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Taxonomic revision of the *Eudicella* White, 1839 complex, with description of three new subgenera (Scarabaeidae, Cetoniinae, Goliathini)

Michele DE PALMA*, Hitoshi TAKANO**, Philippe Léonard*** & Thierry BOUYER****

* School of Life Sciences, Swiss Federal Institute of Technology in Lausanne (EPFL), 1015 Lausanne, Switzerland. Email: michele.depalma@epfl.ch.

** African Natural History Research Trust, Leominster, Herefordshire HR6 9QA, UK.

** Department of Life Sciences, Natural History Museum, London SW7 5BD, UK.

*** Avenue Eugène Ysaye 30, B-4053 Embourg, Belgium.

**** 57 rue Genot, B-4032 Chênée, Belgium.

Summary. Morphological and DNA barcoding analysis of representative taxa in the *Eudicella* White complex identified five distinct subgenera, three of which are established herein: *Eudicella (Coelorrhinella)* n. subg., *Eudicella (Aneurhina)* n. subg., and *Eudicella (Ceratorhinella)* n. subg. The remaining taxa are either assigned to *Eudicella s. str.* or *Eudicella (Coelorrhina)* Burmeister.

Résumé. Des analyses morphologiques et génétiques par Barcoding des taxa représentatifs du genre *Eudicella* White ont permis d'identifier cinq sous-genres distincts, trois d'entre eux établis ici pour la première fois: *Eudicella (Coelorrhinella)* n. subg., *Eudicella (Aneurhina)* n. subg., and *Eudicella (Ceratorhinella)* n. subg. Les taxa restants sont chacun assignés à *Eudicella s. str.* ou *Eudicella (Coelorrhina)* Burmeister.

Keywords. Africa, Scarabaeidae, Cetoniinae, Goliathini, Eudicella, nova subgenera.

Introduction

Since HOLM (1993), the genus *Eudicella* White, 1839 (type species: *Goliathus smithii* MacLeay, 1838) has been split into two subgenera, *Eudicella s. str.* and *Eudicella* (*Cyprolais*) Thomson, 1880 (DE PALMA, 2009). In this issue of *Entomologia Africana* (page 10), DE PALMA & TAKANO synonymized *Cyprolais* with *Coelorrhina* Burmeister, 1842, whose type species is *Cetonia quadrimaculata* Fabricius, 1781 (*contra* KRIKKEN, 1984). Therefore, *Eudicella* currently comprises two subgenera: *E. (Eudicella*) White and *E. (Coelorrhina*) Burmeister.

While HOLM (1993) lumped all species outside *Eudicella s. str.* into one subgenus, ALLARD (1985) had previously recognised two distinct genera (*Coelorrhina* and *Ceratorrhina* [sic] Westwood, 1843) and two speciesgroups within *Coelorrhina*. In fact, *E. (Coelorrhina*), as defined by HOLM (1993), is a heterogeneous group of species and confusion still surrounds the definition of the subgenus and its relationship with *Eudicella s. str.* For example, two highly related species, *E. cupreosuturalis* Bourgoin, 1913 and *E. bouyeri* Leonard & Beinhundner, 2014, are currently assigned to each of the two different subgenera. To further complicate matters, DE PALMA &

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TAKANO (2021, page 9) clarified that *Ceratorhina* Westwood is a junior synonym of *Dicronorhina* Hope, 1837, with type species *Scarabaeus micans* Drury, 1773; thus, *Eudicella s. lat.* requires taxonomic revision.

Morphological and DNA barcoding analysis of representative taxa currently assigned to either *E*. (*Eudicella*) or *E*. (*Coelorrhina*) sensu HOLM (1993) indicate that five subgenera are involved, three of which are established herein.

