Fragmenta entomologica, 53 (2): 283–298 (2021)

eISSN: 2284-4880 (online version)
pISSN: 0429-288X (print version)

Research article
Submitted: July 8th, 2021 – *Accepted*: September 18th, 2021 – *Published*: November 30th, 2021
DOI: 10.13133/2284-4880/547

Phylogenetic placement of a new paleoendemic pill scarab from the Udzungwa Mountains, Tanzania, triggers biogeographic interpretations (Coleoptera: Hybosoridae, Ceratocanthinae)

Vasily V. GREBENNIKOV

Canadian Food Inspection Agency, 960 Carling Ave., Ottawa, ON, K1A 0Y9, Canada – vasily.grebennikov@canada.ca

Abstract

A new pill scarab with peculiar carinate apical halves of the elytra, *Balleriodes sphaera* **gen.** et **sp. nov.**, is described and illustrated from the Udzungwa Mountains, Tanzania. A phylogenetic analysis of 73 terminals and 3118 aligned positions from three DNA fragments placed *Balleriodes* within a newly recognized and strongly supported clade herein informally named the *Synarmostes* group. The group includes three monophyletic species-rich genera: African *Melanophilharmostes* and *Pseudopterorthochaetes*, as well as *Synarmostes* from Madagascar and the Comoro Islands. The discovery of the monotypic genus *Balleriodes* **gen. nov.** in Udzungwa highlights the importance of the ancient and exceptionally biodiverse chain of the Eastern Arc Mountains in Tanzania and Kenya. Three cases of overseas dispersal by the members of the *Synarmostes* group are hypothesized: Africa to Madagascar, Madagascar to Comoros, and Africa to Annobón. Preliminary biogeographical interpretation of the increasingly more resolved pantropical subfamily Ceratocanthinae is presented.

Key words: DNA barcode, ITS2, 28S, forest litter, Afrotropics, Eastern Arc Mountains, *Balleriodes*, new genus, new species.

http://zoobank.org/urn:lsid:zoobank.org:pub:DF5C4463-4C32-4C56-95F1-C7378EAD5869

Introduction

The present study was triggered by a discovery made on October 7, 2014, in the biodiverse and ancient forest of the Udzungwa Mountains, Tanzania (Fig. 1A; Burgess et al. 2007). A sample of sifted forest litter taken on that day revealed a series of highly unusual adult pill scarabs (Figs 1B–F, 2–5). This colloquial term refers to the subfamily Ceratocanthinae of the hybosorid beetle family (Howden & Gill 2000). Most pill scarabs can conglobate, that is to pack body and legs into a tight spheroid (Figs 1B-F, 3, 4) resembling that of pill bugs (Armadillidiidae, terrestrial isopods) using, however, interlocking exoskeletal structures. The subfamily is a pantropical clade of 43 genera and over 366 species (Ballerio & Grebennikov 2016).

The Udzungwa species was, however, notably dissimilar from most other pill scarabs by having the posterior half of elytra distinctly carinate (or deeply grooved, both definitions describe the same morphological manifestation, Figs 1B-F). Beetles' elytra were even and polished anteriorly, while deeply grooved (or markedly carinate) posteriorly. In this respect, these beetles resembled those of the poorly known genus *Synarmostes* Germar, 1843. The latter consists of three named species in Madagascar and one in the Comoro Islands (Figs 3, 4; Ballerio & Grebennikov 2016). Alternatively, although more remotely, carinate elytral apices of the Udzungwa species resembled those of the otherwise much dissimilar genus *Aneilobolus* Hesse, 1948 with four named species in South Africa (Figs 3, 4; Ballerio & Grebennikov 2016). In *Aneilobolus*, however, elytra display the more generalized condition of being carinate throughout most of their entire length, as frequently found in various other pill scarabs, e.g. among *Acanthocerodes* Péringuey, 1901, *Congomostes* Paulian, 1968, *Germarostes* Paulian, 1982 or *Martinezostes* Paulian, 1962 (see images in Ballerio & Grebennikov 2016). Moreover, primitively incapable of enrollment coaptation (=ability to form a nearly perfect spheroid; Ballerio & Grebennikov 2016), *Aneilobolus* is an unlikely sister group to the spheroid-forming *Synarmostes* and the new Tanzanian species.

Monophyly and phylogenetic positions of both *Synarmostes* and *Aneilobolus*, as well as those of the vast majority of other pill scarabs, have never been adequately tested. When included as outgroups in DNA-based analyses (Grebennikov 2019a, b), the Comoro species representing the genus *Synarmostes* formed a strongly supported clade with two sole representatives of two African genera: *Melanophilharmostes* Paulian, 1968 (Figs 3, 4) and *Pseudopterorthochaetes* Paulian, 1977 (Figs 3, 4). The latter two genera were hypothesized to form a clade of 25 named species distributed between Liberia, Ethiopia, and South Africa (Fig. 1A, Ballerio 2016). The sole sequenced member of *Aneilobolus*, on the other hand, formed a strongly supported clade with the Neotropical genera *Germarostes* and *Ceratocanthus* White, 1842 (Grebennikov 2019b). Considering all the uncertainties, the first interpretation of the Udzungwa pill scarab was, therefore, that it might represent the first mainland record of the so far exclusively insular *Synarmostes*.

Assuming that the four named species of *Synarmostes* do form a clade, two lines of circumstantial evidence support this preliminary interpretation. Firstly, it evokes a single and, therefore, the most parsimonious non-reversal origin of the peculiarly carinate apical elytral halves. Secondly, the Udzungwa is spatially close to the Comoro Islands (850 km) and Madagascar (1,450 km), both laying in the same south-east direction (Fig. 1A). If *Synarmostes* is a clade naturally distributed in Madagascar and Comoros, that is across a formidable sea distributional barrier, why then its member cannot also naturally exist in nearby Tanzania? If so, such a trans-Mozambique Channel distribution can be explained by several conflicting biogeographical scenarios. Two main alternatives are the ancient Gondwanan vicariance (documented among beetles only for *Heterogyrus milloti* Legros, 1953, Gyrinidae; Gustafson et al. 2017) versus much later and more frequent dispersal from mainland Africa (Poux et al. 2005; Yoder & Nowak 2006). The presence of *Synarmostes* on the geologically young Comoros Islands (10–15 Mya of the oldest island, Mayotte and 0.5 Mya of the youngest island, Grand Comore; Audru et al. 2010) strongly suggests clade's capacity for overseas dispersal. Even more intriguing, can the Tanzanian species be perhaps a result of the westwards dispersal from Madagascar to the African mainland, that is in the direction opposite to the prevailing route (Ali & Huber 2010; Masters et al. 2021)? Such events, although exceedingly rare among terrestrial non-volant clades, have been convincingly evoked for the skinks of the genus *Cryptoblepharus* Wiegmann, 1834 (Rocha et al. 2006; Blom et al. 2019) and the day-gecko *Phelsuma dubia* Boettger, 1881 (Rocha et al. 2009).

The main alternative hypothesis was that the Udzungwa species is not most closely related to *Synarmostes*, while the genus itself might not necessarily be a clade. This interpretation is not the most parsimonious from the morphological viewpoint, because it implies at least a double origin (or a single origin and at least a single secondary loss) of the posteriorly carinate elytra. If so, will then the new peculiar Udzungwa species be a "paleoendemic" (see in Methods on terminology) sister to a numerically much larger and widely distributed clade? Such hypothesis has been advanced for the recently discovered *Philharmostes ballerioi* Grebennikov, 2019 pill scarab from the nearby Kaguru and Nguru mountains in Tanzania forming a sister to the entire *Philharmostes* group of genera (Grebennikov 2019a) and for the oligotypic weevil genus *Lupangus* Grebennikov, 2017 from the Usambara, Uluguru, and Udzungwa Mountains sister to the speciose genus *Typoderus* Marshall, 1953 (Grebennikov 2017). All these highlands are part of the Eastern Arc Mountains (EAM, Lovett & Wasser 1993; Burgess et al. 2007). If so, shall a new genus be erected to accommodate such a "relict" organism and by doing so to stress the uniqueness of EAM in retaining through time species-poor forest-dependent sisters of widespread species-rich clades?

Table 1. DNA fragments used in the phylogenetic analyses (total number of sequenced terminals, followed by minimal, maximal and aligned length of each fragment, and the first and the last position of each aligned fragment in the concatenated matrix).

Fragment	#	min	max	aligned	positions
COI-5P	72	468	658	658	1 to 658
ITS2	65	206	654	1569	659 to 2227
28S	72	284	648	891	2228 to 3118

To test the aforementioned alternatives, phylogenetic relations between the new Udzungwa species and those of other pill scarabs, including the genera *Synarmostes* and *Aneilobolus*, must be resolved. This task, together with a morphological description of the new Udzungwa species, constitutes the goal of the present paper. Throughout this work, all inferences made to the subfamily Ceratocanthinae refer, strictly speaking, only to the tribe Ceratocanthini, which accommodates all but seven species of pill scarabs (98%). This is because two other species-poor tribes restricted to South America, Ivieolini and Scarabatermitini, are not represented in this analysis, while their phylogenetic position, although revealed as a clade sister to Ceratocanthini using a morphological dataset (Ballerio & Grebennikov 2016), is far from been well established.

