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Phylogeny and systematics of the giant rhinoceros beetles (Scarabaeidae: Dynastini)

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Phylogeny and systematics of the giant rhinoceros beetles (Scarabaeidae: Dynastini)

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Abstract. This report contains the first inclusive phylogenetic analysis and taxonomic structure for the genera presently included within the scarabaeid tribe Dynastini. The study was based upon morphological, biogeographic and molecular data and yielded direct support for the recognition of three subtribes in the Dynastini: Dynastina MacLeay, **New Status** (*Dynastes* Kirby, *Augosoma* Burmeister, *Megasoma* Kirby, *Golofa* Hope), Xylotrupina Hope, **New Status** (*Xylotrupes* Hope, *Allomyrina* Arrow, *Trypoxylus* Minck, *Xyloscaptes* Prell) and Chalcosomina Rowland and Miller, **New Subtribe** (*Chalcosoma* Hope, *Haploscapanes* Arrow, *Beckius* Dechambre, *Eupatorus* Burmeister, *Pachyoryctes* Arrow). The results provide indirect but significant support for the origin of the tribe Dynastini to be of an age no later than the early Late Cretaceous. Molecular and morphological evidence suggests that *Eupatorus* as constituted in current taxonomic literature is not monophyletic, and taxonomic alternatives are discussed to address this deficiency. A plausible explanation is also provided for the perplexing use by F. W. Hope of the family-group names Xylotrupidae and Dynastidae.

Introduction

The remarkable extravagance and variety of male sexual ornaments that have evolved among the giant rhinoceros beetles (tribe Dynastini) have attracted the ardent attention of naturalists for centuries (e.g. Scheuchzer 1732-1737). However, despite this notoriety basic aspects of the biology of this group - which might help reveal how and why such armaments arise and evolve - remain poorly resolved to this day. A conspicuous example is the virtual absence of investigations since Darwinian times that might have focused upon evolutionary relationships among the relatively few genera that compose the Dynastini.

This study attempts to aid such further research by providing the first phylogenetic analyses within the tribe Dynastini (Fig. 1), notwithstanding Rowland (2003). These analyses are based upon morphological, biogeographic and molecular characters from representatives of each of the 13 genera and approximately 70% of the species currently proposed to constitute the tribe. From the results of these analyses we have assembled a relatively robust phylogenetic topology which forms the basis of a first, readily testable taxonomic structure for the tribe – and from which trends in character evolution can be assessed. Further, the phylogenetic analyses provide indirect evidence that suggests a minimum geological age of origin of the tribe. Discussions are also provided concerning enigmatic historical usages of family-group names, as well as present directions for future refinements in the proposed taxonomic system for the tribe Dynastini.

Methods and Materials

Taxon sampling. Ingroup taxa included 20 species representing each genus of the tribe Dynastini (Table 1): *Augosoma* Burmeister, *Golofa* Hope, *Dynastes* Kirby, *Megasoma* Kirby, *Trypoxylus* Minck, *Xyloscaptes*

Prell, *Allomyrina* Arrow, *Xylotrupes* Hope, *Haploscapanes* Arrow, *Chalcosoma* Hope, *Beckius* Dechambre, *Eupatorus* Burmeister, *Pachyoryctes* Arrow. Where possible multiple species are included from genera that contain more than one species to examine monophyly of the genus-groups. Morphological and taxonomic analyses were performed by JMR. Molecular and phylogenetic analyses were performed by KBM.

Outgroup taxa included four species from other tribes and subfamilies within Scarabaeidae (Table 1). The resulting cladograms were rooted with *Polyphylla decemlineata* (Say), a member of the subfamily Melolonthinae.

In addition to the specimens employed in the phylogenetic analyses, the following taxa were examined for development of the descriptions of the subtribes and the key to the subtribes and genera: *Allomyrina pfeifferi* (Redtenbacher), *Augosoma centaurus* (Fabricius), *Beckius beccarii* (Gestro), *Chalcosoma atlas* (Linné), *C. caucasus* (Fabricius), *C. mollenkampi* (Kolbe), *Dynastes granti* Horn, *D. hercules* (Linné), *D. neptunus* (Quensel), *D. satanas* (Moser), *D. tityus* ((Linné), *Eupatorus birmanicus* Arrow, *E. gracilicornis* Arrow, *E. hardwickei* (Hope), *E. siamensis* (Laporte), *Golofa aegeon* (Drury), *G. argentinus* Arrow, *G. clavigera* (Linné), *G. cochlearis* Ohaus, *G. costaricensis* Bates, *G. eacus* Burmeister, *G. imperialis* Thomson, *G. minuta* Sternberg, *G. pelagon* Burmeister, *G. pizarro* Hope, *G. porteri* Hope, *G. pusilla* Arrow, *G. spatha* Dechambre, *G. tersander* (Burmeister), *G. unicolor* (Bates), *G. xiximeca* Moron, *Haploscapanes barbarossa* (Fabricius), *Megasoma acteon* (Linné), *M. anubis* (Chevrolat), *M. cedrosa* Hardy, *M. elephas* (Fabricius), *M. gyas* (Herbst), *M. joergenseni* (Bruch), *M. mars* (Reiche), *M. occidentalis* Bolivar, Jiménez et Martínez, *M. pachecoi* Cartwright, *M. punctulatum* Cartwright, *M. sleeperi* Hardy, *M. thersites* LeConte, *M. vogti* Cartwright, *Oryctes rhinoceros* (Linné), *Pachyoryctes solidus* Arrow, *Trypoxylus dichotom* (Linné), *Xyloscaptes davidis* (Deyrolle et Fairmaire), *Xylotrupes australicus* Thomson, *X. beckeri* Schaufuss, *X. carinulus* Rowland, *X. clinias* Schaufuss, *X. damarensis* Rowland, *X. falcatus* Minck, *X. gideon* (Linné), *X. inarmatus* Sternberg, *X. lorquini* Schaufuss, *X. macleayi* Montrouzier, *X. meridionalis* Prell, *X. mniszechi* Thomson, *X. pachycera* Rowland, *X. pauliani* Silvestre, *X. philippinensis* Endrödi, *X. pubescens* Waterhouse, *X. siamensis* Minck, *X. sumatrensis* Minck, *X. tadoana* Rowland, *X. telemachos* Rowland, *X. ulysses* (Guérin-Méneville).

