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Phylogenetic and biogeographical review of the Drepanocerina (Coleoptera: Scarabaeidae: Oniticellini)

Angela Roggero *, Enrico Barbero & Claudia Palestrini

Department of Life Sciences and Systems Biology, Via Accademia Albertina 13, I-10123 Torino, Italy; Enrico Barbero [enrico.barbero@unito.it]; Claudia Palestrini [claudia.palestrini@unito.it]; Angela Roggero [angela.roggero@unito.it] — * Corresponding author

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Abstract

A phylogenetic analysis of Drepanocerina based on 81 morphological characters was conducted using various analytical approaches (Maximum Parsimony, New Technology Search, Bayesian Inference, and Phylogenetic Networks Analysis). Twelve lineages ranked at the generic level were resolved, with full congruency among the four analytical methods. Results allowed to propose two new genera, which are herein described as *Paraixodina* **gen. nov.** and *Epidrepanus* **gen. nov.** In addition, the previously unknown *Eodrepanus integriceps* and *Sinodrepanus similis* females were identified and described. A biogeographic analysis was performed based on 14 geographic macro-areas, partitioning the subtribe and outgroup distributional ranges. Based on the inferred phylogeny and biogeography, an ancestral distribution and radiation scenario from the Central East Africa macroarea (Afrotropical Region) was proposed. The biogeographic implications of past and present-day relationships within Drepanocerina was discussed.

Key words

Phylogeny, biogeography, taxonomy, Afrotropical, Oriental, Palearctic, ancestral distribution reconstruction, morphology, new genera.

1. Introduction

The oniticelline subtribe Drepanocerina Lansberge, 1875 (Janssens 1946, 1949; Balthasar 1963a) is a taxonomically troublesome group, having undergone many nomenclatural changes throughout the 20th and continuing into the early 21st century (Barbero et al. 2009a). The early systematic history of Drepanocerina was summarized in the review of Janssens (1953), who implicitly recognised three genera in the subtribe, including i) *Drepanocerus* Kirby, 1828, which then comprised 18 Afrotropical and 8 Oriental species, being the genus *Ixodina* Roth, 1851 placed here in synonymy with the former one (Table 1); ii) *Scaptocnemis* Péringuey, 1901 (with *S. segregis* Péringuey, 1901); and iii) *Drepanoplatynus* Boucomont, 1921 (with *D. gilleti* Boucomont, 1921), the two latter ones being Afrotropical and monospecific genera. *Scaptocnemis* was later transferred to Oniticellina (Branco 2010), while *Drepanoplatynus* was maintained in Drepanocerina. Afterwards, eight new *Drepanocerus* species from the Afrotropical and Oriental regions were described (Balthasar 1963b,c; Kryzhanovski & Medvedev 1966; Endrödi 1971, 1976; Biswas 1979) (Table 1).

Simonis & Zunino (1980) revalidated the Afrotropical genus *Cyptochirus* Lesne, 1900 to accommodate three species formerly placed in *Drepanocerus* (Janssens 1953), and a newly described one. Simonis (1981) established the genus *Anoplodrepanus* for two Jamaican species, earlier described in *Drepanocerus*: *D. reconditus* Matthews, 1966 and *D. pecki* Howden, 1976. Simonis (1985) proposed the new Oriental genus *Sinodrepanus* for six species, three previously assigned to *Drepanocerus*, and three newly described. Masumoto et al. (2004) and Ochi et al. (2004) described three new *Sinodrepanus* species from the Oriental region.

Later, Kabakov (2006) described a new *Drepanocerus* species from the Hindu Kush (Afghanistan), which is the only extant Drepanocerine species recorded from the Eastern Palearctic.

More recently, Barbero et al. (2009a) established the genus *Eodrepanus* distributed throughout the Afrotropical and Oriental regions, containing six species previously assigned to *Drepanocerus* (see also Kabakov 2006), and three newly described ones (two extant Afrotropical species, and a fossil one from the Palearctic Region). The latter, *Eodrepanus coopei*, dates from the Eemian interglacial period some 130–114 thousand years ago and is known from only pronotum and elytra (Barbero et al. 2009a) collected from the site of Trafalgar Square (London, UK) (Coope 2000). This fossil species was also recorded from Woolpack Farm, Great Ouse River in Cambridgeshire, UK (Gao et al. 2000).

Subsequently, Krikken (2009) transferred the New-World outlier genus *Anoplodrepanus* Simonis from Drepanocerina to Oniticellina and delimited the former to include the following Old-World ten genera: *Drepanocerus* Kirby, 1828; *Sinodrepanus* Simonis, 1985; *Cyptochirus* Lesne, 1900; *Ixodina* Roth, 1851 (reinstated here as a valid genus); *Eodrepanus* Barbero et al., 2009a; and the newly described *Afrodrepanus*, *Clypeodrepanus*, *Latodrepanus* (the latter a synonym of *Drepanellus*, see Barbero et al. 2009b), *Sulcodrepanus*, and *Tibiodrepanus*, all from the Old World. These taxonomic changes were based on external morphological traits without the use of formal phylogenetic analysis. Branco (2010) corroborated Krikken's (2009) assignment of *Anoplodrepanus* to Oniticellina. Finally, Barbero et al. (2011) synonymized *Sulcodrepanus* Krikken, 2009 with *Tibiodrepanus* Krikken, 2009, and described the new Afrotropical species *Tibiodrepanus tagliaferrii*.

Presently the subtribe Drepanocerina includes ten genera with a total of 53 extant species distributed in the Afrotropical, Palearctic and Oriental regions, and one fossil species recorded from Southern England. The monophyly of the taxon is not entirely secured, although the presence of a basal carina in the pygidium separate Drepanocerina from any other Oniticellini taxa. However, few other potential synapomorphies (i.e., the posterior coxae not close together, or the pubescence of superior surface always very tight or scaly) show scattered occurrence in other Scarabaeinae taxa.

Recent phylogenetic studies primarily assessed basal and the more ancient relationships in Scarabaeoidea (Philips et al. 2004; Philips 2005; Smith et al. 2006; Monaghan et al. 2007; Wirta et al. 2008; Scholtz et al. 2009), and far more is known about some taxa than others. Drepanocerina is a good example of this fragmentary knowledge: although it is a well-characterised group within Oniticellini, its phylogeny at various taxonomic levels has not been elucidated. Furthermore, Drepanocerina was more or less peripherally involved in various morphological (Philips et al. 2004; Philips 2005) and molecular (Monaghan et al. 2007; Wirta et al. 2008) phylogenetic analyses, with incongruent results depicting relationships with other members of Scarabaeinae. On the basis of these studies, the systematic position of Drepanocerina appeared controversial. Besides, Scholtz et al. (2009) later summarized the more recent studies in Oniticellini in which three subtribes (i.e., Oniticellina, Drepanocerina and Helictopleurina) are recognized.

The last hypothesis being the most trusted one, it was thus here employed as a basis for the following phylogenetic analyses within Drepanocerina. The general objectives of the present study were to undertake a phylogenetic analysis with the aim to elucidate relationships among formerly recognised genera, and new genera described herein within the subtribe. Furthermore, we de-

Table 1. List of the 43 Drepanocerina species included in the phylogenetic and geographical analyses, with their distribution defined by the macroareas (code letters as defined in Fig. 2).

Species	Distribution
Afrodrepanus impressicollis (Boheman, 1857)	DFG
Afrodrepanus marshalli (Boucomont, 1921)	ABDFG
Clypeodrepanus digitatus Krikken, 2009	D
Clypeodrepanus striatus (Boucomont, 1921)	DF
Clypeodrepanus strigatus (Janssens, 1953)	ABD
Cyptochirus ambiguus (Kirby, 1828)	CFG
Cyptochirus decellei (Simonis and Zunino, 1980)	CDF
Cyptochirus distinctus Janssens, 1953	ABDF
Cyptochirus trogiformis (Roth, 1851)	CDG
Drepanocerus kirbyi Kirby, 1828	BCDEFG
Drepanocerus orientalis Krikken, 2009	D
Drepanocerus patrizii Boucomont, 1923	CDEFG
Drepanoplatynus gilleti Boucomont, 1921	AD
Eodrepanus bechynei (Janssens, 1953)	ABCDFG
Eodrepanus fastiditus (Péringuey, 1901)	CDFG
Eodrepanus integriceps (Janssens, 1953)	JK
Eodrepanus liuchungloi (Kryzhanovsky & Medvedev, 1966)	J
Eodrepanus morgani Barbero, Palestrini & Roggero, 2009	B
Eodrepanus paolae Barbero, Palestrini & Roggero, 2009	D
Eodrepanus parallelus (Raffray, 1877)	CDFG
Eodrepanus striatulus (Paulian, 1945)	HJK
Ixodina abyssinica Roth, 1851	ABCDFG
Ixodina freyi (Janssens, 1953)	DFG
Ixodina runicus (Arrow, 1909)	HJKL
Ixodina saegeri (Balthasar, 1963)	DFG
Latodrepanus caelatus (Gerstaecker, 1871)	ABCDEFG
Latodrepanus laticollis (Fahraeus, 1857)	BDEFG
Latodrepanus nicolasi Barbero, Palestrini & Roggero, 2009	F
Latodrepanus pulvinarius (Balthasar, 1963)	DG
Latodrepanus schimperi (Janssens, 1963)	C
Latodrepanus simonisi Barbero, Palestrini & Roggero, 2009	AB
Sinodrepanus arrowi (Balthasar, 1932)	K
Sinodrepanus besucheti Simonis, 1985	K
Sinodrepanus similis Simonis, 1985	JK
Sinodrepanus thailandicus Ochi, Kon & Masumoto, 2004	J
Sinodrepanus tsaii Masumoto, Yang & Ochi, 2004	K
Sinodrepanus uenoi Ochi, Kon & Masumoto, 2004	K
Tibiodrepanus hircus (Wiedemann, 1823)	IJKL
Tibiodrepanus setosus (Wiedemann, 1823)	HIJKL
Tibiodrepanus simplex (Kabakov, 2006)	M
Tibiodrepanus sinicus (Harold, 1868)	HIJKL
Tibiodrepanus sulcicollis (Laporte de Castelnau, 1840)	ABCDEFG
Tibiodrepanus tagliaferrii Barbero, Palestrini & Roggero, 2011	BE

fined the species geographical patterns from a substantial distribution database obtained from collected specimens with carefully verified locality records. The distribution data were integrated with respect to the results of the phylogenetic analysis in order to propose an ancestral distribution reconstruction hypothesis on the evolutionary history of Drepanocerina.

2. Material and methods

2.1. Material examined

We studied approximately 7,000 specimens (type and non-type material) belonging to 43 Drepanocerina species (out of 53 described ones; see Table 1) that represent all 10 currently accepted genera (including *Ixodina*). Then, we selected a total of about 500 specimens that were representative of the various Drepanocerina species and dissected them.

Examining the material, we identified a taxonomic problem concernig some *Ixodina* species (i.e., *I. bos*, *I. endroedyi*, *I. kovacsi* and *I. szunyoghyi*) that were described by Endrödi (1971, 1976) exclusively on the basis of the shape of male pronotal horns, while the females of these species are virtually indistinguishable from each other, and identical to the *I. abyssinica* ones. After a careful examination of the genitalia and epipharynx of the five species, we could not identify any significant differences in shape of these structures, thus we preferred to include only *I. abyssinica* in our analysis, till the taxonomic status of the other four species would be clarified using the most appropriate methods.

The institutions and private collectors who loaned us the material examined for this study are listed in the Acknowledgements.

2.2. Morphological analysis

Mouthparts and genitalia of both sexes were dissected and treated following the methods typically employed for Scarabaeoidea (Barbero et al. 2003). Images of male and female genitalia and those of epipharynx were captured using a Leica® DFC320 digital camera connected to a stereoscopic dissecting macroscope (Leica® Z16Apo).

2.3. Phylogenetic analysis

The phylogenetic relationships among the Drepanocerina taxa were analysed using three sets of characters inferred from external features, epipharynx and genitalia of both sexes (Barbero et al. 2009a, 2011).

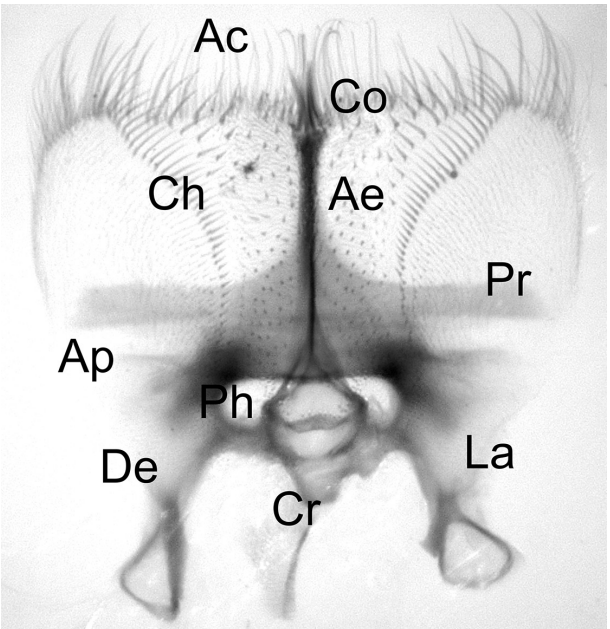

Fig. 1. Scheme of the epipharynx (*S. besucheti*) showing the various parts discussed in the characters list (7. Appendix): Ac = acropariae, Ae = anterior epitorma, Ap = apotormae, Ch = chaetopariae, Co = corypha, Cr = crepis, De = dexiotorma, La = laeotorma, Ph = plegmatic area, Pr = proplegmatium.

Previous studies showed that the epipharynx is a useful tool in Scarabaeoidea systematics (Nel & De Villiers 1988; Nel & Scholtz 1990; Barbero et al. 2003; Medina et al. 2003; Sanmartin & Martin-Piera 2003; Philips et al. 2004; Verdú & Galante 2004), although the structure is not yet so widely employed as it would be desirable. Here, we defined the regions, subregions and structures of the Scarabaeoidea adult epipharynx (Fig. 1) applying the nomenclature formerly proposed for coleopteran larvae (Böving 1936), with the exception of some unnamed parts, which were designated following the terminology proposed by Barbero et al. (2003).

For male genitalia, we followed the terminology by Medina et al. (2013), while we referred to the traditional terminology for Coleoptera female genitalia (Barbero et al. 2003).

The matrix consists of 81 morphological characters (33 binary and 48 multistate) scored for 43 ingroup Drepanocerina species (Table 2) in NDE 0.5.0 (Page 2001). All characters were analysed as unordered and equally weighted. To root the trees, the "*Anoplodrepanus*" terminal was added to accommodate characters scored from *Anoplodrepanus pecki* and *A. reconditus*. It was defined as the outgroup.

