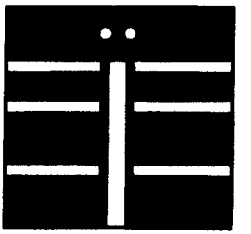
On the genus *Copris* Müller, 1764: Definition and phylogenetic survey of the Afrotropical species-groups (Coleoptera: Scarabaeidae)



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The 97 Afrotropical species of the genus *Copris* are clustered into 48 seemingly monophyletic species-groups. A phylogenetic tree of these species-groups, based on 83 morphological characters, is given, as well as a key, and a list of the species they comprise. A new species is described from southern Zaire: *Copris katangae*.

Sur le genre Copris *Müller, 1764. Définition et examen phylogénétique des groupes d'espèces afro-tropicales (Coléoptères, Scarabaeidae).* — Les 97 espèces du genre *Copris* actuellement connues d'Afrique tropicale sont rangées dans 48 groupes d'espèces très certainement monophylétiques. On donne ici un arbre phylogénétique de ces groupes d'espèces, établi à partir de 83 caractères morphologiques. On donne aussi une clé des groupes d'espèces, et, pour chacun d'entre eux, la liste des taxons qu'ils comprennent. Enfin, on décrit une nouvelle espèce du sud du Zaïre: *Copris katangae*.

Key words: Coleoptera, Scarabaeidae, *Copris*, dung beetles, Afrotropical, phylogenetics, biogeography, new species

INTRODUCTION

Compared with other tropical continents, Africa is characterized by the vast development of herbaceous landscapes, where a great diversity of herbivorous Mammals has developed. The dynamics of African savanna has most probably been an important factor of diversification for these Mammals. It is especially during the pluvial and interpluvial periods of the Plio-Pleistocene that the major radiation of ungulates, especially Bovidae, took place (Sinclair, 1983). The excreta of these animals are used by large numbers of coprophagous beetles. Among them, the genus *Copris* (Fig. 1, a-b) is important by the number of its species (97 in tropical Africa), and the role they play in recycling organic materials. The genus has been considered "recent" by Cambefort (1991) due to its absence from Australia and Madagascar. Only 5 species occur in Western Palaearctic, 71 in Asia (Balthasar, 1963), and 25 in America (Matthews, 1962) where only one crosses the Panama isthmus and extends southwards to Ecuador.

The Afrotropical *Copris* have been the subject of a previous revision (Ferreira, 1961), and of the present one, still in progress (Nguyen-Phung & Cambefort, 1986, 1987a, 1987b; Nguyen-Phung, 1987, 1988a, 1988b, 1988c, 1989; Cambefort, 1992a, 1992b). Here, we aim to establish a phylogeny of the Afrotropical species-groups, a prerequisite for further systematic and biogeographic studies of the genus.

MATERIAL AND METHODS

The taxa

The genus Copris

According to the classification of Balthasar (1963), there are two subfamilies in the family Scarabaeidae, namely Scarabaeinae and Coprinae (see also

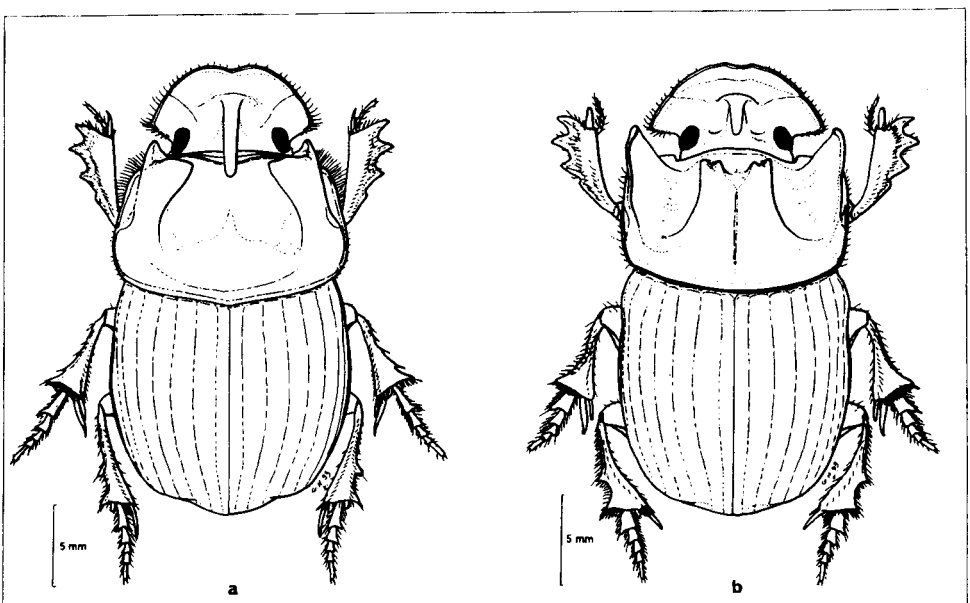

Fig. 1. — Habitus. (a) "concave" pronotum (*C. arcturus*); (b) "convex" pronotum (*C. colmanti*).

Cambefort, 1991). Within the Coprinae, a number of tribes are generally recognized, but it is not established whether they all are monophyletic. Especially, there are some doubts about the pair Coprini/ Dichotomiini. The traditional difference between them is the presence of transverse carinæ on the hind (and sometimes median) tibiæ in the Coprini and their absence in the Dichotomiini. But a carina does not make a tribe, especially in this case, where the carina is likely to be analogous rather than truly homologous. Other analogies and parallelisms seem to have occurred, resulting in genera very similar in appearance but sometimes only distantly related, e.g. *Copris* and *Catharsius* in Africa and Eurasia; *Coptodactyla* and *Thyregis* in Australia; *Dichotomius* and *Ontherus* in the Americas. Obviously, the relationships between all these and related genera need to be reconsidered. *Copris*, type-genus of the tribe Coprini, is characterized by a few apomorphies: the elytral striæ are ten in number, of which the 8th and especially the 9th are sometimes indistinct; the metatibiæ have one transverse carina on their lateral face, this carina not extending on their ventral face; the internal sack of the male genitalia has two principal laminæ: a "conic" one which is basal at rest, and a "lateral parietal", also situated in the basal half of the phallobase at rest (Nguyen-Phung & Cambefort, 1987a) [the other "*Copris*-like" genera have different numbers or shapes of the laminæ (Marchisio, 1983)]. Due to these autapomorphies, the genus seems to be monophyletic.

Afrotropical species-groups

Clustering Afrotropical *Copris* into species-groups, on the basis of external characters, dates back from Ferreira (1961), who exploited the unpublished works of the late André Janssens. We used this system in our previous papers. In the present one, we make important changes based on the study of new characters, and especially of those of the internal sack. What are our species-groups for? In a phylogenetic analysis, it is usually more appropriate to study species. But making a tree would have necessitated a number of characters much larger than the 83 here selected, which has proven very difficult if not impossible. For this reason, we decided to define the smallest possible species-groups on the basis of some appropriate and seemingly apomorphic characters, especially those of external morphology and the male internal sack. From these, we assumed that the species-groups here defined were all monophyletic. Some species-groups are such by definition, being limited to one species; most others cluster 2 to 4 species, the monophyly of which we are also confident; the same holds for the largest group, which contains a dozen species: group *23. integer*.

