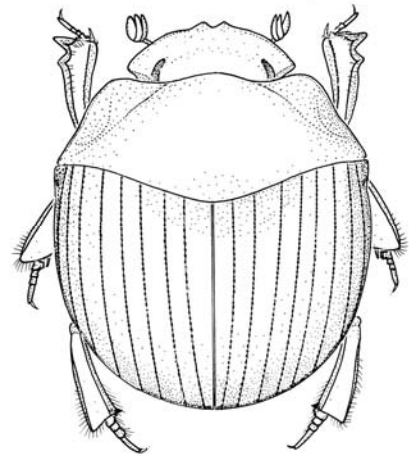


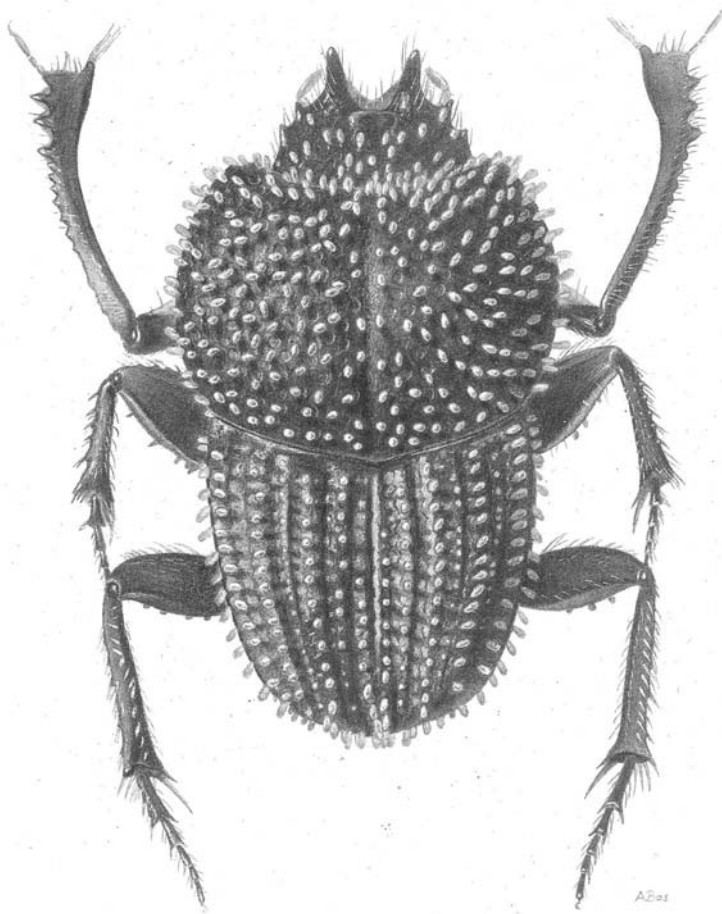
Haroldius

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Frontispiece. Habitus of *Clypeodrepanus digitatus* sp.n. from Kenya, male holotype.

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Drepanocerine dung beetles: a group overview, with description of new taxa (Coleoptera: Scarabaeidae: Scarabaeinae)

J. Krikken

Abstract

The taxonomic and biogeographic status of the genus *Drepanocerus* Kirby, 1828 and related genera is reviewed and discussed. The subtribe Drepanocerina Lansberge, 1875 remains poorly defined, the attributes supporting its monophyly being almost negligible. The morphological diversity of the *Drepanocerus* group of genera is analysed, and the current taxonomic heterogeneity of *Drepanocerus* auctorum is resolved by proposing new genera and regrouping species and subspecies. The following new genera are proposed and keyed along with other group members: *Afrodrepanus* (Afrotropical), *Clypeodrepanus* (Afrotropical), *Latodrepanus* (Afrotropical), *Sulcodrepanus* (Afrotropical), *Tibiodrepanus* (Oriental). *Ixodina* Roth, 1851 (Afrotropical-Oriental) is reinstated as a valid genus. These acts lead to 23 generic recombinations of species-group names. An annotated list of all genera, species and subspecies currently placed in the subtribe Drepanocerina is given. Habitus and character details of representatives of the *Drepanocerus* group and other drepanocerines are depicted. Two new species from East Africa are described and keyed along with congeneric species: *Clypeodrepanus digitatus* and *Drepanocerus orientalis*. The male of *Ixodina freyi* (Janssens, 1953) is recorded and illustrated for the first time – based on a series from Tanzania. The Caribbean genus *Anoplodrepanus* Simonis, 1981 is suggested to belong in the Oniticellina.

Keywords: Drepanocerina, *Clypeodrepanus*, *Drepanocerus*, *Anoplodrepanus*, keys, checklist, new genera, new species, taxonomy, biogeography, ecology, East Africa.

Haroldius 4 (2009): 3-30, figs 1-56, frontispiece.

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Introduction and background

During dung beetle campaigns in East Africa (1972-1981) numerous scarabs were extracted from elephant and other large herbivore mammal dung, including several taxa referable to *Drepanocerus* Kirby, 1828 and related genera. Additionally, Asian relatives were collected from bovine dung during field work in Southeast Asia (1972, 1985-1989); some colleagues also provided taxonomically interesting material from both regions. After a long interval of being beset with other duties, I resumed the study of these drepanocerines and the relevant recent literature. My findings proved interesting enough to justify the present interim report, comprising a taxonomic overview of the group and proposals of new genera and species.

Most members of the subtribe Drepanocerina are small, usually 3.5-8 mm long (total range 2.5-17 mm). Many are more or less cryptic in their dung microhabitat due to a dull, strongly microsculptured integument, more or less covered with bristles, scales and other pilosity, with dung and soil particles adhering to them. They habitually remain motionless when disturbed. Larger species with an oblong, jagged outline, currently placed in *Cyptochirus* Lesne, 1900, show genuine camouflage, resembling coarse, woody elephant dung particles (Krikken, 1983), thus being easily overlooked – also by human collectors. Drepanocerines are reputedly rare, but this is unlikely: although they do not occur everywhere, dung heaps of large herbivorous mammals, like elephant, rhino, and various bovines, may occasionally contain considerable quantities of them, depending, apart from the presence of the dung producers themselves, on geographic location, season, and habitat; of course, the extraction technique applied is crucial (see under Technical remarks). With very few exceptions the ca 55 known Recent species-group taxa in the group live in the Afrotropical and Oriental Regions (details further below).

André Janssens (1953), in his still useful review of the world's Drepanocerina and Oniticellina, placed most species in *Drepanocerus*. Janssens's conception of the genus, however, proved rather heterogeneous, and, not surprisingly therefore, during the 1980s, certain Old World groups of species were revised and placed in different genera, old and new (Simonis & Zunino 1980, Simonis 1985a). A new genus *Anoplodrepanus* Simonis, 1981 was created for two New World species originally combined with *Drepanocerus*. Simonis & Cambefort (1984) reconsidered the monospecific Afrotropical genus *Drepanoplatynus* Boucomont, 1921. Very recently a restart with revisions was made by Barbero et al. (2009), who created a new genus for a widespread Afrotropical-Oriental group of drepanocerine species. In addition to these genus-level actions, several new species were described in both *Drepanocerus* and the other genera, and, of course, faunistic data were added.

In-depth biological information on drepanocerines remains rare – see Lumaret & Cambefort (1980), Cambefort (1981, 1982), Cambefort & Lumaret (1984), and included references, for information on nidification behaviour, ecology, and larval morphology. Whatever the details, it is significant in the present taxonomic context to note that the reproductive biology of the various genera and/or groups of species appears as diverse as their morphology.

The morphological character analysis given in this paper focusses on the *Drepanocerus* group of genera, i.e. the groups of species placed in *Drepanocerus* before 2009 (Table 2 below), or, in other words, *Drepanocerus* sensu Janssens (1953) minus *Cyptochirus* Lesne, 1900 and *Sinodrepanus* Simonis, 1985. This analysis indeed confirms the need for a further subdivision into genera and/or groups of species, the main product here being a taxonomic overview of these supraspecific units, including six new or reinstated genera. Following the generic accounts is a complete annotated list of taxa currently placed in the Drepanocerina, from genus to subspecies level, including more than 20 generic recombinations of the relevant extant species-group names. The New World genus mentioned above is removed from the Drepanocerina.

After the group sections an intriguing new little drepanocerine (see frontispiece) is described from East Africa – it was this species that aroused my interest in the supraspecific classification of the group in the first place. Furthermore, under the collection name label “*Drepanocerus kirbyi*” I encountered a mixed lot, including East African material different from genuine *kirbyi* Kirby, 1828 (the type species of the genus), and equally deserving to be treated as a new species. The male sex of *Ixodina freyi* (Balthasar, 1953) is described here for the first time, based on North Tanzanian material.

The phylogenetic, biogeographic and ecological background of drepanocerines, and the ensuing research challenges, are all discussed at the end of the paper, following the Species accounts. The general intention of the present exercise is fourfold: (a) to outline our current knowledge about the taxonomy of drepanocerines, (b) to get to grips with the continuing taxonomic heterogeneity mentioned, (c) to describe some unknown drepanocerine oddities, and (d) to stimulate others to undertake a critical broad-scope revision of the classification of drepanocerine species. Actually, the reclassification given below is not greatly different from that implied in the key of Janssens (1953), but it is odd that, while he apparently had no hesitation to formally subdivide other groups (like he had, for instance, done in a most durable way with the Gymnopleurini, cf. Janssens, 1940), he explicitly resisted analogous action with respect to his *Drepanocerus*.

This publication is part of an ongoing programme on the classification of scarab genera, supplemented with reports on noteworthy species collected during field campaigns.

Technical notes

Conventional sampling techniques aside, drepanocerines and other beetles living in elephant dung were extracted by using collapsible textile-made sieves (actually modified Winkler sieves), consisting of two main parts: a closed exterior box with attached pyramidal funnel, entirely made of cotton fabric on a metal frame; and an internal, canvas-walled, rectangular box sieve (bottom with 8 mm metal grid), containing the dung sample (narrowly separating it from the exterior box). These contraptions were hung outdoors, in the sun, containing a freshly collected dung sample. Spurred on by the desiccation of the sample the smaller beetles tend to crawl down through the metal grid, falling into the cotton funnel and into the attached collecting jar underneath. Larger forms (like *Cyptochirus* mentioned above) had to be hand picked, not passing through the sieve mesh. Specimens in bovine dung were hand picked or, when abundant, collected by flotation in containers filled with water.

The substance of this paper is straightforward morphological taxonomy, with the underlying argumentation made as transparent as possible in this limited context. Esoteric techniques are avoided, as the primary objective here is to describe the overall taxonomic diversity of the drepanocerines in a most practical way. The adult character diversity of the group is analysed, with particular reference to East African material at hand. Phylogenetic propositions remain limited and tentative – a full analysis would be premature anyway; molecular data are not available, although some forms were recently mentioned, as in Monaghan et al. (2007). For the morphological analysis a DELTA-oriented system for generating a key and diagnoses was used (Dallwitz 2005); the output is not given as-is, but it was adapted and served as a check on the present text of the key and the generic diagnoses of the *Drepanocerus* group.

Some typically drepanocerine features deserve a considered terminology – more on this in the next section. Beware of polymorphism and worn specimens; use major males where appropriate. Measurements are approximate (variable position of body parts and optical distortion may create imprecision). Note the differences between full-face and other views in the pictures; full-face here actually means: maximal surface view, i.e. not necessarily parallel to any pair of the three main body axes. Cluttering the text below with too many references to pictures and specimen details is avoided – the pictures and their captions are quite self-evident, and the

regional origin of the material illustrated is given in the captions (most specimens are from Kenya). Further details may be requested from the author. Scale line with the figures are 1 mm; with figs 49-50 0.5 mm.

Character diversity in the *Drepanocerus* group of genera

A selection of taxonomically significant morphological characters is given in Table 1; the list is primarily based on my own observations on the drepanocerine material at hand. The table contains supposedly derived character states (and consequently potential synapomorphies), as distilled from a much longer list of scarabaeoid characters (de drepanocerine section containing ca 55 characters). The formal generic diagnoses given below were generated from this longer list, as explained in the Technical notes, above. With the concise list of 25 characters in Table 1, the outline of the genera in Table 2, the key, the diagnoses, and the supporting illustrations, the user of this paper should be able to easily get to the name of an extant or newly created genus and its taxonomic content. The study of additional material and revisionary work will undoubtedly lead to further fine-tuning of the generic diagnoses.

Although both the terminology and wording of the characters attempt to avoid quasi-identical and analogous characters, practical description and recognition had priority. One can, for instance, not be sure that the paradiscal elytral ridge in *Ixodina* versus African *Eodrepanus*, respectively, are strictly homologous – for the moment we think they are not; similarly, the ridges on the frontovertex of *Drepanocerus*, *Afrodrepanus*, and other drepanocerines are unlikely to be homologous. The key is practical: the wide separation in the key between certain genera, like *Tibiodrepanus* and *Sulcodrepanus*, which may be closely related, follows from an easily recognizable character (in this case the shape of the protibia), not from their assumed relationships.