These two species were formerly included by mistake in the *Drepanocerus* genus (Matthews 1966; Howden 1976) based on the incorrect recognization of a transversal carina on the base of pygidium (a character present only in Drepanocerina). Once the true taxonomic position of *Anoplodrepanus* within Oniticellini was ascertained (Krikken 2009; Branco 2010), the genus was re-

Table 2. Matrix of the characters.

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Anoplodrepanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cy. ambiguus	1	2	0	0	0	0	1	0	0	0	1	2	0	1	0	2	2	0	0	1	0	0	0	0	0	1	0	3	1	2	0	0	0	0	0	0	2	0	1	0
Cy. decellei	0	2	0	0	0	0	0	2	0	0	0	2	0	1	3	2	2	1	0	1	0	0	0	0	0	1	0	3	1	2	0	0	0	0	0	0	2	0	1	0
Cy. distinctus	1	2	0	0	0	0	0	0	0	0	1	2	0	1	0	2	2	0	0	1	0	0	0	0	0	1	0	3	1	2	0	0	0	0	0	0	2	0	1	0
Cy. trogiformis	0	2	0	0	0	0	0	0	0	0	1	2	0	1	0	2	0	0	0	1	0	0	0	0	0	1	0	3	1	2	0	0	0	0	0	0	2	0	1	0
E. bechynei	1	0	2	1	0	0	1	1	1	0	0	3	0	2	0	1	1	0	1	3	0	0	0	0	0	0	0	2	0	1	0	0	1	0	1	1	0	0	1	1
E. fastiditus	1	0	3	1	0	0	1	1	1	0	0	3	0	2	0	1	1	0	1	3	0	0	1	0	0	0	0	2	0	1	0	0	1	0	1	0	0	0	1	1
E. morgani	1	0	2	1	0	1	1	1	1	0	0	3	0	2	0	1	1	0	1	3	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	1	1
E. paolae	1	0	2	1	0	1	1	1	1	0	0	3	0	2	0	1	1	0	1	3	0	0	0	0	0	0	0	2	0	1	0	0	1	0	1	1	0	0	1	1
E. parallelus	1	0	3	1	0	0	1	1	1	0	0	3	0	2	0	1	1	0	1	3	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	1	1
E. integriceps	1	1	3	1	0	1	0	1	1	0	1	3	0	2	0	1	1	0	1	4	0	0	0	0	0	0	0	2	0	1	0	0	1	0	1	1	0	0	1	1
E. liuchungloi	1	1	3	1	0	1	0	1	1	0	1	3	0	2	0	1	1	0	1	3	0	0	0	0	0	0	0	2	0	1	0	0	1	0	1	1	0	0	1	1
E. striatulus	1	1	3	1	0	1	0	1	1	0	1	3	0	2	0	1	1	0	1	3	0	0	0	0	0	0	0	2	0	1	0	0	1	0	1	1	0	0	1	1
D. kirbyi	2	0	2	3	0	1	1	0	0	0	1	1	0	0	3	0	1	0	0	1	1	0	1	0	0	0	0	2	1	2	0	1	0	0	0	1	0	0	1	0
D. orientalis	2	0	2	3	0	1	1	0	0	0	1	1	0	0	3	0	1	0	0	1	1	0	1	0	0	0	0	2	1	2	0	1	0	0	0	1	0	0	1	0
D. patrizii	2	0	2	3	0	0	0	0	0	0	1	0	0	0	3	2	2	0	0	1	1	0	1	0	0	0	0	2	1	2	0	1	0	0	0	1	0	0	1	0
I. abyssinica	0	3	0	2	0	1	1	0	0	1	0	0	1	3	3	2	1	0	0	2	1	0	1	1	0	0	0	2	1	1	0	0	0	1	2	2	0	3	1	0
Pa. freyi	2	2	2	3	1	2	0	0	0	1	2	4	0	3	1	0	1	0	0	5	1	1	1	0	0	0	0	2	1	1	1	1	0	1	2	2	2	3	1	0
Pa. runica	2	2	2	3	1	2	0	0	0	1	2	4	0	3	3	0	1	0	0	5	1	0	1	0	0	0	0	2	1	1	1	0	0	1	2	2	2	3	1	0
Pa. saegeri	0	3	1	2	1	1	0	0	1	1	2	4	0	3	3	1	0	0	1	5	1	1	0	1	0	0	0	2	0	1	1	1	0	1	2	2	2	3	1	0
Epi. caelatus	0	0	0	1	0	0	3	0	1	0	1	0	3	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0
Epi. pulvinarius	0	0	0	1	0	0	3	0	1	0	1	0	3	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0
Epi. schimperi	0	0	0	1	0	0	3	0	1	0	0	0	3	0	3	0	0	1	0	1	0	0	0	0	0	0	?	?	1	0	0	0	0	0	0	1	1	1	0	0
A. impressicollis	0	3	1	1	0	0	2	0	0	0	1	1	0	1	3	0	2	2	0	4	0	0	0	0	0	0	0	2	0	1	0	0	0	1	0	2	3	2	1	0
A. marshalli	0	2	1	1	0	0	0	0	0	0	1	1	0	1	3	0	3	1	0	4	0	0	0	1	1	0	0	2	0	1	0	0	0	1	0	1	3	2	1	0
Dr. gilleti	0	1	1	1	0	0	0	2	1	0	1	0	0	0	3	0	2	2	0	0	0	0	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	1	1	0
C. digitatus	0	2	5	2	0	0	3	2	0	0	0	0	0	0	3	0	1	2	0	1	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0
C. striatus	0	2	0	2	0	0	0	2	0	0	0	0	2	0	1	0	1	2	0	1	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0
C. strigatus	0	2	0	2	0	0	0	2	0	0	0	0	2	0	3	0	1	2	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0
L. laticollis	3	0	1	3	0	0	0	2	0	0	1	1	2	1	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	2	3	1	1	0
L. nicolasi	3	0	1	3	0	0	0	2	0	0	1	0	2	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	2	3	1	1	0
L. simonisi	3	0	1	3	0	0	0	2	0	0	1	1	2	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	2	3	1	1	0
S. arrowi	0	2	0	0	0	0	1	0	0	0	1	1	0	1	2	1	0	1	2	0	0	0	2	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	1	0
S. besucheti	0	2	1	0	0	0	1	2	0	0	0	2	0	1	2	0	0	1	0	1	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	1	0
S. similis	0	2	0	0	0	0	1	0	0	0	1	1	0	1	2	1	0	1	2	0	0	0	2	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0
S. thailandicus	0	2	0	0	0	0	1	0	0	0	0	1	0	1	2	1	0	1	2	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	1	0
S. tsaii	0	2	1	0	0	0	1	0	0	0	0	2	0	1	2	0	0	1	2	1	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	1	0
S. uenoi	0	2	1	0	0	0	1	2	0	0	0	2	0	1	2	1	1	1	2	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	1	0
T. hircus	3	0	4	0	0	0	1	3	0	0	0	1	1	0	0	2	0	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0
T. setosus	3	2	4	0	0	0	1	0	0	0	0	0	1	0	1	2	1	1	0	1	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	2	0	0	0
T. simplex	3	2	1	0	0	0	1	0	0	0	1	0	0	0	1	2	0	1	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0
T. sinicus	3	2	4	0	0	0	1	3	0	0	0	1	0	0	1	2	1	1	0	1	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0
T. sulcicollis	3	0	4	0	0	1	0	3	0	0	1	0	1	0	1	2	0	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0
T. tagliaferrii	3	0	4	0	0	0	0	3	0	0	0	0	1	0	1	2	0	1	0	1	1	0	0	1	0	0	?	?	1	0	0	0	0	0	0	1	0	0	0	0

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
Anoplodrepanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cy. ambiguus	0	0	0	0	1	0	0	2	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	3	0	0	1	1	0	3	0	0	0	0	0	0	0
Cy. decellei	0	0	0	0	1	0	1	2	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	3	0	0	1	1	0	3	0	0	0	0	0	0	0
Cy. distinctus	0	0	0	0	1	0	1	2	0	0	0	0	0	1	1	2	1	0	0	0	0	1	0	2	0	0	0	3	0	0	1	1	0	3	0	0	0	0	0	0	0
Cy. trogiformis	0	0	0	0	0	1	0	1	2	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	1	0	1	3	0	0	1	1	0	3	0	0	0	0	0	0	0
E. bechynei	0	0	0	1	0	2	0	0	1	0	1	0	0	0	1	2	1	0	0	0	2	3	0	1	0	0	0	1	0	1	0	0	0	1	1	0	2	4	1	0	2
E. fastiditus	0	0	0	1	0	2	0	0	0	0	1	0	0	0	1	1	1	1	0	0	2	3	0	1	0	0	0	1	0	1	2	0	0	0	1	0	2	5	1	0	2
E. morgani	0	0	0	1	0	2	0	1	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	2	4	1	0	2
E. paolae	0	0	0	1	0	2	0	0	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	0	0	1	0	2	4	1	0	2
E. parallelus	0	0	0	1	0	2	0	0	1	0	1	0	0	0	1	2	0	1	0	0	2	3	0	1	0	0	0	1	0	1	2	0	0	1	1	0	2	5	1	0	2
E. integriceps	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	2	1	1	0	0	2	3	0	1	0	0	0	1	1	1	1	0	0	2	0	0	2	4	0	0	2
E. liuchungloi	0	0	0	1	0	2	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	1	1	2	4	1	0	2
E. striatulus	0	0	0	1	0	2	0	1	0	0	0	0	0	0	0	2	1	1	0	0	2	3	0	1	0	0	0	1	0	1	1	0	0	0	1	1	2	4	1	0	2
D. kirbyi	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	2	0	2	0	1	1	0	0	3	0	0	2	1	2	3	0	0	0	6	0	0	2
D. orientalis	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	2	0	2	0	1	1	0	0	3	0	0	2	1	2	3	0	0	0	6	0	0	2
D. patrizii	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	2	0	2	0	1	0	0	1	3	0	0	2	1	2	3	0	0	1	6	0	0	2
I. abyssinica	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	1	0	1	1	1	0	4	0	2	1	1	1	2	0	0	2	1	0	2	0	0	2	3	0	0	0
Pa. freyi	0	0	0	0	0	2	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	5	0	1	1	2	1	2	0	0	1	0	1	2	0	0	1	3	1	0	2
Pa. runica	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	2	0	1	0	0	1	5	0	1	0	2	1	2	0	0	1	1	2	2	0	0	1	3	1	0	2
Pa. saegeri	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	2	0	1	0	1	1	5	0	1	0	2	1	2	0	0	2	1	0	0	1	1	1	3	1	0	2
Epi. caelatus	0	0	0	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	2	1	1	0	0	0	3	1	2	2	1	3	3	0	0	1	1	0	0	0
Epi. pulvinarius	0	0	0	0	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	2	1	1	0	0	0	3	1	2	2	1	3	3	0	0	1	1	0	0	0
Epi. schimperi	0	0	0	0	1	1	1	0	0	1	0	?	?	0	1	0	1	0	0	0	0	2	1	1	0	0	0	3	1	2	?	?	?	?	?	?	?	?	?	?	?
A. impressicollis	0	0	1	0	0	1	1	1	2	0	0	2	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	3	1	1	0	1	0	2	0	0	1	1	0	0	0
A. marshalli	0	0	1	0	0	1	1	1	2	0	0	2	0	0	1	0	1	0	1	1	0	2	0	0	1	0	0	3	0	0	2	1	0	0	0	0	1	3	0	0	0
Dr. gilleti	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	2	1	2	0	0	1	3	1	1	2	1	0	0	0	0	1	2	0	0	0
C. digitatus	0	0	0	0	1	1	1	1	1	0	0	2	1	0	1	2	1	1	0	0	0	0	1	2	0	1	1	2	0	0	2	1	0	3	2	2	2	3	0	0	2
C. striatus	0	0	0	0	1	1	1	1	0	0	0	2	1	0	1	2	0	1	0	0	0	0	1	2	0	1	0	2	0	2	2	1	1	3	2	2	2	3	0	0	2
C. strigatus	0	0	0	0	1	1	1	1	0	0	0	2	1	0	0	0	0	1	0	0	0	0	1	2	0	1	0	2	0	2	2	1	1	3	2	2	2	3	0	0	2
L. laticollis	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	2	1	0	0	0	2	1	1	1	1	3	3	0	0	0	2	0	0	0
L. nicolasi	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	0	2	1	1	1	1	3	3	0	0	0	2	0	0	0
L. simonisi	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	0	2	1	1	1	1	3	3	0	0	0	2	0	0	0
S. arrowi	1	0	0	0	0	1	0	1	2	0	0	1	0	1	1	2	1	1	0	0	0	2	1	2	0	3	0	3	0	3	2	1	1	3	0	0	0	7	0	1	1
S. besucheti	1	0	0	0	0	1	0	1	2	0	0	0	0	1	1	0	1	1	0	0	0	2	1	2	0	3	0	3	0	3	1	0	1	3	0	0	0	7	0	0	1
S. similis	1	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	2	1	2	0	3	0	2	0	3	2	1	1	3	0	0	0	7	0	1	1
S. thailandicus	1	0	0	0	0	1	0	1	2	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	1	3	0	0	0	7	0	0	1
S. tsaii	1	0	0	0	0	1	0	1	2	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	3	0	0	0	7	0	0	1
S. uenoi	1	0	0	0	0	1	0	1	2	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1	3	0	0	0	7	0	0	1
T. hircus	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	2	1	1	0	0	2	1	0	1	0	1	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0
T. setosus	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	2	1	1	0	0	2	1	0	1	0	1	0	3	0	0	1	0	0	0	0	1	0	3	0	0	0
T. simplex	1	0	0	0	0	2	0	1	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	0	1	3	0	0	0
T. sinicus	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	2	1	1	0	0	2	1	0	1	0	1	0	3	0	0	1	0	0	0	0	1	1	3	0	0	0
T. sulcicollis	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	2	1	0	1	0	1	0	3	0	0	0	0	0	2	0	0	0	3	0	0	0
T. tagliaferrii	1	0	0	0	0	1	0	1	1	0	0	?	0	0	0	0	1	1	0	0	2	1	0	1	0	1	0	3	0	0	?	?	?	?	?	?	?	?	?	?	?

moved from Drepanocerina and included in Oniticellina subtribe.

The relationships among Drepanocerina species were inferred by conducting phylogenetic analyses using the methods described below. The resulting trees were examined with FigTree v1.4.0 (Rambaut 2012).

