

Afromontane *Coelocorynus* (Coleoptera: Scarabaeidae: Cetoniinae): Larval descriptions, biological notes and phylogenetic placement

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Key words. Coleoptera, Scarabaeoidea, Cetoniinae, Valgini, Trichiini, Cryptodontina, *Coelocorynus*, larvae, morphology, phylogeny, Africa, Cameroon, Mt. Oku

Abstract. This paper reports the collecting of adult beetles and third-instar larvae of *Coelocorynus desfontainei* Antoine, 1999 in Cameroon and provides new data on the biology of this high-altitude Afromontane genus. It also presents the first diagnosis of this genus based on larval characters and examination of its systematic position in a phylogenetic context using 78 parsimony informative larval and adult characters. Based on the results of our analysis we (1) support the hypothesis that the tribe Trichiini is paraphyletic with respect to both Valgini and the rest of the Cetoniinae, and (2) propose that the Trichiini subtribe Cryptodontina, represented by *Coelocorynus*, is a sister group of the Valgini: Valgina, represented by *Valgus*. The larvae-only analyses were about twofold better than the adults-only analyses in providing a phylogenetic resolution consistent with the larvae + adults analyses. Only one of the ten clades was consistently supported by the analyses of both the larval and adult datasets, while the remaining nine were invariably strongly supported by one but not the other analysis, thus highlighting the importance of employing different data sources.

INTRODUCTION

The Afromontane beetle genus *Coelocorynus* (Figs 1–4) includes 18 named species, 15 of which were described in the last 10 years (Antoine 1999, 2003). The few known *Coelocorynus* specimens were predominantly recorded from altitudes between 2000 m and 3000 m, with the lowest being 950 m and the highest 3900 m. All but one *Coelocorynus* species are known from the East-African highlands located within the triangle formed by southeast Ethiopia, central Tanzania and the easternmost part of the Democratic Republic of Congo (DRC). This genus is reported from the Bale Mountains (Ethiopia), Mt. Kenya and the Aberdare Mountains (Kenya), Mt. Elgon (Kenya/Uganda), the Usambara and Uluguru Mountains (Tanzania), and the Ruwenzori Mountains (along with some other closely adjacent ranges in the west) in Uganda/DRC. This predominantly East-African distributional pattern is disrupted by the Cameroonian species *C. desfontainei* Antoine, 1999, previously known from two males and two females from the Northwest province, including Bafut and Mt. Oku.

Phylogenetic affinities of *Coelocorynus* were uncertain. When proposed, the genus was grouped with the monotypic *Cryptodonte* Burmeister, 1847 and *Pantodinus* Burmeister, 1847 as sub-groups of Dynastinae (cited after Krikken, 1984: 39; the status of Scarabaeoidea family-group names conventionally used throughout this paper are those of Smith, 2006) to form the subtribe Cryptodontina. Kolbe (1909) associated it with *Platygenia* Macleay, 1819 and *Osmoderma* Lepeletier & Serville, 1825, thus transferring it into the poorly defined Trichiini. Krikken

(1984) revised the whole of the Cetoniinae (“Cetoniidae” in his sense) and transferred the genus *Pantodinus* into Incaina, another Trichiini subtribe. Recently, Micó et al. (2008) made the most comprehensive phylogenetic treatment of Cetoniinae so far, employing both larval and adult characters, and concluded that the tribe Trichiini (sensu Smith, 2006) consists of at least three separate lineages: (A) subtribe Trichiina, a sister group to the Valgini; (B) subtribe Osmodermatina, and (C) subtribe Incaina branching off subsequently from Cetoniinae s. str. (Cetoniinae without Trichiini and Valgini). Their analyses, however, did not include representatives of three subtribes critical for testing the basal branching events within the Cetoniinae, namely Microvalgina (Valgini), Platygeniina and Cryptodontina (both Trichiini).

This paper reports the discovery of a *Coelocorynus* breeding site in Cameroon and has six objectives: (1) provide a detailed description and illustrations of *Coelocorynus* larvae; (2) report observations on the biology of this poorly known genus; (3) hypothesise about the phylogenetic position of *Coelocorynus*; (4) test more rigorously the overall monophyly of Cetoniinae hypothesized by Micó et al. (2008); (5) evaluate the relative contribution of larval versus adult characters in resolving the phylogeny of our ingroup, and (6) indicate the most promising directions for future phylogenetic research on the Cetoniinae. Overall, we hope to add to our knowledge of pleurostict Scarabaeidae, a mega-diverse radiation of plant-eating beetles, which includes many agriculture and forestry pests such as “chafers” and “June beetles”, and

TABLE 1. Results of the 12 phylogenetic analyses (columns 1–12). “Dataset” row indicates the three datasets used in the analyses (larvae, adults and combined; characters 1–43, 44–81 and 1–81, respectively). “Ordered/unordered” row indicates whether some multistate characters (7, 11, 13, 16, 25, 30, 37, 52, 54, 67, 77) were ordered. “Successive weighting” row indicates whether successive approximations were used for character weighting. Next three rows indicate tree length, consistency (CI) and retention (RI) indices, and the number of the shortest (= most parsimonious) trees obtained. Taxonomic abbreviations used in the left column are: Val – Valgina, Cryp – Cryptodontina, Trich – Trichiina, Os – Osmodermatina, In – Incaina, Cr – *Cremastocheilus*, Cet(–) – Cetoniinae s. str., consisting of Goliathini + Gymnetini + Cetoniini + Schizorhinini + Diplognathini + Cremastocheilini (i.e., without Valgini and Trichiini). Cell values: Clade present (+) or absent (–) on the strict consensus tree followed by bootstrap value, if applicable. Cell color: Black, grey and white for highly supported, moderately supported and unsupported branches, respectively. Column SV/RSV and row RV/RRV indicate Support Value/Relative Support Value for individual clades and Resolution Value/Relative Resolution Value for individual analyses, respectively (for their meaning and calculation see Material and methods).

Analysis ##	SV/RSV	1	2	3	4	5	6	7	8	9	10	11	12
Dataset		larvae	larvae	larvae	larvae	adults	adults	adults	adults	combin.	combin.	combin.	combin.
Ordered/unord.		unord.	unord.	ordered	ordered	unord.	unord.	ordered	ordered	unord.	unord.	ordered	ordered
Successive weighting		no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
Tree length		175	342	177	330	239	180	245	191	450	490	460	484
CI/RI		31/76	59/90	31/78	60/93	20/68	58/93	19/69	55/93	22/69	52/89	22/70	52/90
# of shortest trees		>1484	>1574	>1484	>1581	>1581	>1582	>1582	814	>1164	>1579	1	>1579
Single fully and most consistently resolved topology													
Valgina	24/100%	+98	+99	+99	+99	+96	+96	+96	+94	+99	+100	+99	+99
Trichiina	18/75%	+85	+85	+85	+85	–/na	–/58	–/50	+/50	+86	+88	+66	+86
Incaina	16/67%	–/na	–/na	–/na	–/na	+74	+74	+75	+66	+82	+86	+71	+88
Val+Cryp	12/50%	+66	+67	+67	+69	–/na	–/na	–/na	–/na	–/50	+61	–/na	+61
Val+Cryp+Trich	14/58%	+63	+76	+76	+78	–/na	–/na	–/na	–/na	+63	+70	–/na	+67
Cet(–) except Cr	17/71%	–/na	–/na	–/57	–/na	+71	+70	+75	+60	+81	+87	+66	+86
Cet(–)	7/29%	–/na	–/na	–/59	–/na	–/na	–/na	–/na	–/na	+74	–/60	+/50	+77
Cet(–)+Os	14/58%	+75	+76	–/70	–/55	–/na	–/na	–/na	–/na	+83	+86	+64	+84
Cet(–)+Os+In	6/25%	–/na	–/na	–/na	–/na	–/na	–/na	–/na	–/na	+70	+74	–/50	+73
CETONIINAE	16/67%	+70	+70	+72	+74	–/na	–/na	–/na	–/na	+82	+86	+75	+89
RV/RRV		12/60%	12/60%	13/65%	11/55%	6/30%	7/35%	6/30%	7/35%	18/90%	19/95%	13/65%	20/100%
Alternative grouping													
Val+Cr+Os	8/33%	–/na	–/na	–/na	–/na	+65	+64	+67	+53	–/na	–/na	–/na	–/na

invasive alien species such as the Japanese beetle, *Popillia japonica* (Newman, 1841).

MATERIAL AND METHODS

Sources, identification and handling of *Coelocorynus* larvae

The field-collected Cameroonian larvae were identified as belonging to *Coelocorynus* based on the following considerations: (1) they were found together with teneral adults of this species in the same log, which was not co-inhabited by any other Scarabaeoidea larvae or adults, and (2) they agree morphologically with the larvae of *C. opacicauda* Arrow, 1926 illustrated in Grebennikov & Scholtz (2004) and Scholtz & Grebennikov (2005), as well as with the larvae identified as such in the National History Museum, London (NHML; see below).

Besides *C. desfontainei*, one author (PŠ) found in the NHML collection one vial containing one third-instar and four second-instar Cetoniinae larvae labelled “*Coelocorynus opacicauda* (Arrow) Aberdare Mts, (Gedye)” and subsequently an adult of *C. opacicauda* labelled “W. Aberdares 10–11,000 ft, Nov 1934 A.J.F. Gedye”. Comparison of the larvae with those collected in Cameroon revealed an overall similarity and presumed congenerity.

Morphological observations and measurements were carried out using an Olympus SZX9 stereomicroscope and Olympus BX 40 light microscope, both equipped with Olympus Camedia 5060 digital cameras. Mouthparts were dissected and mounted on slides in Liquide de Swan. Drawings were made of photographs. Larval habitus images were produced on a flatbed HP-Scanjet 5530 scanner. The Helicon Focus programme was used

to combine several photographs of adults into a single deep-focus image. The brightness and/or contrast of all pictures have been slightly enhanced in Adobe Photoshop.