"Primitive" vs. "evolved" taxa

The genus *Copris*, and especially the Afrotropical species, constitute probably a "recent" cluster, which may have evolved together with the large Mammalian fauna, during the alternative dry and wet episodes of the Plio-Pleistocene period. For this reason, there are probably no true "primitive" or "ancestral" species in the Afrotropical *Copris*, and it is difficult to find any "primitive" species anywhere in the world, i.e. species which display mostly primitive characters, with the possible exception of those of the Oriental subgenus *Microcopris* Balthasar, 1958. Janssens (1947) was one of the first authors to study the relationships between evolution and sexual dimorphism in Scarabaeidae. He formulated three important statements (which, however, might be valid only in the taxon in question):

1. on average, small species are more primitive than large ones;
2. sexual secondary characters of the male are more marked in large (evolved) species than in small (primitive) ones,

Table 1. — List of characters with their state

1	shape of the male horn (0: horn absent; 1: horn long, subsinuate, most often with postero-apical denticles; 2: rather long, with one posterior denticle, basal to median; 3: very short, almost round in section, dorso-ventrally flattened at the apex; 4: middle length, smooth, longitudinally hollowed in gutter, posteriorly bicarinate, each carina with a denticle in its basal third; 5: rather short, more or less flattened dorso-ventrally; 6: relatively long, punctuate or rugose, longitudinally hollowed in gutter, posteriorly bicarinate; 7: relatively long, punctuate or rugose, with one posterior denticle more or less bifurcate; 8: relatively long, punctuate or rugose, with 2 or 3 postero-basal denticles; 9: relatively short, with lateral expansions).
2	internal margin of eye (0: rounded; 1: angular).
3	punctuation of head (0: simple; 1: not).
4	clypeus and frons (0: smooth; 1: not).
5	dorsal surface of genæ (0: smooth; 1: not).
6	occipital carina (0: entire; 1: barely interrupted; 2: distinctly interrupted).
7	ventral surface of clypeus (0: without a margin; 1: margin not entire; 2: margin entire).
8	sulcus of ventral surface of clypeus (0: absent; 1: present).
9	punctuation of ventral surface of genæ (0: sparse; 1: dense).
10	first joint of labial palpi (0: internal side straight; 1: internal side convex).
11	anterior margin of labium (0: straight; 1: emarginate).
12	labial sulcus (0: < half of labium length ; 1: ≥ half of labium length).
13	anterior margin of pronotum (Fig. 2) (0: not in {; 1: in {).
14	anterior margin of pronotum at eye level (0: not or barely broadened; 1: breadth more than doubled).
15	"anterior side" of pronotum (0: divergent; 1: straight).
16	anterior angle of pronotum (0: obtuse or right; 1: acute).
17	"latero-posterior" side of pronotum (0: convex or straight; 1: concave).
18	side of pronotum (0: convex or straight; 1: concave or sinuate).
19	nature of pronotal punctuation (0: simple; 1: not simple).
20	density of pronotal punctuation (0: feeble; 1: strong).
21	median lobe of pronotum (0: absent; 1: < half pronotal breadth; 2: ≥ half pronotal breadth).
22	latero-superior sides of median lobe of pronotum (0: absent; 1: convergent forward; 2: divergent forward).
23	anterior declivity of pronotum: shape (0: absent; 1: plane or convex; 2: concave; 3: *inhalatus* group shape).
24	anterior declivity of pronotum: punctuation (0: declivity absent; 1: smooth or almost smooth; 2: not smooth).
25	lateral carinæ of pronotal declivity (0: absent; 1: partly occurring; 2: entire).
26	pronotum lateral pits: quantity of punctuation (0: pits absent; 1: smooth or almost smooth; 2: not smooth).
27	pronotum lateral pits : quality of punctuation (0: pits absent; 1: merely punctured; 2: with granules or "scales").
28	lateral lobules of pronotum (0: absent or replaced by carinæ; 1: simple; 2: double).
29	disc of pronotum (0: with a longitudinal sulcus at least at rear; 1: not sulcated; 2: absent).
30	surface of pronotal disc (0: punctured or granular; 1: smooth or almost smooth; 2: absent).
31	lateral teeth of pronotal hollow (0: absent; 1: denticulate; 2: not denticulate).
32	punctuation of pronotal hollow (0: absent; 1: sparse; 2: dense).
33	posterior margin of pronotum (0: smooth or almost smooth; 1: crenulate).
34	punctuation of elytral striæ (0: fine and/or sparse; 1: coarse and /or dense).
35	punctuation of elytral interstriæ (0: fine and/or sparse; 1: coarse and /or dense).
36	8th elytral stria (0: almost reaching the elytral apex; 1: not very much passing backwards the first half of elytral length).
37	9th elytral stria (0: distinct in its basal part; 1: entirely indistinct).
38	punctuation of external proepimere (0: uniform; 1: not uniform).
39	longitudinal carina of prosternum (0: absent; 1: present).
40	prosternal hair (0: absent; 1: present).
41	margin of pygidium (0: entire; 1: disappearing at apex).
42	pygidial punctuation: quality (0: strong; 1: feeble).
43	pygidial punctuation: quantity (0: rather dense; 1: sparse).