Genus Eudicella White, 1839

Type species: Goliathus smithii MacLeay, 1838

Re-description: Body depressed, elongate, with the apical elvtral calli more approximated than the humeral calli: dorsum and venter avelutinous and without cretaceous areas: abdominal sternites medially depressed in the male. Clypeus subquadrate, flat, with lateral areas depressed and anterior margin slightly raised and emarginate in the female; almost always armed with a variably developed median horn and lateral projections in the male. Pronotum wider at base, slightly convex, with emarginate basolateral margins and slightly emarginate basomedian (antescutellar) margin; disc with variably deep and dense micropunctures: lateral margins smooth, slightly raised, more upturned in the posterolateral segment. Scutellum wide, nearly equilateral, with lateral grooves exposed. Elvtron wider at humerus, smooth, asetose, without defined striae or costae, with a slightly elevated sutural costa; fine micropunctures scattered or aligned to form longitudinal series, and a line of deeper punctures outlining the sutural costa; apex simple, acute, without apical spine. Pro- and metasternum with variably deep and dense micropunctures and variably long and dense setae. Mesometasternal process broad and apically subtriangular, with setose mesometasternal declivity. Protibia asetose, unidentate or weakly bidentate on the outer margin in the male: tridentate on the outer margin in the female. Meso- and metatibia with long setae on at least the proximal segment, with a median outer denticle in the female. Pars basalis of the aedeagus longer than the parameres; parameres proximally fused, separated at apices.

Subgenus Eudicella (Eudicella) White, 1839 (Figs 1-5)

Type species: Goliathus smithii MacLeay, 1838

Diagnostic characters (male): Clypeus short, concave, with lateral areas more deeply excavated; surface smooth and shiny; lateral margin short, with a long and pointed spine at the anterolateral margin; median, Y-shaped preclypeal horn with long, flattened, variably denticulate and apically tapering branches. Frons broad, flat or slightly concave, without distinct horns or projections, roughly as long as the clypeus and separated from the latter by two slightly raised anteocular elevations; dense and deep microsculpture.

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Figures 1-5. *E.* (*Eudicella*) White. Fig. 1: \bigcirc *E.* (*E.*) *chloe.* a, habitus. b, aedeagus, frontal view. c, aedeagus, lateral view. Fig. 2: \bigcirc *E.* (*E.*) *frantzi*. Fig. 3: \bigcirc *E.* (*E.*) *morgani*. Fig. 4: \bigcirc *E.* (*E.*) *morgani*. Fig. 5: \bigcirc *E.* (*E.*) *frontalis.*

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Pronotum with minute, shallow, dense and often confluent micropunctures. Profemur with a brush of short and dense setae along the anterior side. Protibia armed on the interior margin with a series of irregular, short spines in the male. Parameres short and curved ventrally, fused on the proximal segment and medially widened, flattened dorsoventrally but of variable thickness; ventral surface generally flat and concave but sometimes thickened and with a slight elevation that never forms a distinct knob in lateral view; apex enlarged, flat, generally with subtriangular outline, with more or less angular profile in frontal view; meatus between the free parameres usually long and relatively narrow (Figs 1-5).

List of species:

E. (Eudicella) daphnis (Buquet, 1835)

E. (*Eudicella*) grallii (Buquet, 1836)

E. (Eudicella) smithii (MacLeay, 1838)

E. (Eudicella) morgani (White, 1839)

E. (*Eudicella*) *frontalis* (Westwood, 1841)

E. (Eudicella) tetraspilota Harold, 1879

E. (Eudicella) darwiniana Kraatz, 1880

E. (Eudicella) trimeni Janson, 1884

E. (Eudicella) pauperata Kolbe, 1884

E. (Eudicella) chloe Raffray, 1885

E. (Eudicella) colmanti Braem, 1907

E. (Eudicella) ducalis Kolbe, 1914

E. (Eudicella) aethiopica Müller, 1941

E. (Eudicella) inexpectata Antoine, 1985

E. (Eudicella) frantzi De Palma, 2010 bona sp., stat. rev.

E. (Eudicella) nana Seidel, 2016

Subgenus Eudicella (Coelorrhina) Burmeister, 1842 (Figs 6-10)

Type species: Cetonia quadrimaculata Fabricius, 1781

Diagnostic characters (male): Clypeus long, with preclypeal area elongate and deeply concave, and lateral areas more deeply excavated; surface matt and rugose owing to the dense microsculpture; lateral margin raised, forming a longitudinal ridge with a short, subtriangular, dorsoventrally flattened projection at the anterolateral margin; median, Y-shaped preclypeal horn with short, apically dilated, transversely truncated and variably

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Figures 6-10. E. (Coelorrhina) Burmeister. Fig. 6: A E. (C.) hornimani. a, habitus, dorsal view. b, habitus, ventral view. Fig. 7: $\bigcirc E$. (C.) viridipyga, head, semi-lateral view. Fig. 8: [♀] E. (C.) loricata. Fig. 9: [∧] E. (C.) loricata. a, habitus. b, aedeagus, frontal view. c, aedeagus, lateral view. Fig. 10: F. (C.) quadrimaculata. a, habitus, dorsal view. b, head, semi-lateral view. c, aedeagus, frontal view. d, aedeagus, lateral view.