Voucher specimens used in the molecular analyses are deposited in the JM Rowland Collection (JMRC) or the Museum of Southwestern Biology, University of New Mexico (MSBA, K.B. Miller curator) and bear labels with the indicated identifying codes (Table 1).

Morphological data. Morphological characters were assembled from published sources (Arrow 1908, 1911, 1925, 1937, 1944, 1951; Burmeister 1847; Endrödi 1947, 1951, 1957, 1976, 1985; Hope 1837; Janssens 1949; Lacordaire 1856; Latreille, 1829; Minck 1920; Rowland 2003, 2011) and from direct examination of specimens contained in the JMRC. The latter characters were employed for the descriptions of the subtribes, the key to the subtribes and genera of the Dynastini, and the phylogenetic analyses presented in Figures 1 and 2. The key is diagnostic for male specimens that fully express the secondary sexual characters, and is largely synoptic. The systematic account conforms to the format of Smith (2006) and Bouchard et al. (2011), and the nomenclatural actions are in accord with ICZN (1999).

Morphological characters and states as coded for the phylogenetic analysis are listed as follows, and their distribution among studied taxa is given in Table 2.

1. Mandible incisors: 0, adenticulate; 1, denticulate.
2. Cephalic horn apex (male): 0, acuminate; 1, bifurcate.
3. Lateral cephalic horn armature (male): 0, absent; 1, present.
4. Dorsal cephalic horn armature (male): 0, absent; 1, present.
5. Mesal pronotal horn (male): 0, absent; 1, present.
6. Mesal pronotal horn apex (male): 0, acuminate; 1, bifurcate.
7. Mesal pronotal dense pilosity (male): 0, absent; 1, present.
8. Mesal pronotal accessory horns (male): 0, absent; 1, present.
9. Lateral pronotal horns (male): 0, absent; 1, present.
10. Anterior ventrolateral pronotal apices (male): 0, not developed as horns; 1, developed as horns.
11. Prothoracic legs: 0, essentially sexually monomorphic; 1, decidedly sexually dimorphic.
12. Protibia: 0, tridentate; 1, quadridentate.

13. Paramere dorsal interdigitating teeth: 0, absent; 1, present.
14. Paramere distolateral contours: 0, converging inward; 1, parallel or diverging outward.
15. Paramere apex setation: 0, absent or short and inconspicuous; 1, long and conspicuous.
16. Raspulae: 0, essentially a simple chagrin of flexible filaments; 1, chagrin includes sclerotized spines or indurated patches.
17. Dorsal integument color: 0, dark reddish brown; 1, tan to orangish yellow or greenish yellow to bluish gray with irregular dark spots.

DNA sequences. Methods for DNA extraction, amplification and sequencing closely followed Miller et al. (2007, 2009). DNA was extracted using the Qiagen DNEasy kit (Valencia, California, USA) and the animal tissue protocol. In most cases, thoracic muscle tissue was removed and extracted. In some cases other tissues were extracted.

Four genes were sequenced for analysis, *cytochrome c oxidase II* (COII), *16S rRNA* (16S), *histone III* (H3) and *arginine kinase* (ArgKin). Individual gene fragments are missing for some taxa (Table 1). Primers used for both amplification and sequences were derived from several sources (Table 3). Amplification of COII, 16S and H3 required typical amplification conditions (35 cycles of denaturing: 95°C 1min., annealing: 40-50°C 1 min., elongation: 72°C 1min.). Arginine kinase required nested reamplification with one amplification run using AK168F and AK939R (Table 3) and amplification from this product using nested primers, AK183F and AK933R (Table 3), using the above conditions with sequencing from this final product. Fragments were PCR amplified using TaKaRa Ex Taq (Takara Bio Inc., Otsu, Shiga, Japan) on an Eppendorf Mastercycler ep gradient S Thermal Cycler (Eppendorf, Hamburg, Germany) and visualized by gel electrophoresis. Fragment purification was done using ExoSAP-IT (USB-Affymetrix, Cleveland, Ohio, USA) and cycle-sequenced using ABI Prism Big Dye (ver. 3.1, Fairfax, Virginia, USA) with the same primers as those used in amplification. Sequencing reaction products were purified using Sephadex G-50 Fine or Medium (GE Healthcare, Uppsala, Sweden) and sequenced with an ABI 3130xl Genetic analyzer (Molecular Biology Facility, UNM). Fragments were sequenced in both directions and sequences were edited using Sequencher (Genecodes 1999).

Analysis. Alignment of COI, H3 and ArgKin was straightforward since these markers are length-invariant and were aligned based on conservation of codon reading frame. Alignment of 16S was done using the program Muscle (Edgar 2004) using the default settings. Gaps in the aligned region were treated as missing data.

The phylogeny was estimated using a combined equal-weights parsimony analysis using the program NONA (Goloboff 1995) as implemented by WinClada (Nixon 2002) using the heuristic command settings "hold 10000", "mult*100", "hold/40" and "multiple TBR + TBR". Support for branches was measured using bootstrap values. These were calculated with NONA and WinClada using 1000 replications, 10 search reps, 1 starting tree per rep, "don't do max*(TBR)", and save the consensus of each replication.