44 pygidial punctuation: distribution (0: uniform; 1: not uniform).
45 metasternum (0: entirely punctured; 1: not).
46 meso-metasternal carina (0: absent; 1: present).
47 anterior margin of the first abdominal sternite (0: without a ridge; 1: with a ridge).
48 first abdominal sternite (0: smooth; 1: punctured).
49 apical two teeth of front tibiæ (Fig. 3) (0: equally distant; 1: more or less joined into one).
50 dorsal punctuation of front tibiæ (0: fine and/or sparse; 1: coarse and /or dense).
51 shape of the anterior spur of front tibiæ (0: parallel-sided, apex acute, bent inward and downward; 1: parallel-sided, apex obtuse, bent only downward; 2: as in 1, but broadly rounded and sometimes widened at the apex; 3: as in 1, but bent outward; 4: bent inward in obtuse angle; 5: as in 4, but the externo-apical side of the angle is concave; 6: as in 2, but slightly hooked inward).
52 anterior carinæ of front femora (0: close to each other; 1: distant from each other).
53 punctuation of the anterior half of front femora on the ventral surface (0: fine and/or sparse; 1: coarse and /or dense).
54 punctuation of the ventral surface of middle femora (0: almost uniform; 1: not uniform).
55 punctuation of the ventral surface of middle femora basis (0: fine and/or sparse; 1: coarse and /or dense).
56 "fingers" of hind tibiæ (Fig. 4) (0: short; 1: long).
57 punctuation of the ventral surface of hind femora (0: almost uniform; 1: not uniform).
58 punctuation of the ventral surface of hind femora basis (0: fine and/or sparse; 1: coarse and /or dense).
59 parameres of the ædeagus (Fig. 5) (0: without prickles; 1: prickly).
60 "copulatory" lamina of internal sack (0: absent; 1: present).
61 shape of the "conic" lamina of internal sack (0: absent; 1 to 9: see Fig. 6a-i).
62 shape of the "lateral parietal" lamina of internal sack (0: club like; 1: not).
63 apex of hind tibiæ (0: not bilobate; 1: bilobate).
64 basal transverse sulcus of pygidium (0: regularly parallel-sided, narrow; 1: as in 0, but relatively wide; 2, as in 0, but enlarged in the middle; 3: as in 0, but deeper, with the higher edge sharp, the lower one blunt).
65 anterior row of piliferous punctures on the dorsal surface of hind femora (0: absent; 1: one row with 6 points and less; 2: one row with about a dozen points; 3: 24 points and more in one or two rows).
66 dorsal surface of hind femora (0: entirely punctured except at front; 1: with punctures at rear and at the apex; 2: with punctures alongside the posterior margin only; 3: not punctured except the anterior row of punctures).
67 external area of dorsal surface of hind tibiæ (0: punctured; 1: not).
68 internal row of punctures of dorsal surface of hind tibiæ (0: not united by a carina; 1: united by a carina).
69 female horn (0: absent; 1: short; 2: long).
70 section of the female horn (0: no horn; 1: flattened laterally; 2: flattened transversally).
71 apex of the female horn (0: no horn; 1: truncate or emarginate; 2: acute or complex).
72 "anterior side" of pronotum (0: diverging forwards; 1: straight; 2: absent; 3: converging forwards).
73 anterior angle of pronotum (0: obtuse or right; 1: acute; 2: rounded).
74 "latero-posterior" side of pronotum (0: convex or straight; 1: concave).
75 side of pronotum (0: convex or straight; 1: concave or sinuate).
76 median lobe of pronotum (0: absent; 1: feebly prominent; 2: prominent or very prominent).
77 anterior edge of pronotal median lobe (0: absent; 1: not emarginate; 2: emarginate or bidentate).
78 anterior declivity of pronotal median lobe (0: absent; 1: plane or convex; 2: concave; 3: *inhalatus* group shape).
79 punctuation of anterior declivity of pronotal median lobe (0: absent; 1: smooth or almost smooth; 2: punctured granular or rugose).
80 pronotal lateral lobules (0: absent or replaced by a carina; 1: present).
81 pronotal disc (0: absent; 1: smooth or almost smooth; 2: punctured or granular).
82 lateral teeth of pronotal hollow (0: absent; 1: denticulate; 2: not denticulate).
83 apical two teeth of front tibiæ (0: equally distant; 1: more or less joined into one).

in the same way as, in a given species, they are more marked in large specimens than in small ones (allometry);

3. in the largest (most evolved) species, there are allometric sexual secondary characters in the female too. But these could be taken into account in a few cases only, since primitive species can display apomorphic characters, and vice versa.

The characters

Choice of characters

All the traditional morphological characters have been used: shape of the male and female head and pronotum, of elytræ, of the pygidium, and of the ventral side. In addition, we have used new characters of the ventral side of the head and of the mouthparts, and especially of the laminæ of the internal sack of the male genitalia. According to Zunino (e.g. 1984), this kind of character provides more true synapomorphies than other morphological characters, where parallelisms are more frequent. Female genitalia have failed to give useful characters in the present analysis.

Character coding

To establish the polarity of characters, two outgroups have been selected: the African *Litocopris punctiventris* Waterhouse, type-species of the genus which Janssens (1939) considered a subgenus of *Copris*, and the Australian *Thyregis kershawi* Blackburn, also type-species of its genus, which was considered "ancestral" to *Copris* by Matthews (1976).

— *Litocopris punctiventris.* - It is characterized by only one autapomorphy: the front tibiæ are truncated at a right angle. But the general appearance is rather different from true *Copris*. In addition, the body is densely punctured, on the upper and the lower faces. For these reasons, it seems appropriate to separate it from *Copris* at the generic level.

— *Thyregis kershawi.* - Compared with this species, *Litocopris* and *Copris* form a monophyletic group. For example, they share a conic lamina in the internal sack. Despite the fact that they share a few characters with *T. kershawi*, e.g. the transverse carina on the hind tibiæ, which separate them from all the other genera in the tribe Coprini, the three taxa do not seem to be very closely related (the transverse carina on the hind tibiæ could be a mere analogy). A few autapomorphies are displayed by *Thyregis* (e.g. a transverse carina on the middle tibiæ and a 15-fidous seta in the internal sack): they have not been taken into account here. All the other (states of) characters displayed by this genus are shared by either *Litocopris* or *Copris*, except the absence of a conic lamina and of an anterior row of piliferous punctures on the dorsal surface of hind femora (characters 61 and 65), which we consider autoplesiomorphies. Therefore, all the characters of *Thyregis* reported in the present study are considered primitive (plesiomorphic).

List and matrix of characters

Eighty-three characters have been retained, all the uninformative ones having been excluded. We have also excluded autapomorphies, although Yeates (1992) claims they should be maintained. The characters retained are listed in Table 1, with their states (characters 1 to 68: male; 69 to 83: female). All the characters have been considered unordered. Illustrations of some characters are given. Some additional characters have been illustrated in our previous papers.

Of these 83 morphological characters, the different states present in the 48 species-groups have been included in a matrix (Table 2).

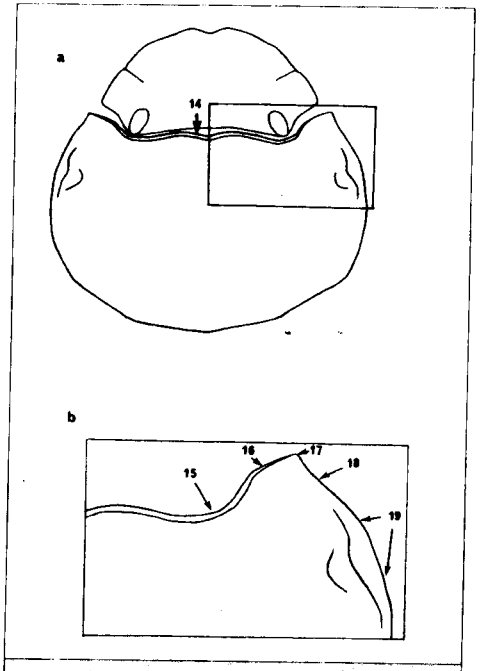

Fig. 2. — Characters of the pronotal anterior and lateral margins. (a) character 14; (b) characters 15 to 19.

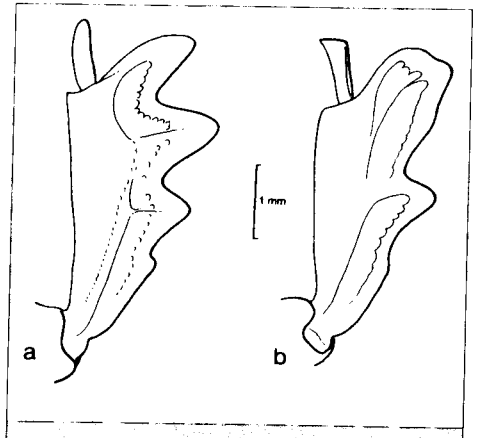

Fig. 3. — Front tibia: teeth (characters 49 and 83) and spur (character 51). (a) apical two teeth equally distant; spur bent outward and broadly rounded (*C. interioris*). (b) apical two teeth more or less joined into one; spur bent inward in obtuse angle (*C. singularis*).