Material is deposited in the Canadian National Collection of Insects, Arachnids and Nematodes (CNCI), the B.D. Gill collection (*C. desfontainei*), and in the NHML (*C. opacicauda*). The morphological terminology used in the present study is adopted from Böving (1936), Ritcher (1966), Lawrence (1991) and Micó et al. (2001).

Morphological datasets and analytical strategy

Eighty one morphological characters were selected for the analysis; the majority were recently explained and illustrated by Micó et al. (2008). New characters were added and some were re-defined; full character descriptions, state definitions and optimization statistics are given in the Appendix. The combined larval and adult morphological matrix included 60 terminals and 81 characters (Table 2). The tree was rooted using a single representative of the family Trogidae. Characters 1–43 are of larval morphology and 44–81 of adult morphology. No polymorphic characters are present in the matrix. Three larval characters (5, 27, 34) are parsimony uninformative and were not included in the analysis. Eleven multi-state characters (7, 11, 13, 16, 25, 30, 37, 52, 54, 67, 77) were analysed as being either ordered (analyses 3, 4, 7, 8, 11, 12; Table 1) or unordered (analyses 1, 2, 5, 6, 9, 10; Table 1); all other multi-state characters were treated as unordered in all analyses. We analysed three separate morphological datasets: Larval (characters 1–43), adult (characters 44–81) and combined (characters 1–81), using for each four possible combinations of ordering and successive weighting

TABLE 2. Matrix of 60 taxa and 81 larval and adult characters used in phylogenetic analysis of Cetoniinae.

Ordered (O) / Uninformative (U)		1	111111112	222222223	333333334	444444445	555555556	666666667	777777778	8
		1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
		U O	O O O	O U O	U O	O O	O O	O	O	
<i>Trox cadaverinus</i>	(Trogidae)	100000--1	0100000?00	0000011000	1000-10100	0110000000	?002100000	0000000200	0000000000	0
<i>Valgus californicus</i>	(Cet. Valgini)	1201101001	1011001110	1000021012	0111010100	0010000110	1000110110	0001110200	0001001101	1
<i>Valgus canaliculatus</i>	(Cet. Valgini)	1201101001	1011001110	1000021012	0111010100	0011000110	1000110110	0001110200	0001001101	1
<i>Valgus hemipterus</i>	(Cet. Valgini)	1201101001	1001001110	1000020012	0111010100	0010000110	1000110110	0000000200	0001001101	2
<i>Coelocorynus desfontainei</i>	(Cet. Trichiini)	0000011010	1001200110	?000011112	0101110100	0012220110	0111010000	000000?110	0000000100	0
<i>Archedinus relictus</i>	(Cet. Trichiini)	0010102211	1001201110	1100101012	1101110100	0011220110	1200100100	1001000110	0000000000	0
<i>Inca clathrata</i>	(Cet. Trichiini)	0100102212	1001000110	1100101112	1111210100	0010221110	0210101000	1001110010	0001001000	2
<i>Osmoderma eremita</i>	(Cet. Trichiini)	1100101102	0001201110	1100101111	1101110110	0011100110	0000100100	0001000100	0001001000	0
<i>Gnorimus variabilis</i>	(Cet. Trichiini)	0010102001	1001100111	1000011111	0101110101	0010010110	1010000100	0000100101	0000000100	2
<i>Iridosoma acahuizotlensis</i>	(Cet. Trichiini)	0000102101	1001101111	1000011111	0111110100	0010010110	0010011100	0100101010	0000000010	2
<i>Trichius fasciatus</i>	(Cet. Trichiini)	0000102001	1001100111	1100011111	0001110100	0010000110	0010010100	0000000100	0000000100	1
<i>Ammaurodes passerinii</i>	(Cet. Cetoniini)	?100101212	0001201110	1100101111	1001110100	0012021110	0211010101	0101101000	1101010000	2
<i>Anisorrhina flavomaculata</i>	(Cet. Cetoniini)	1110101212	0001201110	1100101111	1001110101	0012120110	0211010101	0100110100	1110100000	0
<i>Cheirolasia burkei</i>	(Cet. Cetoniini)	1110101212	0001201110	1100101111	1001112010	0012122110	1210101001	0100002000	1101010000	2
<i>Chlorocalla africana</i>	(Cet. Cetoniini)	1110101212	0001200110	1100101111	1001112011	0012121110	0101010101	0100110100	1101010000	0
<i>Dicronocephalus wallichi</i>	(Cet. Cetoniini)	?110101212	0001201110	1100101111	1001110110	0011100111	0210101000	0001002000	1011000000	2
<i>Eudicella euthalia</i>	(Cet. Cetoniini)	1110101212	0001200110	1100101111	1001112011	0012211110	0211010101	0110112100	1011010000	0
<i>Fornasinius fornasini</i>	(Cet. Cetoniini)	1110101212	0001201110	1100101111	1001210010	0011120110	1210101001	0000100010	1110110000	2
<i>Goliathus orientalis</i>	(Cet. Cetoniini)	1100101212	0001201110	1100101111	1001210001	0011120110	1210101001	0101111001	1011011000	2
<i>Mecynorrhina polyphemus</i>	(Cet. Cetoniini)	1110101212	0001201110	1100101111	1101212010	0011021110	0211010101	0011100100	1101010000	2
<i>Megalorrhina harrisi</i>	(Cet. Cetoniini)	?110101212	0001201110	1100101111	1001111010	0011021110	0211010101	0011111000	1101011000	2
<i>Neoscelis dohrni</i>	(Cet. Cetoniini)	?110101112	0001201110	1100101111	1101113011	0011220110	1211010101	0100112000	1011010000	0
<i>Stephanorrhina princeps</i>	(Cet. Cetoniini)	1110101202	0001200110	1100101111	1001112011	0010112110	1211010101	0100000110	1110100000	0
<i>Aethlessa floralis</i>	(Cet. Cetoniini)	1101101102	0001201110	1100101111	1001113111	0012000110	0010001010	0000000110	0111010000	0
<i>Cetonia carthami</i>	(Cet. Cetoniini)	1111101102	0001201110	1100101111	1001113111	0010000110	0101010101	0000000110	1110101000	0
<i>Euphoria lurida</i>	(Cet. Cetoniini)	1111101102	0001201110	1100101111	1001113111	0010000110	0010001010	0000000110	1110101000	1
<i>Netocia morio</i>	(Cet. Cetoniini)	1101101102	0001201110	1100101111	1001113111	0010000110	0101010101	0000000110	1110101000	0
<i>Oxythrea funesta</i>	(Cet. Cetoniini)	1111101102	0001201110	1100101111	1001113111	0010000110	0010001010	0000000110	1110101000	1
<i>Pachnoda sinuata</i>	(Cet. Cetoniini)	1111101102	0001201110	1100101111	1001113111	0010000110	0101010101	0000000110	1110101000	2
<i>Potosia cuprea</i>	(Cet. Cetoniini)	1111101102	0001201110	1100101111	1001113111	0010000110	0101010101	0000000110	1110101000	0
<i>Stalagmosoma albella</i>	(Cet. Cetoniini)	1101101102	0001200110	1100101111	1001113111	0010000110	1011011101	0000000110	0111010000	0
<i>Tropinota squalida</i>	(Cet. Cetoniini)	1101101102	0001201110	1100101111	1001113111	0010010110	0011010101	0000000000	1110101000	1
<i>Argyripa lansbergei</i>	(Cet. Cetoniini)	?101101212	0001201110	1100101111	1111113111	0011100110	1112011010	0100110110	1111110000	2
<i>Cotinis mutabilis</i>	(Cet. Cetoniini)	1110101212	0001201110	1100101011	1001113111	0012220110	0012010101	0000000110	1111110000	2
<i>Gymnetis flavomarginata</i>	(Cet. Cetoniini)	1111101102	0001201110	1100101011	1001113111	0010000110	0012011101	0000000110	1111110000	2
<i>Hologymnetis cinerea</i>	(Cet. Cetoniini)	1111101102	0001201110	1100101111	1001113111	0010000110	0012010101	0000000110	1111110000	2
<i>Hoplopyga singularis</i>	(Cet. Cetoniini)	1111101102	0001200110	1100111111	1101113111	0010000110	0012011101	?000010110	1111110000	2
<i>Euchroea flavoguttata</i>	(Cet. Cetoniini)	?110101112	0001201110	1100101112	1001113110	0010000110	0010001010	0000000110	1110101000	2
<i>Thaumastopeus pugnator</i>	(Cet. Cetoniini)	?110102212	0001200110	1100101111	1101101110	0010010110	0012011101	0000100100	1101100000	0
<i>Trichaulax macleayi</i>	(Cet. Cetoniini)	1110101212	0001200110	1100101111	1001110110	0010001110	0101010101	0010010100	1110101000	1
<i>Campsira cognata</i>	(Cet. Cetoniini)	?100101212	0001201110	1100101111	1001110110	0010010111	1002111101	0000000210	1110110010	0
<i>Cremastocheilus wheeleri</i>	(Cet. Cetoniini)	?1011011?2	0001201110	1100101111	?11110?10	0010002111	0000100100	0001000100	0011010100	0
<i>Conradtia principalis</i>	(Cet. Cetoniini)	?110101212	0001201110	1100101011	1001112111	0012221110	0111201010	0000000111	1110010000	2
<i>Diplognatha gagates</i>	(Cet. Cetoniini)	?110101212	0001201110	1100101011	1001111110	0010000110	0011010100	0001000010	1110100000	0
<i>Cyclocephala alexei</i>	(Dynastinae)	0011100100	1111001010	110?001110	1001100100	1010000100	1000000000	0000002001	0000000100	1
<i>Oryctes nasicornis</i>	(Dynastinae)	0010100210	1111001010	1100001110	1101100100	1002010100	0200100000	0000000001	0000000101	0
<i>Anomala cincta</i>	(Rutelinae)	0001100000	1101011010	1110011111	1001100101	1010000000	1000000000	0000010000	0000000100	0
<i>Pelidnota virescens</i>	(Rutelinae)	0010100210	1011201010	1100011111	1101100100	1010000100	1000000000	0000001201	1000000100	0
<i>Phyllophaga obsoleta</i>	(Melolonthinae)	0101110000	1101011010	1110011000	1001100101	0110100000	1000000000	0000000000	0000000100	0
<i>Triodontella castillana</i>	(Melolonthinae)	0111110001	1101011010	111?011000	1001000101	0110000100	0000000100	0000000100	0000000000	1
<i>Xylotrupes gideon</i>	(Dynastinae)	1110100212	0101001010	1100201110	1001100?00	1012010100	0200200000	0000000100	0000000100	0
<i>Dynastes hercules</i>	(Dynastinae)	1110100212	0101001010	1100101110	1001100100	1002010100	0200200000	000?001001	0000000100	0
<i>Phileurus sp.</i>	(Dynastinae)	0100100210	1101001010	1100101110	1001100100	1012221110	0000100000	0000000011	0000000101	0
<i>Pentodon idiota</i>	(Dynastinae)	0101100000	1101111010	1100000110	1001100100	10001001?0	0000000000	0000000010	0000000100	0
<i>Phyllognathus excavatus</i>	(Dynastinae)	1100100210	1101001010	1100011110	1001100100	10021001?1	0210111000	000000?101	0000000100	0
<i>Amphimallon solstitialis</i>	(Melolonthinae)	0101110001	1101211010	1110111000	1001100101	1110101000	1000000000	0100011100	0000000101	1
<i>Anoxia orientalis</i>	(Melolonthinae)	0101110001	1101221010	1110011000	1001100100	1010101000	1000000000	0100111100	0000000100	2
<i>Chaetopteroplia segetum</i>	(Rutelinae)	0001100000	1101011010	1100111111	1001100100	1000100000	1000000001	000010020?0	0000000100	1
<i>Propomacrus bimacronatus</i>	(Euchirinae)	1101100322	2011201110	0110111000	1101200100	0110100000	1000000000	0000001110	0000000100	0
<i>Aphodius rufipes</i>	(Aphodiinae)	111120-002	0010000100	0100011000	1001100101	1010001100	1010000000	0000000010	0000000000	0