Material and Methods

DNA sequencing

Live Afrotropical (including Malagasy) specimens of pill scarabs were sampled by sifting forest leaf litter (Grebennikov 2017), while other herein sequenced specimens were assembled from various sources (see Acknowledgments). In all methodological aspects, this study follows closely those of Grebennikov (2019a, b), therefore methods are only briefly described. Three DNA fragments were sequenced and analysed (Table 1, fragment abbreviations are in brackets): mitochondrial cytochrome c oxidase I (COI, the DNA barcode fragment, Hebert et al. 2003), nuclear internal transcribed spacer 2 (ITS2) and

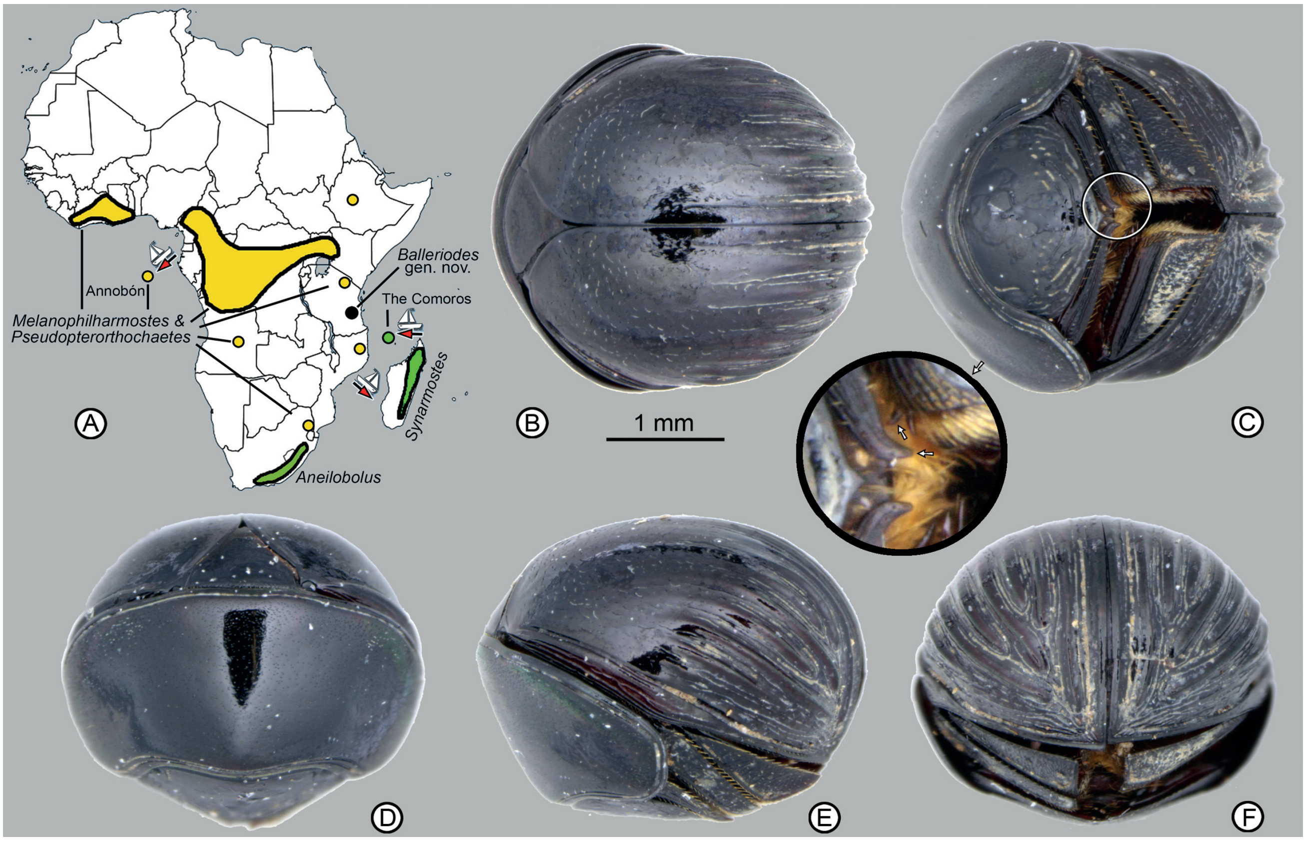

Fig. 1 – A, Distribution of *Balleriodes sphaera* **gen. et sp. nov.** and potentially related and/or similar pill scarabs in Africa and Madagascar. **B-F**: *Balleriodes sphaera* **gen. et sp. nov.**, holotype, habitus (**B**: left lateral, **C**: dorsal, **D**: ventral; **E**: anterior, **F**: posterior).

nuclear 28S ribosomal DNA (28S). Two sources of DNA data were used (Table 2): 64 newly sequenced fragments and 145 sequences from two earlier similarly designed studies (Grebennikov 2019a, b). Sequencing of DNA was performed at the Canadian Centre for DNA Barcode using their standard protocols (CCDB, http://ccdb.ca/). The primers used are listed in Table 2 in Grebennikov (2017). All details on the lab work (such as DNA extraction, amplification, PCR protocols), as well as images of the original electropherograms, habitus images and locality data for all 73 specimens sequenced for this analyses (Table 2, voucher codes starting with CNCCOLVG000) are available online in the Barcode of Life Database (BOLD, Ratnasingham & Hebert 2007) public dataset at dx.doi.org/10.5883/DS-VGDS17. A separate BOLD public dataset dx.doi.org/10.5883/DS-VGDS18 contains only the DNA barcode fragment (and associated metadata) for all nine type specimens of the new species.

Composition of the in- and outgroups

The ingroup of the herein implemented analysis was formed by two representatives of the new Udzungwa species (8752 & 8969), plus four terminals representing the genus *Synarmostes*. One *Synarmostes* was from Grande Comore (9456, courtesy of Brian L. Fisher; sequenced for Grebennikov 2019b) and the remaining three specimens represented three newly sampled and sequenced Malagasy species (Table 2). The taxonomy of *Synarmostes* is presently under review, along with the introduction of numerous new species from both Comoros and Madagascar (Alberto Ballerio, personal communication), therefore in most cases, no species names are provided. The nearest outgroup was formed by two and four representatives from two potentially most closely related African genera *Melanophilharmostes* (7790 & 9116) and *Pseudopterorthochaetes* (9474, 9603, 10271 & 10273), respectively. The distant outgroup was formed by 54 other Ceratocanthinae (including two members of *Aneilobolus*: 9826 & 9468) and seven non-Ceratocanthini Hybosoridae (Table 2). In total, 73 terminals of Hybosoridae formed the matrix. This dataset was based on all 52 Hybosoridae terminals used earlier (Grebennikov 2019b, but except terminals 3669 and 9617, see below), plus 21 newly sequenced specimens/terminals (Table 2).

For different reasons, several terminals mentioned below were not used in the analysis. Considering that the ITS2 fragment of the terminal "3669 *Cryptogenius*" from Bolivia (MH777800) is more than 200 nucleotides longer than the second-longest in the dataset (thus generating numerous gaps in the alignment), this terminal was not used. Considering the peculiarly position of the terminal "9617 *Cyphopisthes*" from the Philippines forming sister to the

Table 2. DNA fragments and their GenBank accession numbers of 73 Hybosoridae (Coleoptera) specimens used in the phylogenetic analysis. GenBank accession numbers in bold are those newly sequenced for this analysis; those in regular font are from Grebennikov (2019a, b).

Voucher	Genus and/or species	Country	COI	ITS2	28S
03705	*Philharmostes basilewskyi*	Tanzania	MH778074	MH777811	MH777854
03710	*Philharmostes*	Tanzania	MH778057	MH777793	MH777837
03712	*Philharmostes werneri*	Tanzania	MH778099	MH777835	MH777879
03718	*Philharmostes pseudumbratilis*	Tanzania	MH778091	MH777829	MH777871
03722	*Cryptophilharmostes mahunkai*	Tanzania	MH778059	MH777795	MH777839
03723	*Cryptophilharmostes mahunkai*	Tanzania	MH778088	MH777826	MH777868
03734	*Afrocloetus*	Tanzania	MH778032	MH981217	MH981212
03738	*Afrocloetus*	Tanzania	MH778030	MH981216	MH981211
03742	*Philharmostes*	Tanzania	MH778078	MH777815	MH777858
03756	*Cryptophilharmostes*	Tanzania	MH778082	MH777819	none
03763	*Cryptophilharmostes merkli*	Tanzania	MH778058	MH777794	MH777838
03767	*Cryptophilharmostes merkli*	Tanzania	MH778060	MH777796	MH777840
07013	*Philharmostes pseudumbratilis*	Tanzania	MH778080	MH777817	MH777860
07017	*Philharmostes grebennikovi*	Tanzania	MH778062	MH777798	MH777842
07027	*Philharmostes ornatus*	Tanzania	MH778065	MH777801	MH777845
07055	*Philharmostes ballerioi*	Tanzania	MH778071	MH777808	MH777852
07058	*Cryptophilharmostes*	Tanzania	MH778066	MH777803	MH777847
07070	*Philharmostes ballerioi*	Tanzania	MH778061	MH777797	MH777841
07131	*Petrovitzostes guineensis*	Cameroon	MH778090	MH777828	MH777870
07790	*Melanophilharmostes carinatus*	Ethiopia	**MW340083**	**MW340104**	**MW340128**
07826	*Aneilobolus*	South Africa	**MW340071**	**MW340096**	**MW340116**
08417	*Philharmostes interruptus*	South Africa	MH778068	MH777805	MH777849
08752	*Balleriodes sphaera*	Tanzania	**MW340084**	**MW340105**	**MW340129**
08766	*Afrocloetus*	Tanzania	MH778014	none	MH981209
08767	*Afrocloetus*	Tanzania	MH778013	MH981214	MH981208
08778	*Afrocloetus*	Tanzania	MH778026	MH981215	MH981210
08907	*Pseudosynarmostes mitsinjo*	Madagascar	MH778069	MH777806	MH777850
08933	*Philharmostes*	Tanzania	MH778098	MH777834	MH777878
08934	*Philharmostes*	Tanzania	MH778085	MH777822	MH777864
08969	*Balleriodes sphaera*	Tanzania	**MW340075**	none	**MW340120**
08978	*Philharmostes*	Tanzania	MH778095	MH777832	MH777875
09116	*Melanophilharmostes poggii*	Eq. Guinea	MH778087	MH777824	MH777866
09213	*Baloghianestes oribatidiformis*	Eq. Guinea	MH778086	MH777823	MH777865
09412	*Baloghianestes*	Ghana	MH778093	none	MH777873
09456	*Synarmostes*	Comoros	MH778075	MH777812	MH777855
09459	*Madrasostes*	Malaysia	MH778097	MH777833	MH777877
09468	*Aneilobolus*	South Africa	MH778096	none	MH777876
09474	*Pseudopterorthochaetes demirei*	Cameroon	MH778070	MH777807	MH777851
09476	*Carinophilharmostes vadoni*	Cameroon	MH778079	MH777816	MH777859
09480	*Baloghianestes oribatidiformis*	Cameroon	MH778094	MH777831	MH777874
09490	*Baloghianestes anceps*	Cameroon	MH778056	MH777792	MH777836
09491	*Baloghianestes oribatidiformis*	Cameroon	MH778089	MH777827	MH777869
09602	*Philharmostes*	Ghana	MH778084	MH777821	MH777863
09603	*Pseudopterorthochaetes*	Ghana	**MW340074**	**MW340098**	**MW340119**
09611	*Nesopalla iviei*	Puerto Rico	MH778083	MH777820	MH777862
09614	*Astaenomoechus*	Panama	MH778067	MH777804	MH777848
09618	*Madrasostes*	Philippines	**MW340080**	**MW340102**	**MW340125**
09709	*Philharmostes*	South Africa	MH778076	MH777813	MH777856
09710	*Philharmostes*	Tanzania	MH778063	MH777799	MH777843
09716	*Ceratocanthus amazonicus*	French Guiana	MH778081	MH777818	MH777861
09720	*Congomostes hintelmanni*	Cameroon	MH916844	MH777802	MH777846
09721	*Congomostes hintelmanni*	Cameroon	MH778009	MH981213	MH981207
09755	*Germarostes*	Mexico	MH778072	MH777809	MH777853
09756	*Anaides laticollis*	Mexico	none	MH777825	MH777867
09760	*Philharmostes*	Madagascar	MH778077	MH777814	MH777857

