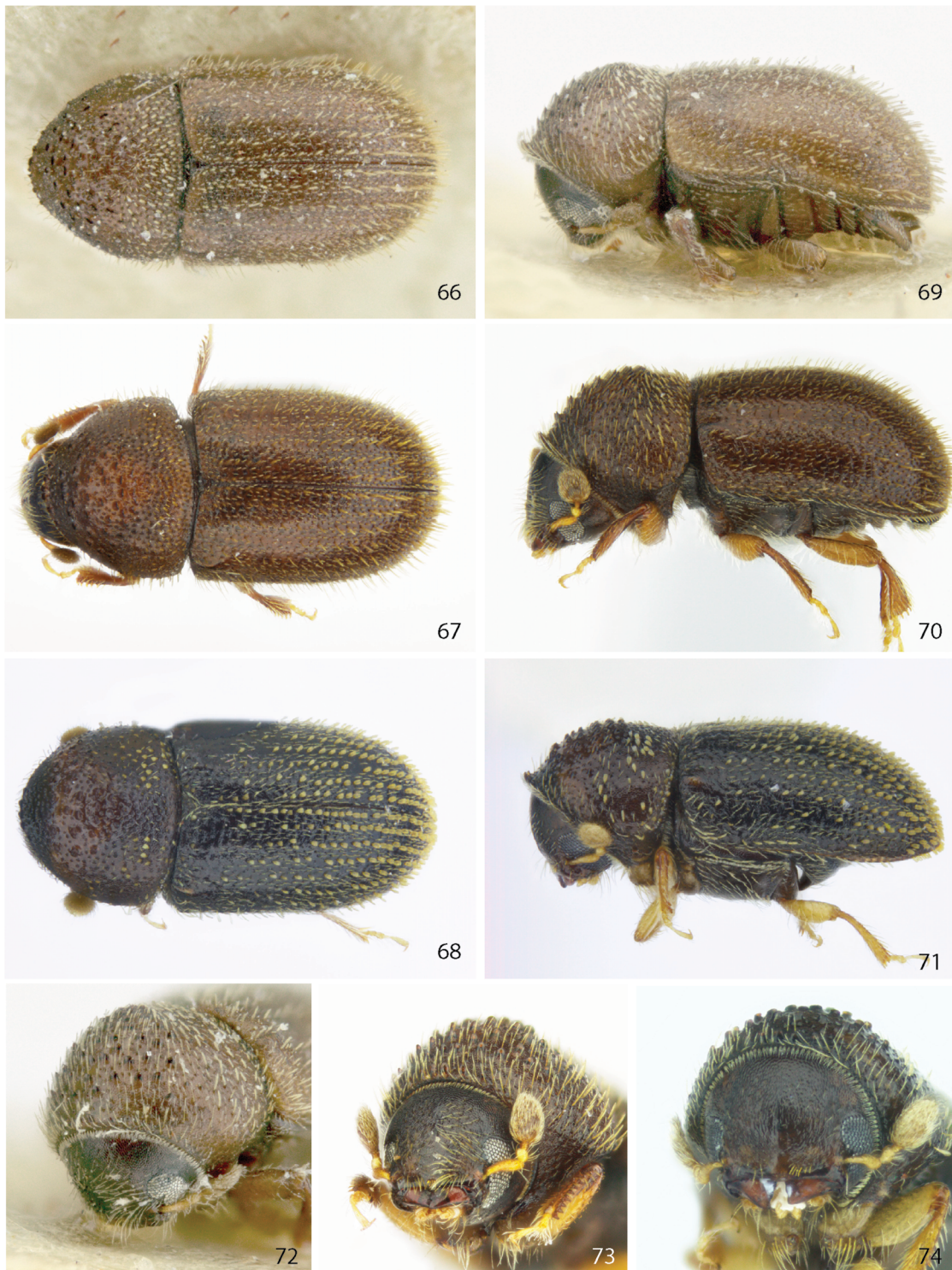
#### Diagnosis

Antennal club large, flattened, without clear sutures; eyes almost entire to deeply emarginated; lateral margin of pronotum short, extended laterally with a curved carina; mesocoxae narrowly separated; third tarsal segment cylindrical; male last tergite visible ventrally, with posterior edge of last abdominal ventrite procurved for reception of tergite.

#### Redescription

**Female** frons simple, convex, sometimes with a longitudinal keel. Eyes slightly to deeply emarginated just above eye mid-length. Antennae with 3, 4, or 5 funicle segments (including the pedicel). Antennal club flat, oval, sutures faint, and procurved if at all visible. Pronotum weakly declivous on the anterior half or two-thirds, with small asperities, 4 to 8 larger



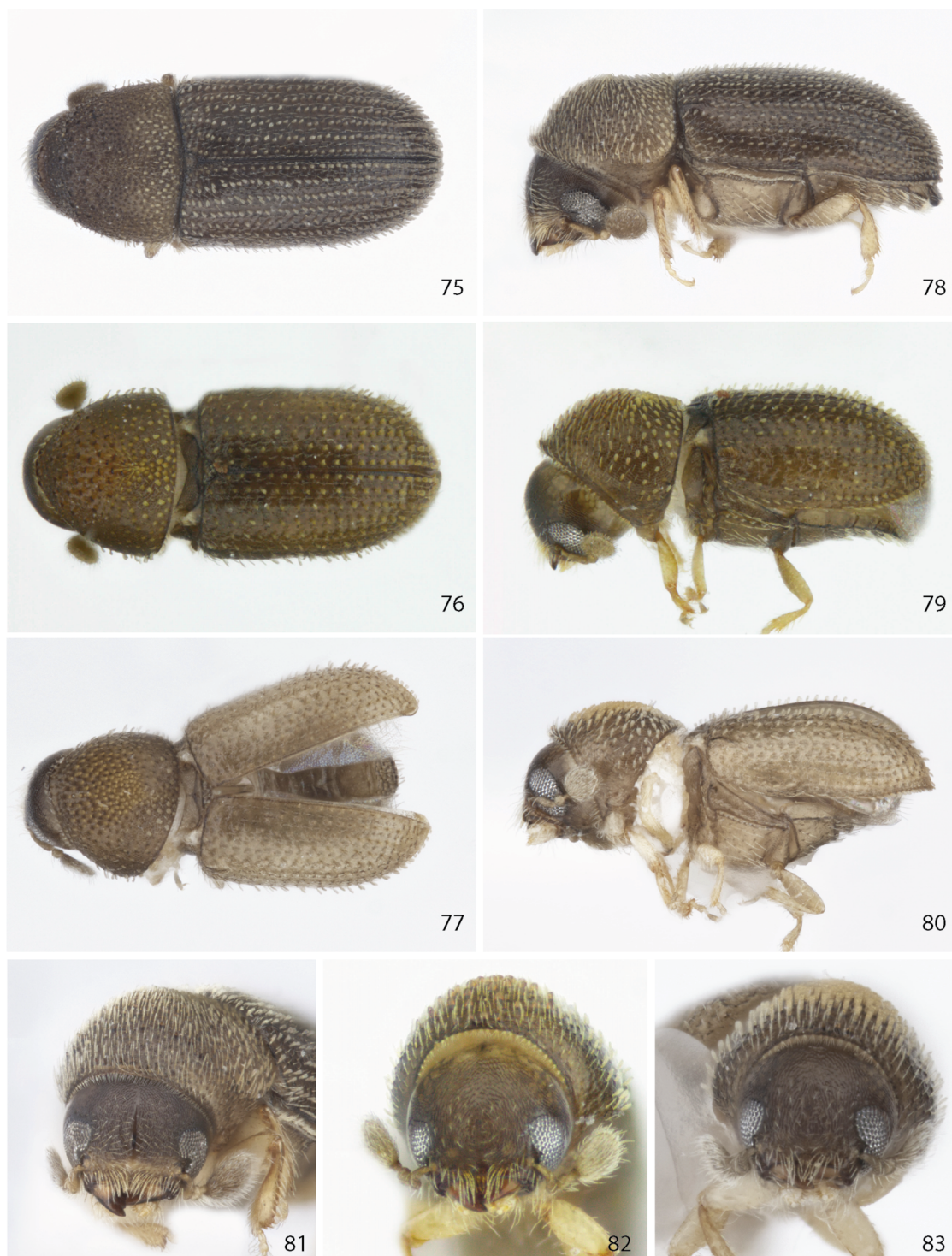


**Figs. 66 to 74.** Dorsal, lateral, and front view of (66, 69, 72) *Afrocosmoderes grobleri* female; (67, 70, 73) *A. grobleri* male; (68, 71, 74) *Afrocosmoderes zambesianus* female.

tubercles or small teeth along the anterior margin; lateral edge of the pronotum with a short, curved carina. Elytra simple, apically broadly rounded; main interstitial setae scale- or bristle-like, with additional ground vestiture absent or consisting of scant hair-like to denser short and scale-like setae. Scutellar shield visible, flat, U-shaped. Postnotum is separated from

metanotum by a membrane. Mesocoxae are narrowly separated. Protibiae gradually widening towards apex, with 4 to 10 lateral socketed denticles. Metatibiae with lateral, socketed denticles on apical third or less. Tarsal segments cylinder-shaped. Setae on metanepisternum either plumose, split, scale- or hair-like. Proventriculus with developed apical plate occupying





