Systematics and phylogeny of Eodrepanus, a new Drepanocerine genus, with comments on biogeographical data (Coleoptera: Scarabaeidae: Oniticellini)

DOI:10.1080/002229309030165 90

Journal of Natural History, 43(29), 2009, ***DOI:*** 10.1080/00222930903016590

Systematics and phylogeny of *Eodrepanus*, a new Drepanocerine genus, with comments on biogeographical data (Coleoptera: Scarabaeidae: Oniticellini)

ENRICO BARBERO, CLAUDIA PALESTRINI and ANGELA ROGGERO

Department of Biologia Animale e dell'Uomo. Via Accademia Albertina 13. I-10123, Torino, Italy *(Authors names in alphabetical order)*

Correspondence: Angela Roggero, Dpt. Biologia Animale e dell'uomo, Via Accademia Albertina 13, I-10123 Torino, Italy. Phone: +39 011 670 4536, Fax + 39 011 670 4508, E-mail: angela.roggero@unito.it.

Abstract. We described here *Eodrepanus* **gen. n.**, currently comprising nine species, six previously assigned to the genus *Drepanocerus* and three described as new (namely, *E. morgani* **sp. n.**, *E. paolae* **sp. n.** and *E. coopei* **sp. n.**). Two of the new species have an afrotropical distribution, whilst the latter is an Eemian fossil species from England. Maximum Parsimony was used to analyze reciprocal relationships among the species of *Eodrepanus* **gen. n.,** and four of the 24 species remaining in *Drepanocerus*. Support for these phylogenies was evaluated using the Bootstrap method and Bayesian Inference as implemented in MrBayes. The biogeography of *Eodrepanus* **gen. n.** was analyzed using several different methods, viz. Analysis of Similarity (Ochiai Index). Dispersal-Vicariance Analysis (DIVA) and Parsimony Analysis of Endemicity (PAE).

Key words. New genus, new species, new combination, Eemian fossil species, phylogeny, biogeography

Running title: Phylogeny and biogeography of *Eodrepanus* gen. n.

Word count: 14093

Introduction

In 1828 Kirby established the genus *Drepanocerus* for the species *D. kirbyi*, based on specimens from the Cape of Good Hope. In the following decades (Table 1), eight new entities were described from both Afrotropical and Indomalayan Regions (*D. laticollis* Fåhraeus, *D. caelatus* Gerstaecker, *D. abyssinicus* Roth, *D. sinicus* Harold, *D. sulcicollis* Castelnau, *D. parallelus* Raffray, *D. fastiditus* Peringuey, and *D. impressicollis* Boheman). Lesne (1900) established the genus *Cyptochirus* (in Drepanocerina subtribe) for a single species, *C. ambiguus*, previously attributed to the genus *Oniticellus* Serville. Nevertheless, some later authors (d'Orbigny 1916, Arrow 1931) regarded the Lesne genus as a synonym of *Drepanocerus*. Gillet (1911) assigned two Indomalayan species (*D. hircus* and *D. setosus*) formerly described as *Copris* by Wiedemann (1823) to *Drepanocerus*. Boucomont (1921) then added two new afrotropical species (*D. marshalli* and *D. striatus*) and, together with Gillet, in 1927 assigned to *Cyptochirus* six species, including also *D. patrizii* (Boucomont 1923). Janssens (1953) provided the overall work devoted to *Drepanocerus* genus, considering 26 species (including those ascribed to the genus *Cyptochirus*) and providing the identification keys for the species. Nine further species were then described in the following years (Balthasar 1963a, 1963b, Kryzhanovsky and Medvedev 1966, Endrödi 1971, 1976, Biswas 1979, Kabakov 2006).

Then, Simonis and Zunino (1980) re-established the genus *Cyptochirus* (comprising four species), and later Simonis (1985a) described *Sinodrepanus* for six indomalayan species, three of which were previously placed in the former genus. Simonis (1985b) also pointed out the evident lack of homogeneity within *Drepanocerus*, and identified some well-differentiated groups of species. Moreover, in the original description of *D.*

parallelus, Raffray (1877) noted the ambiguity of this species, and placed it only tentatively in *Drepanocerus*.

Currently, thirty species (Table 1) are assigned to *Drepanocerus*, whose distribution extends widely from the Afrotropical Region to the Eastern Palearctic and Indomalayan Regions.

We examined the whole genus using the characters traditionally employed in the systematics of Scarabaeoidea. The results showed a high degree of heterogeneity within the genus that explains the difficulties of previous authors in ascribing species to *Drepanocerus*. Subsequent analyses suggested that the genus might not be monophyletic and confirmed the previous hypothesis: within this heterogeneous genus we could recognize several distinct sets of species.

The aim of the present work is to discuss the taxonomic status and resolve the phylogenetic relationships among the here-identified nine species that show a high degree of eveness both in external and internal features. Phylogenetic results were then compared with distribution data, to try to infer the biogeographic history of the species studied here.

Material and methods

Material examined

We examined over 1000 specimens (typical and not-typical material) belonging to thirteen *Drepanocerus* species. The studied species are: *D. kirbyi* Kirby 1828 (type-species of the genus), *D. patrizii* (Boucomont 1923), *D. impressicollis* Boheman 1857, *D. marshalli* Boucomont 1921, *D. bechynei* Janssens 1953, *D. fastiditus* Péringuey

1900, *D. integriceps* Janssens 1953, *D. liuchungloi* Kryzhanovsky and Medvedev 1966, *D. parallelus* Raffray 1877, *D. striatulus* Paulian 1945, and three new species described hereinafter: two from Central Africa, and an Ipswichian fossil species from England.

The material is preserved in the Institutions listed below: Albany Museum, Grahamstown, South Africa (AMG), British Museum, London, UK (BM); Canadian Museum of Nature, Ottawa, Canada (CMN); Chinese Academy of Science, Beijing, China (CAS); Institut Royal de Sciences Naturelles du Belgique, Bruxelles, Belgium (IRSCNB); Lapworth Museum of Geology, Birmingham, UK (BIRUG); Magyar Természettudományi Múzeum, Budapest, Hungary (UNHM); Musée Royale de l'Afrique Centrale,Tervuren, Belgium (MRAC); Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy (MSNG); Museo Zoologico La Specola, Firenze, Italy (MZF); Muséum d'Histoire Naturelle, Genève, Switzerland (MHNG); Muséum d'Histoire Naturelle, Lyon, France (MHNL); Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (MNHUB); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museo Regionale di Scienze Naturali, Torino, Italy (MRSN); Museum für Tierkunde, Dresden, Germany (MTD); Museum of Zoology of Lund University, Lund, Sweden (MZL); Natural History Museum of Los Angeles County, Los Angeles, USA (NHMLAC); Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRS); Naturhistoriches Musem, Basel, Switzerland (NMB); Narodni Muzeum v Praze, Prague, Czech Republic (NMP); National Collection of Insects, Plant Protection Research Institute, Pretoria, South Africa (SANC); Oxford University Museum Natural History, Oxford, UK (OUMNH); Smithsonian Institute, National Museum of Natural History, Washington, USA (NMNH); South African Museum, Cape Town, South

Africa (SAMC); Transvaal Museum, Pretoria, South Africa (TM); Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia (ZIRAS); Zoologische Staatssammlung, München, Germany (ZSM); Zoologisk Museum, Copenhagen, Denmark (MUC).

Part of the examined material belongs to private collections: Barbero, Torino, Italy (CBA); Ballerio, Brescia, Italy (CBL); Bonato, Torino, Italy (CBO); Carpaneto, Roma, Italy (CCP); Dellacasa, Genova, Italy (CDE); Moretto, Toulon, France (CMO); Schillhammer, Wien, Austria (CSC).

Morphological techniques

Mouthparts and genitalia of both sexes were dissected and treated following the methods described in literature for Scarabaeoidea (Barbero *et al.* 2003). Slides of male and female genitalia and mentum were examined and ink-drawings of the structures were made using a binocular microscope Leica® MZ8 (Leica Microsystems GmbH, Wetzlar, Germany) with a drawing tube.

Images of external features (head, pronotum and elytra) and mouthparts (epipharynx) were captured using a Leica® DFC320 digital camera connected to a stereoscopic dissecting scope (Leica® Z16Apo).

Measurements were taken with the software LAS v2.5.0 (Leica® Application Suite), with selected dimensions being Maximum Pronotal Width (PW), Maximum Elytral Length (EL) and Maximum Elytral Width (EW); dimensions of each species are reported in legends of the corresponding photos (Figs. 2-3). Other dimensions used in the identification keys are: the whole body length (dorsal view, d.v.), taken from the anterior edge of the clypeus to the pygidium, and the body width, which is considered as the maximum pronotal width (d.v.).

Characters

Our analysis used the external and genitalic features traditionally employed in phylogenetic analyses within coleopteran taxa. We also examined other anatomical structures employed in phylogenetic analysis, such as the mouthparts. The epipharynx particularly reveals itself very useful as a diagnostic character for both generic and specific level in many taxa of Scarabaeoidea (Nel and De Villiers 1988). Although the systematic value of the epipharynx in adults was already mentioned by Halffter (1961), the structure was studied only occasionally in systematic treatments of Scarabaeoidea (Dellacasa 1977, Cambefort 1979, Nel and Scholtz 1990). In the last few years, however, epipharynx has come to be more widely employed in systematic, phylogenetic and ecological analyses of Coleoptera as a qualitative, discrete character (Barbero *et al.* 2003, Medina *et al.* 2003, Sanmartin and Martin-Piera 2003, Philips *et al.* 2004, Verdú and Galante 2004).

Here, we define regions, subregions, and structures of the epipharynx employing the nomenclature proposed by Böving (1936) for coleopteran larvae except for some unnamed parts, which are nominated following the terminology proposed in Barbero *et al*. (2003).

After examining the external and internal structures of adults, we identified 51 morphological characters of which 20 were from the external features, 5 from the mentum, 11 from the epipharynx, 10 from the male genitalia and 5 from the female genitalia. These characters were used to build a matrix (Table 2) for phylogenetic analysis employing Nexus Data Editor 0.5.0 (Page 2001a).

Cladistic analysis

Parsimony analysis. Character coding was based on the thirteen species listed in the Material section (see above). As pointed by Cobbett *et al.* (2007), inclusion of fossil taxa does not greatly affect the phylogenetic relationships among the extant taxa. Thus, we decided to perform the phylogenetic analyses both including and excluding the fossil species.

All 51 characters (30 binary and 21 multistate) were unordered, and equal weighted. The multistate characters were interpreted as “uncertainty”, and the gaps were treated as “missing”.

After a careful analysis of the other genera currently assigned to Drepanocerina (*Cyptochirus* Lesne 1900, *Anoplodrepanus* Simonis 1981, and *Sinodrepanus* Simonis 1985) we chose the four *Cyptochirus* species as the outgroup. In the analysis, we represent the four species as a single branch to not increase uselessnessly the number of steps of the tree. Trees were rooted by outgroup method.

We carried out a Heuristic Search in PAUP 4.0b.10 (Swofford 1998-2002), using the following settings: stepwise addition with simple addition sequence, TBR branch-swapping, ACCTRAN character-state optimization. The MaxTrees limit was set to automatically increase from the initial setting. The resulting trees were examined with TreeView 1.6.6 (Page 2001b).

We also assessed support for each branch of the tree using the non-parametric Bootstrap method (using the same Heuristic Search settings as above, but with 1.000.000

replications), as implemented in PAUP. Bootstrapping (Felsenstein 1985) probably represents the most widely used method for assessing phylogenetic support for the past decade since it provides relative estimates of nodal support of different parts of the tree. Moreover, in the years alternative measures have been suggested, as Bremer support (Bremer 1988, 1994), Jackknife (Farris *et al.* 1996), and Bayesian phylogenetic support (Rannala and Yang 1996), the last one being now the most popular. There has been recent discussion about the different meaning of bootstrap and bayesian support values (i.e., posterior probability values) and the tendency of bootstrap to give lower values of support compare with bayesian probabilities (Wilcox *et al.* 2002, Alfaro *et al.* 2003, Cummings *et al.* 2003, Holder and Lewis 2003). Here, we compared bootstrap values (confidence measures) and bayesian posterior probabilities (see below for further details).

Bayesian Inference of Phylogeny. As pointed out by Müller and Reisz (2006), the recent development of bayesian methods for phylogenetic analyses has added new alternatives to the study of morphological evolution, apart from cladistic parsimony-based studies. Until now bayesian analyses have been conducted very rarely on morphological data alone (Lewis 2001, Cabrero-Sañudo 2007, Straka and Bogusch 2007), being instead more frequently employed on molecular data or, more likely, on combined data sets of gene sequences and morphological data (Nylander *et al.* 2004, Wiens *et al.* 2005, Fric *et al.* 2007).

By comparing different models of Bayesian Inference on a morphological data set for early eureptiles, Müller and Reisz (2006) showed that the results might be more or less different, depending on the implementation of a gamma-shape parameters best fitting the data set. Following Müller and Reisz (2006), here we used Markov chain Monte

Carlo simulations (i.e., MCMC) to approximate the posterior probabilities of trees and parameters, as implemented in MrBayes v3.1 (Huelsenbeck *et al.* 2001, Ronquist and Huelsenbeck 2003, Ronquist *et al.* 2005).

The analysis was initiated with a random starting tree and run for 1,000,000 generations (two runs, four chains), sampling trees every 100th 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 (usually, 25% of the total). After discarding the trees saved during the "burn-in phase" (as estimated graphically), the remaining trees were summarized in the Bayesian consensus trees, and the topologies of the two runs were compared to detect differences. Analyses were performed with and without the fossil species, as in the parsimony analysis.

Distribution analysis

Distribution data were obtained from specimens labels, and each collection locality was georeferenced; the coordinates data were employed to build digital maps of distribution for each species in GIS environment through Diva-GIS v5.4.0.1 (Hijmans *et al.* 2005). Using the features maps (available from the software home page), nine macroareas were then established reckoning their more generical characteristics of climate, orography, and vegetation, combined with the distribution data of the species:

A. Western Tropical Africa (WTA)

B. West-Central Tropical Africa (CWTA)

C. Southern Africa (SA)

D. South Tropical Africa (STA)

E. East Tropical Africa (ETA)

F. Northeast Tropical Africa (NETA)

G. NE India (NEI)

H. Indochina (IC)

I. S China (SC)

We added a tenth area [J = England (EN)], where the fossil species was found. Successively, we built a binary matrix of species presence/absence (Table 3), coding 0 as absence and 1 as presence. This set of ten macroareas (Fig. 10) was used in the Cluster Analysis (CA), the Parsimony Analysis of Endemicity (PAE) and the Dispersal-Vicariance Analysis (DIVA) (see below).

Similarity Index and Cluster Analysis. Association of similarity based on binary matrices of presence/absence data (Hubálek 1982, Hayek 1994) are ordinarily employed to study the large-scale distribution patterns of species, and to test the measures of association among areas, in various research fields, as biogeography or ecology. Mainly on a basis of studies in which a wide varieties of coefficients were analyzed to evaluate their effectiveness (Hubálek 1982, Hayek 1994, Murguía and Villaseñor 2000), we chose to use the Ochiai Similarity Index (Ochiai 1957), it being one of the few satisfying rather stringent conditions (Hubálek 1982, Bolton 1991), and less affected by the frequency of occurrence (Jackson *et al.* 1989).

Jackson *et al*. (1989) demonstrated also that the dendrogram based on the Ochiai's Index indicates strong similarities in cluster structure, and summarize a size effect.

To test the relationship among the selected areas of Afrotropical and Indomalayan Regions, here we computed the Ochiai Similarity Index on the fauna distribution binary data and then employed the Ochiai Similarity coefficients to build clusters of areas by

UPGMA (i. e. Unweighted Paired Group Method of Averaging), through NTSYSpc 2.20 (Rohlf 1998-2005). Hierarchical Cluster Analysis was used to classify species on the basis of their biogeographical patterns. This numerical procedure identifies relatively homogeneous macroareas of species based on presence/absence data.

Parsimony Analysis of Endemicity. Parsimony analysis of Endemicity (PAE) was originally developed by Rosen (1984, 1988) and Rosen and Smith (1988) to assess area relationships of fossil or extant taxa from different areas, and as originally applied it used localities as units. Later, Morrone (1994) proposed PAE as a tool to detect areas of endemism, using grid-cells as units based on their shared species, where one group of grid-cells defined at least by two taxa represents an area of endemism (Contreras-Medina *et al.* 2007). The method takes as starting point the presence/absence of data for a set of sample localities and a particular taxon. Shared presences are analogous to synapomorphies in phylogenetic systematics, and areas are grouped according to the most parsimonious cladogram, which represent nested sets of areas.

PAE employed the same binary matrix (with data transposed) previously constructed for studies on similarity of areas. To root the area cladograms, one row coded with all zeros was included in the matrix, representing a sample hypothetical area without any of the taxa from the remaining areas.

Two analyses were conducted, one with all the macroareas together, and the other after discarding macroareas with a single species (i.e., A, G and J) because they are not areas of endemism. Parsimony Analysis (Exaustive Search) was performed on data matrices as implemented in PAUP 4.0b.10 (Swofford 1998-2002), and a Majority Rule Consensus Tree was built when more than one cladogram resulted from analysis.

Resulting clades were then examined to identify the centres of species diversity endemism.

Due to the widespread extension of *Eodrepanus* distribution, characterized also by a marked disjunction, we did not employ here a grid-cell matrix.

Analysis of Similarities. One-Way Analysis of Similarities (ANOSIM) was used to examine differences between groups of macroareas. The ten macroares were grouped according to results from CA and PAE. We used as distance measure the euclidean distances as implemented in PAST 1.84 (Hammer *et al.* 2001) employing the binary matrix of presence/absence (Table 3). The test is based on comparing distances between groups (r_B) with distances within groups (r_W), and the test statistic R value (comprised in interval -1/+1) give the amount of similarity, with 0 value indicating completely random grouping. We can have further information about the groups, since for $R > 0.75$ groups are well-separate, for $R > 0.50$ groups are well-specified, although partly superimposed, for $R < 0.25$ groups are scarcely separable.The significance of the test is computed by permutation of group membership, with 100,000 replicates.

Dispersal-Vicariance analysis. The historical biogeography of *Eodrepanus* was explored using dispersal-vicariance analysis (Ronquist 1997) as implemented in DIVA v1.1 (Ronquist 1996). The method reconstructs ancestral distributions in a given phylogeny assuming a vicariance explanation, but at the same time allowing for dispersal and extinction to occur in shaping the current distributional pattern (Ronquist 1997, Sanmartin 2003). As pointed by Sanmartin (2003), optimal reconstructions are those that minimize dispersal and extinction events under a parsimony criterion: dispersal and extinction are unpredictable events that can wipe out the traces of phylogenetically constrained processes like vicariance and duplication. In DIVA, the vicariance events (allopatric speciation) and duplication events (sympatric speciation, i.e. speciation within the 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 distribution of the species were set to ten areas (see the list of macroareas above). We used the single, fully bifurcated tree 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). The other settings were set default values (bound=250, hold=1000, weight=1.000, age=1.000). Results were then compared to choose the better solution to explain biogeographical relationships within the species.

Results

Characters List

1. *Sexual dimorphism*: (0) marked, characterized by horns and laminae well-developed; (1) male and female are clearly identified, but there are not horns and laminae on pronotum and head; (2) absent.

2. *General shape of the head*: (0) wider than long; (1) longer than wide.

3. *Head*: (0) with carinae forming cells; (1) with longitudinal carinae (sometimes carrying horns); (2) simple, with short carinae at vertex, never horns.

4. *Pronotum maximum width/elytra maximum width*: (0) subequal; (1) smaller.

5. *Pronotal carinae*: (0) merging to form well-developed cells; (1) longitudinal, largely and variously sinuate; (2) little developed.