Voucher	Genus and/or species	Country	COI	ITS2	28S
09761	*Philharmostes*	Madagascar	MH778092	MH777830	MH777872
09835	*Chaetodus asuai*	Ecuador	**MW340064**	none	**MW340109**
10203	*Synarmostes*	Madagascar	**MW340063**	**MW340089**	**MW340108**
10238	*Synarmostes tibialis*	Madagascar	**MW340078**	**MW340100**	**MW340123**
10262	*Synarmostes*	Madagascar	**MW340068**	**MW340093**	**MW340113**
10271	*Pseudopterorthochaetes genierorum*	Mozambique	**MW340076**	**MW340099**	**MW340121**
10273	*Pseudopterorthochaetes miomboincola*	Mozambique	**MW340069**	**MW340094**	**MW340114**
10304	*Liparochrus infantus*	Australia	**MW340070**	**MW340095**	**MW340115**
10306	*Liparochrus silphoides*	Australia	**MW340086**	**MW340106**	**MW340131**
10307	*Liparochrus matthewsi*	New Caledonia	**MW340082**	**MW340103**	**MW340127**
10308	*Antiochrus aberrans*	Australia	**MW340066**	**MW340091**	**MW340111**
10322	*Chaetodus irregularis*	Bolivia	**MW340077**	none	**MW340122**
10356	*Germarostes senegalensis*	Brazil	**MW340067**	**MW340092**	**MW340112**
10363	*Germarostes posticus*	Chile	**MW340087**	**MW340107**	**MW340132**
10366	*Pterorthochaetes*	Papua N.G.	**MW340085**	none	**MW340130**
10369	*Cyphopisthes*	Papua N.G.	**MW340081**	none	**MW340126**
10373	*Perignamptus*	Papua N.G.	**MW340072**	**MW340097**	**MW340117**
10376	*Cyphopisthes*	Papua N.G.	**MW340079**	**MW340101**	**MW340124**

rest of the subfamily in both earlier topologies (Grebennikov 2019a, b) and that it did not cluster with two newly added congeners (specimens 10369 and 10376) in preliminary analyses, this terminal was flagged as potentially problematic (possible misalignment, misidentification or contamination; GenBank accession numbers MH778073 and MH777810) and not used.

Considering high confidence in the monophyly of Ceratocanthinae consistently supported by larval (Grebennikov et al. 2004) and adult morphological character (including body conglobation, Ballerio & Grebennikov 2016), the root was placed between this subfamily and the rest of the topology consisting of seven non-Ceratocanthinae Hybosoridae.

Sequence alignment and phylogenetic analysis

Alignment of all three DNA fragments was done separately using the online MAFFT Q-INS-i algorithm (Katoh et al. 2017; https://mafft.cbrc.jp/alignment/server/). No internal parts of DNA fragments were removed before the analysis, even if consisting mainly of insertions/deletions (indels, particularly frequent in ITS2). Inconsistently sequenced 5′-end and 3′-end of ITS2 alignment were trimmed of 19 and 68 positions, respectively. Three aligned single-fragment datasets (Table 1) were concatenated using Mesquite 3.61 (Maddison & Maddison 2020) into a matrix of 3118 positions and containing 50% of completely undetermined characters (mainly due to numerous indels in aligned ITS2 sequences, Table 1). Unrooted topology was built using a Maximum Likelihood (ML) approach, as implemented in CIPRES Science Gateway online platform (Miller et al. 2010; http://www.phylo.org/, tool "RAxML-HPC2 on XSEDE") and using RAxML version 8 (Stamatakis 2014) algorithm. Consistently with the previous analyses (Grebennikov 2019a, b), the CAT approximation to the widely used GTR + G nucleotide substitution model was applied independently for each of three partitions. Support values were generated based on 1000 bootstrap replicates (Stamatakis et al. 2008) and categorized as strong (≥90%), moderate (<90% and ≥75%) and weak (<75%, while clade is present on the consensus tree). The tree was visualized in FigTree v1.4.4. (Rambaut 2020).

A temporal analysis to determine the time of the pill scarab dispersal/-s across the Mozambique Channel, although suggested by a draft manuscript reviewer, is not herein implemented. Without relevant fossil evidence and improved phylogenetic resolution within the Ceratocanthini, it will necessary rely on pre-determined nucleotide substitution rates. This approach will likely overestimate the ages, necessarily using (largely saturated) mitochondrial sequences (as demonstrated Near et al. 2017 for ray-finned fishes).

Morphological methods

The specimens of the new species were imaged *in toto* and two of them then softened in warm water for dissection. Dissected abdomens from both specimens of the new species represented on the phylogenetic tree (Fig. 5) were macerated in a warm water solution of potassium hydroxide and disarticulated to extract and illustrate internal structures (Figs 2A–S). Body parts were imaged when submerged in glycerol or Canada Balsam. Morphological terms for the male terminalia are those of Cristóvão & Vaz-De-Mello (2020). Since the abdomen of the ball-forming pill scarabs is enclosed deeply inside the much larger and difficult-to-access elytral cavity, genitalia dissection required disarticulation of most of the abdomen, meso-, and metathorax. For this reason, male genitalia are imaged for a disarticulated paratype specimen, while the holotype is designated from a structurally intact and, therefore, unsexed, specimen. The holotype is likely a male, judging from two externally visible leg characters suggesting a male in sexually dimorphic pill scarab species: (1.) the apical spur (also called “tooth”) forming apical part of protibia forms nearly right angle with the axis of protibia and (2.) the short and straight inner apical peg (or “spur”; terminology is unstable) of mesotibiae forming a nearly right angle with the axis of mesotibia (insert in Fig. 2C).

Terminology for species-poor clades lacking fossil data and forming sister-groups to species-rich clades

As repeatedly pointed out (Krell & Cranston 2004; Casana & Laurenti 2013), extant species-poor sisters of species-rich clades, particularly when confined to biologically exceptionally stable environments, have been historically called “living fossils”, “primitive” or “basal”. The iconic examples are tuatara (*Sphenodon punctatus* Gray, 1842) from New Zealand sister to all crown scaled reptiles (Squamata), or lungfishes (Dipnoi) forming a clade sister to all crown tetrapods. This terminology is, however, highly misleading and inconsistent with the evolutionary tree-thinking (Omland et al. 2008). Competing (and more sensible) terms are either vague (“relict”, Grandcolas et al. 2014) or require frequently lacking fossil evidence (“paleoendemic”, Wojciechowski 2013). Biology is seemingly lacking a concise term describing an extant geographically restricted poorly diversified clade sister of a much greater and widely distributed extant clade, particularly in a situation when the fossil evidence of the former’s widespread occurrence is inadequate to justify the term “paleoendemic”. The latter term, although not optimal, is used herein for the lack of a better alternative.

Results

The ML analysis resulted in a moderately- to well-resolved tree, except for the basal nodes (Fig. 5). The new Tanzanian species formed a strongly supported clade together with three strongly supported monophyletic genera: *Melanophilharmostes*, *Pseudopterorthochaetes* and *Synarmostes*. *Synarmostes* from the Comoro Islands is nested within its Madagascan congeners (specimen 9456 in Fig. 5). Relationships among these four genera are weakly resolved. This inclusive strongly supported clade (here informally named the *Synarmostes* group) and the Madagascan genus *Pseudosynarmostes* Ballerio, 2008 form a moderately supported sister to a strongly supported clade of two Neotropical genera. The rest of the topology is consistent with both recent DNA analyses utilizing the same terminals (Grebennikov 2019a, b), except that the clade of *Afrocloetus* Petrovitz, 1968 and *Congomostes* Paulian, 1968 is not forming sister to the *Philharmostes* group. Consistent topological similarities include the strongly supported Afrotropical and Madagascan *Philharmostes* group, the basalmost dichotomy of which is formed by *Philharmostes ballerioi* Grebennikov, 2019. South African *Aneilobolus* is recovered as monophyletic and strongly supported sister to the Neotropical clade of *Germarostes* and *Ceratocanthus*; all three genera forming a moderately supported sister to a strongly supported clade of the three Indomalayan and Australasian genera (*Cyphopisthes* Gestro, 1898, *Perignamptus* Harold, 1877, and *Pterorthochaetes* Gestro, 1898). Notably, no regional fauna of pill scarabs (Fig. 5) is monophyletic.

***Balleriodes* gen. nov.**

Type species. *Balleriodes sphaera* sp. nov.,
here designated.