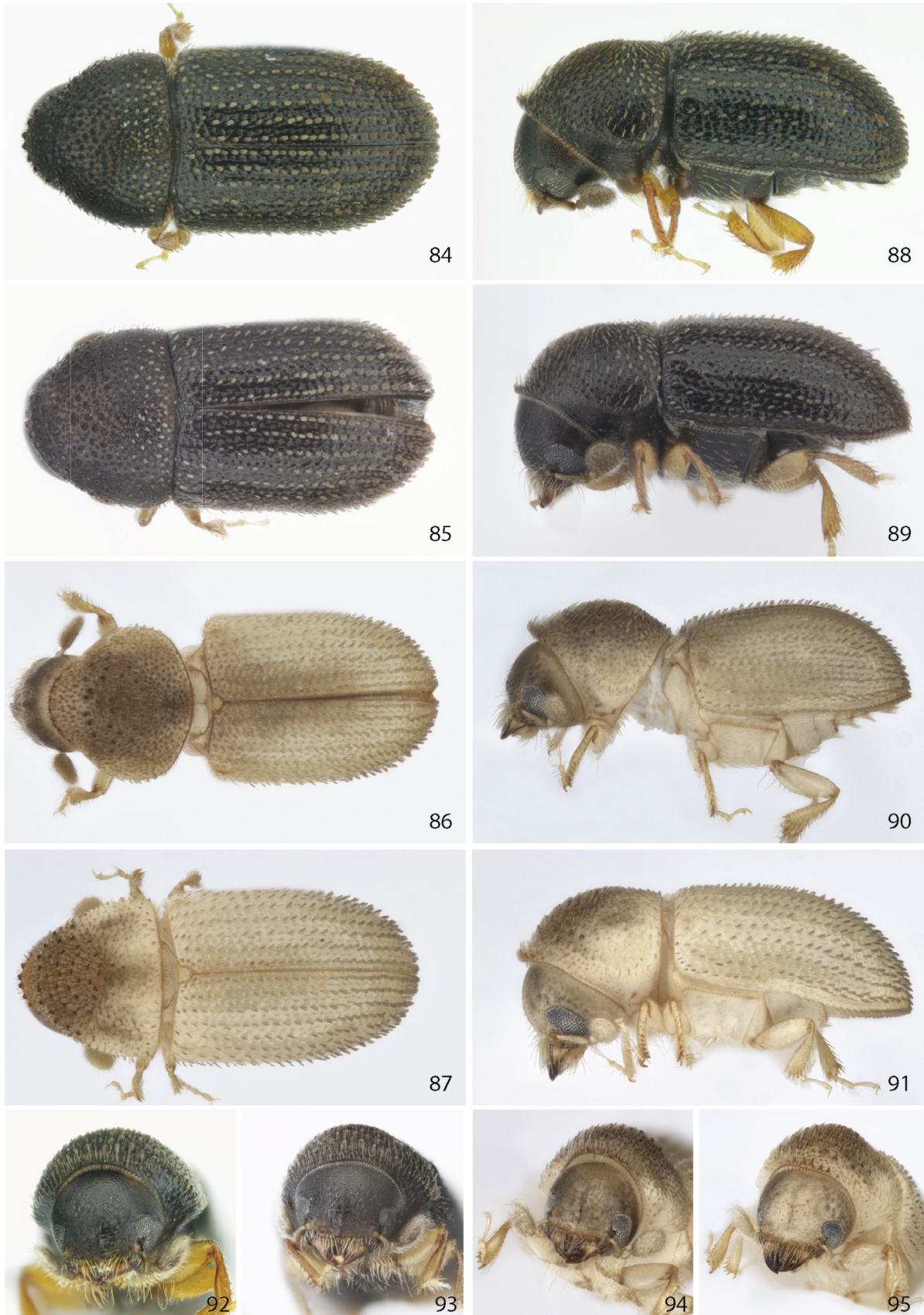
**Figs. 75 to 83.** Dorsal, lateral, and front view of (75, 78, 81) *Afrocosmoderes pellitus* female; (76, 79, 82) *Afrocosmoderes parvus* female; (77, 80, 83) *A. parvus* male.

nearly half the length, smooth or toothed, usually divided by a longitudinal median suture carrying sutural teeth.

**Male** differs from the female in some species by the produced and narrowly rounded anterior margin of the pronotum, sometimes with dense short spatulate golden setae on anterior half or two-thirds, otherwise with narrow bristles. Fifth abdominal

ventrite with a procurved posterior margin that receives the ventrally extended last tergite. Male genitalia apodemes as long or slightly shorter than penis body, broad and leaf-like, free at apex; tegmen open dorsally, ventrally with a pointed, often long manubrium; spiculum gastrale robust, weakly forked apically or a simple rod; basal sclerites large and complex.





**Figs. 84 to 95.** Dorsal, lateral, and front view of (84, 88, 92) *Afrocosmoderes brevicostatus* male; (85, 89, 93) *A. brevicostatus* female; (86, 90, 94) *Afrocosmoderes carinatus* male; (87, 91, 95) *A. carinatus* female.





**Figs. 96 to 104.** Dorsal, lateral, and front view of (96, 99, 102) *Afrocosmoderes seriatus* male; (97, 100, 103) *A. seriatus* female; (98, 101, 104) *Afrocosmoderes madagascariensis* female.

#### *Distribution*

Madagascar, South-East Africa.

#### *Comments*

Since its original description, 12 new species were recently discovered and the diagnosis and description are modified accordingly. *Afrocosmoderes* is distinguished from its sister group

*Hypothenemus* by the large and flattened antennal club which lacks distinct sutures and septum. The male is furthermore of the same size as the female and has fully developed wings and eyes. The sharp carina along the lateral margin of the pronotum, the narrowly separated mesocoxae, a large apical plate of the proventriculus which usually has a median suture, separate this genus from the similar genus *Cosmoderes* Eichhoff, 1878.





**Figs. 105 to 113.** Dorsal, lateral, and front view of (105, 108, 111) *Afrocosmoderes africanus* male; (106, 109, 112) *Afrocosmoderes plenus* male; (107, 110, 113) *A. plenus* female.

There is a variable gender use of the Greek noun *dere*, which is feminine. However, when a final -s is added in the Latinisation of the noun (*deres*), the gender can be changed. The original use of masculine gender for *Cosmoderes* is therefore maintained.

**Table 3.** Character diagnostics based on: (i) the best molecular Bayesian tree topology (treelength = 61), and (ii) one of the eight most parsimonious trees from morphology data using implied weight (treelength = 58)

Character	Molecular tree		Morphology tree	
	RC	HI	RC	HI
1. Eye emargination	0.11	0.67	<b>1.00</b>	<b>0.00</b>
2. Funicle segments	0.20	0.60	0.10	0.75
3. Male frons	0.11	0.67	0.23	0.60
4. Anterior pronotal margin of males	0.11	0.67	0.33	0.50
5. Setae type on male pronotum	0.06	0.75	0.14	0.75
6. Interstrial setae type, posterolaterally	0.11	0.67	0.11	0.67
7. Interstrial pattern of setae	0.00	0.67	0.20	0.67
8. Elytral ground vestiture	0.14	0.67	0.25	0.60
9. Metanepisternal setae type	0.20	0.67	0.22	0.67
10. Metanepisternal setae length	0.10	0.75	0.09	0.80
11. Ventrite setae, main type	0.17	0.67	0.17	0.67
12. Ventrite setae, minor type	0.00	<b>0.50</b>	0.00	0.50
13. Protibial teeth, number	0.07	0.80	0.26	0.67
14. Metatibial teeth	0.09	0.80	0.24	0.67
15. Proventricular anterior plate	0.11	0.67	0.33	0.50
16. Aedeagus, apex	<b>1.00</b>	<b>0.00</b>	<b>1.00</b>	0.00
17. Aedeagus, major basal sclerite	<b>1.00</b>	<b>0.00</b>	<b>0.53</b>	<b>0.33</b>
18. Aedeagus, basal sclerite lateral tooth	<b>1.00</b>	<b>0.00</b>	<b>1.00</b>	<b>0.00</b>
19. Feeding mode	0.42	0.50	<b>0.42</b>	0.50
20. Geographical area (Afr./Mad.)	<b>1.00</b>	<b>0.00</b>	0.25	0.50
Average	0.31	0.52	0.38	0.48

Trees were pruned to contain the same taxa (Supplementary Data). Values better than the average are marked in bold.

**Table 4.** Summary of biology in *Afrocosmoderes* based on new field records

Taxon	Host plant genus (family)	Habitat	Tissue	Gallery type	Broods
<i>A. asper</i>		Liana	Bark		
<i>A. asper</i>		Liana	Wood	Deep tube	
<i>A. brevicostatus</i>		Branch	Bark		
<i>A. carinatus</i>		Branch	Bark		
<i>A. grobleri</i>	<i>Virgilia</i> (Fabaceae)	Branch	Bark	Cave	11 to 13 ( <i>n</i> = 2)
<i>A. grobleri</i>	<i>Virgilia</i> (Fabaceae)	Branch	Bark	Elongate cave	
<i>A. lenifrons</i>		Liana	Bark	Longitudinal	
<i>A. longisetus</i>	<i>Abrus</i> (Fabaceae)	Liana	Bark	Deep spiral	1 to 3 ( <i>n</i> = 8)
<i>A. longisetus</i>	<i>Strongylodon</i> (Fabaceae)	Liana	Bark		
<i>A. longus</i>		Liana	Bark	Irregular	
<i>A. parvus</i>	<i>Dombeya</i> (Sterculiaceae)	Seedling	Bark	Cave	12 ( <i>n</i> = 1)
<i>A. pellitus</i>	<i>Cananga</i> (Annonaceae)	Branch	Bark		
<i>A. pennatus</i>	<i>Landolphia</i> (Apocynaceae)	Liana	Wood	Spiral	
<i>A. pennatus</i>	<i>Strongylodon</i> (Fabaceae)	Liana	Bark		6 to 15 ( <i>n</i> = 6)
<i>A. plenus</i>		Liana	Bark	Cave	4 to 6 ( <i>n</i> = 3)
<i>A. schedli</i>	<i>Landolphia</i> (Apocynaceae)	Liana	Bark		
<i>A. seriatus</i>		Branch	Bark		
<i>A. zambesianus</i>		Twig	Bark		2 ( <i>n</i> = 1)

For further details and geographical data see taxon descriptions.