(Farris, 1969) parameters (Table 1). In total, 12 separate analyses were completed and are summarized in Table 1. Hennig86 (Farris, 1988) searched for the shortest (= most parsimonious) trees (heuristic search; commands “mh*” and “bb*” and then performed successive approximations (Farris, 1969; executed by a string of commands “xs w”, “mh*” and “bb*” repeated in cycles until the tree statistics stabilised). Branch support was assessed using Nona 2.0 (Goloboff, 1999) through bootstrapping 1000 randomly generated trees. Winclada (Nixon, 2002) was used as a shell program to communicate with Nona and to visualise the trees.

Relative Support Value (RSV) and Relative Resolution Value (RRV)

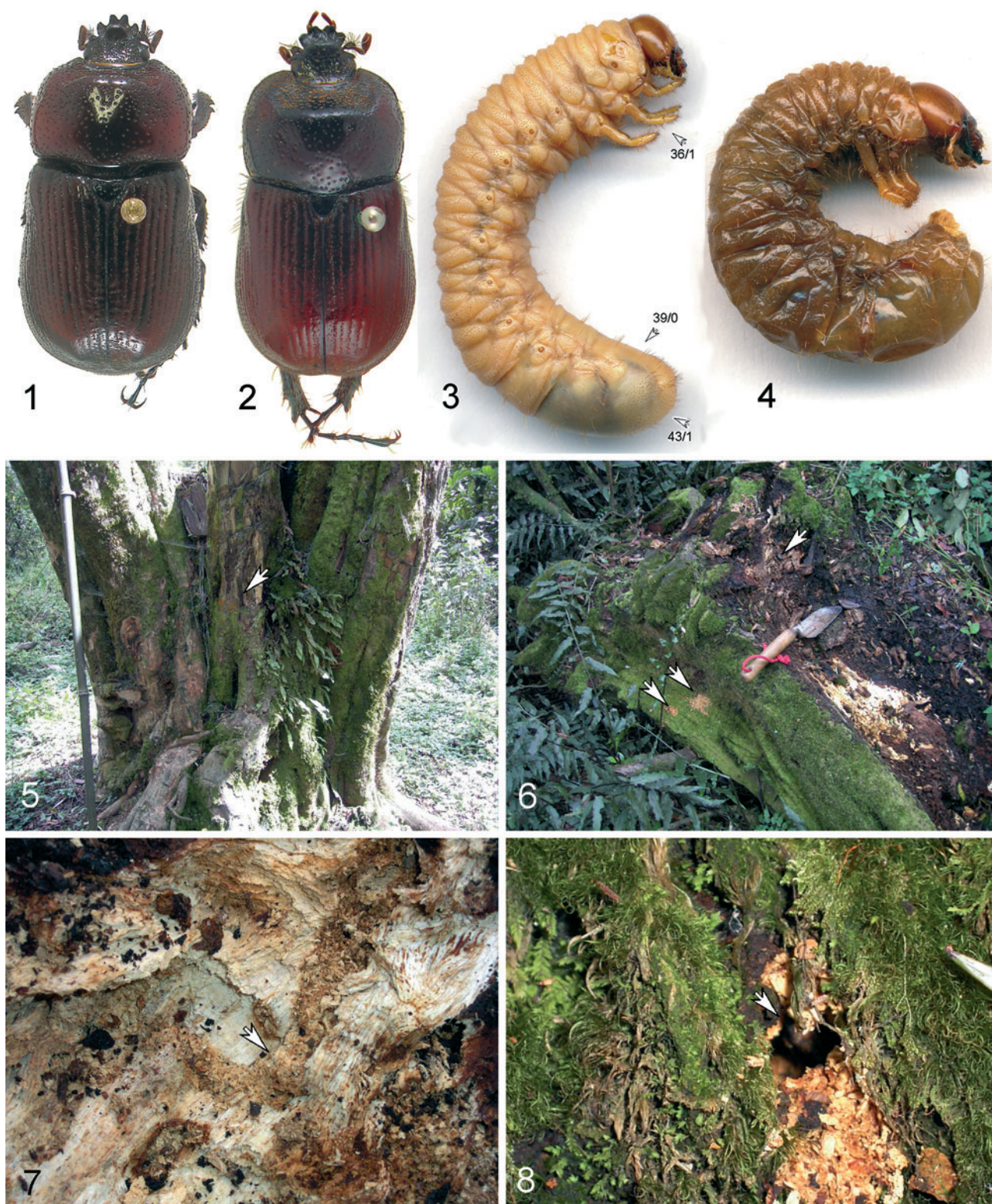
To make an unambiguous judgement on the strength of support for each of the 10 clades highlighted in Table 1 and to compare the capacity of each of the 12 morphological analyses to consistently resolve these clades, we used the recently introduced statistical measures “Relative Support Value” (RSV) and “Relative Resolution Value” (RRV), respectively (Grebennikov & Newton, 2009). They were calculated as a ratio of obtained Support Value (SV) for clades and Resolution Values (RV) for analyses to their possible absolute maxima (see below), respectively. Obtained SV and RV were calculated as sum of horizontal (SV) or vertical (RV) individual cell scores varying from 0 (clade unsupported, i.e., absent on the strict consensus tree and bootstrap <50%; white cell in Table 1) through 1 (clade moder-

ately supported, i.e., present on the strict consensus tree and bootstrap <50% OR absent on strict consensus tree, but bootstrap equal or >50%; grey cell in Table 1) to 2 (clade strongly supported, i.e. present on the strict consensus tree and bootstrap equal or >50%; black cell in Table 1). Maximum possible values for SV and RV (Table 1) for 12 analyses focusing on 10 clades, were 24 and 20, respectively. Maximum possible RSV of 100%, as observed for Valgina (Table 1), indicates that this clade was strongly supported by all 12 analyses, while the lowest RSV of 25%, as observed for the clade of Cetoniina s. str. + Osmodermatinae + Incaina (Table 1), indicates that it was recovered only a few times. Maximum possible RRV of 100%, as observed for analysis 12 (Table 1), indicates that this analysis was capable of resolving all 10 clades and each clade was strongly supported, while the lowest observed RRV of 30%, as recorded for analyses 5 and 7 (Table 1), indicates that they were only partly consistent with the most supported and fully resolved topology (Fig. 25).