6. *Sexual dimorphism (excluding horn presence) in pronotal carinae and punctuation*

shape: (0) absent; (1) present.

7. *Pronotum, punctuation*: (0) uneven, large, rounded, double, more or less thick in cells, always thick and small elsewhere; (1) uniform, rounded, double, more or less thick; (2) large, rounded or ovalar, double, larger at disc (sometimes confluent forming ovalar elongate areolae), more or less sparse, rarefying on carinae.

8. *Pronotum, basal medial angle*: (0) inapparent; (1) marked.

9. *Scutellum*: (0) evident; (1) not clearly visible.

10. *Elytra, basally the striae*: (0) single, never joined; (1) double, joined together.

11. *Elytra, surface*: (0) points at apex and at interstriae 3 and 6; (1) setigerous points evenly widening.

12. *Elytra, III interstria carina*: (0) always missing; (1) present but incomplete; (2) complete.

13. *Elytra, V interstria carina*: (0) evident; (1) absent, or greatly reduced.

14. *Fore tibia*: (0) markedly sexually dimorphic, in males thin, arched, and far more developed than in female; (1) gently sexually dimorphic, never larger in males than in females; (2) not sexually dimorphic.

15. *Fore tibial margin, inner basal tooth*: (0) absent; (1) present.

16. *Medial and hind femura*: (0) equal or a little longer than tibia; (1) much longer than tibia.

17. *Abdominal sides*: (0) covered by elytra; (1) not covered by elytra.

18. *Sternites, medially*: (0) all (1-4) evenly punctuated; (1) unevenly punctuated, punctuation on sternites 2-4 thinner than on sternite 1.

19. *Metasternum, medially longitudinal surface*: (0) flat; (1) humped.

20. *Metasternum, discal surface*: (0) without points; (1) covered with marked points.

21. *Mentum, pubescence*: (0) several long setae; (1) 4 pairs of long setae; (2) 2 pairs of long setae.

22. *Mentum, fore margin*: (0) largely notched; (1) deeply notched; (2) rectilinear.

23. *Mentum, sides*: (0) very rounded; (1) slightly rounded; (2) rectilinear.

24. *Mentum, distal palp*: (0) elongate, twice as long as the first palp; (1) short.

25. *Mentum, distal palp*: (0) rounded; (1) enlarged at apex; (2) ovalar.

26. *Epipharynx, fore margin laterally*: (0) rectilinear; (1) slightly curvilinear; (2) greatly rounded.

27. *Epipharynx,medial notch on fore margin*: (0) absent; (1) narrow, more or less deep; (2) very marked, largely rounded.

28. *Acropariae, setae*: (0) homogeneous in length; (1) short or missing in central part, longer in lateral part.

29. *Chaetopedia*: (0) with bristles and setae evenly mixed; (1) solely latero-apical part with few sparse and thick setae; (2) latero-apical area with thin, dense and very long setae.

30. *Anterior epitorma*: (0) extending till the fore margin; (1) short, never reaching the fore margin.

31. *Anterior epitorma*: (0) rod-like, narrow; (1) triangular-shaped; (2) rectilinear and thick.

32. *Epipharynx, proplegmatium*: (0) simple, linear; (1) two triangular thickening on sides.

33. *Plegmatic area*: (0) arched, well-developed; (1) reduced and lowered; (2) absent.

34. *Crepis, apex*: (0) asymmetrical, left-turned; (1) symmetrical, rectilinear.

35. *Crepis, caudal part*: (0) triangular-shaped; (1) tridentate.

36. *Laeotorma and dexiotorma joining tracts*: (0) rectilinear, sometimes up-turned; (1) down-sloping.

37. *Phallobase*: (0) short; (1) elongate.

38. *Phallobase, features of distal ventral area*: (0) cordiform; (1) subrectangular; (2) arched upward.

39. *Phallobase, distal ventral area*: (0) expanded; (1) narrowed; (2) greatly reduced.

40. *Parameres, on the whole*: (0) subquadrangular or trapezoidal; (1) with inner and outer margins rectilinear and converging to apex; (2) more or less arched.

41. *Aedeagus, parameres*: (0) unarmed; (1) hooked.

42. *Aedeagus, medial tooth of parameres*: (0) absent; (1) present, well-developed; (2) present, reduced, often blunt.

43. *Parameres, inferior tooth*: (0) small; (1) developed; (2) absent.

44. *Parameres, dorsal side*: (0) linear; (1) slightly protrunding; (2) with a well-developed expansion.

45. *Primary lamella*: (0) consisting in separate parts; (1) fused in a single structure.

46. *Primary lamella developing*: (0) horizontally; (1) vertically.

47. *Receptaculum seminis, distal part*: (0) medium sized; (1) enlarged.

48. *Vagina, infundibulum*: (0) not-sclerotized, C-shaped, then variously sinuate; (1) thickened, sigmoidal.

49. *Vagina, sclerotization of infundibular wall*: (0) present; (1) absent.

50. *Vagina, infundibular wall with a sclerotization*: (0) symmetrical, U-shaped or rounded; (1) asymmetrical.

51. *Vagina, dorsal part of infundibular wall*: (0) large ; (1) reduced.

Cladistic analysis

Maximum Parsimony analysis discarding the fossil species led to a single equally parsimonious tree (Statistics: Tree length = 113, Consistency index [CI] = 0.6283, Homoplasy index [HI] = 0.3717, Retention index [RI] = 0.7423, Rescaled consistency index [RC] = 0.4664). Only unambiguous character state changes are shown on the tree (Fig. 9A). Including the fossil species, the analysis (Fig. 9C) showed the same statistics, except for RI (=0.7455) and RC (=0.4684).

Three clades are well-identified on the single tree, on the basis of the synapomorphies that are marked on tree (Fig. 9A). The clade *D. patrizii/kirbyi* is characterized by the head longer than wide on the whole, the fore tibia only slightly dimorphic, the medial and hind femur much longer than tibia, the abdominal sides not covered by elytra, the mentum sides rectilinear, the distal palp of mentum ovalar, the fore margin of epipharynx greatly rounded on sides, the medial notch of fore margin of epipharynx marked and rounded, parameres margins converging to apex, and sclerotization of infundibular wall of vagina absent. Four synapomorphies support the clade consisting of *D. impressicollis/marshalli*: longitudinal and sinuate carinae of pronotum, complete carina of III elytral interstria, fore margin of mentum rectilinear, and inferior tooth of parameres absent.

The hypothesized new genus is well-supported by twelve synapomorphic characters that clearly separate the 9 species of the last-examined clade. Head simple and never carrying horns, pronotum less wide than elytra, pronotal carinae little developed, pronotum expressing a certain amount of sexual dimorphism, elytral striae joined at base, mentum sides slightly rounded, distal palp of mentum short, fore margin medial notch of epipharynx narrow and deep, anterior epitorma short, proplegmatium with triangular thickening on sides, crepis symmetrical, and primary lamella of males fused in a single structure are the characters that validate the clustering of these 9 species, their isolation being confirmed also by the subsequent analyses.

Bootstrap support (1,000,000 replicates) is high for the genera-clades, both the clades *Eodrepanus* species and *patrizii*/*kirbyi* have 100% of congruence, while the value for the clade *impressicollis*/*marshalli* is a little lower (90%). The low values of the clade *impressicollis*+*marshalli*/*Eodrepanus* (76%) is likely due to absence of part of the *Drepanocerus* species in the present analysis. Bootstrap support including fossil taxon gave the same percentages of congruence in the main clades of Bootstrap of extant taxa, but lower values for the internal branches of *Eodrepanus* (53% and 51% instead of 62% and 65% respectively, see Fig. 9)

The Bayesian analysis excluding the fossil species gave a phylogram similar to the consensus tree resulting from parsimony analysis (Fig. 9B), except for the position of *E. morgani* and *E. paolae*. The posterior probabilities are showed in Consensus Tree. The clade *patrizii*/*kirbyi* has an high posterior probability (0.99), while analysis shows a lower support for the monophyly of the clade *impressicollis*/*marshalli*, with a posterior probability of 0.88. Also the monophyly of *Eodrepanus* is assessed by the posterior probability value (1.00). The support for analysis including the fossil species is the same for the clades *patrizii*/*kirbyi*, *impressicollis*/*marshalli* and *Eodrepanus* clade, while for the internal nodes of the new genus the values are usually lower (Fig. 9D). Here, also the position of *E. coopei* remains unresolved in cladogram.

Taxonomy

Eodrepanus gen. n.

= *Paradrepanocerus* Simonis *in litteris* (*partim*)

Type species: *Eodrepanus parallelus* (Raffray, 1877)

Diagnosis. The genus *Eodrepanus* is characterized by the elytral striae split to originate supplementary intervals and by the abdominal segments I-V connected without visible sutures. The phalloteca (male genitalia) is elongate and slim. In females the infundibulum is sigmoidal and the infundibular wall asymmetrical. The epipharynx is very characteristic, with the anterior epitorma never reaching the fore margin, that is notched medially in all the species.

Generic description. Size relatively small (lenght mm 3-6), body elongate and depressed, brown-black, bearing long and thin setae, more or less dense and scatteredly distributed. Head scarcely transverse or not at all; clypeus almost always emarginated anteriorly (except in *E. integriceps*); cephalic armature: a pair of longitudinal, parallel, cariniform gibbosities, variously developed, punctate or not, placed on the posterior half of the head. Pronotal disc longitudinally, more or less widely and deeply depressed and flanked by variously developed longitudinal carinae. Elytra flat or subdepressed, subparallel; each elytral stria consisting of two marked parallel striae, connected at the elytral base and giving rise to supplementary interstriae. Scutellum evident (*E. integriceps*) or not. Metasternum flat or scarcely convex, variously hollowed or furrowed; abdominal segments I-V closely connected, the sutures medially not visible. Hind coxae widely separated. Anterior tibiae bearing externally 3-4 teeth. Sexual dimorphism present, with fore tibiae more or less elongate and bent inwardly in males, longitudinal callosities of pronotum more developed and more setose in female, elytra with an obvious callosity at the base of 3rd interstria in females, only gently swollen in males, abdominal segments more densely punctated in males than in females. Epipharynx generally subpentagonal, fore margin excised medially, epitorma short and hind plegmatic region triangular and bordered by converging tormae. Parameres elongated with curved apexes, ventrally directed. Ventral edge bearing a lobe. Copulative lamella consisting of three differently-developed pieces. Vagina usually strongly asimmetrical, sometimes bearing strong plicae. Infundibulum tubular, obviously sinuate, sigmoid-shaped, distally bulbous.

Distribution. The genus consists of 9 species and is distributed in Afrotropical and Indomalayan Regions (Fig. 1): *E. bechynei*, *E. fastiditus*, *E. morgani*, *E. paolae* and *E. parallelus* are present in the entire subsaharan Africa, from Niger and Eritrea to South Africa. *E. integriceps*, *E. liuchungloi*, *E. striatulus* are located in the Indomalayan region; fossil remains of *E. coopei* were found in England, in deposits dated back to early phase of Ipswichian (Eemian) interglacial age, namely to 120,000 years ago.

Remarks. Simonis (unpublished data) stressed the heterogeneity within *Drepanocerus*, and identified some “groups of species”. He also proposed (unpublished data) the generic name *Paradrepanocerus* for some of these species, but did not give any formal and nomenclatorial valid description. Besides, in *Paradrepanocerus* he grouped species here assigned to the genus *Eodrepanus* together with others (*D. schimperi* Janssens, *D. striatus* Boucomont and *D. strigatus* Janssens), whose phylogenetic relationships are not yet entirely elucidate by us (unpublished data). At any rate, the latter species are entirely different and far separate from *Eodrepanus* species, and do not belong to the new genus here described.

Keys to the species of *Eodrepanus* genus

1. Scutellum clearly visible, narrow and long. Clypeal margin entire, more or less parabolical, slightly produced in the middle. Anterior tibiae in males obviously elongated, strongly bent inward, outer teeth large, the second one very larger than the others. Length 6 mm. China.…………………………..……………………...*integriceps*

- Scutellum lacking. Clypeal margin clearly notched and bidentate. Anterior tibiae not very elongated, scarcely bent inward, gently broadened apically, outer teeth not very large, the second one not very larger than the others. Length 3-5.5 mm ………………2

2. Punctures of the pronotal disc very uneven: large, partly elongate and confluent in the middle, scattered, small or very small on wide, mediolateral callosities…........*parallelus*

- Punctures of the pronotal disc uniform. Mediolateral callosities with wide and dense punctures or more or less clothed with very dense setae….…………………….…….....3

3. Surface of pronotal lungitudinal depression covered by long, annulate and partly confluent punctures, giving rise to long, longitudinal, minute wrinkles..............*bechynei*

- Surface of pronotal lungitudinal depression covered by wide punctures, round or ovalar, not confluent………….………………..…………………………………...……4

4. Punctures of pronotal disc more or less twice longer than wide.……...……….*fastiditus*

- Punctures of pronotal disc round or only slightly longer than wide...………………....5

5. Elytral stria VI with a complete row of setigerous punctures, rather big and evident……………………………………………………………………………...…6

- Elytral stria VI totally lacking of setigerous punctures ……………………………..……7

6. Lamella copulatrix as in Fig 6B. Southern China…………………...……..*liuchungloi*

- Lamella copulatrix as in Fig 4D. Nepal to Indochina………………...……...*striatulus*

7. Vertex bearing two longitudinal, shining carinae. Inner edge of fore femura not dentate apically. Elytra obviously depressed between the sutural and the fifth interstriae; fifth interstria markedly convex…...…………..……………….………………….*paolae*

- Vertex without longitudinal, shining carinae. Inner edge of fore femura dentate apically. Elytra not depressed between the sutural and the fifth interstriae; fifth interstria not convex or only very slightly swollen..…………………..……………………*morgani*

Eodrepanus bechynei **(Janssens 1953) comb. n.**

(Figs 1B, 2A, 3A, 4A, 7A, 8A)

Drepanocerus bechynei Janssens 1953: 33; Ferreira 1962: 35, Ferreira 1968-69: 373, Cambefort 1971: 421, Endrödi 1971: 292, Endrödi 1976: 156, Rougon and Rougon 1977: 666, Doube 1983: 369, Cambefort 1984: 93, Hanski and Cambefort 1991: app. B.9(2), app. B.13, Davis and Dewhurst 1993: 305, Moretto and Bordat 2006: 121.

Diagnosis. Species well-characterized and easily identified, with long, annulate and partly confluent punctures of the pronotal longitudinal depression.

Description. Body elongate, flattened, almost dull. Superior and inferior surface black, pygidium more or less dark brown, legs reddish-brown. Clypeus anteriorly bearing two blunt teeth, widely and not deeply separated. Clypeo-genal angle slightly sinuate, genae evenly curvilinear, scarcely produced. Vertex bearing two feeble, longitudinal callosities separated by a moderate hollow. Punctuation of head deep and quite dense, rather ovoidal on the vertex. Lateral edges bearing some whitish, thick, acuminated setae. Surface of head clothed with light brown, long, erect, sparse setae. Pronotal disc feebly depressed, almost rectangular, bounded at the sides by two longitudinal low ridges. Lateral pronotal thirds gently hollowed in the middle and subcarinate. Lateral edges crenulate. Basal edge feebly and widely angular in the middle. The whole pronotal surface with very dense punctures, long, partly confluent,wrinkled. Setae light yellow, not very long, curved and thick. Scutellum lacking. Elytra elongate, gently narrowed backward, sericeous, feebly shining. Secondary interstriae flat; first four ones equally wide, fifth and sixth ones wider. Elytral intervals smooth, the fifth one carinate and bearing a row of reddish setae, longer apically. Seventh interval carinate and bearing a narrow row of yellow-reddish, short and recumbent setae. Elytral apices bearing long and partially erect setae. Punctures of the whole prosternal surface deep, dense, partly ovoidal. Mesosternum densely punctuated. Metasternal disc feebly concave in the basal half, with rather dense punctures,more or less large. Setae of metasternum light yellow, erect, long, only on the sides. Abdominal segments bearing scattered, uneven punctures. Anterior tibiae obviously bent in the anterior third, bearing three outer teeth; the two distal ones bigger and close together; outer edge crenulated; inner edge entire. Metatibial spur as long as 2/3 of first metatarsal joint.

Type material. Holotype ♂ (IRSNB), ETHIOPIA: Abyssinia, Lake Daka. Paratypes: 1♀ 1♂ (IRSNB), ETHIOPIA: Abyssinia, Lake Daka; 3♀♀(MRAC), DEMOCRATIC REPUBLIC OF THE CONGO: Uvira, xii.1932 (*Burgeon*); 1♀ 2♂♂(NMB), GUINEA: Coyah, Cercle de Dubréka, 15.iv.1951 (*Bechyné*).

Additional material examined. BENIN: Parahoue, 15.iii.2001 (*Bordat*) (MHNL); W du Benin N. P., N Kaobagou, ii-iii.2003 (*Kotchobi and Tchibozo*) (CBA). BURKINA FASO: Cologani (*Bomans*) (CMO); Sanguié, Boromo, Sorobouli Forest, 270 m, 10-15.viii.2005 (*Moretto*)(CMO); Bobodioulasso env., xii.1996 (*Bomans*) (MZF). BURUNDI: Bujumbura, iii-iv.1969 (*Giraudin*) (NMB). CAMEROON: Adamaoua, iv.1976 (*Ngaoundaba and Nicolas*) (MHNL). DEMOCRATIC REPUBLIC OF CONGO: Rwindi Valley, Lake Edward area, viii.1958 (*Koch*) (NMB). IVORY COAST: Koko, 23-26.vi.2000 (*Moretto*) (CMO) (MHNL). ETHIOPIA: Abyssinia, Lake Abasse (*Kovacs*) (UNHM); Kefa region, Jima, Seka env., 31.vii.2002 (*Sforzi and Bartolozzi*) (MZF); Arsi region, Wondo Genet, 1850 m, xii.1990 (*Werner*) (MZF); Shoa province, Lake Langano, 1600 m, xii.1990 (*Werner*) (MZF); Billate River valley, 20 km N of Lake Abaya, viii.1974 (*Remotti*) (MRSN). GAMBIA: Bathurst, i.1968. (*Palm*) (MZL); Bathurst, 22.i.1968 (*Leiler*) (NHRS); Sangajor, 24.i.1968 (*Leiler*) (NHRS); Sangajor, 24.i.68 (*Palm*) (MSNG); Fajara, 21-23.iii.1975 (*Monch)* (UNHM); Waterworks N. R., outside Abuko, 25.ii.1977 (MZL). GHANA: Nabogo, 40 km N of Temale, 21.i.1970 (*Endrödy-Younga*) (UNHM) (TM). GUINEA: Ditinn, 5.iv.1945 (*Clemest*) (SANC). GUINEA BISSAU: Farim, iv-v.1899 (*Fea*) (MSNG). KENYA: Masai Mara G.R., near Serena Lodge, 1550 m, 19.iv.1975 (*Davis and Dewhurst*) (SANC); Masai Mara G.R., Keekorok, 1625 m, 26.iv.1975 (*Davis and Dewhurst*) (SANC); Kitale, Kapenguria env., 2300 m, 22-27.xii.1995 (*Snizek*) (CBA); Kampi Ya Kanzi Maasai Reserve, 1100 m, 30.vii.2003 (*Ballerio*) (CBL); Mount Elgon (*Palm*) (MZL); Mount Elgon, Kaptega, 1980 m, i.1979 (*Leiler*) (NHRS). MOZAMBIQUE: Gorongosa Mounts, 2300 ft, 15.iv.1971 (*Bornemissza and Aschenborn*) (SANC) (NMB); Gorongosa N. P., 15.xii.1972 (*Besnard*) (MHNL). NIGER: Saga, 1.ii.1980 (*Leblanc*) (MHNL). NIGERIA: Kontagora, 75 km S, 19.vii.1974 (*Bornemissza*) (SANC). RWANDA: Kagera N. P., 19.xii.1971 (*Roggeman*) (MSNG). SENEGAL: Ziguinchor, iv.1974 (*Nicolas*) (CMO) (MHNL); Basse Casamance, Boufou, Taei, near Bignona, 24.xi.1961 (NMB). SOUTH AFRICA: Cape Province, Transkei, Magwa Waterfall, 7.xii.1988 (*Endrödy-Younga*) (TM); Eastern Cape Province, Port St. Jones, Silake N. R., 12.iii.2000 (*Bordat*) (MHNL); Natal, Hluhluwe G. R., 6.iv.1974 (*Endrödy-Younga*) (TM); Natal, Hluhluwe G. R., 19.xi.1992, 27.xi.1992 (TM); Natal, Hluhluwe G. R., Inziname, 18.iii.1982 (*Doube*) (SANC); Natal, Umfolozi G. R., 25.viii.1971 (*Bornemisszа and Insley*) (SANC); Natal, Umfolozi, G. R., Mfafa area, 200 m, 23.xi.1977 (*Bernon and Davis*) (SANC); TANZANIA: Serengeti N. P., Western corridor, 1450 m, 27.iv.1975 (*Davis and Dewhurst*) (SANC); Manyara N. P., 1050 m, 1-2.v.1975 (*Davis and Dewhurst*) (SANC); Kilimanjaro, Kibonoto, 1000-1300 m, viii.1905-06 (*Sjöstedt*) (MNHUB). UGANDA: Busoga District, Jinja env., i-iii.1968 (*Rwabuneza*) (MRAC); Queen Elizabeth N.P., Mweya, 912/950 m, 16.viii.1990, 27.viii.1990, 6.x.1990 (*Ieradi*) (CCP); Queen Elizabeth N.P., Rwenshama, 920 m, 31.viii.1990 (*Ieradi*) (CCP). ZAMBIA: Luangwa Valley, Chibembe, 7.x.1984 (*Dellacasa*) (CDE) (CBA) (MSNG).