## Included Species

### Clade A

*Afrocosmoderes asper* sp. nov.

Figures 13 to 15, 21, 27, 28, 31, 32, 35, 36

urn: lsid: zoobank.org: act: C3E49319-2C02-40AA-A6A2-DF5E06C3D18C

**Material examined.** Holotype male: MADAGASCAR, Ankarafantsika NP [−16.264, 46.828], alt. 200 m, 8.5.2015, ex liana [ZMUB]. Allotype and paratypes (7): same data as holotype (3), except 7.5.2015 (4) [ZMUB (5); NHMW (2)].

**Diagnosis.** Male frons impressed and shiny, with dense and long setae distributed along its outer margin; female frons impressed, dull, with short setae over entire impressed area; elytral striae slightly impressed; abdominal ventrites with mixed coarse scale-like and fine split setae.

**Etymology.** The Latin nominative adjective *asper* means rough or unrefined, referring to its rather shaggy, striate and rough appearance.

**Description, male.** Length 1.5 to 1.7 mm, 1.9 to 2.1 × as long as wide; color black. Eyes deeply emarginated. Antennal funicle 5-segmented; club flat, pilose, without sutures. Frons broadly impressed, impunctate and shiny in middle, with setae as long as scapus densely placed along the outer margin of impressed area. Pronotum broader than long, broadly rounded in front, with four tubercles centrally along the margin; anterior two-thirds steeply declivous, densely covered by squared asperities, vestiture consisting of broad erect scales on posterior third, hair-like on anterior half. Elytral interstriae slightly raised, with densely placed rounded to subquadrate scale-like setae in mainly single rows, slightly confused towards posterolateral margins; ground vestiture consisting of short, dense scale-like setae; stria punctures small and shallow, spaced within rows by their diameter, each associated with a fine short seta. Metanepisternum with simple short setae, on abdominal ventrites with a transverse row of course bristles along each posterior margin, intermixed with bi- and trifid small and fine setae; posterior margin of ventrite V procurved to receive the terminal tergite. Protibiae with 7 or 8 lateral denticles on apical



half; metatibiae with 4 fine denticles on apical quarter. Proventriculus with anterior plate undivided, with transverse rows of blunt spines. Aedeagus compact, apodemes clearly shorter than rest of the penis body; basal sclerites with blunt laterally pointed spines near the basal orifice, connected to a dorsally curved hook; apex narrow and tongue-like; spicule as long as aedeagus, curved without fork.

**Female** externally similar to male except frons less impressed with short, scattered setae, the pronotum with slightly more dispersed asperities, and the posterior margin of the last abdominal ventrite transverse.

**Distribution and biology.** Madagascar. Only known from the type locality in north-western Madagascar. It was collected twice from dead lianas. Males and females formed monogamous pairs in a tube-like tunnel into the wood of the liana.

*Afrocosmoderes saetiger* sp. nov.

Figures 29, 30, 33, 34, 37, 38

urn: lsid: zoobank.org: act: 0C63CB04-B9A9-4746-8AA7-922EC6143EA3

**Material examined.** Holotype male: MADAGASCAR, [Mahajanga] Forêt d'Tsimembo, 11 km NNW Soatana [−18.92, 44.41], #BLF4508, ex sifted litter, B. Fischer leg. [CAS]. Allotype female: MADAGASCAR, [Diana Province] Forêt d'Orangea, 3.8 km SE Ramena [−12.262, 49.375] #BLF3200, B. Fischer leg. [CAS].

**Diagnosis.** Male pronotum with broad golden setae on anterior half; elytral striae on central and posterior disk and declivity impressed, punctures large, deep, subcontiguous, interstriae with densely set subquadrate setae, ground vestiture of coarse scale-like setae.

**Etymology.** From the Latin adjective *saetiger* meaning bristly, referring to the coarse striae and dense interstitial setae, particularly on the declivity.

**Description, male.** Length 1.0 to 1.3 mm, 2.3 × as long as wide; color brown. Eyes deeply emarginated. Antennal funicle 3-segmented; club flat, pilose, without sutures. Frons narrowly impressed, with short, scattered setae near eyes and epistoma. Pronotum broadly rounded in front, with few small tubercles centrally along the margin; anterior half steeply declivous, densely covered by small asperities, vestiture consisting of broad golden scales on anterior half, mixed light-colored scale- and hair-like on posterior half. Elytral striae impressed, more deeply so on posterior part, punctures large, deep, subcontiguous; interstriae slightly raised, with densely placed subquadrate scale-like setae in single rows; ground vestiture consisting of short, dense scale-like setae. Metanepisternum with simple short setae, on abdominal ventrites with a transverse row of coarse bristles along each posterior margin, intermixed with small and fine setae; posterior margin of ventrite V procurved to receive the terminal tergite. Protibiae with 7 or 8 lateral denticles on apical half; metatibiae with 6 lateral denticles on apical half.

**Female** externally similar to male except frons convex with scant minute setae, the pronotum with mixed hair-like and bristle-like setae on anterior half, and the posterior margin of the last abdominal ventrite entire.

**Distribution and biology.** Madagascar. Two single specimens were collected from two dry forest localities in western and northern Madagascar. They were sifted from dry litter

indicating breeding in thin branches or lianas as most other species in the genus.

*Afrocosmoderes longus* sp. nov.

Figures 3, 39, 40, 42, 43, 45, 46

urn: lsid: zoobank.org: act: 201C40B3-4CE0-4137-BFD4-6F39D9FD918E

**Material examined.** Holotype male: MADAGASCAR, Ambohitantely special reserve [−18.189, 47.292], 1,500 m alt., 12.V.2015, ex liana, B. Jordal, leg. [ZMUB]. Allotype and paratypes: same data as holotype [NHMW (2); ZMUB (4)].

**Diagnosis.** Male pronotum with broad golden setae on anterior part; body >2.4 × as long as wide; frons in both sexes lightly impressed or grooved just above epistoma.

**Etymology.** The Latin nominative adjective *longus* meaning long, referring to the largest body length to width ratio in the genus.

**Description, male.** Length 1.2 to 1.4 mm, 2.4 to 2.5 × as long as wide; color brown. Eyes deeply emarginated. Antennal funicle 5-segmented; club flat, pilose, without sutures. Frons generally convex, slightly longitudinally grooved in middle, with scant, short setae. Pronotum somewhat narrowly rounded in front, with few small tubercles centrally along the margin; anterior two-thirds steeply declivous, densely covered by small asperities, vestiture consisting of golden scale-like setae on anterior two-thirds, light-colored behind, with hair-like setae intermixed. Elytral striae very slightly impressed, irregular punctures shallow and subcontiguous; interstriae with spatulate setae mainly in single rows, more confused towards posterolateral margins; ground vestiture consisting of coarse but hair-like setae on disk, becoming scale-like on declivity. Metanepisternum with simple setae a little longer than sclerolepidia, on abdominal ventrites with a transverse row of fine bristles along each posterior margin, intermixed with small and fine setae; posterior margin of ventrite V procurved to receive the terminal tergite. Protibiae with 5 or 6 lateral denticles on apical third; metatibiae with 4 or 5 lateral denticles on apical fifth. Proventriculus with anterior plate divided by medial suture, with transverse rows of sharp spines. Aedeagus compact, apodemes clearly shorter than rest of the penis body; basal sclerites with blunt laterally pointed spines near the basal orifice, connected to a dorsally curved hook; apex narrow and tongue-like; spicule as long as aedeagus, curved without fork.

**Female** similar to male except frons with fine short and scant setae, the pronotum with mainly hair-like and few light colored spatulate setae on anterior half, and the posterior margin of the last abdominal ventrite entire.

**Distribution and biology.** Madagascar. Only known from the high-altitude type locality in central Madagascar; it was breeding in a dead hanging liana making irregular tunnels.

*Afrocosmoderes schedli* Johnson

Figures 41, 44, 47

*Euptilius madagascariensis* Schedl, 1963: 65.

*Cosmoderes madagascariensis* (Schedl, 1963)

*Afrocosmoderes schedli* Johnson, 2020: 27, replacement name for *A. madagascariensis* (Schedl, 1963), pre-occupied by *A. madagascariensis* (Schedl, 1961).

**Material examined.** Syntype ('paratype') female: MADAGASCAR, Montagne d'Ambre, 4.XII.1952, K.E. Schedl [NHMW].

New record: MADAGASCAR, Diana, Montagne d'Ambre [–12.54, 49.17], 1,000 m alt., 4.XI.2019, ex *Landolphia?* liana, B. Jordal, leg. [3 ZMUB; 1 NHMW]

**Diagnosis.** Antennal funiculus 4-segmented; frons in both sexes smooth; ground vestiture scale-like, metanepisternal seta split.

**Redescription, male.** Length 1.2 to 1.4 mm, 2.2 to 2.3 × as long as wide, color dark brown. Frons with low obtuse keel on lower half, convex and finely punctured with scant fine setae. Eyes deeply emarginated; antennal funiculus 4-segmented; club flat, pilose, with only a faint trace of a slightly procurved suture on basal fourth. Pronotum with golden spatulate setae on anterior two-thirds. Elytral striae not impressed, interstriae with regular rows of short spatulate setae, each separated within a row by slightly more than their length; ground vestiture of elongated, almost hair-like scales. Metanepisternal setae short and split, some fluffy; largest setae on ventrites spatulate. Protibiae with 6 or 7 lateral denticles on apical half, metatibiae with 5 or 6 lateral denticles on apical fourth. Proventriculus with apical plate undivided, medial suture barely indicated, with transverse rows of sharp granules. Male genitalia with apodemes shorter than penis body, basal sclerites forming a loop with a pair of laterally directed spines, apical penis narrow and tongue-shaped; spicule a simple curved rod.