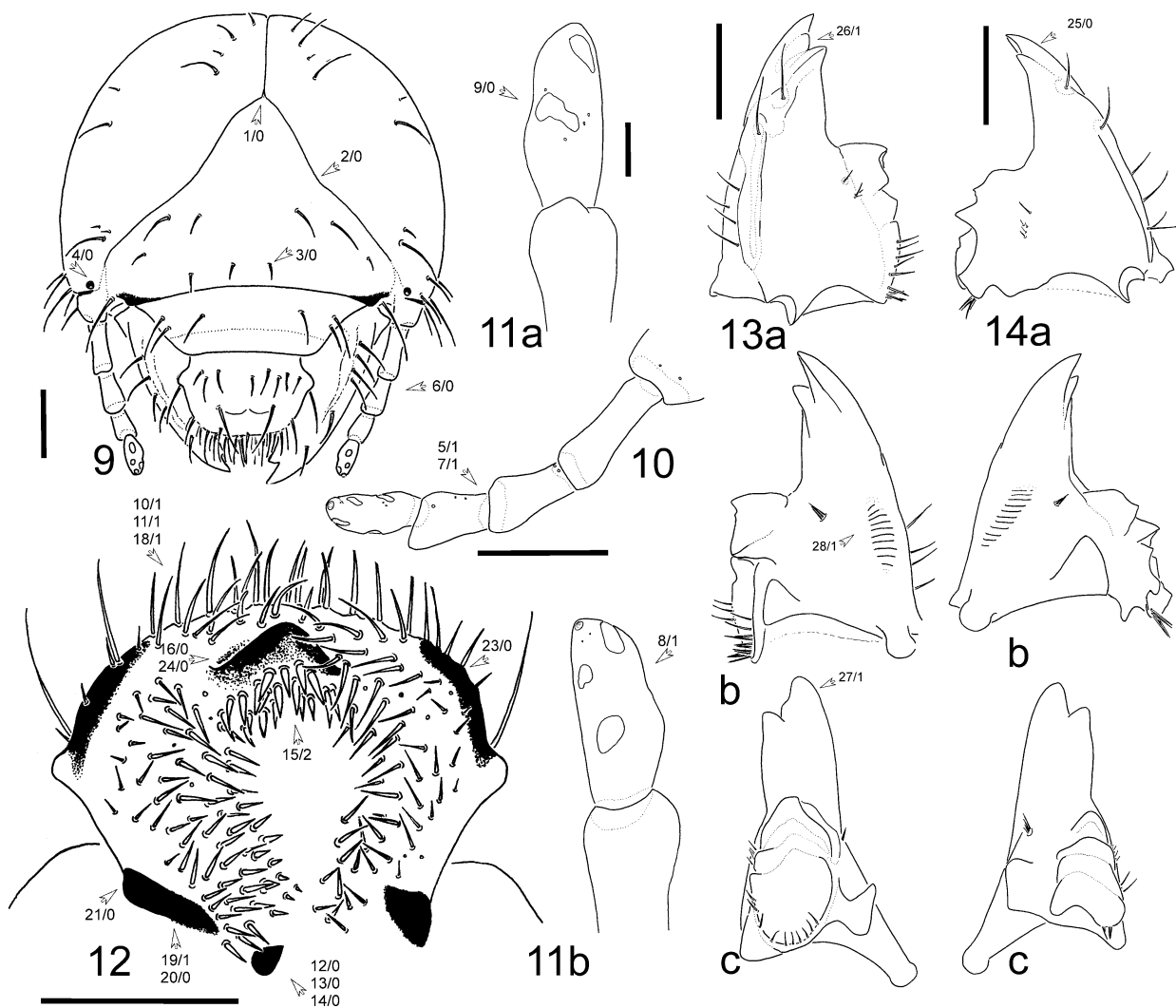
RESULTS

Generic description of third-instar *Coelocorynus* larvae

A typical C-shaped grub (Figs 3, 4); with only a few long setae; abdomen 10-segmented, segments subequal in



Figs 1–8. Habitus of *Coelocorynus* adults (1, 2) and larvae (3, 4) and the habitat of *Coelocorynus* in the forest at 2800 m on Mt. Oku above Elak village, Northwest Province, Cameroon (5–8). 1, 3 – *C. desfontainei*; 2, 4 – *C. opacicauda*; 5 – standing tree with arrow pointing to location where an adult male was removed from a 1cm diameter gallery; 6 – partially rotten trunk on ground with larvae and newly emerged adults (upper arrow pointing to an adult beetle; two lower arrows indicating frass below two adult exit holes); 7 – feeding burrows of larvae in rotten wood backfilled with frass (indicated by arrow); 8 – close-up of adult exit hole, illustrated in Fig. 6 (indicated by arrow), with frass below. Arrows with small numbers in Fig. 3 point to the character states described in Appendix.



Figs 9–14. *Coelocorynus desfontainei*, third-instar larva. 9 – head capsule; 10 – right antenna, lateral view; 11 – ultimate antennomere of right antenna, ventral view (a) and dorsal view (b); 12 – epipharynx; 13 – left mandible, dorsal (a), ventral (b) and medial (c) views; 14 – right mandible, dorsal (a), ventral (b) and medial (c) views. Scale bars: 9, 10, 12–14 – 1 mm; 11a,b – 0.2 mm. Arrows with small numbers point to the character states described in Appendix.

size except for slightly prolonged segments IX and X; body length 46–58 mm.

Head as in Figs 9 and 21; maximum width 5.6–5.8 mm; head surface with fine microsculpture, yellowish brown; antennifer, postclypeus and labrum brown; chaetotaxy as figured; frontal sutures evenly sinuate to lyriform; dorsal endocarina not protruding further than anterior part of epicranial suture; clypeus trapezoidal, anteclypeus membranous, postclypeus heavily sclerotized with 2 exterior and 1 anterior setae on each side; frontoclypeal suture distinct along entire length; single pigmented or unpigmented stemma present on each side of head.

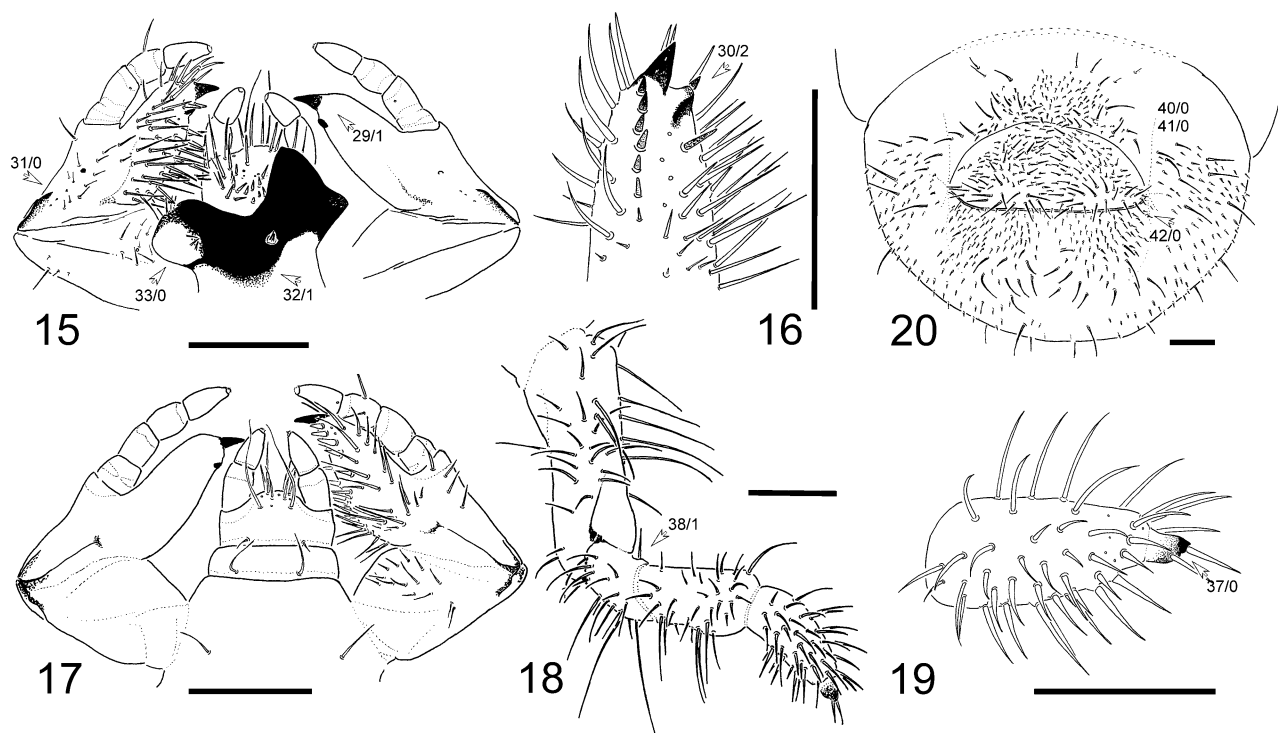
Antennae (Figs 10–11, 23–24) with 4 subequal antennomeres devoid of setae; antennomere I slightly longer than others; antennomere III with ventral and apically protruding portion bearing sensory area on its dorsal surface; antennomere IV with 2 ventral and 3 dorsal sensory spots and a small apical field with a few minute sensilla.

Labrum nearly symmetrical; anterior margin convex, with numerous setae; middle of lateral margin with dis-

tinctly projecting tubercle; dorsal surface with 2 transverse rows of setae; posterior row with 8–13 setae and 2 long setae beneath lateral tubercle; anterior row with 1 paramedian and 1 lateral seta on each side.

Epipharynx (Figs 12, 22) with well sclerotized and prominent haptomeral process bearing apical field of pore-like sensilla and 3–4 lines of stout, spine-like setae posteriorly; acroparia with about 30 long setae; clithra and epizygum absent; lateral margin of epipharynx with strong medial tubercle and heavily sclerotised anteriorly; acanthoparia with 4–6 irregularly located setae; setae on chaetoparia located in 5–6 longitudinal rows, setae in medial rows stout, almost spine-like; plegmata and proplegmata absent; pedium moderately broad; dextortorma bar-like, longer than laeotorma, right pternotorma absent; laeotorma triangular with posterior pternotorma; haptolachus with sensory cone and 4–5 pores, sclerotised plate absent; crepis faintly sclerotised, indistinct.