Distribution. The species extends from NW to NE Afrotropical region, reaching soutward South Africa (Natal and Cape Province). It was quoted also from other localities (data not verified) in Niger (Rougon and Rougon 1977), Ivory Coast (Cambefort 1984), Democratic Republic of Congo (Ferreira 1962) and Tanzania (Janssens 1953).

Eodrepanus coopei **sp.n.**

(Figs 1A, 5A, 5D)

Diagnosis. This fossil species is easily identified on the basis of pronotal punctuation, that clearly differs from the other species ones. Both pronotal and elytral features assigned the species to the new genus here described.

Description. General shape of the pronotal surface as in the genus. Punctures evenly distributed, in the discal area larger and slightly longitudinally elongate. Elytra elongate.

Type material. Holotype (pronotum) (BIRUG), GREAT BRITAIN: England, Trafalgar Square, London. Paratypes (1 pronotum, 3 left elytrae) (BIRUG), GREAT BRITAIN: England, Trafalgar Square, London.

Distribution. At present, we know the species only from the typical locality. Besides, Gao *et al.* (2000) pointed out that fossil remains similar to *E. coopei* ones were recorded from deposits of Woolpack Farm, Great Ouse River, Cambridgeshire (UK), but we could not examine the material. The fossil remains of the species (Coope 1979, 2000) were found in deposits dated back to early phase of Ipswichian (Eemian) interglacial age, namely to 120,000 years ago.

Etymology. The species was named after Dr. Russel Coope, who first identified the fossil and placed it in *Drepanocerus* genus, and gave us the material on loan. Successively, the same Coope housed the specimens from Trafalgar Square in the Lapworth Museum of Geology, University of Birmingham, UK.

Remarks. Both the sites (Trafalgar Square, in London and Woolpack Farm, in Cambridgeshire) were characterized by regional mixed oak forest and temperate fauna, with locally open areas in river valleys (high herb pollen levels) that supported rhinoceros and giant deer (Stuart 1976, 1982). The vertebrate assemblages of either Trafalgar Square and Woolpach Farm sites resembles the “hippopotamus fauna” characteristic of the Ipswichian age (Franks 1960, Sutcliffe 1995). At present, eight localities are included in the list of Eemian sites (Coope 2000), all located in SE England at Lower Thames Valley, and characterized by the very same suite of exotic dung beetles. Sites with analogous characteristics of England ones were identified in various areas of Europe till Far East (Zagwijn 1996), and similar assemblages of interglacial beetles are present in other parts of continental Europe (Coope 2000).

***Eodrepanus fastiditus* (Peringuey, 1900) comb. n.**

(Figs 1C, 2B, 3B, 4B, 5B, 5E, 7B, 8B)

Drepanocerus fastiditus Peringuey 1900: 111, 113; Gillet 1911: 100, Boucomont 1921: 204 205, Janssens 1953: 33, Ferreira 1954: 258, Ferreira 1955: 81, Ferreira 1958: 149, Ferreira 1962: 36, Ferreira 1967a: 44, Ferreira 1968-69: 374, Endrödy-Younga 1982: 17, Doube 1983: 369, Hanski and Cambefort 1991: app. B.8, Davis and Dewhurst 1993: 305.

Diagnosis. Species similar to *E. bechynei*, differing mainly by the punctures of the longitudinal pronotal depression that are ovalar, not confluent, and more or less twice longer than wide.

Description. Body elongate, flattened. Upper surface black, head shining, inferior surface, pygidium and legs black or dark brown. Clypeus bearing anteriorly two blunt teeth, widely and not deeply separated. Clypeal edge sinuate, genae subdentate anteriorly. Vertex bearing two feeble, longitudinal callosities separated by a moderate hollow. Punctuation of head deep and dense, ovoidal posteriorly. Lateral edges bearing some whitish, thick, acuminated setae. Antennal club brown. Pronotal disc in males gently depressed. Pronotal surface evenly covered by large, ovalar, quite dense punctures. Disc in females narrowly depressed, densely punctate, bordered laterally by two longitudinal rows of thick, light brown, very dense setae. Lateral pronotal thirds gently hollowed in the middle and subcarinate. Basal edge feebly and widely angular in the middle. Scutellum lacking. Elytra elongate, gently narrowed backward, sericeous, feebly shining. Elytral intervals smooth, the fifth one carinate and bearing a row of reddish setae, longer apically. Seventh interval carinate and bearing a narrow row of yellow-reddish, short and recumbent setae. Elytral apices bearing long and partially erect setae. Third interstria, in females, obviously tubercolate basally, tubercle densely setose; in males the base of third interstria is only convex. Punctures of the whole prosternal surface deep, dense, partly ovoidal. Mesosternum punctate. Metasternal disc longitudinally impressed in the middle, with more or less large punctures. Setae of metasternum light, scanty. Abdominal segments bearing scattered, uneven punctures. Anterior tibiae obviously bent in the anterior third, bearing three outer teeth; the two distal ones bigger and close together; outer edge crenulated; inner edge entire. Metatibial spur as long as1/2 of first metatarsal joint.

Type material. Holotype ♂ (SAMC), SOUTH AFRICA: Natal, Estcourt. Paratypes: 2♂♂ 1♀ (SAMC), SOUTH AFRICA: Natal, Estcourt.

Additional material examined. BURUNDI: Kyriama, 1500 m, viii.1987 (*Giannatelli*) (CBO). DEMOCRATIC REPUBLIC OF THE CONGO: Rwindi Valley, Lake Edward area, viii.1958 (*Koch*) (NMB); Kivu, Bukavu, vi-1954 (*Brédo*) (NMP). ERITREA: “Eritrea”, 12.ix.1914 (*Hauschild*) (MUC); ETHIOPIA: Arsi Region, Wondo Genet, 1850 m, xii.1990 (*Werner*) (MZF). KENYA: Swam river, Adrukoit, 1360 m, 25.i.1979 (*Leiler*) (NHRS); Masai Mara G. R., Keekorok, 1625 m, 26.iv.1975 (*Davis and Dewhurst*) (SANC); Masai Mara G. R., Mara River near Serena Lodge, 1500 m, 19.iv.1975 (*Davis and Dewhurst*) (SANC); Meru N. P., Bwatherongi, 700 m, 1.xii.1975 (*Dewhurst*) (SANC); Mount Elgon N. P., 2300 m, 3.ix.1986 (*Zoia*) (CBA); Mount Elgon N. P., near Chepnyalil Cave, 2500 m, 24-28.i.1992 (*Merki*) (UNHM); Rongo, 8 km E, 1300 m, 24.xi.1975 (*Dewhurst*) (SANC). MOZAMBIQUE: Gorongosa Mts., 2.300 ft, 15.iv.1971 (*Bornemissza and Aschenborn*) (SANC); Gorongosa N. P., 11-28.i.1972 (*Bornemissza and Kirk*) (SANC). RWANDA: Bugesera, 10.iii.1972 (*Roggeman*) (MRAC). SOUTH AFRICA: "Cap land" (NMB); Cape Province, Zuurberg, 19/20.viii.1989 (*Minet*) (MHNL); Cape Province, East London, x.1966 (*Zumpt*) (NMB); Cape Province, Eastern Cape, Grahamstown, ix.1909 (*Ledoux*) (NMNH); Cape Province, Glenthorpe, Grahamstown, 3.xi.1981 (*Weaving*) (AMG); Cape Province, Kudu Reserve, 16.ii.1982 (*Weaving*) (AMG); Cape Province, Transkei, Magwa waterfall, 7.xii.1988 (*Endrödy-Younga*) (TM); Cape Province, Transkei, Port St. Jones, Silaka, 2.xii.1987 (*Endrödy-Younga*) (TM); Cape Province, Transkei, Silaka Forest Reserve, 2.xii.1988 (*Endrödy-Younga*) (TM); Natal (*Andrewes*) (BM); Natal, Bushland's Halt, 17.i 1986 (*Aschenborn*) (NHMLAC); Natal, Cathedral Peaks Forest Station, 75 km WSW Estcourt, 7-31.xii.1979 (*Peck and Peck*) (CMN); Natal, Cathedral Peaks Forest Station, 75 km WSW Estcourt, 1400 m, 30-31.xii.1979 (*Peck and Peck*) (CMN); Natal, Drakenberg, Cathedral Peak Station, 18.i.1996 (*Endrödy-Younga*) (TM); Natal Drakenberg, Champagne Castle, 13.iv.1990 (*Klimaszewski*) (TM); Natal, Dukuduku forest Station, 7.iv.1974 (*Endrödy-Younga*) (TM); Natal, Estcourt (*Andrewes*) (BM); Natal, Estcourt (*Haviland*) (SANC); Natal, Frere (SAMC); Natal, Frere, viii.1891 (*Marshall*) (BM); Natal, Frere, ix.1891 (*Marshall*) (BM); Natal, Frere, viii.1892 (*Marshall*) (BM); Natal, Hluhluwe G. R., i.1986 (MSNG) (CBA); Natal, Hluhluwe G. R., 15.xi.1985 (NHMLAC); Natal, Hluhluwe G. R., 16.xi.1985 (*Aschenborn*) (NHMLAC); Natal, Hluhluwe G. R., 6.xii.1985 (*Aschenborn*) (MSNG); Natal, Hluhluwe G. R., 19.ix.1992 (*Endrödy-Younga*) (TM); Natal, Hluhluwe G. R., 22.x.1985 (*Fox and Byrne*) (TM); Natal, Hluhluwe G. R., 19.xi.1992, 27.xi.1992 (*Endrödy-Younga*) (TM); Natal, Hluhluwe G. R., Bobbiesdrif Riverine forest, 13.i.1986

(*Aschenborn*) (NHMLAC); Natal, Hluhluwe G. R., Bobbiesdrif Riverine forest, 15.i.1986 (*Aschenborn*) (MSNG); Natal, Hluhluwe G. R., Inziname, 10-11.ii.1982 (*Davis*) (SANC); Natal, Hluhluwe G. R., Inziname, 17.i.1986 (*Aschenborn*) (TM) (NHMLAC); Natal, Hluhluwe, Morris Farm, 13.i 1986 (*Aschenborn*) (NHMLAC); Natal, Ithala G. R., 24.xi.2002 (*Endrödy-Younga*) (TM); Natal, Ithala G. R., 18-19.ii.2003 (*Fouquè*) (CMO); Natal, middle Karkloof forest, 1300 m, 11.xii.1989 (*Endrödy-Younga and Klimaszewsky*) (TM); Natal, Ladysmith, 21 km N, 11.xii.1980 (*Davis*) (SANC); Natal, Mkuzi G. R., 12-15.xii.1981 (*Doube, Macqueen Davis and Flanagan*) (SANC); Natal, Mpumalanga, Nwaswitsaka Reserve, 8.xii.1997 (*Bellamy*) (TM); Natal, Mpumalanga, Pilgrims Rest, 25.ix.2006 (*Snäll*) (NHRS); Natal, Mtubatuba, 21/29.viii.1971 (*Bornemissza and Insley*) (SANC); Natal, Mtunzini, ix.1949 (*Koch*) (TM); Natal, Pietermaritzburg 1919 (*Schwarze*) (NMP); Natal, Umfolozi G. R., 21/26.viii.1971 (*Bornemissza and Insley*) (SANC); Natal, Umfolozi G. R., 6.iv.1974 (*Endrödy-Younga*) (TM); Natal, Umfolozi G. R., Mbuzzana area, 28.iii.1972 (*Olsen*) (SANC); Natal, Weza Forest Station, 22.xi.1989 (*Endrödy-Younga and Klimaszewsky*) (TM); Natal, Winterton (*Bordat and Bordat*) (CMO); Orange Free State, Vredefort, 29.xi.1970 (*Bornemissza*) (SANC); Transvaal, Argent, 7-16.xii.1953 (*Capener*) (ZSM); Transvaal, Barberton, 16 km N, 24.x.1986 (*Endrödy-Younga*) (TM); Transvaal, Berlin Forest Station, 9.xii.1986 (*Endrödy-Younga*) (TM); Transvaal, Bloemhof, xii.1962 (*Zumpt*) (NMB); Transvaal, Boekenhoutskloof, 30 km NE Pretoria, 7.xi.1975, 4.xi.1976, 8.x.1976, 22.x.1976, 26.i.1978 (*Stickler*) (SANC); Transvaal, Boekenhoutskloof, 30 km NE Pretoria, 22.xi.1977, 17.x.1977 (*Bernon*) (CMN); Transvaal, Bundu Inn, 24.iii.1974 (*Endrödy-Younga*) (TM); Transvaal, Castle Gorge, 41 mi W Pretoria, 5.xii.1970 (*Bornemissza*) (SANC); Transvaal, Gauteng, Cullinan Windy

Brow, 9.i.2002 (*Endrödy-Younga*) (TM); Transvaal, Hazyview, 31.x.1990 (*Klimaszewski*) (TM); Transvaal, Johannesburg, i-ii.1952 (*Zumpt*) (NMB) (IRSNB); Transvaal, Johannesburg, iv.1950 (*Capener*) (TM); Transvaal, Johannesburg, xi.1950 (*Zumpt*) (IRSNB) (NMB); Transvaal, Klaserie, 3.v.1981 (*Endrödy-Younga*) (TM); Transvaal, Kruger N. P., Satara, 19.ii.1982 (*Doube and Macqueen*) (SANC); Transvaal, Moloto Area, 21.iv.1976 (*Culligan*) (SANC); Transvaal, Nash Scott G. R., 1.ix.1986 (*Edwardes*) (CBA); Transvaal, Nelshoogte Forest Station, 3.xii.1986, (*Endrödy-Younga*) (TM); Transvaal, Nylsvley, at river, 3.ix.1975 (*Endrödy-Younga*) (TM); Transvaal, Nylsvley, Smith farm (*Motz*) (UNHM); Transvaal, Nylsvley, Smith farm, 13.xii.1975, 15.xii.1975, 24.i.1976, 27-29.ii.1976, 27.iii.1976, 27.iv.1976 (*Endrödy-Younga*) (TM); Transvaal, Piet Retief, iii.1918 (*Brauns*) (TM); Transvaal, Piet Retief, 37 kms E, 18.x.1972 (*Olsen*) (SANC); Transvaal, Pretoria 24.v.1904 (*Swierstra*) (TM); Transvaal, Pretoria, v.1968 (*Jones*) (TM); Transvaal, Rietondale, near Pretoria, 21.ix-15.x.1981 (*Davis*) (SANC); Transvaal, Roodeplaat Dam N. R., 14.viii.1974 (*Strydom*) (TM); Transvaal, Shilouvane, Pietersburg (SAMC); Transvaal, Soutpan Pretoria, 8.ii.1973, (*Endrödy-Younga*) (TM); Transvaal, Uitsoek Forest Station environments, 13.xii.1986 (*Endrödy-Younga*) (TM); Transvaal, Waterberg, 11.ii.1976 (*Strydom*) (TM); Transvaal, Waterberg, 12.ii.1976 (*Strydom*) (TM); Transvaal, Zeerust, 32 km E, 9.i.1973 (*Davis*) (SANC); Transvaal, Zoutpansberg District, xi-1924. Coll. H.J. Heske (TM); Western Cape Province, Vredenburg, 13 km NE, 10 m ca., 28.iv.1976 (*Davis and Aschenborn*) (SANC). TANZANIA: Serengeti N. P., W corridor, 1450 m, 27.iv.1975 (*Davis and Dewhurst*) (SANC); Tanganyika, Mount Meru E slope, 5,700 fts, 26.i.1966 (*Szunyoghy*) (UNHM); Udzungwa Mts. N. P., 700 m, 20.vii.2004, (*Bartolozzi and Sforzi*) (MZF). UGANDA: Queen Elizabeth N. P., Mweya 912/950 m, 17.viii.1990, 19.ix.1990 (*Ieradi*) (CCP); Queen Elizabeth N. P., Rwenshama 920 m, 27.ix.1990 (*Ieradi*) (CCP). ZAMBIA: Luangwa Valley, Chibembe, 7.x.1984 (*Dellacasa*) (CDE); Luangwa Valley, Mfuwe, 7.x.1984 (*Dellacasa*) (CDE). ZIMBABWE: Glen Clova, 21.iv.1971 (*Bornemisszza and Aschenborn*) (SANC); Harare area, 8.xii.1989 (*Holter and Sommer*) (MUC); Harare area, 22.i.1991 (*Holter*) (MUC); Houtberg, 19.x.1954 (*Ferreira*) (MZL); Inyazura, 9 Kms S, 13.xi.1972 (*Davis*) (SANC); Kyle G. R., 22.iv.1971 (*Bornemisszza and Aschenborn*) (SANC); Lowdale, 8.iv.1973 (*Duke*) (TM); Matabeleland, S Kumalo, 16.ii.1991 (*Gardiner*) (MUC); Matabeleland, S Matopos G. P., Whovi Wild Area, 18.ii.1991 (*Gardiner*) (MUC); Matopos G. P., 16.iii.1998 (*Bernaud and Bernaud*) (MHNL); Salisbury, 21.v.1972 (*Duke*) (TM).

Distribution. The species is known from E and S Africa. The species was also quoted from various localities of Guinea-Bissau (Ferreira 1968-69), Democratic Republic of Congo (Janssens 1953), South Africa (Janssens 1953, Ferreira 1968-69, Endrödy-Younga 1982) and Zimbabwe (Ferreira 1955), but data are not verified, hence were not listed above.

***Eodrepanus integriceps* (Janssens, 1953)**

(Figs 1A, 2C, 6A, 7C, 8C)

Drepanocerus integriceps Janssens 1953: 34; Balthasar 1963c: 70, Bedzek and Krell 2006: 156.

Diagnosis. The species is easily recognizable by the shape of the clypeus and the presence of the scutellum.