We recognize that at least some of the morphological characters may not be independent (Rowland 2003). To explore the effect of inclusion of morphological character on the resulting cladogram, we also ran the analysis with only the combined molecular data using the same commands as above.

Results

The parsimony analysis resulted in a fully resolved cladogram (Fig. 1, length = 4216, CI = 40, RI = 47). Dynastini is monophyletic, though with relatively low support (bs<50), and since only a few outgroups were included, broader conclusions about the monophyly of the group are not here warranted. Within Dynastini, support for most groupings is relatively strong. Two larger monophyletic groups within the tribe are indicated. One includes the African genus *Augosoma*, sister to a clade including the New World genera *Golofa*, *Dynastes* and *Megasoma*, each of which is monophyletic with strong support (bs>85 in each case). Within this group, *Dynastes* and *Megasoma* are sister to each other with strong support (bs=88) and *Golofa* is sister to that clade, also with good support (bs=84). The other large monophyletic group includes all the Palearctic and Oriental genera (bs=90). Within this group, there are two additional larger clades. The first (bs=76) includes *Trypoxylus*, *Xyloscaptes*, *Allomyrina* and a monophyletic

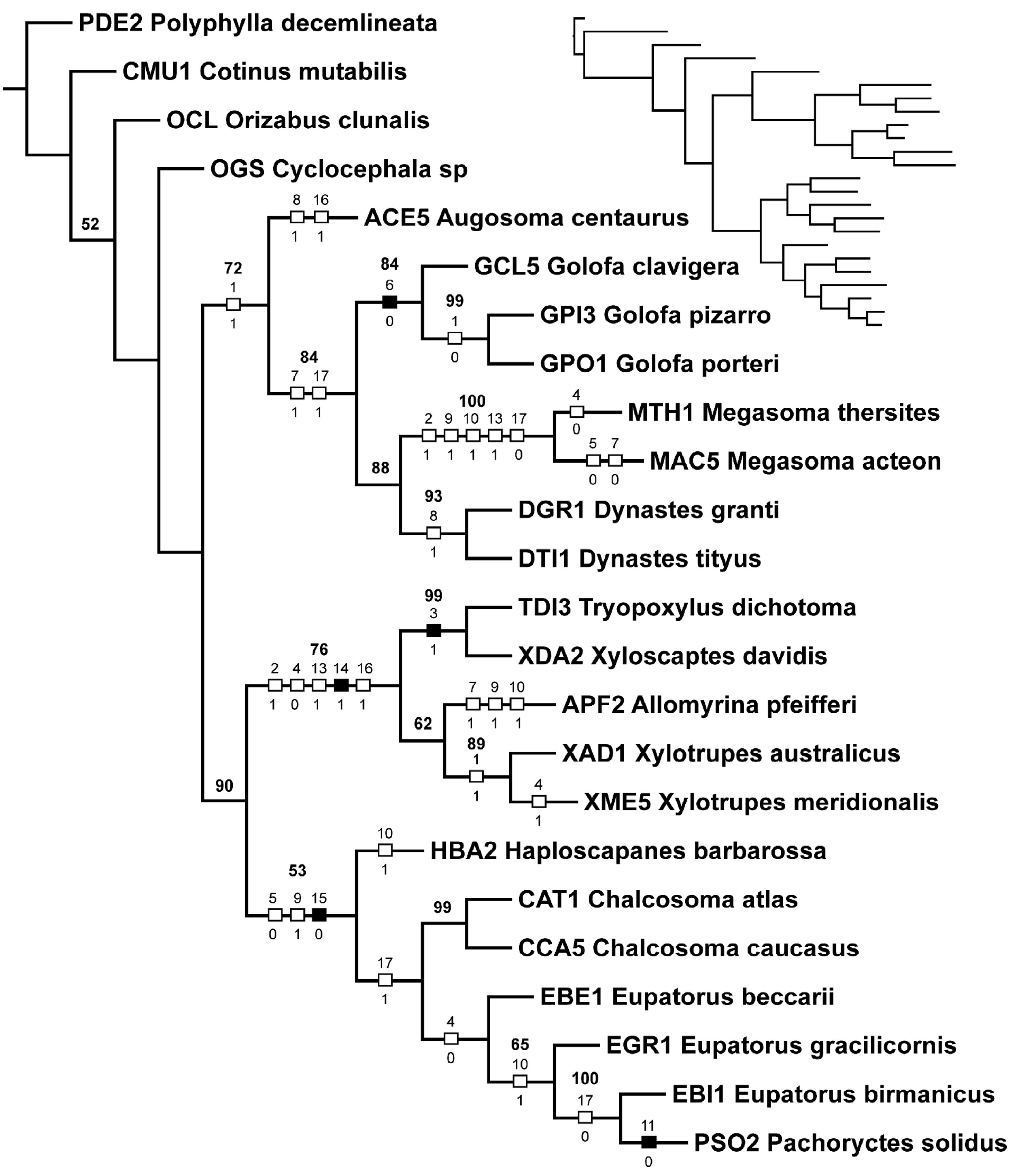

Figure 1. Single most parsimonious cladogram resulting from analysis of morphological and molecular data (16S, COII, H3 and arginine kinase) for Dynastini with morphological character state transformations mapped using "fast" (ACCTRAN) optimization in WinClada. Numbers immediately above hashmarks are morphological character numbers. Numbers below hashmarks are character state numbers derived on that branch. Numbers in bold above branches are bootstrap support values. Inset branching diagram is single most parsimonious cladogram from analysis of all data with branch lengths proportionate to number of character state transformations mapped using "fast" optimization.