Maximum Parsimony Analysis (Heuristic Search)**.** This was performed in PAUP 4.0b.10 (Swofford 2002). The software default settings (stepwise addition with simple addition sequence, tree bisection–reconnection branch-swapping, ACCTRAN character-state optimization) were applied with the multistate characters interpreted as "uncertainty", and the gaps treated as "missing". The MaxTrees limit was set to automatically increase from the initial setting. Trees were rooted by the outgroup method, and the strict consensus was calculated.

Statistical support for each branch was assessed using the non-parametric bootstrap method (Felsenstein 1985), with the same heuristic search settings as above, but with 100,000 replications, as implemented in PAUP. The following bootstrap values were applied to support the clades: weak (50–63%), moderate (64–75%), good (76–88%), and strong (89–100%) (Wahlberg et al. 2003).

New Technology Search. The morphological dataset was also analyzed through TNT (Goloboff et al. 2003, 2008) within the New Technology Search option, selecting all four search methods (Sectorial Search, Ratchet, Drift and Tree Fusing) with the defaults settings. The synapomorphies common to all trees were mapped onto the resulting trees. Tree statistics were calculated using a TNT script (stats.run). Relative support values were calculated using symmetric resampling, bootstrap standard and jackknife with 1,000 iterations, as implemented in TNT (Sharkey et al. 2012), while the Bremer support was calculated using the TNT script (Goloboff et al. 2008).

Bayesian Inference of Phylogeny. Following Müller & Reisz (2006), here the Markov chain Monte Carlo simulations (MCMC) was used to approximate the posterior probabilities of trees and parameters, as implemented in MrBayes v3.2 (Huelsenbeck et al. 2001; Ronquist & Huelsenbeck 2003; Ronquist et al. 2011).

The analysis was initiated with a random starting tree and run for 2,500,000 generations (two runs, eight chains), sampling trees every 100 generations, with rate heterogeneity modelled by equal distribution. Posterior clade probabilities were used to assess nodal support. The trees sampled during the burn-in phase (i.e. before the chain had reached its apparent target distribution) were discarded (25% of the total). The remaining trees were summarized in the Bayesian Majority Rule consensus trees, and the topologies of the two runs were compared to detect differences.

For the graphic exploration of MCMC convergence in Bayesian phylogeny, TRACER v1.6 (Rambaut et al. 2013) was then employed to analyze the results obtained from Bayesian MCMC runs, and to check for trends that might suggest problems with MCMC convergence; the lnL probability plot was examined for stationarity.

Phylogenetic Networks Analysis. Phylogenetic networks were calculated by Splits Tree 4.13.1 (Huson & Bryant 2006) to analyze the distances among taxa and assess the monophyly of clades. The test of monophyly (see Kaygorodova & Livetseva 2007) assessed the monophyly of the lineages using the Neighbor-Net method (Bryant & Moulton 2004). In addition, the bootstrap support of splits (100,000 runs) was included.

2.4. Biogeographical analysis

Delimitation of specific ranges and definition of macroareas. The distribution data were obtained from specimen labels, and each locality was georeferenced to be used to build digital maps of the distribution for each species in GIS environment through QGis v 2.0.1 (QGIS Development Team 2013). The species distributions were subsequently examined employing the spatial correlation analysis as implemented in SAM v4.0 (Rangel et al. 2010), and the localities were grouped according to the specific shared range patterns. The bioclimatic variables used in the procedure (the generic grids at 10 arc-minutes resolution of annual mean temperatures, mean diurnal range, isothermality, temperature seasonality, temperature annual range, annual precipitation, and precipitation seasonality) were obtained from WorldClim database (Hijmans et al. 2005), and 14 macroareas were thence defined (Fig. 2) that covered the Drepanocerina and outgroup (i.e., Jamaica) distribution. Successively, a binary data matrix of species presence/absence in the identified macroareas was built, coding 0 for absence and 1 for presence to summarize the distribution data of Drepanocerina. This matrix was applied in the dispersal-vicariance analysis.

Dispersal-Vicariance Analysis. The historical biogeography of Drepanocerina was explored using Dispersal-Vicariance analysis (Ronquist 1997) as implemented in DIVA v1.1 (Ronquist 1996). In DIVA, the vicariance events (allopatric speciation) and duplication events (sympatric speciation, i.e. speciation within a defined area) carry a cost of zero, whereas dispersal and extinction events cost one per unit area added or deleted from the distribution (Ronquist 1997). The species distribution was set to 14 areas (Fig. 2, list of macroareas). We used the two fully bifurcated trees obtained in the parsimony analysis, constraining the maximum number of unit areas in ancestral distributions to two, three and four successively (optimization settings maxareas = 2, 3 and 4). Additional settings were set default values (bound = 250, hold = 1000, weight = 1.000, age = 1.000). Results were compared, and the optimal solution that explained the biogeographical relationships within the species was chosen.

Subsequently, RASP (Statistical Dispersal-Vicariance Analysis method, Yu et al. 2010a) was employed to test the results of DIVA analysis. Condensed trees were calculated from the trees of the Parsimony Analysis

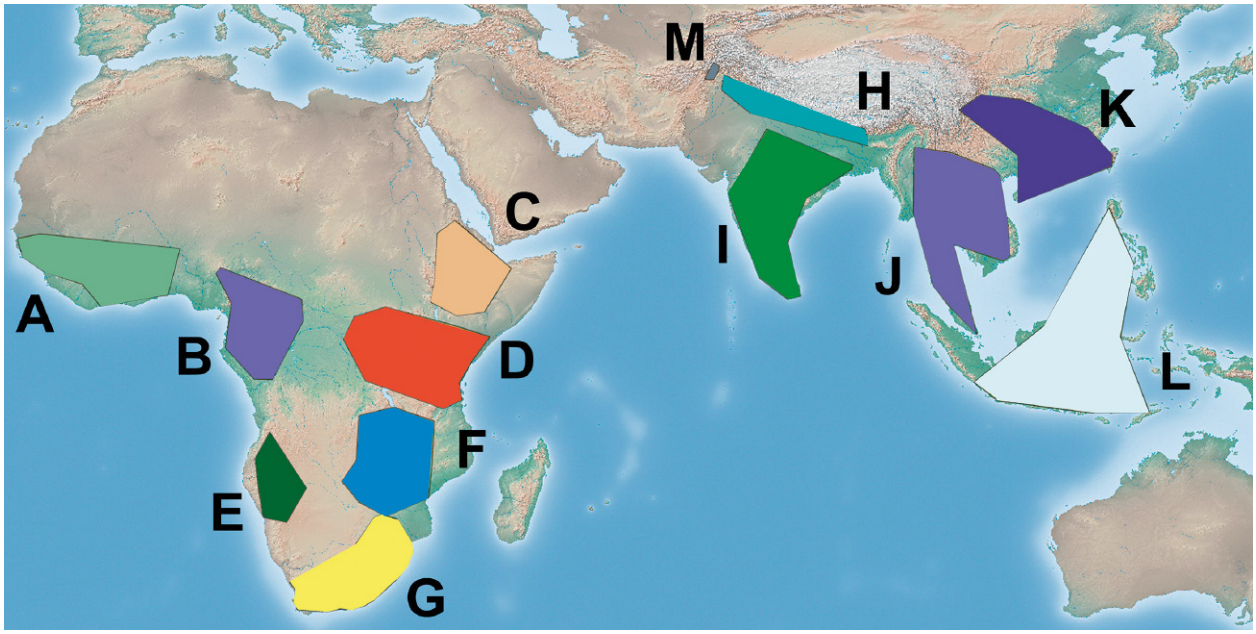

Fig. 2. Map of 13 out of the 14 macroareas identified: W Africa (A), CW Africa (B), E Africa (C), CE Africa (D), SW Africa (E), SE Africa (F), S Africa (G), N India (H), C and S India (I), Indochina (J), S China (K), Sunda shelf and Philippines (L), Hindu Kush (M, in Palarctic Region); Jamaica (N, for the outgroup) not included.

and the Bayesian Inference (separately and together), as implemented in RASP. The maximum number of areas was kept as 2. The software integrates DIVA analysis, furnishing statistical support for ancestral range reconstructions (Yu et al. 2010b; Ali et al. 2012).

3. Results

3.1. Phylogenetic analysis

The morphology-based phylogenetic relationships inferred from the different approaches supported well-defined taxa, which were ascribed to the ten genera herein known (Krikken 2009; Barbero et al. 2011), and two new genera here described as *Paraixodina* **gen. nov.**, and *Epidrepanus* **gen. nov.** The characters supporting the monophyly of the identified genera were listed in Table 3.

The Maximum Parsimony analysis generated two trees (Length = 407, CI = 0.390, HI = 0.609, RI = 0.755, RC = 0.295; strict consensus in Fig. 3) conflicting only in the relationships among the three lineages *T. sulcicollis*, *T. tagliaferrii* and *T. hircus* + *T. setosus* + *T. sinicus* (shown as a trichotomy in Fig. 3). Strong bootstrap support was observed for the different genera, but the analysis did not resolve most of the intergeneric relationships, for which very low support values were obtained (not shown in Fig. 3).

The New Technology Search analysis resulted in two trees, which were identical to those of Maximum Parsimony analysis (Total fit = 46.94 and 46.90, Adjusted homoplasy 34.06 and 34.10), and the clade-supporting synapomorphies common to the two trees were examined (Table 3). Resampling showed congruent, and significant results for the Drepanocerina generic clades, but most intergeneric relationships among genera remained equivocal. The resulting values of resampling analyses were written onto the Maximum Parsimony consensus tree (Fig. 3). Here, the relative support values were calculated by symmetric resampling, bootstrap standard, jackknife, and Bremer support, respectively: *Tibiodrepanus* (89, 82, 88, 88.4), *Eodrepanus* (100 for all four methods), *Clypeodrepanus* (99 for all four methods), *Drepanocerus* (96, 91, 97, 97.7), *Paraixodina* (88, 81, 88, 88.7), *Latodrepanus* (99 for all the four methods), *Epidrepanus* (93, 88, 91 and 91.1), *Afrodrepanus* (94, 91, 93, 93.6), *Cyptochirus* (97, 92, 96, 96.6), and *Sinodrepanus* (98, 96, 98, 98.7). While each genus was well-supported, the support values of the phylogenetic relationships among the genera were not calculated in the analysis, except for the *Ixodina* + *Paraixodina* (moderate/good: 81, 71, 84, 88.3), and *Epidrepanus* + *Latodrepanus* (very weak: 47, 38, 42, 42.2) clades. Thus, the support values for *Epidrepanus* + *Latodrepanus* were notably lower than for *Ixodina* + *Paraixodina*. Furthermore, the average group support for symmetric resampling, bootstrap standard, and jackknife were respectively 46.4, 43.2, 45.6.

A majority rule 50% consensus tree was produced from Bayesian Inference, with clade credibility values from all the trees retained in the analysis (Fig. 4). The results are similar to Parsimony analysis, with the monophyly of genera and the intrageneric relationships showing high rate of credibility, while the intergeneric

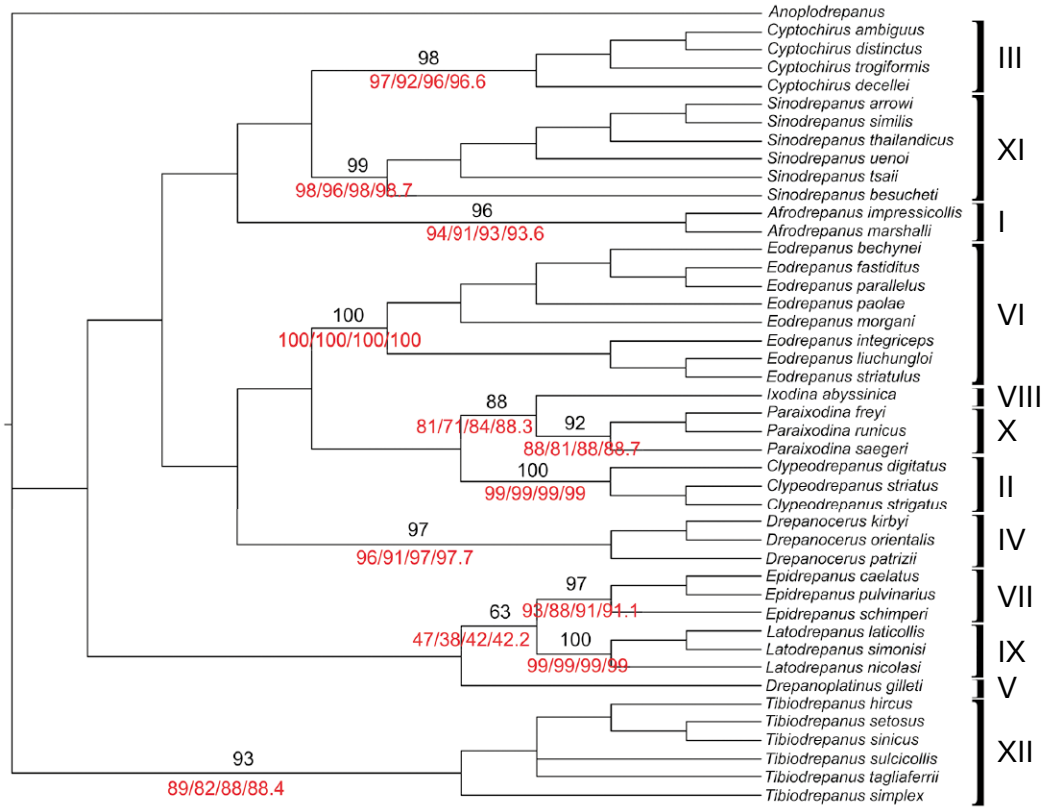

Fig. 3. Strict Consensus from MP analysis (Length = 407, CI = 0.986). The Bootstrap support values (Majority rule 50%) are shown above the branches, while the resampling (symmetric resampling, bootstrap strandard, and jackknife respectively) and the Bremer support values from TNT are shown below branches in red.