Mandibles (Figs 13–14) prominent; right with 2, left with 3 scissorial teeth; scrobis with 3–5 setae; dorsal



Figs 15–20. *Coelocorynus desfontainei*, third-instar larva. 15 – labium and maxillae, dorsal view; 16 – apex of left maxilla, medio-ventral view; 17 – labium and maxillae, ventral view; 18 – right metathoracic leg; 19 – claw of right metathoracic leg; 20 – last abdominal segment, ventral view. Scale bars: 1mm. Arrows with small numbers point at character states as described in Appendix.

carina present; dorso- and ventro-molar setae present, ventro-molar setae aggregated to form a rim; ventral stridulatory area present on both mandibles, with about 10–15 transverse ridges and with apical asperities less distinct; molar lobes of both mandibles with sharp projections; posterior margin of calyx in medial aspect concave on right mandible, flattened and convex on left; right and left mandible with 10 and 12 setae on each brustia, respectively.

Maxilla (Figs 15–17) with several hair-like setae on cardo and labacobarria dorsally; stipes with 10–11 faint setae dorsally; maxillary stridulatory area much reduced posteriorly, with 2–6 small or minute recurved spines and one conical process dorsally on middle of basal part of stipes; galea and lacinia (Fig. 16) fused forming mala; galeo-lacinial suture absent; galeal uncus falcate; lacinial unci reduced with 2 apical stout setae and preapical sclerotized tubercle; mala with numerous long stout setae dorsally and with a longitudinal row of 4–7 spine-like setae and about 20 hair-like setae ventrally; maxillary palpus with 4 palpomeres and segment-like palpifer.

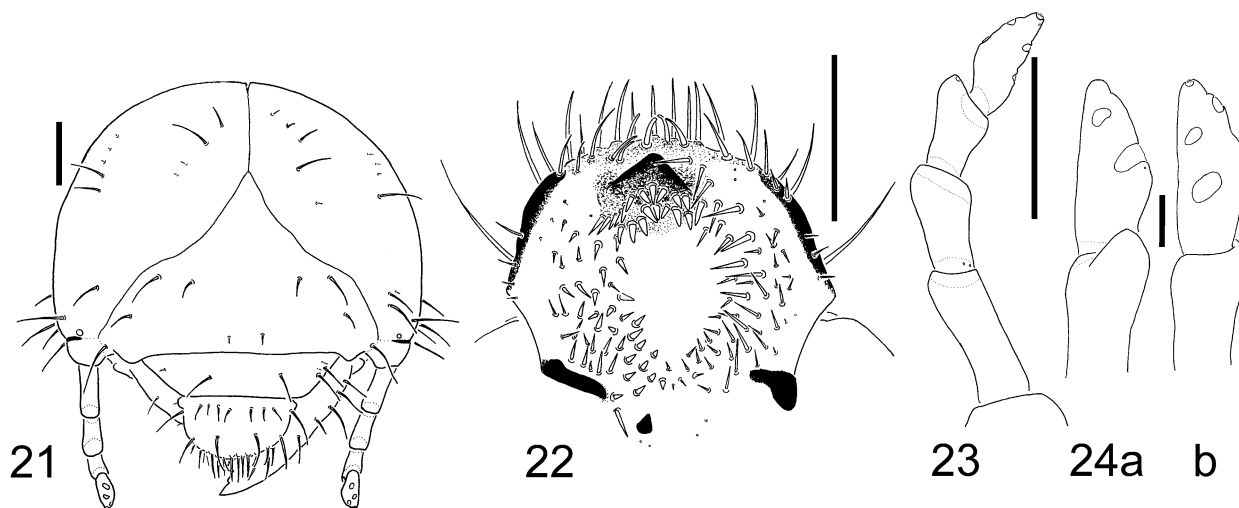
Hypopharynx with hypopharyngeal sclerome (Fig. 15) asymmetrical, with strong protruding truncate process and a few seta-like tegumentary expansions medio-posterior to the process; left lateral lobe membranous, with 3–4 seta-like tegumentary expansions; glossa with about 10 short stout setae in medio-proximal area and about 20 long setae and 10 pores on distal half; labial palpi two-jointed.

Thorax with all legs (Figs 18–19) subequal and with similar tarsal claws (Fig. 19); claws cylindrical, rounded at apex, with 2 apical setae and minute tip; prothoracic sclerite present; mesothoracic spiracle with C-shaped respiratory plate; distance between lobes of respiratory plate about half of, or equal to, maximum diameter of respiratory plate; metathoracic spiracles present, highly reduced and non-functional; each dorsal sub-lobe with 3–5 rows of short setae, posterior row with short and few long setae; venter with about 10 long setae on each segment.

Abdomen 10-segmented; segments IX and X separate, slightly longer than others and not distinctly thickened; chaetotaxy on abdominal segments I–VII as on thorax, chaetotaxy on segments VIII–IX much reduced; raster (Fig. 20) without clearly distinguishable septula, palida and hamate; anal slit transverse, dorsal anal lobe with numerous small spiny setae and few long setae in 2 rows; lower anal lip with numerous short and long setae; abdominal spiracles I and VIII largest, all others smaller and subequal in size.

Diagnostic characters of third-instar *Coelocorynus* larvae

Coelocorynus desfontainei Antoine, 1999 (Figs 3, 7, 9–20). Maximum width of head capsule 5.6 mm ($n = 1$); stemma on each side of head pigmented; apical half of ultimate antennomere in lateral view almost cylindrical, without protrusions; epipharynx with gymnoparia indistinct or absent, right chaetoparia with 65–71 and left with 51–53 setae; ventral stridulatory area on mandibles with 10–12 ridges; maxillary stridulatory area with 2–3 small



Figs 21–24. *Coelocorynus opacicauda*, third-instar larva. 21 – head capsule; 22 – epipharynx; 23 – right antenna, lateral view; 24 – right ultimate antennomere, ventral (a) and dorsal (b) views. Scale bars: 21–23 – 1 mm; 24 – 0.2 mm.

recurved spines posteriorly; greatest length of mesothoracic spiracles 0.625 mm and distance between lobes subequal to, or as long as, spiracular plate.

Coelocorynus opacicauda Arrow, 1926 (Figs 4, 21–24). Maximum width of head capsule 5.8 mm ($n = 1$); stemma on each side of head unpigmented; apical half of ultimate antennomere in lateral view more or less conical, with protrusion bearing apical sensory area; epipharynx with gymnoparia more or less developed, each chaetoparia with about 50 setae; ventral stridulatory area on mandible with 13–15 distinct ridges; maxillary stridulatory area with 5–6 recurved spines posteriorly; greatest length of mesothoracic spiracles 0.600 mm and distance between lobes subequal to half the length of spiracular plate.

Biology of *Coelocorynus*

Larvae of *C. desfontainei* were recorded by B.D. Gill in early May 2006 in standing and fallen dead wood at an altitude of around 2,800 m on Mt. Oku, Northwest Province, Cameroon. The first adult was collected inside dead wood of a large moss-covered standing tree (Fig. 5). A small hole on the outside of the trunk (roughly 1 cm diameter) had an accumulation of frass below the hole. The hole was excavated and a male beetle found. Several days later a partially rotten tree trunk lying on the ground nearby was observed with two holes and a telltale accumulation of granular frass (Fig. 6–8) on the moss and lichens below the holes. These holes were excavated and a single teneral female was found in the larger of the two galleries. The rest of the log was chopped open to expose one more adult, plus the remains of several adults that had died in their pupal chambers. Several larvae were found feeding in the soft rotten wood. The larval feeding galleries meandered through the rotten wood and were densely packed with frass (Fig. 7). All the adults collected had recently emerged as they had no obvious signs of wear on their legs or clypeus. The accumulation of granular frass below the holes indicated they had excavated their emergence tunnels but then remained in their

tunnels, at least during the day. No other scarab larvae or adults were found in rotting wood at this altitude, although dynastine and cetoniine larvae were found in rotting wood on Mt. Oku below 2000 m.

Another observation on *Coelocorynus* biology was made by VVG in October 2001 on the western slope of Mt. Kenya at the meteorological station on the Naro Moru Route (altitude 3050 m). Five live adults of *C. opacicauda* Arrow, 1926, along with some unhatched eggs, were excavated at about chest height from under the bark of a dead standing tree at the upper edge of the montane forest. The eggs were kept in a container and at least two first-instar larvae were obtained. These larvae were illustrated and scored for a phylogenetic analysis of Scarabaeoidea (Grebennikov & Scholtz, 2004; Scholtz & Grebennikov, 2005).

Results of the cladistic analysis

The results of 12 parsimony analyses of morphological data are summarized in Table 1. The most consistently resolved topology of the Cetoniinae basal branching events presented in Fig. 25 represents a majority rule consensus tree obtained from the strict consensus and bootstrap trees of each of 12 analyses. Relative support values are plotted against each clade in Fig. 25. To facilitate further discussion, all 12 analyses are grouped into three sets based on the source of data: larval (analyses 1–4), adult (analyses 5–8), and combined (analyses 9–12); the former two are also termed “partial”. For convenience, Cetoniinae s. str. is defined as Cetoniinae without Valgini and Trichiini.