Description. Only males known. Body elongate, flattened, moderately shining, black, with edges of head, pronotum and elytra dark brown, legs reddish brown. Clypeus entire, narrowly produced in the middle. Clypeal and genal edges rectilinear, clypeo-genal angles convex. Vertex bearing two feeble, longitudinal, smooth callosities, connected posteriorly. Punctuation of head evenly deep and quite dense. Lateral edges bearing some whitish, acuminated setae. Pronotal disc feebly depressed, almost circular. Lateral pronotal thirds gently, longitudinally hollowed and subcarinate. Lateral edges serrulate. Basal edge widely angular and depressed in the middle. Punctures evenly dense, flat, round or feebly ovalar. Setae light, long, curved anteriorly and laterally, long, erect and scattered elsewhere. Scutellum narrow. Elytra elongate, very gently narrowed backward. Secondary interstriae flat. First five ones equally wide, sixth one obviously wider. Elytral intervals more or less punctuate and setose, the fifth one bearing a row of reddish setae. Seventh interval carinate and bearing a narrow row of yellow-reddish, short and recumbent setae. Elytral apices bearing long and partially erect setae. Prosternum deeply punctate. Mesosternum punctate. Metasternum unevenly and quite densely punctuate, punctures umbilicate. Abdominal segments bearing rather big punctures, dense on the sides, more scattered in the middle. Fore tibiae long and strongly bent inward, bearing three outer teeth; the two distal ones close together, the second one very developed; outer edge crenulate. Antero-superior edge of fore femura dentate distally. Metatibial spur as long as 2/3 of first metatarsal joint.

Type material. Holotype ♂ (IRSNB), CHINA: Ganchouen (=Guizhou), Kouy-Tchéou, 1910 (*P. Cavalerie*). Paratype: 1♂ (MNHN), CHINA: Mou-Pin, 1870 (*A. David*).

Distribution. The species is known only from the typical localities in Southern China.

Eodrepanus liuchungloi **(Kryzhanovsky and Medvedev, 1966)**

(Figs 1A, 2D, 6B, 7D, 8D)

Drepanocerus liuchungloi Kryzhanovsky and Medvedev 1966: 396; Bedzek and Krell 2006: 156.

Diagnosis. We cannot obtain on loan the female holotype. Here, we studied a single male specimen preserved in CAS and identified as *E. liuchungloi* (see below). The species is very similar to *E. striatulus* but can be distinguished by the shape of the male genitalia (primary lamella).

Description. Body elongate, flattened, shining. Uniformely black, with legs reddish brown. Clypeus narrow and gently protruding, bearing two teeth, not deeply separated. Clypeo-genal junction notched. Vertex bearing two feeble, longitudinal callosities. Punctuation of head evenly deep and quite dense. Lateral edges bearing some whitish, acuminated setae. Antennal club brown. Pronotal disc feebly depressed, bounded laterally by two slight longitudinal callosities. Lateral pronotal thirds gently hollowed in the middle and subcarinate. Lateral edges obviously denticulate. Basal edge feebly and widely angular in the middle. Punctures evenly dense and uniformely wide. Scutellum lacking. Elytra elongate, gently narrowed backward. Secondary interstriae flat. First five ones equally wide, sixth one obviously wider. Elytral intervals more or less punctuate and setose, the fifth one bearing a row of reddish setae, short and erect. Seventh interval carinate and bearing a narrow row of yellow-reddish, short and recumbent setae. Elytra in males only very slightly swollen at the base of third and fourth intervals. Elytral apices bearing long and partially erect setae. Prosternum deeply punctate. Mesosternum punctate. Metasternum bearing a slight, longitudinal furrow in the middle of the hind half, surface evenly and very densely punctate, except for a little, ovoidal, nearly impunctate space in the fore half. Abdominal segments bearing rather big punctures, dense on the sides, a bit less dense in the middle. Inner edge of fore tibiae moderately bent in the anterior two-thirds, bearing three outer teeth; the two distal close together, the second one bigger than other two; outer edge crenulate. Antero-superior edge of fore femura dentate distally. Metatibial spur as long as 2/3 of first metatarsal joint.

Type material. Holotype ♀ (CAS), CHINA: S Yunnan, Damonlung, 40 km SE Cheli, 640 m, 28.vi.1957 (*Shun-Ju*).

Additional material examined. CHINA: 1 ♂, Guizhou, Maolan, Libo, 26.x.1998 (*Li*) (CAS).

Distribution. The species is known only from S China, near the boundaries of Myanmar and Laos.

Eodrepanus morgani **sp.n.**

(Figs 1A, 2E, 6C, 7F, 8E)

Diagnosis. The species can be recognized by even and rounded pronotal punctuation, the vertex not bearing longitudinal carinae and elytra not depressed between the sutural and the fifth interstriae.

Description. Body elongate, rather flattened, scarcely shining. Upper surface black, with edges of head, pronotum and elitra brown. Inferior surface, pygidium, and legs reddish-brown. Clypeus bearing anteriorly two blunt teeth, widely and not deeply separated. Clypeal and genal edges evenly curvilinear. Vertex bearing two feeble, longitudinal callosities separated by a moderate hollow. Punctuation of head deep and quite dense, rather ovoidal on the vertex. Lateral edges bering some whitish, thick, acuminated setae. Surface of head clothed with light brown, long, erect, sparse setae. Pronotum transverse. Disc feebly depressed, rectangular, bounded at the sides by two longitudinal low ridges. Lateral pronotal thirds gently hollowed in the middle and subcarinate. Lateral edges strongly denticulate. Basal edge feebly and widely angular in the middle. The whole pronotal surface with very dense punctures, wide, flat, round or feebly ovoidal. Setae light, long, curved and thin anteriorly and on the edges, shorter, thick, erect on the discal callosities. Scutellum lacking. Elytra elongate, gently narrowed backward, sericeous, feebly shining. Secondary interstriae flat but rather deep; First four ones equally wide, fifth one 1/2 wider than the four one and obviously broadened basally, sixth one wider twice the fifth one. Elytral intervals smooth, the fifth one bearing a row of reddish setae, short and erect in the first 4/5, long and curved in the last fifth. Seventh interval carinate and bearing a row of yellow-reddish, short and recumbent setae. Elytral apices bearing long and partially erect setae. Punctures of the whole prosternal surface deep, dense, partly ovoidal. Mesosternum not punctuated. Disc of metasternum gently humped anteriorly, feebly concave in the basal half; narrowly smooth in the middle of the fore half, with rather dense punctures, large or very large and umbilicate elsewhere. Setae of metasternum light, scattered, erect, not very long, a bit denser on the sides. Abdominal segments bearing rather big, even, umbilicate punctures. Anterior tibiae obviously bent in the anterior third, bearing three outer teeth; the two distal teeth bigger and close together. Outer edge of fore tibiae entirely crenulate. Inner edge entire, abruptly broadened basally. Antero-superior edge of fore femura broadened distally. Metatibial spur as long as ½ of first metatarsal joint.

Type material. Holotype ♂, CENTRAL AFRICAN REPUBLIC: Bayanga, 16.iii-6.iv.1996 (*P. Moretto*) (CMO). Paratypes: 3 ♂♂, same locality and date as holotype (CMO).

Distribution. Known only from the typical locality.

Etymology. The species was named after the son of our colleague Philippe Moretto, who collected the specimens and gave us on loan.

***Eodrepanus paolae* sp.n.**

(Figs 1A, 2F, 6D, 7G, 8F)

Diagnosis. The species can be identified by even and rounded pronotal punctuation, the vertex bearing two longitudinal carinae and elytra obviously depressed between the sutural and the fifth interstriae.

Description. Body elongate, flattened, head and pronotum rather shining. Upper surface brown-black, with some bronze lustre on the head. Ventral surface and pygidium brown-black, legs dark reddish-brown. Clypeus narrowed anteriorly, bearing two blunt teeth, widely and not deeply separated. Clypeal edges hardly sinuate, genae subparallel. Vertex bearing two small, longitudinal carinae separated by a moderate hollow. Punctuation of head deep and quite dense, rather ovoidal on the vertex. Lateral edges bearing some whitish, thick, acuminated setae. Surface of head clothed with light brown, long, erect, sparse setae. Pronotum transverse. Disc feebly depressed, rectangular, bounded at the sides by two longitudinal low ridges, and internally by two other, less elevated, longitudinal callosities. Lateral pronotal thirds gently hollowed in the middle and subcarinate. Lateral edges crenulate. Basal edge feebly and widely angular in the middle. The whole pronotal surface with very dense punctures, wide, flat, round or feebly ovoidal. Setae light, long, curved and thin anteriorly and on the edges, scattered, thick, erect on the discal ridges. Scutellum lacking. Elytra elongate, gently narrowed backward, sericeous, feebly shining. Discal area obviously flattened. Secondary interstriae flat but rather deep; First four ones equally wide, fifth one wider than the four one and a bit broadened basally, sixth one wider twice the fifth one. Elytral intervals smooth, the fifth one convex, bearing a row of reddish, short and erect setae in the apical third. Seventh interval carinate and bearing a row of yellow-reddish, short and recumbent setae. Elytral apices bearing long and partially erect setae. Punctures of the whole prosternal surface deep, dense, partly ovoidal. Mesosternum deeply punctuated. Disc of metasternum gently humped anteriorly, feebly furrowed in the basal half; narrowly smooth in the middle of the fore half, with rather dense punctures, large or very large and umbilicate elsewhere. Setae of metasternum light, scattered, erect, not very long, denser on the sides. Abdominal segments bearing rather big, even, umbilicate punctures. Anterior tibiae gently bent in the anterior half, bearing three outer teeth; the two distal teeth bigger and close together. Outer edge of fore tibiae entirely crenulate. Inner edge entire, not broadened basally. Antero-superior edge of fore femura not broadened distally, antero-inferior edge strongly carinate. Metatibial spur curved inward, as long as ½ of first metatarsal joint.

Type material. Holotype ♂ (MNHG), BURUNDI: Rumeza, 2200 m, viii.1987 (*Giannatelli*).

Distribution. Known only from the typical locality.

Etymology. The species was named after the daughter of CP, one of the authors.

Eodrepanus parallelus (Raffray, 1877)

(Figs 1D, 2G, 3C, 4C, 5C, 5F, 7H, 8G)

Drepanocerus parallelus Raffray 1877: 314; Gillet 1911: 100, d’Orbigny 1916: 31, Boucomont 1921: 204 226, Janssens 1939: 9, Janssens 1953: 33, Janssens 1956: 345, Ferreira 1962: 36, Ferreira 1968-69: 376.

Diagnosis. Species characterized by the uneven size and the dense, elongate, partially confluent punctures of the pronotal disc.

Description. Body elongate, flattened, moderately shining. Uniformely black, with edges of head and legs reddish brown. Clypeus bearing anteriorly two teeth, widely and not deeply separated. Clypeal and genal edges evenly curvilinear, genae anteriorly obviously dentate. Punctuation of head deep and dense on the clypeus, superficial and very dense elsewhere. Antennal club brown. Pronotal disc feebly depressed, bordered laterally by two longitudinal callosities. Lateral pronotal thirds gently hollowed in the middle. Lateral edges crenulate. Punctures dense, elongate, partially confluent in the middle, gently ovalar and dense on the sides, smaller and scattered on the callosities. Setae light, long, thick and curved anteriorly and on the edges, shorter and rare elsewhere. Scutellum lacking. Elytra elongate, gently narrowed backward, sericeous, feebly shining. Secondary interstriae flat. First four ones equally wide, fifth and sixth ones obviously wider. Elytral intervals smooth, the fifth one bearing a row of reddish setae, short and erect. Seventh interval carinate and bearing a narrow row of yellow-reddish, short and recumbent setae. Elytral apices bearing long and partially erect setae. Prosternum deeply punctate. Mesosternum punctate. Metasternum longitudinally hollowed in the middle, very minutely punctate on the disc, punctures dense and big elsewhere. Abdominal segments bearing rather big punctures on the sides, almost smooth in the middle. Fore tibiae obviously bent in the anterior third, bearing three outer teeth; the two distal ones bigger and close together; outer edge crenulate; inner edge entire. Antero-superior edge of fore femura dentate distally. Metatibial spur as long as 2/3 of first metatarsal joint.

Type material. Holotype ♂ (IRSNB), ETHIOPIA: Abyssinie, Tembiène, x.1876.

Additional material examined. BURUNDI: Urundi Plain, Ruzizi, 29.vi.1940 (*Brédo*) (IRSNB). DEMOCRATIC REPUBLIC OF THE CONGO: Albert N. P., Lubilia River, Lake Edward emb., 912 m, 31.vii.1956 (*Vanschuytbroeck*) (MSNG); Albert N. P., Molindi River, near Kibuga Lake, 30.iv-2.v.1934 (*de Witte*) (IRSNB); Rwindi Valley, Lake Edward area, viii.58 (*Koch*) (NMB); Garamba N. P., Morubia, 11.vi.1951 (*Verschuren*) (MNHN); Kivu, Bukavu (NMP); Semliki Forest, viii.59 (*Koch*) (NMB); "Zaire" (MNHUB). ERITREA: "Eritrea Colony" (*Jensen-Haarup*) (MUC); "Eritrea" 12.ix.1914 (*Hauschild*) (MUC); Keren (MNHUB); Gura, xii.1936-iii.1937 (*Nicotra*) (CMN). ETHIOPIA: "Abyssinia", 1850 (*Schimper*) (NMB); "Abyssinia" (*Raffray*) (MCG); "Abyssinia" (ZSM); Abyssinia, Arar (MNHUB); Abyssinia, Lac Daka (IRSNB); Abyssinia, Boulè-Boulè River (IRSNB); Scirè, 1936 (*Brasavola*) (MCT); Shoa Province, Lake Langano, 1600 m, xii.1990 (*Werner*) (MZF); Welega Region, Nekemte, Sire environments, 26.vii.2002 (*Sforzi and Bartolozzi*) (MZF). KENYA: Amboseli, 11.iii.1970 (*Palm*) (MZL); Amboseli, 22.i.1986 (*Minetti*) (CMO); Elgon Mount, 1980 m (*T. Palm*) (MSNG); Kampi Ya Kanzi Maasai Reserve, 1100 m, 30.vii.2003 (*Ballerio*) (CBL); Kanziko, ix.1936 (*Mac Arthur*) (BM) (NMNH); Marsabit N. R., near Gof Bongole, 1010 m, 18.v.1975 (*Davis and Dewhurst*) (SANC); Masai Mara G. R. near Serena Lodge, 1550 m, 25.xi.1975 (*Dewhurst*) (SANC); Meru, Nkubu, 1500 m, 1-10.iv.1987 (*Mourglia*) (CBO); Meru district, Meru N. P., 6.ii.1983 (*Mourglia*) (CBA); Meru N. P., Leopard Rock, about 600 m, 14.xi.1975 (*Dewhurst*) (SANC); Naivasha, 16.i.1981 (*Gangloff*) (MHNL); Thowa River, vii.1935 (*Mac Arthur*) (NMNH); Tsavo N.P., 4.xii.1974 (*Kingston*) (OUMNH); Tsavo West N. P., 31 Kms W of HQ, 850 m, 4.v.1975 (*Davis and Dewhurst*) (SANC). MALAWI: Mulanje Mts., 1000 m, x.1991 (*Dudley*) (CMO). MOZAMBIQUE: Beira District, Vila de Manica, 30.viii.1964 (USNM); Lourenço Marques, xii.1959 (*Haaf*) (NMB); Machipanda, 8.i.1972 (*Bornemissza and Kirk*) (SANC). RWANDA: Butare region, Astrida, x.1952 (*Laurent*) (NMP). SOUTH AFRICA: Natal, Malvern, vii.1897 (*Marshall*) (BM); Natal, Hluhluwe G. R., 19.xi.1992, 27.xi.1992, 28.xi.1992 (*Endrödy-Younga*) (TM); Natal, Hluhluwe G. R., i.1986 (MSNG); Natal, Umfolozi G. R., 25.viii.1971 (*Bornemissza and Insley*) (SANC); Natal, Umfololozi G. R., 6.iv.1974 (*Endrödy-Younga*) (TM). TANZANIA: Serengeti N. P., Lake Ndutu area, 4.vii.1992, 9.vii.1992, ii.1993 (*Foster*) (OUMNH); Serengeti N. P., Western corridor, 1450 m, 27.iv.1975 (*Davis and Dewhurst*) (SANC). UGANDA: Busoga district, Jinja env., i-iii.1968 (*Rwabuneza*) (NMB); Kasese, 600 m, 13-19.xi.1994 (*Snizek*) (CBA); Queen Elizabeth N. P., Mweya, 912/950 m, 16.viii.1990, 7.ix.1990, 21.ix.1990 (*Ieradi*) (CCP). ZAMBIA: Luangwa Valley, Chibembe, 7.x.1984 (*Dellacasa*) (CDE); Luangwa Valley, Mfuwe,7.x.1984 (*Dellacasa)* (CDE). ZIMBABWE: Glen Clova, 21.iv.1971 (*Bornemissza and Aschenborn*) (SANC); Harare area, Mogena, 16.ii.1990 (*Madsen*) (ZSM); Kyle G. R., 22.iv.1971 (*Bornemissza and Aschenborn*) (SANC); Rekometjie, 8-9.i.1982 (*Doube and Macqueen*) (SANC).

Distribution. The species spreads in the whole E Africa, from Ethiopia to South Africa (Natal). Janssens (1953) reported *E. parallelus* also from other localities of Rwanda and Democratic Republic of Congo, but we could not verify the data.

***Eodrepanus striatulus* (Paulian, 1945)**

(Figs 1A, 2H, 3D, 4D, 7E, 8H)

Drepanocerus striatulus Paulian 1945: 140; Janssens 1953: 31, Balthasar 1963a: 69, Biswas 1979: 341, Masumoto 1987: 130, Hanboonsong *et al.* 1999: 467, Kabakov and Napolov 1999: 72, Sewak 2006: 220, Bedzek and Krell 2006: 156.

Diagnosis. The species is very similar to *E. liuchungloi*, but can be distinguished by shape of the male genitalia (primary lamella).

Description. Body elongate, flattened, shining. Uniformely black, with legs dark reddish brown. Clypeus narrow and gently protruding, bearing two blunt teeth, not deeply separated. Clypeal and genal edges evenly curvilinear. Vertex bearing two feeble, longitudinal callosities. Punctuation of head evenly deep and quite dense. Lateral edges bearing some whitish, acuminated setae. Antennal club brown. Pronotal disc feebly depressed, bounded laterally by two longitudinal callosities. Lateral pronotal thirds gently hollowed in the middle and subcarinate. Lateral edges obviously denticulate. Basal edge feebly and widely angular in the middle. Punctures evenly dense; in males uniformely wide, in females feebly ovoidal and umbilicate on the discal depression, round, double and deeper on the callosities, wide and round on the sides. Moreover, in females there are two longitudinal band of short, dense, light setae bordering the discal depression. Scutellum lacking. Elytra elongate, gently narrowed backward. Secondary interstriae flat. First five ones equally wide, sixth one obviously wider. Elytral intervals more or less punctate and setose, the fifth one bearing a row of reddish setae, short and erect. Seventh interval carinate and bearing a narrow row of yellow-reddish, short and recumbent setae. In females each elytron bears an evident callosity at the base of third and fourth intervals; in males these callosities are hardly perceptible or totally lacking. Elytral apices bearing long and partially erect setae. Prosternum deeply punctate. Mesosternum punctate. Metasternum bearing a slight, longitudinal furrow in the middle of the hind half, unevenly and quite densely punctate. Abdominal segments bearing rather big punctures, dense on the sides, very scattered in the middle. Inner edge of fore tibiae moderately bent in the anterior two-thirds, bearing three outer teeth; the two distal close together, the second one bigger than other two; outer edge crenulate. Antero-superior edge of fore femura dentate distally. Metatibial spur as long as 2/3 of first metatarsal joint.