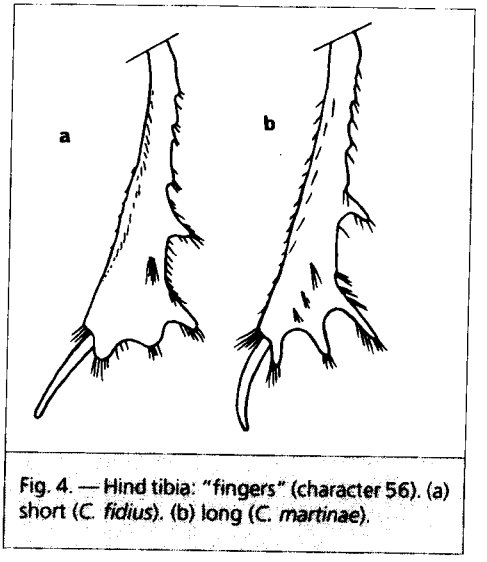

Fig. 4. — Hind tibia: "fingers" (character 56). (a) short (*C. fidius*). (b) long (*C. martinae*).

PHYLOGENETIC ANALYSIS

At present, a number of microcomputer programs of phylogenetic analysis are available. They use the classical methods of Wagner parsimony (Kitching, 1992; Siebert, 1992; Darlu & Tassy, 1993). We have analysed the matrix of Table 2 with the Macintosh programs Paup (Swofford, 1992), and MacClade (Maddison & Maddison, 1993) to enter the data and improve the analysis.

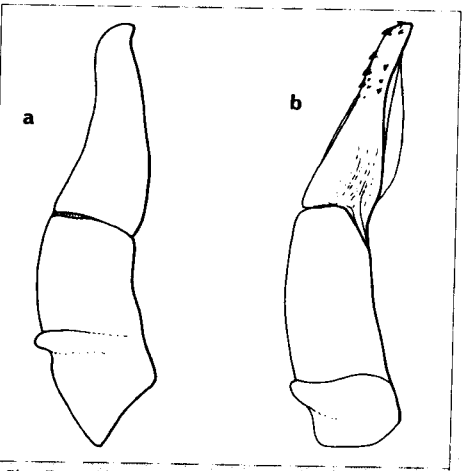

Fig. 5. — Parameres of the ædeagus (character 59). (a) without prickles (*C. afgoi*). (b) prickly (*C. cassius*).

Table 2. — Matrix of characters of the groups of Afrotropical *Copris*.

	1 2 3 4 5 6 7 8 12345678901234567890123456789012345678901234567890123456789012345678901234567890123
Thyregis	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Litocopris	01000000010100000001000000000000000000000000011000301010110010111000000000000000000
1. *mesacanthus*	20000000000100000101000000002212111110010000111001601100100020101110111100000000000
2. *coriarius*	20000000000100000101000000002212101110010000110001611010010020101110111100100000000
3. *fidius*	20010000000100100101000000002211101110000000111101601010010020101111212100100000000
4. *bootes*	11100000111100100001000000002212110010000001110001300101100020102111212100000000210
5. *arcturus*	11100000011010111111000000002212010010000000110000301010010020102111111120112220100
6. *phylax*	11100000011110001111000000002222010010000000110001301010010020102111111120122120000
7. *gilleti*	11100000000111011111000000002212111010000000010111001110110020102111212111100000211
8. *typhoeus*	11100000000110111111000000002212110110005001111101301001000020122111212301100000220
9. *diversus*	31000000110101100000000000001000100000000001100003010000000301011011111000101201 00
10. *megaceratoides*	10000000110100010001222121210100001101001000001100131111011003013300022221002212 1000
11. *cornifrons*	41011000111100100100222202100100000010100001110000300101000030122110111000122220200
12. *inhalatus*	51000011011100000011123112110000110110000001110000500000000140003300111000122321000
13. *simonettai*	61000020101010111011122200000000110111010011111010500000000140122310211111122220001
14. *afgoi*	51000020001000101111122202100000100110000001111001401000000140122210111101111120000
15. *singularis*	51000020001000101111122202110000100110000000111011401000000140122210111101111120001
16. *sexdentatus*	11000211010011001110212201110000011110010000111001501000000141021210111001111120000
17. *caelatus*	71000111000011011111112212110000101010010000111101501100100141022211111011012120000
18. *ritsemae*	71000121000011011111112212110000001010010001011001501110110141022210111001112120000
19. *jacchus*	11000020000010011111112212200000010110000000111001001000000141023210112001121210000
20. *laius*	11000020100010011111112221220110001011100000011000014010000001410232102120011212200 00
21. *anceus*	61100201100011111010222222210100000111000000110001000000000141023310122011121220001
22. *capensis*	61100021100011111010122221210100010110000000110001400000000141003310111000021220100
23. *integer*	61000020000010011111221212210100010110000001111111401000000140023210111101111120001
24. *draco*	11000020100011010111111212220100010110000000111000140100000004103321021100101112 1100
25. *colmanti*	61000020001111100110121122210100000110100011111001300000000041023210211001221111 00
26. *corniger*	61000021000101100110121122111000101101000111111013000000000410032101111001211111 00
27. *atropolitus*	61000001101110000100221110000100010011100$10111100300100100050122300111020022211100

28.	*morphaeus*	611000010001111000102221200001000100111001101010001000000000500333101111200111201 00
29.	*tridens*	810000111111000111001111021100001000100000111100003010001000701123001110001111001 00
30.	*antares*	510002201001000001011122121100001000100000001111005010000100701212001111001111200 00
31.	*obesus*	810002201001010001011222121100001000110000011111002010000100701223011111001111200 00
32.	*nepos*	810002010001010001011212121100001000100000011101001011001000601311001110001111200 00
33.	*phungae*	800002000001010001011122121100000000000000001010012011101100701211011110001121200 00
34.	*cribricollis*	800002100001110011011122121100001000100100001101014011101100701311001110000111200 00
35.	*gazellarum*	800002100001110001011122121110001011100110001100005011101100701311001110000111200 00
36.	*insidiosus*	900002110000000001011122121100000001100000001111014011101100701211001110000111220 00
37.	*katangae*	800002211000010001011222121100000000100000001110014011101100701221001110001111200 00
38.	*orion*	810112010001010001001121121100000001100010$$111100301000000801312001110001111101 00
39.	*gracilis*	810001100001010001011122111100000001100000011111003000000008010220011100001112000 00
40.	*sinon*	810001100001010001001122111100000001100000011111003000000008010220011100001112000 00
41.	*orphanus*	810002211001010000001122221101000101100000011101001010000000701012011110000111201 00
42.	*amyntor*	810002100001010000001222121101001101110000101101002010000000701023011110000121200 00
43.	*carmelita*	810002000001010000001121121101001001110001101101002010000000701312011110000111101 00
44.	*interioris*	810002001001010000001121111201001101110000101001002000000000701323011110000121101 00
45.	*armiger*	810002200000010001001222121101000001100000111111000010000010900222001110000111201 00
46.	*humilis*	810002200000001000001222121101000001100000111111000010000010900222101111001111201 00
47.	*misellus*	810002200000001000001111121100000001101000$111110020000000119002221011110001112000 00
48.	*urus*	910102210000000000001112021001000101101000$111110130000000109002120011100001112010 00

