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Barcoding analysis and taxonomic revision of *Goliathus* Lamarck, 1802 (Scarabaeidae, Cetoniinae)

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Summary. We conducted barcoding analysis of valid taxa in the genus *Goliathus* Lamarck, 1802 and clarified their relationships. Specimens of *Goliathus goliatus* (Drury, 1770) sampled in tropical rainforests from Cameroon to Kenya display degrees of genetic and phenotypic separation that, however, do not seem to justify subspecific splitting. ***Goliathus meleagris* Sjöstedt, 1927**, which is localized in the Miombo woodlands of southern Democratic Republic of the Congo, Democratic Republic of Congo, and neighbouring areas of Angola and Zambia, **is raised from synonymy with *Goliathus orientalis* Moser, 1909 and ranked subspecifically under *Goliathus goliatus* status rev., bona ssp.** The moderate genetic separation, the eco-geographic isolation, and the presence of transitional populations in the Maniema and Tanganyika Provinces of D. R. C., together indicate that a single species with two subspecies are involved. We also provide historical arguments and present new material indicating that the type locality of *Goliathus orientalis,* "landeinwärts von Lindi" is in a region between Songea and the eastern shore of Lake Malawi in southwest Tanzania. ***Goliathus orientalis* is recognized as a good species, bona sp.** and ***Goliathus usambarensis* Preiss, 1933** (type locality: Usambara Mountains) **is ranked subspecifically** under it, s**tatus rev.**. *Goliathus regius* Klug, 1835, *Goliathus cacicus* (Olivier 1789) and *Goliathus albosignatus* Boheman, 1857 are confirmed good species. Notably, *Goliathus albosignatus* forms a separate cluster that is equidistant from the sister genus *Fornasinius* Bertoloni, 1853 and the outstanding *Goliathus* species-group, suggesting early separation of *Goliathus albosignatus* from a common ancestor. All valid *Goliathus* taxa are illustrated.

Sommaire. Nous avons barcodé des échantillons appartenant à différents taxons du genre *Goliathus* Lamarck, 1802 et clarifié leurs relations. Les spécimens de *Goliathus goliatus* (Drury, 1770) échantillonnés dans les forêts tropicales humides allant du Cameroun au Kenya présentent des degrés de séparation génétique et phénotypique qui ne semblent pas justifier une séparation subspécifique. ***Goliathus meleagris* Sjöstedt, 1927,** est localisée dans les forêts de *Brachystegia* ou Miombo, du sud de la République démocratique du Congo ou R. D. C., et dans les régions limitrophes de l'Angola et de la Zambie. Elle est **sortie de la synonymie avec *Goliathus orientalis* Moser, 1909 et classée comme sous-espèce de *Goliathus goliatus*, status rev., bona ssp.** La séparation génétique faible mais marquée, l'isolement éco-géographique et la présence de populations de transition dans les provinces du Maniema et du Tanganyika en R. D. C. appuient l'idée que deux sous-

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espèces d'une même espèce sont impliquées. Nous fournissons des arguments historiques et du nouveau matériel qui montrent clairement que la localité type de *Goliathus orientalis*, « landeinwärts von Lindi », désigne une région située entre Songea et la rive est du lac Malawi, dans le sud-ouest de la Tanzanie. ***Goliathus orientalis*** est reconnu comme **une bonne espèce, bona sp.** et ***Goliathus usambarensis* Preiss, 1933** (localité type: monts Usambara) **est classée comme sous-espèce de *Goliathus orientalis*, status rev.**. *Goliathus regius* Klug, 1835, *Goliathus cacicus* (Olivier 1789) et *Goliathus albosignatus* Boheman, 1857 sont confirmées comme de bonnes espèces. *Goliathus albosignatus* forme un groupe distinct qui est équidistant du genre frère *Fornasinius* Bertoloni, 1853 et d'un groupe formé des autres espèces de *Goliathus*, suggérant une séparation précoce de *Goliathus albosignatus* à partir d'un ancêtre commun aux trois groupes. Tous les taxons valides sont illustrés.

Keywords. Coleoptera, Cetoniinae, Goliathini, *Goliathus*, Africa, status rev., bona species, bona subspecies, Barcode.

Introduction

The genus *Goliathus* (type species: *Scarabaeus goliatus* Drury, 1770) was reviewed adequately by WIEBES (1968) and illustrated lavishly by LACHAUME (1983). Currently, six species of *Goliathus* are recognized: *Goliathus goliatus* (Drury, 1770), *Goliathus cacicus* (Olivier 1789), *Goliathus regius* Klug, 1835, *Goliathus albosignatus* Boheman, 1857 (with a doubtful subspecies, *Goliathus a. kirkianus* Gray, 1864), *Goliathus orientalis* Moser, 1909 and *Goliathus usambarensis* Preiss, 1933. *Goliathus atlas* Nickerl, 1887 is often treated as a natural hybrid between *G. regius* and *cacicus*. This paper will discuss and revise the taxonomy of the genus.

WIEBES (1968) treated *G. meleagris* and *G. usambarensis* as junior synonyms of *G. orientalis* and ranked both *G. regius* and *G. orientalis* subspecifically under *G. goliatus*. Subsequent authors treated *G. goliatus, G. regius* and *G. orientalis* as separate species (e.g., NAGAI & SAKAI, 1998). Notably, confusion still surrounds the identification of *G. orientalis* and its relationship with both *G. meleagris* (currently treated as a synonym of *G. orientalis*) and *G. usambarensis* (raised recently to species level; BAUDET, 2013).

MAWDSLEY (2013) reviewed the *Goliathus* taxa from southern Democratic Republic of the Congo (D. R. C.) and Tanzania. In line with earlier reviewers (e.g., WIEBES, 1968), he treated *G. usambarensis* (type locality, Usambara Mountains, northeast Tanzania) as a junior synonym of *G. orientalis* (type locality, "interior of Lindi", southern Tanzania). BAUDET (2013) instead proposed to raise *G. usambarensis* from the synonymy with *G. orientalis*. However, both authors erroneously interpreted *G. orientalis* as the taxon from the Katanga plateaus in southern D. R. C. The study of the *G. orientalis* holotype indicates that it is distinct from the specimens of

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southern D. R. C., which belong to *G. meleagris* (type loc., Katinda, currently in the Haut-Katanga Province, D. R. C.).

Identification of *Goliathus orientalis* Moser, 1909

The *G. orientalis* holotype (Fig. 1) is housed in the Museum für Naturkunde (MNHB), Berlin, Germany. The taxon was described as a local form (*sensu* subspecies) of *G. giganteus* Lamarck, 1817 (a synonym of *G. goliatus*). The brief description states that the specimen was collected in the interior of Lindi ("*landeinwärts von Lindi*"). A printed note attached to the specimen, added by museum's staff at a later time (probably in the first half of the twentieth century), states that the specimen was probably collected in a forested area in the highlands between Usagara and Lake Malawi or Mahenge, therefore in an indefinite region in south or south-central Tanzania ("*vermutlich in den Regenwaldenklaven vor der deutschostafrikanischen Randterrasse von Usagara bis zum Nyassasee oder in Mahenge*").