Type material. Holotype ♂ (IRSNB), VIETNAM: Tonkin, Hoa-Binh Region, 1928 (*De Cooman*). Paratype: 1 ♀ (IRSNB), VIETNAM: Tonkin, Hoa-Binh Region, 1928 (*De Cooman*).

Additional material examined. INDIA: Meghalaya, 3 km E Tura, 1500 m, 4.v.1999 (*Dembicky and Pacholatko*) (ZIRAS); Meghalaya, 9 km NW of Jowai, 1400 m, 12.v.1999 (*Dembicky and Pacholatko*) (NMB). LAOS: CE Boli, Kham Xai Province, 8 km NE Ban Nape, 600 m ca., 1-18.v.2001 (*Pacholatko*) (NMB). MYANMAR: Kachin State, Indawgyi Lake, 7 km S Lonton, 250 m ca., 20-25.v.1999 (*Schillhammer and Schuh*) (CSC). NEPAL: Syange, Himalaya, Annapurna Mts., Marsyangdi Khola, 1100 m, 27.v.1993 (*Ahrens*) (MTD). VIETNAM: Vànyen, River Noire, 1923-24 (*Dussault*) (NMB); 52 km SW Lang Son, 370 m, 27.iv.-6.v.1996 (*Pacholatko and Dembicky*) (NMB); Bac Kan Province, Ba Be National Park, 296 m, 19-viii-2005, (*Hayes*) (OXF); Tonkin, Hoa Binh, vii.1934 (*De Cooman*) (NMB); Tonkin, Hoa-Binh (CMN).

Distribution. At present, the species is present in Nepal, NE India, N Myanmar, C Laos, and N Vietnam (Fig. 1A). It was reported also from Thailandia (Masumoto 1987; Hanboonsong *et al.*, 1999) and China (Balthasar 1963a), as well as from other localities of India (Biswas, 1979) and Vietnam (Kabakov and Napolov, 1999). Besides, we could not verify these distribution data. A very old, single specimen from "*Mesepet*", collected by W. Helfer (1810-1840) is present in NMP collection, but we could not place exactly the locality, that could be in Myanmar (Tenasserim Province, or Mergui-Archipel), or India (area around Calcutta). We excluded that the specimen could be collected from the Andamane Islands, where Helfer was killed just after he disembarked.

Biogeographical analysis

Similarity and Cluster Analyses. The cluster (Fig. 10B) based on the Ochiai similarity matrix clearly separates the Afrotropical and Indomalayan macroareas. Within the Indomalayan region, NE India (G) and Indochina (H) are more closely related, while S China (I) was the first to split. In Afrotropical region, WTA (A) and CWTA (B) are well-separated from the whole Eastern part of Africa (C, D, E, F), which is supported by widespread species, as *E. fastiditus* and *E. parallelus*. Only *E. bechynei* shows a disjunct distribution between an eastern (A+B) and a western component (C, D, E, F), with a major barrier constituted by the tropical forest (rain forest) in Congo Basin. On the basis of the cluster, we identified ETA (E), as the area characterized by the greater species richness.

Parsimony Analysis of Endemicity. The first analysis based on an exaustive search on all the 10 macroareas (A-J) led to four most parsimonious cladograms (Statistics: Tree length = 10, CI = 0.9000, HI = 0.1000, CI excluding uninformative characters = 0.8333, HI excluding uninformative characters = 0.1667, RI = 0.9231, RC = 0.8308), which agree on the basal separation between the Afrotropical and Indomalayan regions. They only differed in the reciprocal position of the Indomalayan (G, H and I) and Palearctic

(J) macroareas. Relationships among the Afrotropical macroareas are instead the same in all the trees, and identical to the ones obtained in the Similarity Analysis, with the W macroareas (A and B) separated from a equal-level clade constituted by S and E macroareas (C, D, E, F). In the 50% Majority Rule Consensus Tree the consensus percentages are 100% for the Afrotropical macroareas, while relationships among Indomalayan and Palearctic macroareas were unresolved.

In the second analysis, where the macroareas with a single species were excluded (Huang *et al.* 2007), the exaustive search gave a single tree, that confirmed the former results (Fig 10C, Statistics: Tree length = 8, CI = 1.0000, HI = 0.0000, CI excluding uninformative characters = 1.0000, HI excluding uninformative characters = 0.0000, RI = 1.0000, RC = 1.0000).

Anosim. Analyses were performed grouping macroareas in 4 groups (AB; CDEF; GHI; J), and then in 5 groups (AB; CDF; E; GHI; J). Results showed significant differences among groups in both analyses (Table 4), with r_B always greater than $r_{W,}$ and R >0.75 (meaning that groups are well-separate). Statistics validated the macroareas relationships proposed in former analyses.

Dispersal Vicariance Analysis. After analyzing the optimizations setting maxareas to different values (Table 5), we chose the results of maxareas=4, with 15 dispersals required, on the basis of the less-ambiguity criterion. We then examined all the possible optimal distributions for the chosen optimal recostruction (Fig. 11).

The first recostruction suggests a wide distribution of ancestor (Fig. 11A) in the Afrotropical (E) and Indomalayan (GHI) regions, followed by a vicariance event. The Afrotropical ancestor extend its range (duplications and dispersals) splitting across great part of the Afrotropical region. This hypothesis remains invariate in all the recostructions; after extending into the Palearctic region (+J), the Indomalayan ancestor underwent two vicariance events, and a single dispersal event.

The second reconstruction (Fig. 11B) suggests a more widespread ancestral distribution, including the Afrotropical (E), Palearctic (J) and Indomalayan (more or less extended) regions. The Afrotropical clade of *Eodrepanus* is recostructed as above, whereas within the Indomalayan region several dispersal events take place that extended the range of this clade.

The last recostructions (Fig. 11C, D, E) are similar to the second one, differences involving only the Indomalayan distribution.

Particularly noteworthy is the reconstruction of the Afrotropical clade, that is invariant in all the analysis, even if setting maxareas to different values.

Discussion

Maximum Parsimony and Bayesian Inference confirmed both the hypothesized polyphyly of *Drepanocerus* and the monophyly of *Eodrepanus* **gen. n.**, which is definied by twelve synapomorphic characters (Fig. 9A).

In the phylogenetic tree inferred from analysis of the extant species alone, *Eodrepanus* is constituted by two major clades, with the Afrotropical species well-separated from the Indomalayan ones. Including fossil species, phylogenetic analysis gave a similar tree and showed the close relationships of the Palearctic fossil and the Indomalayan species. Phylogenetic relationships among *E. coopei*, *E. morgani*, *E. paolae* and the two main clades *E. fastiditus-bechynei-parallelus* and *E. striatulus-liuchungloi-integriceps* were unresolved both in parsimony and bayesian reconstructions (Fig. 9C, D). One possible explanation is the high number of missing characters for *E. coopei* (there are only fossils remains of pronotum and elytra), as well as the missing characters for the yet-unknown females of *E. morgani* and *E. paolae*.

Results from Analysis of Similarity and Parsimony Analysis of Endemicity showed two primary biogeographical patterns: an Afrotropical and an Indomalayan clade. The most parsimonious biogeographic recostruction in DIVA postulates an evolutionary scenario in which the Afrotropical clade of *Eodrepanus* genus evolved in East Africa (macroarea E) and secondarily dispersed to West, Central and South Africa. The Indomalayan clade was more or less widely distributed (G, H, I), depending on the recostruction.

As for the origin of colonization of Palearctic Region, it can be hypothesized that a widespread ancestor would be present in both Afrotropical and Indomalayan regions (Fig. 11). This ancestor then dispersed and colonized Palearctic Region likely from the Indomalayan Region (*E. coopei* is more strictly related to the Indomalayan species, see Fig. 9).

Successively, these tropical fauna extinguished in the Palearctic by subsequent climatic changes (lowering of temperature, see Sanmartin *et al.* 2001), and the Afrotropical component are isolated from Indomalayan ones by the break up of Arabian-Indian disjunction due to progressive drying of these areas. The two components remain secluded, with the actually disjoint distribution.

Aknowledgement

This research was supported by grants from the Italian Ministero dell’Istruzione, dell’Università e della Ricerca (MIUR). We are greatly indebted for the loan of material and useful information to various curators of the many institutions enlisted above (see Material and Methods): A. H. Kirk-Spriggs (AMG), F. Génier (CMN), A. Drumont (IRSCNB), G. Cuccodoro (MHNG), V. Marengo (MHNL), A. Taghavian (MNHN), J. Frisch (MNHUB), M. Uhlig (MNHUB), M. de Meyer (MRAC), R. Poggi (MSNG), O. Jäger (MTD), O. Martin (MUC), L. Bartolozzi (MZF), R. Danielsson (MZL), W. Xie (NHMLAC), B. Viklund (NHRS), E. Sprecher (NMB), N. E. Adams [†] (NMNH), J. Hájek (NMP), Z. Simmons (OUMNH), R. Staals (SANC), M. Cochrane (SAMC), J. Harrison (TM), O. Merkl (UNHM), A. Frolov (ZIRAS), M. Baher (ZSM). We are grateful to dr. A. Simonis (Torino) for the useful information. We are also indebted to the many private collectors and researchers who either provided us with material (see list in Material and Methods), and in particular we would thank: dr. M. Bai (CAS) who send us the *E. liuchungloi* specimen, and dr. H. Schillammer (NHMW), who gave us his *E. striatulus* specimens from Myanmar to study. We are very grateful to Prof. G. Russel Coope (Tigh Na Cleirich, Foss, Perthshire, Scotland, UK), who gave us on loan the fossil material to study. We would also thank dr. Isabel Sanmartin (Real Jardin Botánico de Madrid, Spain), for her many suggestions that greatly helped us to improve the text.

References

Alfaro ME, Zoller S, Lutzoni F. 2003. Bayes or Bootstrap? A Simulation Study Comparing the Performance of Bayesian Markov Chain Monte Carlo Sampling and Bootstrapping in Assessing Phylogenetic Confidence. Molecular Biology and Evolution 20:255–266.

Arrow GJ. 1931. The Fauna of British India, including Ceylon and Burma. Part III. Coleoptera Lamellicornia (Coprinae). Taylor and Francis, London. 428 pp.

Balthasar V. 1963a. Neue Arten der Familie Scarabaeidae. 111. Beitrag zur Kenntnis der Scarabaeoidea Col. Časopis Čekoslovenké Spolecnosti Entomologické 60:284–295.

Balthasar V. 1963b. Oniticellini. Eine neue Art von *Drepanocerus*. 113. In: de Saeger H, Baert P. Beitrag zur Kenntnis der Scarabaeoidea. Col. Parc National de la Garamba. Mission H. de Saeger, 40:131–134.

Balthasar V. 1963c. Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region (Coleoptera: Lamellicornia). Band 2, Coprinae. Verlag der tschechoslowakischen Akademie der Wissenschaften, Prag. 628 pp.

Barbero E, Palestrini C, Roggero A. 2003. Revision of the genus Phalops Erichson, 1848 (Coleoptera: Scarabaeidae: Onthophagini). Monografie del Museo Regionale di Scienze Naturali, Torino. 378 pp.

Bedzek A, Krell F-T. 2006. Scarabaeidae Scarabaeinae Oniticellini. Vol 3. In: Löbl I, Smetana A. Catalogue of Palearctic Coleoptera. Apollo Books, Stenstrup. pp 157–158.

Biswas S. 1979. Studies on the scarab beetles (Coleoptera: Scarabaeidae) of North India. Part II. Three new species and two new records from India. Journal of the Bombay Natural History Society 76:338–342.

Bolton HC. 1991. On the Mathematical Significance of the Similarity Index of Ochiai as a Measure for Biogeographical Habitats. Australian Journal of Zoology 39:143–156.

Boucomont A. 1921. Synopsis des Onticellini d’Afrique. Revue de zoologie et de botanique Africaines 9:197–234.

Boucomont A, Gillet JJE. 1927. Coleopterorum Catalogus auspiciis et auxilio W. Junk editus a S. Schenkling. Pars 90. Fam. Scarabaeidae. Subfam. Coprinae II. Berlin. 168 pp.

Böving AG. 1936. Description of the larva of *Plectris aliena* Chapin and explanation of new terms applied to the epipharynx and raster. Proceedings of the Entomological Society of Washington 38:169–185.

Bremer K. 1988. The limits of aminoacid sequence data in angiosperm phylogenetic reconstruction. Evolution 42:795–803.

Bremer K. 1994. Branch support and tree stability. Cladistics 10:295–304.

Cabrero-Sañudo FJ. 2007. The phylogeny of Iberian Aphodiini species (Coleoptera, Scarabaeoidea, Scarabaeidae, Aphodiinae) based on morphology. Systematic Entomology 32:156–175.

Cambefort Y. 1971. Scarabaeinae récoltés dans le Fouta Djalon (Guinée). Bulletin de l’I.F.A.N. 3:420–424.

Cambefort Y. 1979. Données préliminaires sur la taxonomie des *Caccobius* Thomson *s. lat.* (Coleoptera, Scarabaeoidea, Scarabaeinae). Nouvelle Revue d'Entomologie 2:119-128.

Cambefort Y. 1984. Étude écologique des Coléoptères Scarabaeidae de Côte d’Ivoire. Travaux des Chercheurs de la Station de Lamto, Lamto. 294 pp.

Cobbett A, Wilkinson M, Wills MA. 2007. Fossils impact as Hard as Living Taxa in Parsimony Analyses of Morphology. Systematic Biology 56:753–766.

Contreras-Medina R, Vega IL, Morrone JJ. 2007. Application of parsimony analysis of endemicity to Mexican gymnosperm distributions: grid-cells, biogeographical provinces and track analysis. Biological Journal of the Linnean Society 92:405–417.

Coope GR. 1979. Late Cenozoic fossil Coleoptera: Evolution, Biogeography, and Ecology. Annual Review of Ecology and Systematics 10:247–267.

Coope GR. 2000. The climatic significance of coleopteran assemblages from the Eemian deposits in southern England. Netherlands Journal of Geosciences 79:257–267.

Coope GR. 2001. Biostratigraphical distinction of interglacial coleopteran assemblages from southern Britain attributed to Oxygen Isotope Stages 5e and 7. Quaternary Science Reviews 20:1717–1722.

Cummings MP, Handley SA, Myers DS, Reed DL, Rokas A, Winka K. 2003. Comparing Bootstrap and Posterior Probability Values in the Four-Taxon Case. Systematic Biology 52:477–487.

d’Orbigny H. 1916. Voyage dans l’Afrique Orientale Anglaise 1912-1913 par M. Guy Babault. Résultats Scientifiques. Insectes Coléoptères Scarabaeidae Onthophagini et Oniticellini. Blondel la Rougery [?], Paris. 33pp.

Davis ALV, Dewhurst CF. 1993. Climatic and biogeographical associations of Kenyan and northern Tanzanian dung beetles (Coleoptera: Scarabaeidae). African Journal of Ecology 31:290–305.

Dellacasa G. 1977. Morfologia dell’epifaringe negli *Aphodius* adulti. Studi di sistematica sugli Aphodiinae VII. (Coleoptera, Scarabaeidae). Memorie della Società entomologica italiana 56:229–232.

Doube BM. 1983. The habitat preference of some bovine dung beetles in Hluhluve Game Reserve, South Africa. Bulletin of Entomological Research 73:357–371.

Endrödi S. 1971. The scientific results of the Hungarian Zoological Expedition to Tanganyika. 16. Coleoptera: Lamellicornia (*partim*). Folia Entomologica Hungarica 24:289–311.

Endrödi S. 1976. Lamellicornia (Coleoptera) aus Ghana. II. Annales Historico-Naturales Musei Nationalis Hungarici 68:155–164.

Endrödy-Younga S. 1982. An annotated check-list of dung associated beetles of the Savanna Ecosystem Project study area, Nylsvley. South African National Scientific Programmes Report 59:1–34.

Farris JS, Albert VA, Kallersjo M, Lipscomb D, Kluge A. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12:99–124.

Felsenstein J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39:783–791.

Ferreira MC. 1954. Monografia dos Escarabeídos da África do Sul. III parte tribo Oniticellini. 1. Géneros *Drepanocerus* Kirby e *Scaptocnemis* Péring. Revista da Facultade de Ciências de Lisboa 4:245–280.

Ferreira MC. 1955. Catálogo dos Escarabídeos existentes no Museu Dr. Álvaro de Castro. Memorias do Museu Dr. Álvaro de Castro 3:55–86.

Ferreira MC. 1958. Os Escarabídeos do Transvaal Museum (Tribos Scarabaeini, Gymnspleurini [*sic!*] e Oniticellini). Boletim da Sociedade dos Estudos de Moçambique 27:131–150.

Ferreira MC. 1962. Coprinae (Coleoptera Lamellicornia) Fam. Scarabaeidae. In: de Saeger H, Baert, P. Parc National de la Garamba. Mission H. de Saeger. 30. 123 pp.

Ferreira MC. 1967a. Os Escarabídeos da sub-região natural da África do Sul. IX. Chaves para determinação das espécies dos géneros *Drepanocerus* Kirby, *Euoniticellus* Janssens, *Tiniocellus* Péringuey, *Liatongus* Reitter e *Oniticellus* Serville (Tribo Oniticellini). Arquivos do Museu Bocage 1:39–47.

Ferreira MC. 1967b. Os Escarabídeos de Moçambique. I. Revista de entomología de Moçambique 10:5–778.

Ferreira MC. 1968-69. Os Escarabídeos de Africa (sul do Saára). Revista de entomología de Moçambique 11:1–1088.

Franks JW. 1960. Interglacial Deposits at Trafalgar Square, London. New Phytologist 59:145–152.

Fric Z, Wahlberg N, Pech P, Zrzavý J. 2007. Phylogeny and classification of the *Phengaris-Maculinea* clade (Lepidoptera: Lycaenidae): total evidence and phylogenetic species concepts. Systematic Entomology 32:558–567.

Gao C, Keen DH, Boreham S, Coope GR, Pettit ME, Stuart AJ, Gibbard PL. 2000. Last Interglacial and Devensian deposits of the River Great Ouse at Woolpack Farm, Fenstanton, Cambridgeshire, UK. Quaternary Science Reviews 19:787–810.

Gillet JJE. 1911. Coleopterorum Catalogus auspiciis et auxilio W. Junk editus a S. Schenkling. Pars 38. Fam. Scarabaeidae. Subfam. Coprinae I. Berlin. 100 pp.

Halffter G. 1961. Monografía de las especies norteamericanas del género *Canthon* Hoffsg. (Coleopt., Scarab.). Ciencia 20:225–320.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4:1–9. Free Software. The program is available at: http://palaeo-electronica.org/

Hanboonsong Y, Chunram S, Pimpasalee S, Emberson RW, Masumoto K. 1999. The dung beetle fauna (Coleoptera, Scarabaeidae) of Northeast Thailand. Elytra 27:463–469.

Hanski I, Cambefort Y. 1991. Dung beetle ecology. Princeton University Press, Princeton. 481 pp.

Hayek LAC. 1994. Analysis of amphibian biodiversity data. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS. Measuring and monitoring biological diversity. Standard methods for amphibians. pp. 207–269. Smithsonian Institution Press, Washington.

Hijmans RJ, Guarina L, Jarvis A, O’Brien R, Mathur P. 2005. DIVA-GIS. v5.4.0.1. Free Software. The program is available at: www.diva-gis.org/

Holder M, Lewis PO. 2003. Phylogeny Estimation: Traditional and Bayesian Approaches. Nature Reviews Genetics 4:275–284.

Huang X, Lei F, Qiao G. 2007. Areas of endemism and patterns of diversity for aphids of the Qinghai-Tibetan Plateau and the Himalayas. Journal of Biogeography 35:230–240.

Hubálek Z. 1982. Coefficients of association and similarity, based on binary (presence-absence) data: an evaluation. Biological Reviews of the Cambridge Philosophical Society 57:669–689.

Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP. 2001. Bayesian Inference of Phylogeny and Its Impact on Evolutionary Biology. Science 294:2310–2314.

Jackson DA, Somers KM, Harvey HH. 1989. Similarity coefficients: measures of co-occurrence and association or simply measure of occurrence? The American Naturalist 133:436–453.

Janssens A. 1939. Mission G. F. de Witte 1933-1935. Oniticellini, Coleoptera Lamellicornia fam. Scarabaeidae. Institut des Parcs Nationaux du Congo Belge, Exploration du Parc National Albert 25:1–22.

Janssens A. 1953. Mission G. F. de Witte. Oniticellini (Coleoptera Lamellicornia). Institut des Parcs Nationaux du Congo Belge, Exploration du Parc National de l’Upemba 11:1–118.

Janssens A. 1956. Contribution à l’étude de la faune entomologique du Ruanda-Urundi (Mission P. Basilewsky 1953). XC. Coleoptera Scarabaeidae Scarabaeinae. Annales du Musée Royal du Congo Belge C. Zoologie 51:343–356.

Kabakov ON. 2006. Lamellicorn beetle from subfamily Scarabaeinae of the fauna of Russia and adjacent countries. Tovarichestvo nauchnykh izdanii 142:1–374 [in Russian].

Kabakov ON, Napolov A. 1999. Fauna and ecology of Lamellicornia of subfamily Scarabaeinae (Coleoptera, Scarabaeidae) of Vietnam and some parts of adjacent countries: South China, Laos and Thailand. Latvijas Entomologs 37:58–96.

Kirby W. 1828. A description of some Coleopterous Insects in the Collection of the Rev. F.W. Hope, F.L.S. The Zoological Journal 3:520–525.

Kryzhanovsky OL, Medvedev SI. 1966. Dung Beetles of the Subfamily Coprinae (Coleoptera: Scarabaeidae) in Yunnan Province of South-Western China, Part 1. Revue d'Entomologie de l'URSS 45:387–400. [In Russian].

Lesne P. 1900. Coléoptères. In: Michel C. Mission de Bonchamp. Vers Fachoda à la rencontre de la mission Marchand à travers l'Ethiopie. pp. 498–501. Plon-Nourrit and Cie, Paris.

Lewis PO. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50:913–925.

Masumoto K. 1987. Coprophagid beetles from northwest Thailand (I). Entomological review of Japan 42:125–131.

Medina CA, Scholtz CH, Gill BD. 2003. Morphological variation and systematics of *Canthon* Hoffmansegg 1817, and related genera of new world Canthonini dung beetles. Deutsche Entomologische Zeitschrift 50:23–68.

Moretto P, Bordat P. 2006. Les scarabéides coprophages du Parc National du Niokolo-Koba au Sénégal (Coleoptera, Scarabaeoidea). Nouvelle revue d'entomologie 23:115–145.

Morrone JJ. 1994. On the identification of areas of endemism. Systematic Biology 43:438–441.

Müller J, Reisz RR. 2006. The Phylogeny of Early Eureptiles: Comparing Parsimony and Bayesian Approaches in the Investigation of a Basal Fossil Clade. Systematic Biology 55:503–511.

Murguía M, Villaseñor JL. 2000. Estimating the quality of the records used in quantitative biogeography with presence-absence matrices. Annales Botanici Fennici 37:289–296.

Nel A, De Villiers WM. 1988. Mouthparts Structure in Adult Scarab Beetles (Coleoptera: Scarabaeoidea). Entomologia Generalis 13:95–114.

Nel A, Scholtz CH. 1990. Comparative morphology of the mouthparts of adult Scarabaeoidea (Coleoptera). Entomology Memoirs 80:1–84.

Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey JL. 2004. Bayesian phylogenetic analysis of combined data. Systematic Biology 53:47–67.

Ochiai A. 1957. Zoogeographical Studies on the Soleoid Fishes found in Japan and Its Neighbouring Regions. II. Bulletin of the Japanes Society of Scientific Fisheries 22:526–530 [in Japanese].

Page RDM. 2001a. Nexus Data Editor v0.5.0. Free Software. The program is available at: http: //taxonomy.zoology.gla.ac.uk/rod/rod.html.

Page RDM. 2001b. TreeView v1.6.6. Free Software. The program is available at: http://taxonomy.zoology.gla.ac.uk/rod/rod.html.

Philips TK, Pretorius E, Scholtz CH. 2004. A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. Invertebrate Systematics 18:53–88.

Raffray A. 1877. Coléoptères Lamellicornes rapportés d'Abyssinie et Zanzibar. Descriptions des espèces nouvelles. Revue et Magasin de Zoologie Pure et Appliquée (Series 3) 4:312–336.

Rannala B, Yang Z. 1996. Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. Journal of Molecular Evolution 43:304–311.

Rohlf FJ. 1998-2005. NTSYSpc - Numerical Taxonomy and Multivariate Analysis System v2.20. Exeter Software, Setauket New York.

Ronquist F. 1996. DIVA v. 1.1. User's Manual. Software free available at http://www.ebc.uu.se/systzoo/research/diva/diva.html

Ronquist F. 1997. Dispersal-Vicariance Analysis: A New Approach to the Quantification of Historical Biogeography. Systematic Biology 46:195–203.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Ronquist F, Huelsenbeck JP, van der Mark P. 2005. MrBayes v3.1 Manual, Software free available at http://mrbayes.net

Rosen BR. 1984. Reef coral biogeography and climate through the Late Cenozoic: just islands in the sun or a critical pattern of islands? In: Brenchley P. Fossils and climate. John Wiley and Sons, London. pp. 201–262.

Rosen BR. 1988. From fossils to earth history: applied historical biogeography. In: Myers AA, Giller PS. Analytical biogeography. Chapman and Hall, London. pp. 437–481.

Rosen BR, Smith AB. 1988. Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from late Cretaceous to Recent, using a new method. Gondwana and Tethys, Special Publications of the Geological Society of London 37:275–306.

Rougon C, Rougon D. 1977. Contribution à l'étude de la faune entomologique de la République du Niger. Bulletin de l'I.F.A.N. 39:653–681.

Sanmartin I. 2003. Dispersal vs. vicariance in the Mediterranean: historical biogeography of the Palearctic Pachydeminae (Coleoptera, Scarabaeoidea). Journal of Biogeography 30:1883–1897.

Sanmartin I, Enghoff H, Ronquist F. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biological Journal of the Linnean Society 73:345–390.

Sanmartin I, Martin-Piera F. 2003. First phylogenetic analysis of the subfamily Pachydeminae (Coleoptera, Scarabaeoidea, Melolonthidae): the Palearctic Pachydeminae. Journal of Zoological Systematics and Evolutionary Research 41:2-46.

Sewak R. 2006. Insecta: Coleoptera: Scarabaeidae: Coprinae (Dung Beetles). In: Alfred JRB. Fauna of Arunachal Pradesh. Part 2, Invertebrates. State Fauna Series, Zoological Survey of India, Kolkata. pp 191–224.

Simonis A. 1981. *Anoplodrepanus*, nuovo genere di Oniticellini (Coleoptera, Scarabaeidae). Bollettino del Museo di Zoologia dell'Università di Torino 7:87–94.

Simonis A. 1985a. Un nuovo genere e tre nuove specie di Drepanocerina (Coleoptera: Scarabaeidae: Oniticellini). Revue Suisse de Zoologie 92:93–106.

Simonis A. 1985b. Aspetti filogenetici della sistematica dei Drepanocerina (Coleoptera, Scarabaeidae) e loro implicazioni zoogeografiche. Atti XVI Congresso Nazionale Italiano di Entomologia, Palermo-Erice-Bagheria, 28.v/1.vi.1985, pp 293–298. Palermo.

Simonis A, Zunino M. 1980. Il genere *Cyptochirus* Lesne (Coleoptera, Scarabaeoidea, Oniticellini). Bollettino del Museo di Zoologia dell'Università di Torino 4:21–40.

Straka J, Bogusch P. 2007. Phylogeny of the bees of the family Apidae based on larval characters with focus on the origin of cleptoparasitism (Hymenoptera: Apiformes). Systematic Entomology 32:700–711.

Stuart AJ. 1976. The History of the Mammal Fauna During the Ipwichian/Last Interglacial in England. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 276:221–250.

Stuart AJ. 1982. Pleistocene Vertebrates in the British Isles. Longman, London. 212 pp.

Sutcliffe AJ. 1995. Insularity of the British Isles 250000-300000 years age: the mammalian, including human, evidence. In: Preece RC. Island Britain: a Quaternary Perspective. Geological Society of London, Special Publication No. 96, London. pp. 127–140.

Swofford DL. 1998-2002. PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4b.10. Sinauer Associates, Sunderland, MA.

Verdú JR, Galante E. 2004. Behavioural and morphological adaptations for a low-quality resource in semi-arid environments: dung beetles (Coleoptera, Scarabaeoidea) associated with the European rabbit (*Oryctolagus cuniculatus* L.). Journal of Natural History 38:705–715.

Wiedemann CRW. 1823. Zweihundert neue Käfer von Java, Bengalen und den Vorgebirgen der Gutten Hoffnung. Zoologisches Magazin 4:107–183.

Wiens J, Bonnet RM, Chippindale PT. 2005. Ontogeny discombobulates phylogeny: Paedomorphosis and higher-level salamander relationships. Systematic Biology 54:91–110.

Wilcox TP, Zwickl DJ, Heath TA, Hillis DM. 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. Molecular Phylogenetics and Evolution 25:361-371.

Zagwijn WH. 1996. An Analysis of Eemian Climate in Western and Central Europe. Quaternary Science Review 15:451-469.

Tables

Table 1. List of the thirty species assigned to *Drepanocerus* Kirby according to Janssens (1953), modified adding the species described afterwards. The asterisks indicate the species here studied.

	Species	**Distribution**
1	*D. abyssinicus* Roth 1851	Afrotropical Region
2	*D. bechynei* Janssens 1953*	Afrotropical Region
3	*D. bos* Endrödi 1976	Afrotropical Region
4	*D. caelatus* Gerstaecker 1871	Afrotropical Region
5	*D. endroedyi* Endrödi 1976	Afrotropical Region
6	*D. fastiditus* Péringuey 1900*	Afrotropical Region
7	*D. freyi* Janssens 1953	Afrotropical Region
8	*D. hircus* Wiedemann 1823	Oriental Region
9	*D. impressicollis* Boheman 1857	Afrotropical Region
10	*D. integriceps* Janssens 1953*	Oriental Region
11	*D. kazirangensis* Biswas 1979	Oriental Region
12	*D. kirbyi* Kirby 1828	Afrotropical Region
13	*D. kovacsi* Endrödi 1976	Afrotropical Region
14	*D. laticollis* Fåhraeus 1857	Afrotropical Region
15	*D. liuchungloi* Kryzhanovsky & Medvedev 1966*	Oriental Region
16	*D. marshalli* Boucomont 1921	Afrotropical Region
17	*D. parallelus* Raffray 1877*	Afrotropical Region
18	*D. patrizii* Boucomont 1923	Afrotropical Region
19	*D. pulvinarius* Balthasar1963	Afrotropical Region
20	*D. runicus* Arrow 1909	Oriental Region
21	*D. saegeri* Balthasar 1963	Afrotropical Region
22	*D. schimperi* Janssens 1953	Afrotropical Region
23	*D. setosus* Wiedemann 1823	Oriental Region
24	*D. simplex* Kabakov 2006	Eastern Palearctic Region
25	*D. sinicus* Harold 1868	Oriental Region
26	*D. striatulus* Paulian 1945*	Oriental Region
27	*D. striatus* Boucomont 1921	Afrotropical Region
28	*D. strigatus* Janssens 1953	Afrotropical Region
29	*D. sulcicollis* Laporte de Castelnau 1840	Afrotropical Region
30	*D. szunyoghyi* Endrödi 1971	Afrotropical Region

Table 2. Matrix of the 51 characters employed in the phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cyptochirus	0	0	0	0	0	0	0	0	0	0	0	0	0	0/2	0	0	0
D.patrizii	0	1	1	0	0	0	0	1	0	0	1	1	0	1	0	1	1
D.kirbyi	0	1	1	0	0	0	0	1	0	0	1	1	0	1	0	1	1
D.impressicollis	2	0	1	0	1	0	1	0	0	0	0	2	0	2	0	0	0
D.marshalli	0	0	1	0	1	0	1	0	0	0	0	2	0	2	0	0	0
E.bechynei	1	0	2	1	2	1	2	0	1	1	0	1	0	2	1	0	0
E.fastiditus	1	0	2	1	2	1	2	0	1	1	0	1	0	2	1	0	0
E.integriceps	?	0	2	1	2	?	1	1	0	1	1	0	1	?	1	0	0
E.liuchungloi	?	0	2	1	2	?	2	1	1	1	1	0	1	?	0	0	0
E.morgani	?	0	2	1	2	?	1	0	1	1	0	0	1	?	1	0	0
E.paolae	?	0	2	1	2	?	2	0	1	1	0	1	0	?	0	0	0
E.parallelus	1	0	2	1	2	1	2	0	1	1	0	1	1	2	1	0	0
E.striatulus	1	0	2	1	2	1	2	1	1	1	1	1	1	2	0	0	0
E.coopei	?	?	?	1	2	?	2	1	1	1	0	1	1	?	?	?	?

Table 2. (continued)

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Cyptochirus	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0
D.patrizii	0	0	1	1	1	2	0	2	2	2	0	1	0	0	0	0	0
D.kirbyi	0	1	1	1	1	2	0	2	2	2	0	1	0	0	0	0	0
D.impressicollis	0	0	1	0	2	0	0	0	0	0	1	1	0	0	0	1	0
D.marshalli	0	0	1	0	2	0	0	0	0	0	1	1	0	0	0	1	0
E.bechynei	1	1	0	1	1	1	1	0	1	1	1	0	1	2	1	2	1
E.fastiditus	1	1	0	1	1	1	1	1	0	1	1	2	1	2	1	1	1
E.integriceps	0	0	0	2	0	1	1	0	1	1	1	2	1	0	1	2	1
E.liuchungloi	0	0	0	2	0	1	1	0	0	1	1	2	1	1	1	1	1
E.morgani	0	0	0	1	0	1	1	0	1	1	1	0	1	0	1	1	1
E.paolae	0	0	1	1	0	1	1	0	1	1	1	0	1	0	1	1	1
E.parallelus	1	1	1	1	1	1	1	0	1	1	1	2	1	0	1	0	1
E.striatulus	0	0	1	2	0	1	1	0	0	1	1	0	1	1	1	1	1
E.coopei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table 2. (continued)

	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Cyptochirus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D.patrizii	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	-	-
D.kirbyi	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	-	-
D.impressicollis	0	0	1	0	0	0	1	1	2	0	0	1	0	0	0	0	1
D.marshalli	0	1	0	0	0	0	1	1	2	0	0	1	0	0	0	0	1
E.bechynei	1	0	1	0	1	2	1	1	1	0	1	0	0	1	0	1	1
E.fastiditus	0	1	1	0	0	2	1	2	0	1	1	1	0	1	0	1	0
E.integriceps	1	0	1	2	2	0	1	1	1	0	1	0	?	?	?	?	?
E.liuchungloi	0	0	1	2	2	2	1	2	1	0	1	0	?	?	?	?	?
E.morgani	0	1	1	0	1	2	1	2	0	2	1	0	?	?	?	?	?
E.paolae	0	1	1	1	2	2	1	2	0	1	1	0	?	?	?	?	?
E.parallelus	0	1	1	0	1	2	1	1	1	0	1	1	0	1	0	1	0
E.striatulus	1	0	1	2	2	2	1	2	0	0	1	0	1	1	0	1	1
E.coopei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table 3. Binary matrix of absence/presence of the *Eodrepanus* species. See text (Material and Methods) for the list of macroareas.

	A	B	C	D	E	F	G	H	I	J
E. bechynei	1	1	1	1	1	1	0	0	0	0
E. coopei	0	0	0	0	0	0	0	0	0	1
E. fastiditus	0	0	1	1	1	1	0	0	0	0
E. integriceps	0	0	0	0	0	0	0	0	1	0
E. liuchungloi	0	0	0	0	0	0	0	1	1	0
E. morgani	0	1	0	0	0	0	0	0	0	0
E. paolae	0	0	0	0	1	0	0	0	0	0
E. parallelus	0	1	1	1	1	1	0	0	0	0
E. striatulus	0	0	0	0	0	0	1	1	0	0

Table 4. Results of ANOSIM.

	r_W	r_B	R	$p_{(same)}$
Analysis 1	7.6	27.4	0.88	0.00040
Analysis 2	8.5	25.67	0.76	0.00053

Table 5. Results of DIVA, number of nodes are reported in Fig. 11F.

Node	**Optimal distributions at each node**		
	maxareas = 2	**maxareas = 3**	**maxareas = 4**
10	E	E	E
11	E	E	E
12	BE	BE	BE
13	E	E	E
14	I/HI	I/HI	I
15	H/GI/HI	H/GI/HI/GHI	GI/HI/GHI
16	GJ/HJ/IJ	GJ/HJ/GHJ/IJ/GIJ/HIJ	GHJ/GIJ/HIJ/GHIJ
17	EG/EH/EI/EJ	EGH/EGI/EHI/EGJ/EHJ/EIJ	EGHI/EGHJ/EGIJ/EHIJ

Captions to figures

Fig. 1. Maps of distribution of the nine *Eodrepanus* species: A, *E. coopei* (black star); *E. morgani* (black cross); *E. paolae* (black rhombus); *E. striatulus* (black square); *E. integriceps* (black dot); *E. liuchungloi* (black triangle). B, *E. bechynei*. C, *E. fastiditus*. D, *E. parallelus*.

Fig. 2. Male facies: A, *E. bechynei* (PW = 1.87 mm, EL = 1.91 mm, EW = 1.94 mm); B, *E. fastiditus* (PW = 1.72 mm, EL = 1.83 mm, EW = 1.79 mm); C, *E. integriceps* (PW = 2.51 mm, EL = 2.50 mm, EW = 2.64 mm); D, *E. liuchungloi* (PW = 1.81 mm, EL = 1.77 mm, EW = 1.91 mm); E, *E. morgani* (PW = 2.05 mm, EL = 2.00 mm, EW = 2.20 mm); F, *E. paolae* (PW = 2.17 mm, EL = 2.16 mm, EW = 2.25 mm); G, *E. parallelus* (PW = 2.18 mm, EL = 2.21 mm, EW = 2.19 mm); H, *E. striatulus* (PW = 1.67 mm, EL = 1.68 mm, EW = 1.76 mm).

Fig. 3. Female facies: A, *E. bechynei* (PW = 1.80 mm, EL = 1.78 mm, EW = 1.83 mm); B, *E. fastiditus* (PW = 1.80 mm, EL = 1.84 mm, EW = 1.84 mm); C, *E. parallelus* (PW = 2.34 mm, EL = 3.31 mm, EW = 2.28 mm); D, *E. striatulus* (PW = 1.52 mm, EL = 1.49 mm, EW = 1.58 mm).

Fig. 4. Genitalia: A, *E. bechynei*; B, *E. fastiditus*; C, *E. parallelus*; D, *E. striatulus*.

Fig. 5. Left elytron: A, *E. coopei*; B, *E. fastiditus*; C, *E. parallelus*. Pronotum: D, *E. coopei* , with details of punctuation, right: central disc, left: side; E, *E. fastiditus*; F, *E. parallelus*.

Fig. 6. Male Genitalia: A, *E. integriceps*; B, *E. liuchungloi*; C, *E. morgani*; D, *E. paolae*.

Fig. 7. Epipharynx: A, *E. bechynei*; B, *E. fastiditus*; C, *E. integriceps*; D, *E. liuchungloi*; E, *E. striatulus*; F, *E. morgani*; G, *E. paolae*; H, *E. parallelus*.