Table 1. Summary of taxonomically significant generic character states

Cl	La	Eo	Ix	Ti	Su	Dr	Af	Si	Cy	25 (presumably derived) character states:
Cl	1. Clypeal apex shining brown, delimited from remainder of head
Cl	2. Clypeofrontal transition (male) with median protrusion
.	Dr	Af	.	.	3. Frons with pair of longitudinal ridges
La	4. Frontovertex with single transverse ridge
.	Dr	.	.	Cy	5. Deplanate pronotum with symmetric pattern of ridged depressed cells
La	6. Pronotum cushion-like, with symmetric non-ridged depressions
.	.	.	Ix	7. Pronotum with central hole laterally bridged by paramedian ridges
.	.	Eo	8. Elytral epipleuron emarginate at humerus
.	Af	.	Cy	9. Elytral epipleuron reduced, narrow
.	.	.	Ix	10. Elytral disc deplanate inside distinct arcuate ridges
.	.	Eo	11. Elytral disc deplanate inside distinct parallel ridges
Eo	12. Elytra with strong parepipleural ridge from humeral umbone caudad
.	Dr	13. Elytra deplanate, with raised interstriae 1, 3 and 5
.	.	.	.	Ti	Su	14. Posthumeral depression present, followed by parepipleural ridge
.	Af	.	.	15. Elytra with heavily (umbilicate-)punctate striae
.	Dr	.	.	.	16. Integument of elytra with symmetric (yellow) colour pattern
.	Af	Si	Cy	17. Proepimeral surface steeply declivous / excavate
.	Af	.	.	18. Metasternum with pattern of impressions
La	19. Metepisternum with sharp longitudinal fold
.	Dr	20. Abdomen laterally strongly expanded-ridged
.	.	Eo	Si	.	21. Protibia with 2-3 external denticles only
.	.	.	.	Ti	22. Protibia with fine 4th denticle sitting on transverse apex
Cl	Af	.	.	23. Protibial apex male collinear with 4th external denticle
.	Si	Cy	24. Most of integument with close cover of appressed scales
.	Si	.	25. Parameres with separate sclerotized accessory projections

Cl La Eo Ix Ti Su Dr Af Si Cy

generic abbreviations:

Cl	<i>Clypeodrepanus</i>	Su	<i>Sulcodrepanus</i>
La	<i>Latodrepanus</i>	Dr	<i>Drepanocerus</i>
Eo	<i>Eodrepanus</i>	Af	<i>Afrodrepanus</i>
Ix	<i>Ixodina</i>	Si	<i>Sinodrepanus</i>
Ti	<i>Tibiodrepanus</i>	Cy	<i>Cyptochirus</i>

Table 2. Outline of the *Drepanocerus* group of genera as reclassified in this paper

Clypeodrepanus (Afrotropical) – clypeus shining brown; pronotum broadly convex, with shallow midline depression; elytron strongly punctate-striate; clypeofrontal transition (male) with median protrusion

digitatus, striatus, strigatus

Latodrepanus (Afrotropical) – broad cushion-like pronotum with symmetric pattern of slight depressions; frontovertex with distinct transverse elevation; elytra generally convex, striation superficial or absent; metepisternum folded into crest

laticollis, caelatus, pulvinarius, schimperi

Eodrepanus (Afrotropical-Oriental) – elytron with parallel geminate-aciculate striae; humeral section of epipleuron emarginate; parepipleural ridge complete; habitus deplanate, parallel-sided; protibia 3-dentate

bechynei, coopei, fastiditus, integriceps, liuchungloi, morgani, paolae, parallelus, striatulus

Ixodina (Afrotropical-Oriental) – pronotum on base with 2-3 forward protrusions on either side, paramedians bridging deep central hollow; elytron with deplanate disc delimited by arcuate paradiscal ridge

abyssinica, bos, endroedyi, freyi, kovacsi, runica, saegeri, szunyoghi

Tibiodrepanus (Oriental) – protibia with fine, sharp denticle on transverse apical edge, outer edge with 3 larger denticles; pronotum medially and laterally more or less impressed, male may have larger protrusion(s)

hircus, kazirangensis, setosus, simplex, sinicus

Sulcodrepanus (Afrotropical) – pronotum with uninterrupted median impression, limited (in male) by elevated high plate on either side; head without any protrusions; elytron with superficial striation; protibia simply 4-dentate

sulcicollis

Drepanocerus (Afrotropical) – pronotal disc deplanate, with symmetric pattern of bristle-bearing ridges separating ca 10 depressed cells (complete in female); deplanate elytron with raised interstriae 1, 3, 5, and distinct yellow pattern; abdomen laterally expanded well beyond elytral edge

kirbyi, orientalis, patrizii

Afrodrepanus (Afrotropical) – elytron with 8 rows of very large, deep punctures; epipleuron reduced, adjacent metepisternum concave; symmetric metasternal pattern of impressions; frons with pair of longitudinal costae

impressicollis, marshalli

In this paper the term interstriae (plural) refers to the intervals between the elytral striae. Among drepanocerines a stria (if distinct at all) varies from a simple punctate line to pairs of striolae and deep umbilicate-punctate series of punctures. The basic number of elytral striae (from suture to epipleuron) is eight, usually with six between suture and humeral umbone. A pair of fine, aciculate parallel striolae on the elytra (as in *Eodrepanus*) is here termed a geminate stria, supposedly originating from longitudinally confluent annulate-aciculate punctures.

Note the terminology of the elytral elevations (ridges, tubercles) from the suture (= median line) to the epipleura: juxtasutural, paradiscal (immediately bordering a deplanate disc, usually interstria 5), parepipleural (at short distance above epipleuron, usually interstria 8), epihumeral (on the humeral umbone), and juxtepipleural (= superiorly limiting the epipleuron).

The terminology with regard to the relief pattern (longitudinal elevations and other elements) on the pronotum runs from the midline (median) to the sides (marginal) as follows: median or central, paramedian, sublateral, lateral, submarginal, and marginal. This terminology is particularly relevant in *Ixodina*. Head and pronotum may have a symmetrically arranged pattern of depressions, in *Drepanocerus*, and more strongly so in *Cytochirus*, forming (more or less polygonal) cells separated by low bristle-bearing ridges.

Strial features aside, the microsculpture is usually, even on a single individual, complex: punctures (for instance on the pronotum) may be simple and distinct, annulate (annular), isodiametric or anisodiametric, very elongate (and confluent), etc. The inner area of annular punctures usually is microgranulose (in some species subcircular-microstriolate) – this is a common type of microsculpture among drepanocerines. A cover of dense fine aciculate streaks or other type of microsculpture may be present on the interstitial surface of the elytra (microstriolation), obliterating the normal striation – the same is the case with microgranulate or simply scabrous surfaces. Punctures may have a fine (sub)appressed seta, a long coarse (erect) simple bristle, a claviform bristle (which may be rolled-up scales), or different types of scales. The colour of these types of pilosity varies from pale (whitish) to black (for instance in bristles and scales of *Cytochirus* species).

As for genital characters, a synthesis explaining their (homologous) diagnostic, or for that matter, phylogenetic significance has, in my opinion, not been achieved. In most genera the parameral structure is simple, and consequently only salient sclerotized complexity was taken into account. The mouthparts are diverse, but a taxonomic, let alone phylogenetic evaluation, requires further detailed study, which is beyond the scope of this paper.

Key to the *Drepanocerus* group of genera and close relatives

Group description

Pygidial circumference with ridge; basal ridge very distinct. Pygidial surface frequently with pattern of small, variably pronounced (non-marginal) symmetric protrusions. Dorsal body surface with distinct, but variably raised protrusions, at least in males (different according to genus: symmetrically arranged ridges, costae, horns); these may be limited to one part only: head, pronotum, or elytra. Integument (at least dorsally) generally matt or sericeous, black or brown (one genus excepted: yellow elytral markings present; in other species legs and ventral parts may be more or less yellow). Much of body bearing numerous setae, bristles, scales, or a combination of these, but never (as in close relatives outside the *Drepanocerus* group: *Cytochirus*, *Sinodrepanus*) extensively covered with appressed scales, and never with close pubescence. Most of body with dense microsculpture (different according to genus: punctate, annulate, striolate, granulate, reticulate, simply scabrous, etc.); annular punctation common. Clypeal apex usually bidentate-emarginate (denticles may be blunted, apical edge may then look bisinuate). Pronotal base at most with obtuse median angle (but in *Drepanocerus* more produced), which never completely covers any small scutellum (in many species scutellum indistinct anyway, irrespective of cover by pronotum). Elytral epipleuron present, usually distinct in lateral view, but rarely much broader than adjacent interstria (section at humerus may be narrow, or emarginate, as in *Eodrepanus*). Humeral umbone distinct, striae 6 and 7 usually reaching humeral umbone (in some taxa forming more or less distinct humeral incisions); juxtépipleural stria (8) may be indistinct. Protibia varies in shape, with 3 or 4 distinct denticles on outer edge, but always lacking the combination of a broader brush on a truncate apex. Mesocoxae widely separated, parallel; mesometasternal suture straight, (sub)transverse. Metacoxae distinctly separated. Abdomen with 6(-7) more or less fused ventrites; abdominal ventrites may have strong lateral impressions. Tarsi all 5-segmented; meso- and metatarsal segments 1 about as long as 2-4 combined. Antenna 8-segmented. Parameres relatively simple, moderately sclerotized, at most with slight projections (not separated from main structure). Body length 2.5-8 mm (representatives of the related *Cytochirus* and *Sinodrepanus* are usually longer).

Key

1. Most of integument visible, lacking (locally) close cover of fine scales, though usually with numerous setae and/or bristles. Up to ca 8 mm long. *Drepanocerus* group of genera. 3
 - Integument, including entire dorsum, largely concealed by close cover of fine appressed (mostly greyish/brownish) scales, more or less mixed with other types of pilosity. Proepisternum steeply declivous, glabrous, lighter brown, posteriorly delimited by sharp ridge. Scutellum very distinct. Usually longer than 8 mm. Both head and pronotum lacking any long projections. 2
2. Head and pronotum may have symmetric protrusions and depressions, but lacking cover of cells separated by low bristle-bearing ridges. Protibia broad, in male with oblique, apico-internally slightly protruding apex, and 2 or 3 denticles on outer edge. Parameres complex, with symmetrically extended lateral and medio-apical projections (upper side view). Habitus elevated, elytra relatively shorter, 7.5-13 mm long. Asia. *Sinodrepanus*
 - Both head and pronotum with numerous symmetrically arranged, well-defined, densely squamiferous, depressed cells separated by low bristle-bearing ridges (ca 10 on pronotum). Protibia of male distally curved inward, usually with long thumb-like apico-internal extension, and with 4 denticles on outer edge. Parameres with shorter projections. Habitus remarkably elongate-deplanate, dorsal outline parallel-sided, 8-17 mm long. Africa. *Cytochirus*
3. Elytral disc lacking discrete, straight, strictly parallel geminate striae (if present, pair of striolae undulate and encompassing punctures). Elytral disc may be delimited by sharpish paradiscal ridge, which is then more or less curved and pronotal and other characters different. 4
 - Elytral disc with impunctate, discrete, straight, strictly parallel geminate striae, interstria 3 may have protrusion at base. Pronotal and elytral disc of most species laterally delimited by low, (nearly) straight, paradiscal (usually more or less setose) elevation; pronotal disc at most shallowly depressed. Protibia with total of 3 denticles on outer edge, apical edge lacking 4th denticle. Humeral section of elytral epipleuron strongly emarginate. Parepipleural ridge high, and continuous from humeral umbone. Dorsal body outline oblong, parallel-sided, surface generally deplanate. *Eodrepanus*
4. Elytron lacking well-defined, curved paradiscal ridge. Pronotum lacking central-transverse hollow quasi-tunnelling under any longitudinal elevations. 5
 - Elytron with fine, uninterrupted, sharpish ridge evenly curving from base (inside humerus) to apicosutural corner, encompassing feebly striate, generally deplanate disc. Pronotum with symmetrically arranged longitudinal elevations (2 or 3 ridges starting from base forward, on either side), separated by (shining) central-transverse hollow, which is quasi-tunnelling laterad under paramedian elevations. Two distinct epihumeral ridges present. Scutellum distinct. Protibia with total of 4 denticles on outer edge. *Ixodina*

5. Clypeal apex with colour and microsculpture not greatly different from remainder of head. Postclypeal surface never with small roundish or transverse protrusion well in front of eyes (if so, pronotal and other characters very different). 6
- Clypeal apex shining brown, and well delimited from matt remainder of head. Male with short but distinct median protrusion on postclypeal surface. Pronotum broadly convex, with, at most, very slight symmetrical protrusions and/or depressions. Elytral striae broad, deep, very distinctly punctate. Dorsal outline of elytra evenly rounded, not oblong. Pronotum with abundant upright bristles and/or scales in annulate punctures, most elytral interstriae also with row of upright bristles and/or scales. Metacoxae very widely separated. Protibial apex more or less transverse (may be apico-internally produced, in male). Scutellum indistinct. Africa. *Clypeodrepanus*
6. Protibia usually with 4 larger denticles, all along outer edge, apex with movable spur and tarsus only. Africa. 7
- Protibia with fine (4th) denticle sitting on transverse apex, adjacent to tarsus and movable spur, outer edge with 3 larger denticles and proximal serration. Elytron finely punctate-striate (not geminate-striate), interstria 5 raised, usually with numerous bristles, parepipleural ridge distinct, not connected to humeral umbone. Pronotum broadly impressed laterally; major males (of at least some species) with conspicuous pronotal protrusion(s). Scutellum minute. Asia. *Tibiodrepanus*
7. Frontoververtex without transverse protrusion. Pronotum with different elevations and depressions. Elytral striation usually distinct (albeit superficial in some species) 8
- Frontoververtex with single transverse protrusion (somewhere between anterior border of eyes and vertex, in some species interrupted medially, curved). Pronotum broadly, strongly convex (cushion-like) and densely punctate, with various shallow, symmetrically arranged depressions (not separated by narrow ridges); bristles long, mostly far apart. Elytral disc generally convex, with obsolete or very superficial striae, and with more or less raised interstriae 3 and 5 (which each may have narrow longitudinal ridge). Generally uniformly black. Metepisternum with longitudinal (ridged) fold. *Latodrepanus*
8. Elytral disc uniformly black, interstriae 1 and 3 not raised and lacking thick bristles. Pronotum with depressions, but lacking symmetric cells separated by low bristle-bearing ridges; any median impression of pronotum not divided into two cells. Abdomen laterally at most slightly expanded (indistinct from above). . 9
- Elytral disc black or brown, with distinct symmetric pattern of yellow markings. Alternate (odd) interstriae raised, with bristles; striae superficial. Pronotum (at least in females) deplanate, with numerous symmetrically arranged depressed cells separated by low bristle-bearing ridges (limited to basal surface in males having excessive pronotal ornamentation). Abdomen laterally strongly expanded, with sharp ridge along elytron (very distinct from above). Head elongate, genae laterally virtually straight (subparallel to median), frontoververtex with pair of long, anteriorly more or less convergent ridges. *Drepanocerus*
9. Elytron with superficial, fine punctate striation only; posthumeral surface of elytral margin depressed, lacking deep punctures, at most with slight parepipleural ridge. Elytral epipleuron high, distinct. Proepisternal surface not concave. Metasternum without symmetric impressions. Protibia unmodified, with obliquely oriented apico-external denticle. Pronotum with median concavity over most of its length, in males limited by high ridge or plate on either side. Clypeogenal edge interrupted-incised. Entire head without any elevations. *Sulcodrepanus*
- Elytron with 8 rows of (more or less umbilicate) large, deep striae punctures, each double row separated by narrow ridge; posthumeral surface of elytral margin not generally depressed. Elytral epipleuron reduced, very narrow. Proepisternal surface distinctly concave. Metasternum with distinct, symmetrically arranged impressions. Protibial apex straight, transverse, apico-external denticle perpendicular. Pronotal disc (at least in males) concave, with or without pair of projections, but lacking plate on either side. Clypeogenal edge not interrupted-excised. Frontoververtex with pair of low longitudinal costae. *Afrodrepanus*

Diagnoses of genera in the *Drepanocerus* group

Clypeodrepanus gen.n.