Diagnosis. The only known species of the genus can be immediately recognized among all pill scarabs (including most similar *Synarmostes*) by the unique combination of the following easily observed characters: body black, non-metallic, without prominent pubescence or punctures (although sparse fine surface sculpturing is present), in conglobate position nearly circular in dorsal view and nearly globular in 3-dimensional shape. Most notably (and uniquely with allopatric *Synarmostes*), adults of the new genus have elytra with markedly developed longitudinal striation only in posterior halves. Adult beetles of the new genus additionally differ from those of *Synarmostes* in having a single apical outer spur on protibia apices (two in *Synarmostes*), head lacking a transverse furrow on vertex, parameres with a basal projection, and relatively larger basal piece of male genitalia (Alberto Ballerio, personal communication). Additionally, the type species of this monotypic genus displays two characters seemingly unique within all of Ceratocanthinae (Alberto Ballerio, personal communication): remarkably long and dense setae on the fore tarsi (arrow in Fig. 2L) and the transparent membrane adjacent to the ventral surface of parameres (arrows in Figs 2P–R).

Description. Body black; without pubescence; without much microsculpture; non-metallic; in fully conglobate position visible part of legs (tibiae) and elytral apical halves often covered with dirt-like coating (Figs 3–4); neatly circular in dorsal view and nearly globular in 3-dimensional shape. Enrollment coaptations (ability to make a perfect ball) present. Head with interocular bridge (=“genal canthus”) completely subdividing compound eye into dorsal and ventral parts (Fig. 2A); dorsal eye small, ellipse-shaped, with major axis about four times greater than minor axis (Fig. 2A). Antennae with 10 antennomeres (Fig. 2G). Mandibles in apical part without teeth (in addition to mandibular apex, Figs 2E–F). Maxillae with distal palpomere longer than combined length of both preceding ones (Fig. 2C). Pronotum evenly convex, sparsely, and

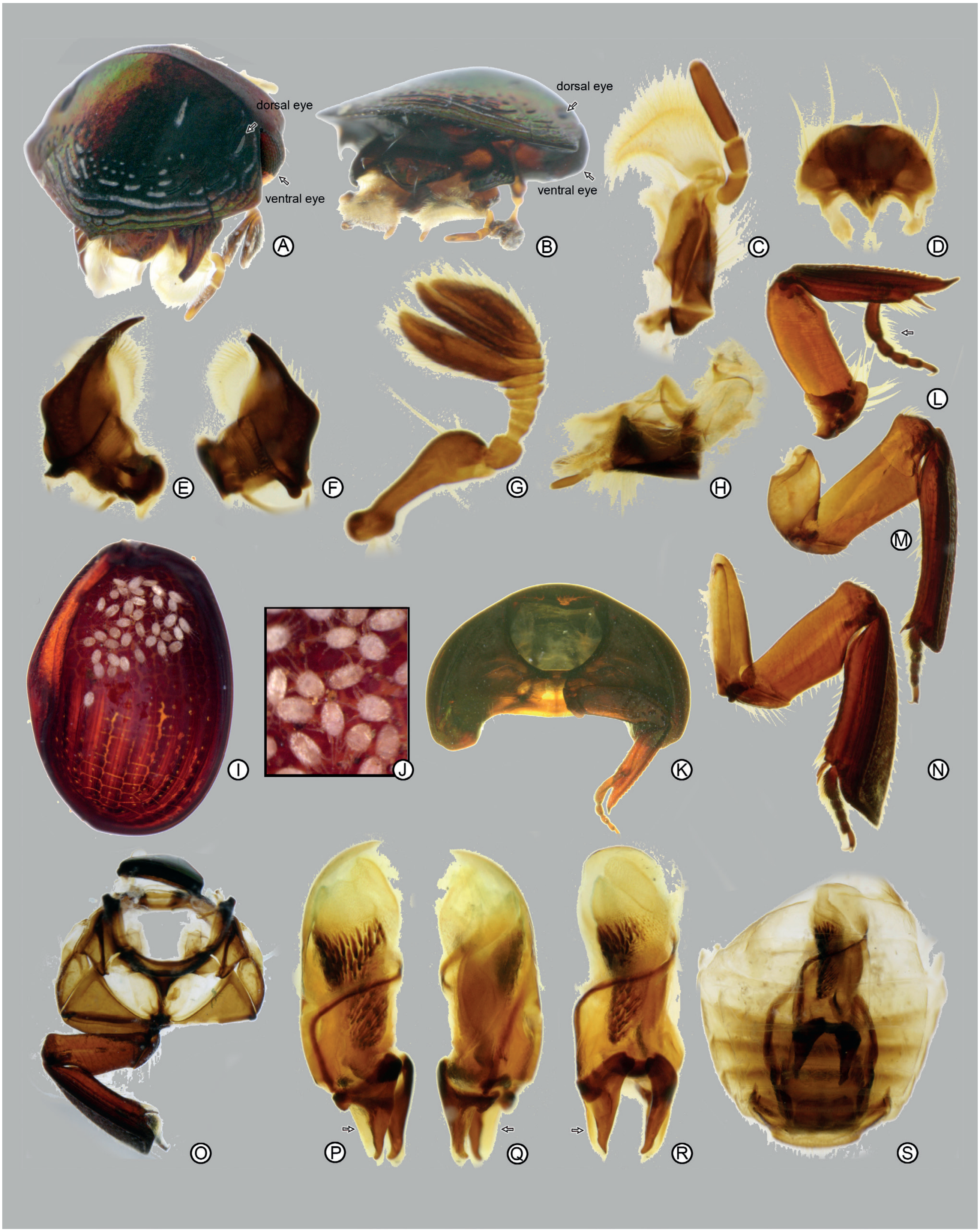

Fig. 2 – *Balleriodes sphaera* **gen. et sp. nov.**, paratypes (**A-R**, specimen 8969, **S**, specimen 8752), details. **A-B**, head, fronto-dorsal (**A**) and frontal (**B**); **C**, maxilla; **D**, labrum; **E-F**, mandibles; **G**, antenna; **H**: labium; **I-J**, elytron in ventral view showing phoretic mites (**J**, enlarged); **K**, prothorax, ventral view; **L-N**, fore, middle and hind left legs; **O**, pterothorax, ventral view; **P-R**, phallobase and parameres, right lateral (**P**), left lateral (**Q**) and dorsal (**R**) views; abdomen, with male genitalia *in situ*. Images are not to scale.

shallowly punctured, its anterior and posterior margins not swollen (Fig. 1D), marginal bead complete. Elytra longitudinally striate on dorsal side in posterior half, and not striate in anterior half, with sparse shallow transverse comma-shaped punctures. Metathoracic wings absent. Protibiae with fine serration on distal third of outer side and with a larger apical outer tooth (Fig. 2L). Male genitalia with parameres almost symmetrical, basally with a projection (Figs 2P–R). Female genitalia and sexual dimorphism not studied.

Species composition and distribution. This genus is monotypic and its known distribution is limited to the type locality of its only species (see below).

Etymology. The generic name is a patronymic, derived by adding the Latin suffix -*odes* to the family name of Alberto Ballerio (Brescia, Italy), in recognition of his role in triggering my interest in the evolution of pill scarabs. Gender masculine.

Balleriodes sphaera **sp. nov.**
Figs 1B–F, 2A–S, 3, 4, 5)

Type locality. Tanzania, the Udzungwa Mountains, 7.8419º S 36.8546º E, 1083 m.

Description. The morphological description is the same as that given above for the genus. Holotype maximal body length (in enrolled position, Fig. 1B): 3.2 mm (variation: 3.2 – 3.4, n = 3), maximal body width 3.0 (variation: 3.0 – 3.2 mm, n = 3), maximal body height in lateral view (Fig. 1D): 2.6 mm. DNA of holotype: MW393776 (COI); DNA data of paratypes: MW340075, MW340084, MW393773–5, MW393777–9 (COI), MW340105 (ITS2) and MW340120, MW340129 (28S).

Material examined. Holotype (deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada), not sexed, “TANZANIA, Udzungwa Mts., -7.8419 36.8546, 1083m, 7.x.2014, sift03, V.Grebennikov”, “CNCCOLVG00008750”. Paratypes (deposited together with the holotype), eight specimens 8751–55 and 8968–70, same data as holotype (of them specimen 8968 is in the collection of Alberto Ballerio; see Acknowledgements).

Distribution. This species is known only from the type locality.

Biology. All specimens were taken in a single sifting sample in the montane rainforest, although a total of 13 sifting samples was taken in the Udzungwa Mountains (sample list in Table 1 in Grebennikov 2017). Phoretic mites were detected under the elytra of both dissected paratypes (Figs 2I, J).

Etymology. The species epithet is the Latin noun meaning “ball, globe, sphere”, with reference to the peculiarly globular shape of conglobate specimens of the new species, likely most closely approaching a perfect sphere among all Ceratocanthinae (and, therefore, of all Coleoptera); in apposition.

Discussion

Evolution of the posteriorly carinate elytra in pill scarabs

Even though elytra are variously carinate/grooved in different pill scarabs (see images in Ballerio & Grebennikov 2016), only *Balleriodes* and *Synarmostes* present two acutely different elytral surfaces: even and polished anterior part versus deeply grooved (or notably carinate) posterior part. If Fig. 5 correctly reflects the relationships among the four genera forming the *Synarmostes* group, then the two most parsimonious interpretations exist. One suggests that the aforementioned elytral morphological peculiarity is a non-reversed novelty evolving twice: in the Most Recent Common Ancestor (MRCA) of *Balleriodes* and, in parallel, in that of *Synarmostes*. Equally parsimonious alternative advocates for a single origin of this character in the MRCA of a clade formed by three genera of the *Synarmostes* group (both aforementioned ones, plus *Pseudopterorthochaetes*), with a subsequent reversal in MRCA of the latter. Morphological data, however, suggest that the genera *Melanophilharmostes* and *Pseudopterorthochaetes* form a clade (Ballerio 2016), which, therefore, casts doubts on both interpretations. Since the relationships among all four genera within the *Synarmostes* group are only weakly resolved, *Balleriodes* and *Synarmostes* may form a clade. If true, this would evoke a single non-reversed origin of this peculiar elytral character. Lack of resolution within the *Synarmostes* group renders all these alternatives presently unresolved.