DISCUSSION

Position of *Coelocorynus* and re-evaluation of Micó et al’s (2008) hypothesis on Cetoniinae phylogeny

We hypothesise that the genus *Coelocorynus* is a sister-group of the tribe Valgini, represented in our analysis by three *Valgus* species. Other branching events in the monophyletic Cetoniinae revealed by our analysis (Table

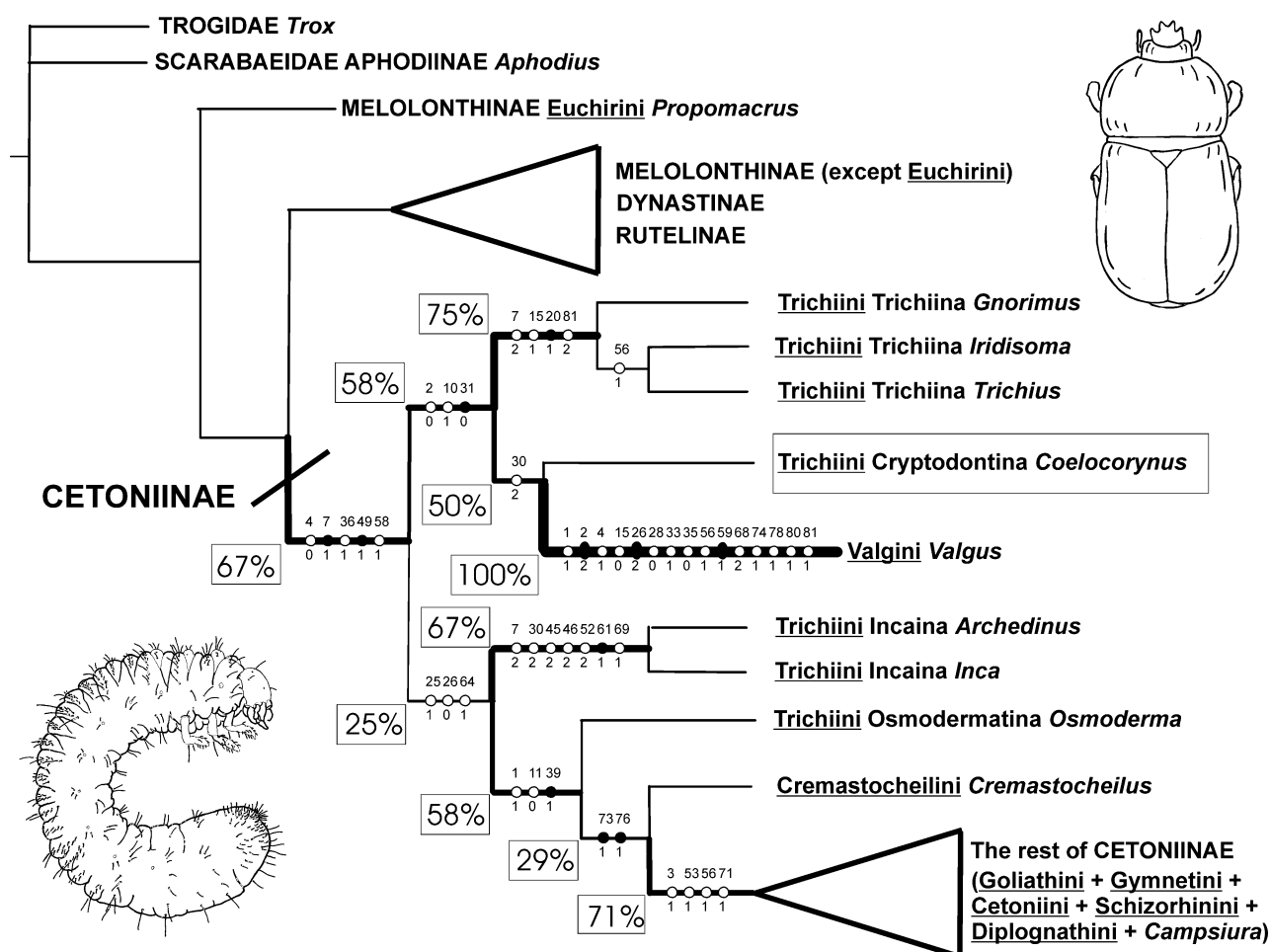


Fig. 25. Consensus phylogeny of the Cetoniinae based on combined analyses of data on larval and adult morphology with some characters ordered and all characters successively weighted (analysis 12). Unambiguously optimized characters are superimposed on internodes; character numbers are above circles; numbers of newly acquired apomorphic character states are below circles; black circles indicate unique evolutionary events; white circles indicate parallelisms or reversals. Boxed Relative Support Values (expressed in percent) are proportional to the width of internodes and reflect the overall relative confidence in the hypothesis that a clade is monophyletic. An adult and a larva of *Coelocorynus* are illustrated by outline drawings; position of this taxon is boxed on the cladogram.

1 and Fig. 25) fully agree with those proposed by Micó et al. (2008). This is not surprising, because our matrix relied heavily on their data for character selection and taxon sampling. We deviated from these authors however, in the analytical methodology and therefore, in the resulting degree of confidence associated with a monophyly hypothesis for each resolved clade. Instead of using bootstrap or Bremer values suitable to represent clade stability in an individual analysis, we calculated “Relative Support Value” (RSV; as explained in Material and methods), which represents clade stability in multiple analyses. Among the most parsimonious clades depicted in Fig. 25, the weakest were Cetoniinae s. str. and Cetoniinae s. str. + Osmodermatina + Incaina with RSV of 29% and 25%, respectively. The most strongly supported clade is Valgini with a RSV of 100%. This high support is considered a sampling artefact because this relatively diverse tribe has more than 30 genera and was represented in our analyses by three congeneric *Valgus* species. All remaining seven clades highlighted in our analyses have intermediate RSV ranging from 50% (Valgini + Crypto-

dontina) to 75% (monophyly of the three Trichiina genera).

Relative contribution of larval versus adult characters

Availability of larval and adult characters scored for the same set of terminals permits a comparison of the ability of individual partial datasets to resolve clades in a way consistent with those obtained from the combined dataset. The results indicate that, with the single exception of Valgini (or, rather, the genus *Valgus* represented in the analyses by three species), a clade consistently supported by one partial dataset becomes invariably and consistently rejected by the other. This phenomenon is illustrated by the shading of individual cells in Table 1, with black indicating strong support for a clade, and white indicating lack of support. Contrary to the topologies obtained from the combined and adult analyses (columns 9–12, 5–8, respectively), those based on larval characters (columns 1–4) were not able to determine whether two clades were monophyletic: Incaina and Cetoniinae s. str. without *Cremastocheilus*. Conversely, adult analyses (#5–8) were

plagued by recovering a presumably artificial group of Valgini + Osmoermatina + *Cremastocheilus* (the lowest row of Table 1), thus rejecting three monophyletic groups consistently recovered in the larval and combined analyses (columns 1–4 and 9–12, respectively): Valgini + Cryptodontina; Valgini + Cryptodontina + Trichiina; and Cetoniina s. str. + Osmoermatina + Incaina. Adult analyses also did not support monophyly of either Trichiina or Cetoniinae. Two other clades, Cetoniinae s. str. and Cetoniinae s. str. + Osmoermatina + Incaina, recovered in the combined analyses as most parsimonious, were not detected in the partial analyses. The overall contribution of each of the 12 analyses to resolving the tree in a manner consistent with the most parsimonious hypothesis is measured by “Relative Resolution Value” (Table 1). Comparison of these values for the three data-sets suggests that adult-based topologies (value 30–35%) were only half as good as those based on larvae (value 55–65%); this conclusion was also reached by Micó et al., 2008, without, however, measuring the RRV), while combined analyses provided the most resolved and, simultaneously, the most parsimonious trees (value 65–100%). These results highlight the importance of bringing at least two independent character sets into the analysis to achieve statistically sound results, which, hopefully, reflect the true evolutionary history of the group.

Direction of further research

Monophyly of Valgini will remain uncertain until members of the termitophilous subtribe Microvalgina, and their completely unknown larvae, are included in the analysis. Besides Microvalgina, Platygeniina is the only Cetoniinae subtribe outside of Cetoniinae s. str. not represented in our analysis. Although third-instar larvae of *Platygenia barbata* (Afzel, 1817) have been collected from oil palm in Nigeria and subsequently described (Jerath & Unny, 1965), the description is not detailed enough to permit character scoring. The non-monophyletic “tribe” Trichiini, with (a) the Valgini and (b) the rest of Cetoniinae derived from within it, requires a new set of tribes and subtribes to adequately reflect the new phylogenetic findings (also proposed, although not implemented, by Smith et al., 2006).

ACKNOWLEDGMENTS. This project was supported by the Charles University Grant Agency (grant #GAUK 119207) and by the Ministry of Education of the Czech Republic (grant #MŠMT ČR-0021620828) to PŠ. Canadian co-authors BDG and VVG want to acknowledge the hospitality of their Cameroonian hosts E.C. Suh, N. Godlove A., G. Chuyong (all of University of Buea) and P. Tamanji (Université de Yaoundé II). Alexander von Humboldt Foundation (www.avh.de) is acknowledged for creating a World network of former Fellows, which brought BDG and VVG in touch with the colleagues in Cameroon thus leading to successful completion of their trip. Fieldwork in Cameroon for VVG was supported by a research grant provided by E. Hintelmann (Munich, Germany) through a scientific foundation she has established at the Zoologische Staatssammlung München (http://www.zsm.mwn.de/events/wiss_preise.htm) in memory of her late husband R.J.H. Hintelmann. H. Laubvogel and H.-U. Raake (Universitätsbibliothek, Museum für Naturkunde, Humboldt-Universität zu Berlin, Germany) helped locate

the difficult-to-find 1909 Kolbe paper. K. McLachlan-Hamilton (Canadian Food Inspection Agency, Ottawa) reviewed this MS prior to submission.