Female externally similar to male except frons smooth to epistoma, vestiture on pronotum with fine setae only, and last ventrite straight.

**Distribution and biology.** Madagascar. Recollected in this study from the type locality in northern Madagascar. Mature specimens were dissected from irregular tunnels under bark of a dead hanging liana.

*Afrocosmoderes lenifrons* sp. nov.

Figures 8, 48, 51, 54

urn: lsid: zoobank.org: act: 46E95FFD-DEC1-46E1-AE56-1708B23FB908

**Material examined.** Holotype female: MADAGASCAR, Diana, Montagne d'Ambre [–12.54, 49.17], 1,000 m altitude, 03.11.2019, ex liana, B. Jordal leg. [ZMUB]. Allotype male: MADAGASCAR, Fianarantsoa, Ranomafana NP [–21.253, 47.421], 950 m alt., 31.10.2012, in EtOH trap, B. Jordal, leg. [ZMUB]. Paratype: same data as holotype [NHMW].

**Diagnosis.** Male pronotum on its anterior third with only hair-like setae; protibiae with 7 or 8 lateral denticles on apical half; frons smooth, except for a tiny central pit.

**Etymology.** Composed by the stem of the Latin nominative adjective *lenis* (m/f), meaning smooth, and the noun *frons*, referring to the flat and smooth frons in both sexes.

**Description, female.** Length 1.3 to 1.5 mm, 2.1 to 2.2 × as long as wide; color dark brown. Eyes deeply emarginated. Antennal funicle 4-segmented; club flat, pilose, without sutures. Frons convex, smooth, with a tiny pit slightly marked in center; vestiture of scant, short setae. Pronotum somewhat narrowly rounded in front, with 4 or 6 small tubercles at center of anterior margin, middle two largest; anterior two-thirds steeply declivous, densely covered by small asperities, vestiture consisting of hair-like setae on anterior two-thirds, light-colored spatulate setae behind, with hair-like setae intermixed. Elytral striae not impressed, punctures shallow, irregular and indistinct; interstriae with spatulate setae in regular single rows, each seta separated within rows by their length or slightly more;

ground vestiture consisting of hair-like setae on disk, scale-like on declivity. Metanepisternum with simple setae a little longer than sclerolepidia, on abdominal ventrites with a transverse row of coarse bristles along each posterior margin, intermixed with small and fine setae. Protibiae with 7 or 8 lateral denticles on apical half; metatibiae with 5 or 6 lateral denticles on apical fourth.

**Male.** Similar to female except posterior margin of ventrite V procurved to receive the terminal tergite (internal characters not dissected).

**Distribution and biology.** Madagascar. Collected from the north and south-east of the island. One collection was from a dead liana.

**Comments.** Distinguished from *A. pennatus* by the hair-like ground vestiture on elytral disc (versus clearly scale-like), the more rounded spatulate shape of the interstitial setae, and by the tiny pit in the middle of the frons (vs. turgid shiny line).

*Afrocosmoderes pennatus* (Schedl)

Figures 16, 22, 49, 50, 52, 53, 55, 56

*Miocryphalus pennatus* Schedl, 1953: 79

*Afrocosmoderes pennatus* (Schedl), combination by Jonson et al. (2020).

**Material examined.** Lectotype, male: MADAGASCAR, Montagne d'Ambre, K. E. Schedl, leg. 1952 [NHMW].

New records: MADAGASCAR, Diana Prov., Montagne d'Ambre [–12.54, 49.17], 1,000 m alt., 04.11.2019, ex liana, B. Jordal leg.; Madagascar, Fianarantsoa Prov., Ranomafana NP, Centre ValBio [–21.253, 47.421], 950 m alt., 29.9.2012, ex *Strongylodon craveniae* liana; same data, except EtOH trap; same data except Vato trail [–21.292, 47.421], 1,100 m alt., 4.10.2012, ex *Landolphia* liana [ZMUB].

**Diagnosis.** Antennal funiculus 5-segmented; male pronotum with broad golden setae; metanepisternal setae short and simple.

**Redescription, male.** Length 1.4 to 1.6 mm, 2.0 to 2.2 × as long as wide, color brown. Frons with longitudinal low and shiny turgidity; eyes deeply emarginated; antennal funiculus 5-segmented. Pronotum with golden narrowly spatulate setae. Elytral ground vestiture consisting of scale-like short setae from base to apex, interstitial setae short and spatulate, spaced within rows by the length a seta. Metanepisternal setae short and simple; largest setae on ventrites coarse long bristles. Protibiae with 7 or 8 lateral denticles on apical half, metatibiae with 5 or 6 lateral denticles on apical third. Proventriculus with apical plate divided by medial suture, on some plates with limited rows of blunt or sharp teeth, some plates entirely smooth except along medial suture. Male genitalia with apodemes shorter than penis body, basal sclerites forming a loop with a pair of laterally directed spines, apical penis narrow and tongue-shaped; spicule a simple curved rod.

Female similar to male, except for last abdominal ventrite straight and pronotum with narrow, light setae.

**Distribution and biology.** Madagascar. Recollected several times from the type locality north on the island, and from southern parts, in Ranomafana. Specimens were dissected from different types of fallen dead or hanging *Strongylodon* (Fabaceae) and *Landolphia* (Apocynaceae) lianas. Egg tunnels appeared spiral, partly under bark but terminally deeper in the woody tissue of the liana. Brood size varied between 6 and 15 eggs or larvae (Table 4).

*Afrocosmoderes onfertus* sp. nov.

Figures 6, 57, 60, 63

urn: lsid: zoobank.org: act: F3E24685-7DB5-4780-B582-6BDD81D04F40

**Material examined.** Holotype, female: MADAGASCAR, Andasibe NP, Botanical Garden [–18.941, 48.426]. Malaise trap, MA-01-08B-09, 2001, B. Fischer, leg. [CAS].

**Diagnosis.** Female frons with a longitudinal obtuse carina from epistoma to upper level of eyes; interstitial setae on elytra in part in multiple confused rows, very dense; ground vestiture of coarse scale-like setae about one-quarter to half the width of main setae.

**Etymology.** Based on the Latin participle *confertus*, meaning crowded together, dense, in close order, referring to the densely set and slightly confused interstitial setae.

**Description, female.** Length 1.6 mm, 2.2× as long as wide; color dark brown. Eyes deeply emarginated. Antennal funicle 4-segmented; club flat, pilose, without sutures. Frons convex, shallowly punctate, reticulate, with a low median carina from epistoma to upper level of eyes; vestiture consisting of scant, short, fine setae, except dense on epistoma. Pronotum broadly rounded in front, with two larger and a few smaller apical tubercles; anterior three-quarters steeply declivous, densely covered by small asperities, vestiture consisting of fine hair-like setae on anterior two-thirds, light-colored spatulate setae intermixed behind. Elytral striae very slightly impressed, punctures irregular in size, some places deeply impressed, others shallow; interstriae with main setae broad and truncated in single rows in part, elsewhere, particularly toward the sides with strongly confused multiple rows; ground vestiture consisting of scale-like setae; striae setae fine, slightly longer than ground vestiture. Metanepisternum with simple setae slightly longer than sclerolepidia, on abdominal ventrites with a transverse row of coarse bristles along each posterior margin, intermixed with small and fine setae. Protibiae with 9 lateral denticles on apical two-thirds; metatibiae with 5 lateral denticles on apical sixth.

**Male** not known.

**Distribution and biology.** Madagascar. Only known from the type locality, in a typical eastern lowland rainforest. A single specimen was collected in a Malaise trap.

**Comments.** This species is very similar to *A. pennatus* and *A. longisetus*, but the interstitial setae are slightly broader and truncated (versus spatulate) and closer within a row where they are separated by less than the length of a seta (versus most setae separated by 1 to 2 × their length); rows tend to be confused, particularly in posterolateral parts, and the ground vestiture consist of coarse setae.

## Clade B

*Afrocosmoderes longisetus* sp. nov.

Figures 5, 9, 18, 23, 58, 59, 61, 62, 64, 65

urn: lsid: zoobank.org: act: BD914F9B-7F29-4DAA-BE41-7C500E40F96B

**Material examined.** Holotype, female: MADAGASCAR, Ranomafana NP, Valo [–21.250, 47.420], 1,100 m alt., ex *Abrus* liana, 6.X.2012, B. Jordal, leg. [ZMUB]. Allotype and paratypes: same data as holotype; same data except Centre ValBio [–21.253, 47.421], 950 m alt., ex *Strongylodon craveniae* liana, 29.IX.2012 [ZMUB (6); NHMW (2)].

**Diagnosis.** Antennal funiculus 4-segmented; male pronotum with hair-like bristles; interstitial setae near lateral margin long and bristle-like; ground vestiture of dense, short, scale-like setae.