(bs=89) *Xylotrupes*. The second, more weakly supported clade (bs=53) includes the genera *Haploscapanes*, a monophyletic (bs=99) *Chalcosoma, Beckius, Eupatorus* and *Pachyoryctes* nested within *Eupatorus* Burmeister. Analysis of the combined molecular data alone (without including morphology) resulted in exactly the same topology.

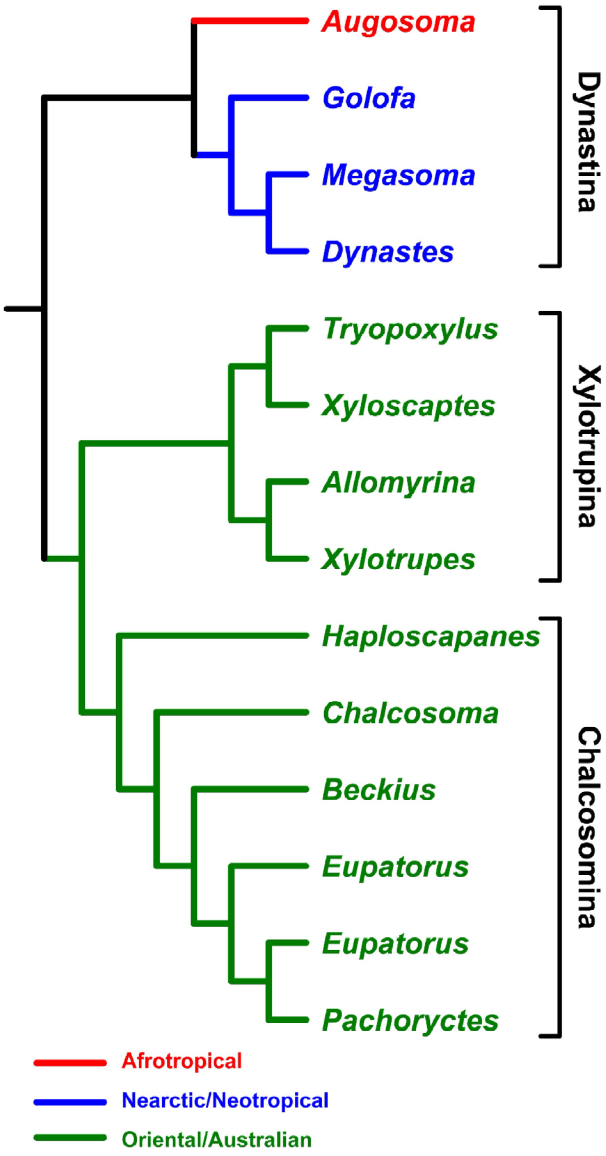

Figure 2. Summary phylogeny of Dynastini genera, distribution and classification based on results of combined phylogenetic analyses.

Discussion

Based upon the results of the phylogenetic analyses we propose recognition of three well-supported subtribes, the African and New World clade Dynastina and two Old World clades, Xylotrupina and the new subtribe Chalcosomina (Fig. 2). Further, our analyses found that the west African genus *Augosoma* is sister to the clade containing the American genera *Dynastes, Megasoma* and *Golofa* (Figs. 1, 2). This evidence supports the origin of the tribe Dynastini as no later than the early Late Cretaceous, when the South American and African continental tectonic plates separated and thus initiated the vicariant differentiation of their respective biotas (Wegener 1929; Reyment 1969; Berggren and Hollister 1978; Moullade and Guérin 1982). This proposed geologic age of origin of the tribe Dynastini is not inconsistent with the direct, though limited evidence documented in the fossil record of Mesozoic scarabaeid beetles (Krell 2000).

Hope (1837, 1845a, 1845b) and Burmeister (1847) present formal and informal taxonomic treatments regarding the Dynastini. Here we examine these treatments for the inferences they might contain regarding these authors' concepts of the relationships among the genera of this tribe. Hope (1837, 1845b) recognized MacLeay's family Dynastidae, and in Hope (1845a) he created the apparent additional family Xylotrupidae, but he did so, perplexingly, in order to accommodate the new genus *Dipelicus*, a pentodontine. One might infer from the latter that either Hope (1845a) perceived *Xylotrupes* to be more closely allied morphologically to *Dipelicus* than it is to *Dynastes*, which seems unlikely; or that Hope wrote Xylotrupidae, but should rather have written Xyloryctidae, which seems quite likely from the following evidence. Hope (1837) introduced the new genus *Xyloryctes* at the head of six new pentodontine genera. Then Hope (1845a) introduced the additional new pentodontine genus *Dipelicus,* but enigmatically created the family Xylotrupidae to contain that new genus. Darren Mann obtained the F. W. Hope archives at Oxford University Museum which contain Hope's manuscript notes from the historical period in question. These revealed that, other than *Xylotrupes,* all of the recognised genera that Hope listed in his notes under Xylotrupidae are oryctines or pentodontines: *Oryctes, Oryctoderus, Cheiroplatys, Tetradosata*(?), *Apothrix*(?) and *Phileurus depressus* - which is a junior synonym of the pentodontine *Semanopterus subcostatus* Laporte (Endrödi 1985: 416-417). Moreover, Hope did not list *Xyloryctes* among these, but did list *Xylotrupes*, and under the latter are listed five trivial names: *juba, latipes, curtus, porcellus, ixion* - all of which are names of pentodontines, and none of which

Table 1. Taxa and specimens used in phylogenetic analysis of Dynastini. JMRC = JM Rowland Collection, MSBA = Museum of Southwestern Biology, University of New Mexico.