REFERENCES

- ANTOINE P. 1999: Quelques espèces nouvelles ou peu connues de la famille des Cetoniidae (Coleoptera) – VII. *Entomol. Afr.* **4**: 2–16.
- ANTOINE P. 2003: Révision du genre *Coelocorynus* Kolbe (Coleoptera, Cetoniidae, Trichiinae). *Coléoptères* **9**: 127–150.
- BÖVING A.G. 1936: Description of the larva of *Plectris aliena* Chapin and explanation of new terms applied to the epipharynx and raster. *Proc. Entomol. Soc. Wash.* **38**: 169–185.
- FARRIS J.S. 1969: A successive approximation approach to character weighting. *Syst. Zool.* **18**: 374–385.
- FARRIS J.S. 1988: *Hennig86*. Published by the author, Port Jefferson Station, NY, USA.
- GOLOBOFF P. 1999: *NONA, Version 2*. Published by the author, Tucumán, Argentina.
- GREBENNIKOV V.V. & NEWTON A.F. 2009: Good-bye Scydmaenidae, or why the ant-like stone beetles should become megadiverse Staphylinidae sensu latissimo (Coleoptera). *Eur. J. Entomol.* **106**: in press.
- GREBENNIKOV V.V. & SCHOLTZ C.H. 2004: The basal phylogeny of Scarabaeoidea (Insecta: Coleoptera) inferred from larval morphology. *Invertebr. Syst.* **18**: 321–348.
- JERATH M.L. & UNNY K.L. 1965: Larvae of six genera of Cetoniinae from Eastern Nigeria (Coleoptera: Scarabaeidae). *Coleopt. Bull.* **19**: 59–64.
- KOLBE H. 1909: Über die Cryptodontinen, ein verbindendes Glied zwischen den Dynastiden und den melitophilen Lamellicornien. *Entomol. Rdsch.* **26**: 81–83.
- KRIKKEN J. 1984: A new key to the suprageneric taxa in the beetle family Cetoniidae, with annotated list of the known genera. *Zool. Verh.* **210**: 1–77.
- LAWRENCE J.F. 1991: Order Coleoptera (general discussion, family key, various family treatments). In Stehr F.W. (ed.): *Immature Insects. Vol. II*. Kendall/Hunt, Dubuque, Iowa, pp. 144–658.
- MICÓ E., VERDÚ J.R. & GALANTE E. 2001: Larval morphology of some Anisoplinini grain beetles with a key to their larvae (Coleoptera: Scarabaeoidea: Rutelidae: Anomalinae). *Eur. J. Entomol.* **98**: 311–320.
- MICÓ E., MORÓN M.A., ŠÍPEK P. & GALANTE E. 2008: Larval morphology enhances phylogenetic reconstruction in Cetoniidae (Coleoptera: Scarabaeoidea) and allows the interpretation of the evolution of larval feeding habits. *Syst. Entomol.* **33**: 128–144.
- NIXON K.C. 2002: *WinClada, Version 1.0000*. Published by the author, Ithaca, NY.
- RITCHER P.O. 1966: *White Grubs and their Allies: A Study of North American Scarabaeoid Larvae*. Oregon State University Press, Corvallis, 219 pp.
- SCHOLTZ C.H. & GREBENNIKOV V.V. 2005: Scarabaeiformia Crowson, 1960. In Beutel R.G. & Leschen R.A.B. (eds): *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. Vol. 4 Arthropoda: Insecta, Part 38. Coleoptera, Beetles Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyhaga partim.)*. Walter de Gruyter, Berlin, pp. 345–425.
- SMITH A.B.T. 2006: A review of the family-group names for the superfamily Scarabaeoidea (Coleoptera) with corrections to nomenclature and a current classification. *Coleopt. Soc. Monogr.* **5**: 144–204.

SMITH A.B.T., HAWKS D.C. & HERATY J.M. 2006: An overview of the classification and evolution of the major scarab beetle clades (Coleoptera: Scarabaeoidea) based on preliminary molecular analyses. *Coleopt. Soc. Monogr.* 5: 35–46.

Received April 11, 2008; revised and accepted November 21, 2008

APPENDIX. List of 81 morphological characters used in the analysis.

The abbreviation “MMŠG” followed by a number indicates the character used by Micó et al. (2008); abbreviation “mod.” indicates whether it was significantly re-worded compared to the original source. Character statistics: ci – consistency index; ri – retention index; SW – successive weighting on scale 0 to 10. Character state optimization refers only to the characters illustrated in Fig. 25 (i.e., informative at basal splits within the ingroup and excluding autapomorphies, also excluding autapomorphies for the highly supported Valgini, represented only by three *Valgus* species).

Larvae

1. Epicranial suture [MMŠG: 1]: not extending between frontal suture = 0 (Fig. 9); extending between frontal suture = 1. State 1 is a synapomorphy for Osmodermatina + Cetoniinae s. str. (with a parallelism in Valgini and numerous cases of ambiguity inside Cetoniinae s. str.). ci=20; ri=75; SW=1.

2. Frontal suture [MMŠG: 2]: not sinuate or smoothly sinuate = 0 (Fig. 9); bisinuate (concave) = 1; sinuate (convex) = 2. State 0 is a synapomorphy for Trichiina + Cryptodontina + Valgini (with a subsequent reversal in Valgini and parallelism in Incaina: *Archedinus*). ci=28; ri=54; SW=1.

3. Anterior frontal setae [MMŠG: 3]: present = 0 (Fig. 9); absent or reduced = 1. State 1 is a synapomorphy for Cetoniinae s. str. except *Cremastocheilus* (with numerous parallelisms and reversals both inside and outside this clade). ci=6; ri=48; SW=0.

4. Stemmata [MMŠG: 4]: present = 0 (Fig. 9); absent = 1. State 0 is a synapomorphy for Cetoniinae (with a subsequent reversal in Valgini, *Cremastocheilus* and some other Cetoniini s. str.). ci=14; ri=77; SW=1.

5. Antenna: with three joints = 0; with four joints = 1 (Fig. 10); with five joints = 2.

6. Relative size of antenna [length of antenna (A) / length of cranium (C)] [MMŠG: 5]: A/C (1 = 0 (Fig. 9); A/C > 1.1 = 1.

7. Relative length of antennomeres [MMŠG: 6, mod.]: second antennomere longer than the rest (first, third and fourth subequal) = 0; first antennomere longer than the rest = 1 (Fig. 10); first segment as long as the apical segment = 2. State 1 is a synapomorphy for Cetoniinae (with three subsequent independent changes to state 2 in Trichiina, Incaina and Schizorhynchini: *Thaumastopeus*). ci=50; ri=89; SW=4.

8. Number of dorsal sensory spots on antenna [MMŠG: 7, mod.]: a single sensory spot = 0; two or three = 1 (Fig. 11b); four or more = 2; one or two (states 0 and 1 can occur on the same specimen) = 3.

9. Number of ventral sensory spots [MMŠG: 8, mod.]: three or less than three = 0 (Fig. 11a); four or more = 1; three to five (both states 0 and 1 can occur on a single specimen) = 2.

10. Shape of epipharynx [MMŠG: 9]: asymmetric = 0; bilobed or not lobed = 1 (Fig. 12); trilobed = 2. State 1 is a synapomorphy for Trichiina + Cryptodontina + Valgini (with a parallelism in Incaina: *Archedinus*). ci=28; ri=73; SW=2.

11. Clithrum of epipharynx [MMŠG: 10, mod.]: present = 0; absent = 1 (Fig. 12); present, absent, or variable in each specimen = 2. State 0 is a synapomorphy for Osmodermatina + Cetoniinae s. str. (with a parallelism in Dynastinae). ci=50; ri=90; SW=4.

12. Sclerotized plate on epipharynx [MMŠG: 11]: absent = 0 (Fig. 12); present = 1.

13. Sensory cone on haptolachus of epipharynx [MMŠG: 12, mod.]: sensory cone well developed = 0 (Fig. 12); well defined but extremely reduced (tiny cone) = 1; sensory cone not defined = 2. We consider a sensory cone as reduced when the apical sensilla remains in a sensory field on a large oval plate.

14. Third nesium (next to laeotorma): present = 0; absent = 1 (Fig. 12).

15. Vestiture on haptomerum of epipharynx [MMŠG: 13]: bare = 0; with a transverse row of stout setae interrupted by the haptomeral process = 1; with transverse row(s) of stout setae under the haptomeral process = 2 (Fig. 12). State 1 is a synapomorphy for Trichiina. ci=28; ri=72; SW=2.

16. Haptomerum of epipharynx [MMŠG: 14, mod.]: without heli = 0 (Fig. 12); one to four heli = 1; with more than four heli = 2.

17. Sensilla on haptomerum [MMŠG: 15] (not illustrated): grouped on a more or less prominent cone = 0; not grouped on a cone or absent = 1.

18. Epizygum on epipharynx [MMŠG: 16]: present = 0; absent = 1 (Fig. 12).

19. Tormae on epipharynx: fused = 0; separate = 1 (Fig. 12).

20. Dextiotorma on epipharynx [MMŠG: 17]: straight = 0 (Fig. 12); bent mesally = 1. State 1 is a synapomorphy for Trichiina. ci=100; ri=100; SW=10.

21. Pternotormae on epipharynx [MMŠG: 18, mod.]: present and extended mesally = 0; not extended mesally or absent at least on one side = 1 (Fig. 12).

22. Number of setae on acanthoparia of epipharynx [MMŠG: 19, mod.] (not illustrated): absent or less than four (if more than four then very short and indistinct) = 0; more than five = 1.

23. Plegmata on epipharynx [MMŠG: 20]: absent = 0 (Fig. 12); present = 1.

24. Proplegmata on epipharynx: absent = 0 (Fig. 12); present = 1.

25. Number of scissorial teeth on right mandible [MMŠG: 21, mod.]: two = 0 (Fig. 14a); three = 1; four = 2. State 1 is a synapomorphy for Incaina + Osmodermatina + Cetoniinae s. str. ci=66; ri=95; SW=6.

26. Number of scissorial teeth on left mandible [MMŠG: 22]: four = 0; three = 1 (Fig. 13a); two = 2. State 0 is a synapomorphy for Incaina + Osmodermatina + Cetoniinae s. str. (with a subsequent change to state 1 in two genera of Gymnetini). ci=28; ri=72; SW=2.

27. Apex of mandible [MMŠG: 23]: tridentate = 0; not tridentate = 1 (Fig. 13c). Only in *Valgus* is there a single apical tooth, which is separated by a scissorial notch from the second tooth in dorsal view, and also by another notch from the third tooth in ventral view.