"$" indicates ambiguous state of character

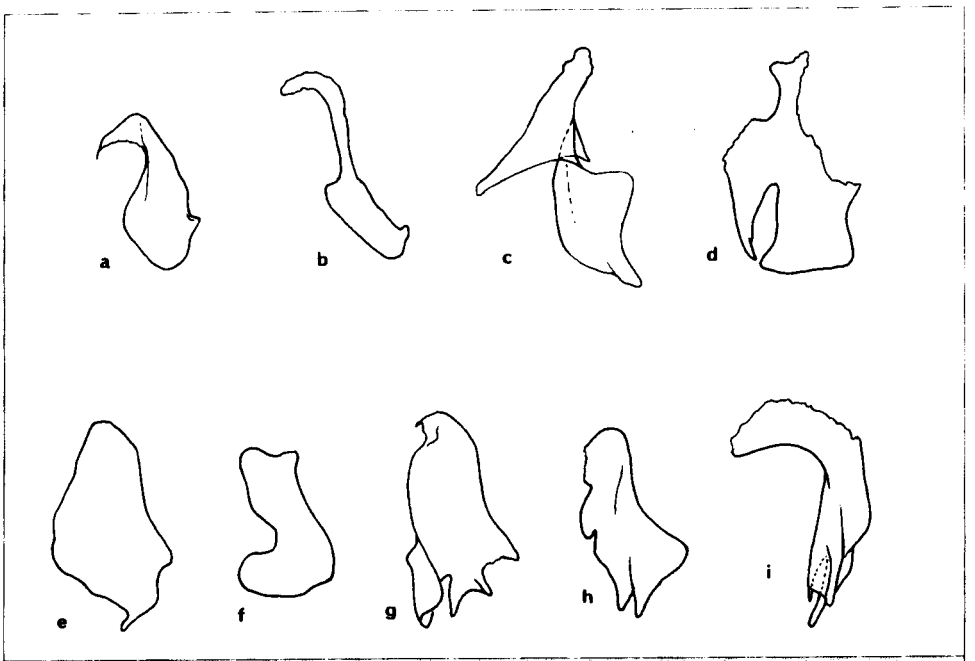

Fig. 6. — States 1 to 9 of the "conic" lamina (character 61). (a) state 1 (*Litocopris punctiventris*); (b) state 2 (*Copris fidius*); (c) state 3 (*C. megaceratoides*); (d) state 4 (*C. simonettai*); (e) state 5 (*C. atropolitus*); (f) state 6 (*C. nepos*); (g) state 7 (*C. phungae*); (h) state 8 (*C. orion*); (i) state 9 (*C. misellus*).

When all the characters are given the same weight (namely 1), the program extracts 4 trees of the same length, namely 604 steps, with a minimum possible length of 144 steps and a maximum possible of 1301. Their fit measures are as follow:

CI = 0.23
HI = 0.77
RI = 0.602 and
RC= 0.144.

These indices, especially the consistency index *CI*, are low enough, but this could be expected due to the rather large number of terminal taxa (species-groups) and characters (Siebert, 1992). Moreover, it should be kept in mind that we are processing small species-groups, all from the same geographical origin (tropical Africa), and probably rather "recent" (Plio-Pleistocene?). Therefore, we must expect a significant amount of homoplasies and parallelisms. From these 4 trees, a strict consensus tree was computed by the program (Fig. 7). Due to the fact that we have used the option "heuristic search" of the program Paup (Swofford, 1992), instead of "exhaustive", or even "branch and bound" (which both have proven very difficult or even impossible due to the large number of characters and taxa), it is not sure that the trees we have obtained were the most parsimonious possible. But we consider that the consensus tree we present in figure 7 gives a satisfactory picture of the relationships between the species-groups of Afrotropical *Copris*, although it could be improved in the future.

KEY TO THE SPECIES-GROUPS

Observation 1. - Correct placement of isolated females is often difficult. Isolated minor males can be placed through their internal sack characters.