Genus	Species	Code	Voucher deposition	Extracted tissue (see footnotes)	GenBank #(COII/16S/H3/ArgKin)
Outgroup					
Polyphylla	*decemlineata*	KBMC-PDE2	JMRC	1	-/JX994048/-/JX994005
Cotinus	*mutabilis*	KBMC-CMU1	JMRC	1	JX994068/JX994045/JX994025/JX994004
Orizabus	*clunalis*	KBMC-OCL1	JMRC	1	JX994069/JX994046/-/-
Cyclocephala	sp.	KBMC-OGS	MSBA	2	JX994070/JX994047/-/-
Ingroup					
Allomyrina	*pfeifferi*	KBMC-APF2	JMRC	1	JX994049/JX994026/JX994006/JX993994
Augosoma	*centaurus*	KBMC-ACE5	JMRC	3	JX994050/JX994027/JX994007/JX993995
Beckius	*beccarii*	KBMC-EBE1	JMRC	2	JX994055/JX994032/JX994012/-
Chalcosoma	*atlas*	KBMC-CAT1	JMRC	2	JX994051/JX994028/JX994008/-
Chalcosoma	*caucasus*	KBMC-CCA5	JMRC	3	JX994052/JX994029/JX994009/JX993996
Dynastes	*granti*	KBMC-DGR1	JMRC	1	JX994053/JX994030/JX994010/JX993997
Dynastes	*tityus*	KBMC-DTI1	JMRC	1	JX994054/JX994031/JX994011/-
Eupatorus	*birmanicus*	KBMC-EBI1	JMRC	2	JX994056/JX994033/JX994013/-
Eupatorus	*gracilicornis*	KBMC-EGR1	JMRC	2	JX994071/-/-/-
Golofa	*clavigera*	KBMC-GCL5	JMRC	3	JX994057/JX994034/JX994014/JX993998
Golofa	*pizarro*	KBMC-GPI3	JMRC	3	JX994058/JX994035/JX994015/-
Golofa	*porteri*	KBMC-GPO1	JMRC	3	JX994059/JX994036/JX994016/-
Haploscapanes	*barbarossa*	KBMC-HBA2	JMRC	1	JX994060/JX994037/JX994017/JX993999
Megasoma	*acteon*	KBMC-MAC5	JMRC	3	JX994061/JX994038/JX994018/JX994000
Megasoma	*thersites*	KBMC-MTH1	JMRC	2	JX994062/JX994039/JX994019/-
Pachyoryctes	*solidus*	KBMC-PSO2	JMRC	2	JX994063/JX994040/JX994020/-
Trypoxylus	*dichotom*	KBMC-TDI3	JMRC	3	JX994064/JX994041/JX994021/-
Xyloscaptes	*davidis*	KBMC-XDA2	JMRC	1	JX994065/JX994042/JX994022/JX994001
Xylotrupes	*australicus*	KBMC-XAD1	JMRC	1	JX994066/JX994043/JX994023/JX994002
Xylotrupes	*meridionalis*	KBMC-XME5	JMRC	1	JX994067/JX994044/JX994024/JX994003

[1] Collected as live adults, then frozen or placed in EtOH, and muscle tissue dissected into absolute EtOH.
[2] Muscle tissue isolated from dead, dried adults, muscle tissue dissected dry into sealable vials.
[3] Procured as frozen larvae, muscle tissue dissected into absolute EtOH.

have otherwise ever been associated with *Xylotrupes* or are now associated with Dynastini. The latter evidence thus is strong that Hope simply mistakenly used the names Xylotrupidae and *Xylotrupes* in the above publications and manuscript notes where he should have used the names Xyloryctidae and *Xyloryctes*. Darren Mann provided the following additional supportive insights regarding Hope's heretofore perplexing use of the family name Xylotrupidae: *"I have been through some of Hope's archives and found the name Xylotrupidae in his own hand, although in the same notebook, on three separate occasions. This usage included several genera beneath, Oryctes, Xylotrupes, etc. So my guess would be that he wanted to create a new 'group name' for the genus Dipelicus and just lost track of what was Xyloryctes and Xylotrupes more a lapsus memoriae than a lapsus calami."* Moreover, the several foregoing facts suggest that considerable caution should be used in inferring Hope's concepts of relationships among the genera of the Dynastini by his use of the family names Dynastidae (Hope 1837, 1845b) and Xylotrupidae (Hope 1845a). Regarding formal nomenclature, whether or not Hope (1845a) mistakenly used the name Xylotrupidae rather than Xyloryctidae does not affect the status of the name Xylotrupidae according to the ICZN (pers. comm. Andrew Smith).

Burmeister (1847) segregated Dynastidae into the two informal categories *"Dynastidae lasiopygi"* containing *Golofa, Theogenes* and *Dynastes*; and *"Dynastidae liparopygi"* containing *Augosoma, Xylotrupes, Eupatorus, Chalcosoma* and *Megasoma;* and of which he wrote: [p. 246] *"Dynastidae liparopygi. Sie bewohnen die westliche halbkugel und zerfallen in drei natürliche Gattungen."*; and [pp. 262-263]

Table 2. Taxa and morphological character states coded for phylogenetic analysis of Dynastini. Morphological characters and code states are described in the Materials and Methods on pp. 2-3.

	000000000	11111111
	123456789	01234567
Augosoma centaurus	100111010	01000110
Golofa clavigera	100110100	01000101
Golofa pizarro	000110100	01000101
Golofa porteri	000110100	01000101
Dynastes granti	100111110	01000101
Dynastes tityus	100111110	01000101
Megasoma thersites	110011101	11010100
Megasoma actaeon	11010-001	11010100
Trypoxylus dichotom	011011000	01011110
Xyloscaptes davidis	011011000	01011110
Allomyrina pfeifferi	010011101	11011110
Xylotrupes australicus darwinia	110011000	01011110
Xylotrupes meridionalis	110111000	01011110
Haploscapanes barbarossa	00010-001	11000000
Chalcosoma atlas	00010-001	01000001
Chalcosoma caucasus	00010-001	01000001
Beckius beccarii	00000-001	01000001
Eupatorus gracilicornis	00000-001	11000001
Eupatorus birmanicus	00000-001	11000000
Pachyoryctes solidus	00000-001	10000000

"Dynastidae lasiopygi. Man kann nach der Bildung der Unterkiefer, mit denen der übrige Körperbau ganz in Harmonie bleibt, noch zwei natürliche Unterabtheilungen feststellen." Burmeister thus considered *Dynastidae lasiopygi* and *Dynastidae liparopygi* as natural groupings (pers. comm. Joachim Willers).