It is possible only to speculate on the precise type locality of *G. orientalis*, but taking into consideration the recent capture of this species in southwest Tanzania (see below) and researching the history of the exploration of this region by German entomologists, there is a credible argument to suggest that the type locality of *G. orientalis* is, in fact, in southwest Tanzania. It is highly unlikely from an ecological and biogeographic perspective that a population of *Goliathus* (with the exception of *G. albosignatus*) is found in the hills around Lindi. As Lindi was the major port in southern German East Africa at the turn of the twentieth century (EWERBECK, 1902), it is possible that a shipment of specimens out of Tanzania could be imprecisely labelled from their port of departure.

At the time of description, the holotype specimen was in Moser's private collection rather than in the MNHB, which likely rules out the specimen's provenance from a State-funded expedition to German East Africa. The first major entomologist to have passed through Lindi before the turn of the twentieth century was Friedrich Fülleborn on his journey inland to the highland regions around Lake Tanganyika and Lake Malawi (FÜLLEBORN, 1906). But as his expedition was funded by the Hermann and Elise WENTZEL Foundation, which was set up to benefit the Royal Prussian Academy of Sciences in Berlin, the scientific samples collected on that expedition were deposited in the MNHB. It is not inconceivable that some specimens from this expedition may have ended up in private hands, but it is highly unlikely that the MNHB would have allowed an example of a prized *Goliathus* specimen to be sold or exchanged. Moreover, if MOSER, a Berliner, had become aware of the presence of a new form of *Goliathus* in the MNHB

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Figs 1-3 : *Goliathus orientalis* Moser, 1906**. Fig. 1:** ♂ holotype (in MNHB). **a**, dorsal view. **b**, ventral view. **c-d**, aedeagus. **Fig. 2:** ♂ specimen (Mbinga District, Ruvuma Region, Tanzania). **Fig. 3:** ♀ specimen (*ditto*).

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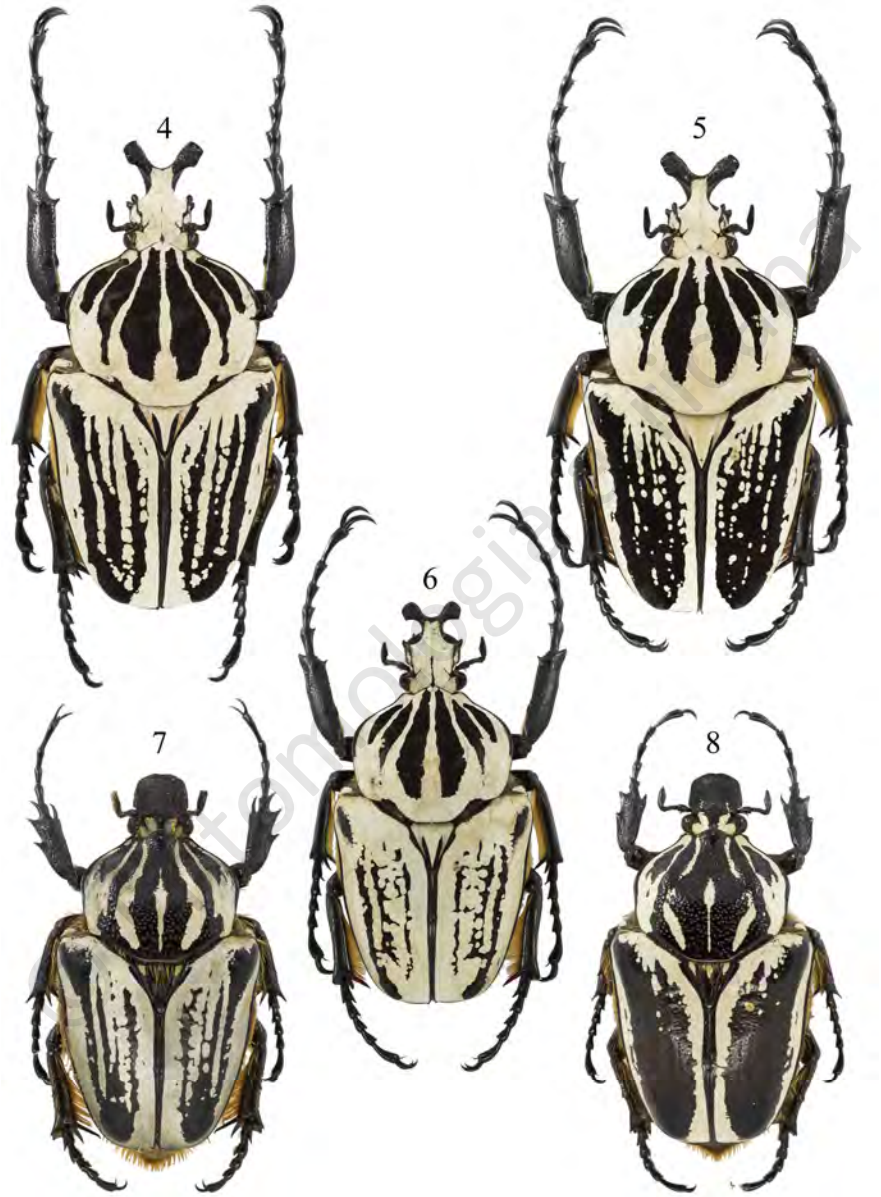

Figs 4-8: ***Goliathus orientalis usambarensis*** Preiss, 1933**. Figs 4-6:** ♂ specimens (Usambara Mountains, Tanga Province, Tanzania). **Figs 7-8:** ♀ specimens (*ditto*).

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from the Fülleborn expedition, it is likely that he would have described it much earlier than 1909, since the first descriptions of new species from this expedition were published in 1900 (KARSCH, 1900).

Between 1900 and 1905, Eugen HINTZ (1903) and Johann ERTL (1904-05) passed through Lindi, the latter travelling to Kigonsera and the mission station of Peramiho. ERTL had his own private collection, which was eventually sold to the Zoologische Staatssammlung München (ZSM) museum, Munich, Germany, after his death in 1924 (HORN *et al*., 1990). In the summer of 1905, the Maji Maji Rebellion broke out in southern Tanzania and would last two years, with the fallout from the end of the conflict continuing for many years after. During the rebellion, fierce attacks on both German military and religious personnel were commonplace limiting the movement of people (and specimens) out of Tanzania (GIBLIN & MONSON, 2010).

Based on the above, we conclude the type specimen of *G. orientalis* was likely collected after FÜLLEBORN in 1900 and before the start of the Maji Maji Rebellion in 1905, and that the type locality of "*landeinwärts von Lindi*" refers to the highland region between Songea and the eastern shore of Lake Malawi, roughly at the same latitude as Lindi. This is further corroborated by photographs in our hands of one male and one female specimen of a *Goliathus* collected recently in a named village of the Mbinga District (Ruvuma Region) in southwest Tanzania (Figs 2-3). Notably, the male specimen is virtually identical to the *G. orientalis* holotype, especially with respect to the arrangement and shape of the elytral lines, as well as the colour of the ventral surface of the body. The population of *G. orientalis* in southwest Tanzania appears to be very localised, with only a few specimens having ever been collected. Entomological explorations of the Matengo Highlands in 1935-36 by Hans ZERNY, curator of the Vienna Museum, only yielded *G. albosignatus* (KNIRSCH, 1942).