Generic diagnosis

Head generally transverse, without pattern of symmetrically arranged depressed cells separated by ridges. Frontoververtex (well behind clypeus) without any protrusions. Clypeal surface in front smooth and colour a well-delimited shining lighter brown. Clypeal outline anteriorly emarginate-bidentate, margin (male) anteriorly with raised denticles (long, upright in major males of at least one species). Lateral margin of clypeus generally evenly curved or straight, distinctly angulate-dentate, or simply unmodified. Clypeogenal edge at suture (full-face view)



Figs 1-15. Habitus, oblique (1-12), lateral view (13); forebody, dorsal (14); forebody, axial (15). – 1, 13-15. *Clypeodrepanus digitatus* (1, holotype, 13, paratype male, 14, paratype female, 15, paratype male; all Kenya); 2, *Latodrepanus laticollis* (Kenya); 3, *Eodrepanus bechyneni* or nr (Kenya); 4, *Ixodina abyssinica* (Kenya); 5, *Ixodina freyi* (Tanzania); 6, *Tibiodrepanus hircus* (Indonesia: Bali); 7, *Sulcodrepanus sulcatus* (Kenya); 8, *Drepanocerus orientalis* (Kenya, holotype); 9, *Afrodrepanus impressicollis* (Kenya); 10, *Sinodrepanus* nr *falsus* (Thailand); 11, *Cyptochirus trogiformis* (Kenya); 12, *Anoplodrepanus pecki* (Jamaica, paratype). – Males, unless mentioned otherwise.

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abrupt. Male median postclypeal protrusion (on or just behind clypeofrontal transition) transverse-short, or roundish-short.

Pronotum generally broad, convex, midline moderately impressed; without pair of very broad anterior projections, without slender basomedian forward projection, without pair of long, slender, acuminate, forward projections, without longer low paramedian elevations delimiting discal-median depression, without high crest delimiting median depression on either side. Pronotal sides (dorsal view) with marginal edge (more or less) evenly rounded to obtuse anterolateral angle, edge (in lateral view) rounded or straight posteriorly. Basal edge of pronotum fully, widely rounded. Prothoracic underside on either side flat or very slightly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture consisting of (sub)isodiametric annular punctures. Scutellum between basosutural angles of elytra indistinct.

Elytral disc generally more or less convex, distinctly striate-punctate (8 very distinct striae), with stria punctures distinct, simple (relatively deep), with rough, usually microgranulose-microreticulate interstriae. Elytron with simple juxtepleural ridge, epipleuron unmodified, at most narrow but not emarginate-sinuate behind humerus. Elytral interstria 8 minimal, due to strong, complete striation; humeral umbone simple or slightly incised by striae, no distinct depression behind humeral umbone; elytral base lacking isolated protrusion. Elytral colour virtually uniformly black or brown. Regular discal interstriae with slender bristles or with coarse (distally expanded) bristles, all interstriae nearly equally elevated or at least flat.

Surface of abdominal ventrites medially flat. Metasternum between widely separated mesocoxae generally slightly convex. Metepisternum more or less flat, unmodified. Metacoxae very widely separated. Proximal abdominal ventrites with sutures medially more or less effaced. One or more distal abdominal ventrites laterally impressed-compacted (note anteanal ventrite). Abdominal sides at most slightly expanded beyond epipleura, and indistinct from above. Pygidium with small (variably pronounced) elevations.

Legs usually slender. Protibia straight to very slightly curved, or distal section strongly curved inward (male protibia modified in at least one species), with total of 4 external denticles, distinctly serrate proximally. Protibial apex with simply straight edge and more or less perpendicular apico-external denticle, in major male of one known species with strongly produced interior apex (may have tuft of long setae on produced apico-internal apex, male of the same species). Male protibia with external denticles standing out normally or (sub)perpendicular to axis. Metatarsal segment 1 about equal to or slightly shorter than segments 2-4 combined.

Parameres simple, lacking accessory projections separate from main structure (in dorsal view).

General body shape normally compact to slightly elongate. Pilosity generally abundant, with numerous bristles and/or simple setae predominant, or with (quasi-)claviform bristles predominant. Body very small; usual length 3.5-4 mm.

Type species

Clypeodrepanus digitatus sp.n.

Geographic range

Afrotropical (East), 3 spp.

Comments

The three species in this genus have a characteristically smooth, shining brown clypeal apex, with (in the males) a distinct median protrusion on the clypeofrontal transition. The species are keyed below, after the description of the new species *C. digitatus*. Major males of this species look very different from their known congeners, by the long digitate-penicillate, curved protibiae and very long, upright clypeal denticles. Both pronotum and elytra are little modified in terms of elevations and concavities.

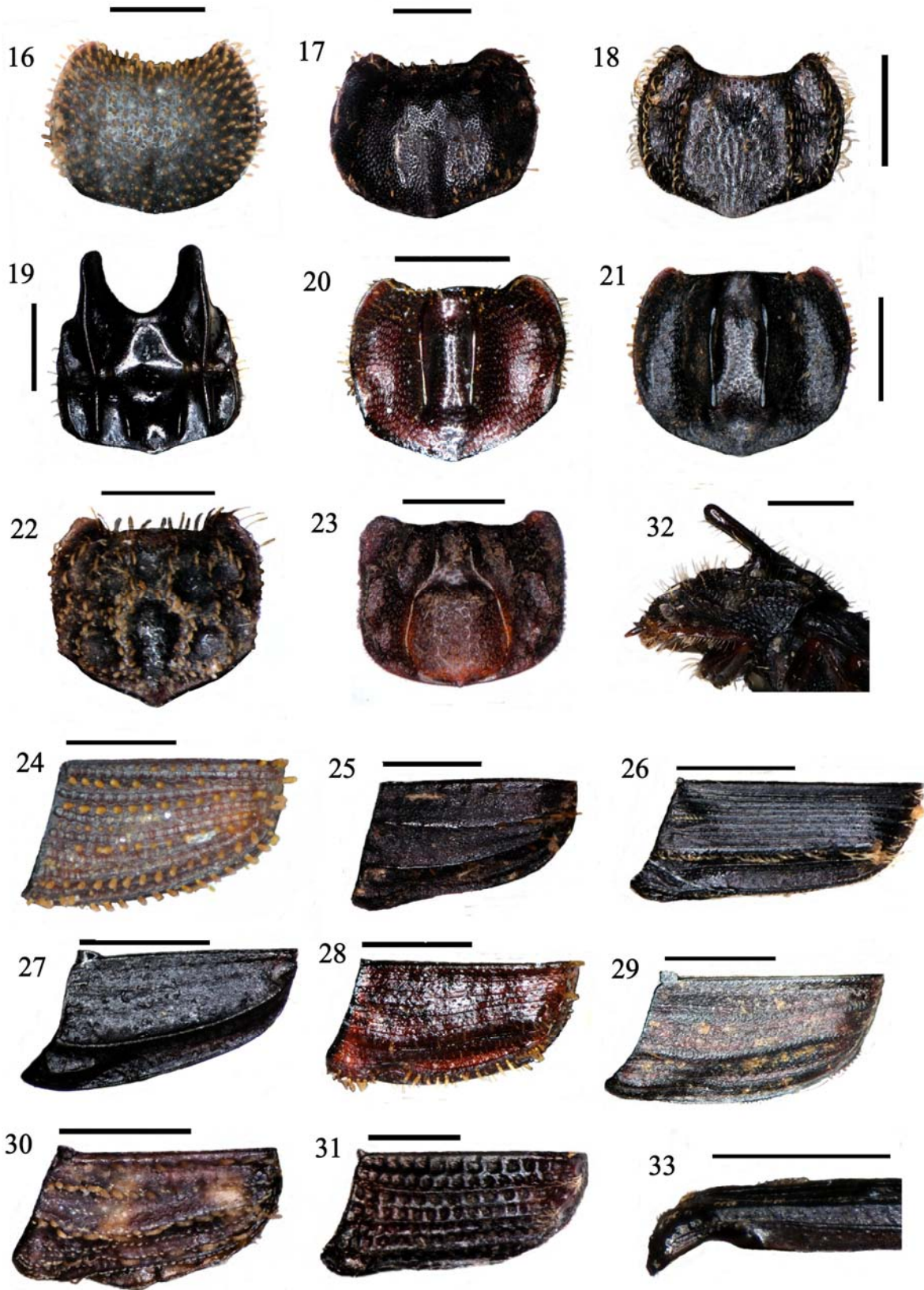
Etymology

The prefix *Clypeo* to *drepanus* refers to the characteristic clypeus; *drepanus* (apparently referring to sickle-shaped horns, or to the Cape) derived from *Drepanocerus*, as also employed by Simonis et al. for their new genus-group names; masculine noun.

***Latodrepanus* gen.n.**

Generic diagnosis

Head generally transverse, without pattern of symmetrically arranged depressed cells separated by ridges. Frontovertex with single transverse elevation (may be interrupted medially), situated somewhere between anterior border of eyes and vertex. Clypeal surface in front black or brown, just like remainder of head. Clypeal outline anteriorly emarginate-bisinate to emarginate-bidentate. Lateral margin of clypeus generally evenly



Figs 16-33. Pronotum, dorsal (16-23); left elytron, dorsal (24-31); forebody, lateral (32); anterior section of elytron, lateral, showing humeral emargination (33). – 16, 24, *Clypeodrepanus digitatus* (Kenya, holotype); 17, 25, *Latodrepanus laticollis* (Kenya); 18, 26, 33, *Eodrepanus bechynei* or nr (Kenya); 19, 27, *Ixodina abyssinica* or nr (Kenya); 32, *Ixodina freyi* (Tanzania; note position of head and prothorax); 20, 28, *Tibiodrepanus hircus* (Indonesia: Bali); 21, 29 *Sulcodrepanus sulcatus* (Kenya); 22, 30, *Drepanocerus orientalis* (Kenya, holotype; 30, elytron with abdominal expansion); 23, 31, *Afrodrepanus impressicollis* (Kenya). – All males.

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curved or straight, multidentate and/or -sinuate (but not always). Clypeogenal edge at suture (full-face view) abrupt, excised. Median postclypeal protrusion (on or just behind clypeofrontal transition) absent.

Pronotum generally convex (cushion-like, “swollen”), with symmetric pattern of shallow impressions; without pair of very broad anterior projections, without slender basomedian forward projection, without pair of long, slender, acuminate, forward projections, without longer low paramedian elevations delimiting any discal-median depression, without high crest delimiting any median depression on either side. Pronotal sides (dorsal view) with marginal edge (more or less) evenly rounded to obtuse anterolateral angle, edge (in lateral view) sinuate posteriorly. Basal edge of pronotum medially fully rounded. Prothoracic underside on either side flat or very slightly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture consisting of (sub)isodiametric annular punctures, or densely to crowdedly simply punctate. Scutellum between basosutural angles of elytra small or narrow but distinct, or indistinct (as in the type species).

Elytral disc generally more or less convex, very superficially striate or lacking any striae; interstriae with scabrous, usually microgranulose-microreticulate, sparsely bristle-bearing surface. Elytra at most with a few minor ridges. Elytron with simple, strongly elevated juxtepleural ridge, with epipleuron unmodified, at most narrow but not emarginate-sinuate behind humerus, with at most slight parepleural ridge; humeral umbone simple or slightly incised by striae (or with ridges), surface behind umbone depressed; elytral base lacking isolated protrusion. Elytral colour virtually uniformly dark (black-brown). Regular discal interstriae with few bristles (slender bristles and/or coarse, distally expanded bristles); all interstriae more or less equally elevated, surface flat; or distinctly, alternately elevated (i.e. narrow ridges on odd interstriae).

Surface of abdominal ventrites medially flat. Metasternum between mesocoxae generally slightly elevated to tectiform in front; disc with single median impression. Metepisternum folded, with sharpish longitudinal ridge near lateral wing of metasternum. Metacoxae narrowly separated. Proximal abdominal ventrites with sutures medially more or less effaced. One or more distal abdominal ventrites laterally distinctly impressed-compacted. Abdominal sides at most slightly expanded beyond epipleura, and indistinct from above. Pygidium convex, at most slightly uneven (for instance, a slight ridge or ill-defined tubercles).

Protibia robust, straight to very slightly curved, with total of 4 external denticles (standing out normally), proximally more or less serrate. Protibial apex with normal oblique apico-external denticle (4), neither with apico-internal protrusion, nor with tuft of long setae. Metatarsal segment 1 about equal to or slightly shorter than segments 2-4 combined.

Parameres simple, lacking accessory projections separate from main structure (in dorsal view).

General body shape compact to slightly elongate. Pilosity generally sparse, with numerous bristles and/or simple setae and/or (quasi-)claviform bristles predominant. Body small; usual length 4-5 mm.

Type species

Drepanocerus laticollis Fahraeus, 1857.

Geographic range

Afrotropical, 4 spp.

Comments

The frons has a transverse protrusion in both sexes, its detailed position and shape varying among species; the metepisternum is abruptly folded. In addition to being characteristically swollen, the pronotal surface has superficial impressions and also a fine punctation, not directly striking as annulate. The type species stands apart from the others in that its elytral striation is absent, and its scutellum indistinct. The scutellum of other species (like *L. caelatus*) is minute but distinct. Initially the groups of *caelatus* and *laticollis* were considered separate (sub)genera, but this view was abandoned awaiting more data on the diversity inside *Latodrepanus*.

Etymology

The prefix *Lato* to *drepanus* refers to the name of the type species; masculine noun.

***Eodrepanus* Barbero, Palestrini & Roggero, 2009**

Generic diagnosis

Head generally transverse, without pattern of symmetrically arranged depressed cells separated by ridges. Frontovortex at most with slight (sub)longitudinal elevation(s). Clypeal surface in front black or brown, like posterior surface of head. Clypeal outline anteriorly emarginate-bidentate or emarginate-bisinate (rounded in one Oriental species). Lateral margin of clypeus generally evenly curved or straight. Clypeogenal edge at suture

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(full-face view) usually abrupt, but excision may be obsolescent. Median postclypeal protrusion (on or just behind clypeofrontal transition, male) absent.

Pronotum deplanate, with elongate, broad, very shallow discal-median depression, with low paramedian (glabrous or more or less setose) costa or ridge delimiting discal depression on either side (both sexes); paramedian elevations not developing into higher crests or very broad anterior projections; pronotum also without slender basomedian forward projection, without pair of long, slender, acuminate, forward projections. Pronotal sides (dorsal view) with marginal edge (more or less) evenly rounded to obtuse anterolateral angle, edge (in lateral view) sinuate posteriorly. Basal edge of pronotum medially rounded off. Prothoracic underside on either side flat or very slightly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture consisting of isodiametric annular punctures and/or anisodiametric (elongate, confluent) annular punctures. Scutellum between basosutural angles of elytra poorly distinct or minute (more distinct in one Oriental species).