Fig. 8. Mentum: A, *E. bechynei*; B, *E. fastiditus*; C, *E. integriceps*; D, *E. liuchungloi*; E, *E. morgani*; F, E. *paolae*; G, *E. parallelus*; H, *E. striatulus*.

Fig. 9. A, Maximim Parsimony Tree of the extant taxa, with Bootstrap values reported below branches (value< 50% are not reported). Characters synapomorphies are reported above branches (state changes: black dots = 1; grey dots = 2). Tree statistics are reported in text. B, Bayesian Consensus Tree with extant taxa derived from analysis of morphological characters, with posterior clade probabilities below branches. C, Maximum Parsimony Tree with the fossil species. D, Bayesian Consensus Tree with fossil species, the posterior clade probabilities values are below branches.

Fig. 10. A, Map of the ten (A-J) ecological macroareas. B, Cluster of Similarity Matrix (Ochiai Index). C, PAE Tree excluding macroareas with a single species.

Fig. 11. Dispersal-Vicariance analysis. Settings: maxareas=4, bound=250, hold=1000, weight=1.000, age=1.000. Optimal reconstruction requires 15 dispersals. A-E, the hypotheses were traced on branches; F, Tree with numbers of nodes.

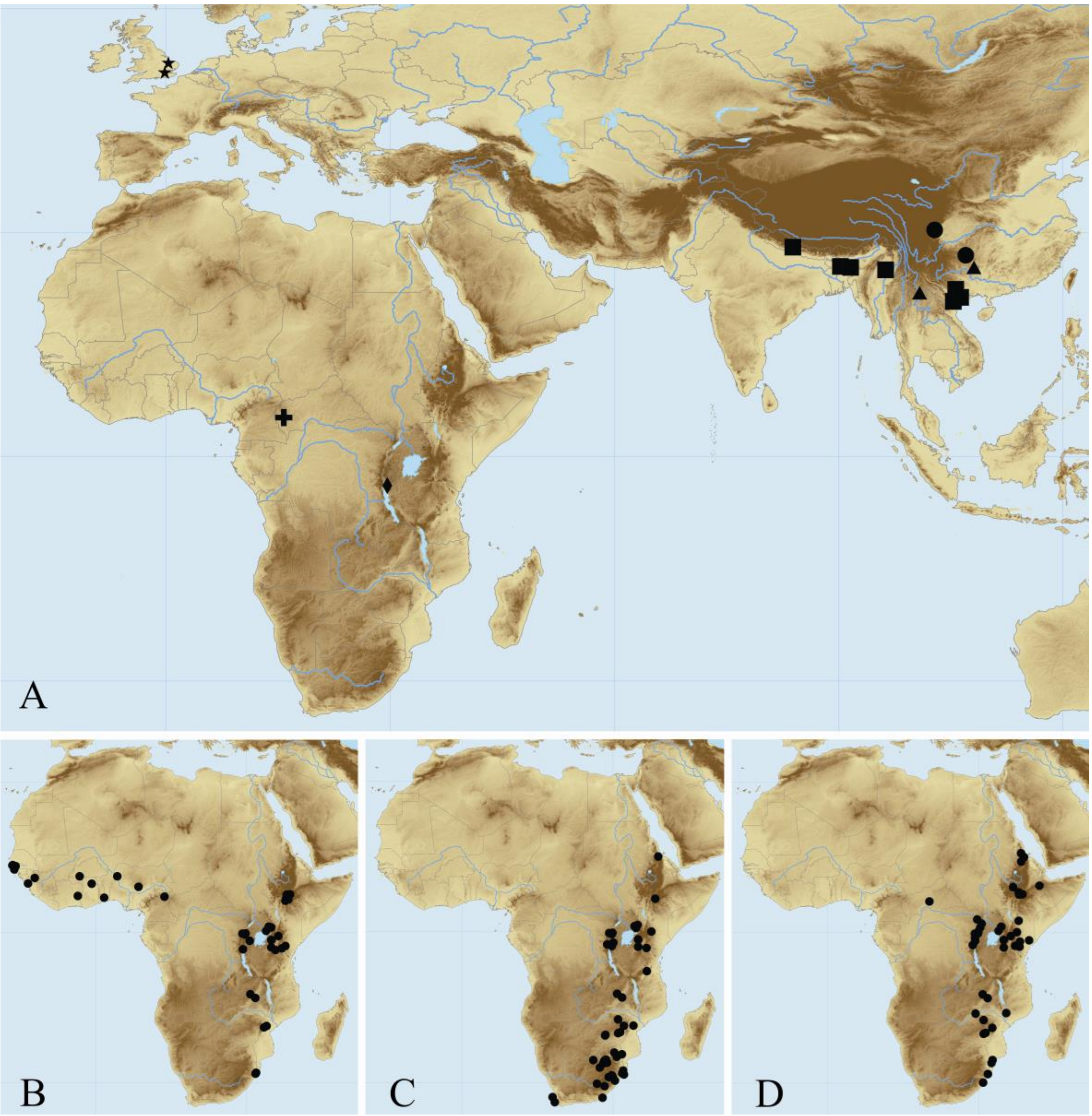

Fig. 1.

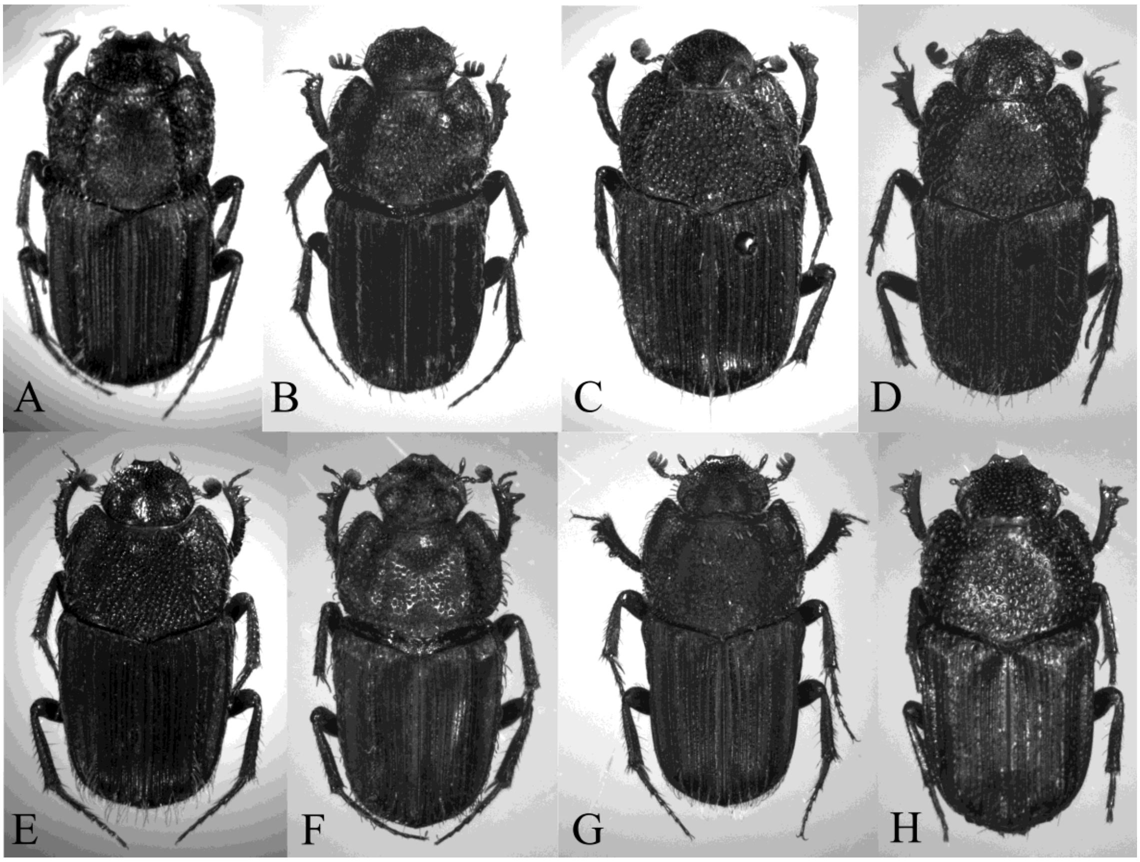

Fig. 2.

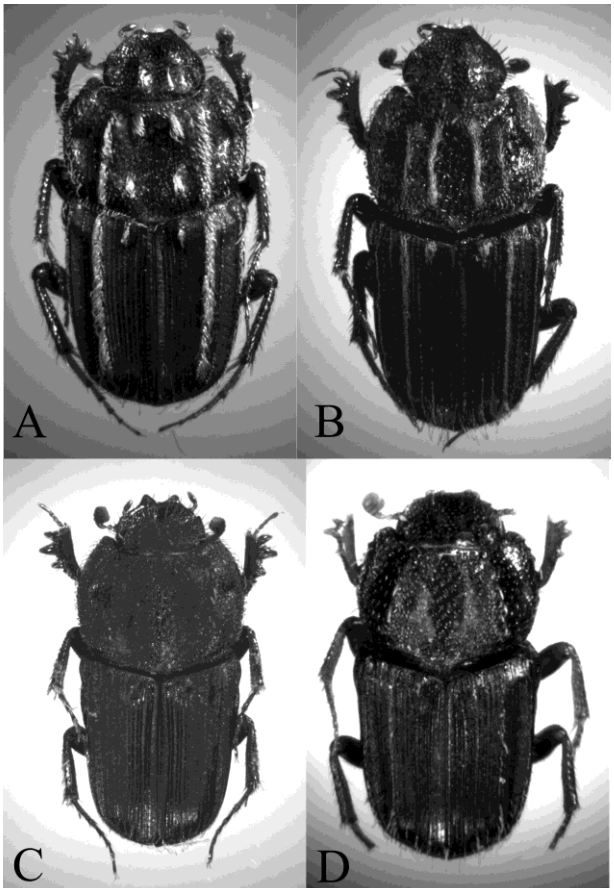

Fig. 3.

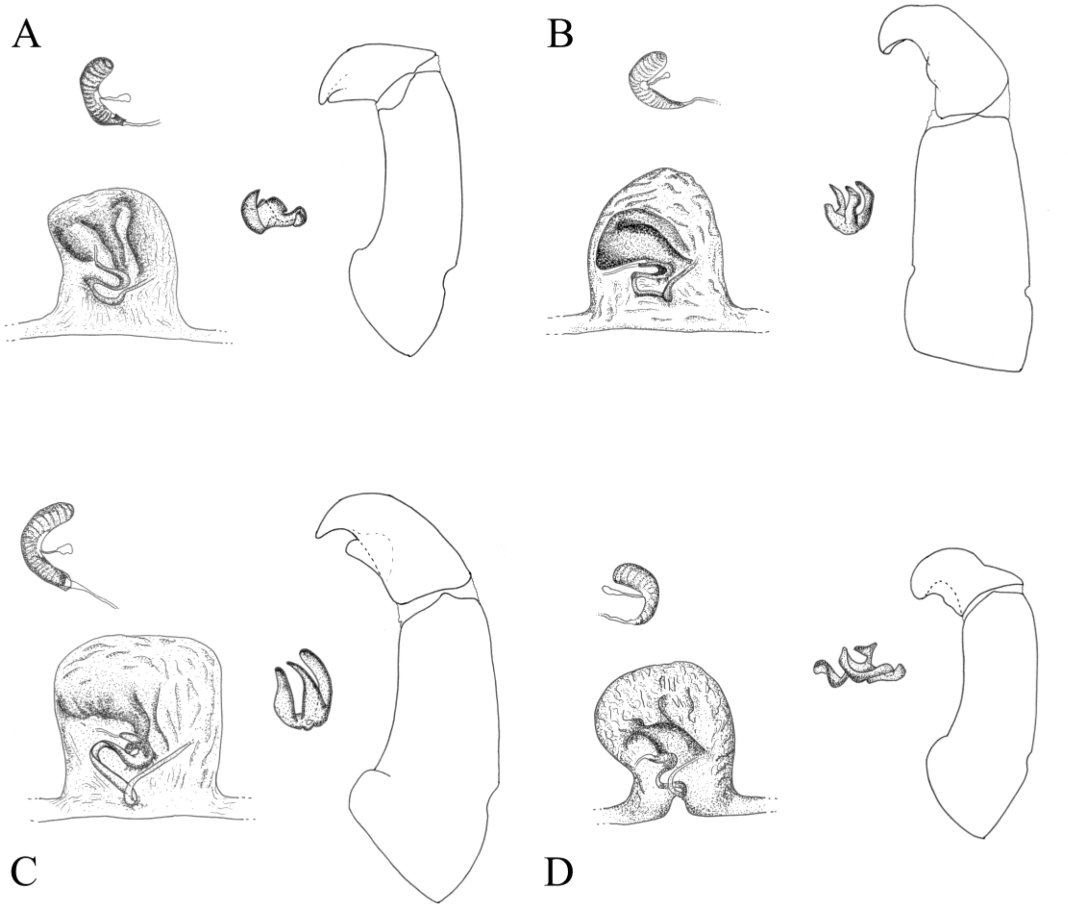

Fig. 4.

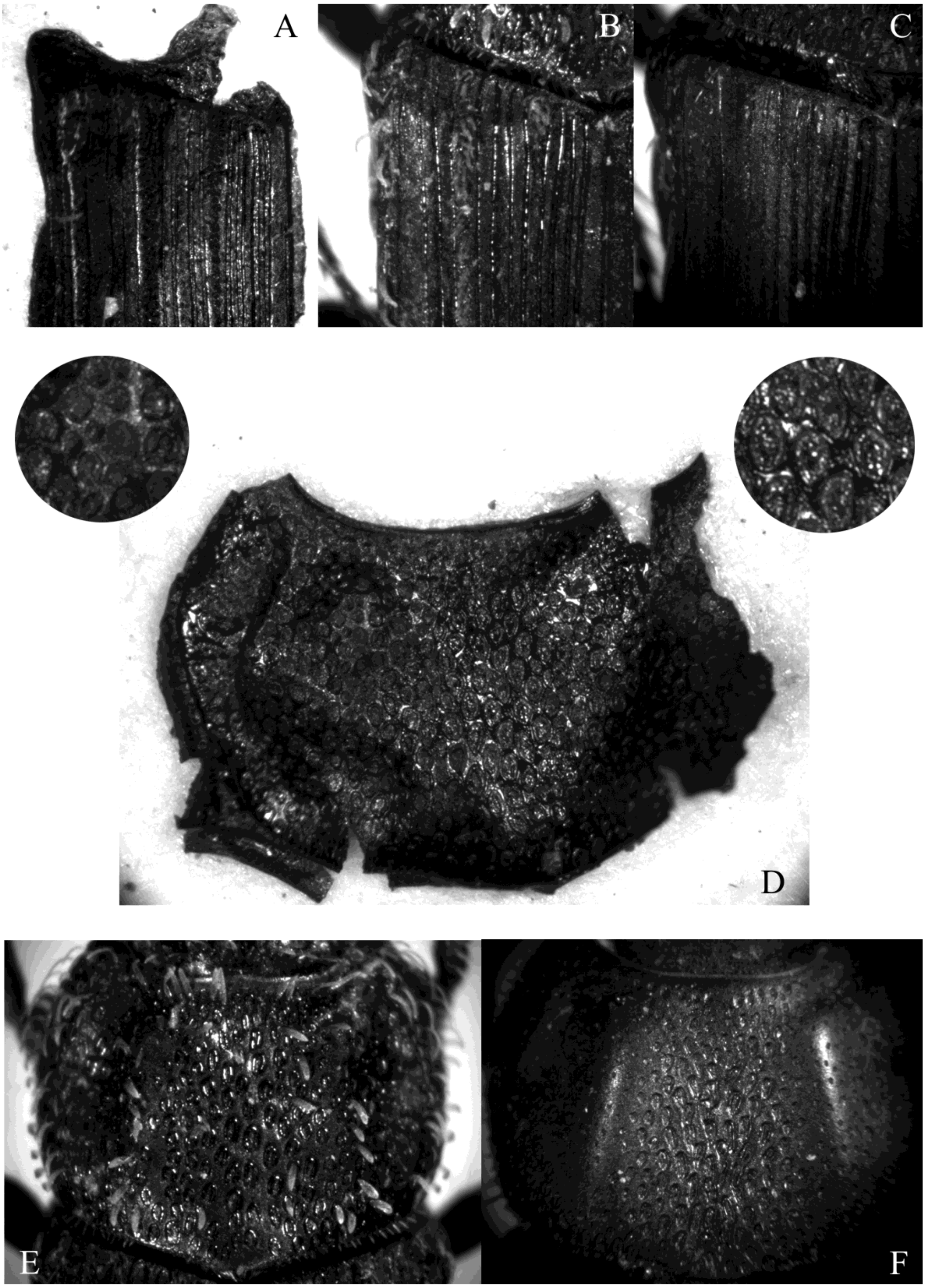

Fig. 5.

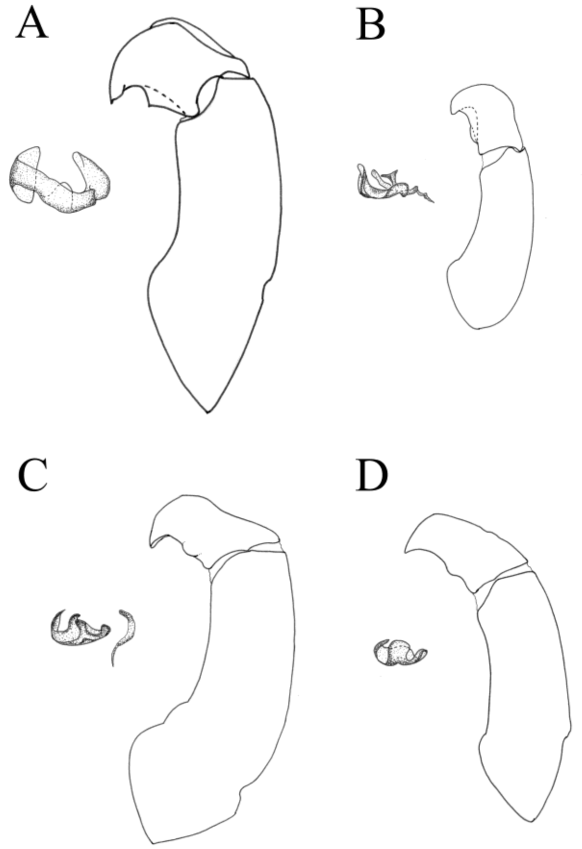

Fig. 6.