Observation 2. - The key broadly follows the phylogenetic tree. However,

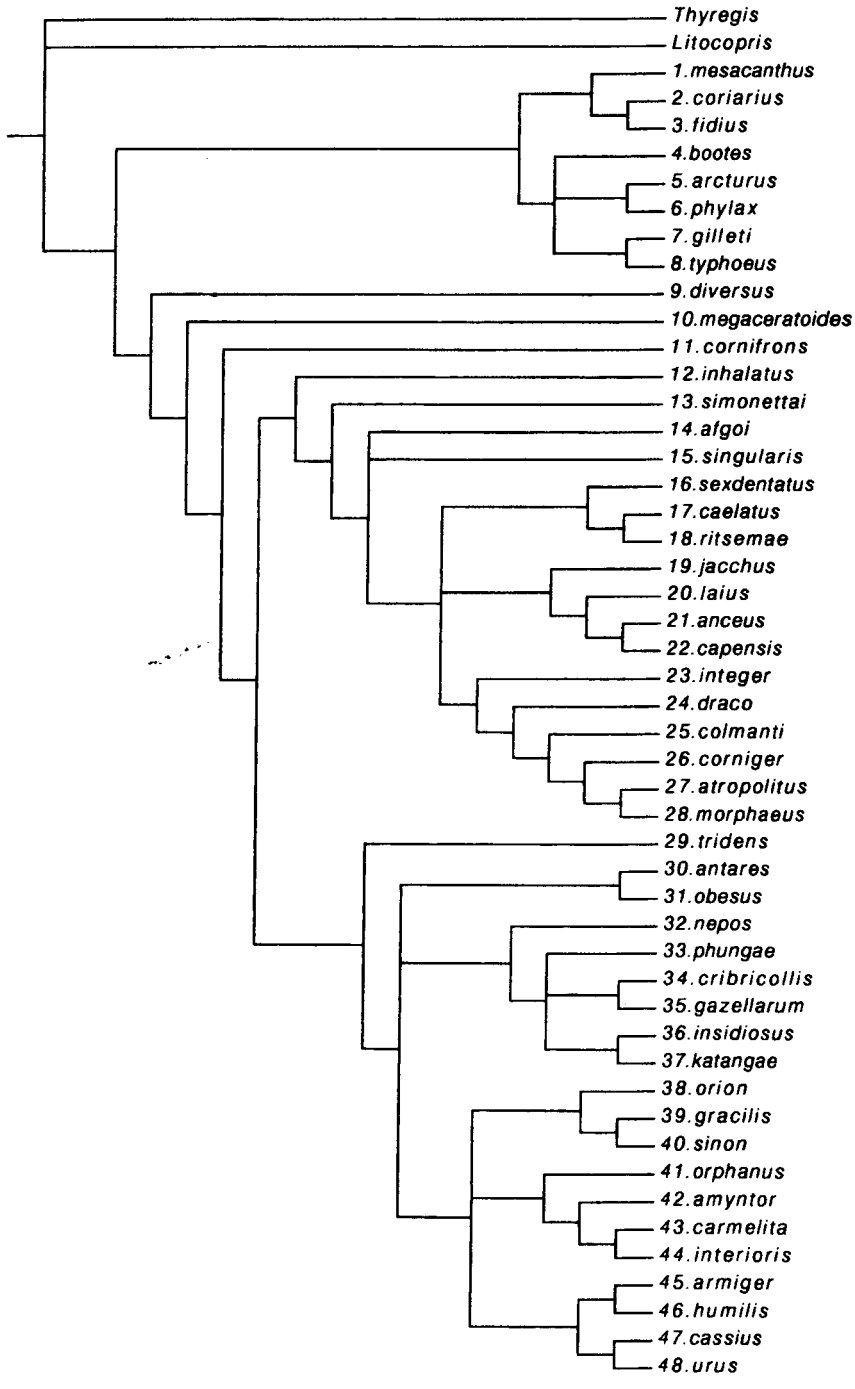

Fig. 7. — Phylogenetic tree (strict consensus of 4 trees: see text) of the species-groups of Afrotropical *Copris*.

for practical purposes, the order of the species-groups has been modified in some occasions, and some characters have been used at a different level in the key and in the tree (e. g.: male parameres prickly).

Observation 3. - The so-called "typical" *Copris* structure of male pronotum is that of the type-species: *C. lunaris* (L.) (Fig. 1b).

1 – Pronotum of major males strongly concave, the concavity limited on both sides by an elevated, toothed carina (Fig. 1a) 2
– Pronotum of males never strongly concave 3

2 – Smaller species (15-20 mm), with sexual secondary characters less marked ..... groups *1-3*
– Larger species (20-25 mm), with sexual secondary characters very marked ..... groups *4-8*

3 – Parameres of males prickly ..... groups *45-48*
– Parameres of males not prickly 4

4 – Pronotum of males not having the typical *Copris* structure; 9th elytral stria separated from the 10th at basis ..... group *9. diversus*
– 9th elytral stria never separated from the 10th at basis, except in a small species with typical *Copris* structure of pronotum. 5

5 – One large (18-24 mm), punctured species of West Africa; males with long and curved cephalic horn; females with the pronotal structure normally typical of males ..... group *10. megaceratoides*
– Other characters; females never with the typical structure of male pronotum 6

6 – Dorsal surface of the head (including the horn but except sometimes the vertex) completely without punctures in males, and almost completely in females ..... group *11. cornifrons*
– Dorsal surface of head always punctured, at least on genæ; sides of male horn always granular or rugose 7

7 – Pronotum partly granular or rugose 8
– Pronotum punctured, without granules, asperities, nor rugosities 19

8 – Transverse section of cephalic horn of male wider than long, its apex blunt or emarginate 9
– Transverse section of cephalic horn of male longer than wide, at least in the apical third 10

9 – Middle-sized to large (17-23 mm) species seemingly absent from Somalia and Kenya ..... group *12. inhalatus*
– One small (12-13 mm) species from Somalia ..... group *14. afgoi*

10 – Females similar to males, with long cephalic horn; pronotum of both sexes with a narrow median lobe and without lateral lobules; one Somalian species ..... group *13. simonettai*
– Females never similar to males 11

11 – Apical two teeth of anterior tibiæ more or less joined together, especially in females 12
– Apical two teeth of anterior tibiæ not joined together 13

12 – Apical two teeth of anterior tibiæ almost united into one (fig. 3b) ..... group *15. singularis*
– Apical two teeth of anterior tibiæ joined together, but not united into one ..... group *23. integer*

13 – Large or apterous species; cephalic horn of male very long 14
– Winged species; either middle-sized (15-18 mm) with proportionally long cephalic horn, or larger (22-30 mm) with proportionally short cephalic horn 16

14 – Middle-sized (18-20 mm), apterous species from the Cape region. ..... group *16. sexdentatus*
– Large (22-32 mm), winged species 15

15 – Large species (22-26 mm); male pronotum without lateral lobules ..... groups *19-20*
– Large or very large species (26-32 mm); male pronotum with lateral lobules .. .. group *24. draco*

16 – Middle sized (15-18 mm) species; pronotal disc entirely punctured ..... groups *17-18*
– Larger (22-30 mm) species; pronotal disc smooth 17

17 – Anterior declivity of the pronotum rugosely punctured, neither smooth nor granulate ..... groups *21-22*
– Anterior declivity of the pronotum

either smooth or granulate 18

18 – Median lobe of male pronotum narrow, its apex narrower than 1/4 of pronotal width ..... group *25. colmanti*
– Median lobe of male pronotum wider than 1/4 of pronotal width. ..... group *26. corniger*

19 – Male pronotum with median lobe not wider than lateral lobules ..... group *29. tridens*
– Median lobe of male pronotum always wider than lateral lobules 20

20 – Large (20-23 mm); dorsal surface almost smooth; three species from the mountain ranges of East-Central Africa ..... groups *27-28*
– Smaller (11-20 mm); at least sides of the pronotum punctured 21

21 – Disc of pronotum punctured; occipital carina distinctly interrupted on both sides 22
– Disc of pronotum smooth except in small (11-13 mm) species whose occipital carina is indistinctly interrupted on both sides 27

22 – Conic lamina of internal sack bilobate (Fig. 6f); two species from the mountain ranges of East-Central Africa. ..... group *32. nepos*
– Conic lamina never bilobate 23

23 – Pronotal disc strongly punctured ..... groups *34-35*
– Pronotal disc feebly punctured 24

24 – Internal edge of eyes distinctly angular ..... groups *30-31*
– Internal edge of eyes in regular curve 25

25 – Male pronotum with typical *Copris* structure; median lobe of pronotum not so wide as half of pronotal width ..... group *33. phungae*
– Other characters 26

26 – Section of cephalic horn much wider than long at basis, with lateral expansions on both sides ..... group *36. insidiosus*
– Section of cephalic horn longer than wide; median lobe of pronotum wider than half of pronotal width ..... group *37. katangae*

27 – Spur of fore tibiæ turned outward, not widened; conic lamina of internal sack incised and divided into two sharp lobes at basis (Fig. 6h) 28
– Spur of fore tibiæ more or less widened and/or turned inward; basis of conic lamina not bilobed 29

28 – Larger (15-18 mm); median lobe of pronotum separated from lateral lobules by distinct excavations ..... group *38. orion*
– Smaller (11-13 mm); pronotal lateral excavations almost indistinct ..... groups *39-40*

29 – Smaller (13-16 mm); clypeus almost bidentate ..... group *41. orphanus*
– Larger (15-20 mm); clypeus not bidentate 30

30 – Basal sulcus of pygidium shallow ..... group *42. amyntor*
– Basal sulcus of pygidium well-marked and deep ..... groups *43-44*

DEFINITION OF THE SPECIES-GROUPS

Species-groups *1-3*

Species included. - group *1*, *C. mesacanthus* Harold, 1878 (2 ssp.); group *2*, *cambeforti* Nguyen-Phung, 1988, *coriarius* Gillet, 1907, *serius* Nguyen-Phung, 1987, and *vankhaii* Nguyen-Phung, 1988 (2 ssp.); group *3*, *fidius* (Olivier, 1789) (key *in* Nguyen-Phung, 1988b).