The habitus of *G. orientalis* is overall similar to that of specimens collected in abundance in the Usambara Mountains in the last two or three decades (see *G. usambarensis* below). The pronotum is creamy white with relatively short and basally divergent bands. The elytra are very dark brown with longitudinal series of partly coalescent creamy white dots ("lines" hereafter). In addition to the sutural and marginal lines, five discal lines are present (#1-5 from the elytral suture to external elytral margin). Lines #1 and 5 are obsolete and fused with the sutural and marginal lines, respectively, whilst lines #2-4 appear distinct and extend from the base to the apex of elytron, converging and fusing at the apical callus. The underside of the body is dark green.

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The following status is established for MOSER's taxon:

***Goliathus orientalis* Moser, 1909 (*nec auct.*) bona sp.**
Goliathus giganteus orientalis Moser, 1909

Identification of *Goliathus usambarensis* Preiss, 1933

PREISS (1933) described *G. goliathus usambarensis* from the Usambara Mountains in northeast Tanzania. According to the author, the new taxon has several features in common with *G. orientalis* and *G. meleagris*, while it is significantly differentiated from the forms inhabiting the rainforests of central Africa and Cameroon ("*Sie hat manches Gemeinsame mit G. orientalis Mos. und G. meleagris Sjöst läßt aber in überwiegendem Maßb eine eigene Entwicklungsrichtung erkennen und ist von den Formen des zentralafrikanischen un kameruner Regenwaldgebietes bereits weit abgerückt*.").

The three syntypes of *G. usambarensis* illustrated by PREISS (1933) are similar to the holotype and aforementioned specimens of *G. orientalis*. However, the analysis of a large number of specimens collected in the Usambara Mountains revealed some differences (Figs 4-8). In virtually all male specimens, elytral line #3 is narrow, incomplete, and somehow compressed between lines #2 and #4. Also, the colour of the ventral surface of the body is darker than in the specimens of *G. orientalis* from southwest Tanzania. In a minority of the specimens, the creamy white markings invade most of the elytral surface, allowing the brown background to display only at the humeral and apical calli and through variably developed vertical streaks. Conversely, the creamy white lines can be extremely reduced in other specimens; all intermediates can be found. The unequivocal identity of this taxon makes a lectotype designation unnecessary.

Although the habitus of *G. usambarensis* is similar to that of *G. orientalis*, the geographic isolation and minor albeit consistent differences in the arrangement and shape of the elytral lines, as well as the colour of the ventral surface of the body, lead us to consider *usambarensis* as a sufficiently differentiated subspecies of *G. orientalis.* Such determination guarantees the stability of taxonomic nomenclature, as the name *usambarensis* has been in use for at least two decades to identify *Goliathus* specimens originating from the Usambara Mountains. Of note, ENDRÖDI's name *preissi* (1951) was explicitly created for an "aberration" of *G. goliathus* [sic] and, therefore, is unavailable under Article 45.6.2 of the ICZN. Furthermore, ENDRÖDI (1951) unscrupulously selected the reference specimen among PREISS' syntypes of *G. usambarensis*.

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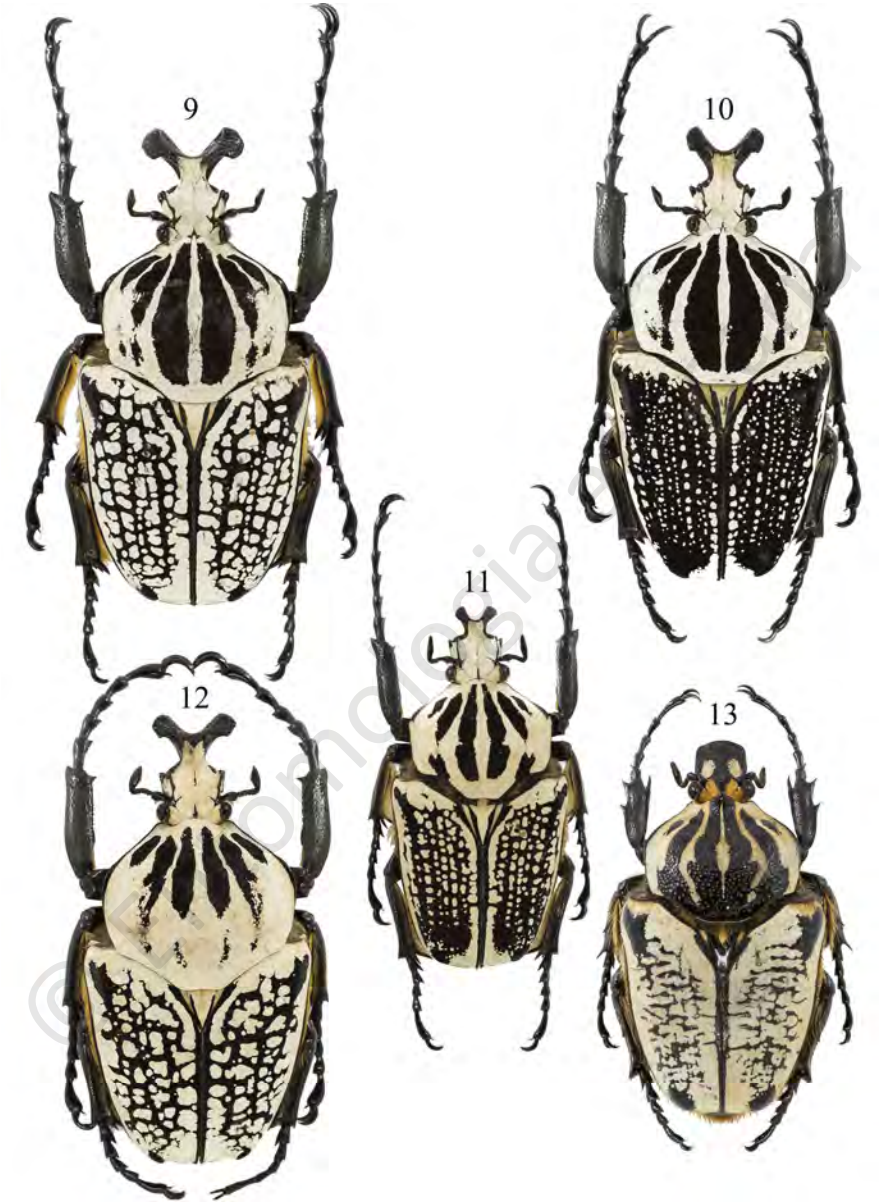

Figs 9-13: ***Goliathus goliatus meleagris*** Sjöstedt, 1927**. Figs 9-12:** ♂ specimens (9, Koni, Shaba Province, Zaïre; 10, Upemba National Park, "Katanga", D. R. C.; 11, Koni, Shaba Province, Zaïre; 12. Kundelungu National Park, Haut-Katanga Province, D. R. C.). **Fig 13:** ♀ specimen (Koni, Shaba Province, Zaïre).