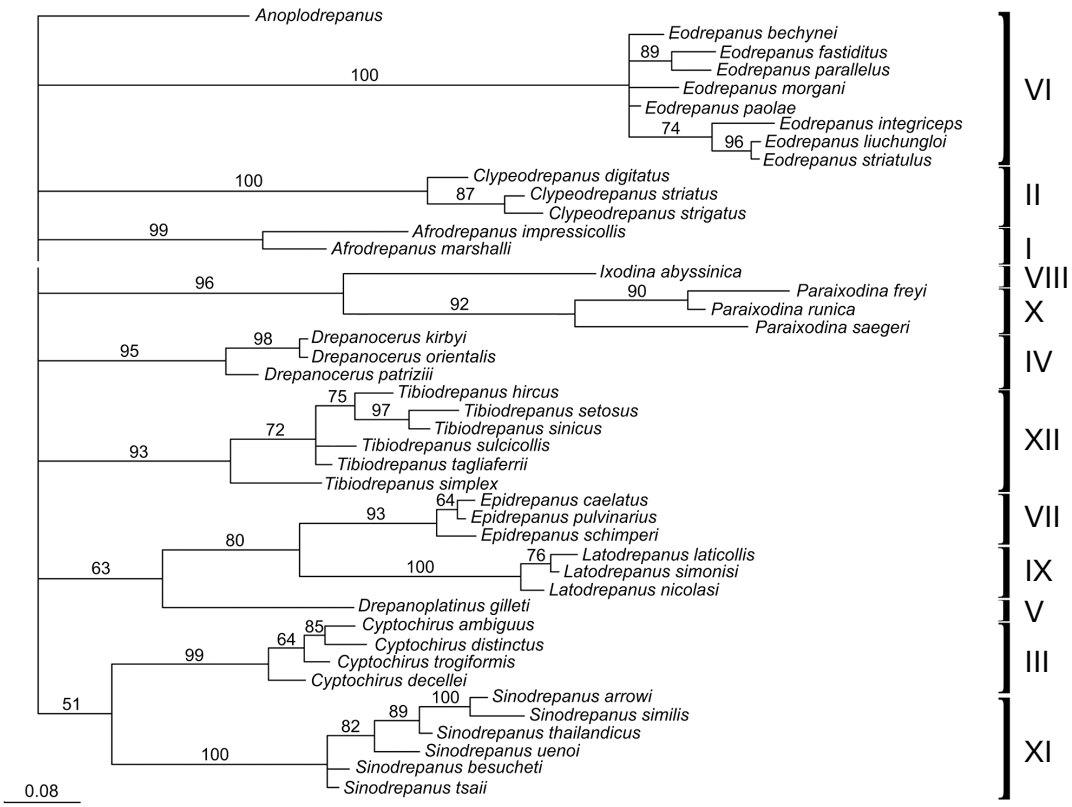

Fig. 4. Bayesian Inference 50% majority rule consensus tree.

Table 3. List of characters distinguishing the genera, from Maximum Parsimony and TNT analyses. For the character states see Appendix.

Afrodrepanus	20:4; 34:1; 37:3; 38:2; 43:1; 47:1; 52:2; 59:1; 64:0
Clypeodrepanus	8:2; 18:2; 25:1; 27:1; 28:1; 30:0; 39:0; 45:1; 52:2; 53:1; 63:1; 75:2; 76:2
Cyptochirus	3:0; 16:2; 26:1; 28:3; 29:1; 30:2; 36:0; 37:2; 62:1; 67:1
Drepanocerus	1:2; 4:3; 21:1; 23:1; 29:1; 30:2; 32:1; 42:1; 53:1; 59:1; 60:2; 73:2; 78:6
Drepanoplatynus	2:1; 18:2; 26:2; 32:1; 36:0; 54:1; 64:2; 67:1
Eodrepanus	1:1; 8:1; 9:1; 12:3; 14:2; 15:0; 16:1; 19:1; 20:3; 33:1; 35:1; 40:1; 44:1; 46:2; 61:2 70:1; 72:0; 78:4
Epidrepanus	3:0; 7:3; 39:0; 48:0; 55:1; 70:2
Ixodina	7:1; 13:1; 16:2; 46:0; 55:2; 56:1; 59:1; 65:1; 81:0
Latodrepanus	1:3; 4:3; 15:0; 22:1; 23:1; 36:2; 68:2; 71:1
Paraixodina	5:1; 11:2; 12:4; 31:1; 37:2; 48:0; 61:1; 66:2; 77:1; 79:1
Sinodrepanus	7:1; 15:2; 41:1; 63:1; 64:2; 66:3; 70:3; 72:0; 73:1; 81:1
Tibiodrepanus	1:3; 16:2; 21:1; 24:1; 29:1; 41:1

Table 4. Results of DIVA from the two MP trees (see Fig. 7 for the nodes' numbers), only the multiple hypotheses are listed.

Node	Optimal distribution – ancestral of terminals	
	TREE 1	TREE 2
	maxareas = 2	maxareas = 2
45	CD F DF DG	CD F DF DG
46	D DF	D DF
62	DJ	DJ
63	DH DJ DK DL	DH DJ DK DL
76	B AD BD AF BF	B AD BD AF BF
77	F BF DF	F BF DF
78	D BD DF	D BD DF
83	BI DI EI BJ DJ EJ BK DK EK BL DL EL	BI EI BJ EJ BK EK BL EL
84	B BD E DE	B BD E DE DI DJ DK DL
85	BM DM EM	BM DM EM
86	D BD DE DM	D BD DE DM
87	BN DN EN MN	BN DN EN MN

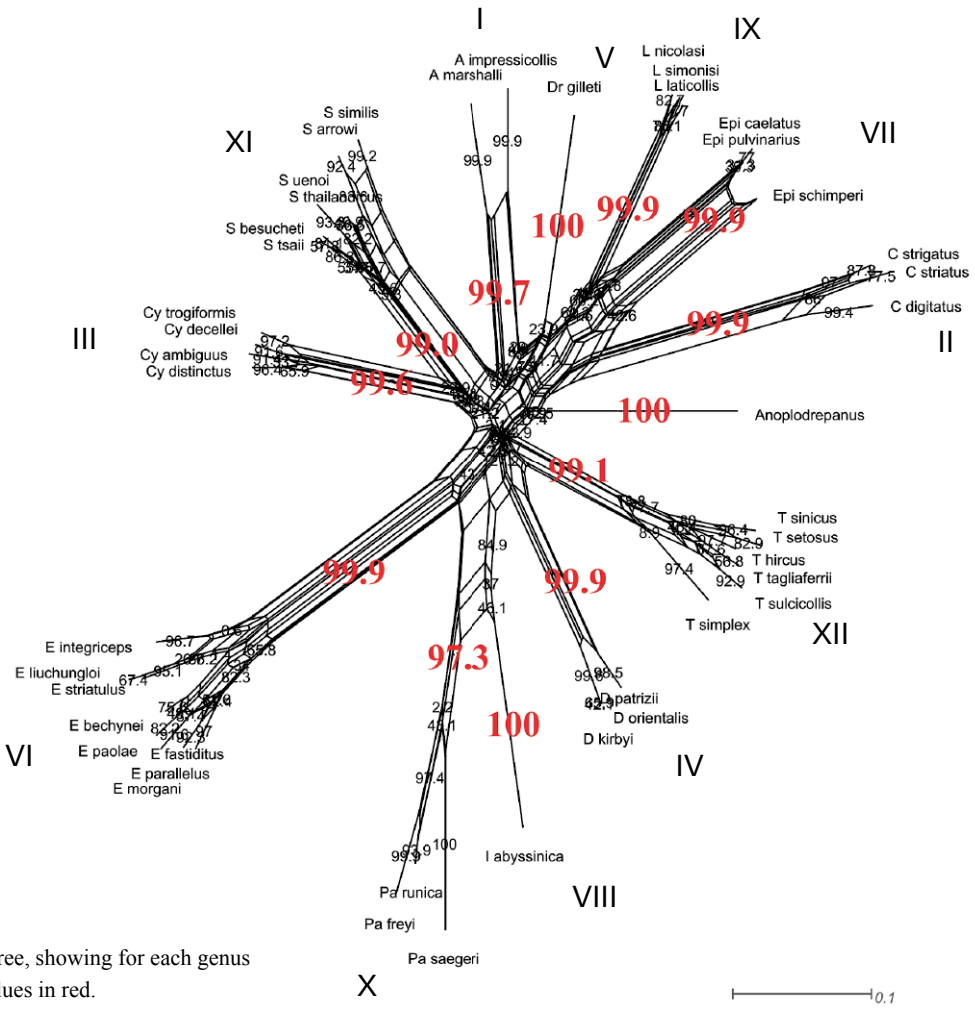

Fig. 5. Splits tree, showing for each genus the support values in red.

relationships were far from resolved, i.e. the nodes were collapsed. The chain swap information for the two runs generated equal results for proportion of successful state exchanges between chains. The resulting statistics of the two runs were studied employing TRACER, and confirmed the correctness of the Bayesian Inference.

The Phylogenetic Networks analysis computed the distances to splits by NeighborNet Equal Angle algorithm, and the resulting network splits tree (Fig. 5) had recomputed fit = 95.02, and LS fit = 99.62. Resampling using the bootstrap method confirmed the genus level groups already evidentiated in the former analyses, with

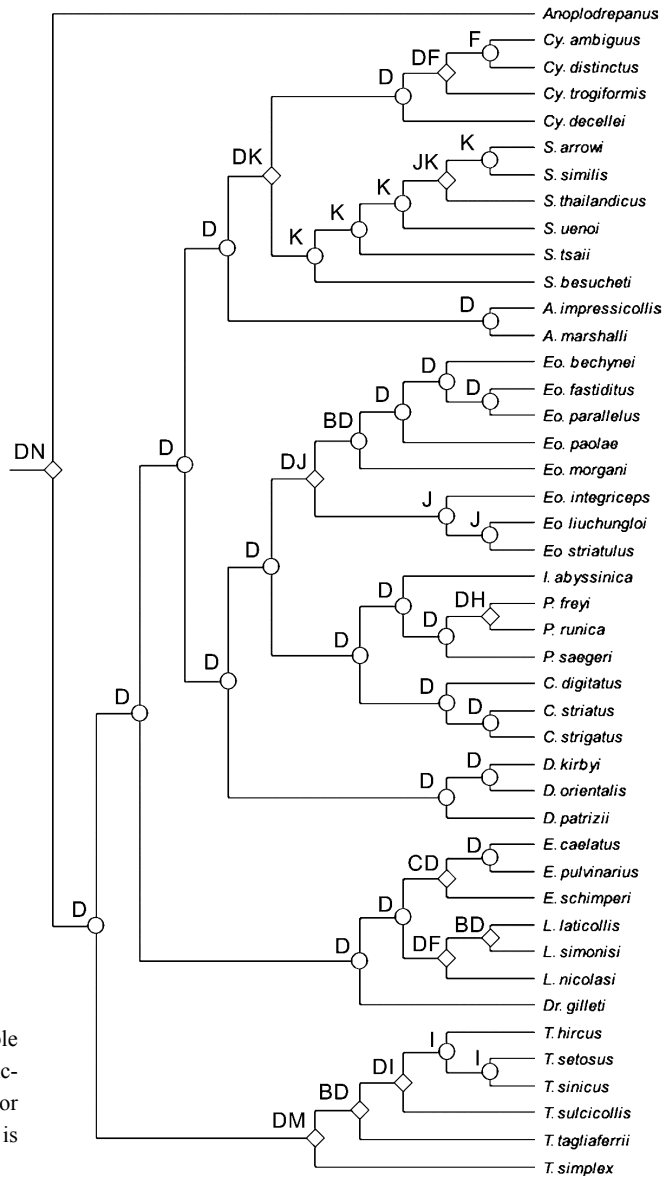

Fig. 6. DIVA optimal reconstruction, in which the most probable ancestral distributions are shown. Where more than one reconstruction is possible, alternative distributions are listed in Table 4. For the number of nodes please see Figure 7. Each vicariant event is marked by a rhomb and each dispersal event by a circle.

the following support values: 97.3 for *Paraixodina*, 99.0 for *Sinodrepanus*, 99.1 for *Tibiodrepanus*, 99.6 for *Cyptochirus*, 99.7 for *Afrodrepanus*, 99.9 for *Clypeodrepanus, Drepanocerus*, *Epidrepanus*, *Latodrepanus* and *Eodrepanus* (and necessarily 100 for the monospecific genera *Drepanoplatynus* and *Ixodina*).

3.2. Biogeographical analysis

The species distributions were listed based on the identified macroareas A–N (Table 1). Most species were found to be distributed in more than one macroarea, and some taxa exhibited a wide geographic distribution, i.e. represented in more than five macroareas from the entire Afrotropical or Oriental regions (but no species occurred in both these regions). Fourteen species were collected from a single area. Three genera (*Eodrepanus*, *Paraixodina*, and *Tibiodrepanus*) were present in both the Afrotropical and Oriental regions, while one genus (*Sinodrepanus*) was recorded only from the Oriental region, and the other genera were recorded only from the Afrotropical region.

Congruent results were gained in the Dispersal-Vicariance Analysis, after analysing the optimizations setting maxareas to different values (14, 4, 3, and 2 areas respectively). The majority of nodes showed invariant ancestral areas, only few nodes giving alternative hypotheses (Table 4). The results of maxareas = 2 (with 97 dispersals required) were chosen, since provided the optimal result based on the "less-ambiguity" criterion. Subsequently, all the possible optimal distributions for the chosen optimal reconstruction on both trees from Parsimony analysis were examined, obtaining almost identical results. Here, the optimal reconstruction is shown for the first tree (Fig. 6).