**Etymology.** A nominative new Latin adjective, referring to the long setae near the lateral margins of the elytra.

**Description, male.** Length 1.3 to 1.5 mm, 2.2 to 2.3 × as long as wide; color dark brown. Eyes deeply emarginated. Antennal funicle 4-segmented; club flat, pilose, without sutures. Frons convex, impressed just above epistoma, surface reticulate and scarcely pubescent, with a faint longitudinal turgidity in the middle. Pronotum weakly constricted and slightly extended in front, with 4 or 6 smaller tubercles along the margin; anterior three-quarters steeply declivous, densely covered by slightly smaller asperities, vestiture consisting of fine hair-like setae on anterior two-thirds, with light-colored spatulate setae intermixed behind. Elytral striae not impressed, irregular punctures shallow; interstriae with main broad, spatulate setae, except long bristles at interstriae 9 and 10; striae setae fine and as short as a puncture; ground vestiture consisting of dense scale-like, almost hair-like setae. Metanepisternum with long, simple setae, on abdominal ventrites with a transverse row of coarse bristles along each posterior margin, intermixed with small and fine setae; posterior margin of ventrite V procurved to receive the terminal tergite. Protibiae with 7 or 8 lateral denticles on apical three-quarters; metatibiae with 5 or 6 lateral denticles on apical third. Proventriculus with large anterior plate divided by medial suture, surface mainly smooth. Aedeagus with apodemes shorter than rest of the penis body; basal sclerites two rings, a larger apical ring with three thin and detoured spines, and a contiguous smaller basal ring with a caudally curved extension similar to the tegmental manubrium; apex broadly rounded; terminal plates large; spicule as long as aedeagus, curved with a sharp angle near the apical end.

**Female** externally similar to male, except for last abdominal ventrite.

**Distribution and biology.** Madagascar. Collected repeatedly in rainforest southeast on the island (Ranomafana). It was taken from dead hanging *Abrus* and *Strongylodon* lianas, both in the plant family Fabaceae.

**Comments.** This species is similar to *A. pennatus* and was serendipitously discovered by examining slide prepared male genitalia which are very different. Externally it can only be distinguished by the long bristle-like setae near the lateral margin of the elytra and the 4-segmented funiculus, and to a lesser degree, by the narrower and more acuminate shape of the short scale-like ground vestiture.

DNA sequences previously submitted to GenBank with voucher name CrCor01 were from this species, not *A. pennatus*.

*Afrocosmoderes grobleri* (Schedl)

Figures 24, 66, 67, 69, 70, 72, 73

*Miocryphalus grobleri* Schedl, 1961: 349.

*Afrocosmoderes grobleri* (Schedl, 1961), combination by Johnson et al. (2020).

*Hypocryphalus caplandicus* Schedl, 1965: 115, **syn. nov.**

**Material examined.** Paratype male: SOUTH AFRICA, Cape Prov., Grootvadersbosch, 13.XII.1956, J. H. Grobler [NHMW]. Paratype of *Hypocryphalus caplandicus*: SOUTH AFRICA, Cape Prov., Grootvadersbosch, 15.I.1957, J. H. Grobler [NHMW].

New records: SOUTH AFRICA; Knysna, Gouna/Grootdrai [–33.946, 23.054], ex *Virgilia oroboides* trunk, 6.XI.2006, B. Jordal leg.; same data except Millwood Road [–33.889, 22.997], 7.XI.2006 [ZMUB].



**Diagnosis.** Antennal funiculus 5-segmented; elytral interstriae with rather long bristle-like setae, ground vestiture mainly hair-like.

**Redescription, male.** Length 1.5 to 1.8 mm, 2.0 to 2.1 × as long as wide, color brown. Frons slightly impressed longitudinally on median third; eyes deeply emarginated; antennal funiculus 5-segmented. Pronotum with coarse asperities and hair-like setae on its anterior half. Elytral striae not impressed; vestiture consisting of narrow interstitial bristles increasing in length towards declivity, intermixed with coarse elongated scale-like ground vestiture. Metanepisternum with long, fine setae, on ventrites with fine irregular bristles and finer setae intermixed. Protibiae with 7 lateral denticles on apical two-thirds, metatibiae with 6 lateral denticles on apical third. Proventriculus with apical plate large, divided by a tuberculate medial suture, surface otherwise entirely smooth. Male genitalia with apodemes shorter than penis body, basal sclerites forming a slightly twisted loop, penis apically broadly rounded; spicule a simple curved rod.

**Female** similar to male except for the last abdominal ventrite.

**Distribution and biology.** South Africa. Collected several times from *Virgilia oroboides* (Fabaceae), in the Knysna area in the Western Cape province. Pairs of male and female were found only at the early stage of egg laying ( $n=2$ ), whereas females were always alone when larvae had developed ( $N=20$ ). Two well-developed broods contained 11 and 13 larvae. This species makes cave-like or elongated tunnel-like caves under relatively thick bark, where eggs are laid in scattered clutches. The larvae will extend the cave and finally make their own feeding tunnels away from the cave.

**Comments.** The species *Hypocryphalus caplandicus* is identical to *Miocryphalus grobleri*. These two species were collected in the same habitat by Grobler, and Schedl probably overlooked the fact that he had already published some specimens as *M. grobleri* as there are no particularly notable differences between the two.

*Afrocosmoderes zambesianus* sp. nov.

Figures 68, 71, 74

urn: lsid: zoobank.org: act: A45A89AA-E466-4963-8944-C6D2E89C8FEF

**Material examined.** Holotype, female: TANZANIA, Udzungwa NP [−7.868, 36.844], 1,000 m alt., 12.XI.2009, B. Jordal, leg. [ZMUB].

**Diagnosis.** Female frons with sharp longitudinal carina; pronotum rather short and broad; main interstitial setae spatulate, in rows; ground vestiture rather dense and hair-like.

**Etymology.** With the addition of the suffix *-anus* to the noun Zambesian (region), forming a masculine nominative adjective, referring to the biogeographical region within which the type locality is located (Tanzania).

**Description, female.** Length 1.3 mm, 2.2 × as long as wide; color reddish black. Eyes deeply emarginated. Antennal funicle 5-segmented; club flat, pilose, without sutures. Frons convex, with sharp longitudinal keel from epistoma to upper level of eyes, surface rugosely reticulate and scarcely pubescent. Pronotum broadly rounded in front, about 4 smaller tubercles along the margin, slightly impressed without asperities just behind front margin, with coarse asperities on the remaining anterior central two thirds being steeply declivous; vestiture consisting of long, fine hair-like setae on anterior two-thirds, with light-colored spatulate setae intermixed behind. Elytral

striae not impressed, punctures obscure; interstriae with main setae in rows, broad and spatulate, except more elongated at interstriae 9 and 10; striae setae fine; ground vestiture hair-like. Metanepisternum with long, broad but unifid setae, on abdominal ventrites with a transverse row of fine bristles, intermixed with small and fine setae. Protibiae with 4 lateral denticles on apical one-third; metatibiae with 3 apical lateral denticles.

**Male** not known.

**Distribution and biology.** Tanzania. Only known from the type locality where it was collected as a single mature female and two offspring larvae in a terminal broken twig of a small seedling.

*Afrocosmoderes pellitus* (Schedl)

Figures 7, 11, 12, 75, 78, 81

*Erioschidias pellitus* Schedl, 1953: 79

*Afrocosmoderes pellitus* (Schedl), combination by Jonson et al. (2020).

**Material examined.** Holotype and paratype, females: MADAGASCAR, Mt. d'Ambre [NHMW].

New record: MADAGASCAR, Diana prov., Montagne d'Ambre [−12.54, 49.17], 1,000 m alt., ex *Cananga odorata* branch, 2.XI.2019, B. Jordal, leg. [ZMUB].

**Diagnosis.** Antennal funiculus 3-segmented; frons in both sexes with longitudinal carina; elytral ground vestiture hair-like; vestiture on abdominal ventrites fine bristles.

**Description, male.** Length 1.3 to 1.5 mm, 2.2 to 2.5 × as long as wide, color light brown. Frons convex, with sharp median carina from epistoma to vertex; eyes deeply emarginated; antennal funiculus 3-segmented. Pronotum on its anterior half with fine asperities and hair-like setae. Elytral striae not impressed; interstitial setae spatulate or subquadrate, separated within rows by less than their length; ground vestiture hair-like. Metanepisternal setae long, split or trifid; setae on abdominal ventrites thin and hair-like. Protibiae with 7 or 8 lateral denticles on apical half, metatibiae with 5 lateral denticles on apical third. Proventriculus with apical plate large, divided by a tuberculate medial suture, surface of some plates containing transverse row of rounded teeth, others entirely smooth. Male genitalia with apodemes shorter than penis body, basal sclerites consisting of rounded individual pieces, penis apically broadly rounded; spicule a simple curved rod.

**Female** externally similar to the male, except for the last abdominal ventrite.

**Distribution and biology.** Madagascar. Recollected here from the type locality in the northern part of the island. Mature specimens were dissected from a *Cananga odorata* branch (Annonaceae), which is an introduced tree used in the perfume industry (ylang-ylang tree).

**Comments.** This species is, together with *A. longus* sp. nov. and *A. seriatus*, the most elongated species in the genus.

*Afrocosmoderes parvus* sp. nov.

Figures 76, 77, 79, 80, 82, 83

urn: lsid: zoobank.org: act: DEA5A130-4FCF-4F0D-92DD-757CABA1C41E

**Material examined.** Holotype, male: MADAGASCAR, Ankarafantsika NP [−16.264, 46.828], 200 m alt., ex *Dombeya* seedling, 9.V.2015, B. Jordal, leg. [ZMUB]. Allotype female and two paratypes: same data as holotype [ZMUB].

**Diagnosis.** Body length <0.9 mm; frons smooth; antennal funiculus 3-segmented; eyes entire; male pronotum slightly

produced, anterior slope with broad golden setae; elytral ground vestiture absent.

**Etymology.** This is the smallest species known in the genus and is here given the Latin nominal adjective *parvus* which means small.