Three overseas dispersals in the Synarmostes group

Overseas dispersal of terrestrial animals is a fascinating subject (de Queiroz 2014) detectable in its footprint in the present biogeographical patterns. At least three such events are detectable in the *Synarmostes* group. Two of them pertain to the monophyletic genus *Synarmostes*, presently endemic to two adjacent, although geologically grossly dissimilar island systems. They are the continental and never submerged island of Madagascar and the volcanic and relatively recent Comoro Islands. Phylogenetically nested within the otherwise exclusively African *Synarmostes* group, the biogeographic past of this genus is pivoted on whether its presence on Madagascar might be attributed to factors other than overwater dispersal. To address this question, the relative age of the MRCA of *Synarmostes* must be estimated.

It seems unlikely that Ceratocanthinae crown group (let alone the genus *Synarmostes*) might be older than 120 million years (Myr). The latter is the minimal age of the opening of the Mozambique Channel, which presently separates Africa and Madagascar by minimally 430 km of

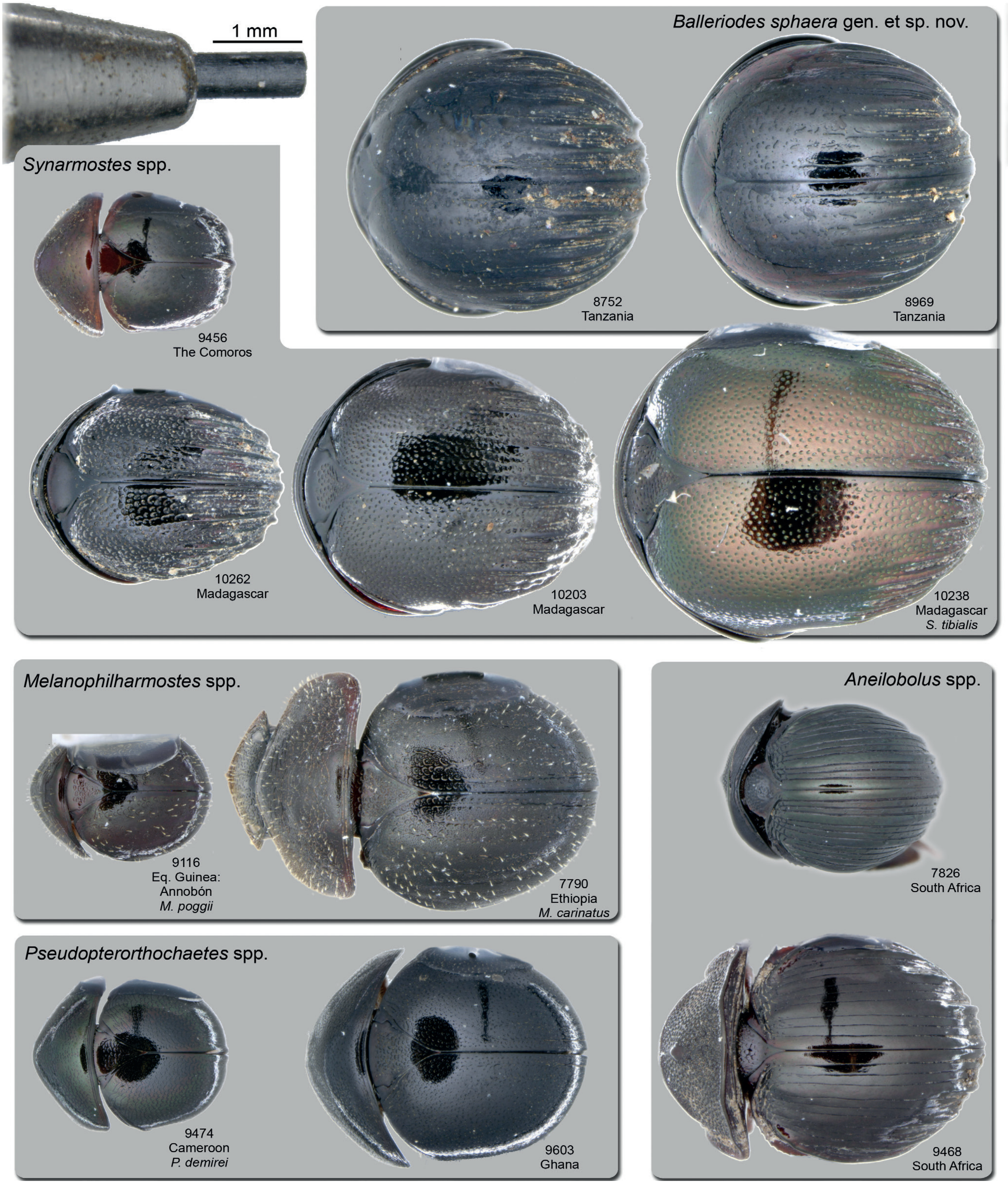

Fig. 3 – Habitus of select ingroup and outgroup pill scarabs, dorsal view; images are to scale.

the sea (Reeves 2014). Two circumstantial pieces of evidence support this temporal interpretation. Firstly, fossil records of pill scarabs (reviewed in Ballerio & Grebennikov 2016; Poinar & Ballerio 2017) provide no evidence that the age of crown Ceratocanthini is greater than that of the Oligocene. Secondly, the only DNA-based age estimate suggests that the more inclusive clade of Hybosoridae separated from its sister (Glaphyridae plus Ochodaeidae) 130–69 Myr ago (fig. S9 in McKenna et al. 2015). If the opening of the Mozambique Channel predates the origin

Fig. 4 – Habitus of select ingroup and outgroup pill scarabs, left lateral view; images are to scale.

of the pill scarab crown group, which seems likely, then the plate tectonic vicariance can hardly be a significant biogeographical factor for this clade. The only feasible alternative is, therefore, the overwater dispersal to Madagascar. This interpretation is consistent with the dispersal strategy hypothesized for other relatively young endemic Malagasy clades arriving at the island from predominantly Africa. Examples include *Madagasikara* Köhler et Glaubrecht, 2010 river snails (Köhler & Glaubrecht 2010), *Aulonogyrus* Motschulsky, 1853 whirligig beetles (Gustafson

2018), distantly related clades of dung beetles (Miraldo et al. 2008), *Crematogaster* Lund, 1831 ants (Blaimer 2012), as well as the overwhelming majority of non-volant terrestrial vertebrates (Vences 2004) such as chameleons (Tolley et al. 2013), colubrid snakes (Nagy et al. 2003) and all four radiations of non-volant terrestrial mammals: tenrecs (Afrosoricida), euplerid carnivores, lemurs, and nesomyine rodents (Poux et al. 2005; Gunnell et al. 2019).

After having likely dispersed from Africa to Madagascar, members of *Synarmostes* probably completed at least one more sizable overseas travel, that is from Madagascar to the Comoro Islands (and likely among the latter). This is strongly suggested by the presence of the genus on the entirely volcanic Comoros archipelago and the nested position of the only analysed Comoro specimen within its strongly monophyletic and otherwise exclusively Madagascan congeners. This is consistent with numerous other examples of Comoros harbouring out-of-Madagascar recent overwater immigrants of primarily Madagascan radiations such as Mantellidae frogs (the genera *Mantydactylus* Boulenger, 1895, *Boophis* Tschudi, 1838, and *Blommersia* Dubois, 1992; Hutter et al. 2018; Vences et al. 2003; Glaw et al. 2019, respectively) or *Hemidactylus* Oken, 1817 geckos (Rocha et al. 2005). Both species of the Comoro lemurs, however, are also present in Madagascar and are likely results of human-mediated dispersal (Pastorini et al. 2003).

The third and presently the last known case of overseas dispersal within the *Synarmostes* group is that of the recently described *Melanophilharmostes poggii* Ballerio, 2016 known solely from the island of Annobón, Equatorial Guinea, on the western side of the African continent (Fig. 1A). This is the only member of Ceratocanthinae known from the otherwise highly imbalanced and depauperate terrestrial fauna of this small island (17 km^2), that notably lacks any amphibians (Ceríaco et al. 2018). Annobón is of relatively recent volcanic origin (not earlier than 4.8 Mya ago, Lee et al. 1994) and is located some 350 km from the nearest African mainland (Gabon) and 180 km from the nearest island (São Tomé). The overseas dispersal is the only natural source of its terrestrial fauna, and it is of predominantly African origin (e.g. Jesus et al. 2009, but perhaps not so for the weevil *Aethiopacorep africanus* (Hustache, 1932) of likely American origin; Grebennikov & Anderson 2021).

Balleriodes*, a possible paleoendemic of the Eastern Arc Mountains*

Sister-group relationships between *Balleriodes* and the genus *Pseudopterorthochaetes* (nine named species, widely distributed in Africa) is weakly resolved and, therefore, might be an analytical artefact. Regardless of what exactly constitutes sister of *Balleriodes*, it seems plausible to assume that it is a speciose and widely distributed clade, and also a member of the *Synarmostes* group. If so, the genus *Balleriodes* currently known from a single sampling event in the Udzungwa Mounts might be considered (with etymological reservations described in Methods) as a paleoendemic, that is a species-poor lineage geographically restricted to exceptionally stable habitat, and sister of a species-rich and widely distributed clade. Similar conclusions were made about two other newly discovered EAM beetle clades: the weevil genus *Lupangus* (Grebennikov 2017) and *Philharmostes ballerioi* pill scarab (Grebennikov 2019a). Each of these clades likely defines an old (pre-Miocene) dichotomy and is sister to much larger and widely distributed clades. Other (not too numerous and not necessarily strictly endemic to EAM) examples are: *Xenoperdix* Dinesen, Lehmberg, Svendsen, Hansen, and Fjeldså, 1994 partridge from Udzungwa and Rubeho, a clade likely divergent from its Asian sister in the early Oligocene (Wang et al. 2017), *Boulengerula* Tornier, 1896 caecilians likely divergent from its African sister in the late Cretaceous (Roelants et al. 2007) or Kupeaeae monocots likely divergent from their pantropical sister in the late Cretaceous (Mennes et al. 2013).