28. Stridulatory area on mandibles [MMŠG: 24]: absent or greatly reduced (less than four ridges, or only with indistinct microridges) = 0; present = 1 (Fig. 13b).

29. Lacinia and galea [MMŠG: 25]: not fused = 0; fused, forming mala = 1 (Fig. 15).

30. Number of unci of lacinia [MMŠG: 26]: three = 0; two = 1; only one or absent = 2 (Fig. 16). State 2 is a synapomorphy for Cryptodontina + Valgini (with a parallelism in Incaina and one member of Gymnetini). ci=33; ri=78; SW=2.

31. Number of stridulatory teeth on maxilla [MMŠG: 27, mod.]: less than four, or more than four, but the stridulatory teeth extremely reduced = 0 (Fig. 15); five or more normally developed teeth = 1. State 0 is a synapomorphy for Trichiina + Cryptodontina + Valgini. ci=100; ri=100; SW=10.

32. Tegumentary expansions on right side of hypopharyngeal scleroma (just below scleroma) [MMŠG: 28]: present = 0; absent = 1 (Fig. 15).

33. Tegumentary expansions on left side of hypopharyngeal scleroma [MMŠG: 29]: present = 0 (Fig. 15); absent = 1.

34. Spiracles (not illustrated): biforous = 0; cribriform = 1.

35. Number of holes in respiratory plate of thoracic spiracle [MMŠG: 30] (not illustrated): 0–15 holes across diameter = 0; 16–59 holes across diameter = 1; more than 60 tiny holes across diameter = 2.

36. Relative size of legs [MMŠG: 31]: three pairs of legs of different size, length increasing from first to third pair = 0; all pairs of similar size = 1 (Fig. 3). State 1 is a synapomorphy for Cetoniinae (with a parallelism in *Trox*). ci=50; ri=93; SW=4.

37. Last segment of legs [MMŠG: 32, mod.]: with weakly developed claw with two setae = 0 (Fig. 19); tarsungulus with several setae and a well developed sclerotized claw = 1; tarsungulus with several setae and a tiny sclerotized claw at apex = 2; tarsungulus with several setae = 3.

38. Relative size of leg segments [MMŠG: 33, mod.]: trochanter longer than tibiotarsus = 0; trochanter shorter than tibiotarsus = 1 (Fig. 18).

39. Abdominal segments IX and X [MMŠG: 34]: not fused = 0 (Fig. 3); fused = 1. State 1 is a synapomorphy for Osmodermatina + Cetoniinae s. str. (with reversal in Goliathini: *Goliathus*). ci=50; ri=96; SW=4.

40. Palidium on raster of last abdominal segment [MMŠG: 35]: absent = 0 (Fig. 20); present = 1.

41. Hamate setae on raster of last abdominal segment [MMŠG: 36]: absent = 0 (Fig. 20); present = 1.

42. Anal slit [MMŠG: 37]: transverse = 0 (Fig. 20); Y-shaped = 1.

43. Anal tergite [MMŠG: 38]: with an area demarked by a special sulcus = 0; without sulcus = 1 (Fig. 3).

Adults

44. Surface of frons [MMŠG: 39]: convex = 0; concave = 1; with accessories = 2.

45. Clypeal surface [MMŠG: 40]: flattened or slightly convex = 0; slightly concave = 1, deeply concave or excavated = 2. State 2 is a synapomorphy for Incaina (with numerous parallelisms outside this clade). ci=13; ri=40; SW=0.

46. Anterior border of male clypeus [MMŠG: 41]: straight, slightly curved or sinuate = 0; clearly notched = 1; armed = 2. State 2 is a synapomorphy for Incaina (with parallelism in Cryptodontina and other cases outside Incaina). ci=16; ri=56; SW=0.

47. Ventral surface of labium [MMŠG: 42]: flattened or convex = 0; partially or slightly concave = 1; completely or deeply concave = 2.

48. Anterior border of labrum [MMŠG: 43]: exposed = 0; hidden = 1. Weakly sclerotized labrum is reduced or completely covered by clypeus and other mouthparts.

49. Preocular notch [MMŠG: 44]: absent = 0; present = 1. State 1 is a synapomorphy for Cetoniinae. ci=100; ri=100; SW=10.

50. Antennal scapus [MMŠG: 45]: rounded = 0; widened and depressed = 1. Anterior and posterior border of the basal antennomere clearly expanded, offering a nearly flattened external surface that covers the antennal insertion when disturbed.

51. Length of male antennal club [MMŠG: 46]: as long as or shorter than funicle = 0; clearly longer than funicle = 1.

52. Sexual dimorphism of head [MMŠG: 47]: absent = 0; slight = 1; accentuated = 2. State 2 is a synapomorphy for Incaina (with numerous parallelisms outside this clade). ci=15; ri=68; SW=1.

53. Apex of galea [MMŠG: 48]: toothed = 0; rounded, not toothed = 1. State 1 is a synapomorphy for Cetoniinae s. str. except *Cremastocheilus* (with two parallelisms outside and one reversal inside this clade). ci=14; ri=71; SW=1.

54. Central third of posterior border of pronotum [MMŠG: 49]: straight or curved = 0; clearly sinuate = 1; lobed = 2. Backward expansion of the posterior pronotal border forms a rounded lobe usually covering most of scutellum. A sinuate posterior pronotal border projects beyond the basal border of scutellum.

55. Pronotal disc [MMŠG: 50, mod.]: simply convex = 0; with depressions or prominences = 1; with depression and prominences only in males = 2.

56. Basal third of pronotum [MMŠG: 51]: reduced = 0; projected = 1. State 1 is a synapomorphy for Cetoniinae s. str. except *Cremastocheilus* (with three parallelisms outside this clade). ci=25; ri=85; SW=2.

57. Anterolateral border of pronotum [MMŠG: 52]: with margin = 0; without margin, rounded = 1.

58. Procoxae [MMŠG: 53]: transverse, slightly prominent = 0; nearly conical and clearly prominent = 1. State 1 is a synapomorphy for Cetoniinae (with a subsequent reversal in Cryptodontini). ci=33; ri=87; SW=2.

59. Metacoxae [MMŠG: 54]: close together = 0; widely separated = 1.

60. Posterolateral corner of metacoxa [MMŠG: 55]: short, rounded = 0; prominent, acute = 1.

61. Inner sides of base of protibia [MMŠG: 56]: without tooth = 0; with tooth = 1. State 1 is a synapomorphy for Incaina. ci=100; ri=100; SW=10.

62. External border of male protibia [MMŠG: 57, mod.]: with two to three teeth = 0; without a tooth or with an apical one = 1.

63. Inner border of male protibia [MMŠG: 58, mod.]: simple = 0; toothed or serrate = 1.

64. Preapical ventral border of protibia [MMŠG: 59]: simple, flattened = 0; toothed = 1. State 1 is a synapomorphy for Incaina + Osmodermatina + Cetoniinae s. str. (with four reversals inside Cetoniinae s. str. and parallelism in two among three members of Valgini). ci=12; ri=30; SW=0.

65. Dorsal surface of mesotibia [MMŠG: 60]: with keels or spines = 0; without keels or spines = 1.

66. Dorsal surface of metatibia [MMŠG: 61]: with keels or spines = 0; without keels or spines = 1.

67. Sexual dimorphism of protarsus [MMŠG: 62]: absent = 0; slight = 1; accentuated = 2.

68. Onychium [MMŠG: 63]: long = 0; short = 1; absent = 2. We take as a reference the dorsoventral basal width of one tarsal claw (as long as the dorsoventral basal width of tarsal claw or shorter).

69. Preprosternum [MMŠG: 64]: without projection = 0; with erect tubercle or strong spine = 1. State 1 is a synapomorphy for Incaina (with numerous parallelisms outside this clade). ci=7; ri=47; SW=0.

70. Postprosternum [MMŠG: 65]: without projection = 0; with erect tubercle or strong spine = 1.

71. Mesometasternum [MMŠG: 66]: without projection = 0; with tubercle = 1. State 1 is a synapomorphy for Cetoniinae s. str. except *Cremastocheilus* (with one parallelism and one reversal outside and inside this clade, respectively). ci=33; ri=92; SW=3.

72. Proepimeron [MMŠG: 67]: nearly flattened or scarcely concave = 0; deeply concave = 1. The strong and wide depression on the proepimeron in a number of Cetoniinae allows for the reception of the basal distal half of the profemur and as a consequence, the thickness of the latero-posterior side of pronotum is reduced.

73. Dorsal part of mesepimeron [MMŠG: 68]: completely covered or nearly so = 0; clearly exposed = 1. State 1 is a synapomorphy for all Cetoniinae s. str. (with two reversals inside this clade). ci=33; ri=92; SW=3.

74. Proepisternal keel [MMŠG: 69]: absent or weakly defined = 0; clearly defined and outstanding = 1.

75. Scutellum [MMŠG: 70]: completely exposed = 0; partly covered or completely covered = 1.

76. Posthumeral elytral emargination [MMŠG: 71]: weak or absent = 0; wide and deep, well defined = 1. State 1 is a synapomorphy for all Cetoniinae s. str. (with two reversals inside this clade). ci=33; ri=92; SW=3.

77. Fifth abdominal sternum [MMŠG: 72]: nearly as long as fourth = 0; longer than fourth = 1.

78. Fifth abdominal spiracle [MMŠG: 73]: annular = 0; tuberculiform = 1.

79. Pygidium [MMŠG: 74]: wider than long = 0; as long as wide, or slightly longer than wide = 1.

80. Propygidium [MMŠG: 75]: covered by elytra = 0; largely exposed = 1.

81. Dorsal vestiture [MMŠG: 76]: absent = 0; setiferous = 1; pruinose or cretaceous = 2. State 2 is a synapomorphy for Trichiina (with one reversal inside this clade and multiple reversals and parallelisms outside it). ci=9; ri=34; SW=0.