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Figs 14-18: ***Goliathus goliatus meleagris*** Sjöstedt, 1927. **Fig. 14:** ♂ specimen (Lubemba, Haut-Katanga Province, D. R. C.). **a**, dorsal view. **b**, aedeagus. **Figs 15-18:** ♂ specimens (15, Lubemba, Haut-Katanga Province, D. R. C.; 16**,** "M'Pala" [Tanganyika Province, D. R. C.], Guillemé, in IRSNB.; 17, "Kabambarré" [Maniema Province, D. R. C.], Delhaize 1900, in IRSNB.**;** 18, Wakipingi, Busanga, north of Kolwezi, D. R. C.)

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It is thus unclear why recent authors included the name *preissi* Endrödi in the synonymy (e.g. MAWDSLEY, 2013).

G. orientalis usambarensis seems restricted to the montane tropical moist forests of the Usambara Mountains. The localization of the nominal taxon in the highlands of southwest Tanzania makes it likely that isolated populations of this species exist, or may have existed, in other forests of the Eastern Arc Mountains.

The following status is established for PREISS' taxon:

***Goliathus orientalis usambarensis* Preiss, 1933 stat. rev.**
Goliathus goliathus usambarensis Preiss, 1933
Goliathus usambarensis Preiss, 1933 (BAUDET, 2013)
[*G. goliathus ab. preissi* Endrödi 1951; unavailable name]

Identification of *Goliathus meleagris* Sjöstedt, 1927

SJÖSTEDT (1927) described *G. meleagris* as a good species. The three-line description ("♂ - *G. gigantis orientali Mos. maxime affinis, sed vittis nigris pronoti multo majoribus, elytris totis rotunde et dense albo maculatis facillime distinguendus*") captures the most notable differences between the habitus of the new taxon and that of *G. orientalis*, which evidently SJÖSTEDT considered the sister taxon. The author indicates Katanga in the D. R. C. as the type locality of *G. meleagris*. Months later, SJÖSTEDT (1928) published a more detailed description of *G. meleagris* together with a photograph of the holotype, a large specimen of 102 mm. The image, description and type locality unequivocally establish the identity of *G. meleagris*, which is the taxon localized in the plateaus of the former Katanga Province in the D. R. C. and neighbouring areas of northeast Angola and northern Zambia. At variance with *G. goliatus*, which is a tropical evergreen rainforest dweller, *G. meleagris* is found in deciduous woodlands in the Central Zambezian Miombo ecoregion.

The vast majority of *G. meleagris* specimens can be distinguished from *G. orientalis* by the markings on pronotum and elytra (Figs 9-13). As mentioned by SJÖSTEDT (1927, 1928), the elytral marks of *G. meleagris* are not aligned to form longitudinal lines as in *G. orientalis s. lat.*, but are arranged as inhomogeneously dispersed maculae of variable size and shape, generally on a black rather than brown background. Moreover, the pronotal bands of the central pair converge basally (except for specimens with reduced pronotal markings), whereas they often diverge in *G. orientalis*. In the female, the microsculpture of the pronotum is relatively deep, large and sparse in both

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G. orientalis and *G. meleagris*, compared to some other taxa in this genus (see below).

G. meleagris is currently treated as a synonym of *G. orientalis*. In order to better understand its relationship with *G. orientalis* and *G. goliatus*, we conducted barcoding analysis of representative members of genus *Goliathus*.

Barcoding analysis of *Goliathus*

Muscle tissue or eggs were removed from each specimen and submitted to the Biodiversity Institute of Ontario in Guelph, Canada for DNA extraction, amplification, and sequencing of cytochrome c oxidase subunit I (COI-5P), as described by HEBERT *et al.* (2003).

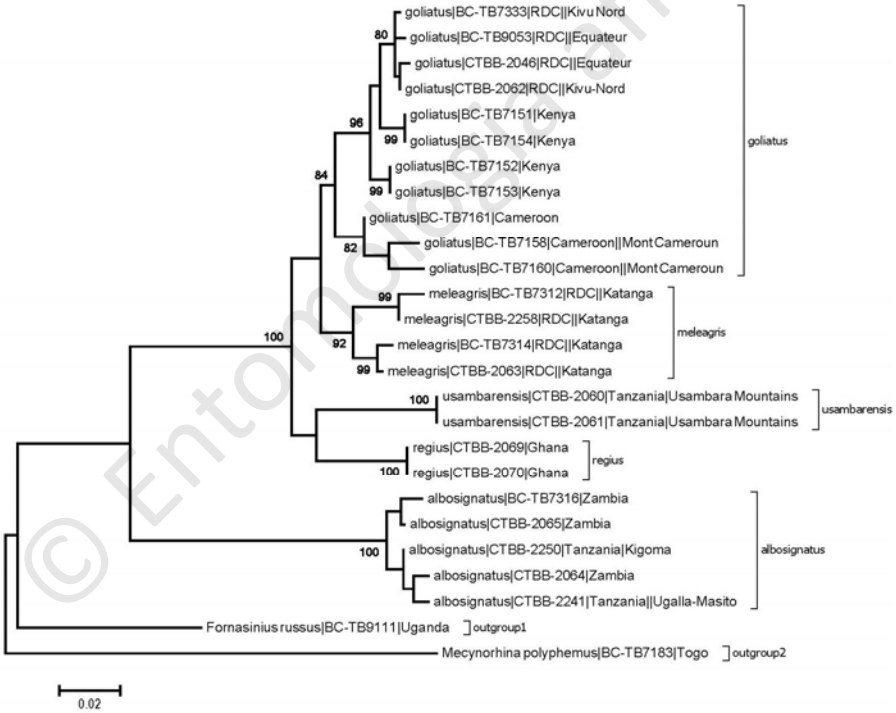

Figure 39. Neighbour-Joining Tree (Maximum Composite Likelihood model, generated by MEGA 6.06 from complete sequences of 658 bp CO1-5P obtained in BOLD) of 24 *Goliathus* specimens and representative outgroup genera (*Fornasinius* and *Mecynorhina s. str.*).