**Description, male.** Length 0.7 to 0.9 mm, 2.1 to 2.3 × as long as wide; color brown. Eyes entire. Antennal funicle 3-segmented; club flat, pilose, without sutures. Frons convex, smooth, scarcely pubescent. Pronotum narrowly rounded in front, weakly produced with 4 smaller tubercles along the margin, anterior half declivous with asperities, vestiture consisting of broad golden setae on anterior half, on posterior third scales paler and mixed with fine hair-like setae. Elytral striae not impressed, irregular punctures shallow; interstriae with main setae spatulate, in rows; striae setae fine and hair-like; ground vestiture absent. Metanepisternum with long, split setae, on abdominal ventrites with a transverse row of coarse bristles, intermixed with small and fine setae; posterior margin of ventrite 5 procurved to receive terminal tergite. Protibiae with 4 or 5 lateral denticles on apical one-third; metatibiae with 3 or 4 apical denticles. Proventriculus with large anterior plate divided by tuberculate medial suture, surface either smooth or with transverse rows of rounded teeth. Aedeagus with apodemes shorter than rest of the penis body; basal sclerites Y-shaped, with some smaller additional unconnected pieces; apex broadly rounded; spicule shaped as a curved rod, as long as aedeagus.

**Female** similar to male, except less narrowly rounded in front of pronotum, with only hair-like setae on anterior two-thirds of the pronotum.

**Distribution and biology.** Madagascar. Only known from the type locality where it was collected from a 3 cm thick stem of a dead *Dombeya* seedling (Sterculiaceae). Five teneral specimens remained in a partly abandoned gallery shaped as a cave, where last stage larvae made independent tunnels away from the early-stage cave.

#### Clade C

*Afrocosmoderes brevicostatus* sp. nov.

Figures 84, 85, 88, 89, 92, 93

urn: lsid: zoobank.org: act: 2BA537EA-3360-4BEE-BA50-B413964F0F13

**Material examined.** Holotype, male: MADAGASCAR, Andasibe, Mantadia National Park [−18.861, 48.447], 900 m alt., ex unknown branch, 15.V.2015, B. Jordal, leg. [ZMUB]. Allotype and paratype (1): same data as holotype [ZMUB].

**Diagnosis.** Frons with short longitudinal carina just above epistoma; antennal funiculus 3-segmented; male pronotum produced; elytral ground vestiture hair-like.

**Etymology.** The Latin nominative adjective *costatus* refers to the longitudinal keel in the frons, adding the prefix *brevi-*, meaning short, which describes its short length.

**Description, male.** Length 1.2 mm, 2.1 to 2.2 × as long as wide; color dark brown. Eyes emarginated. Antennal funicle 3-segmented; club flat, pilose, without sutures. Frons convex, smooth, except short, narrow, sharp carina from epistoma to upper level of eyes, scarcely pubescent. Pronotum narrowly rounded in front, distinctly produced with about 6 tubercles along the margin, distinctly larger than asperities on anterior two-thirds, vestiture consisting of hair-like setae on anterior two-thirds, intermixed with pale scales on posterior third. Elytral striae not or very slightly impressed, irregular punctures shallow; interstriae with main setae spatulate

to subquadrate, in rows; striae setae and ground vestiture similarly hair-like. Metanepisternum with short, split and almost fluffy setae, on abdominal ventrites with a transverse row of coarse bristles, intermixed with small and fine setae; posterior margin of ventrite 5 procurved to receive terminal tergite. Protibiae with 4 or 5 lateral denticles on apical one-third; metatibiae with 3 or 4 denticles on apical one-fourth. Proventriculus with large anterior plate divided by tuberculate medial suture, surface either smooth or with transverse rows of rounded, occasionally smaller and sharp teeth. Aedeagus with apodemes shorter than rest of the penis body; basal sclerites V-shaped, further apically with a series of necklace-shaped small sharp sclerites; apex broadly rounded; spicule shaped as a curved rod, as long as aedeagus.

**Female** externally similar to male, except pronotum broadly rounded in front.

**Distribution and biology.** Madagascar. Only known from the type locality in a lowland rainforest where a few mature offspring were collected under bark of a 3 cm thick dead branch.

*Afrocosmoderes carinatus* sp. nov.

Figures 2, 86, 87, 90, 91, 94, 95

urn: lsid: zoobank.org: act: 4829B9DC-0E8C-4096-866F-12B607C8BF2A

**Material examined.** Holotype, male: MADAGASCAR, Diana, Montagne d'Ambre [−12.54, 49.17], 1,000 m alt., 4.XI.2019, B. Jordal, leg. [ZMUB]. Allotype female and two paratypes: same data as holotype [ZMUB].

**Diagnosis.** Frons with longitudinal carina from epistoma to vertex; antennal funiculus 3-segmented; male pronotum produced; elytral ground vestiture hair-like.

**Etymology.** The Latin nominative adjective *carinatus* refers to the sharp longitudinal keel in the frons, particularly well developed in the male.

**Description, male.** Length 1.1 to 1.3 mm, 2.1 to 2.2 × as long as wide; immature color light brown. Eyes emarginated. Antennal funicle 3-segmented; club flat, pilose, without sutures. Frons convex, smooth, except narrow, sharp carina present from epistoma to vertex, scarcely pubescent. Pronotum narrowly rounded in front, distinctly produced with about 6 tubercles along the margin, slightly larger than asperities on anterior two-thirds, vestiture consisting of hair-like setae on anterior two-thirds, intermixed with pale scales on posterior third. Elytral striae not impressed, punctures shallow; interstriae with main setae triangularly spatulate, in rows; striae setae and scant ground vestiture similarly hair-like. Metanepisternum with short, split setae, on abdominal ventrites with a transverse row of coarse bristles, intermixed with small and fine setae; posterior margin of ventrite 5 procurved to receive terminal tergite. Protibiae with 4 or 5 lateral denticles on apical one-third; metatibiae with 4 denticles on apical one-fourth. Proventriculus with large anterior plate divided by tuberculate medial suture, surface either smooth or with transverse rows of rounded, occasionally smaller and sharp teeth. Aedeagus with apodemes shorter than rest of the penis body; basal sclerites V-shaped, other sclerites elongated; apex broadly rounded; spicule shaped as a curved rod, as long as aedeagus.

**Female** externally similar to male, except pronotum broadly rounded in front.

**Distribution and biology.** Madagascar. Only known from the type locality in a northern mountainous rain forest. Six immature adult specimens were dissected from the bark of a 2 cm thick branch.



*Afrocosmoderes seriatus* sp. nov.

Figures 10, 25, 96, 97, 99, 100, 102, 103

urn: lsid: zoobank.org: act: 641CD2F6-0269-4DE4-AEDE-CC03200421C7

**Material examined.** Holotype, male: MADAGASCAR, Diana, Montagne d'Ambre [–12.54, 49.17], 1,000 m alt., 3.XI.2019, B. Jordal, leg. [ZMUB]. Allotype female and paratypes: same data as holotype (3, ZMUB); same data except 2.XI.2019, leg. J. Eliassen [5, ZMUB; 2, NHMW]; MADAGASCAR, Diana, Special reserve d'Ambre, 3.5 km SW Sakaramy [–12.54, 49.17], leg. B. Fischer [2, CAS].

**Diagnosis.** Frons in both sexes with very faint trace of longitudinal carina just above epistoma to upper level of eyes; antennal funiculus 3-segmented; male pronotum with broad golden setae; metanepisternal setae long and split; small bifid setae intermixed on abdominal ventrites.

**Etymology.** The Latin nominative adjective *seriatus* refers to the tidy regular rows of interstitial setae.

**Description, male.** Length 1.2 to 1.3 mm, 2.3 to 2.5 × as long as wide; color brown. Eyes emarginated. Antennal funicle 3-segmented; club flat, pilose, without sutures. Frons convex, smooth, except for a faint short carina present just above epistoma, scarcely pubescent. Pronotum broadly rounded in front, with about 6 tubercles along the margin, distinctly larger than asperities on anterior two-thirds, vestiture consisting of dense, broad, golden scale-like setae becoming paler and sparser on posterior one-third, intermixed with hair-like setae. Elytral striae not impressed, punctures distinct, spaced by half their diameter; interstriae with main setae triangularly spatulate, in regular rows; striae setae and ground vestiture similarly hair-like, each seta about two times as long as a striae puncture. Metanepisternum with long, split setae, on abdominal ventrites with a transverse row of coarse bristles, intermixed with fine split setae; posterior margin of ventrite 5 procurved to receive terminal tergite. Protibiae with 5 or 6 lateral denticles on apical one-third; metatibiae with 4 denticles on apical one-fourth. Proventriculus with large anterior plate divided by tuberculate medial suture, surface either smooth or with transverse rows of rounded, occasionally smaller and sharp teeth. Aedeagus with apodemes shorter than rest of the penis body; basal sclerites V-shaped, other sclerites elongated and feather-like; apex broadly rounded; spicule shaped as a curved rod, as long as aedeagus.

**Female** externally similar to male, except pronotum with only hair-like setae on anterior two-thirds.

**Distribution and biology.** Madagascar. Only known from three nearby rain forest localities in the Montagne d'Ambre area in the north of the island. Old broods were dissected from irregular maturation tunnels under bark of branches 2 and 5 cm in diameter. Two specimens were also sifted from forest litter.

*Afrocosmoderes madagascariensis* (Schedl)

Figures 98, 101, 104

*Ptilopodius madagascariensis* Schedl, 1961: 133.

*Afrocosmoderes madagascariensis* (Schedl), combination by Jonson et al. (2020).

**Type material.** Holotype female: MADAGASCAR, Joffreville, 600 m, 16.XII.1952, Dr K. E. Schedl leg. [MNHN]; paratypes: same data as holotype [NHMW].

**Diagnosis.** Antennal club 3-segmented; metanepisternal setae split; elytral ground vestiture scale-like; spatulate interstitial setae near lateral margin mixed with bristle-like setae.