The reconstruction suggested that the ingroup taxa ancestral distribution was located in macroarea D (i.e.,

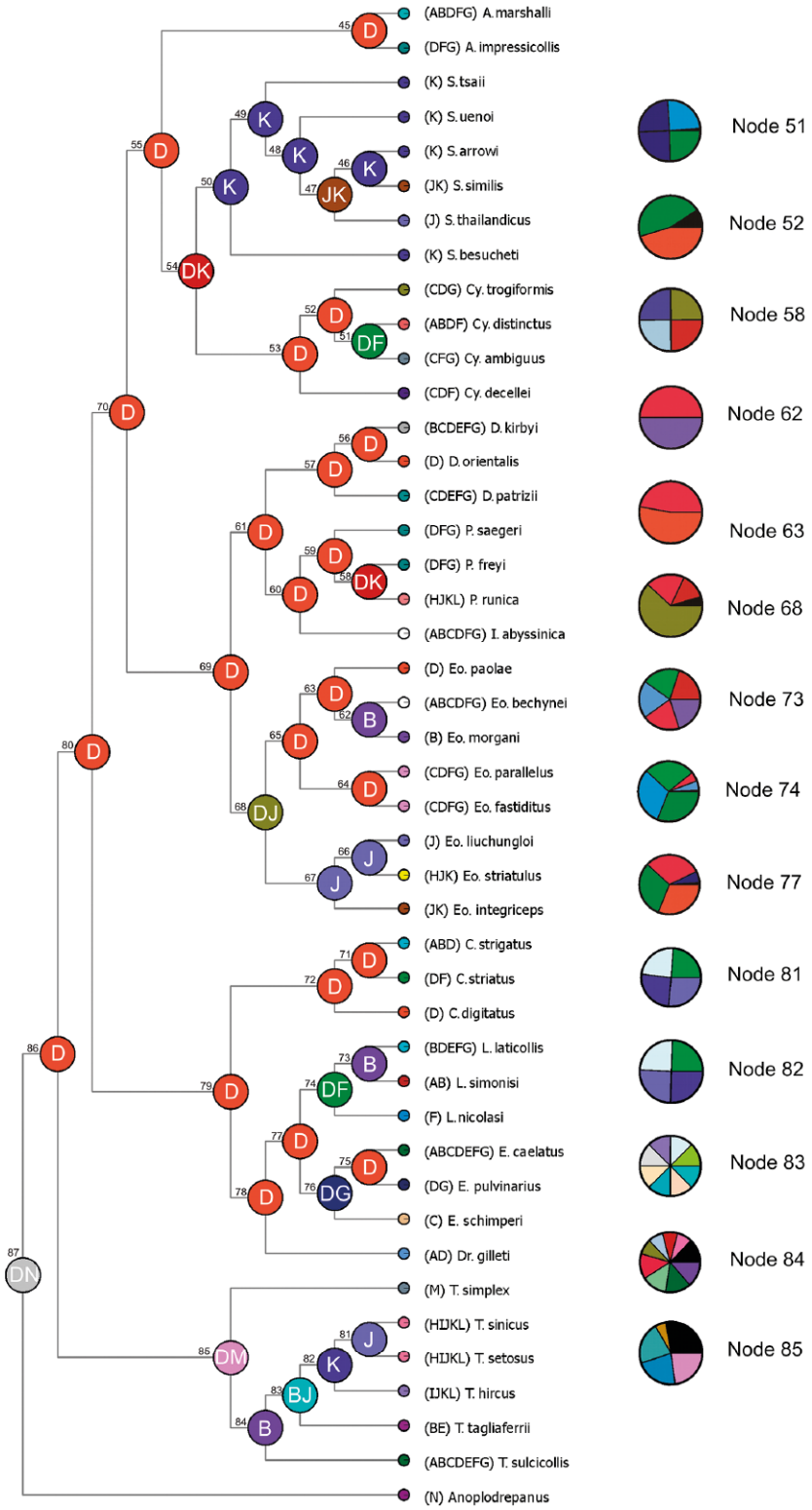

Fig. 7. Graphical results of ancestral optimal distributions at each node of the condensed tree from the trees of Maximum Parsimony and Bayesian Inference analyses (S-DIVA in RASP), showing only the most likely state for each node. The full sets of alternative hypotheses and their relative likelihoods are shown in the pie charts on the right (see also the Table 5, for the detailed list of the equiprobable alternatives).

Central East Africa). On the basis of the proposed reconstruction, the ancestors inhabited Central East Africa and did not initially undergo a dispersal or vicariant event in the Afrotropical region, i.e. several basal dichotomies occurred in D (nodes 86, 80, 79, 78,77, 70, 69 and 56). Although mostly of these nodes are poorly supported in the phylogenetic analysis (Figs. 3, 4), this did not change the result of a basal diversification into genus level taxa

Table 5. Results of the S-DIVA, with the optimal reconstructions percent values for both MP and BI trees together. The nodes marked in grey gave many equiprobable hypotheses.

Node	Node P	Optimal reconstruction
45	P=0.99	D 100.00
46	P=0.99	K 99.87 / JK 0.13
47	P=0.89	JK 100.00
48	P=0.81	K 99.60 / JK 0.40
49	P=0.45	K 100.00
50	P=1.00	K 95.66 / JK 4.34
51	P=0.85	DF 24.66 / DG 24.66 / CD 24.66 / F 24.66 / CF 0.45 / BC 0.45 / AC 0.45 / FG 0.00
52	P=0.64	D 45.38 / DF 45.33 / DG 3.99 / CD 3.99 / FG 0.62 / CF 0.62 / BC 0.04 / AC 0.03
53	P=0.99	D 81.17 / DF 16.28 / CD 1.54 / DG 0.36 / CF 0.27 / FG 0.22 / BC 0.14 / AC 0.01 / BG 0.00
54	P=0.50	DK 95.40 / FK 1.42/ CK 1.40 / DJ 1.08 / GK 0.30 / BK 0.20 / DF 0.13 / FJ 0.02 / CJ 0.02 / AK 0.01 / GJ 0.01 / CD 0.01 / DG 0.00 / BC 0.00
55	P=0.31	D 84.20 / DK 15.08 / DJ 0.49 / FK 0.19 / GK 0.03 / FJ 0.01 / GJ 0.00
56	P=0.98	D 100.00
57	P=0.95	D 100.00 / DF 0.00
58	P=0.90	DK 24.94 / DL 24.94 / DH 24.94 / DJ 24.94 / FJ 0.04 / GJ 0.03 / FL 0.03 / FK 0.03 / FH 0.03 / GL 0.03 / GK 0.03 / GH 0.02
59	P=0.92	D 96.29 / DL 0.93 / DK 0.92 / DJ 0.92 / DH 0.92 / GJ 0.00 / FJ 0.00 / GL 0.00 / FL 0.00 / GK 0.00 / FK 0.00
60	P=0.96	D 98.83 / DL 0.29 / DJ 0.29 / DK 0.29 / DH 0.29 / GJ 0.01 / FJ 0.01 / BG 0.00 / BF 0.00 / BD 0.00 / CJ 0.00 / GL 0.00 / FL 0.00 / CL 0.00
61	P=0.28	D 100.00
62	P=0.32	B 49.99 / BD 49.96 / BG 0.02 / BF 0.01 / BC 0.01
63	P=0.33	D 52.95 / BD 47.05
64	P=0.89	D 100.00
65	P=0.46	D 83.48 / BD 16.52 / BG 0.00 / BF 0.00
66	P=0.96	J 99.23 / JK 0.77
67	P=0.75	J 99.90 / JK 0.10
68	P=1.00	DJ 61.99 / BD 20.00 / DK 13.26 / BJ 3.13 / JK 0.64 / BK 0.32 / GJ 0.21 / FJ 0.21 / CJ 0.21 / AJ 0.01 / DH 0.00 / BG 0.00 / BF 0.00
69	P=0.21	D 97.50 / DJ 2.50
70	P=0.07	D 96.98 / DK 2.07 / DJ 0.96
71	P=0.87	D 100.00
72	P=1.00	D 100.00
73	P=0.76	B 20.02 / BD 20.00 / AD 20.00 / BF 19.99 / AF 19.99 / BG 0.00 / AG 0.00
74	P=1.00	DF 30.99 / F 30.99 / BF 27.25 / BD 5.05 / AD 5.05 / AF 0.65 / FG 0.00 / BG 0.00
75	P=0.64	D 99.69 / BG 0.09 / BD 0.09 / CG 0.06 / CD 0.06 / FG 0.00 / DF 0.00 / AG 0.00
76	P=0.93	CD 99.75 / BC 0.10 / CG 0.10 / BG 0.02 / BD 0.02 / CF 0.00 / AC 0.00 / FG 0.00
77	P=0.80	D 31.09 / DF 30.82 / BD 30.80 / CD 6.29 / AD 0.76 / BC 0.18 / BG 0.07 / FG 0.00 / CF 0.00 / AG 0.00
78	P=0.63	D 97.14 / DF 0.93 / BD 0.93 / CD 0.89 / AD 0.11
79	P=0.31	D 98.67 / DF 0.61 / BD 0.61 / CD 0.08 / AD 0.04
80	P=0.24	D 89.57 / DK 4.86 / DJ 2.69 / BD 2.01 / FK 0.23 / CK 0.22 / JK 0.09 / BK 0.07 / FJ 0.07 / BJ 0.05 / GK 0.05 / CJ 0.05 / GJ 0.02 / AK 0.01 / BG 0.00 / AJ 0.00 / BF 0.00
81	P=0.97	J 26.37 / K 25.71 / L 23.96 / I 23.96
82	P=0.75	K 25.44 / J 25.40 / L 24.58 / I 24.58
83	P=0.39	BJ 12.51 / EJ 12.51 / BK 12.50 / BL 12.50 / BI 12.50 / EL 12.49 / EI 12.49 / EK 12.49
84	P=0.72	B 13.68 / E 13.66 / DE 13.66 / BD 13.66 / DJ 8.11 / DL 8.11 / DK 8.11 / DI 8.11 / EK 1.84 / BK 1.84 / EJ 1.75 / BJ 1.75 / BL 1.12 / EL 1.12 / BI 1.12 / EI 1.12 / FJ 0.18 / GJ 0.18 / CJ 0.18 / AJ 0.18 / FK 0.12 / GK 0.12 / CK 0.11 / AK 0.11 / DH 0.03 / EH 0.02 / BH 0.02 / EF 0.00 / FL 0.00 / FI 0.00 / GL 0.00
85	P=0.93	DM 22.88 / BM 21.94 / EM 21.92 / KM 5.58 / JM 4.78 / LM 3.43 / IM 3.43 / DE 2.87 / BD 2.87 / DL 1.22 / DK 1.22 / DJ 1.22 / DI 1.22 / EJ 0.87 / BJ 0.87 / EK 0.64 / BK 0.64 / BL 0.55 / EL 0.55 / EI 0.55 / BI 0.55 / HM 0.04 / GJ 0.02 / FJ 0.02 / CJ 0.02 / AJ 0.02 / GK 0.01 / FK 0.01 / CK 0.01 / AK 0.01 / DH 0.00 / EH 0.00 / BH 0.00 / FM 0.00 / GM 0.00 / EF 0.00
86	P=1.00	D 75.72 / BD 6.25 / DE 5.86 / DM 3.71 / DJ 3.13 / DK 2.09 / DL 0.93 / DI 0.93 / BJ 0.22 / EJ 0.22 / JM 0.16 / FK 0.11 / CK 0.11 / BK 0.07 / DF 0.07 / JK 0.06 / EK 0.06 / GK 0.06 / EM 0.05 / BM 0.05 / KM 0.04 / FJ 0.02 / CJ 0.02 / GJ 0.01 / DH 0.01 / CD 0.01 / LM 0.00 / IM 0.00 / EL 0.00 / AK 0.00 / BL 0.00 / EI 0.00 / AD 0.00 / BI 0.00 / DG 0.00 / FG 0.00 / CF 0.00 / AB 0.00 / EF 0.00 / CG 0.00 / BG 0.00 / FM 0.00 / HM 0.00 / EG 0.00
87	P=1.00	DN 74.71 / BN 7.17 / EN 6.04 / MN 3.84 / JN 3.74 / KN 2.24 / LN 0.91 / IN 0.91 / FN 0.22 / CN 0.13 / GN 0.07 / HN 0.01 / AN 0.01

taken place in area D. Range extension of taxa was suggested only in terminal nodes via duplications and dispersals, with a large number of Drepanocerina species splitting across a large part of the Afrotropical Region (Fig. 6). Vicariant events were proposed several times for the clade *Cyptochirus* + *Sinodrepanus* (Central East Africa and Southern China vicariance), and again within *Cyptochirus* (Central East Africa and South East Africa), and within *Sinodrepanus* (Indochina and Southern China). In the *Eodrepanu*s clade (Fig. 6) a vicariant event was hypothesized (Central East Africa and Indochina), while a Central West Africa and Central East Africa vicariance was not evidentiated here (although it was enlisted in the RASP analysis, see below). A vicariant event (Central East Africa and Northern India) was also detected for in the clade *P. freyi* + *P. runica* (Fig. 6). For the *Epidrepanus*

clade a vicariant event was proposed (East Africa and Central East Africa), while for *Latodrepanus* clade two vicariant event were shown (Central East Africa and South East Africa, and Central West Africa and Central East Africa). The *Tibiodrepanus* clade was characterised by three vicariance events in the proposed reconstruction (Fig. 6): Central East Africa and Hindu Kush (Eastern Palearctic), Central West Africa and Central East Africa, and Central East Africa and Indochina. It is noteworthy that geographically congruent vicariance events occurred several times independently in Drepanocerina, even in phylogenetically distant clades (Fig. 6). Furthermore the terminal wide distribution is a common but "homoplasious" trait in the various Drepanocerina clades.

The S-DIVA method implemented in RASP was used to construct the possible ancestral ranges of Drepanocerina. In the first analysis (not shown), the two Maximum Parsimony trees were used. The optimal distribution at each node for these trees gave a P value = 1.00 for all nodes with a unique option (100%) for the majority of nodes. In some nodes, alternative hypotheses were suggested, but they were often equiprobable.

The results were compared to those from DIVA, confirming the former results. For nodes 52, 67, 81, 82, 86 and 87 the analysis gave the 25% for each option, for node 68 50% for each option, for node 76 the 20% for each option, for nodes 77, 78 and 85 the 33.33% for each option, for node 83 the 8.33% for each option, and for node 84 23.08% for four options and 7.69% for one option.

The optimal distribution for each node for the trees from Bayesian Inference (not shown here) was similar to the former one, but for most of nodes there were more alternative hypotheses. Also the third analysis (including the trees from both Maximum Parsimony and Bayesian Inference) gave congruent results, with a P value at each node often lower than 1.00 in the reconstruction (Table 5). The macroarea D (Central East Africa) was suggested as possible ancestral range in some of the more basal nodes, confirming the results previously gained using DIVA. Besides, it was noteworthy that for many nodes the ancestral distribution remained uncertain, or at least equally probable (Fig. 7).

3.3. Taxonomy

3.3.1. Genus *Paraixodina* gen. nov.

Type species. *Drepanocerus runicus* Arrow, 1909.

Diagnosis. *Paraixodina* is close to *Ixodina* in the morphological characters, but can be distinguished from it by the presence of 3 longitudinal ridges on the frontovertex in *Paraixodina*. *Ixodina* instead carries two tubercles on the frontovertex. Besides, the epipharynx and the genitalia of both sexes show a very different shape in the two genera, allowing for their easy identification.