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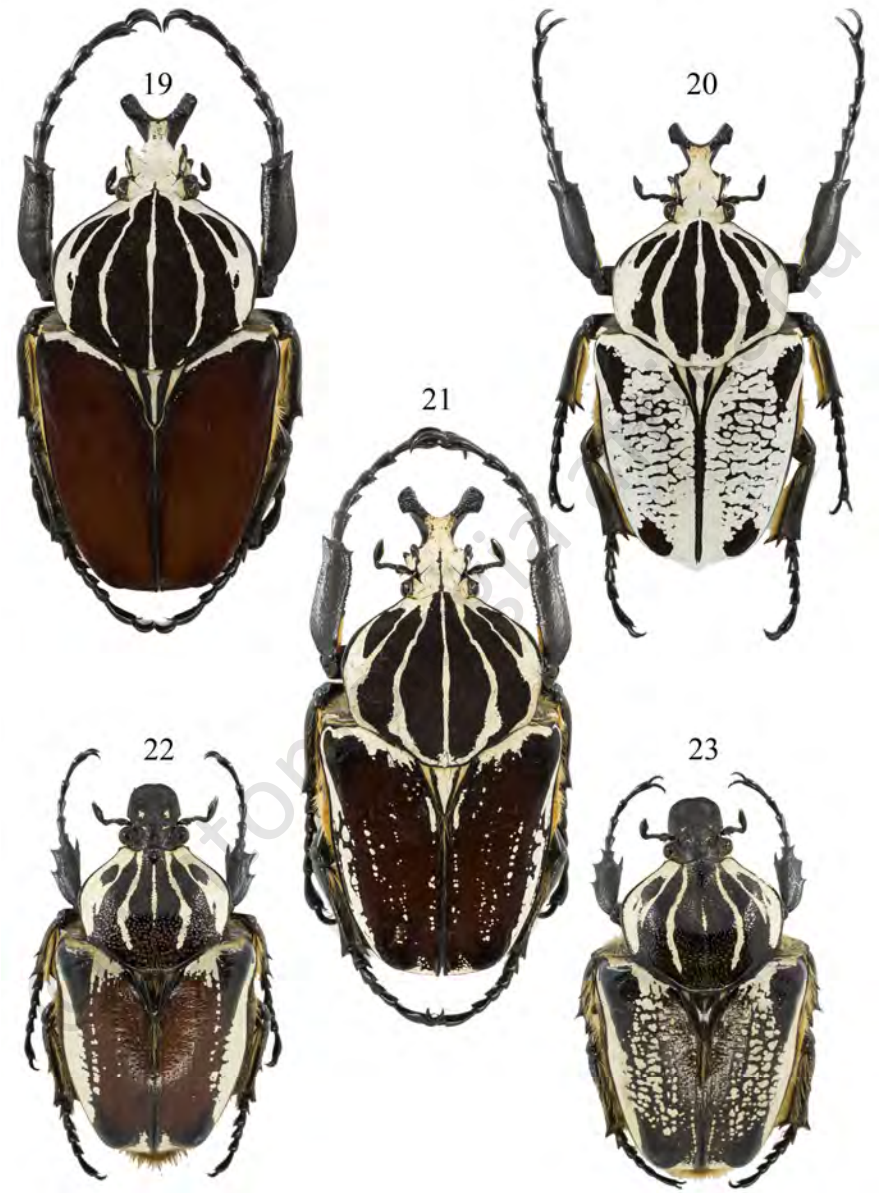

Figs 19-23: ***Goliathus goliatus s. str.*** (Drury, 1770). **Fig. 19:** ♂ specimen (Gabon). **Fig. 20:** ♂ specimen (Buea, Southwest Province, Cameroon). **Fig. 21:** ♂ specimen (Nandi Hills, Kenya). **Fig. 22:** ♀ specimen (Kibale Forest, Uganda). **Fig. 23:** ♀ specimen (Nandi Hills, Kenya).

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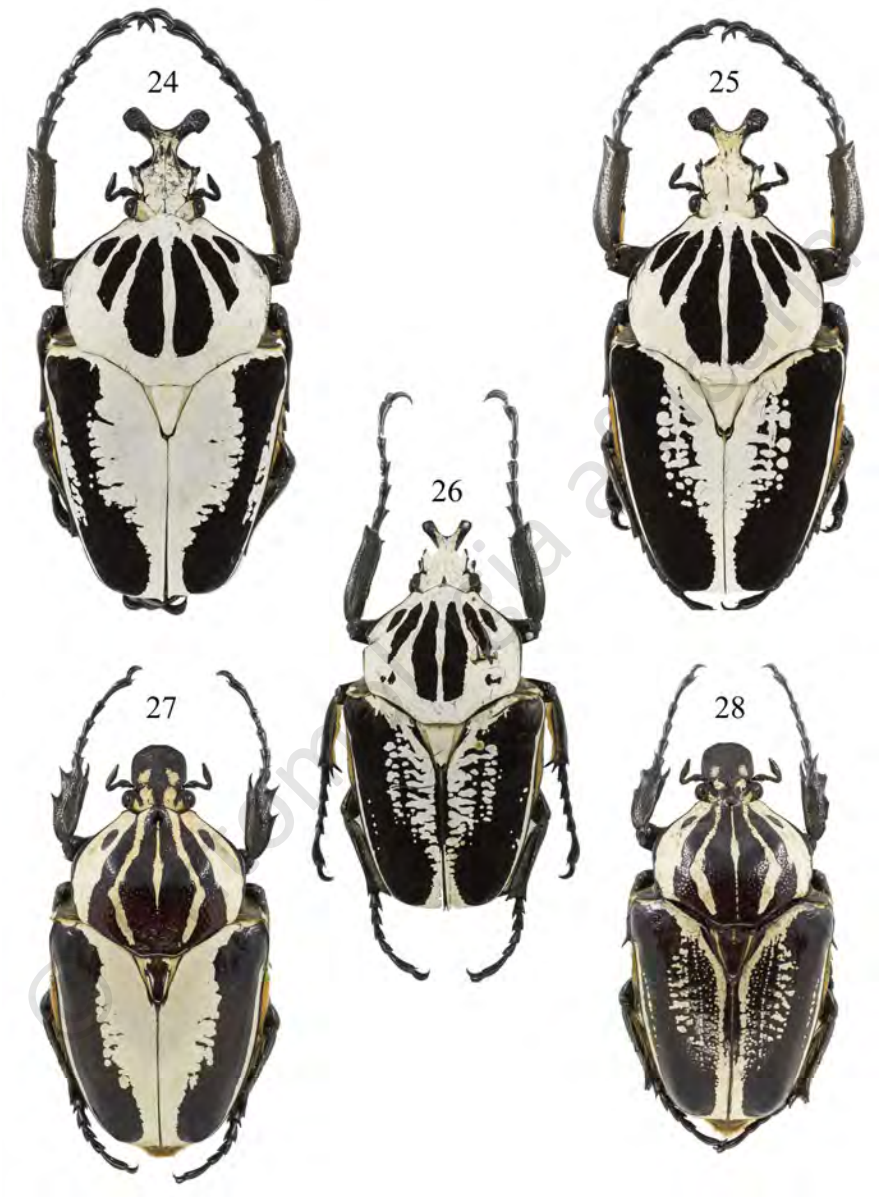

Figs 24-28: ***Goliathus regius*** Klug, 1835**. Figs 24-26:** ♂ specimens (24-25, Issia, Côte d'Ivoire; 26. Taï Forest, Côte d'Ivoire). **Figs 27-28:** ♀ specimens (Issia, Côte d'Ivoire).