**Redescription, female.** Length 1.2 to 1.3 mm, 2.2 × as long as wide, color dark brown. Frons flattened, rugose, with a short longitudinal obtuse carina just above epistoma; eyes deeply emarginated; antennal funiculus 3-segmented. Pronotum with coarse asperities on anterior half. Elytral striae not impressed, vestiture consisting of elongated spatulate interstitial setae, near lateral margins mixed with fine bristles; ground vestiture of scale-like minute setae. Metanepisternal setae long and split. Protibiae with 5 or 6 lateral denticles on apical half.

**Male** not known.

**Distribution.** Madagascar. It is only known from a northern mountain rainforest locality near Montagne d'Ambre.

**Comments.** Type specimens have some characters hidden by glue and some setae are abraded. DNA sequences were previously submitted to GenBank under this name (Pistone et al. 2018) but those sequences are from *A. zambesianus* sp. nov.

### Incertae sedis

*Afrocosmoderes africanus* (Schedl), comb. nov.

Figures 105, 108, 111

*Stephanorhopalus africanus* Schedl, 1977: 396.

*Ernoporicus africanus* (Schedl, 1977), combination by Wood and Bright, 1992.

*Eidophelus africanus* (Schedl, 1977), combination by Johnson et al., 2020.

**Type material.** Holotype male: [SOUTH AFRICA] Natal [NHMW].

**Diagnosis.** Male pronotum broad, with broad golden setae over most of its surface; eyes entire; antennal funiculus 5-segmented.

**Redescription, male.** Length 1.1 mm, 1.9 × as long as wide, color dark black. Frons flattened, smooth; eyes entire; antennal funiculus 5-segmented. Pronotum broadly rounded, with dense broad and golden scale-like setae almost reaching posterior margin. Elytral striae very slightly impressed; interstitial setae broader than long, densely placed in mainly regular rows (confused near base), ground vestiture absent.

**Female** not known.

**Distribution.** South Africa. It is only known from the type locality in Natal.

**Comments.** This species has previously been treated in three different genera. However, the characteristic golden broad setae on the pronotum are unmistakably male *Afrocosmoderes*. Characteristics of legs and venter are not clearly seen on the type, but protibiae have most likely fewer than five lateral denticles.

*Afrocosmoderes plenus* sp. nov.

Figures 1, 17, 20, 106, 107, 109, 110, 112, 113

urn: lsid: zoobank.org: act: 18E21A35-B930-4848-8784-D9028E233CBF

**Material examined.** Holotype, male: MADAGASCAR, Ankarafantsika NP [–16.264, 46.828], 200 m alt., ex liana, 9.V.2015 [ZMUB]. Allotype and paratypes (4): same data as holotype [ZMUB, NHMW (2)]; MADAGASCAR, Parc National Montagne d'Ambre, Petite Lac Road, ex Malaise trap MA-01-01D-07, B. Fischer, leg. [1, CAS].

**Diagnosis.** Stout tiny species 1.9 to 2.0 × as long as wide, male pronotum narrowly prolonged, with broad golden setae; eyes entire, funicle 3-segmented; ground vestiture absent.

**Etymology.** From the Latin nominative adjective *plenus*, meaning rounded or chubby, referring to the overall stout body shape of this otherwise small species.

**Description, male.** Length 0.9 to 1.0 mm, 1.9 to 2.0 × as long as wide; color dark blackish brown. Eyes entire. Antennal funicle 3-segmented; club flat, pilose, without sutures. Frons convex, relatively smooth, weakly wrinkled, with a faint turgidity on vertex. Pronotum narrowly rounded in front, with about 6 tubercles along the margin, distinctly larger than asperities on anterior two-thirds, vestiture consisting of dense, broad, golden scale-like setae becoming paler and sparser on posterior one-fifth, intermixed with fine hair-like setae. Elytral striae not impressed, punctures obscure; interstriae with main setae subquadrate, slightly longer than wide, in regular rows; striae setae hair-like, ground vestiture generally absent except a few fine setae near elytral suture. Metanepisternum with short, simple setae, on abdominal ventrites with a transverse row of coarse bristles, intermixed with fine setae; posterior margin of ventrite 5 procurved to receive terminal tergite. Protibiae with 5 or 6 lateral denticles on apical one-third; metatibiae with 3 or 4 denticles on apical one-fourth. Proventriculus with large smooth anterior plate divided by tuberculate medial suture, or open with transverse rows of blunt spines. Aedeagus not dissected.

**Female** externally similar to male, except frons and vertex smooth, pronotum broadly rounded in front, with only hair-like setae on anterior two-thirds.

**Distribution and biology.** Madagascar. Collected in two forest localities in the northwest and northern parts of the island. Broods were dissected from bark of a dead liana where the female made a cave-like egg tunnel. Brood size ranged between 4 and 6 eggs in putatively the early stage of reproduction ( $n=3$ ).

*Afrocosmoderes niger* (Schedl)

*Erioschidias niger* Schedl, 1961: 131.

*Afrocosmoderes niger* (Schedl), combination by Jonson et al. (2020).

**Type material.** Holotype female: MADAGASCAR, Perinet, 20.XI.1952, Dr K. E. Schedl leg. [MNHN].

**Diagnosis.** Antennal funiculus 4-segmented; elytral ground vestiture hair-like, interstitial setae increasing in thickness from thin bristles near the base to broad spatulate setae on the declivity.

**Redescription, female.** Body length 1.5 mm, 2.2 × as long as wide. Frons convex, smooth; eyes emarginated; antennal funiculus 4-segmented. Elytral interstriae with main setae on basal fifth fine and bristle-like, then broader and spatulate toward declivity and apex; elytral ground vestiture hair-like. Protibiae with 5 lateral denticles on apical third; vestiture on metanepisternum scant, consisting of short, narrow scales.

**Male** not known.

**Distribution.** Madagascar. It is only known from the type locality in an eastern lowland rainforest.

**Comments.** The holotype in MNHN is the only material of this species. Due to loan restrictions at MNHN, pictures could not be produced. However, the species is easily recognized by eg the interstitial setae changing from almost hair-like near the base of elytra to spatulate on the declivity.

## Key to Species in *Afrocosmoderes*

Unless otherwise stated, the distribution is Madagascar.

1. Protibiae with 4 to 6 denticles along its lateral edge (if 6 denticles, then elytral ground vestiture scant and hair-like) ..... 2

- Protibiae with 7 to 10 denticles along the outer lateral edge (if only 6 denticles, then lower central frons grooved, or metatibia with 5 to 6 denticles) ..... 10
2. Elytral ground vestiture mixed hair- and scale-like; elytral declivity slightly flattened, ... *A. madagascariensis*
- Elytral ground vestiture either hair-like or absent; declivity gently rounded ..... 3
3. Basal fourth of interstriae with bristle- or hair-like setae ... *A. niger*
- Interstitial setae spatulate or broad bristles from base to apex ..... 4
4. Eyes slightly to strongly emarginated; elytral ground vestiture consisting of small setae scattered on interstriae ... 5
- Eyes entire; elytral ground vestiture absent ..... 8
5. Antennal funicle 5-segmented; lateral elytral interstriae with mixed scale- and bristle-like setae; metanepisternal setae unid (Tanzania) ..... *A. zambesianus*, sp. nov.
- Antennal funicle 3-segmented; lateral interstriae with spatulate setae only; metanepisternal setae split ..... 6
6. Anterior margin of male pronotum broadly rounded, setae on anterior slope broad, golden scale-like; smallest setae on abdominal ventrites bifid; frons in both sexes with only a slight trace of a carina ... *A. seriatus*, sp. nov.
- Anterior margin of male pronotum narrowly extended, setae on anterior slope hair-like; smallest setae on ventrites simple; male frons with sharp longitudinal carina ..... 7
7. Setae on elytral interstriae subquadrate; male frontal carina extending to upper level of eyes ... *A. brevicostatus*, sp. nov.
- Setae on interstriae triangular (cuneate); male carina extending to vertex ..... *A. carinatus*, sp. nov.
8. Interstitial setae broader than long, slightly confused within rows near lateral margins; male pronotum broadly rounded in front (South Africa) ..... *A. africanus*
- Interstitial setae slightly longer than broad, uniseriate; male pronotum produced anteriorly (Madagascar) ... 9
9. Antennal funicle 5-segmented; metanepisternal setae short and unid; body length 1.9 to 2.0 × as long as wide; elytral declivity commencing on anterior third ... *A. plenus*, sp. nov.
- Antennal funicle 3-segmented; metanepisternal setae long and split; body length 2.2 to 2.3 × as long as wide; elytral declivity commencing on posterior third ... *A. parvus*, sp. nov.
10. Frons in both sexes impressed, more strongly so in males which also have long setae around an impunctate concave area; general habitus appears rough, striae impressed; abdominal ventrites along its posterior margin with fine trifid setae between coarse bristles ... *A. asper*
- Frons convex or only slightly grooved, with at most scattered setae; general body appearance smooth (except rough in *A. saetiger*); all setae on abdominal ventrites unid ..... 11
11. Elytral ground vestiture hair-like throughout; male frons carinate ..... *A. pellitus*
- Elytral ground vestiture scale-like at least on posterior half: male frons smooth or grooved ..... 12
12. Antennal funicle 3-segmented; striae punctures on elytra large, deep, subcontiguous, striae impressed on declivity; appearing rough, setae in interstitial rows very dense .... *A. saetiger*, sp. nov.