Description. Drepanocerina of small or very small size, 2.4–4.5 mm. Head lacking any transverse carinae, vertex bearing a triplet of sublongitudinal ridges. Pronotum bearing three variably modified costae on each side. Scutellum visible. Elytral disc obviously deplanate, V elytral interstria distinctly curved and strongly carinate. Humeral callosities bearing two short longitudinal carinae. Protibiae 4-toothed. Metathoracic episterna not longitudinally depressed and lacking any sharp longitudinal carina. Anterior part of metasternal disc with a longitudinal carina. Abdomen not laterally expanded beyond elytral edges. Abdominal ventrites deplanate, sutures not effaced medially. ***Male genitalia:*** Aedeagus with phallobase relatively slender; parameres curved apically, and carrying small expansions protrunding ventrally; endophallus sclerites partly reduced, with a lamella fairly developed, quadrangular and laminar, the others smaller and less sclerotized. ***Female genitalia:*** Receptaculum seminis tubular, simple; vagina carrying an asymmetrical, semicircular (comma-shaped) sclerotization; the infundibular tube with even diameter along the whole length, sclerotized, only slightly curved around midlenght, and the ends rectilinear. ***Epipharynx:*** Fore margin deeply notched in *P. freyi* and *P. runicus*, sublinear in *P. saegeri*; acropariae and acanthopariae with setae very long and thick, longer in the median part; apophobae long and thin; the anterior epitorma never reaching the fore margin, more or less enlarged and well-sclerotized; chaetopariae linear, reduced and short; crepis poor-developed; proplegmatium scarcely sclerotized, thin; plegmatic area expanded; corypha constituted by some short and thick setae; haptomerum anteriorly with some thick setae, and posteriorly with a pubescence short and thinner.

Distribution. The genus shows a wide distribution both in Afrotropical (Ivory Coast, Democratic Republic of Congo, Kenya, Zambia, Mozambico, and South Africa) and Oriental (North-Central India, Nepal, S China, Myanmar, Thailand, Indochina, Malaysia, and Indonesia) regions.

Etymology. The name refers to closeness of the new genus to *Ixodina*, based on the external features.

Checklist of *Paraixodina* species. *P. freyi* (Janssens, 1953), *P. runica* (Arrow, 1909), *P. saegeri* (Balthasar, 1963).

3.3.2. Genus *Epidrepanus* gen. nov.

Type species. *Oniticellus caelatus* Gerstaecker, 1871.

Diagnosis. *Epidrepanus* is morphologically very close to *Latodrepanus* and *Clypeodrepanus*, but can be easily distinguished from the former by the features of the odd elytral interstriae, which are carinate in *Latodrepanus* but not carinate both in *Epidrepanus* and *Clypeodrepanus*. The main differences between *Epidrepanus* and *Clypeodrepanus* lie in the shape of the scutellum, which is not

visible in *Clypeodrepanus*, and visible in *Epidrepanus*, and in the clypeal apex, which is markedly different (shining brown) from the remaining portion of the head in *Clypeodrepanus*, but indifferentiated in *Epidrepanus*. *Epidrepanus* shows the epipharynx and genitalic structures of both sexes well differentiated from those in other species, thus these structures can be usefully employed in taxon identification.

Description. Drepanocerina of medium size, 3.5–6.0 mm. Head bearing only a transverse carina, entire or medially interrupted, placed between anterior border of eyes and vertex. Pronotum lacking carinae or ridges, only longitudinally depressed at the base. Scutellum minute but distinct. Elytral disc obviously convex, elytral striae not geminate. Odd elytral interstriae neither markedly curved nor strongly carinate, striae wide but not deep, not distinctly punctate. Humeral callosities bearing one short longitudinal carina. Protibiae 4-toothed. Metathoracic episterna bearing a more or less strong, longitudinal carina, parallel to the internal edge. Abdomen not laterally expanded beyond elytral edges. Abdominal ventrites deplanate, sutures not effaced medially. ***Male genitalia:*** Aedeagus with phallobase stout, almost as long as the parameres; parameres subrectilinear, and carrying small expansions protrunding ventrally; endophallus sclerites well-developed and sclerotized, the principal one constituted by various parts slightly arched. ***Female genitalia:*** Receptaculum seminis tubular, carring a thickened collar in proximal part; vagina elongate, wrinkled, with a membranaceous protrusion laterally, and a large, almost circular sclerotization; in the infundibular tube, very tightly C-reversed medial part carrying a large, desclerotized area and a lateral expansion well developed, and rectilinear and elongate distal part toward the receptaculum seminis. ***Epipharynx:*** Fore margin feebly notched; acropariae and acanthopariae with setae long and thick; apophobae short and dense, extended; the anterior epitorma never reaching the fore margin, and carrying a sclerotized expansion in the middle; chaetopariae sinuate, short and thick; crepis not much developed, asymmetrical; proplegmatium tapering toward the external sides; plegmatic area semiovalar and reduced; corypha constituted by few long and thick setae; haptomerum with a well-developed and dense pubescence, constituted by short and thick bristles mixed to thinner setae.

Distribution. The genus shows a wide distribution in the Afrotropical region, from Guinea to Ethiopia eastward and to Cameroon, Democratic Republic of Congo, Malawi and Tanzania southward.

Etymology. The new genus is named after the epipharynx, whose characters allowed to separate *Epidrepanus* from the genus *Latodrepanus*.

Checklist of *Epidrepanus* species. *E. caelatus* (Gerstaecker, 1871), *E. pulvinarius* (Balthasar, 1963), *E. schimperi* (Janssens, 1963).

3.3.3. Genus *Eodrepanus* Barbero, Palestrini & Roggero, 2009

Description of female of *Eo. integriceps* (Janssens, 1953) (Fig. 8A,B)**.** The females of *Eo. integriceps* differ from males in the following characters: Anterior clypeal edge entire but straight, not narrowly produced. Pronotal disc widely depressed. Scutellum evident, long and narrow. Elytral interstriae bearing setigerous punctures. Metasternum and abdomen bearing very wide umbilicate punctures, unevenly serrate. Anterior tibiae shorter and wider than in males, only gently bent inward, outer teeth smaller than in males. Body clothed with long and scattered setae. ***Female genitalia:*** Receptaculum seminis with a rounded and slightly expanded apex (as *Eo. striatulus*), carring a very reduced thickened collar in proximal part; vagina with a large well-sclerotized, asymmetrical and expanded infundibular wall, as the other species of *Eodrepanus* (Barbero et al. 2009a), but furthermore carrying a characteristic U-reverse shaped thickening; the infundibular tube S-reverted, with a small desclerotized area in medial part, and a rectilinear, elongate distal part toward the receptaculum seminis. ***Epipharynx:*** Identical to that of male (Barbero et al. 2009a).

Distribution. *Eodrepanus integriceps* was previously known only from southern China, and the species distribution is now extended to Burma.

Material. BURMA: 2 ♀♀, Shan region, Shan highlands, Mong Hkok, 25–28.VII.2005, ex cattle dung local collectors, purchased from Li Jinke (OUMNH).

3.3.4. Genus *Sinodrepanus* Simonis, 1985

Description of female of *S. similis* Simonis, 1985 (Fig. 8C,D)**.** The females of *S. similis* differ from males in the following characters: Anterior clypeal notch a little narrower and deeper, the teeth bigger. Posterior angle of genae slightly less marked. Anterior tibiae less curved, the three external teeth more developed. Longitudinal inner gibbosities of pronotum obviously less evident. Interstria VI weakly narrower in the apical 4/5. ***Female genitalia:*** Receptaculum seminis with uniform diameter and rounded apex; vagina evenly sclerotized, with a large and symmetrical infundibular wall; the infundibular tube evident and well-sclerotized, with the distal part toward the receptaculum seminis complex, very thick, and very sclerotized, the medial part C-reverted, and the distal part toward ovary elongate and tapering. ***Epipharynx:*** Fore margin slightly notched; acropariae and acanthopariae with setae long and thick; apophobae short and dense, extended; the anterior epitorma well-sclerotized reaching the fore margin; chaetopariae well-developed, sinuate, and dense; crepis asymmetrical, blunt; proplegmatium evident, thick and enlarged on sides; plegmatic area narrow; corypha constituted by few long and thick setae; haptomerum with a dense pubescence, with many short, thick bristles.

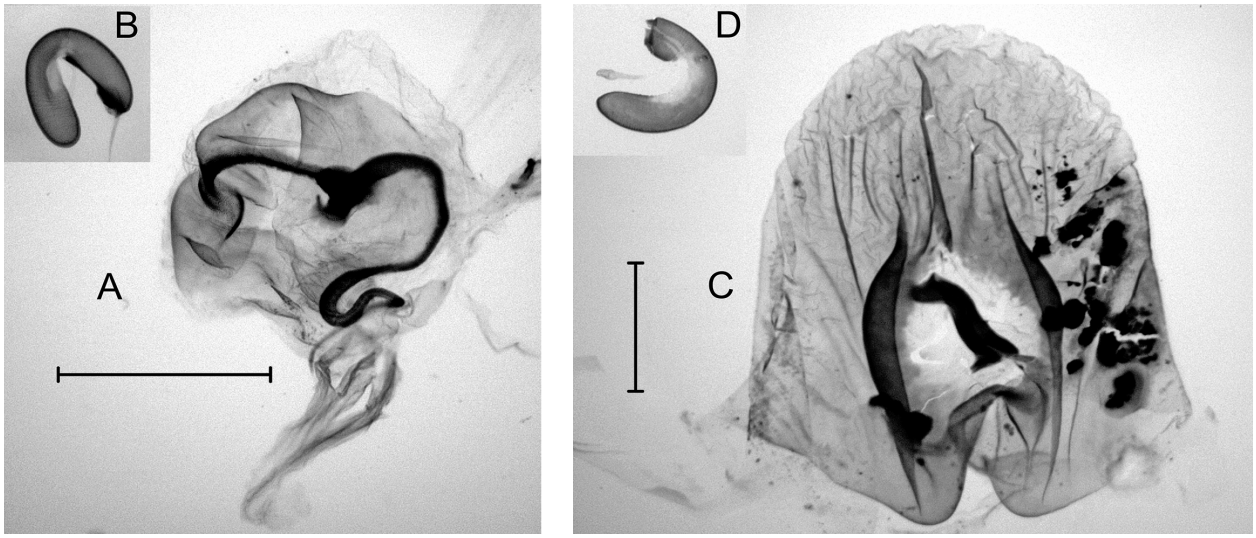

Fig. 8. *Eodrepanus integriceps*, vagina, ventral view with the infundibular wall (**A**) and receptaculum seminis (**B**); *Sinodrepanus similis*, vagina, ventral view with the infundibular wall (**C**) and receptaculum seminis (**D**). Scalebars = 0.5 mm.

Distribution. The species was known only from the type locality in Thailand, thus the distribution is extended to Vietnam and China.

Material. VIETNAM: 1 ♀ Bac Kan prov, Ba Be National Park N 22°24′59.2″ E105°38′02.3″ (OUMNH); **CHINA**: 1 ♀ West Fujian prov, Tongguzhang 1500 m (OUMNH).

4. Discussion

Our study presents the most comprehensive phylogenetic analysis on the Drepanocerina to date, using morphological data, the results then being compared to geographical data. A dataset of 81 morphological characters was used in four approaches, including Maximum Parsimony Analysis, New Technology Search, Bayesian Inference, and Phylogenetic Networks Analysis to infer phylogenetic relationships and reconstruct the biogeographic history of the Drepanocerina. The multiple methodologies gave congruent results. Resampling analyses high values yielded ten well-supported lineages in which twelve genera were identified, thus differing from taxonomy in the recent literature (Krikken 2009). The two new genera were here named *Epidrepanus* gen. nov. and *Paraixodina* gen. nov. The Afrotropical *Epidrepanus* includes three species that were previously but tentatively placed in *Latodrepanus* (Krikken 2009), while the Afrotropical and Oriental *Paraixodina* comprehends three species formerly included in *Ixodina* (Krikken 2009). We considered the statistical support for *Epidrepanus* + *Latodrepanus* insufficient to maintain the two genera together as a unique taxon. The relatively high statistical support for *Ixodina* + *Paraixodina* must be carefully evaluated since four of the *Ixodina* species has been currently excluded from the analysis (see Material & Methods above). Furthermore, with regard to both genus pairs, they showed a very high degree of morphological difference which corresponds to that between the other genera.

The twelve genera identified show well-defined and distinguished features that highlight unique patterns for each taxon in Drepanocerina subtribe (Table 3) by virtue of their peculiar morphology. Furthermore, within each genus the species show marked similarities in the general features of the various anatomical traits here examined. The twelve Drepanocerina genera can be exactly separated by examining the set of morphological characters most diversified in the epipharynx (Fig. 9), since each of them shows unique and well-defined characters in the overall shape, the pubescence (mainly, the chaetopariae and the corypha) and the sclerotized structures (i.e., the tormae). *Latodrepanus* and *Epidrepanus* constitute two distinct taxa on the basis of the very different overall shape of the epipharynx (Fig. 9): in *Latodrepanus* species the epipharynx does not have an incisure on the anterior margin (unique within the subtribe), and carries a corypha with numerous and thick setae (Barbero et al. 2009b), while in *Epidrepanus* the anterior margin is notched, and the corypha consists of few, long setae. Actually, *Epidrepanus* shares with the majority of Drepanocerina genera the characteristic notch on the anterior margin, but this incisure can be more or less deep. In some genera (i.e., *Eodrepanus*, *Paraixodina*, and *Drepanocerus*) the anterior margin shows a very deep notch, albeit variously shaped: widely V-shaped in *Eodrepanus*, tightly V-shaped in *Drepanocerus*, while it is large, rounded, and so deeply incised to reach the plegmatium in *Paraixodina* (Fig. 9).

Furthermore, these three genera can be easily distinguished by the overall shape of the epiphanryx, and also by the various parts forming the epipharynx, which show marked differences. For example, in *Paraixodina* the anterior epitorma is very distinctive, being shaped as

a large, well-sclerotized and short plate; in *Eodrepanus* the anterior epitorma doesn't ever reach the anterior margin, but carries a thick, evident transversal sclerotization at base. Lastly, in *Drepanocerus* the anterior epitorma is well-sclerotized, and reaches the anterior margin, as is the majority of Drepanocerina genera. *Ixodina* also shows a peculiar anterior epitorma that is well-developed anteriorly, but characteristically never reaches the plegmatic area posteriorly. The medial sclerotized area is well-differentiated across the genera, being A-shaped in *Clypeodrepanus*, *Drepanocerus* and *Epidrepanus*, while it is widely arched in *Sinodrepanus*, *Cyptochirus* and *Tibiodrepanus*. Also the absence (as in *Clypeodrepanus*) or the presence (as in *Eodrepanus*, *Latodrepanus*, *Sinodrepanus* and *Tibiodrepanus*) of the variously-shaped apotormae contribute to a clear characterization of the genera (Fig. 9).