The geographical distribution covers the entire expanse of humid or subhumid Afrotropical savannas and woodlands. Only one species is widespread and distributed in the western part of the continent, west of the Great Rift: *C. coriarius* Gillet.

Species-groups *4-8*

Species included. - group *4*, *C. bootes* Klug, 1855; group *5*, *arcturus* Gillet, 1907; group *6*, *phylax* Gillet, 1908; group *7*, *gilleti* Kolbe, 1907; group *8*, *martinae* Nguyen-Phung, 1988, and *typhoeus* Gerstaecker, 1884 (key *in* Nguyen-Phung, 1988c).

Pronotal disc concave, large. Species apparently restricted to elephant dung and very localized, in forest (*C. arcturus* and *phylax*) or eastern, subhumid woodlands.

Species-group *9*

Species included. - *C. diversus* Waterhouse, 1891, and *usambaricus* Gillet, 1908.

Small to medium-sized species distributed in the eastern woodlands, east of the Great Rift.

Species-group *10*

Species included. - *C. megaceratoides* Waterhouse, 1891.

A large species, with a patchy distribution in West African humid savannas, from Senegal to North Zaire.

Species-group *11*

Species included. - *C. cornifrons* Boheman, 1860, and *moffartsi* Gillet, 1907.

A group with disjunct distribution. *C. moffartsi* occurs from West Africa to West Kenya and Rwanda-Burundi, mostly in plateau grasslands. On the basis of internal sack and external characters, we group this species with *C. cornifrons*, a species distributed in Southern Africa.

Species-group *12*

Species included. - *C.davisi* Nguyen-Phung & Cambefort, 1986, *inhalatus* Quedenfeldt, 1884 (4 ssp.), and *rugosus* Gillet, 1908 (key *in* Nguyen-Phung & Cambefort, 1986).

The group occurs mostly in the eastern part of the continent.

Species-group *13*

Species included. - *C. simonettai* Cambefort, 1992.

This Somalian species offers a unique character among Afrotropical *Copris*: the sexual secondary characters of the female are well marked and similar to those of the male.

Species-group *14*

Species included. - *C. afgoi* Cambefort, 1992.

The species small size, reduced sexual secondary characters, and restricted geographical distribution in Somalia allow to assume its primitive character and "ancestral" status.

Species-group *15*

Species included. - *C. singularis* Nguyen & Cambefort, 1987.

As the preceding one, the species is rather small, with reduced secondary sexual characters. The structure of its anterior tibiæ, with the apical two teeth almost united in one, is a clearly apomorphic character, shared with groups *13* and *23*. The distribution is restricted to a few localities in East Africa.

Species-group *16*

Species included. - *C. sexdentatus* Thunberg, 1818, and *sphaeropterus* Harold, 1877.

The two apterous species have a relict status in a few South African localities.

Species-groups *17-18*

Species included. - group *17*, *C. caelatus* (Fabricius, 1794), and *victorini* Boheman, 1857; group *18*, *ritsemae* Harold, 1875, and *vrydaghi* Ferreira, 1962.

The groups are characterized by a strong punctuation and restricted to South Africa.

Species-groups *19-20*

Species included. - group *19, C. jacchoides* Nguyen-Phung & Cambefort, 1986, and *jacchus* (Fabricius, 1775); group *20, C. laiiformis* Nguyen-Phung & Cambefort, 1986, *laioides* Boucomont, 1932, and *laius* Harold, 1868 (2 ssp.) (key to both groups: Nguyen-Phung & Cambefort, 1987b).

The groups cover most of the dry areas in tropical Africa, west of the Great Rift.

Species-group *21-22*

Species included. - group *21, C. anceus* (Olivier, 1789); group *22, capensis* Waterhouse, 1891.

Species-groups *21-22* are restricted to South Africa.

Species-group *23*

Species included. - *C. angustus* Nguyen-Phung & Cambefort, 1987, *bidens* Kolbe, 1893, *dracunculus* Ferreira, 1959, *elphenor* Klug, 1855, *elphenorides* Felsche, 1910, *integer* Reiche, 1847, *jahi* Nguyen-Phung & Cambefort, 1987, *pauliani* Nguyen-Phung & Cambefort, 1987, *renwarti* Nguyen-Phung & Cambefort, 1987, *simulator* Nguyen-Phung & Cambefort, 1987, and at least two undescribed species (key *in* Nguyen-Phung & Cambefort, 1987a).

The species-group with the largest number of taxa occurring in all the humid and subhumid African savannas and woodlands.

Species-group *24*

Species included. - *C. draco* Arrow, 1906, and *truncatus* Felsche, 1910.

The first species is the largest of African *Copris*, and one of the largest of the genus. It probably occurs (or occurred) in elephant dung, in a few localities in Angola, probably in humid woodlands. The second species has been found in evergreen rainforest, from Guinea to Cameroun and Zaire.

Species-group *25*

Species included. - *C. colmanti* Gillet, 1908.

This species has been found in the eastern evergreen rainforest: Gabon, Congo, Zaire.

Species-group *26*

Species included. - *C. corniger* Sahlberg, 1823, *denticulatus* Nguyen-Phung, 1988a, *fallaciosus* Gillet, 1907, and one undescribed species (key *in* Nguyen-Phung, 1988a).

This group has a basically eastern and southern distribution in woodlands.

Species-groups *27-28*

Species included. - group *27, C. atropolitus* Gillet, 1910, and *wiesei* Kolbe, 1914; group *28, morphaeus* Gillet, 1933.

The two groups occur in the East-Central mountain ranges.

Species-group *29*

Species included. - *C. tridens* Felsche, 1901.

A rainforest species distributed from Guinea to Zaire.

Species-groups *30-31*

Species included. - group *30, C. antares* Ferreira, 1958; group *31, obesus* Boheman,

1857, *subsidens* Péringuey, 1901, and one undescribed species.

The two groups occur in Southern Africa.

Species-group *32*

Species included. - *C. amabilis* Kolbe, 1914, *nepos* Gillet, 1908.

Another group from the mountains and plateaus of East-Central Africa.

Species-group *33*

Species included. - *C. phungae* Cambefort, 1992 (2 ssp.).

A still poorly known group from evergreen rainforest (Ivory Coast and Gabon).

Species-groups *34-35*

Species included. - group *34*, *C. cribricollis* Gillet, 1910; group *35*, *gazellarum* Gillet, 1918.