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Twenty-four specimens of five *Goliathus* taxa yielded complete sequences and were included in the phylogenetic analyses: *G. goliatus* (11 specimens from Cameroon, D. R. C. and Kenya), *G. regius* (2 specimens from Ghana), *G. albosignatus* (5 specimens from Zambia and Tanzania), *G. o. usambarensis* (2 specimens from Usambara Mountains, Tanzania) and *G. meleagris* (4 specimens from the former Katanga Province in D. R. C.). Additional samples were analysed that yielded incomplete sequences; although the results were consistent with those obtained from specimens with complete sequences, incomplete sequences were excluded. To analyse the data, a neighbour-joining tree was constructed in BOLD using the Mega 6.06 software (TAMURA *et al*., 2013).

Sequence analysis revealed two major clusters that separate *G. albosignatus* from the other taxa (Fig. 39). Three main subgroups can be further identified in the larger cluster: *G. o. usambarensis*, *G. regius* and *G. goliatus* plus *meleagris*. Therefore, at odds with current taxonomy, *G. meleagris* appears more closely related to *G. goliatus* than to *G. o. usambarensis*. Because specimens of *G. goliatus* from fairly disjunct localities (Cameroon to Kenya) cluster separately from *G. meleagris*, the latter taxon is construed to represent a good subspecies of *G. goliatus*.

The following status is established for SJÖSTEDT's taxon:

***Goliathus goliatus meleagris* Sjöstedt, 1927 stat. rev.**

Goliathus meleagris Sjöstedt, 1927
Goliathus orientalis auct. (*nec* Moser, 1909)

The subspecific ranking of *meleagris* under *goliatus* is further supported by eco-geographic considerations and morphological differences. *G. goliatus s. str*. inhabits ecoregions in western to eastern central Africa that encompass both low- and high-altitude tropical rainforests. Conversely, *G. g. meleagris* seems restricted to subtropical woodlands in southern central Africa. In D. R. C., the boundary (contact zone?) between the two subspecies may lie in the Southern Congolian Forest-Savanna Mosaic ecoregion, which separates the sparsely wooded plateaus of southern D. R. C. from the tropical forests of north and northeast D. R. C. Ecologic specialization may have, therefore, contributed to the separation of *G. g. meleagris* from *G. goliatus s. str*.

G. g. meleagris can be distinguished from *G. goliatus s. str*. by the somewhat steeper anterior declivity of the pronotum in the large male specimens. In the female, the microsculpture of the pronotum is generally larger, deeper and sparser in *G. g. meleagris* than in the nominate subspecies. Although the colour of the elytra can almost always readily separate the two

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taxa, some *G. g. meleagris* specimens resemble certain forms of *G. goliatus s. str.* with dark brown elytra, with reduced or virtually absent white marking (Figs 16 & 18). For example, a series of *G. g. meleagris* specimens with reduced elytral markings has been collected recently in the vicinity of Lubemba, Haut-Katanga Province, near the Zambian border.

Overall, the shape of the pronotum in the male, the microsculpture of the pronotum in the female, the allopatric distribution and ecological specialization, along with the modest divergence, together indicate that *meleagris* represents a well-differentiated subspecies of *G. goliatus*.

Of interest is our finding at the Institut royal des Sciences naturelles de Belgique (IRSNB), Brussels, Belgium, of a number of specimens collected in Kabambarré (= Kabambare, about 100 Km East of Kasongo; Maniema Province) and in the M'Pala region (Tanganyika Province), which lie in the aforementioned boundary zone. Some of these specimens display intermediate features between *goliatus* and *meleagris* (see, e.g., the pronotal markings) and could, therefore, represent transitional forms (Figs 16-17). It is noteworthy that all the specimens from M'Pala, which were collected by Father Guillemé presumably between 1891 and 1897, display black elytra with extremely reduced white marks.

Revised taxonomy of genus *Goliathus*

As discussed above, barcoding analysis suggests that *G. goliatus* (with ssp. *meleagris*), *G. regius* and *G. o. usambarensis* form a cluster of closely related species (max. 6-7% divergence; figure 40).

	albos.	*goliatus*	*meleagr.*	*usamb.*	*regius*	*F. russus*
albosignatus		16.1%	16.1%	17.1%	16.1%	15.8%
goliatus	16.1%		4.4%	6.9%	6.6%	15.5%
meleagris	16.1%	4.4%		6.5%	6.3%	15.6%
usambarensis	17.1%	6.9%	6.5%		7.0%	16.2%
regius	16.1%	6.6%	6.3%	7.0%		17.1%
F. russus	15.8%	15.5%	15.6%	16.2%	17.1%	

Figure 40. Table of the mean genetic distance (in percentage, %) between five *Goliathus* taxa and the outgroup *Fornasinius russus* (Kolbe, 1884).

Notably, the four taxa were treated as conspecific by WIEBES (1968), who ranked *orientalis* (*sensu auct.*; i.e. *meleagris*) and *regius* subspecifically under *goliatus*. Although arguments can be put forward in support of conspecificity and subspecific ranking (e.g., the disjoint distribution of the four taxa), we view *G. regius* and *G. orientalis* as too differentiated from *G. goliatus* to justify their lumping into a single species.

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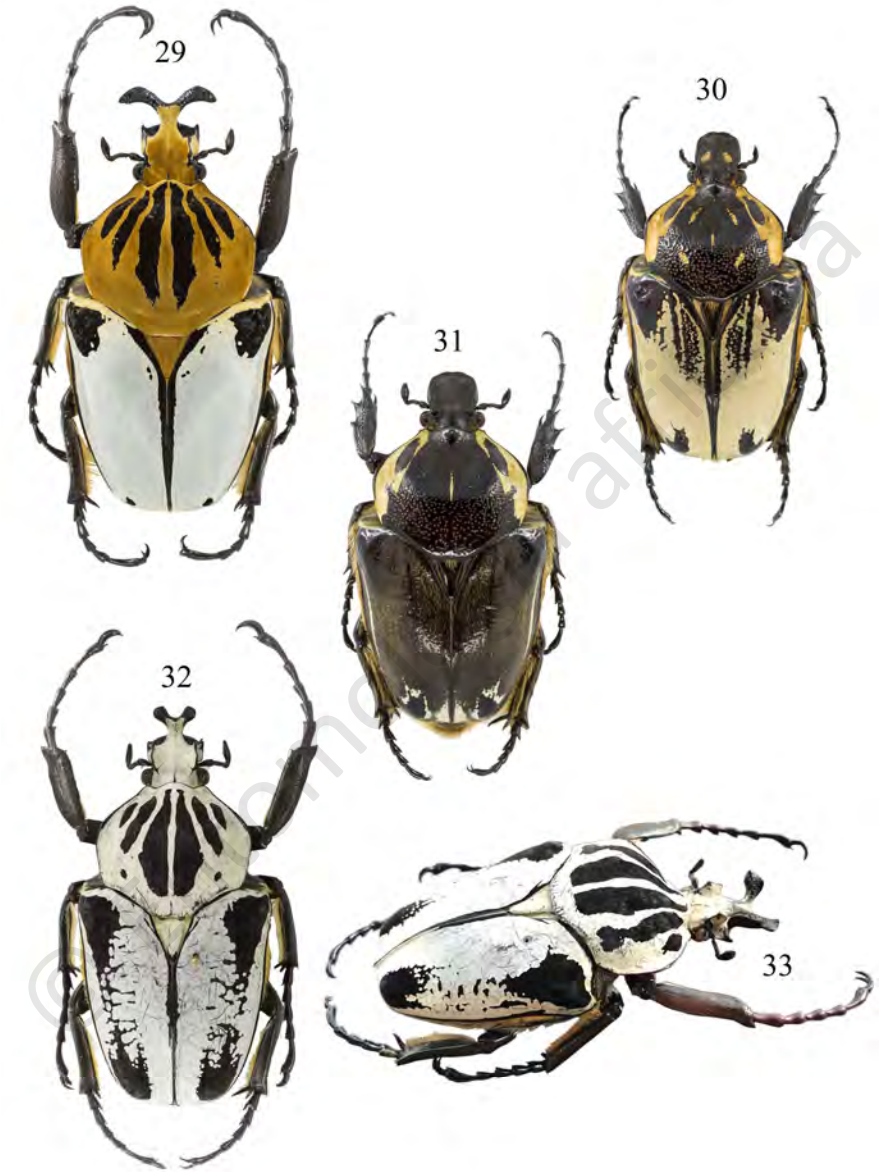