The genitalia of both sexes (not shown here, but see appendix with the matrix characters list) allow to point out well-defined patterns of the various genera as well. In *Cyptochirus* the endophallus lamellae are large, well-sclerotized plates, which are clearly differentiated at the specific level; in this genus the parameres of the aedeagus carry a short and large lamina inward folded. The parameres are instead hook-shaped, and more or less elongate in *Sinodrepanus* as well as in *Tibiodrepanus*. Besides, the two genera are easily separated by the very different overall shape of the parameres that are shorter and enlarged in the ventral part in *Tibiodrepanus*, and more elongate in *Sinodrepanus*. Also *Eodrepanus* shows a characteristic hook-shaped expansion on the apex of parameres, but the general features of aedeagus are so markedly differentiated that a common evolutionary pattern could never be hypothesized for these genera. Unlike what was observed in most of the genera, in *Sinodrepanus* the lamellae of endophallus are numerous, well-sclerotized, and extremely complicated. Also in *Eodrepanus* (Barbero et al. 2009a) the endophallus lamellae are very characteristic, and very different from the *Sinodrepanus* ones, being constituted by a trifurcate single lamella that cannot be found in any other Drepanocerina genus.

Drepanocerus aedeagus has short and thick parameres, carrying a large, folded lamina anteriorly, and in the endophallus a large, subrectangular lamella and some accessory lamellae are found. Also the *Ixodina* aedeagus is very peculiar, with unarmed parameres, and elongate apex, while the endophallus lamella is saddle-shaped, and similar to those found in *Clypeodrepanus* and *Paraixodina*. Besides, the aedeagus of *Paraixodina* is very different from that of *Ixodina*, and shows noticeable protrusions on the parameres, while the endophallus lamellae are almost inapparent, constituted by few, simple and poorly sclerotized laminar expansions. Simple lamellae, but more sclerotized, are found also *Clypeodrepanus*. *Latodrepanus* has a very characteristic aedeagus, carrying unarmed, subrectangular and elongate parameres, and a fan-shaped endophallus lamella (Barbero et al. 2011). In *Epidrepanus* the parameres are more expanded ventrally, carriyng a short hook apically. Also the endophallus is very different from *Latodrepanus*, with more lamellae to form a complex three-dimensional structure.

In *Cyptochirus* the elongate vagina has an inverted U-shaped sclerotization on the infundibular wall, as it is found in many other Drepanocerina genera. Despite the superficial similarities, the sclerotization has distinctive features in each genus: symmetrical and rather elongate in *Cyptochirus*, asymmetrical, short and large in *Tibiodrepanus*, elongate and thick in *Clypodrepanus*, symmetrical, large and squared in *Ixodina*. The vagina of *Paraixodina* instead show a poor-sclerotized, asymmetrical comma-shaped (larger on right) sclerotization, markedly different from the symmetrical U-shaped sclerotization of the *Ixodina* species. The sclerotization of the infundibular wall is symmetrical, rounded and evident in *Sinodrepanus*, greatly asymmetrical, and characteristically more expanded on left in *Eodrepanus*. Although in some genera the infundibular wall sclerotization is almost inapparent, morphological patterns nevertheless can be identified, since also the infundibulum shows well-defined characters. In *Drepanocerus* the infundibulum shows a well sclerotized and plurisinuate distal part toward the ovarium. Sometimes, as in *Latodrepanus* species, the infundibular wall is very enlarged, rounded and well-sclerotized. Conversely, *Epidrepanus* shows a less sclerotized area on the infundibular wall, narrower and elongate, with a peculiar incisure in basal part.

The twelve genera can be clearly separated also by the external features, mainly the pronotum, the elytra and the body ventral side. While *Paraixodina* has a marginate base of the pronotum, all the other genera are characterised by the pronotal base not marginate. Besides, also the elytra allow to distinguish the Drepanocerina genera on the basis of several characters. The genus *Epidrepanus* is the only one with the third elytral interstria bearing protuberance or tubercles, while the other genera do not have whatsoever protuberance or tubercles. Furthermore, *Epidrepanus* is clearly distinguishable from *Latodrepanus*, since the scutellum is visible only in the first genus and the omeral callosities bears one short carina in *Epidrepanus*, and two carinae in *Latodrepanus.* The elytral striae geminate, and the elytral epipleuron emarginate at humerus can separate *Eodrepanus* from all the other genera.

Although both *Tibiodrepanus* and *Sinodrepanus* bear in the elytra a posthumeral depression followed by a parepipleural ridge, they are so markedly different that cannot be considered phylogenetically close.

The metasternum and abdominal segments show distinct patterns in the twelve lineages: on the anterior part of metasternal disc a longitudinal carina is visible in *Paraixodina*, and absent in *Ixodina*; in the central-posterior part of metasternal disc a longitudinal groove is present medially in *Paraixodina* and *Epidrepanu*s, and absent in *Ixodina* and *Latodrepanus*. Only the genus *Eodrepanus* is characterised by the abdominal segments fused medially, while the other genera have distinct abdominal segments with clearly visible sutures. *Afrodrepanus* has abdominal segments transversally carinate, while the other genera do not have any carina on abdominal segments.

To date, the subtribe Drepanocerina is characterised by a wide distribution, which covers the Afrotropical and Oriental regions, and marginally reaches the Palaearctic region. A close examination of each species distribution related to area climatic characteristics allowed to identify 14 macroareas representative of the full distributional range in Drepanocerina.

The integration of morphological characters and geographical data analysed using the Dispersal-Vicariance Analysis method resulted in a viable biogeographic hypothesis for Drepanocerina, in which Central East Africa (macroarea D, Fig. 2) was the ancestral range of the subtribe. The ancestral Drepanocerine lines migrated from Central East Africa (D) throughout the Afrotropical Region, without a well-defined trend, although two main diverging dispersal routes were identified: B (West) and F (South). Migration to the Oriental region (macroareas H – L) occurred independently at least four times in four distinct lineages, due to vicariance events. The present-day Palearctic distribution (macroarea M) is geographically marginal and immediately neighbouring the Oriental Region, and it supports a single species, *Tibiodrepanus simplex* (Barbero et al. 2011).

However, it is likely that in the past the subtribe Drepanocerina was more widely distributed in the Palaearctic, with other species colonising the region when paleoclimatic conditions were more favourable, as evidenced by the extinct *Eo. coopei* from Eemian England deposits (Barbero et al. 2009a).

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7. Appendix

List of the morphological characters used in phylogenetic analysis (matrix in Table 2).

Epipharynx (Figs. 1, 9)

The epipharynx is an extremely complex structure placed in the inferior part of the clypeus, and is divided into a sclerotized, mostly basal part and a membranous part. The tormae are the supporting sclerotized parts, and are conventionally considered a single, internal region. The epipharynx whole surface is usually divided in four main regions (i.e. the pariae, the pedia, the haptolachus, and the haptomerum). Each region is further divided in various subregions. Here, the most noteworthy were marked on Fig. 1. According to the literature (see Barbero et al. 2003 for further details) they can be defined as follows: 1) the acropariae (Ac) are the antero-marginal pariae subregions carrying usually long setae, and correspond to the anterior margin of the epipharynx; 2) the corypha (Co) is the medial antero-apical haptomerum subregion constituted usually by some large and thick setae; 3) the chaetopariae (Ch) are the internal pariae subregions with thick setae forming a single row from the fore margin to the tormae; 4) the anterior epitorma (Ae) is the medial, thick-sclerotized subregion of the tormae extending from the base of epipharynx till the fore margin; the apotormae (Ap) are the latero-anterior, usually tapering, subregions of the tormae; 5) the proplegmatium (Pr) is a thickened pliciform subregion of the tormae extending transversely along the entire surface; the plegmatic area (Ph) is an area circumscribed by the joining tormae in the basal part of epipharynx; 6) the crepis (Cr) is the basal, well sclerotized, usually asymmetrical, haptolachus subregion; 7) laeotorma (La) and dexiotorma (De) are the two transversal, basal, respectively left and right, tormae subregions.

1. Epipharynx, on the whole the anterior part: (0) squared; (1) cordiform, with the fore margin clearly arched; (2) subtrapezoidal; (3) crescent-shaped, rounded.

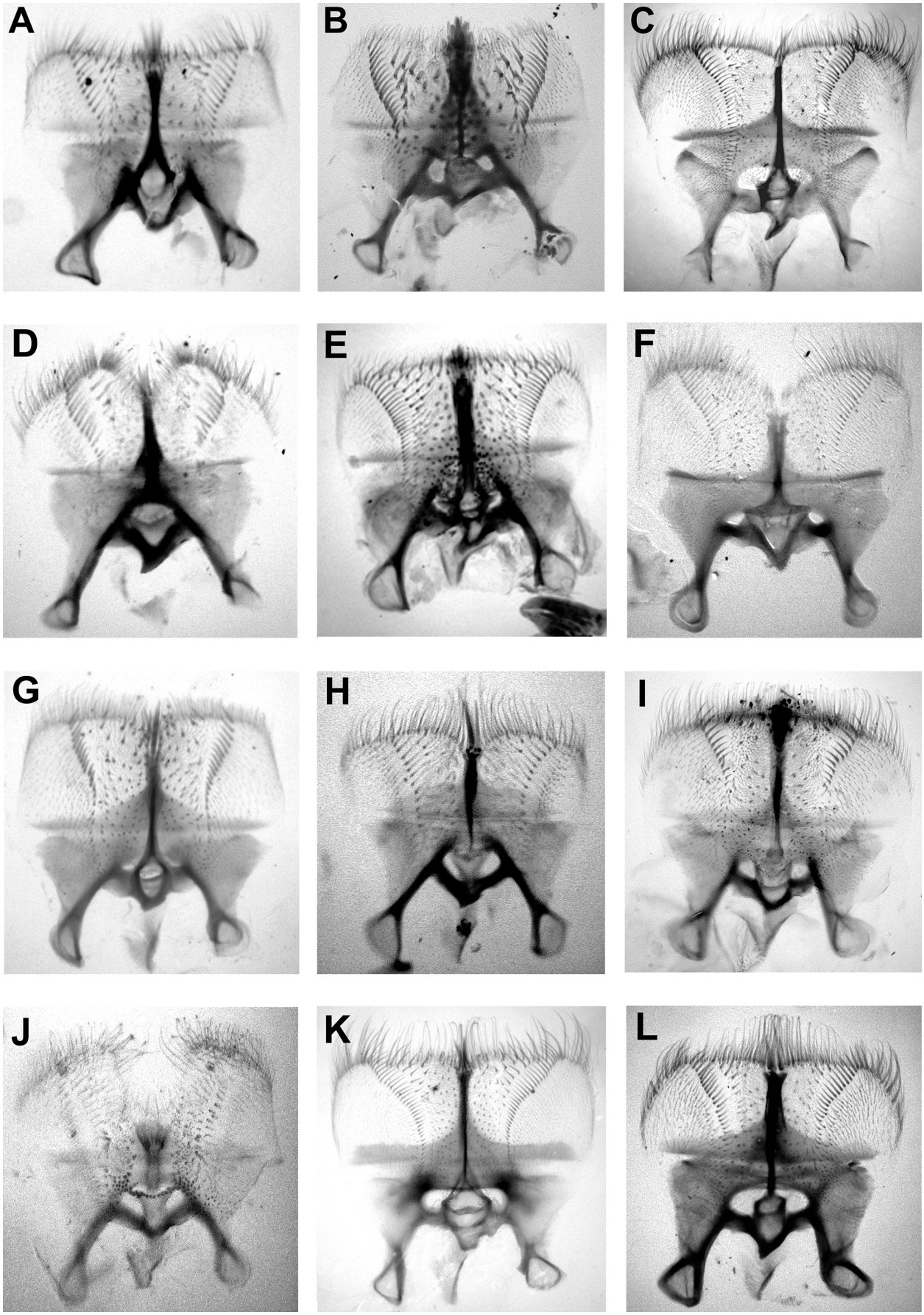

Fig. 9. Epipharynx. **A**: *Afrodrepanus marshalli*; **B**: *Clypeodrepanus digitatus*; **C**: *Cyptochirus distinctus*; **D**: *Drepanocerus kirbyi*; **E**: *Drepanoplatinus gilleti*; **F**: *Eodrepanus fastiditus*; **G**: *Epidrepanus pulvinarius*; **H**: *Ixodina abyssinica*; **I**: *Latodrepanus nicolasi*; **J**: *Paraixodina freyi*; **K**: *Sinodrepanus besucheti*; **L**: *Tibiodrepanus tagliaferrii*.

2. Epipharynx, length/width ratio: (0) > 0.75 and < 0.9; (1) > 0.9; (2) > 0.65 and < 0.75; (3) < 0.65.
3. Epipharynx fore margin (Fig. 9): (0) only slighly notched in the middle; (1) linear or convex; (2) deeply V-notched, the notch narrow; (3) largely but often not-deeply notched, sometimes the notch extending till the chaetopariae; (4) barely sinuate in the middle; (5) largely concave.
4. Acropariae: (0) setae longer on sides, slightly shorter towards the midline, where the setae are again long; (1) setae longer on sides and shorter to midline; (2) setae shorter on sides and longer on midline; (3) setae evenly long.
5. Chaetopariae on the whole: (0) well-developed; (1) vestigial.
6. Chaetopariae, setae: (0) dense; (1) scattered; (2) almost inapparent.
7. Chaetopariae: (0) rectilinear or only slightly arched; (1) arched, usually at 1/2 lenght; (2) angulate at half of lenght; (3) more or less bisinuate.
8. Corypha: (0) constituted by few conspicuous long setae; (1) absent, with a row of short and thin setae from the apex of anterior epitorma to epipharynx fore edge; (2) constituted by many long and thick setae; (3) reduced, constituted by few short and thick setae.
9. Anterior epitorma: (0) extending till the fore margin of the epipharynx; (1) never reaching the fore margin of epipharynx.
10. Anterior epitorma, at the base: (0) reaching the crepis; (1) not reaching the crepis.
11. Anterior epitorma: (0) thin or very thin, almost filiform; (1) thicker, as wide as half of the corypha; (2) very thick, almost as wide as the corypha.
12. Anterior epitorma, on the whole: (0) rod-like, of equal width along the whole length till the base; (1) slightly widening toward the base starting at least by 2/3 of the length; (2) widening to base at less than 1/3 of the length; (3) largely expanded only at 1/5 of the lenght; (4) expanded along the entire length.
13. Anterior epitorma, at apex: (0) simple, rectilinear; (1) enlarged, triangular-shaped; (2) enlarged, rounded; (3) enlarged, rhomboid.
14. Anterior epitorma at base: (0) expanding in a globose area; (1) progressively widening in a triangular-shaped area; (2) carrying a thick rectilinear expansion; (3) rectilinear.
15. Apotormae: (0) triangular shaped, well-developed, thick; (1) triangular-shaped, reduced, thinner; (2) filiform to apex, pointing laterally; (3) not present.
16. Proplegmatium, position: (0) along the midline from anterior margin to crepis; (1) in the hind part; (2) in the fore part of the epypharynx.
17. Proplegmatium, the triangular area reaching up to: (0) half the length of the anterior epitorma; (1) the apex of the anterior epitorma; (2) less than one third of the length of the anterior epitorma; (3) only the basal fifth of anterior epitorma.
18. Proplegmatium, on sides: (0) closely joined to the whole basal sclerotization; (1) with a sclerotized connection in medial half part; (2) joined only in the central third.
19. Proplegmatium: (0) tapering to sides; (1) widened only on sides; (2) truncated at sides, sometimes enlarged.
20. Plegmatic area: (0) reduced, narrow and lowered, inner sclerotized structure absent; (1) present, broad, well-developed, subquadrangular, inner sclerotized structure absent; (2) ovalar, with a biconvex sclerotized structure in the middle; (3) semilunar, small, inner sclerotized structure absent; (4) absent or greatly reduced, inner sclerotized structure absent; (5) present, almond-shaped, with a largely triangular-shaped inner sclerotized structure.
21. Plegmatic area forming: (0) 2 small openings; (1) a single opening; (2) no opening.
22. Crepis, on the whole: (0) evident, well-developed; (1) evident, but less developed; (2) vestigial, inapparent.
23. Laeotorma and dexiotorma joining tract (the pternotormae): (0) rectilinear; (1) down-turned; (2) upturned.
24. Laeotorma and dexiotorma joining sclerotized tract: (0) short; (1) elongate.