Arrow (1908) revised the genus *Eupatorus* to contain *E. hardwickei, E. gracilicornis, E. beccarii, E. birmanicus* and *E. siamensis* by synonymizing *Alcidosoma* which Laporte (1867) had created for *A. siamensis*. This arrangement was followed in Endrödi (1976, 1985). However, our results indicate that under this concept *Eupatorus* is not monophyletic because *Pachyoryctes solidus* is nested among *Eupatorus* species (Fig. 1). That is, *E. gracilicornis* is sister to the clade containing *E. birmanicus* and *Pachyoryctes solidus*, and the latter three species form a clade that is sister to *B. beccarii*. To improve the classification with respect to the latter, we follow Dechambre (1992) in which *E. beccarii* was transferred to *Beckius* Dechambre. Our morphological and biogeographic observations are consistent with this approach, as are the notations, if not the actions, of Arrow (1908), Gestro (1876), Laporte (1867), Endrödi (1976) and Dechambre (1992). Further, we compared non-type specimens of *E. siamensis, E. birmanicus, E. hardwickei* and *E. gracilicornis* and found that *E. siamensis* and *E. birmanicus* are similar in the following respects: 1) they have dorsal pronotal horns which are larger than the basolateral horns, 2) their pronotal integument is rugose and without well-defined pits and 3) they are not known to express tan-colored individuals. Arrow (1908) found *E. siamensis* and *E. birmanicus* to have "curiously different sexual armature c [but] which are so closely alike in all other respects." We found that *E. hardwickei* and *E. gracilicornis* differ from *E. siamensis* and *E. birmanicus* in having: 1) dorsal pronotal horns that are smaller than the basolateral horns, 2) polished pronotal integument with well-defined pits and 3) predominately tan-colored individuals. Further, in spite of Arrow (1908) placing *P. solidus* in its own monotypic genus relative to *E. siamensis and E. birmanicus,* these three species display a pattern of character states from which it is not difficult to imagine that *P. solidus* could be sister to one and not both *E. siamensis* or *E. birmanicus: P. solidus* is compressed lengthwise in general body proportions compared to *E. siamensis* and *E. birmanicus*; the pronotal dorsolateral horns are strong in *E. siamensis* and *E. birmanicus*, weak in *P. solidus*; pronotal anterolateral apices are strong horns in *E. siamensis* and *E. birmanicus*, weak horns in *P. solidus*; proleg sexual dimorphism is strong in *E. siamensis* and *E. birmanicus*, weak in *P. solidus*; mandible incisors are blunt and distinctly laterally lobed in *E. siamensis* and *E. birmanicus*,

Table 3. Primers used for amplification and sequencing of gene fragments for Dynastini specimens.

Gene	Primer	Direction	Sequence (5'-3')
16S	16S[1]	For	CGCCTGTTTATCAAAAACAT
	16S[1]	Rev	CTCCGGTTTGAACTCAGATCA
COII	9b[2]	Rev	GTACTTGCTTTCAGTCATCTWATG
	F-lue[2]	For	TCTAATATGGCAGATTAGTGC
	R-lys[2]	Rev	GAGACCAGTACTTGCTTTCAGTCATC
	Ef1á Cho10[3]	Rev	ACRGCVACKGTYTGHCKCATGTC
	For3[3]	For	GGYGACAAYGTTGGTTTYAAY
H3	Haf[4]	For	ATGGCTCGTACCAAGCAGACGGC
	Har[4]	Rev	ATATCCTTGGGCATGATGGTGAC
ArgKin	AK168F[5]	For	CAGGTTTGGARAAYCACGAYTCYGG
	AK939R[5]	Rev	GCCNCCYTCRGCYTCRGTGTGYTC
	AK183F[5]	For	GATTCTGGAGTCGGNATYTAYGCNCCYGAYGC
	AK933R[5]	Rev	CCCTCAGCYTCRGTGTGYTCNCCRCG

[1]Simon et al. (1994); [2]Whiting (2002); [3]Danforth et al. (1999); [4]Colgan et al. (1998); [5]Wild and Maddison (2008).

sharp and indistinctly laterally lobed in *P. solidus*; prosternal apex is broadly acuminate and orthogonal in *E. birmanicus*, truncate and reflected inward in *E. siamensis* and *P. solidus*; anterodorsal margin of phallobase is sharply defined with midline furrow extending to margin in *E. birmanicus* and *P. solidus*, less defined in *E. siamensis* and midline furrow vague, not extending to margin; paramere blades are short in *E. birmanicus* and *P. solidus*, long and attenuate in *E. siamensis*; paramere orifice is wide and round in *E. birmanicus* and *P. solidus*, narrow and elliptical in *E. siamensis*. It is indeed notable that the male of *P. solidus* has much reduced pronotal armature compared to *siamensis* and *birmanicus*, but it is also observed that the largest males of *P. solidus* have a similar pronotal armature to the small males of *E. siamensis*. Moreover, large males of *P. solidus* appear to express the pronotal armature phenotype typical of the subordinate males of ancestral lineages of *Eupatorus*. This seems also to parallel the expression in *P. solidus* of an essentially female proleg phenotype. Relatively rapid phylogenetic switching between and among such intraspecific alternative developmental phenotypes within conditionally polymorphic lineages appears to be commonplace in the Dynastini (Rowland 2003) and other groups of scarabaeid beetles (Rowland and Emlen 2009), and these phylogenetic events can produce considerable difficulties for the taxonomists of affected groups (West-Eberhard 2003). Thus, the questions regarding *Eupatorus* framed above might best be addressed with robust phylogenetic methods including molecular analyses that incorporate all of the taxa concerned, and consulting the necessary type specimens. According to Endrödi (1976) the type of *A. siamensis* is lost, however Endrödi designated a neotype which he deposited in “meiner Sammlung”, and which is now possibly in the Hungarian Natural History Museum, Budapest. Endrödi (1976) further reported that the type specimen of *E. birmanicus* is in The Natural History Museum, London, as is the type of *E. gracilicornis* and the lectotype of *P. solidus*. The type of *Dynastes hardwickei* is in the Oxford University Museum.