- Antennal funicle 4- or 5-segmented; strial punctures on average shallow, cuticle generally smooth, all main setae separated by the length of a seta or more ..... 13
- 13. Male frons slightly grooved; abdominal ventrites with all setae hair-like ..... 14
  - Male frons smooth; largest setae on ventrites coarse and bristle-like ..... 15
- 14. Interstrial main setae bristle-like, variable in length and thickness; male pronotum on its anterior slope with fine bristles and hair-like setae; body  $<2.2 \times$  as long as broad (South Africa) ..... *A. grobleri*
  - Main interstrial setae broad scales; male pronotum with golden scales on its anterior slope; body  $2.4 \times$  as long as broad (Madagascar) ..... *A. longus*, sp. nov.
- 15. Metanepisternal setae split; male pronotum with golden scales on its anterior slope ..... *A. schedli*
  - Metanepisternal setae mainly unifold; male pronotum with only hair-like setae on its anterior slope ..... 16
- 16. Interstrial setae transverse at tips, in broad confused rows, intermixed with coarse semierect scale-like ground vestiture ..... *A. confertus*, sp. nov.
  - Interstrial setae spatulate, in regular rows; ground vestiture semirecumbent tiny bristles or scales ..... 17
- 17. Elytral interstriae 9 and 10 with mixed long hair-like and shorter bristle-like setae; metanepisternal setae long ..... *A. longisetus*, sp. nov.
  - Interstrial setae all short and bristle-like; metanepisternal setae short ..... 18
- 18. Antennal funicle 5-segmented; main setae on elytral interstriae spaced within a row by their length or less, ground vestiture dense and scale-like; body length  $>1.4$  mm ..... *A. pennatus*
  - Antennal funicle 4-segmented; main setae on elytral interstriae spaced within a row by  $1.5$  to  $2.0 \times$  their length, ground vestiture hair-like and more spaced on disc, denser and scale-like on declivity; body length  $<1.4$  mm ..... *A. lenifrons*, sp. nov.

## Discussion

### Contrasting Diversification Patterns

*Afrocosmoderes* is one of the oldest origins of bark beetle lineages in Madagascar (e.g. Jordal 2021a,b, 2023, 2024). As the sister group to the enormously diverse *Hypothenemus*, it stands in stark contrast with its many fewer species produced, and a restricted distribution largely confined to Madagascar. *Hypothenemus* is found all over the world, with nearly 200 species currently recognized, which is a gross underestimate of the real diversity (Kambestad et al. 2017). Such widespread diversity is in part due to its inbreeding mating system, in which siblings mate before dispersal and makes them preadapted for successfully colonizing new areas (Kirkendall 1993, Jordal et al. 2001). *Afrocosmoderes*, on the other hand, is entirely outbreeding, with monogamous pairs being established after dispersal to a new host plant. At a global scale, it is evident that normal outbreeding species are more restricted in their distribution (Jordal et al. 2001), a pattern which fits the sister comparison between the two genera.

The phylogenetic structure in *Afrocosmoderes* indicates a gradual and slow diversification over time, beginning soon after the origin of the genus. Even though the genus could be somewhat undersampled, as noticed from the 12 new species discovered in this study, it cannot compete for diversity with its sister group. It is therefore a noteworthy observation that *Hypothenemus* delayed diversification for quite some time compared to *Afrocosmoderes*, or experienced significant extinction of its earliest lineages. The young age of crown *Hypothenemus* was also demonstrated in a recent molecular studies based on voluminous AHE data, estimating an even younger crown age around 20 Ma (Johnson et al. 2018). The lack of old extant lineages therefore limits our possibility to study the early evolution of sib-mating in *Hypothenemus*.

The geographical origin of *Afrocosmoderes* is somewhat uncertain. Even though outgroup sampling was fairly substantial and relevant, some small Asian genera were not included. Nevertheless, it seems most likely that the *Hypothenemus-Afrocosmoderes* clade stems from a southern Palearctic or Indomalayan ancestor, two areas which overlap considerably in Trypophloeini genera (Johnson et al. 2018, 2020a,b). It seems clear that *Afrocosmoderes* did not colonize Madagascar from Africa, as all known African species were nested within the Malagasy clade. Instead, the African members originated from one or several colonizations of the mainland, especially if one takes the MrBayes tree topology into account. Trade winds turned and northern Madagascar experienced westward wind directions already in late Oligocene and early Miocene (Ali and Huber 2010, Samonds et al. 2012). These new opportunities never resulted in substantial species radiation on the mainland, however, with only three current species known. Limited speciation is a general trend in other beetles too, where scolytine beetles have been studied in more detail (Jordal 2013, Bukontaite et al. 2015, Eliassen and Jordal 2021, Jordal 2021b).

### Confusing Morphology

Despite the Paleocene origin of *Afrocosmoderes*, it is unusually difficult to distinguish species based on morphological characters alone. In fact, the mismatch between molecular and morphological data urged for new DNA analyses of eight additional *Afrocosmoderes* specimens to check for possible contamination of DNAs during our laboratory work. However, all new samples had a perfect match with the original data for 28S. It is also clear that the incongruent morphological affinities were not due to a rapid, recent radiation of the genus. Instead, the phylogenetic analyses revealed very gradual diversification, with extended time between divergence events resulting in well supported relationships between species or deeper lineages. *Afrocosmoderes* is a prime example of slow morphological evolution and the uniform shape of these beetles is therefore yet another warning against underestimating tropical insect diversity (Li and Wiens 2023).

Taxonomic research in the past illustrates further some of the morphological difficulties described above. Six species in *Afrocosmoderes* were previously described in other genera and in most cases, they have been transferred further, in total involving nine different genera, of which six genera are still in current use. It is clear from these disparate taxonomic acts, and

the morphological challenges experienced in this study, that diagnostic features are hard to discover and define. A series of discriminating characters for species identification were nevertheless developed here (see Methods section), although these were largely ambivalent in the phylogeny reconstruction (Table 3). For instance, reduced emargination of the eyes and the number of funicle segments appeared somewhat, but not entirely, correlated with small body size. Some other characters are likely under strong sexual selection such as the male-female dimorphic pronotum which evolved independently in several species groups. It is therefore not surprising that these kinds of characters have little phylogenetic signal, despite being useful in species diagnostics.

The best clues to affiliate species are found in the male genitalia. This type of morphological characters are often uniform and therefore rarely used to differentiate species of bark beetles. Instead, they have proven useful in grouping higher taxa (e.g. Jordal et al. 2002, Johnson et al. 2020b, Jordal 2021a). In *Afrocosmoderes*, both trends appear, with distinct gross similarities across larger groups of species, yet at the same time there was great variation in genitalia between otherwise near identical species. Distinct species differences in the male genitalia are often a result of sexual selection and is usually observed in insects with multiple matings (Eberhard 1985). There are few examples of multiple mating in bark beetles, but at least in certain *Aphanarthrum* Wollaston there are huge genitalic differences between closely related species known to mate competitively in the tunnel opening or in communal breeding systems under bark (Jordal et al. 2006). It was not clear from the limited observations in this study if multiple matings occurred at any significant scale, but high colonization densities were observed in some of the species collected.

## Antiquity of Behaviors

Behavior is a crucial set of traits that helps define *Afrocosmoderes* species. Their strict preference for either branches or lianas of different plant families separates clades with high support. This is a different type of host preference compared to the typical bark beetle communities in boreal forests in which groups of species, or even entire higher-level taxa, are defined by host plant families or orders. This study contained few observations, and the identification of lianas was uncertain, but the phylogenetic results nevertheless documented a strikingly conserved host preference with respect to lianas. There are very few examples of similar functional host preferences. *Scolytodes* Ferrari has several species rich clades utilizing leaf petioles (Jordal and Kirkendall 1998), *Aphanarthrum* has clades specific to succulents versus shrubs (Jordal 2006), or *Kissophagus* that feed on climbing vines (Pfeffer 1995), but each of these examples involve a single host genus. Only further studies will reveal if the phylogenetically unrelated lianas used by *Afrocosmoderes* are functionally related to each other, or if the host preference pattern observed is a mere coincidence of common lianas being more available to the beetle.

Breeding biology and family structure can also be quite unique for a bark beetle species and varied considerably between species in *Afrocosmoderes*. Laying eggs in clusters is a dramatic shift away from the normal egg niche deposits observed in most bark beetle females, but clusters were observed in three unrelated species (cave and tube structures, see Table 4). This type of egg laying is most commonly observed

in various smaller groups across the several tribes previously included in Cryphalini (see Johnson et al. 2020b). Most *Cryphalus* do this whereas only sporadically observed in *Eidophelus* and *Trypophloeus*. Clustered egg laying is the rule in the sib-mating *Hypothenemus* and is regarded as one of the prerequisites for permanent inbreeding to evolve (Kirkendall 1983, 1993, Kirkendall et al. 2015). It is logical that permanent inbreeders lay their eggs in clusters so that siblings are close for mating when they mature. However, the underlying process favouring clustered egg laying in normal outbreeders such as *Afrocosmoderes* is not known.

Reproduction in small twigs, thin branches and in lianas does not facilitate great brood sizes. This is largely due to the rapid desiccation of thin breeding material and does not allow for extended egg laying. Also, the amount of nitrogen-rich phloem is limited in such plant material which likely reduces the number of eggs that can be produced. Populations are nevertheless healthy and stable, which is possible due to the steady provision of breeding material at a rate much higher than natural tree falls in the forest.

## Specimen Collection Statement

**Nagoya Protocol:** The authors attest that all legal and regulatory requirements, including export and import collection permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study.

## Nomenclature

This article and the nomenclatural act(s) it contains have been registered in Zoobank ([www.zoobank.org](http://www.zoobank.org)), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:25B2F303-41A0-4C0E-A8F2-8BE3E4EBC2F5.

## Author Contributions

Bjarte Jordal (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Funding acquisition [lead], Investigation [lead], Methodology [lead], Project administration [lead], Resources [lead], Software [lead], Supervision [lead], Validation [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead])

## Supplementary Material

**Supplementary material** is available at *Insect Systematics and Diversity* online.

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## Conflicts of Interest

None declared.

## Data Availability

DNA sequence data are available from GenBank with accession numbers given in Table 2. The various matrices used in the analyses are found in Supplementary Material online.

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