Elytral disc generally distinctly deplanate (between both striae 6, on either side of suture), with geminate-aciculate striae; striae punctures indistinct, narrow interstriae not distinctly microsculptured. Elytra with very distinct, straight (glabrous or more or less setose) longitudinal paradiscal ridge (interstria 5). Elytra with simple juxtepleural ridge, with epipleuron distinctly emarginate below humerus; high, sharpish parepleural ridge connected to humeral umbone, no posthumeral depression; umbone simple or slightly incised by striae; elytral base with or without roundish tubercle on base of interstria 3. Elytra virtually uniformly dark coloured (black-brown). Regular discal interstriae at most with inconspicuous bristles, all more or less equally elevated or just flat (apart from the basal tubercle just mentioned).

Surface of abdominal ventrites generally flat. Metasternum between mesocoxae generally not distinctly elevated. Metepisternum slightly longitudinally concave. Metacoxae widely separated. Proximal abdominal ventrites with sutures medially strongly effaced. Distal abdominal ventrites not impressed-compacted. Abdominal sides at most slightly expanded beyond epipleura, and indistinct from above. Pygidium convex, at most slightly uneven (for instance, with slight transverse fold).

Protibia straight to very slightly curved (distal section more strongly curved inward in one Oriental species), with total of 3 external denticles, usually gap between denticles 1-2 slightly wider than between 2-3; proximal serration usually distinct. Protibial apex with normally oblique apico-external denticle, or with oblique edge directed proximally, collinear with apex of apico-external denticle (i.e. male protibia of one Oriental species with apices of external denticles slightly “shifted” proximad); lacking apico-internal tuft of long setae. Metatarsal segment 1 about equal to or slightly shorter than segments 2-4 combined.

Parameres simple, lacking accessory projections separate from main structure (in dorsal view).

General body shape oblong, more or less parallel-sided. Pilosity varies, usually with numerous bristles and/or simple setae predominant. Body very small to small; usual length 3.5-5 mm.

Type species

Drepanocerus parallelus Raffray, 1877 (original designation).

Geographic range

Afrotropical, 5 spp, Oriental, 3 spp; Europe, 1 fossil sp.

Comments

Along with the proposal of the genus, the included species were reviewed (Barbero et al. 2009). Two morphologically distinct groups of species may be recognized in *Eodrepanus*: the bulk of the species (including the type species) have a low longitudinal elevation on either side of the pronotal and elytral disc, a bidentate-bisinate clypeus, normally slender 3-dentate protibiae, and an indistinct scutellum; an Oriental species, however, has a rounded clypeal apex, long, curved protibiae (with three quasi-backward-shifted denticles on their outer edge), and, last but not least, a distinct scutellum (*integriceps*). Barbero et al. (l.c.) present arguments to join both groups in a single genus.

The emarginate elytral epipleuron, the elytral striation, the 3-dentate protibia, and the characters determining the appearance of “parallel deplanation” of the dorsal side, jointly set this *Eodrepanus* apart from other genera of the *Drepanocerus* group.

***Ixodina* Roth, 1851 stat.n.**

Generic diagnosis

Head generally transverse, without pattern of symmetrically arranged depressed cells separated by ridges. Frontoververtex (well behind clypeus) without any protrusions or with (sub)longitudinal elevation(s), in some species with triplet of ridges. Clypeal surface in front black or brown, like posterior surface of head. Clypeal outline anteriorly emarginate-bisinate or emarginate-bidentate. Lateral margin of clypeus generally evenly

curved or straight, or distinctly angulate-dentate (multidentate or -sinuate in some species). Clypeogenal edge at suture (full-face view) abrupt. Median postclypeal protrusion (on or just behind clypeofrontal transition, male) absent.

Pronotum in both sexes with central-transverse hole and basic pattern of (variably modified) longitudinal elevations, starting from 2-3 costae on either side of pronotal base (in some species giving rise to pair of very slender to very broad anterior projections, from halfway pronotum); central hole quasi-tunnelling laterad under longitudinal elevations (tunnel usually with membranous cover). Pronotal sides (dorsal view) with marginal edge straight or rounded, evenly rounded to obtuse anterolateral angle or forming blunted anterolateral angle; edge (in lateral view) sinuate posteriorly. Pronotal base medially at most slightly protruding. Prothoracic underside on either side flat or very slightly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture usually consisting of (sub)isodiametric annular punctures, central hole usually smooth. Scutellum between basosutural angles of elytra small, narrow, but distinct.

Elytral disc generally distinctly deplanate (between both striae 6 on either side of suture), matt; disc very superficially striate, with stria punctures variably distinct, simple, and without distinctly microsculptured interstriae. Elytra with distinct, evenly curved paradiscal ridge (from inside humerus to apicosutural area, interstria 5); additional discal ridge may be present (a raised interstria 3). Elytron with sharply elevated juxtepleural ridge; epipleuron unmodified, at most narrow but not emarginate-sinuate behind humerus, at most with very slight parepleural ridge; humeral umbone with (usually two) well-defined ridges, distinct depression behind umbone; elytral base without isolated protrusion. Elytral colour virtually uniformly dark (black-brown). Regular discal interstriae with or without bristles, any bristles usually slender, erect.

Surface of abdominal ventrites generally flat. Metasternum between mesocoxae generally not distinctly elevated. Metepisternum more or less flat, unmodified. Metacoxae widely separated. Proximal abdominal ventrites medially separated by sutures. Distal abdominal ventrites laterally not impressed-compacted. Abdominal sides at most slightly expanded beyond epipleura, and indistinct from above. Pygidium convex, at most slightly uneven.

Protibia straight to very slightly curved, with total of 4 simple external denticles, variably serrate proximally; apex with distally oriented oblique apico-external denticle, neither with special protrusions, nor with tuft of long setae. Metatarsal segment 1 about equal to or shorter than segments 2-4 combined.

Parameres simple, lacking accessory projections separate from main structure (in dorsal view).

General body shape normally compact to slightly elongate. Pilosity limited compared to most other drepanocerines, bristles and/or simple setae predominant. Legs may be very light coloured (yellow); ventral side may be symmetrical patterned with yellow; several parts may be more shining than is usual in most genera. Body very small to small; usual length 2.5-5 mm.

Type species

Ixodina abyssinica Roth, 1851, by monotypy.

Geographic range

Afrotropical 9 spp+sspp, Oriental 1 sp.

Comments

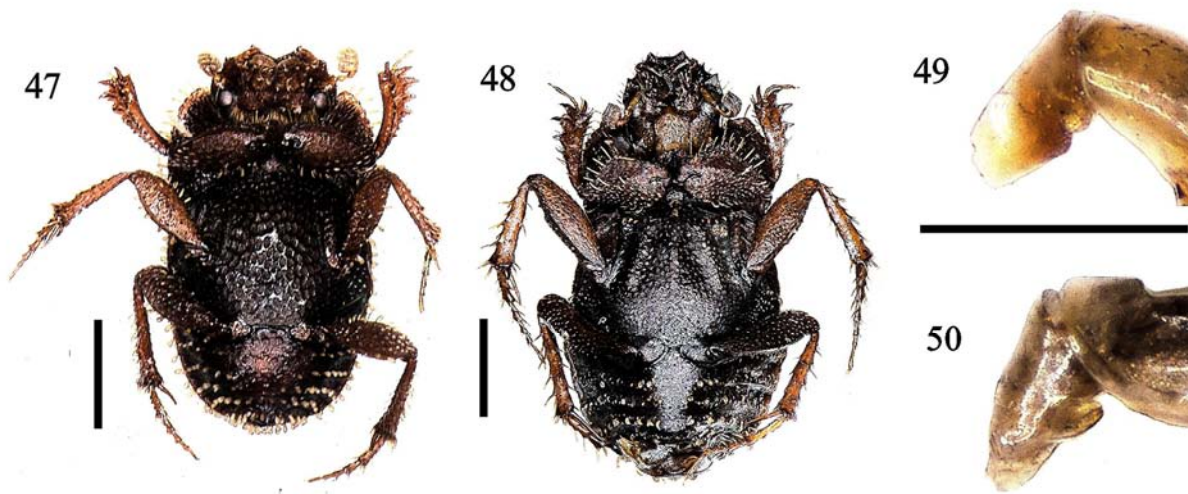
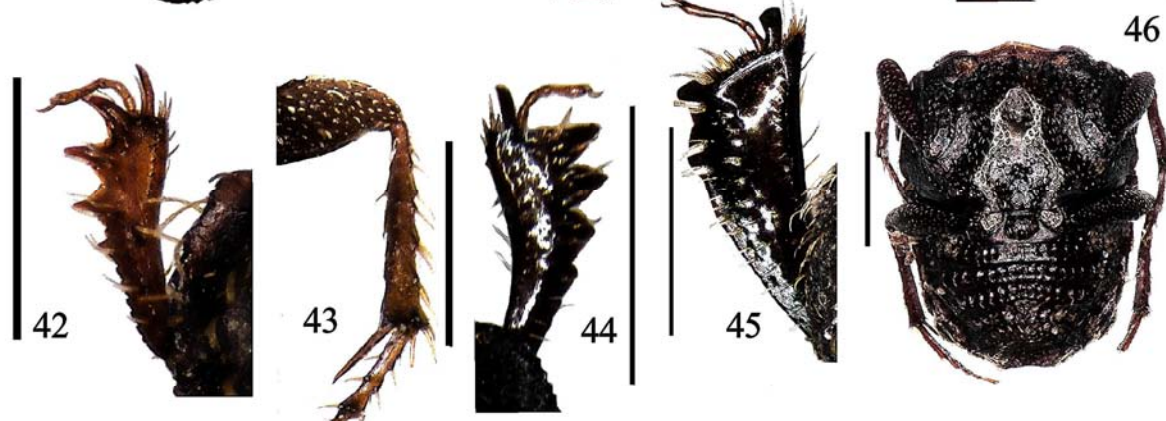
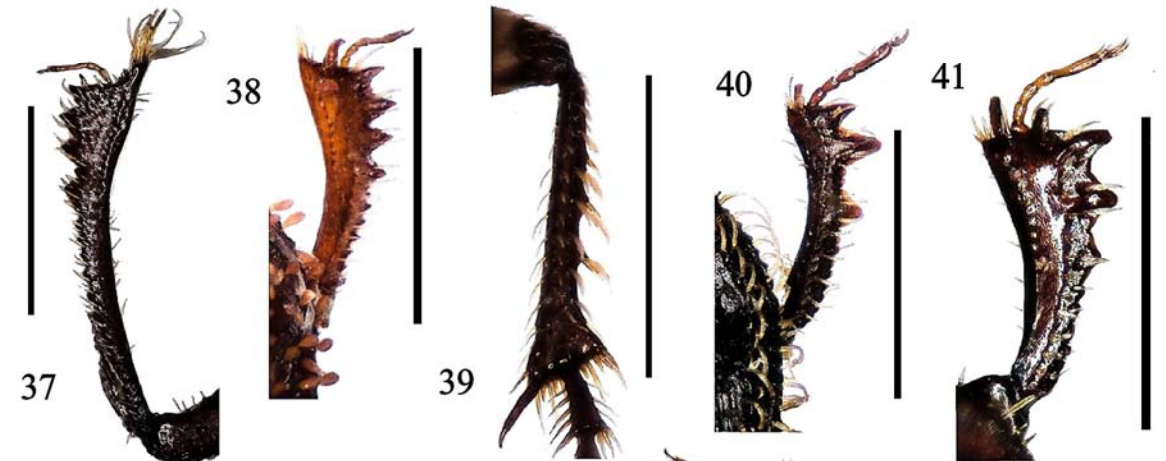
The curved paradiscal ridge on the elytron and the ridges bridging the central pronotal hollow on either side are the two most characteristic, apparently synapomorphic features of *Ixodina*, which for a long time has been treated as a mere synonym of *Drepanocerus*. A simple comparison of the pictures of *Ixodina* with those of other genera in this paper (like *Drepanocerus*) should convince everyone of the justification of the revised status of *Ixodina*. Note the change in gender compared to *Drepanocerus* and the consequent changes in species-group names suffixes. Endrödi's key (1976) is incomplete and outdated.

The genus is internally quite diverse and most species are polymorphic. Various groups of species may be recognized, like those with the robust *abyssinica*-like pronotal protrusions, and those with the more slender pronotal structure shown by, for instance, the Asian *runica*. Note also *I. freyi*, the male of which, with its remarkable pronotal ornamentation, is described below for the first time; its frontovertex, like the minute *saegeri* (which is only ca 2.5 mm long), has 3 longitudinal ridges, the outer ridges being convergent anteriorly. The pronotal sides and base of these two species are more rounded compared to *abyssinica*-like forms. Some *Ixodina* species have lighter (brown to yellow) legs and a shiny ventral side patterned with yellow markings.

More on the basic structure of the pronotal relief pattern of *Ixodina* in the section on *I. freyi* below.

→

Figs 34-50. Head, full-face (1-3); protibia, upper side (37, 38, 40, 41-42, 44, 45); metatibia, underside (39, 43); metapectus (46); ventral side (47, 48); parameres, lateral (49, 50). – 34, 37-39, 47, 49, *Clypeodrepanus digitatus* (34, holotype, 37, 39, paratype, 38, minor male paratype; 47, paratype female; all Kenya); 35, *Latodrepanus laticollis* (Kenya); 36, 42, 43, 48, 50, *Drepanocerus orientalis* (Kenya, holotype); 40, *Eodrepanus becheynei* or nr (Kenya); 41, *Tibiodrepanus hircus* (Indonesia: Bali); 44, 46, *Afrodrepanus impressicollis* (Kenya); 45, *Sinodrepanus nr falsus* (Thailand). – Males, unless mentioned otherwise.



***Tibiodrepanus* gen.n.**

Generic diagnosis

Head generally transverse, without pattern of symmetrically arranged depressed cells separated by ridges. Frontoververtex without any protrusions. Clypeal surface in front black or brown, like posterior surface of head. Clypeal outline anteriorly emarginate-bidentate. Lateral margin of clypeus generally evenly curved or straight, with single distinct denticle delimiting clypeogenal excision (at suture, full-face view). Median postclypeal protrusion (on or just behind clypeofrontal transition, male) absent.