Systematics

Tribe DYNASTINI MacLeay, 1819

Original spelling and citation: Dynastidae MacLeay, 1819: 64
Type genus: *Dynastes* MacLeay, 1819: 22

Subtribe DYNASTINA MacLeay, 1819, NEW STATUS

Original spelling and citation: Dynastidae MacLeay, 1819: 64
Type genus: *Dynastes* MacLeay, 1819: 22
Synonym: Megasominae Swainson, 1840: 210 [stem *Megasomat-*]. Type genus: *Megasoma* Kirby, 1825. Family-group name attributed to Imhoff (1856) in A. B. T. Smith (2006: 175); incorrect original stem formation, not in prevailing usage.
Type genus: *Megasoma* Kirby, 1825: 566

Subtribe XYLOTRUPINA Hope, 1845, NEW STATUS

Original spelling and citation: Xylotrupidae, Hope 1845: 7
Type genus: *Xylotrupes* Hope, 1837: ix

Subtribe CHALCOSOMINA, NEW SUBTRIBE

Original spelling and citation: Chalcosomina Rowland and Miller, 2012
Type genus: *Chalcosoma* Hope, 1837: 86

Tribe DYNASTINI MacLeay

Description. Endrödi (1985) constitutes the most recent comprehensive taxonomic review of the Dynastinae, in which he provides the following morphological description of the Dynastini relative to the other tribes of the subfamily: *"This tribe includes the biggest species of the whole family Melolonthidae. Most species display very strong sexual dimorphism. Horns of males often very long, head and pronotum [horns] in females usually almost absent. Fore legs of males mostly longer than in females. Also elytra in many species different: in male smooth, in female strongly sculptured. Mandibles mostly incised on apex, outer side straight or lobed. Antennae 10-jointed, club in both sexes short. Form of prosternal process highly variable. Propygidium either with or without a stridulatory area. Claw-joint of anterior tarsi strongly thickened only in Dynastes neptunus Quensel and D. satanas Moser; apex of basal-joint of hind tarsi rarely spiniformly produced."*

Subtribe DYNASTINA MacLeay

Included genera. *Augosoma* Burmeister, *Golofa* Hope, *Dynastes* Kirby, *Megasoma* Kirby.

Description. Clypeus mesal margin: deeply emarginate in *Augosoma*, entire to slightly emarginate in *Dynastes*, widely emarginate in *Megasoma* and slightly emarginate in *Golofa*. **Male cephalic horn apex:** Acuminate in *Augosoma, Dynastes* and *Golofa*, bifurcate in *Megasoma*. **Male cephalic horn armature:** Denticulate in *Augosoma, Dynastes* and some *Golofa*, adenticulate in *Megasoma* and some *Golofa*, serrate in most *Golofa;* armature is dorsal in all genera. **Male cephalic horn length in longest-horned species:** Long in all genera. **Male cephalic horn length of shortest-horned species:** Long in *Augosoma*, medium in *Dynastes*, short in *Megasoma* and *Golofa*. **Female frons:** Tuberculate and lateral in position in *Augosoma* and *Megasoma*, tuberculate and mesal in position in *Dynastes* and *Golofa;* tubercles large in *Augosoma* and *Megasoma* and small in *Dynastes* and *Golofa*. **Mandible incisor:** Denticulate in *Augosoma, Dynastes, Megasoma* and some *Golofa*, adenticulate in other *Golofa*; denticles asymmetrical and dominant denticle mesal in *Augosoma, Dynastes* and *Megasoma*, lateral in *Golofa*. **Maxillary lacinia:** Denticles mesally directed, usually number one to three in *Augosoma, Dynastes* and *Megasoma*, and four or more in most *Golofa*. **Dorsal pronotum of major males:** With single mesal horn or boss in *Augosoma, Dynastes, Megasoma* and most *Golofa*, and simply convex in some *Golofa*. **Mesal pronotal horns apex:** Apically bifurcate in *Augosoma, Dynastes* (even if inconsistently or minutely so), *Megasoma* and some *Golofa*, and apically acuminate in other *Golofa*. **Mesal pronotum dense pilosity:** Absent in *Augosoma*, present in *Dynastes, Megasoma* and *Golofa*. **Mesal pronotal accessory horns:** Paired lateral accessory horns present in *Augosoma* and most *Dynastes*, accessory horns absent in *Megasoma, Golofa* and one species of *Dynastes*. **Male anterior ventrolateral pronotal apices:** Not developed as horns in *Augosoma, Dynastes* and *Golofa*, developed as horns in *Megasoma*. **Male pronotal horn length of longest-horned species:** Long in *Augosoma, Dynastes* and *Golofa*, medium in *Megasoma*. **Male pronotal horn length of shortest-horned species:** Long in *Augosoma*, medium in *Dynastes,* absent in *Megasoma* and *Golofa*. **Pronotal architecture of female:** Vaguely complex in *Augosoma*, simply convex in *Dynastes, Megasoma* and *Golofa.* **Pronotal integument of male:** With some anastomosing sculpture in *Augosoma*, other genera without anastomosing sculpture. **Pronotal integument of female:** With considerable anastomosing sculpture in *Augosoma* and *Dynastes,* with little or no anastomosing sculpture in *Megasoma* and *Golofa*. **Prolegs:** Sexually dimorphic in *Augosoma, Dynastes* and some *Megasoma* and *Golofa;* sexually monomorphic in some small *Megasoma* and *Golofa*. **Elytra of female:** Dorsal integument essentially as in male in *Augosoma* and *Megasoma* and some *Dynastes* and *Golofa*, significantly different from male in some *Dynastes* and *Golofa*. **Dorsal integument color:** Uniformly dark red/brown/black in *Augosoma*, some *Dynastes* and *Megasoma*, colored in some *Dynastes* and *Golofa*. **Dorsal pilosity:** No species conspicuously hirsute in *Augosoma* and *Dynastes,* one species conspicuously hirsute in *Golofa*, several species conspicuously hirsute in *Megasoma*. **Paramere dorsal conjunction:** Without interdigitating teeth in *Augosoma, Dynastes* and *Golofa*, with interdigitating teeth in *Megasoma*. **Paramere apex:** Lateral contours converging inward. **Paramere apex setation:** Long and conspicuous. **Raspulae:** With enlarged, sclerotized plate in *Augosoma* and spines in some *Golofa*, without such structures in *Dynastes, Megasoma* and most *Golofa*.