These observations are consistent with the exceptionally stable biological past of the wet forests in Udzungwa (and in other forested blocks of EAM), which are under the direct influence of the moisture from the Indian Ocean and, therefore, are thought to have persisted uninterruptedly since the Oligocene (Lovett & Wasser 1993). Most importantly, these presently widely isolated and relatively small forests have likely survived as wet refugia supporting the existence of the forest-dependent biota during Miocene uplift of the East African plateau resulting in gradual fragmentation of the forest cover (Bobe 2006) and also during dramatic and repeated subsequent forest expansion/shrinkage cycles. The latter coincided with the Pleistocene glacial cycles (Plana 2014) when the Afrotropical rainforest repeatedly shrank to about 10% of its present size (Fig. 4 in Hamilton & Taylor 1991).

The putative paleoendemic organisms such as *Balleriodes* constitute, however, a tiny fraction among species endemic to Udzungwa and to other EAM (for vertebrates see Appendix 1 in Burgess et al. 2007). The majority are so-called "neoendemics" resulting from more recent speciation events likely achieved through the "species-pump" (Papadopoulou & Knowles 2015). Such events are hypothesized when repeatedly connected and disconnected EAM forests enriched each other with genetically very close, although sufficiently distinct lineages, leading to sympatry of two (as *Afrocloetus* Petrovitz, 1968 pill scarabs in Udzungwa; Grebennikov 2019b) and more closest relatives. When sufficiently studied, these events are thought to coincide with and were likely driven by the repeated cycles of the African forest size fluctuations taking place in the Pleistocene (Maley 1996).

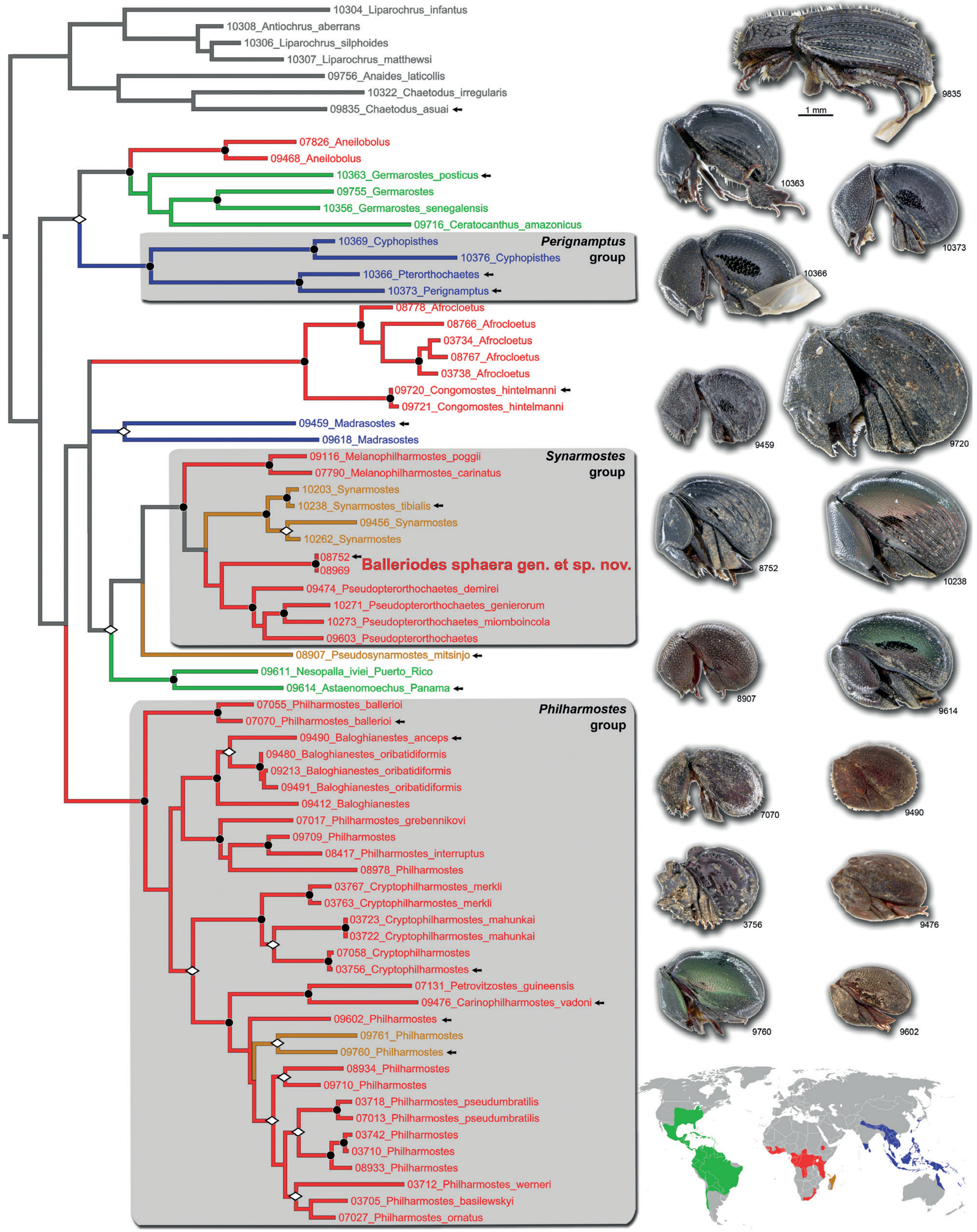

Fig. 5 – Maximum likelihood tree of Ceratocanthinae pill scarabs (Coleoptera: Hybosoridae), as reconstructed by RAxML from the three-fragment concatenated matrix. *Balleriodes sphaera* **gen. et sp. nov.** is inside the monophyletic *Synarmostes* group. Branches with ML bootstrap support percentage ≥90 are marked by black circles; those with bootstrap <90 and ≥75 are marked by open rhombi. Colours of Ceratocanthinae taxa and branches indicate their biogeographical region. Habitus images are to scale; small black arrows indicate imaged specimens.

Phylogenetic classification of pill scarabs

Necessarily mirroring the poorly resolved phylogeny, the taxonomy of pill scarabs remain unsatisfactory. On one hand, taxa remain recognized, even if thought to be non-monophyletic (Scarabatermitini or *Philharmostes* Kolbe, 1895; Ballerio & Grebennikov 2016 and Grebennikov 2019a, respectively) or synonymous (*Afrocloetus* and *Congomostes*; Grebennikov 2019b). On the other, except for three informal generic groups (see below), most of Ceratocanthini genera are not arranged into named monophyletic groups. The only three exceptions are:

- the Afrotropical (including Madagascar) ***Philharmostes* group** of seven genera first proposed by Ballerio (2000) and subsequently recovered as a clade using either adult morphology or DNA sequences (Ballerio & Grebennikov 2016, Grebennikov 2019a, respectively);
- the Indomalayan and Australasian ***Perignamptus* group** first defined in Ballerio 2009 as "*Perignamptus*, *Madrasostes*, and *Macrophilharmostes*, as well as a few species currently placed in other genera, namely *Besuchetostes jaccoudi* Paulian, 1977, *Besuchetostes howdeni* Paulian, 1979, *Cyphopisthes inexpectatus* Paulian, 1981, and *Eusphaeropeltis sabah* Paulian, 1989", plus perhaps monotypic *Oxymorostes* Ballerio, 2009. Notably, if monophyletic, this clade will render at least three genera paraphyletic. The present analysis, although not specifically designed for this purpose, recovered *Perignamptus* in a strongly supported clade with two other Indomalayan and Australasian genera (Fig. 5), but not with *Madrasostes* Paulian, 1975, as originally thought (Ballerio 2009);
- The herein newly defined and monophyletic ***Synarmostes* group** of four Afrotropical (including Madagascar) genera. Remarkably (and similar to the mammalian clade Afrotheria, Seiffert 2007) this clade is strongly supported by genetic data, but its morphological support remains elusive.

The emergence of the global biogeographic pattern of pill scarabs

Ceratocanthinae phylogeny in Fig. 5 lacks representatives from about half of the subfamily's 44 valid genus-group names, most notably from two species-poor South American tribes: Ivieolini and Scarabatermitini. Moreover, it is inferred from only three relatively short DNA fragments. Notwithstanding these limitations, this is the most representative and simultaneously, the most resolved DNA-based pill scarab phylogeny reconstruction to date. Specifically, it includes multiple representatives from all four main regions: the Afrotropical Region, Madagascar, the Neotropical Region, and the Indomalayan plus Australasian Region (herein considered as a unity). Remarkably, none of the so geographically-defined terminals forms a single clade, suggesting the subfamily's complex biogeographic past. The most notable geographical aspects of this phylogenetic tree are as follows:

- the genus *Aneilobolus* (four named species in South Africa) is not most closely related to any African or Madagascan members, but is instead placed in a strongly supported clade with Neotropical species (see also Ballerio & Grebennikov 2016);
- the Afrotropical clade of *Afrocloetus* and *Congomostes* is not sister to the *Philharmostes* group (as previously recovered with weak support, Grebennikov 2019a, b);
- none of the Malagasy pill scarabs has a sister group other than Afrotropical ones, suggesting the "out-of-Africa" hypothesis (Yoder & Nowak 2006);
- none of the Indomalayan and Australasian pill scarabs has strongly supported sister group from the Neotropical region, suggesting their "out-of-Africa" origin, as repeatedly evoked for plants (Zhou et al. 2012) and animal such as *Acanthodactylus* Wiegmann, 1834 lizards (Tamar et al. 2016), primates, and hominoids (Stewart & Disotell 1998).

Remaining biogeographic uncertainties of pill scarabs

Herein presented molecular data are not sufficient to test the South American origin of the subfamily, as hypothesized based on the morphological evidence (Ballerio & Grebennikov 2016). Present topology equally well suggests that Africa might be the subfamily's birthplace. Three factors contribute to this uncertainty. Firstly, the precise position of Ceratocanthinae within Hybosoridae is far from firmly established (Ocampo & Hawks 2006). Secondly, the phylogenetic position of both South American tribes supposedly forming a clade defining the first split within the subfamily (Ballerio & Grebennikov 2016) must be re-addressed. Thirdly, the basalmost dichotomies within the tribe Ceratocanthini are only weakly resolved. Last but not least, no quantitative attempt has been made to date pill scarab evolution, which is a pre-requirement when relating the latter to the plate tectonic events. All these uncertainties will be, hopefully, soon addressed.