Figs 29-31: ***Goliathus cacicus*** (Olivier, 1789). **Fig. 29:** ♂ specimen (Banco Forest, Côte d'Ivoire). **Fig. 30:** ♀ specimen (Ashanti Region, Ghana). **Fig. 31:** ♀ specimen (Banco Forest, Côte d'Ivoire). **Figs 32-33:** ***Goliathus atlas*** Nickerl, 1887. ♂ specimens (Taï Forest, Côte d'Ivoire; ex coll. K. Klingbeil).

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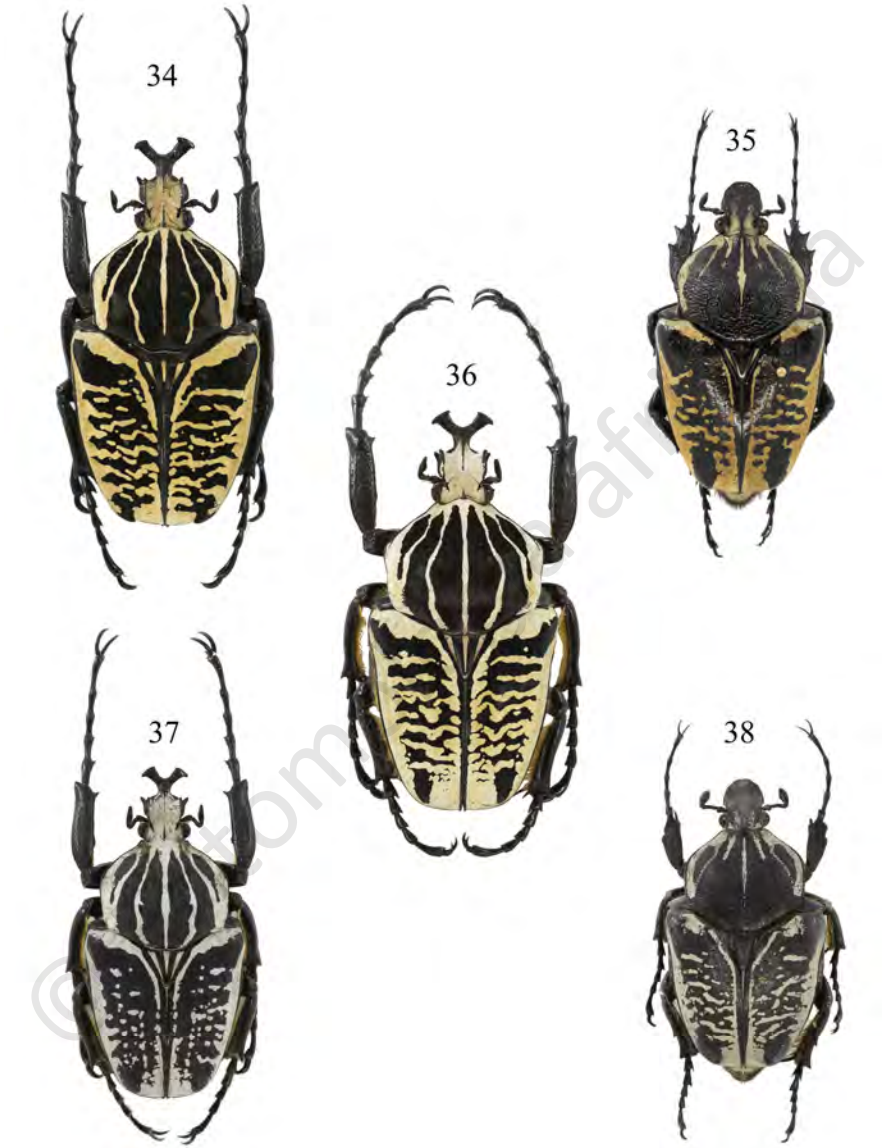

Figs 34-38: ***Goliathus albosignatus*** Boheman, 1857. **Fig. 34:** ♂ specimen (Bulawayo, Zimbabwe). **Fig. 35:** ♀ specimen (*ditto*). **Figs 36-38:** ***Goliathus albosignatus kirkianus*** Gray, 1864. **Figs 36-37 :** ♂ specimens (36, Masasi District, Mtwara Region, Tanzania; 37, Uluguru Mountains, Morogoro Region, Tanzania). **Fig. 38:** ♀ specimen (Mazabuka, Southern Province, Zambia)

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Among the *Goliathus* species, ***G. goliatus s. str***. (Figs 19-23**)** has the broadest distribution range in sub-Saharan Africa. It is found from Benin to Kenya and from southern Chad to central D. R. C. It seems that the Eastern Rift Valley defines the eastern limit of its distribution; in Kenya, *G. goliatus* is found in the Nandi Hills at the edge of the Rift Valley. We sampled the nominal subspecies from 4 distinct areas: southwest Cameroon, northwest D. R. C. (Equateur Province), eastern D. R. C. (Nord Kivu Province) and western Kenya. Although some geographic populations cluster separately, the degree of inter-group divergence (1.5-3.5%) does not significantly exceed intra-group divergence (0.5-2.0%; data not shown), making taxonomic splitting untenable. The high-altitude *G. goliatus* populations of southwest Cameroon display significant variation in the colour of the elytral tegument, which ranges from uniform dark brown to entirely white with black marks at the humeral and apical calli. Such colour morphs (and their intermediates) are encountered in a given population at the expected Mendelian frequency, as seen in other Cetoniinae genera (e.g., *Mecynorhina* (*Megalorhina*); DE PALMA & FRANTZ, 2010). Also, the cephalic armature of *G. goliatus* specimen from western Kenya shows some peculiarities, such as the externally pointed anteocular crests. Nevertheless, these character states (colour of integument; structure of cephalic armature) are best interpreted as derived phenotypes associated with geographical isolation. Undoubtedly, *G. g. meleagris* stands out as a good subspecies, as discussed above.