The two groups occur in drier savannas and woodlands, group *34* east and group *35* west of the Great Rift.

Species-group *36*

Species included. - *C. insidiosus* Péringuey, 1901 (with at least one undescribed subspecies, or even species).

The group occurs in the Eastern mountain range, from Uganda to Zimbabwe.

Species-group *37*

Species included. - *C. katangae* sp. nov.

Diagnosis

Holotype (male): elongated, black, shining. Head broadly emarginated anteriorly, with punctures rugose and dense on the clypeus and genæ, vanishing posteriorly; cephalic horn relatively high, with rugosities on lateral sides and two posterior denticles. Pronotum: median lobe wider than one third of pronotal width, its antero-superior edge in } whose middle angle is directed posteriorly; this lobe flanked with a short and acute lobule on either side; anterior declivity slightly concave, densely punctured in the middle; lateral excavations moderately deep, smooth; pronotal punctures rather dense and strong on the sides, feeble and sparse on the disc, which has a marked longitudinal sulcus; lateral sides sinuated at the rear of anterior angles, which are obtuse. Elytræ smooth and shining, their striæ relatively wide and strongly punctured; interstriæ subconvex, with microscopic punctures. Pygidium with punctures uniformly strong and rather dense. Apex of terminal spur of front tibiæ in obtuse inward angle. Internal sack with two laminæ (Fig. 8).

Length: 19.5-21 mm. Width: 10.5-11 mm.

Female unknown.

Holotype: [Southern Zaire: Shaba], Kaniama - 1931. R. Massart. (Musée royal de l'Afrique centrale, Tervuren).

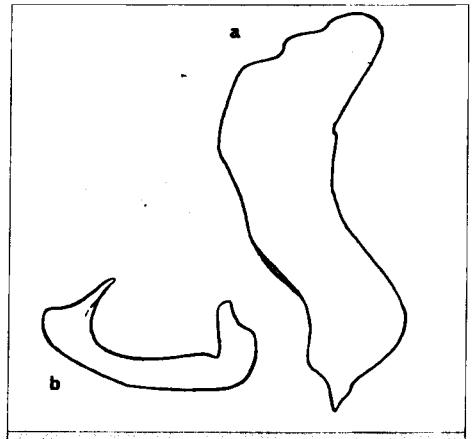

Fig. 8. — *Copris katangae* n. sp., laminæ of the internal sack.

- Paratypes. 2 males: Elisabethville [Lubumbashi], Novembre 1911. Elisabethville [Lubumbashi], 1935, Dr. Richard leg. (Muséerroyal de l'Afrique centrale, Tervuren, and Muséum national d'Histoire naturelle, Paris).

Species-group *38*

Species included. - *C. algol* Nguyen-Phung, 1989, *complexus* Nguyen-Phung, 1989, *jucundus* Gillet, 1933, and *orion* Klug 1835 (4 ssp.) (key in Nguyen-Phung, 1989).

The group is widespread in the humid savannas and woodlands of the whole tropical Africa.

Species-groups *39-40*

Species included. - group *39*, *C. gracilis* Waterhouse, 1891; group *40*, *evanidus* Klug, 1855, *puncticollis* Boheman, 1857, *sinon* (Olivier, 1789), and *fallax* Felsche, 1910.

Two groups of small species, occurring in dry savannas and woodlands.

Species-group *41*

Species included. - *C. macer* Péringuey 1901, *orphanus* Guérin, 1849 (2 ssp.), and *vilhenai* Ferreira, 1962.

A group of humid woodlands, often on plateaus.

Species-group *42*

Species included. - *C. amyntor* Klug, 1855, and *harrisi* Waterhouse, 1891 (3 ssp.).

A group from East African humid woodlands (probably erroneously quoted from West Africa).

Species-groups *43-44*

Species included. - group *43*, *C. carmelita* Fabricius, 1801 (2 ssp.); group *44*, *interioris* Kolbe, 1897.

Two groups widespread in humid and subhumid savannas and woodlands, west of the Great Rift.

Species-groups *45-48.*

Species included. - group *45*, *C. armiger* Gillet, 1910, and *garambae* Cambefort, 1992; group *46*, *decellei* Cambefort, 1992, *dudleyi* Cambefort, 1992, and *humilis* Gillet, 1908; group *47*, *angolensis* Ferreira, 1962, *cassius* Péringuey, 1901, *eburneus* Cambefort, 1992, and *misellus* Péringuey, 1901; group *48*, *bovinus* Gillet, 1908, *camerunus* Felsche, 1904, *urus* Boheman, 1857, and *youngai* Balthasar, 1967 (key of all these groups *in* Cambefort, 1992a).

The groups are well characterized in the whole genus by their male parameres prickly. They occur in humid savannas and woodlands, as well as in the rainforest.

SUMMARY AND CONCLUSIONS

A phylogenetic tree is presented of the 48 seemingly monophyletic species-groups of Afrotropical *Copris*. The species-groups are generally small: 1 or 2, sometimes up to 4 species, with the sole exception of species-group *23. integer* (12 species). Many species-groups have a restricted distribution in tropical Africa, but some are more widespread, e.g.: *2. coriarius, 12. inhalatus, 20. laius, 23. integer, 38. orion, 40. sinon, 41. orphanus, 44. interioris, 47. cassius, 48. urus.*

The species-groups are divided into two principal lines. The first line (species-groups *1-8*) is characterized by a "concave" pronotum. It is represented by a smaller number of species (12 out of 97), and is probably older than the second line. The second line (species-groups *9-48*) is characterized by a "convex" pronotum. It comprises the other 85 described species, and a few more not yet described. It is divided into two main clusters. Most of

the species in the first cluster (species-groups *12-28*) have the pronotal punctuation rugose or granulose and possess a third lamina in the internal sack. The species of the second cluster (species-groups *29-48*) have the pronotal punctuation simple and only two laminæ in the internal sack.

The vast majority of Afrotropical *Copris* inhabit the grasslands and woodlands (savannas). In the lowland evergreen rainforest, there are only a few species: *C. arcturus* and *phylax* (species-groups *5-6*), *truncatus* (*24*), *colmanti* (*25*), *tridens* (*29*), *phungae* (*33*), *carmelita* (*43*), and *camerunus* (*48*). With the exception of species-groups *5-6*, forest species are less closely related to each other than to grassland species. The same is true for the mountain opposed to lowland species. Therefore, it is likely that the ancestors of the recent species-groups have differentiated in grasslands (savannas), of mainly East Africa, and have invaded the other areas and biomes during the climatic fluctuations of the Plio-Pleistocene, following the mammals whose dung they use. But a detailed analysis of the biogeography of Afrotropical *Copris*, and of their relationships with mammals, still remains to be done (Nguyen-Phung & Cambefort, in prep.).

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The curators of the *Institut royal des Sciences naturelles* (Brussels) and *Musée royal de l'Afrique centrale* (Tervuren) put their rich series of Afrotropical *Copris* at our disposal; M. Gilbert Hodebert skillfully drew Fig.. 1 a-b; and Dr Thierry Bourgoin helped with microcomputer programs and techniques. Sincere thanks to them all.

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