Acknowledgements – Alberto Ballerio (Brescia, Italy) variably supported this project, particularly by advising on Ceratocanthinae taxonomy and morphology; he, Bruce D. Gill (Ottawa, Canada), and Claudia Hemp (Bayreuth, Germany) critically read an earlier version of the manuscript prior to its submission. Jon Lovett (Leeds, UK) advised on plant EAM paleoendemics. Sixtus Assey (Turiani, Tanzania) helped in organizing Tanzanian fieldwork. Brian L. Fisher (San Francisco, USA), Balsama Rajemison, and Tiana Vololontiana (both Antananarivo, Madagascar) helped in organizing Madagascar fieldwork; Brian also collected and made available the only sequenced specimens (9456) of *Synarmostes* from Comoros. The following individuals facilitated the accumulation of 21 newly sequenced terminals: Giulio Cuccodoro (Geneva, Switzerland), François Génier (Ottawa, Canada), Maurice Leponce (Brussels, Belgium), Marek Wanat (Wroclaw, Poland), Cristiano Lopes-Andrade (Viçosa, Brazil), Andrew B.T. Smith (Ottawa, Canada), and Alexey Tishechkin (Sacramento, USA). Tanzanian and Malagasy authorities facilitated this project with research permits 2014-200-NA-2014-123 and 249/18-MEEF/SG/DGF/DSAP/SCB, respectively.

References

Ali J., Huber M. 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. Nature, 463: 653–656. Doi: https://doi.org/10.1038/nature08706

Audru J.C., Bitri A., Desprats J.F., Dominique P., Eucher G., Hachim S., Jossot O., Mathon C., Nédellec J.L., Sabourault P., Sedan O. 2010. Major natural hazards in a tropical volcanic island: a review for Mayotte Island, Comoros archipelago, Indian Ocean. Engineering Geology, 114: 364–381. Doi: https://doi.org/10.1016/j.enggeo.2010.05.014

Ballerio A. 2000. A new genus and species of Ceratocanthidae from Tanzania (Coleoptera: Scarabaeoidea). African Zoology, 35: 131–137.

Ballerio A. 2009. Unusual morphology in a new genus and species of Ceratocanthinae from New Guinea (Coleoptera: Scarabaeoidea: Hybosoridae). The Coleopterists Bulletin, 63: 44–53. Doi: https://doi.org/10.1649/0010-065X-63.1.44

Ballerio A. 2016. A first phylogenetic appraisal of two allied genera of Afrotropical Ceratocanthinae: *Melanophilharmostes* and *Pseudopterorthochaetes* (Coleoptera: Hybosoridae). Fragmenta entomologica, 48: 33–52. Doi: https://doi.org/10.4081/fe.2016.159

Ballerio A., Grebennikov V.V. 2016. Rolling into a ball: phylogeny of the Ceratocanthinae (Coleoptera: Hybosoridae) inferred from adult morphology and origin of a unique body enrollment coaptation in terrestrial arthropods. Arthropod Systematics and Phylogeny, 74: 23–52.

Blaimer B.B. 2012. Acrobat ants go global – origin, evolution and systematics of the genus *Crematogaster* (Hymenoptera: Formicidae). Molecular Phylogenetics and Evolution, 65: 421–436. Doi: http://dx.doi.org/10.1016/j.ympev.2012.06.028

Blom M.P.K., Matzke N.J., Bragg J.G., Arida E., Austin C.C., Backlin A.R., Carretero M.A., Fisher R.N., Glaw F., Hathway S.A., Iskander D.T., McGuire J.A., Karin B.R., Reilly S.B., Rittmeyer E.N., Rocha S., Sanchez M., Stubbs A.L., Vences M., Moritz, C. 2019. Habitat preference modulates trans oceanic dispersal in a terrestrial vertebrate. Proceedings of the Royal Society B: Biological Sciences, 286, 20182575: 10 pp. Doi: https://doi.org/10.1098/rspb.2018.2575

Bobe R. 2006. The evolution of arid ecosystems in eastern Africa. Journal of Arid Environment, 66: 564–584. Doi: https://doi.org/10.1016/j.jaridenv.2006.01.010

Burgess N.D., Butynski T.M., Cordeiro N.J., Doggart N.H., Fjeldså J., Howell K.M., Kilahama F.B., Loader S.P., Lovett J.C., Mbilinyi B., Menegon M., Moyer D.C., Nashanda E., Perkin A., Rovero F., Stanley W.T., Stuart, S.N. 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biological Conservation, 134: 209–231. Doi: https://doi.org/10.1016/j.biocon.2006.08.015

Casana D., Laurenti P. 2013. Why coelacanths are not ‘living fossils’. Bioessays, 35: 332–338. Doi: https://doi.org/10.1002/bies.201200145

Ceríaco L.M.P., Marques M.P., Bauer, A.M. 2018. Miscellanea Herpetologica Sanctithomae, with a provisional checklist of the terrestrial herpetofauna of São Tomé, Príncipe and Annobon islands. Zootaxa, 4387: 91–108. Doi: https://doi.org/10.11646/zootaxa.4387.1.4

Cristóvão J.P., Vaz-De-Mello F.Z. 2020. The terminalia of the superfamily Scarabaeoidea (Coleoptera): specific glossary, dissecting methodology, techniques and previously unrecorded sexual dimorphism in some difficult groups. Zoological Journal of the Linnean Society, 191: 1001–1043. Doi: https://doi.org/10.1093/zoolinnean/zlaa079

de Queiroz A. 2014. The Monkey’s Voyage: How Improbable Journeys Shaped the History of Life. Basic Books, New York, 368 pp.

Glaw F., Hawlitschek O., Glaw K., Vences M. 2019. Integrative evidence confirms new endemic island frogs and transmarine dispersal of amphibians between Madagascar and Mayotte (Comoros archipelago). The Science of Nature, 106, 19: 19 pp. Doi: https://doi.org/10.1007/s00114-019-1618-9

Grandcolas P., Nattier R., Trewick S. 2014. Relict species: a relict concept? Trends in Ecology and Evolution, 29: 655–663. Doi: https://doi.org/10.1016/j.tree.2014.10.002

Grebennikov V.V. 2017. Phylogeography and sister group of *Lupangus*, a new genus for three new flightless allopatric forest litter weevils endemic to the Eastern Arc Mountains, Tanzania (Coleoptera: Curculionidae, Molytinae). Fragmenta entomologica, 49: 37–55. Doi: https://doi.org/10.4081/fe.2017.229

Grebennikov V.V. 2019a. First DNA analysis of pill scarabs (Coleoptera: Hybosoridae: Ceratocanthinae) reveals multiple paraphyly of Afrotropical *Philharmostes* and detects its basal dichotomy formed by a new wingless species. European Journal of Entomology, 116: 52–63. Doi: https://doi.org/10.14411/eje.2019.006

Grebennikov V.V. 2019b. Miocene uplift and Pleistocene forest connectivity drove evolution of large-bodied Afrotropical pill scarabs (Coleoptera: Hybosoridae: *Afrocloetus* and *Congomostes*). Arthropod Systematics and Phylogeny, 77: 417–431. Doi: https://doi.org/10.26049/ASP77-3-2019-3

Grebennikov V.V., Anderson R.S. 2021. Late Miocene eastwards transatlantic dispersal of flightless anchonine weevils (Coleoptera: Curculionidae: Molytinae). Zootaxa, 4952: 55–70. Doi: https://doi.org/10.11646/zootaxa.4952.1.3

Grebennikov V.V., Ballerio A., Ocampo F., Scholtz C.H. 2004. Larvae of Ceratocanthidae and Hybosoridae (Coleoptera: Scarabaeoidea): study of morphology, phylogenetic analysis and evidence of paraphyly of Hybosoridae. Systematic Entomology, 29: 524–543. Doi: https://doi.org/10.1111/j.0307-6970.2004.00257.x

Gunnell G.F., Boyer D.M., Friscia A.R., Heritage S., Manthi F.K., Miller E.R., Sallam H.M., Simmons N.B., Stevens N.J., Seiffert E.R. 2018. Fossil lemurs from Egypt and Kenya suggest an African origin for Madagascar's aye-aye. Nature Communications, 9, 3193: 12 pp. Doi: https://doi.org/10.1038/s41467-018-05648-w

Gustafson G.T. 2018. Cenozoic out-of-Africa dispersal shaped diversification of the whirligig beetle genus *Aulonogyrus* (Coleoptera: Gyrinidae: Gyrinini). Arthropod Systematics and Phylogeny, 76: 295–302.

Gustafson G.T., Prokin A.A., Bukontaite R., Bergsten J., Miller K.B. 2017. Tip-dated phylogeny of whirligig beetles reveals ancient lineage surviving on Madagascar. Scientific Reports, 7, 8619: 9 pp. Doi: https://doi.org/10.1038/s41598-017-08403-1

Hamilton A.C., Taylor D. 1991. History of climate and forests in tropical Africa during the last 8 million years. Climatic Change, 19: 65–78. Doi: https://doi.org/10.1007/978-94-017-3608-4_8

Hebert P.D.N., Cywinska A., Ball S.L., deWaard J.R. 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society B: Biological Sciences, 270: 313–321. Doi: https://doi.org/10.1098/rspb.2002.2218

Howden H.F., Gill B.D. 2000. Tribes of New World Ceratocanthinae, with keys to genera and descriptions of new species (Coleoptera: Scarabaeidae). Sociobiology, 35: 281–329.

Hutter C.R., Lambert S.M., Andriampenomanana Z.F., Glaw F., Vences M. 2018. Molecular phylogeny and diversification of Malagasy bright-eyed tree frogs (Mantellidae: *Boophis*). Molecular Phylogenetics and Evolution, 127: 568–578. Doi: https://doi.org/10.1016/j.ympev.2018.05.027

Jesus J., Nagy Z.T., Branch W.R., Wink M., Brehm A., Harris J. 2009. Phylogenetic relationships of African green snakes (genera *Philothamnus* and *Hapsidophrys*) from São Tomé, Príncipe and Annobon islands based on mtDNA sequences, and comments on their colonization and taxonomy. Herpetological Journal, 19: 41–48.