G. regius (Figs 24-28) clearly represents a separate species (min. 6-7% divergence from closest taxa). It is broadly distributed in Western Africa, from Sierra Leone to Togo. The species is fairly common in both pristine and degraded patches of the Western and Eastern Guinean lowland forests; the corresponding author encountered this species at several localities in Ghana. The colour of pronotum and elytra is fairly constant throughout the distribution range. The females can be readily distinguished from those of *G. goliatus s. lat.* by the significantly shallower and sparser microsculpture of the pronotum.

G. cacicus (Figs 29-31), which we could not barcode owing to the lack of freshly collected material, is unquestionably a distinct species. Its distribution in West Africa partly overlaps with that of *G. regius*, from which it is highly differentiated (post-clypeal horns of the male very divergent and curved; brown integument of the pronoto-scutellum and silvery elytra; more elongated tarsi). The two species occasionally hybridize to generate the taxon ***atlas*** (Figs 32-33), which shows characters of both parental species with variable penetrance, e.g., yellowish pronoto-scutellum; medially interrupted black sutural line; broken elytral bands; and deflected post-clypeal horns in

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the large males (Fig. 33, showing a specimen of 97 mm). *G.* "*atlas*" has been collected in fair numbers at localities where the two species cohabit, such as the Taï Forest in Côte d'Ivoire and the Volta Region in Ghana, supporting the notion that it represents a natural hybrid.

Unfortunately, we could not barcode specimens of *G. orientalis* from the type locality. We here took a conservative approach and treated *G. usambarensis* as a good subspecies of *G. orientalis* localized in the Usambara Mountains, although differences with the nominate taxon appear at best minor. We currently ignore whether the distribution range of *usambarensis* involves other mountain forests in the Eastern Arc Mountains of Kenya and Tanzania. Nevertheless, the very disjoint localization of *G. orientalis s. str.* in southwest Tanzania suggests that other populations of *G. orientalis* exist, or may have existed, in the mid-altitude forests along the Eastern Arc Mountains. Based on the records known to us, the Eastern Rift Valley may represent the natural boundary separating *G. goliatus s. lat.* from *G. orientalis*.

G. albosignatus (Figs 34-38) shows important anatomical differences with members of the *goliatus*/*orientalis*/*regius* complex, for example, the hammer-shaped post-clypeal horns of the male, the elongated tarsi, and the presence of cretaceous marks on the pygidium. Unlike other *Goliathus* species, *G. albosignatus* develops in *Hyrax* dung, as do various *Fornasinius* species (MAQUART & MALEC, 2017). The marked divergence (16-17%) between *G. albosignatus* and the surveyed taxa in the *goliatus*/*orientalis*/*regius* complex might suggest early separation of the two groups, which may have occurred in parallel to the radiation of *Fornasinius* from a common ancestor.

G. albosignatus is currently split into two subspecies (WIEBES, 1968; NAGAI & SAKAI, 1998). *G. a. kirkianus* is localized north of the Zambezi River. The main character used to differentiate the two taxa appears spurious (black or yellow setae on meso- and meta-tibiae in the nominal and *kirkianus* subspecies, respectively). However, the two subspecies are here retained until results of barcoding analysis of specimens from south of the Zambezi River become available to us.

Our study is mainly limited by the small sample number, which prevented statistical analysis of the data, and the unavailability of fresh *G. cacicus* specimens for barcoding. However, the barcoding data are largely corroborated by morphological and eco-geographic data. A paper dealing with the phylogeny and supra-specific classification of the Goliath beetles *s. lat.*, which include *Goliathus*, *Argyrophegges* Kraatz, 1895, *Fornasinius* and *Hegemus* Thomson, 1881, is currently in preparation.

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The valid taxa in the genus *Goliathus*, and the distribution of taxa revised in this paper (Figure 41), is shown below.

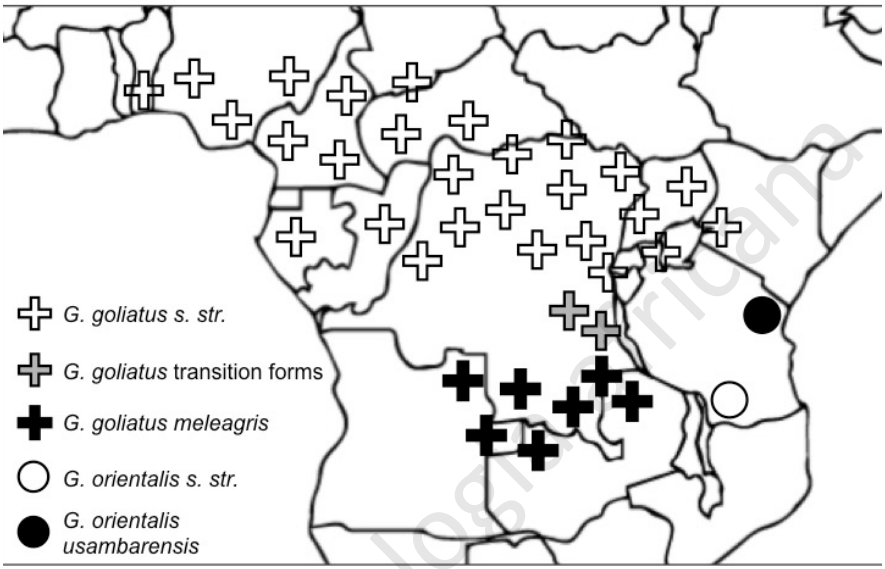

Figure 41. Distribution map of *G. goliatus* and *G. orientalis.*

***1. Goliathus goliatus* (Drury 1770)**

Benin, Nigeria, Cameroon, Central African Republic, Chad (south), Gabon, Equatorial Guinea (?), Republic of the Congo, Democratic Republic of the Congo (north and central), Rwanda, South Sudan (?), Uganda, Kenya (west).

***Goliathus goliatus meleagris* Sjöstedt, 1927 stat. rev.**

Angola (northeast), Democratic Republic of the Congo (south), Zambia.

***2. Goliathus orientalis* Moser, 1909 (*nec auct.*) bon. sp.**

Tanzania (southwest).

***Goliathus orientalis usambarensis* Preiss, 1933 stat. rev.**

Tanzania (northeast).

***3. Goliathus regius* Klug, 1835**

Sierra Leone, Liberia, Republic of Guinea, Côte d'Ivoire, Burkina Faso (?), Ghana, Togo.

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***4. Goliathus cacicus* (Olivier, 1789)**

Sierra Leone, Liberia, Republic of Guinea (?), Côte d'Ivoire, Ghana.

***Goliathus atlas* Nickerl, 1887** [natural hybrid *G. regius* x *cacicus*]
Côte d'Ivoire, Ghana.

***5. Goliathus albosignatus* Boheman, 1857**

Republic of South Africa (northeast), Zimbabwe.

***Goliathus albosignatus kirkianus* Gray, 1864**

Malawi, Zambia, Mozambique, Tanzania.

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