Head

25. Clypeal apex: (0) without a shining brown band; (1) with a shining brown band, clearly distinguishable.
26. Frontoclypeal area: (0) with longitudinal carinae not mutually in touch (can be expanded into horns); (1) with carinae contacting each other (thus forming cells); (2) without carinae.
27. Clypeofrontal transition in males: (0) without median protrusion; (1) with median protrusion.
28. Frontovertex in males: (0) with single transverse rcarinae; (1) unarmed; (2) wth a pair of longitudinal carinae; (3) carinae forming cells.
29. Clypeo-genal junction: (0) very feebly or not notched; (1) strongly notched.

Pronotum

30. Pronotum: (0) without carinae; (1) only with longitudinal carinae; (2) with symmetric pattern of ridged depressed cells.
31. Pronotal base: (0) not marginate; (1) marginate.
32. Pronotal basal medial angle: (0) scarcely marked or inapparent; (1) well marked.

Elytra

33. Elytral striae: (0) not geminate; (1) geminate.
34. Elytral base: (0) not carinate; (1) carinate.
35. Elytral disc concavity: (0) absent; (1) present, and subrectangular; (2) present, narrowed posteriorly.
36. Humeral callosities bearing: (0) no carina; (1) one short carina; (2) two short carinae.
37. Carina of third elytral interstria: (0) absent; (1) only a proximal tubercle is present; (2) present but not extending until the apex; (3) extending from base to apex.

38. Elytral interstriae: (0) I–III and V entirely or partly convex but never sharply carinate; (1) I–III and V neither carinate nor strongly convex; (2) III and V with sharp uninterrupted carina; (3) V with sharp uninterrupted carina.
39. Tuft of long setae on elytral apices: (0) absent; (1) present.
40. Elytral epipleuron at humerus: (0) not emarginate; (1) emarginate.
41. Posthumeral depression: (0) absent; (1) present (in front of parepipleural ridge).

Abdomen

42. Abdominal sides: (0) covered by elytra; (1) not covered by elytra.
43. Abdominal ventrites: (0) not transversely raised nor ridged; (1) transversely raised or ridged.
44. Sutures between abdominal ventrites: (0) not effaced medially; (1) effaced medially.
45. Ranges of very thick setae on abdominal ventrites: (0) only in lateral parts; (1) on all parts.
46. Metasternal disc: (0) evenly smooth; (1) evenly punctuate; (2) punctuate with smooth longitudinal median area.
47. Metasternal disc anteriorly: (0) not carinate; (1) carinate.
48. Metasternal disc: (0) with median longitudinal sulcus; (1) without median longitudinal sulcus.
49. Number of foveae on posterior part of metasternal disc: (0) one; (1) none; (2) two.
50. Metepisternum: (0) without sharp longitudinal fold; (1) with sharp longitudinal fold.

Legs

51. Basal inner margin of fore tibia: (0) without a tooth; (1) with a small tooth.
52. Male protibia: (0) anterior rim of the last tooth forming a right angle with the tibial axis never collinear with the last external denticle; (1) anterior rim of the last tooth forming an acute angle with the tibial axis collinear with the 3rd external denticle; (2) anterior rim of the last tooth forming an obtuse angle with the tibial axis.
53. Metatibial spur: (0) as long as 3/4 of the first tarsomere; (1) equal or subequal to the first tarsomere.
54. Pubescence of the upper surface: (0) never scaly; (1) scaly.

Female genitalia (Figs. 10, 11)

55. Receptaculum seminis: (0) bulging, larger at apex than at base; (1) evenly uniform, gently rounded but never expanded at apex; (2) tapering to apex, that is pointed.
56. Receptaculum seminis, proximal part (from the insertion of ductus receptaculi to the desclerotized area of glandula receptaculi, that is the medial part): (0) shorter than the distal part; (1) longer than the distal part; (2) equal to distal part.
57. Vagina, on the whole: (0) equal length and width; (1) elongate.
58. Apex of vagina: (0) wrinkled; (1) simple folded.
59. Vagina, infundibular wall: (0) large; (1) small.
60. Infundibular area: (0) well-sclerotized, evident; (1) less sclerotized and less marked; (2) not sclerotized, almost inapparent.
61. Infundibular wall: (0) symmetrical; (1) asymmetrical, more expanded to the right; (2) asymmetrical, with a triangular, expanded part to the left.
62. Infundibulum, sclerotized part: (0) U-reverted shaped thick [till forming a ring]; (1) U-reverted narrow; (2) rounded; (3) semioval, with a large rounded notch in the basal part; (4) subtrapezoidal, with the smaller base distal, and the central part desclerotized; (5) inverted comma-shaped, the more expanded part to the right.
63. Well sclerotized, bilobed portion at the base of the infundibular wall: (0) absent; (1) present.
64. Vagina, lateral folds: (0) absent, (1) present, but asymmetrical and poorly defined; (2) symmetric and evident.
65. Infundibular tube, distal portion: (0) rectilinear; (1) upward turned.
66. Infundibular tube, distal portion: (0) expanded, tapering toward the receptaculunm seminis; (1) tubular; (2) a sleeve only slightly thickened; (3) bilobed and greatly sclerotized.
67. Infundibular tube, distal portion connected to receptaculum seminis: (0) elongate; (1) short.
68. Infundibular tube, the central portion connected to vagina: (0) reversed-S shaped with loose loops; (1) reversed-S shaped with tight loops; (2) only slightly sinuate, often subrectilinear; (3) reversed-C shaped.
69. Infundibular tube, in the median part: (0) evenly well sclerotized; (1) desclerotized.
70. Infundibular tube, the central portion: (0) simple, tubular; (1) evenly expanded, but never carrying a lateral protrusion; (2) evenly expanded, carrying an expansion to right; (3) extremely expanded, saccular, decreases sharply at the beginning of the distal tube to the ovary.

Male genitalia (Fig. 12)

71. Phallobase: (0) elongate, longer than twice the parameres; (1) intermediate, as long as twice the parameres; (2) shorter than twice the parameres.
72. Parameres, on the whole: (0) curved, tapering to apex; (1) subrectilinear, in general subquadrangular.
73. Parameres, basal expansion: (0) absent; (1) present, simple and rounded, but enlarged basally; (2) present, triangular, large, pointed at apex; (3) present, bifid.
74. Parameres, medial expansion: (0) laminar, large at base, rounded apically; (1) finger-like, narrow well-developed; (2) triangular-shaped, well-developed, often sharp; (3) absent.
75. Endophallus lamellae, on the whole: (0) well developed, variously shaped; (1) less developed; (2) vestigial.
76. Lamellae, principal sclerite: (0) well developed, and sclerotized; (1) less developed, often little scle-

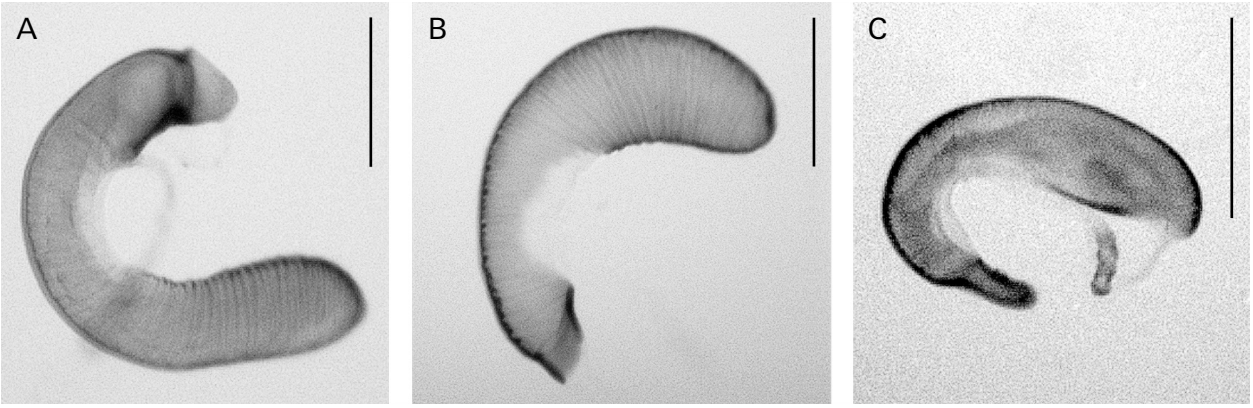

Fig. 10. Receptaculum seminis. **A**: *Epidrepanus caelatus*; **B**: *Latodrepanus laticollis*; **C**: *Ixodina abyssinica*. Scalebars = 0.1 mm.

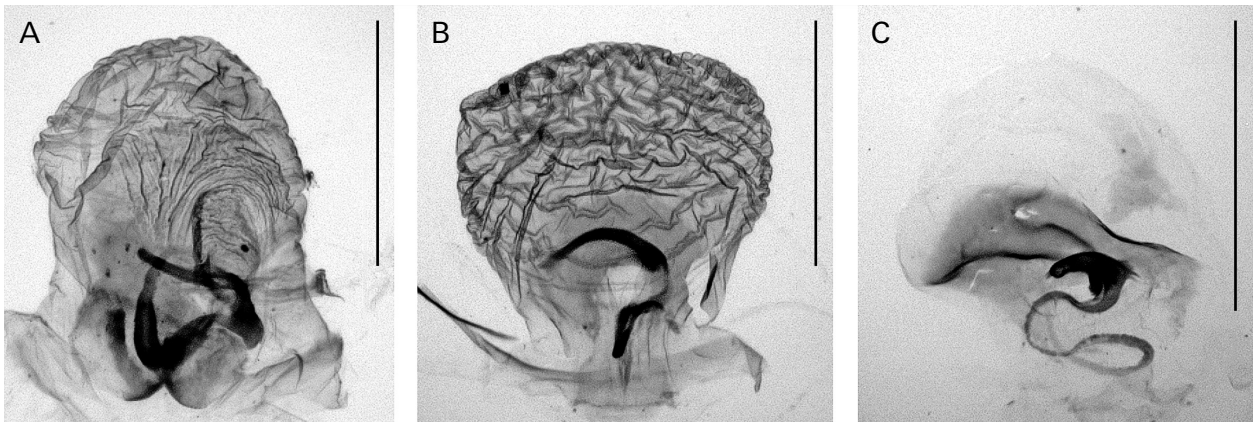

Fig. 11. Vagina, ventral view with the infundibular wall. **A**: *Epidrepanus caelatus*; **B**: *Afrodrepanus impressicollis*; **C**: *Eodrepanus parallelus*. Scalebars = 0.5 mm.

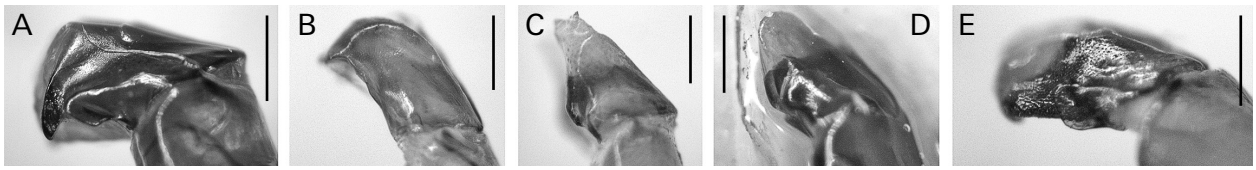

Fig. 12. Aedeagus, parameres. **A**: *Sinodrepanus arrowi*; **B**: *Eodrepanus fastiditus*; **C**: *Drepanocerus kirbyi*; **D**: *Ixodina abyssinicus*; **E**: *Clypeodrepanus strigatus*. Scalebar (A) = 0.5 mm; scalebars (B–E) = 0.2 mm.

rotized; (2) greatly reduced, very little sclerotized, almost inapparent.

77. Lamellae, principal sclerite consists of: (0) several parts, more or less equivalent; (1) several parts, but with a prevalent lamella, the other reduced, (2) a single lamella, variously shaped.
78. The principal sclerite (single), or the more developed lamella is constituted by: (0) a plate (or some plates) simple, laminar, and large; (1) a semicircular plate with a perpendicular C-shaped expansion at one side, and two smaller plates; (2) two plates, a subpyramidal one, and a subrectangular one with folded apical laminae of one apex; (3) a subrectangular, laminar plate small but evident, with folded margins, and two smaller plates sometimes reduced and almost inapparent; (4) trifurcate lamella with short apices; (5) trifurcate lamella with sharp, elongate parts; (6) three rectangular and flat plates, one carrying a filiform expansion in basal part; (7) greatly complex plates, constituted by various well-developed parts.
79. Lamellae, secondary sclerites: (0) well developed and sclerotized; (1) medium development, less sclerotized than the principal lamellae; (2) vestigial and poorly sclerotized.
80. Lamella greatly modified, very sclerotized, large and hook-shaped: (0) absent; (1) present.
81. Raspula: (0) present, well-developed but not markedly sclerotized, more or less extended; (1) very pronounced, and extended over the wall of endophallus; (2) reduced.