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denticulate branches, often with a small tubercle at the base of the branches. Frons almost completely excavated, with the exception of a narrow rear margin from which project two basofrontal horns. Basofrontal horns vertically raised and curved ventrally, apically pointed, either medially approximated or broadly spaced. Pronotum with distinct and sparse micropunctures. Profemur with a brush of short and dense setae along the anterior side. Protibia unarmed on the interior margin in the male. Parameres short and straight, largely fused and medially widened, flattened dorsoventrally but of variable thickness; ventral surface medially thickened to form a distinct knob in lateral view; apex abruptly narrowed, elongate and bent ventrally, terminally rounded in frontal view; meatus between the free parameres limited to the apices (Figs 6-10).

List of species:

- E. (Coelorrhina) quadrimaculata (Fabricius, 1781)
- *E.* (*Coelorrhina*) *hornimani* (Bates, 1877)
- E. (Coelorrhina) loricata (Janson, 1877)
- E. (Coelorrhina) viridipyga (Lewis, 1879)
- E. (Coelorrhina) cornuta (Heath, 1904)
- E. (Coelorrhina) babaulti (Allard, 1983)
- E. (Coelorrhina) ruteri (Allard, 1983)
- E. (Coelorrhina) takanoi Oram, 2015

Subgenus Eudicella (Coelorrhinella) n. subg. (Figs 11-13)

Type species: Goliathus (Eudicellus) auratus Westwood

Diagnostic characters (male): Clypeus long, with preclypeal area elongate and deeply concave, and lateral areas more deeply excavated; surface matt and rugose owing to the dense microsculpture; lateral margin proximally raised, with a broad, subtriangular or subquadrate, dorsoventrally flattened projection at the anterolateral margin; median, T-shaped preclypeal horn with variably dilated, truncate apex and a central tubercle. Frons excavated medially, from the sides of which project two basofrontal horns. Basofrontal horns short, flat, horizontally projected and apically pointed. Profemur with a brush of short and dense setae along the anterior side. Protibia unarmed on the interior margin. Parameres short and ventrally curved, fused on the proximal segment, flattened dorsoventrally; ventral surface flat and concave, medially widened and thickened, but never forming a distinct knob in lateral view; apex dilated, with subtriangular outline, with more or less angular profile; meatus between the free parameres short and narrow (Figs 11-13).

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Figures 11-15. *E.* (*Coelorrhinella*) **n.** subg. and *E.* (*Aneurhina*) **n.** subg. Fig. 11: \mathcal{J} *E.* (*C.*) *aurata.* a, habitus, dorsal view. b, habitus, ventral view. c, head, semi-lateral view. d, aedeagus, frontal view. e, aedeagus, lateral view. Fig. 12: \mathcal{Q} *E.* (*C.*) *aurata.* Fig. 13: \mathcal{J} *E.* (*C.*) *selene.* a, habitus. b, head, semi-lateral view. Fig. 14: \mathcal{J} *E.* (*A.*) *mutica.* a, habitus, dorsal view. c, aedeagus, frontal view. d, aedeagus, lateral view. Fig. 15: \mathcal{Q} *E.* (*A.*) *mutica.*

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List of species:

E. (*Coelorrhinella*) *aurata* (Westwood, 1841)

E. (Coelorrhinella) selene (Kolbe, 1899)

Subgenus Eudicella (Aneurhina) n. subg. (Figs 14-15)

Type species: Coelorrhina mutica Janson, 1915

Diagnostic characters (male): Clypeus quadrate, unarmed, with lateral areas slightly depressed; anterior margin straight, not emarginate; surface matt and rugose owing to the dense microsculpture. Frons medially slightly convex, without anteocular elevations. Profemur without a brush of short and dense setae along the anterior side. Protibia unarmed on the interior margin. Parameres short and ventrally curved, fused on the proximal segment, flattened dorsoventrally; ventral surface flat and concave; apex dilated, flat, with subtriangular outline but without angular profile; meatus between the free parameres long and narrow (Figs 14-15).