Pronotum without pair of very broad anterior discal projections, with slender basomedian forward projection (in male of one species only), without pair of long, slender, acuminate, forward projections; disc with low, more or less curved paramedian elevation delimiting broad median depression on either side (in both sexes), in male of some species with higher (plate-like, variably shaped) crest delimiting this depression on either side. Pronotal sides (dorsal view) with marginal edge evenly rounded to obtuse anterolateral angle, rounded or subsinuate to obtuse posterolateral angle; edge (in lateral view) sinuate posteriorly. Basal edge of pronotum medially protruding slightly, rounded off. Prothoracic underside on either side flat or very slightly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture consisting of (sub)isodiametric annular punctures. Scutellum between basosutural angles of elytra minute.

Elytral disc generally distinctly deplanate (between both striae 6 on either side of suture), variably striate-punctate, with striae punctures distinct, simple, without distinctly microsculptured interstriae, or with rough (microgranulose-microreticulate) interstriae. Elytra with slightly raised interstria 5, or this interstria forming slightly curved paradiscal ridge. Elytron with simple juxtepleural ridge, with epipleuron unmodified, at most narrow but not emarginate-sinuate behind humerus, with variably distinct parepleural ridge behind depression posteriorly delimiting humeral umbone, without any isolated protrusion on base. Elytra virtually uniformly dark coloured (black-brown), matt to sericeous. Regular discal interstriae with slender bristles, with coarse (distally expanded) bristles, and/or with fine setae, interstria 3 may be slightly raised.

Surface of abdominal ventrites generally flat. Metasternum between mesocoxae generally not distinctly elevated. Metepisternum more or less flat, unmodified. Metacoxae narrowly separated. Proximal abdominal ventrites with sutures medially more or less effaced. Distal abdominal ventrites laterally not impressed-compacted. Abdominal sides at most slightly expanded beyond epipleura, and indistinct from above. Pygidium with small (variably pronounced) elevations.

Protibia straight to very slightly curved, with total of 4 denticles, distinctly serrate proximally; slender denticle 4 sitting on transverse apical edge next to tarsus, apico-internal angle not produced and without tuft of long setae; 3 external denticles standing out normally. Metatarsal segment 1 about equal to or slightly shorter than segments 2-4 combined.

Parameres simple, or with slight accessory projections separate from main structure (in dorsal view).

General body shape normally compact to slightly elongate. Pilosity generally abundant, bristles and/or simple setae predominant. Body very small to small; usual length 4-5 mm.

Type species

Copris setosus Wiedemann, 1823.

Geographic range

Oriental, with slight transgression, 5 spp (see comments hereafter).

Comments

The fine (4th) denticle sitting on the protibial apex is the primary attribute of *Tibiodrepanus*. The translation of the description of *Drepanocerus simplex* Kabakov (2006), kindly provided by our colleague Frolov, explicitly mentions this attribute, and consequently *simplex* is recombined with *Tibiodrepanus*. The same applies to *Drepanocerus kazirangensis* Biswas (1980), the forward-directed apical denticle being explicitly mentioned in the original description. These recombinations are tentative, as the descriptions and associated pictures of both species are generally insufficient; types were inaccessible. Note pictures of male genitalia of *simplex* in Kabakov (2006). Whatever, both species certainly do not belong in *Drepanocerus* as here conceived.

Pronotal ornamentation of males diverse according to species, and polymorphic within species. Close to the Afrotropical genus *Sulcodrepanus*, as previously implied in Simonis (1985b), but different in the modified protibia, which for *Tibiodrepanus* may well constitute a decisive generic synapomorphy. As I cannot give a definite synapomorphy for both genera combined, *Sulcodrepanus* is kept separate; it simply is a taxon with a rather basic morphology.

Etymology

The prefix *Tibio* to *drepanus* refers to the characteristic protibial apex; masculine noun.

***Sulcodrepanus* gen.n.**

Generic diagnosis

Head generally transverse, without pattern of symmetrically arranged depressed cells separated by ridges. Head surface generally evenly convex, without any protrusions, entirely black-brown, matt. Clypeal outline anteriorly emarginate-bisinate or emarginate-bidentate. Lateral margin of clypeus generally evenly curved or straight. Clypeogenal edge at suture (full-face view) abrupt, shallowly excised.

Pronotum, stronger male modifications aside, generally deplanate, with elongate, broad shallow discal-median depression or with (at least in male) sharply defined median longitudinal impression; without pair of very broad anterior projections, without slender basomedian forward projection, without pair of long, slender, acuminate, forward projections (but male of single known species has plate-like crest delimiting median depression on either side). Pronotal sides (in dorsal view) with marginal edge evenly rounded to obtuse anterolateral angle, posterolateral angle rounded off; lateral edge (in lateral view) sinuate posteriorly. Basal edge of pronotum medially protruding slightly, rounded off. Prothoracic underside on either side flat or very slightly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture consisting of annular punctures. Scutellum between basosutural angles of elytra small but distinct.

Elytral disc generally distinctly deplanate (between both striae 6 on either side of suture); surface very superficially striate, with striae punctures distinct, simple, with rough, usually microgranulose-microreticulate interstriae. Elytra at most with slightly raised interstria 5. Elytron with sharply elevated juxtepleural ridge, with epipleuron unmodified, at most narrow but not emarginate-sinuate behind humerus, at most with very slight parepleural ridge, with (usually two) ridges on humeral umbone, with distinct depression behind humeral umbone; elytral base without isolated protrusion. Elytral colour virtually uniformly dark (black-brown). Regular discal interstriae at most with few, inconspicuous bristles, interstria 3 slightly raised.

Surface of abdominal ventrites generally flat. Metasternum between mesocoxae generally declivous in front. Metacoxae narrowly separated. Proximal abdominal ventrites with sutures medially more or less effaced. Distal abdominal ventrites laterally not impressed-compacted. Abdominal sides at most slightly expanded beyond epipleura, and indistinct from above. Pygidium with small (variably pronounced) elevations.

Protibia straight to very slightly curved, with total of 4 external denticles standing out normally, distinctly serrate proximally; apex with normal, oblique apico-external denticle (4), without apico-internal protrusion and/or tuft of long setae. Metatarsal segment 1 about equal to or slightly shorter than segments 2-4 combined.

Parameres simple, lacking accessory projections separate from main structure (in dorsal view).

General body shape normally compact to slightly elongate. Pilosity generally sparse, short. Body small; usual length 4.5-5 mm.

Type species

Drepanocerus sulcicollis Castelnau, 1840.

Geographic range

Afrotropical, 1 sp.

Comments

The head is simple, lacking both marginal and non-marginal protrusions. The other non-sexual characters are also relatively simple and can hardly be qualified as derived; they are very similar to those of the Asian *Tibiodrepanus*. That genus, however, has the modified protibiae, with the 4th denticle sitting on the transverse tibial apex, in both sexes – apparently an autapomorphy. Further work has to establish whether these two drepanocerine groups are genuinely related, for instance, in a paraphyletic way, rendering a joint subgeneric level classification perhaps more appropriate.

Etymology

The prefix *Sulco* to *drepanus* refers to the name of the type species; masculine noun.

***Drepanocerus* Kirby, 1828**

Generic diagnosis

Head more or less elongated, without pattern of symmetrically arranged depressed cells separated by ridges, but with pair of longitudinal ridges on frontovertex. Clypeal surface in front black or brown, like posterior surface of head. Clypeal outline anteriorly emarginate-bidentate, margin (in males of two species) anteriorly may have reflexed median projection. Lateral margin of clypeus distinctly angulate-dentate, i.e. with one or more distinct denticles. Clypeogenal edge at suture (full-face view) more or less abrupt. Median postclypeal protrusion (on or just behind clypeofrontal transition, male) absent.

Pronotum with constant pattern of ridges separating numerous symmetrically arranged cells (up to 12, details depending on species); cells may be obliterated by male ornamentation); without pair of very broad anterior projections, without slender basomedian forward projection, with pair of long, slender, acuminate, forward projections (male of one species), without longer lower or higher paramedian elevation delimiting discal-median depression on either side. Pronotal sides with marginal edge (dorsal view) forming blunted (or slightly emarginate-dentate) anterolateral angle; edge (in lateral view) sinuate posteriorly. Pronotal base distinctly produced medially, angular. Prothoracic underside on either side flat or very slightly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture consisting of (sub)isodiametric annular punctures. Scutellum between basosutural angles of elytra small, but distinct.

Elytral disc generally distinctly deplanate (between both striae 6 on either side of suture), very superficially striate, with striae punctures variably distinct, simple, with scabrous or plainly microreticulate interstriae. Elytron with simple, distinct juxtepleural ridge, with epipleuron unmodified, at most narrow in front, but not emarginate-sinuate below humeral umbone, at most with slight parepleural ridge; humeral umbone simple or slightly incised by striae, with distinct posthumeral depression; elytral base lacking isolated protrusion, immarginate. Elytra and other body parts with well defined (symmetric) yellow markings on black-brown background. Regular discal interstriae with fine bristles; interstriae 1, 3 and 5 distinctly raised, with coarser bristles.

Surface of abdominal ventrites medially flat. Metasternum between mesocoxae broad, declivous in front. Metepisternum slightly concave. Metacoxae narrowly separated. Proximal abdominal ventrites with sutures medially more or less effaced. One or more distal abdominal ventrites laterally distinctly impressed-compacted (anteanal sternite "constricted"). Abdominal sides very broadly expanded, forming lateral ridge, very distinct from above. Pygidium with small (variably pronounced) elevations.

Protibia straight to very slightly curved, with total of 4 external denticles standing out normally, distinctly serrate proximally. Protibial apex with normal oblique apico-external denticle (4), neither with apico-internal protrusion, nor with tuft of long setae. Metatarsal segment 1 about equal to or slightly shorter than segments 2-4 combined.

Parameres simple, lacking accessory projections separate from main structure (in dorsal view).

General body shape oblong, more or less parallel-sided. Pilosity including numerous bristles of various shapes and sizes, and simple setae; no close cover of scales. Body small; usual length 4-8 mm.

Type species

Drepanocerus kirbyi Kirby, 1828.

Geographic range

Afrotropical, 3 spp.

Comments

The colour pattern, the head shape, the pronotal cells, the elytral details, and the expanded abdominal sides are most characteristic for the few species here left in *Drepanocerus*, and some of the attributes concerned may constitute synapomorphies. The pronotal cells may be more or less "pushed away" in male *kirbyi* by a pair of pronotal protrusions. *Cyptochirus* species have similar pronotal cells, and their heads have them as well, but otherwise the species are all simply very different.

The three named species of *Drepanocerus* (one new) are briefly keyed below, in the section Species accounts. Note that the males, as usual, may be quite polymorphic in their sexual characters (in two species).

***Afrodrepanus* gen.n.**

Generic diagnosis

Head generally transverse, without pattern of numerous symmetrically arranged depressed cells separated by ridges. Frontovortex with (sub)longitudinal elevations, usually with pair of ridges (may anteriorly be connected by transverse elevation). Clypeal surface in front black or brown, like posterior surface of head. Clypeal outline anteriorly emarginate-bidentate, margin (male) anteriorly with slender reflexed median projection (in one species). Lateral margin of clypeus generally evenly curved or straight. Clypeogenal edge at suture (full-face view) not excised. Median postclypeal protrusion (on or just behind clypeofrontal transition) absent.

Pronotum with (at least in male) sharply defined median longitudinal impression (broad); without pair of very broad anterior projections, without slender basomedian forward projection; in one species with pair of long, slender, acuminate, forward projections (male); with low paramedian (more or less setose) elevation delimiting discal depression on either side (both sexes), but without high crest delimiting median depression on either side. Pronotal sides with marginal edge (dorsal view) forming blunted or concavely arcuate-dentate anterolateral angle, sides more or less parallel (in dorsal view); edge (in lateral view) sinuate posteriorly. Prothoracic underside on either side distinctly concave in front of coxal-marginal ridge. Predominant pronotal microsculpture consisting of (sub)isodiametric annular punctures. Scutellum between basosutural angles of elytra small but distinct, or completely indistinct.

Elytral disc generally deplanate, disc and sides very distinctly striate-punctate, with rows of roundish punctures, which are (very) deeply impressed (more or less umbilicate), with narrowed ridges between rows of striae punctures. Elytron with simple juxtepleural ridge, with epipleuron reduced, very narrow over most of its length, with interstria 8 minimal, due to strong, complete striation; humeral umbone simple or slightly incised by striae, depression behind humeral umbone lacking; isolated protrusion on elytral base absent. Elytral colour virtually uniformly dark coloured (black-brown). Discal interstriae indistinct or narrow (if distinct, more or less equally elevated or just flat, or alternately elevated, i.e. interstriae 1, 3 and 5).

Surface of abdominal ventrites (transversely) more or less raised (or more narrowly ridged). Metasternum between mesocoxae generally with symmetric pattern of distinct impressions. Metepisternum distinctly concave. Metacoxae narrowly separated. Proximal abdominal ventrites medially separated by sutures. Abdominal sides at most slightly expanded beyond epipleura, and indistinct from above. Pygidium with small (variably pronounced) elevations.

Protibia straight to very slightly curved, with total of 4 external denticles (proximal denticle may be very small), distinctly serrate proximally. Protibial apex with simple transverse edge and more or less perpendicular apico-external denticle (4), without apico-internal projection and/or tuft of long setae. Metatarsal segment 1 longer than segments 2-4 combined.

Parameres simple, lacking accessory projections separate from main structure (in dorsal view).

General body shape normally compact to slightly elongate. Pilosity generally sparse, body sculpture generally coarse. Body small; usual length 4-5 mm.

Type species

Drepanocerus impressicollis Boheman, 1857.

Geographic range

Afrotropical, 2 spp.

Comments

Barbero et al. (2009) provides data also justifying the removal of the two species from *Drepanocerus* to a separate genus. Characteristic are the heavily punctate striae, the reduced elytral epipleuron, an uninterrupted clypeogenal edge, and more.

Etymology

The prefix *Afro* to *drepanus* refers to the African range of the genus; masculine noun.

Annotated list of all drepanocerine taxa

Van Lansberge (1875) appears to be the author of the family-group name (as Drépanocérides), but note also the concepts in two influential keys: Drepanocerides in Janssens 1946 and [subtribe] Drepanocerina in Janssens 1949. The annotated list of included taxa below is based on Boucomont (1921), Janssens (1953), Balthasar (1963), Ferreira (1973), and subsequent documented or otherwise reliable species identifications (i.e. those established by taxonomists). Post-1953 papers describing taxonomic novelties (see also Introduction) are all included in full in the References. The list summarizes the new nomenclatural acts proposed in this paper. The usage of some names (which may represent species complexes) definitely requires a reinvestigation based on more extensive material. Note that the paper on *Anoplodrepanus* by Simonis (1981) was missed by The Zoological Record.