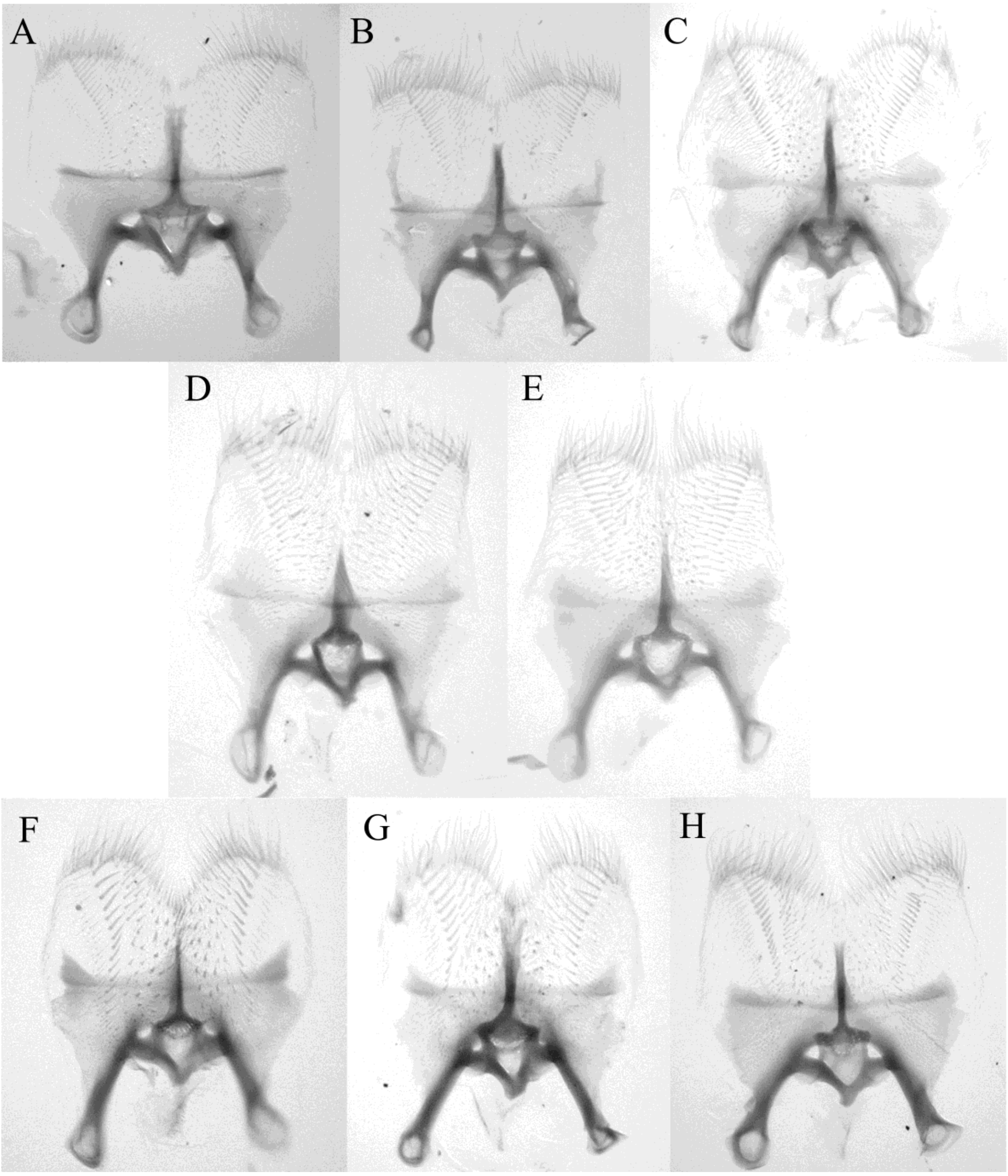

Fig. 7.

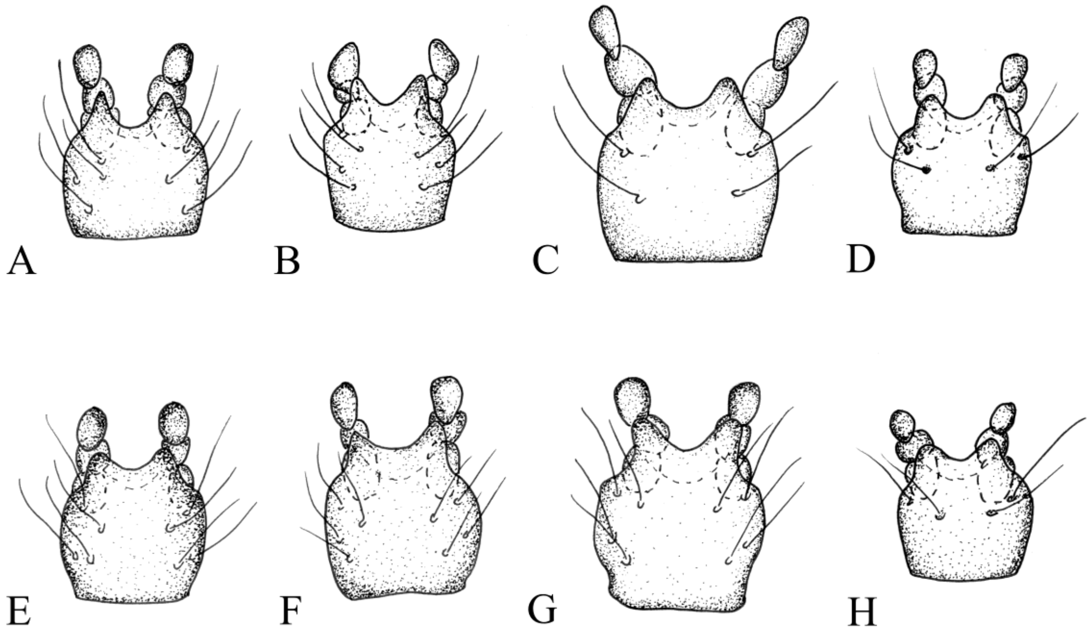

Fig. 8.

C **D**

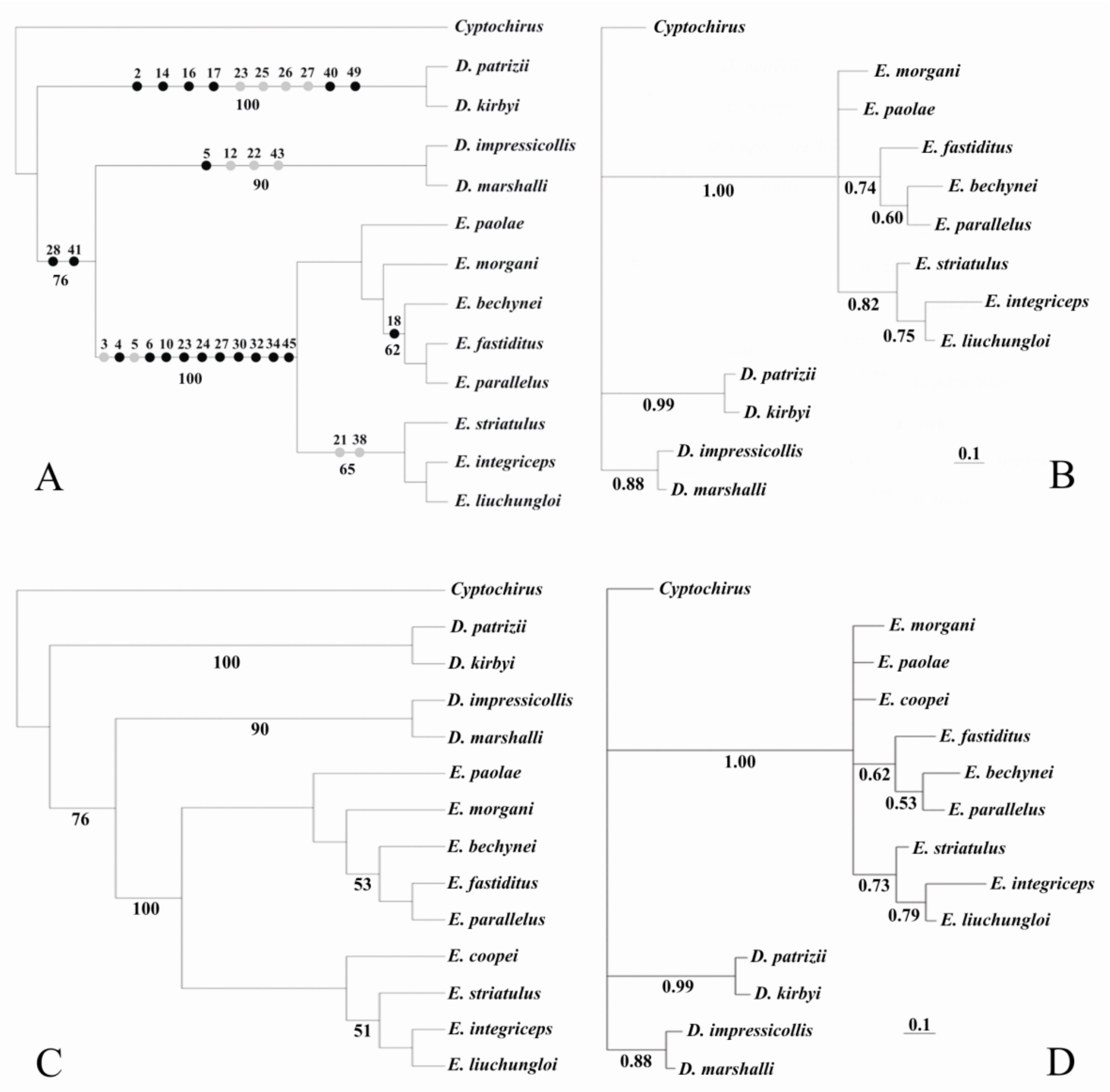
Cyptochirus
2 14 16 17 23 25 26 27 40 49
100
D. patrizii
D. kirbyi
5 12 22 43
90
D. impressicollis
D. marshalli
28 41
76
E. paolae
E. morgani
E. bechynei
18
62
E. fastiditus
E. parallelus
3 4 5 6 10 23 24 27 30 32 34 45
100
E. striatulus
21 38
65
E. integriceps
E. liuchungloi
A
Cyptochirus
E. morgani
E. paolae
E. fastiditus
1.00
0.74
E. bechynei
0.60
E. parallelus
E. striatulus
0.82
E. integriceps
0.75
E. liuchungloi
D. patrizii
0.99
D. kirbyi
D. impressicollis
0.1
0.88
D. marshalli
B
Cyptochirus
D. patrizii
100
D. kirbyi
D. impressicollis
90
D. marshalli
E. paolae
76
E. morgani
E. bechynei
53
E. fastiditus
100
E. parallelus
E. coopei
E. striatulus
51
E. integriceps
E. liuchungloi
C
Cyptochirus
E. morgani
E. paolae
E. coopei
E. fastiditus
1.00
E. bechynei
0.62
0.53
E. parallelus
E. striatulus
E. integriceps
0.73
0.79
E. liuchungloi
D. patrizii
0.99
D. kirbyi
D. impressicollis
0.1
0.88
D. marshalli
D

Fig. 9.

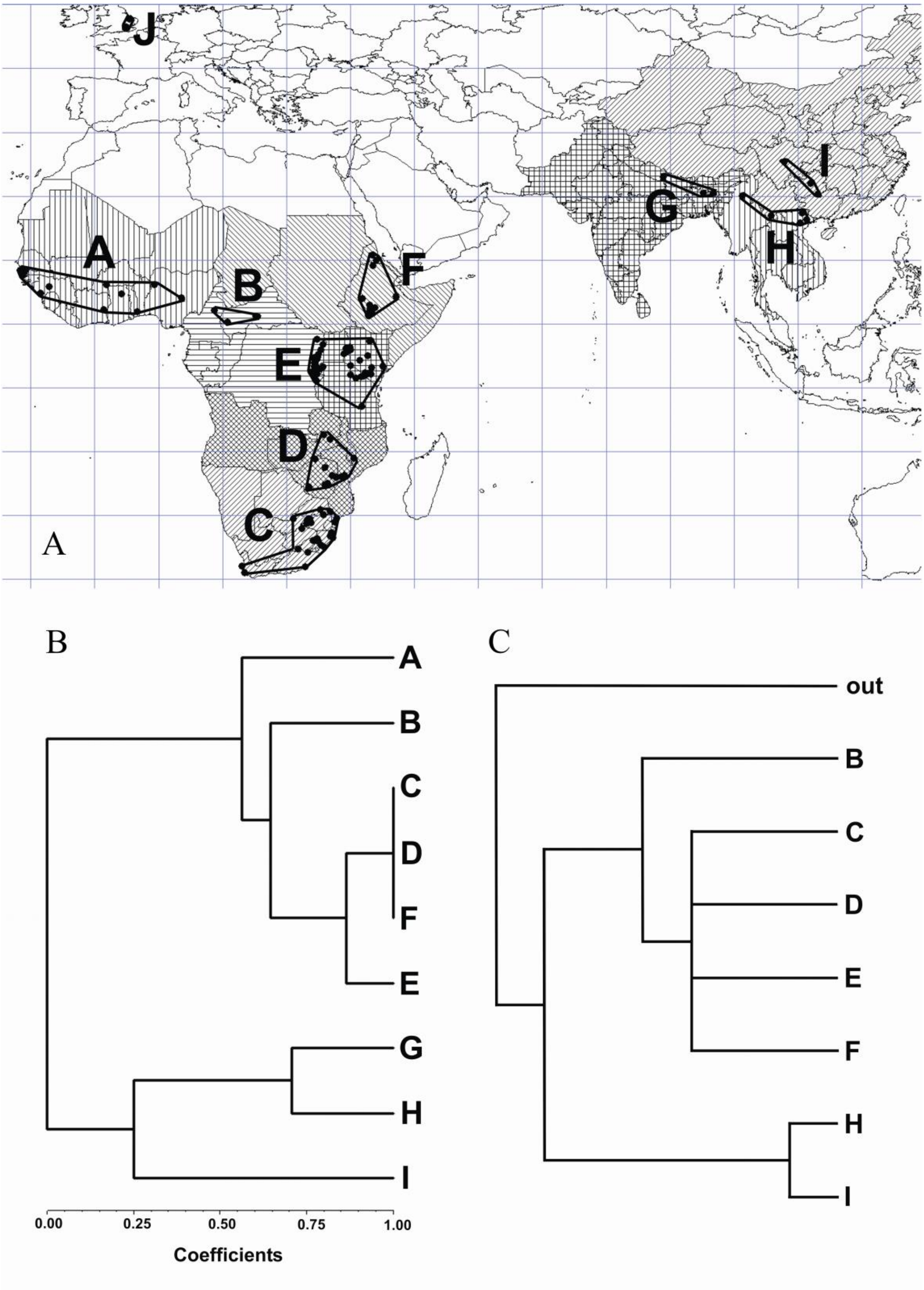
A
J
A
B
F
E
D
C
G
H
I
B
A
B
C
D
F
E
G
H
I
0.00
0.25
0.50
0.75
1.00
Coefficients
C
out
B
C
D
E
F
H
I

Fig. 10.

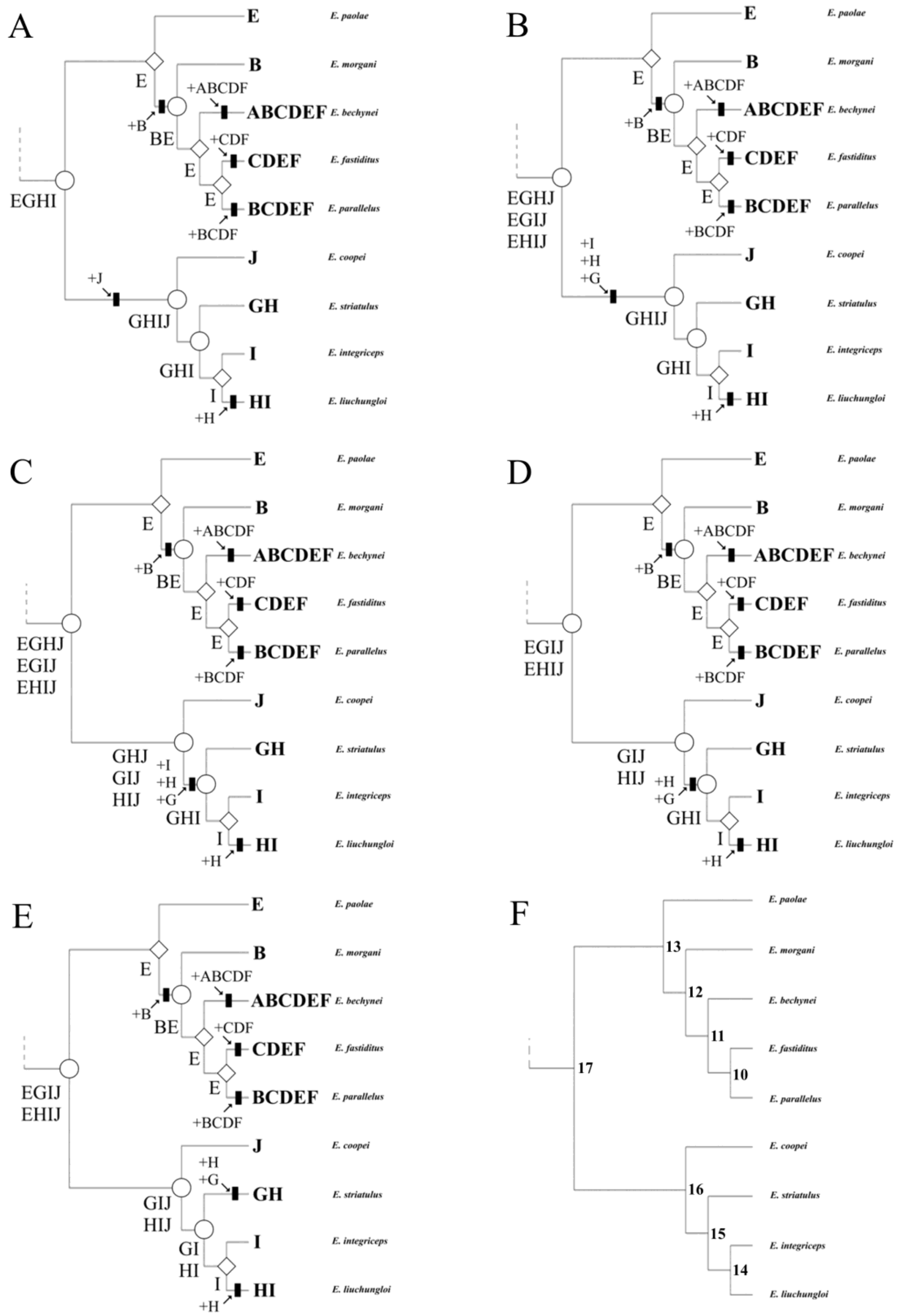
A
E
E. paolae
B
E. morgani
E
+ABCDF
ABCDEF
E. bechynei
+B
BE
+CDF
CDEF
E. fastiditus
EGHI
E
E
BCDEF
E. parallelus
+BCDF
J
E. coopei
+J
GHIJ
GH
E. striatulus
I
E. integriceps
GHI
I
HI
E. liuchungloi
+H
B
E
E. paolae
B
E. morgani
E
+ABCDF
ABCDEF
E. bechynei
+B
BE
+CDF
CDEF
E. fastiditus
EGHJ
EGIJ
EHIJ
E
E
BCDEF
E. parallelus
+BCDF
+I
+H
+G
J
E. coopei
GHIJ
GH
E. striatulus
I
E. integriceps
GHI
I
HI
E. liuchungloi
+H
C
E
E. paolae
B
E. morgani
E
+ABCDF
ABCDEF
E. bechynei
+B
BE
+CDF
CDEF
E. fastiditus
EGHJ
EGIJ
EHIJ
E
E
BCDEF
E. parallelus
+BCDF
J
E. coopei
GHJ
GIJ
HIJ
+I
+H
+G
GH
E. striatulus
I
E. integriceps
GHI
I
HI
E. liuchungloi
+H
D
E
E. paolae
B
E. morgani
E
+ABCDF
ABCDEF
E. bechynei
+B
BE
+CDF
CDEF
E. fastiditus
EGIJ
EHIJ
E
E
BCDEF
E. parallelus
+BCDF
J
E. coopei
GIJ
HIJ
+H
+G
GH
E. striatulus
I
E. integriceps
GHI
I
HI
E. liuchungloi
+H
E
E
E. paolae
B
E. morgani
E
+ABCDF
ABCDEF
E. bechynei
+B
BE
+CDF
CDEF
E. fastiditus
EGIJ
EHIJ
E
E
BCDEF
E. parallelus
+BCDF
J
E. coopei
+H
+G
GH
E. striatulus
GIJ
HIJ
GI
HI
I
E. integriceps
I
HI
E. liuchungloi
+H
F
E. paolae
13
E. morgani
12
E. bechynei
11
E. fastiditus
17
10
E. parallelus
E. coopei
16
E. striatulus
15
E. integriceps
14
E. liuchungloi

Fig. 11