List of species:

E. (Aneurhina) mutica (Janson, 1915)

Subgenus Eudicella (Ceratorhinella) n. subg. (Figs 16-19)

Type species: Eudicella cupreosuturalis Bourgoin, 1913

Diagnostic characters (male): Clypeus short, concave, with a central carina and lateral areas more deeply excavated; surface smooth and shiny; lateral margin short, with a broad, subtriangular, centrally depressed, vertically raised and apically pointed projection at the anterolateral margin; median. Y-shaped preclypeal horn with long, flattened and apically tapering branches. Frons moderately narrow, rugose or with deep punctures, from the sides of which project two basofrontal horns. Basofrontal horns short, flat, horizontally projected and apically pointed. Pronotum with variably deep and dense micropunctures. Profemur with a brush of short and dense setae along the anterior side. Protibia unarmed on the interior margin. Parameres short and ventrally curved, fused on the proximal segment, flattened dorsoventrally; ventral surface medially widened, thickened and with a slight elevation that never forms a distinct knob in lateral view; apex enlarged and thickened, without angular profile; meatus between the free parameres short and wide (Figs 16-19).

List of species:

E. (Ceratorhinella) preissi (Moser, 1912)

- E. (Ceratorhinella) cupreosuturalis Bourgoin, 1913
- E. (Ceratorhinella) bouyeri Leonard & Beinhundner, 2014

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Figures 16-19. *E.* (*Ceratorhinella*) **n.** subg. Fig. 16: \mathcal{J} *E.* (*C.*) *cupreosuturalis.* a, habitus, dorsal view. b, habitus, ventral view. c, head, semi-lateral view. d, aedeagus, frontal view. e, aedeagus, lateral view. Fig. 17: \mathcal{J} *E.* (*C.*) *bouyeri.* Fig. 18: \mathcal{Q} *E.* (*C.*) *bouyeri.* Fig. 19: \mathcal{J} *E.* (*C.*) *bouyeri.* Fig. 19: \mathcal{J} *e.* (*C.*) *preissi.* a, habitus, dorsal view. b, habitus, ventral view. c, head, semi-lateral view. d, aedeagus, frontal view. e, aedeagus, lateral view. b, habitus, ventral view. c, head, semi-lateral view. d, aedeagus, frontal view. e, aedeagus, lateral view. e, head, semi-lateral view. d, aedeagus, frontal view. e, aedeagus, lateral view. e, head, semi-lateral view. d, aedeagus, frontal view. e, aedeagus, lateral view.

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Key to subgenera*

1-Protibia armed with denticles on interior margin ... E. (Eudicella) White

- Protibia unarmed on interior margin
- 2 Clypeus unarmed and profemur without a dense brush of setae

... E. (Aneurhina) n. subg.

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- Clypeus armed and profemur with a dense brush of setae ... 3
- 3 Frons almost completely excavated, with basofrontal horns vertically raised and ventrally curved ... *E. (Coelorrhina)* Burmeister

- Frons partly excavated with basofrontal horns projecting anteriad 4

4-Clypeus without central carina; clypeal horn T-shaped, apically truncated ... *E. (Coelorrhinella)* n. subg.

- Clypeus with central carina; clypeal horn Y-shaped, with divergent and apically pointed branches ... *E. (Ceratorhinella)* n. subg.

*: The key refers to males. Females are difficult to assign to subgenera.

DNA barcoding analysis

Muscle tissue or eggs were removed from four of the five subgenera recognised or first established in this study 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). The subgenus *Aneurhina* could not be analysed owing to the lack of modern material. 42 individuals belonging to 12 putative ingroup taxa yielded successful sequences. *Megalorhina* Westwood and *Cheirolasia* Westwood were selected as outgroup taxa.

Sequences were aligned using MUSCLE in MEGA version X (KUMAR et al., 2018) and phylogenetic tree searches were performed using Bayesian Inference (BI) and Maximum Likelihood (ML). BI analyses were performed using MrBayes version 3.2.7a (RONQUIST et al., 2012). Metropolis-coupled Markov chain Monte Carlo (MCMC) analyses were run with four chains (one cold and three heated) for 10,000,000 generations sampling every 100 generations, discarding the first 25% as burn-in. The two runs converged with the standard deviation of split frequencies 0.003. ML analyses were performed on CIPRES using the RAxML BlackBox utility (STAMATAKIS et al., 2008) with default settings and a GTR+FO+G4m model. Support for clades was evaluated for BI using posterior probabilities and ML using non-parametric bootstrapping. Trees were visualised and annotated in FigTree version 1.4.4.