The species-group names are arranged within their genus in alphabetical order. Numbers of known species and subspecies numbers are given as [s] spp. Where appropriate the species-group names show the original genus combination in brackets. The country (region) records were drawn from the literature and from material at hand, but the indications must remain tentative awaiting full revisions. A few exceptional regional records appear to be new and are marked with a double exclamation mark !!. The abbreviation LS is followed by a reference to the latest synopsis of the genus (actually, only Barbero et al. 2009 has a genuinely revised key, i.e. to the species of *Eodrepanus*). TR marks the region where the type locality of the valid name is situated (where more than one region is mentioned). Some comments given behind forward slash /. One species-group name is left with *Drepanocerus* auctorum, and the status of some *Tibiodrepanus* species needs to be checked (see under generic account above).

As for geographic terminology, national boundaries and geographic names vary in the course of time. In this paper Congo-B and Congo-K stand for the countries of which Brazzaville and Kinshasa, respectively, are the capital cities. South Africa stands for the Republic of South Africa and its enclaves/satellites; older records may pertain to a different concept, which may be a further source of imprecision. Old Abyssinian records are regarded as coming from Ethiopia. Note that Zanzibar in older literature frequently means the sultanate, i.e. the coastal region of Kenya and Tanzania, plus the islands.

Subtribe **DREPANOCERINA** Lansberge, 1875

- *Drepanocerus* group of genera:

***Clypeodrepanus* gen.n.**, type species: *digitatus* – Afrotropical, 3 spp

C. digitatus **sp.n.**, this paper – Kenya

C. striatus (Boucomont, 1921) – Tanzania (*Drepanocerus*) **comb. n.**

C. strigatus (Janssens, 1953) – Congo-K (TR), Benin, Ivory Coast (*Drepanocerus*) **comb. n.**

***Latodrepanus* gen.n.**, type species *laticollis*, Afrotropical, 4 sp

L. caelatus (Gerstaecker, 1871) – Congo-K, Ethiopia, Guinea, Ivory Coast, Kenya, Tanzania (TR) (*Oniticellus*) **comb. n.** / = *setiger* Raffray, 1877

L. laticollis Fahraeus, 1857 – Benin, Congo-B, Congo-K, Guinea, Ivory Coast, Kenya, South Africa (TR), Tanzania, Zimbabwe, (*Drepanocerus*) **comb. n.**

L. pulvinarius Balthasar, 1963b – Kenya, Tanzania (TR) (*Drepanocerus*) **comb. n.**

L. schimperi Janssens, 1953 – Ethiopia / male undescribed (*Drepanocerus*) **comb. n.**

***Eodrepanus* Barbero, Palestrini & Roggero, 2009**, type species: *parallelus* – Oriental, Afrotropical, 9 spp / LS Barbero et al. 2009

E. bechynei (Janssens, 1953) – Benin, Burkina Fasso, Burundi, Cameroon, Congo-K, Ethiopia (TR), Gambia, Ghana, Guinea, Guinea Bissau, Ivory Coast, Kenya, Mozambique, Niger, Nigeria, Rwanda, Senegal, SA, Tanzania, Uganda, Zambia, Tanzania (*Drepanocerus*)

E. coopei Barbero et al., 2009 – UK (England) fossil: Eemian

E. fastiditus (Peringuey, 1901) – Burundi, Congo-K, Eritrea, Ethiopia, Guinea Bissau, Kenya, Mozambique, Rwanda, South Africa (TR), Tanzania, Uganda, Zambia, Zimbabwe (*Drepanocerus*)

E. integriceps (Janssens, 1953) – China:S (*Drepanocerus*) / [odd element in the genus]

E. liuchungloi (Kryzhanovskiy & Medvedev, 1966) – China:S (*Drepanocerus*)

E. morgani Barbero et al., 2009 – Central African Republic

E. paolae Barbero et al., 2009 – Burundi

E. parallelus (Raffray, 1877) – Burundi, Congo-K, Ethiopia (TR), Eritrea, Kenya, Malawi, Mozambique, Rwanda, SA, Tanzania, Uganda, Zambia, Zimbabwe (*Drepanocerus*)

Haroldius 4 (2009)

E. striatulus (Paulian, 1945) – China:S, India:NE, Indonesia (Java!!), Laos, Myanmar, Nepal, Thailand, Vietnam (TR) (*Drepanocerus*)

Ixodina Roth, 1851, **stat. n.**, type species: *abyssinica* – Oriental, Afrotropical, 10 spp+sspp / note feminine usage by Roth / LS Endrödi 1976

I. abyssinica abyssinica Roth, 1851 – Cameroon, Congo-K, Djibouti, Ethiopia (TR), Guinea, Ivory Coast, Niger (*Drepanocerus*)

I. abyssinica tangana (Endroedi, 1971) – Tanzania (TR), Kenya (*Drepanocerus*) **comb. n.**

I. bos (Endroedi, 1976) – Ghana (*Drepanocerus*) **comb. n.**

I. endroedyi (Endroedi, 1976) – Ghana (*Drepanocerus*) **comb. n.**

I. freyi (Janssens, 1953) – South Africa (TR), Tanzania!! (*Drepanocerus*) **comb. n.** / male described this paper

I. kovacsi (Endroedi, 1976) – Ethiopia (*Drepanocerus*) **comb. n.**

I. runica (Arrow, 1909) – China:S, Indonesia (East to Flores!!), Myanmar (TR), Vietnam (*Drepanocerus*) **comb. n.**

I. saegeri (Balthasar, 1963a) – Congo-K, Kenya (*Drepanocerus*) **comb. n.**

I. szunyoghysi szunyoghysi (Endroedi, 1971) – Kenya, Tanzania(TR) (*Drepanocerus*) **comb. n.**

I. szunyoghysi occidentalis (Endroedi, 1976) – Ghana (*Drepanocerus*) **comb. n.**

***Tibiudrepanus* gen.n.**, type species: *setosus*, Oriental, 5 spp

T. hircus (Wiedemann, 1823) – Indonesia (Java TR, Bali), Philippines (Luzon) (*Copris*) **comb. n.**

T. kazirangensis (Biswas, 1980) – India:NE (*Drepanocerus*) **comb.n.** / [precise relationships uncertain]

T. setosus (Wiedemann, 1823) – India, Indonesia (Sumatra!!), Sri Lanka (*Copris*) **comb. n.**

T. simplex (Kabakov, 2006) – Afghanistan (*Drepanocerus*) **comb.n.** / [precise relationships uncertain]

T. sinicus (Harold, 1868) – China:S (TR), India, Laos, Myanmar, Thailand, Vietnam (*Drepanocerus*) **comb. n.** / = *setosus* Boheman, 1858 non Wiedemann, 1823

T. sp. – Indonesia (Sulawesi!!) / [female, species identity uncertain, *hircus* or near]

***Sulcodrepanus* gen.n.**, monospecific, Afrotropical

S. sulcicollis (Castelnau, 1840) – Cameroon, Congo-K, Ethiopia, Mozambique, Guinea, Ivory Coast, Kenya, South Africa (TR) (*Drepanocerus*) / = *dispar* Boheman, 1857 **comb. n.**

Drepanocerus Kirby, 1828, type species: *kirbyi* – Afrotropical, 3 spp

D. kirbyi Kirby, 1828 – Congo-K, Ethiopia, Kenya?, Mozambique, Rwanda, South Africa (TR), Tanzania / [original spelling *kirbii*] / = *furcifer* Castelnau, 1840

D. orientalis **sp.n.**, this paper – Kenya (TR), Tanzania

D. patrizii Boucomont, 1923 – Kenya (TR), South Africa / = *arthuri* Boucomont, 1936

Drepanocerus auctorum, 1 name

status of species to be assessed

D. planus (Fabricius, 1801) – Indonesia (Java) (*Ateuchus*)

***Afrodrepanus* gen.n.**, type species: *impressicollis*, 2 spp

A. impressicollis (Boheman, 1857) – Kenya, South Africa (TR), Tanzania, Zimbabwe (*Drepanocerus*) **comb. n.** / = *natalensis* Harold, 1859

A. marshalli (Boucomont, 1921) – Burundi, Congo-K, Guinea, Ivory Coast, Rwanda, Zimbabwe (*Drepanocerus*) **comb. n.**

- other genera:

Sinodrepanus Simonis, 1985, type species: *falsus* – Oriental, Southeast Palaearctic, 8-9 spp / LS Simonis 1985a

S. arrowi (Balthasar, 1932) – China:S (TR), Vietnam (*Drepanocerus*) / Balthasar 1963c [name not in Simonis 1985a, precise identity to be reassessed]

S. besucheti Simonis, 1985 – China:S

S. falsus (Sharp, 1875) – India:NE, Laos (TR), Thailand, Vietnam, (*Oniticellus*) / = *exsul* Sharp, 1875 (Janssens 1953)

S. rex (Boucomont, 1912) – China:S (*Drepanocerus*) / ? = *arrowi*, q.v.

S. rosannae Simonis, 1985 – China:S

S. similis Simonis, 1985 – China:S, Thailand (TR)

S. thailandicus Ochi et al, 2004 – Thailand

Haroldius 4 (2009)

S. tsaii Masumoto et al, 2004 – China (Taiwan)

S. uenoi Ochi et al, 2004 – China:S

Cyptochirus Lesne, 1900, type species: *ambiguus* – Afrotropical, 4 spp / LS Simonis & Zunino 1980

C. ambiguus (Kirby, 1828) – Congo-K, South Africa (TR) (*Onitis*)

C. decellei Simonis & Zunino, 1980 – Burundi, Congo-K, Kenya, Rwanda (TR), Somalia, Uganda

C. distinctus Janssens, 1953 – Burundi, Central African Republic, Congo-B, Congo-K (TR), Gabon, Guinea, Ivory Coast, Kenya, Senegal, Tanzania, Zambia, (*Drepanocerus*)

C. trogiformis (Roth, 1851) – Ethiopia (TR), Kenya, Somalia, Uganda (*Eurysternus*)

Drepanoplatynus Boucomont, 1921, monospecific – Afrotropical / Simonis & Cambefort 1984

D. gilleti Boucomont, 1921 – Congo-K (TR), Ivory Coast

Scaptocnemis Peringuey, 1901, monospecific – Afrotropical

S. segrégis Peringuey, 1901 – Burundi, Congo-K, Malawi, Tanzania, Zimbabwe (TR)

- **transferred** from Drepanocerina to Oniticellina (see Discussion, further below):

Anoplodrepanus Simonis, 1981, type species: *reconditus* – Neotropical (Caribbean), 2 spp / LS Simonis 1981

A. pecki (Howden, 1976) – Jamaica (*Drepanocerus*)

A. reconditus (Matthews, 1966) – Jamaica (*Drepanocerus*)

Total: ca 55 spp + sspp

Species accounts

Clypeodrepanus digitatus sp. n. (figs 1, 13-16, 24, 37-39, 47, 49, 51, frontispiece)

The major males of this species are very remarkable, and although undoubtedly related to *C. striatus* and *C. strigatus*, the head and protibiae are quite different, as indicated in the diagnosis and brief key given below, and shown in the pictures. Polymorphism in the new species is strong, and it could well be that a similar polymorphism exists in its congeners. The three species all share a broad shining brown clypeal margin and a clypeofrontal protrusion in the male; the females are roughly similar. For more characters of *Clypeodrepanus* see the generic diagnosis above.

Material examined

KENYA: Coast: Shimba Hills, 28/xii/1972, J Krikken 66, 350-400m, savanna with forest patches, from elephant dung, 1 paratype. Meru NP: SE section, 26/xii/1978, J Krikken 281, 550m, deciduous orthophyll savanna, from elephant dung, 1 paratype. Samburu: Samburu Game Lodge, 28/v/1976, J Krikken 207, 850m, deciduous orthophyll savanna, from elephant dung, 1 paratype. Tsavo East NP: Lion Hill nr Voi, 26/xi/1974, J Krikken & A L van Berge Henegouwen 133, 500-600m, deciduous orthophyll savanna, from elephant dung, 3 paratypes. Ndololo (in Voi R forest), 25/xii/1972, J Krikken 65, 550m, riverine forest, from elephant dung, 24 paratypes. Voi Safari Lodge, 26/xi/1974, J Krikken & A L van Berge Henegouwen 132, 600m, deciduous orthophyll savanna, from elephant dung, 4 paratypes. Voi: Mzinga, 21/xii/1972, J Krikken 49, 600m, deciduous orthophyll savanna, from elephant dung, 12 types, incl. **holotype**, paratypes. Tsavo West NP: Shaitana Lava Flow, 07/xii/1974, J Krikken & A L van Berge Henegouwen 163, 900m, deciduous orthophyll savanna, from elephant dung, 2 paratypes.

48 males and females, in 8 records. All in RMNH Leiden.

Description (holotype, male)

Body length ca 4 mm. Habitus convex-deplanate, with “oversized” forebody. Colour generally black-brown, matt, clypeal margin (including dental stalks) shining; elytra and legs brown. Dorsum and abdomen with conspicuous, more or less evenly distributed, erect, claviform pale-brown bristles, mostly sitting in distinct, large (sub)annular punctures. Remainder of body as well legs with numerous bristles and finer setae. General surface microreticulate-microgranulose or simple scabrous; most annular punctures with microgranulose internal surface.

Clypeal apex broadly emarginate, dentate with long upright stalk on either side (provided with long fine setae); clypeal surface crowdedly annulate-punctate, margins (and stalks) shining; clypeogenal margin broadly excised between genal angle and denticle on lateral clypeal margin; suture vague, curving onto frons. Frontoververtex crowdedly annulate-punctate, with numerous claviform bristles, with small but distinct, transverse, short postclypeal protrusion (i.e. well in front of eyes); vertex slightly concave over entire width. Eye foramina very narrow, with 5 or 6 rows of minute facets over their widest point. Ratio interocular distance / maximum (transverse, single) width ca 20.

Pronotum transverse, surface evenly, moderately convex, disc with long, shallow median impression; anterior declivity very short, slight, lacking any protrusions; any circumferal margination indistinct; postvertexal border straight; anterior section of lateral border (full-face view) strongly curving to (subrectangular) anterolateral angle; sides in dorsal view widely, evenly rounded to hardly distinct posterolateral angle; base very widely, evenly rounded; lateral declivity with impression near edge. Pronotal surface crowded with annular punctation, punctural shape and size somewhat varying; many of the larger punctures with claviform bristle; microsculpture on lateral declivities slightly scabrous; bristle length roughly equalling punctural diameter, punctural density (away from median impression) 15-20 / 0.25 sq.mm. Scutellum indistinct.