Katoh K., Rozewicki J., Yamada K.D. 2017. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics, bbx, 108: 1–7. Doi: https://doi.org/10.1093/bib/bbx108

Köhler F., Glaubrecht M. 2010. Uncovering an overlooked radiation: molecular phylogeny and biogeography of Madagascar's endemic river snails (Caenogastropoda: Pachychilidae: *Madagasikara* gen. nov.). Biological Journal of the Linnean Society, 99: 867–894. Doi: https://doi.org/10.1111/j.1095-8312.2009.01390.x

Krell F.-T., Cranston P.S. 2004. Which side of the tree is more basal? Systematic Entomology, 29: 279–281. Doi: https://doi.org/10.1111/j.0307-6970.2004.00262.x

Lee D.C., Halliday A., Fitton J., Poli G. 1994. Isotopic variations with distances and time in the volcanic islands of the Cameroon line: evidence for a mantle plume origin. Earth Planet Science Letters, 123: 119–138. Doi: https://doi.org/10.1016/0012-821X(94)90262-3

Lovett J.C., Wasser S.K. 1993. Biogeography and Ecology of the Rain Forests of Eastern Africa. Cambridge University Press, Cambridge, 351 pp.

Maddison W.P., Maddison D.R. 2020. Mesquite: a modular system for evolutionary analysis. Version 3.5. Program and documentation, available at: http://mesquiteproject.org.

Maley J. 1996. The African rain forest – main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. Proceedings of the Royal Society of Edinburgh, 104B: 31–73. Doi: http://dx.doi.org/10.1017/S0269727000006114

Masters J.C., Génin F., Zhang Y., Pellen R., Huck T., Mazza P.P.A., Rabineau M., Doucouré M., Aslanian E. 2021. Biogeographic mechanisms involved in the colonization of Madagascar by African vertebrates: Rifting, rafting and runways. Journal of Biogeography, 48: 492–510. Doi: https://doi.org/10.1111/jbi.14032

McKenna D.D., Wild A.L., Kanda K., Bellamy C.L., Beutel R.G., Caterino M.S., Farnum C.W., Hawks D.C., Ivie M.A., Jameson M.L., Leschen R.A.B., Marvaldi A.E., McHugh J.V., Newton A.F., Robertson J.A., Thayer M.K., Whiting M.F., Lawrence J.F., Ślipiński A., Maddison D.R., Farrell B.D. 2015. Beetles survived the end Permian mass extinction to diversify during the Cretaceous terrestrial revolution. Systematic Entomology, 40: 835–880. Doi: http://dx.doi.org/10.1111/syen.12132

Mennes C.B., Smets E.F., Moses S.N., Merckx V.S.F.T. 2013. New insights in the long-debated evolutionary history of Triuridaceae (Pandanales). Molecular Phylogenetics and Evolution, 69: 994–1004. Doi: http://dx.doi.org/10.1016/j.ympev.2013.05.031

Miller M., Pfeiffer W., Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, Louisiana, 2010: 1–8. Doi: https://doi.org/10.1109/GCE.2010.5676129

Miraldo A., Wirta H., Hanski I. 2011. Origin and diversification of dung beetles in Madagascar. Insects, 2: 112–127. Doi: https://doi:10.3390/insects2020112

Nagy Z.T., Joger U., Wink M., Glaw F., Vences M. 2003. Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from nuclear and mitochondrial gene phylogenies. Proceedings of the Royal Society of London B: Biological Sciences, 270: 2613–2621. Doi: https://doi.org/10.1098/rspb.2003.2547

Near T.J., Eytan R.I., Dornburg A., Kuhn K.L., Moore J.A., Davis M.P., Wainwright P.C., Friedman M., Smith W.L. 2012. Resolution of ray-finned fish phylogeny and timing of diversification. Proceedings of the National Academy of Sciences, 109: 13698–13703. Doi: https://doi.org/10.1073/pnas.1206625109

Ocampo F.C., Hawks D.C. 2006. Phylogenetic analysis of the scarab family Hybosoridae and monographic revision of the New World subfamily Anaidinae (Coleoptera: Scarabaeoidea). 2. Molecular phylogenetics and systematic placement of the family Hybosoridae (Coleoptera: Scarabaeoidea). Bulletin of the University of Nebraska State Museum, 19: 7–12.

Omland K.E., Cook L.G., Crisp M.D. 2008. Tree thinking for all biology: the problem with reading phylogenies as ladders of progress. BioEssays, 30: 854–867. Doi: https://doi.org/10.1002/bies.20794

Papadopoulou A., Knowles L.L. 2015. Genomic tests of the species-pump hypothesis: recent island connectivity cycles drive population divergence but not speciation in Caribbean crickets across the Virgin Islands. Evolution, 69: 1501–1517. Doi: https://doi.org/10.1111/evo.12667

Pastorini J., Thalmann U., Martin R.D. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. Proceedings of the National Academy of Sciences, 100: 5879–5884. Doi: doi.org/10.1073/pnas.1031673100

Plana V. 2004. Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest. Philosophical Transactions of the Royal Society B: Biological Sciences, 359: 1585–1594. Doi: http://dx.doi.org/10.1098/rstb.2004.1535

Poinar G., Ballerio A. 2017. Remarks on some Ceratocanthinae (Coleoptera: Hybosoridae) in Dominican amber. Zootaxa, 4286: 125–128. Doi: https://doi.org/10.11646/zootaxa.4286.1.9

Poux C., Madsen O., Marquard E., Vieites D.R., de Jong W.W., Vences M. 2005. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. Systematic Biology, 54: 719–730. Doi: https://doi.org/10.1080/10635150500234534

Rambaut A. 2020. FigTree. Version 1.4.4. Program and documentation, available at: http://tree.bio.ed.ac.uk/software/figtree/.

Ratnasingham S., Hebert P.D.N. 2007. BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes, 7: 355–364. Doi: http://dx.doi.org/10.1111/j.1471-8286.2007.01678.x

Reevers C. 2014. The position of Madagascar within Gondwana and its movements during Gondwana dispersal. Journal of African Earth Sciences, 94: 45–57. Doi: https://doi.org/10.1016/j.jafrearsci.2013.07.011

Rocha S., Carretero M.A., Harris, D.J. 2005. Diversity and phylogenetic relationships of *Hemidactylus* geckos from the Comoro Islands. Molecular Phylogenetics and Evolution, 35: 292–299. Doi: https://doi.org/ 10.1016/j.ympev.2004.11.023

Rocha S., Carretero M.A., Vences M., Glaw F., Harris D.J. 2006. Deciphering patterns of transoceanic dispersal: the evolutionary origin and biogeography of coastal lizards (*Cryptoblepharus*) in the Western Indian Ocean region. Journal of Biogeography, 33: 13–22. Doi: https://doi.org/10.1111/j.1365-2699.2005.01375.x

Rocha S., Vences M., Glaw F., Posada D., Harris D.J. 2009. Multigene phylogeny of Malagasy day geckos of the genus *Phelsuma*. Molecular Phylogenetics and Evolution, 52: 530–537. Doi: https://doi.org/10.1016/j.ympev.2009.03.032

Roelants K., Gower D.J., Wilkinson M., Loader S.P., Biju S.D., Guillaume K., Bossuyt, F. 2007. Patterns of diversification in the history of modern amphibians. Proceedings of the National Academy of Sciences, 104: 887–892. Doi: https://doi.org/10.1073pnas.0608378104

Seiffert E.R. 2007. A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. BMC Evolutionary Biology, 7, 224: 13 pp. Doi: https://doi.org/10.1186/1471-2148-7-224

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics, 30: 1312–1313. Doi: https://doi.org/10.1093/bioinformatics/btu033

Stamatakis A., Hoover P., Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology, 57: 758–771. Doi: https://doi.org/10.1080/10635150802429642

Stewart C.-B., Disotell T.R. 1998. Primate evolution — in and out of Africa. Current Biology, 8: R582–R587. Doi: https://doi.org/10.1016/S0960-9822(07)00367-3

Tamar K., Carranza S., Sindaco R., Moravec J., Trape J.F., Meiri S. 2016. Out of Africa: Phylogeny and biogeography of the widespread genus *Acanthodactylus* (Reptilia: Lacertidae). Molecular Phylogenetics and Evolution, 103: 6–18. Doi: https://doi.org/10.1016/j.ympev.2016.07.003

Tolley K.A., Townsend T.M., Vences M. 2013. Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. Proceedings of the Royal Society B: Biological Sciences, 280, 1759, 20130184: 8 pp. Doi: http://dx.doi.org/10.1098/rspb.2013.0184

Vences M. 2004. Origin of Madagascar's extant fauna: a perspective from amphibians, reptiles and other non-flying vertebrates. Italian Journal of Zoology, Supplement 2: 217–228. Doi: http://dx.doi.org/10.1080/11250000409356639

Vences M., Vieites D.R., Glaw F., Brinkmann H., Kosuch J., Veith M., Meyer A. 2003. Multiple overseas dispersal in amphibians. Proceedings of the Royal Society B: Biological Sciences, 270: 2435–2442. Doi: http://dx.doi.org/10.1098/rspb.2003.2516

Wang N., Kimball R.T., Braun E.L., Liang B., Zhang Z. 2017. Ancestral range reconstruction of Galliformes: the effects of topology and taxon sampling. Journal of Biogeography, 44: 122–135. Doi: http://dx.doi.org/10.1111/jbi.12782

Wojciechowski M.F. 2013. The origin and phylogenetic relationships of the Californian chaparral 'paleoendemic' *Pickeringia* (Leguminosae). Systematic Botany, 38: 132–142. Doi: https://doi.org/10.1600/036364413X662024

Yoder A. D., Nowak M.D. 2006. Has vicariance or dispersal been the predominant force in Madagascar? Only time will tell. Annual Review of Ecology, Evolution, and Systematics, 37: 405–431. Doi: http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110239

Zhou L., Su Y.C.F., Thomas D.C., Saunders R.M.K. 2012. 'Out-of-Africa' dispersal of tropical floras during the Miocene climatic optimum: evidence from Uvaria (Annonaceae). Journal of Biogeography, 39: 322–335. Doi: 10.1111/j.1365-2699.2011.02598.x