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Figure 20. Maximum Likelihood tree of *Eudicella s. lat.* and Goliathini outgroup taxa. Numbers above branches indicate bootstrap values/posterior probabilities. Scale bar indicates substitution rate per site.

The phylogenetic inferences based on BI and ML recovered identical topologies. The tree resulting from the ML analysis is shown in fig. 20. The monophyletic *Eudicella s. lat.* includes two distinct, well-supported lineages, with *E.* (*Ceratorhinella*) recovered as sister to *E.* (*Coelorrhina*) + *E.* (*Coelorrhinella*) + *E.* (*Eudicella*). Intra-subgeneric average pairwise distances (APWD) ranged from 0.5 to 13.6% and inter-subgeneric APWD ranged from 15.5 to 26.4%. The APWD between the ingroup and outgroup taxa was 21.9%.

Discussion

The results of this study indicate that all known *Eudicella s. lat.* species can be grouped into five distinct subgenera according to well-defined morphological characters expressed in the male (see key above). Molecular

analyses, while limited in scope (based only on a small region of the mitochondrial gene and with incomplete taxon sampling), corroborated key results obtained by studying morphological and anatomical characters, including the structure of the aedeagus. Individuals of each of the 12 sampled taxa clustered into the five subgenera and their monophyly was supported by strong bootstrap (>90) and posterior probability (100) values. Of note, *E.* (*Ceratorhinella*) forms a separate lineage from that encompassing the other subgenera, making HOLM's (1993) proposition to lump all taxa outside *Eudicella s. str.* into one subgenus untenable. In the future, additional taxa and especially the subgenus *Aneurhina* should be sequenced to clarify phylogenetic relationships within and across the subgenera.

Two oddities may be recognised in the genus, *E. (Aneurhina) mutica* and *E. (Ceratorhinella) preissi.* The former has been assigned here to a new monotypic subgenus. ALLARD (1985) had placed *mutica* in his group 1 of the *Coelorrhina*, together with *aurata* and *selene* ("*Le premier groupe comprend trois espèces centro-occidentales. Les tubercules basaux sont aplatis, triangulaires ou absents. Tibias verts. Apex des paramères élargi, subtriangulaire.*"). *E. (Aneurhina) mutica* is here placed in a separate subgenus largely on account of the completely unarmed clypeal armature and the absence of a dense brush of setae on the anterior margin of the profemur in the male, which are unique features among the *Eudicella* (the dense distal brush of setae on the profemur is here considered an important symplesiomorphy). The structure of the aedeagus is most similar to that of *E. (Coelorrhinella) selene*, which may suggest phylogenetic proximity of *Aneurhina* to that subgenus.

Whereas *E.* (*Ceratorhinella*) *preissi* shows high genetic divergence from *cupreosuturalis* (APWD of 19.7%) and some remarkable morphological characters (deep and sparse punctures on the pronotum and markedly setose pro- and metasternum in both sexes), it agrees well with the other taxa in the subgenus in several other respects, namely the structure of the aedeagus and the general clypeal armature (ALLARD, 1985; HOLM, 1993). Geographic isolation of *E.* (*Ceratorhinella*) *preissi* – a montane species found in the Iringa region of Tanzania – may have contributed to the high degree of genetic divergence and the presence of apomorphic traits (e.g., the deep pronotal punctuation) that, nevertheless, do not seem to support the assignment of *preissi* to a new subgenus.

It may be argued that at least some of the *Eudicella* subgenera identified here would merit full generic status. Indeed, taking into consideration the genetic divergences, the clypeal and aedeagal structure, along with other characters (armature of the protibia, setation of profemur,

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punctuation of the pronotum, etc.), discrete and homogenous species-groups can be identified. However, the degree of separation does not seem to exceed that observed in the sister genus *Mecynorhina* Hope, which is currently split into five subgenera (DE PALMA & FRANTZ, 2010). In our view, *Eudicella s. lat.* represents a Cetoniine genus undergoing evolutionary radiation into distinct genera, and within certain speciose subgenera such as *Eudicella s. str.* and *E. (Coelorrhina*), even the boundaries at the species level are, in fact, difficult to resolve (DE PALMA, 2009; SEIDEL, 2016).

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