Elytra generally evenly convex, uniformly dark brown, matt; juxtasutural zone slightly depressed, apicosutural angle normally concealed due to tight elytral fit; humeral umbone slightly elevated, with regular elytral striae over its surface; elytral basal edge slightly raised; epipleuron narrow at humerus, with row of the usual claviform bristles; juxtepleural ridge distinct. Elytron with 8 straight to slightly curved, broad, well-defined, subparallel striae; stria punctures deep, transverse, simple, mostly separated by 2-4 punctural widths (estimated in stria direction), slightly crenulating interstitial edges. Interstitial surface at most slightly convex; interstriae 2, 3, 5, 7 with single row of fully developed claviform bristles (up to ca 15), interstriae 1, 4, 6 with smaller and fewer bristles, interstria 8 very narrow, lacking bristles; several interstitial punctures in which bristles are based less well defined than on, for instance, pronotum.

Antennal club large, club segment 1-2 darker brown than 3; scapus unmodified. Mentum short, transverse, centre raised, anterior edge concave; maxillae relatively robust. Sides of propectus scabrous, more or less microreticulate, crowded with large, roundish, superficial punctures, most of them with short bristle; coxal-marginal (proepisternal) ridge straight; proepisternal surface slightly concave. Preprosternum simply tectiform, postprosternum unmodified. Mesosternum short, narrow, mesometasternal suture straight. Metasternum evenly convex, surface with very crowded, somewhat honeycomb-like punctation, punctures large, shallow, internally microreticulate, most of them with (usually small) bristle. Metacoxae very widely separated. Abdominal ventrites 1-6 each with transverse row of superficial punctures bearing claviform bristle; surface more or less microreticulate; basomedian surface with sutures slightly effaced; anteanal and anal sternites laterally impressed. Pygidium semielliptic, with strongly ridged circumference; surface microreticulate, centrally with +-like protrusion separating shallow surrounding impressions; numerous claviform bristles present.

Protibia long, very slender, distally curved inward, with 4 larger denticles on outer edge (perpendicular to tibial axis) and proximal serration (diminishing to base); tibial apex oblique, with fine, elongate-acuminate, apically curved spur; internal edge running apically into long thumb-like, penicillate, slightly down-bent projection; pencil hairs long, about 3 times thumb length, issuing from upperside of thumb; underside of protibial length with ridge. Profemur straight, slender, underside with numerous superficial bristle-bearing punctures. Meso- and metafemora equally straight, slender, and with bristles in similar punctures. Meso- and metatibiae straight, slender, distally dilated into transversely subelliptic apical crest, which has both long and short spines; outer side with at least 5 small fossorial, spine-bearing protrusions; mesotibia with short and long acuminate spur, metatibia with single long acuminate spur, longer spurs about as long as tarsal segments 1. Protarsus very fine; meso- and metatarsi robust, tarsal segments 1 nearly as long as 2-4 combined; all tarsi with fine sickle-shaped claws. Approximate length proportions metatibial spur // metatarsal segments 1-5: 7//9/5/3/3/4.

Parameres simple, fig. 49 (paratype).

Measurements in mm (dorsal view). Maximum width of head 1.1. Median length of pronotum 1.6, maximum width 2.3. Sutural length of elytra 1.3, maximum width combined 1.9.

Etymology

The species name refers to the produced protibial apex of major males.

Diagnostic notes and variation

Major males of *Clypeodrepanus digitatus* should be easily recognizable from the shape of their head, pronotum, and protibiae. Females and extreme minor males may be harder to recognize, lacking the characteristic hypertrophic features of major males. The lateral denticle on the clypeus occurs in both sexes and the extravagant cover of claviform bristles may also be a helpful diagnostic feature. Females have the apical protibial edge not obliquely produced into an apico-internal angle or thumb-like protrusion. Furthermore, there are the absence of the postclypeal protrusion and the elongated upright clypeal denticles; the body of females is generally smaller and more slender.

Sexual dimorphism aside, polymorphism is considerable. Minor males do not have the thumb-like protibial extension, the postclypeal protrusion and apical denticles are less developed, and they are smaller and more slender (pronotum less broad), like females. The general colour varies from black to medium brown, somewhat rufous. Body length 3-4 mm.

Key to *Clypeodrepanus* species (males)

1. Postclypeal protrusion transverse. 2
- Postclypeal protrusion roundish. *strigatus*
2. Pronotum with pair of callosities topping distinct anterior declivity. Protibia very slightly curved and not digitate-penicillate. *striatus*
- Pronotum only with midline impression, general surface evenly convex. Protibia (major males) very long and slender, distally curved inward and digitate-penicillate. *digitatus*

***Drepanocerus orientalis* sp.n.** (figs 8, 22, 30, 36, 42, 43, 48, 50, 56)

Initially, this species was considered to belong to *D. kirbyi*, the type species of the genus, and it still stands under this name in collections. The type localities of both *Drepanocerus kirbyi* and its synonym *Oniticellus furcifer* Castelnau, 1840 are the Cape (South Africa), and the males of both, i.e. of the species *Drepanocerus kirbyi*, are horned. I found it quite peculiar that the abundant *kirbyi*-like material from eastern Africa seen had no specimens with horns at all, and on closer inspection detected some other differences. Consequently, I consider them two different species. The three species in *Drepanocerus* as here conceived are keyed after the description and diagnosis of this new species.

Material examined

KENYA: Coast: Kilifi, 26/xii/1973, P J J H Kuijten & F Bouricius, sea-level, sifted from cow dung, 2 paratypes. N of Malindi, 10/v/1976, J Krikken 203, sea-level, wooded cultivated area, from cattle dung, 1 paratype. Shimba Hills, 28/xii/1972, J Krikken 66, 350-400m, savanna with forest patches, from elephant dung, 1 paratype. Masai Mara GR: Talek Gate, 16/xii/1978, J Krikken 276, 1650m, deciduous orthophyll savanna, from cow dung, 5 paratypes. 5 km E of Keekorok, 21/iv/1981, J Krikken et al. 344, 1600m, deciduous orthophyll savanna, from elephant dung, 1 paratype. Tsavo East NP: Ndololo (in Voi R forest), 25/xii/1972, J Krikken 65, 550m, riverine forest, from elephant dung, 20 types, incl. **holotype**, paratypes. Voi, 31/i/1972, C Smeenk, 1 paratype. 25/vii/1971, C Smeenk, from elephant dung, 1 paratype. Voi: Mzinga, 21/xii/1972, J Krikken 49, 600m, deciduous orthophyll savanna, from elephant dung, 34 paratypes. Rift Valley: Kapsabet: Baraton AHRS, 10/ix/1976, H Straat, from fresh cattle dung, 1 paratype. TANZANIA: Morogoro, 24/vii/1973, P J J H Kuijten & F Bouricius, from cow dung, 1 paratype. 68 males and females, in 11 records. All in RMNH Leiden.

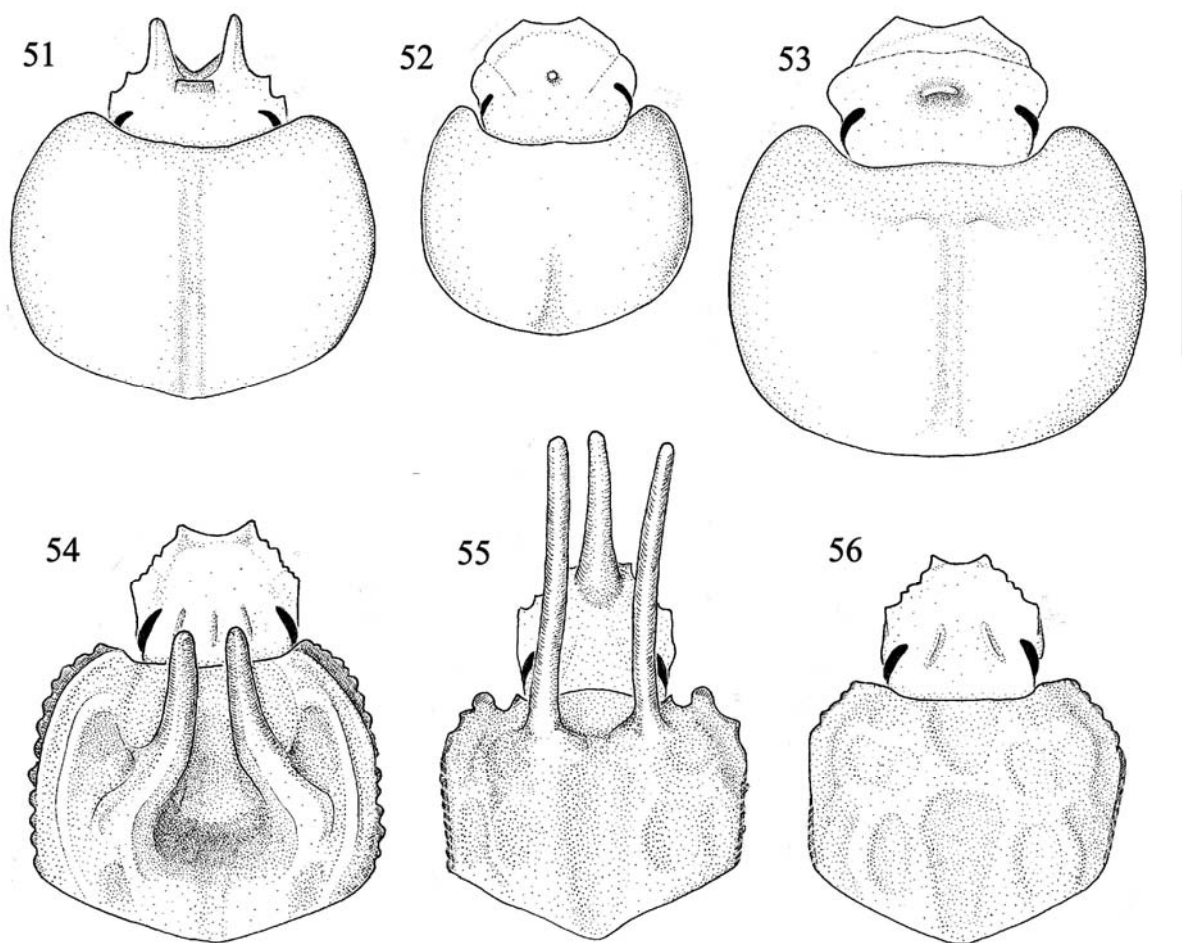
Description (holotype, male)

Body length ca 4 mm. Habitus deplanate, though deep-bodied, somewhat parallel-sided. Colour generally black-brown, matt; pronotal margins, elytra and legs brown, and elytra with distinct yellow markings. Dorsum with conspicuous, unevenly distributed bristles of various types, like: simple, long, erect; thickened, long, recurved; both usually brownish; much smaller, thickened, recurved, whitish bristles. Surface generally with crowded, superficial (sub)annular punctures, their interior microreticulate-striolate; background largely microreticulate, locally indistinct in a more scabrous surface.

Head elongate. Clypeal apex broadly emarginate, dentate on either side; clypeal surface scabrous, finely, abundantly annulate-punctate, with numerous scattered long bristles; clypeogenal margin broadly, evenly concave between anterior genal denticle and first denticle on multidentate-sinuate clypeal side; clypeogenal suture virtually effaced. Gena with well-defined lateral declivity topped by straight ridge (parallel to median axis), anteriorly ending in distinct angle. Frontovortex vaguely, somewhat irregularly annulate-punctate, also with numerous scattered long bristles; interocular surface raised medially, with pair of long, sharpish, anteriorly convergent ridges. Eye foramina narrow, with 5 or 6 rows of minute facets across their widest point. Ratio interocular distance / maximum (transverse, single) eye width ca 12.

Pronotum with disc deplanate, covered by symmetric pattern of shallow depressions separated by ridges bearing thick, recurved bristles: a basomedian and anteromedian cell; a basoparamedian and anteroparamedian cell; a basolateral and anterolateral cell, and a marginal cell; lateral declivity of prothorax below pronotal margin steep, posteriorly finely sharply punctate-setose, and topped by subsinuate pronotal edge (lateral view); postvertexal edge of pronotum straight in dorsal view; anterior section of lateral border curving to blunted anterolateral angle; posterior section almost straight to obtuse posterolateral angle; basal edge of pronotum on either side roughly oblique-straight to produced, shortly rounded median angle. Pronotal surface between ridges without pilosity, crowded with annular punctation, though locally vague and scabrous; pronotal edges with simple long bristles, many annuli on ridges with long, thickened, more or less recurved bristle. Diameters of annuli in basomedian cell ca 0.1 mm. Scutellum small, very short, but distinct, sides roundish.

Elytra with deplanate disc, side depressed behind distinct humeral umbone, dorsal outline of lateral elytral edge straight; general colour brown, matt, with transverse yellow marking over interstriae 2-6(-7) at ca 0.3 from elytral base, and with similar marking over interstriae 3-6 at short distance from apex; basal edge of elytra very slightly raised; epipleuron moderately broad behind humerus, with numerous whitish, curved, small bristles; juxtopleural ridge very distinct. Elytron with 8 nearly straight, very superficial, ill-defined, catenate striae;



Figs 51-56. Male forebody, dorsal outline. – 51, *Clypeodrepanus digitatus*, 52, *strigatus*, 53, *striatus*. 54, *Ixodina freyi*. 55, *Drepanocerus kirbyi*, 56, *orientalis*.

strial punctures simple, separated mostly by 1-2 punctural diameters, vaguely crenulating interstrial edges. Surface of interstriae 1, 3, 5 elevated, each with row of thick, recurved, brownish bristles (ca 15 on interstria 5), interspersed with fine, whitish, recurved bristles; non-elevated interstriae with similar fine bristles; background microsculpture mainly microreticulate-striolate.

Antennal club large, dark brown, segments 1-5 light brown; scapus unmodified. Mentum short, transverse, anteriorly shallowly emarginate, surface medially excavate. Sides of propectus scabrous, more or less microreticulate, crowded with large, superficial, annular punctures, several with long bristle; coxal-marginal suture curved forward, proepisternal surface virtually flat. Preprosternum subtecliform, postprosternum unmodified. Mesometasternal suture vague; anterior side of metasternum strongly declivous to mesosternum, intercoxal surface on either side with longitudinal ridge at some distance from narrowly raised midline; metasternal surface crowded with annular punctation, punctures large, shallow, on disc lacking bristle, on lateral wings many with small, recurved, whitish bristle. Metacoxae distinctly separated. Abdominal ventrites medially slightly shiny, laterally matt, generally microreticulate; sutures more or less effaced; anal-anteanal ventrites strongly impressed-compacted; sides expanded beyond elytral border, their tips yellowish. Pygidium semielliptic, with strongly ridged circumference, centrally with inverse Y-shaped protrusion separating shallow, microreticulate surrounding impressions; numerous bristles present, mainly on protrusion (few larger, many small claviform bristles).

Protibia slender, slightly curved inward, with 4 larger acuminate denticles on outer edge and fine proximal serration; tibial apex unmodified, with slender, slightly curved, elongate-acuminate terminal spur; underside of protibial length with slight ridge. Profemur robust, straight, expanded in front, surface crowded with punctures, several bearing a variably long bristle. Meso- and metafemora more slender, equally straight, and with numerous bristles in similar punctation. Meso- and metatibiae straight, slender, distally dilated into transversely subelliptic apical crest, with has numerous, both long and short spines; outer side with ca 5 small fossorial, spine-bearing protrusions; mesotibia with short and long acuminate spur, metatibia with single long acuminate spur, longer

spurs about as long as tarsal segments 1. Protarsus very fine; meso- and metatarsi robust, tarsal segments 1 about as long as 2-4 combined; all tarsi with fine sickle-shaped claws. Approximate length proportions metatibial spur // metatarsal segments 1-5: 12// 12/5/4/3/6.

Parameres, fig. 50 (holotype).

Measurements in mm (dorsal view). Maximum width of head 1.0. Median length of pronotum 1.6, maximum width 1.9. Sutural length of elytra 1.7, maximum width combined 2.1.

Etymology

The species name refers to its occurrence in eastern Africa.

Diagnostic notes and variation

This is a small species lacking any longer sexually dimorphic male cephalic and pronotal projections. The simple key hereafter separates the three species now included in *Drepanocerus*. Smaller females of *D. patrizii*, a species sympatric with *orientalis* (they were collected on the same sites), may be confused with those of their congeners, but they are usually immediately recognized by a different colour pattern, for instance, by the elytra lacking the large yellow elytral markings characteristic of the *kirbyi* “twin”; usually *patrizii* is larger, up to 8 mm long. The protrusions on the male head and pronotum of *kirbyi* and *patrizii* are polymorphic.

The markings on the elytron of *orientalis* are quite variable; the anterior set may, for instance, be separated and shifted, forming two smaller markings. Some individuals are lighter, others darker. The dentation on the clypeal sides varies, and may be obsolescent. Sexual dimorphism seems absent.

Body length 3.5-4 mm.

Key to *Drepanocerus* species (males)

1. Elytra with two distinct (anterior and antepical) yellow markings. Any longer clypeal horn not complanate-dilated. 2
- Elytra with more or less symmetric pattern of yellow and black-brown, but lacking two distinct, larger sets of markings. Males with clypeal projection, which is long, complanate, apically dilated, reflexed in major males. *patrizii*
2. Head with single clypeal horn, pronotum with pair of forward directed horns. *kirbyi*
- Head and pronotum without long projections. *orientalis*

Ixodina freyi (Janssens, 1953) (figs 5, 32, 54)

Hereafter the polymorphism of *freyi* is briefly described. The species clearly belongs in *Ixodina*. A major male is illustrated. The species was originally recorded from Zululand; our series comes from the Serengeti in North Tanzania, and was collected from buffalo dung. The basic relief structure of *Ixodina*, as evident in the female of *freyi*, is as follows. They usually have 3 ridges on either side of their pronotal base, a paramedian bordering the median depression, a sublateral, usually merging with the paramedian at the central hole, thence continuing anteriorly, and splitting again; the space between the posterior and anterior two forks may be raised, obliterating the separation between them. In (the males of) some species secondary elevations may arise slightly in front of the basal section. The lateral (3rd) ridge runs from the base forward, in some species also bridging the central-transverse hole. Finally, there is a submarginal (4th) ridge on the anterolateral surface of the pronotum, at some distance from the edge.

Material examined

TANZANIA: Serengeti NP: 25 km S of Seronera: nr Lake Magadi, 12/1/1973, J Krikken 95, 1500m, deciduous orthophyll savanna, from buffalo dung, 7 male and female spms. – 1 record. All in RMNH Leiden.

Diagnosis notes

Clypeal sides distinctly multidentate-crenulate. Frontovortex with triplet of (sub)longitudinal ridges. Pronotal sides widely evenly rounded and strongly undulate-crenulate. Elytron with raised interstria 3. Major males with slender, raised pair of stalks, directed forward, from about halfway paramedian ridges, bridging central hole (fig. 32). Minor males only with indication of these stalks, i.e. with (in lateral view) triangular denticle on the (paramedian) ridge bridging the central hole (over the “tunnel”), and a smaller denticle posteriorly on the same ridge, slightly in front of pronotal base. Females with basic *Ixodina* pattern, as explained above, and illustrated in Janssens (1953, fig. 13). Dorsum and other parts with numerous long erect setae. Entirely black. Body length 3.5-4.5 mm.

Discussion

Delimitation and position of the Drepanocerina

Within the Scarabaeinae the subtribe continues to be morphologically poorly defined: their members have eight antennal segments (like all Oniticellini, the related Onthophagini usually have nine), a ridged pygidial base, and a generally matt, heavily (micro)sculptured, (mostly uniformly) brownish-black integument, richly provided with bristles and scales (Janssens, 1949, and others). Curiously, in his 1953 review Janssens remained completely silent about the three subtribes he formerly recognized in the Oniticellini Kolbe, 1905, i.e. the Oniticellina Kolbe, 1905, Drepanocerina Lansberge, 1875, and Helictopleurina Janssens, 1946 (for nomenclature see also Smith 2006). Janssens's (1953) review also contains some inconsistencies and errors, for instance, with respect to the presence of a ridge along the pygidial base and the presence of elytral epipleura. To complicate matters further, the New World *Anoplodrepanus*, originally placed in *Drepanocerus* and described long after Janssens published his review, have a simply convex pygidium, without a basal ridge (more on this further below, under Historical biogeography). The presence of a ridge is just what should distinguish Drepanocerina from Oniticellina, which have a gradual pygidial-propygidial transition. With some difficulty an operational definition to sort out the *Drepanocerus* group of genera has been composed (Group description, heading the key to the genera above) and this includes the pygidial ridge. All in all, whether, after further research, morphological and otherwise, a sufficient set of apomorphies will prove to support the monophyly of a subtribe Drepanocerina remains to be seen. At present this support is almost negligible.

Recent efforts to construct a phylogeny of the subfamily Scarabaeinae and its components (see Scholtz & Grebennikov 2005 and included references, and molecular work, like Monaghan et al. 2007) have not really shed more light on the position of the Drepanocerina in the system, the resolution of these phylogenies being insufficient for this purpose. They confirm, however, the consensus view that: (i) Oniticellina and Drepanocerina are closely related and may be sister groups, or, in some way, have paraphyletic relationships; (ii) the Oniticellini as such constitute a derived clade in the phylogeny of the Scarabaeinae; (iii) the Onthophagini and Oniticellini may be sister groups (Philips et al. 2004, Monaghan l.c.) – certainly if some oddities are reassessed. Much earlier, Simonis (inter alia 1985) already presented a concise discussion of the phylogenetic position and diversity of the Drepanocerina, drawing special attention to the potential taxonomic value of genital characters.

Subdivision of the group

In the absence of a full recent synopsis of the supraspecific taxonomic units (no overall key published since Janssens 1953, no broader underpinned phylogeny either), this paper gives an updated overview of the Drepanocerina as traditionally conceived, with emphasis on *Drepanocerus* auctorum, here called the *Drepanocerus* group of genera. In spite of the extensive descriptive information available, this group remained, without question, a very heterogeneous assemblage of species, judged from their adult morphology alone – see figs 1-9 etc. Consequently, complementary to the genera recognized up till Barbero et al. (2009), the formal addition of supraspecific taxa appears justified, or even unavoidable, and, although in certain respects still tentative, a generic reclassification of the *Drepanocerus* group is proposed in this paper accordingly. Clearly, this classification is capable of improvement, but for the time being there is absolutely no case for maintaining the traditional broad concept of a large genus *Drepanocerus* – not as a single clade based on evident synapomorphies (which is also the main reason for ranking the supraspecific units in the present classification as full genera).

Historical biogeography

Recent drepanocerine genera (like Oniticellini in general) are essentially Afrotropical-Oriental in their distribution; some widespread drepanocerine species reach the Lesser Sunda Islands and Sulawesi in the East, others inhabit South China, and one is known from Afghanistan, close to the border with Northwest Pakistan (Kabakov 2006). The seemingly most remarkable exception would be *Anoplodrepanus*, comprising two upland species from Jamaica. Drepanocerina are not known from Madagascar (which has its own endemic oniticelline subtribe Helictopleurina); they do not now occur in the Mediterranean area (some Oniticellina do). Drepanocerines were, however, recorded from what is now temperate Europe, i.e. from Eemian deposits in England (70-100 000 years BP, one site being London's Trafalgar Square, see Coope 2000); the material concerned was recently referred to *Eodrepanus* by Barbero et al. (2009). These Eemian records show how fast (relatively speaking) distributions may change, which in itself is a strong warning signal against any easy biogeographic speculation. Furthermore, although the African continent seems to have the highest Recent drepanocerine diversity (in terms of numbers of taxa), the "Caribbean connection" and "the signal from Trafalgar Square", render an easy (and perhaps intuitive) conclusion about drepanocerine roots in Africa and an ancient Tethys distribution premature (note the view of Simonis, 1981 – no argued phylogeography given at the time). Matthews (1966), when describing the first drepanocerine from Jamaica, had a very different hypothesis, invoking the Bering Land Bridge to explain a dispersion of Oniticellini into the New World.

Actually, having both *Anoplodrepanus* species before me (one species illustrated here, fig. 12), I can confirm that they are certainly Oniticellini, but see no case whatsoever to keep them in the Drepanocerina (whatever their phylogenetic reality as a subtribe may turn out to be, see also comment above, under Delimitation and position of the Drepanocerina). Consequently, I can do little else than suggest a formal transfer of *Anoplodrepanus* to the Oniticellina.

It should indeed be mentioned at this point that other groups of Scarabaeinae have a large-scale geographic distribution more or less similar to the drepanocerine situation, i.e., Afrotropical-Oriental-South Palaearctic, with some oddities in the California-Mexico-Caribbean region, but their history needs not necessarily be the result of the same processes (as suggested by Matthews 1966). For a recent discussion with emphasis on the Oniticellina, see Philips & Bell (2008) and included references. This trans-Atlantic pattern is, with some variations, found in several other groups of organisms, where it is indeed usually thought to indicate a formerly more widespread, possibly Tethys-related, Cenozoic historical distribution for these groups (see Simonis 1983, 1985, Liebherr 1988, etc.). Note that according to Iturralde-Virent (2006) and others the present Caribbean terrestrial biota were formed after the Middle Eocene (<40 Ma), those of Jamaica, however, being considerably younger.

I have not seen (published records of) drepanocerines from Arabia, and on the species level they nowadays do not seem to “cross” the Afro-(Palaearctic-)Oriental boundary: both sides do not share any species, but the recent Afghan record, for instance, shows again that our factual knowledge is still limited – a further scrutiny of “the Arabian-Iranian gap” might well turn up additional drepanocerine material.

For a recent biogeographical synthesis on the Scarabaeinae, see Davis et al. (2002).

Ecology

In Africa most drepanocerines are widespread, diurnal savanna-steppe inhabitants, associated with large herbivorous dung producers; with possibly one or two exceptions, they do not have elements typical of plain multistratal evergreen forest, but some may occur in wide open spaces and riverine forest frequented by herbivorous mammals, and the same applies to the Asian situation. Our own collections of drepanocerines from Southeast Asia (*Tibiodrepanus*, *Ixodina*) with ecological data all come from bovine dung in open terrain, usually near settlements with domesticated water buffalo and other bovines (our intensive baited pitfall trapping in closed forest, away from edges, never yielded any drepanocerines). Their locally patchy occurrence (one dung heap containing numerous individuals, another nearby, deposited at the same time, containing almost nothing) suggests that aggregation pheromones are at work, a phenomenon well known in other dung beetle groups. Janssens (1953) gave observations on associations with bird excrements, but these were never reconfirmed. Cambefort (1984) differentiates the ecology of ten drepanocerine species on the basis of his studies in Ivory Coast, indicating, for instance, that some may not be totally dependent on large herbivore dung. Simonis & Cambefort (1984) consider *Drepanoplatynus gilleti* a hygrophilic African forest species, but still associated with bovines and elephants. Davis & Dewhurst (1994) analyse original and literature data pertaining to the Scarabaeinae of Kenya and Northern Tanzania, speculating on their possible faunal evolution in relation to the ecological history of the region, and listing eleven drepanocerine species for their region (without going into species-level detail). Kabakov & Napolov (1999) give faunistic and ecological data for seven Southeast Asian species.

The total ranges of some species in Africa and Asia (accepting their species-level homogeneity, cf. the case of *Drepanocerus kirbyi* above) are remarkably extensive within their continent (judged, for instance, from the country records in the Annotated list of drepanocerine taxa, given above); any gaps seem to reflect under-sampling and/or lack of published records, though the presence of a “Congo Basin gap” may indicate that extensive forest cover is an ecological barrier to some species (Barbero et al. 2009).

For an overview of what is known of the reproductive biology and immature stages of drepanocerines and other Oniticellini, see Cambefort & Lumaret (1984) – as mentioned before, there appears to be considerable diversity. For a broader ecological perspective and some additional data, see also the compilation of Hanski & Cambefort (1991).

Research questions

In *conclusion*, drepanocerine scarabs still pose a set of interrelated systematic and biogeographic challenges for future research, including:

- (a) their monophyly, as shown by cladistic considerations, and their position in the overall phylogeny of Scarabaeinae;
- (b) their internal phylogeny and consequent classification from genus down to species level;
- (c) the ensuing explanation of any biogeographic peculiarities resulting from this broader phylogenetic context;
- (d) the resolution of poorly understood variation and polymorphism in some species complexes;
- (e) the description of additional species-level novelties by sampling hitherto ignored scarabaeine faunas;
- (f) the verification and gap-filling of reported distributions of described taxa; and, last but not least,
- (g) an expansion of our knowledge on taxonomically relevant biological features.

Although the comparative morphology and anatomy of some organ systems (like mouthparts, reproductive system, integumental microstructure) may provide taxonomically relevant data, the application of molecular techniques may prove a more rewarding base for reconstructing drepanocerine evolution and elucidating the position of drepanocerines versus the other Oniticellini.

Hopefully, the present overview of the group will stimulate others to produce a broad-scope taxonomic revision beyond both the classic review of Janssens (1953) and the useful but somewhat mosaic work published since.

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