Subtribe XYLOTRUPINA Hope

Included genera. *Allomyrina* Arrow, *Xylotrupes* Hope, *Trypoxylus* Minck, *Xyloscaptes* Prell.

Description. Clypeus mesal margin: Slightly emarginate in *Allomyrina*, deeply emarginate in *Xylotrupes*, widely emarginate in *Trypoxylus,* entire in *Xyloscaptes*. **Male cephalic horn apex:** Bifurcate in all genera. **Male cephalic horn armature:** Adenticulate in *Allomyrina* and some *Xylotrupes,* denticulate in *Trypoxylus, Xyloscaptes* and other *Xylotrupes*; denticles dorsal in some *Xylotrupes*, lateral in *Trypoxylus* and *Xyloscaptes*. **Male cephalic horn length of longest-horned species:** Medium in *Allomyrina* and *Xyloscaptes*, long in *Xylotrupes* and *Trypoxylus*. **Male cephalic horn length of shortest-horned species:** Medium in *Allomyrina*, *Trypoxylus* and *Xyloscaptes*, short in *Xylotrupes*. **Female frons:** Tuberculate with small tubercles in all genera; position mesal in *Allomyrina*, lateral in *Xylotrupes,* with both mesal and lateral tubercles in *Trypoxylus* and *Xyloscaptes*. **Mandible incisor:** Adenticulate in *Allomyrina, Trypoxylus, Xyloscaptes* and *Xylotrupes florensis*, denticulate in other *Xylotrupes*; mostly asymmetrical and laterally dominant. **Maxilla lacinia:** Denticulate in all genera; denticles directed mesally, numbering four or more in *Allomyrina* and *Xylotrupes,* and three or less in *Trypoxylus* and *Xyloscaptes*. **Dorsal pronotum of major males:** With single mesal horn in all genera except *Xylotrupes inarmatus*. **Mesal pronotal horns apex:** Apically bifurcate in all genera except *Xylotrupes inarmatus*. **Mesal pronotum dense pilosity:** Present only in *Allomyrina*. **Mesal pronotal accessory horns:** Present only in *Xylotrupes florensis*. **Male anterior ventrolateral pronotal apices:** Developed as horns only in *Allomyrina*. **Male pronotal horn length of longest-horned species:** Short in *Allomyrina and Trypoxylus,* medium in *Xyloscaptes*, long in *Xylotrupes*. **Male pronotal horn length of shortest-horned species:** Short in *Allomyrina* and *Trypoxylus*, medium in *Xyloscaptes*, absent in *Xylotrupes inarmatus*. **Pronotal architecture of female:** Complex in *Allomyrina, Trypoxylus* and *Xyloscaptes,* simply convex in *Xylotrupes*; architecture vague in *Allomyrina,* pronounced in *Trypoxylus* and *Xyloscaptes*. **Pronotal integument of male:** No anastomosing sculpture in any genus. **Pronotal integument of female:** Considerable anastomosing sculpture in *Allomyrina*, little anastomosing sculpture in *Xylotrupes, Trypoxylus* and *Xyloscaptes*. **Prolegs:** Sexually dimorphic in all genera. **Elytra of female:** Dorsal integument significantly different from male in *Trypoxylus*, essentially the same as in male in *Allomyrina, Xylotrupes* and *Xyloscaptes*. **Dorsal integument color:** Uniformly dark red/brown/black in all genera. **Dorsal pilosity:** Not conspicuous in *Trypoxylus* and *Xyloscaptes*, conspicuous in *Allomyrina* and *Xylotrupes pubescens*. **Paramere dorsal conjunction:** With interdigitating teeth in all genera; teeth strong, dominant tooth evaginates from left side into right side in *Allomyrina, Xylotrupes* and *Trypoxylus*; teeth weak, dominant tooth evaginates from right side into left side in *Xyloscaptes*. **Paramere apex:** Lateral contours parallel or diverging outward. **Paramere apex setation:** Long and conspicuous. **Raspulae:** With enlarged, sclerotized spines in all genera.

Subtribe CHALCOSOMINA, New Subtribe

Included genera. *Haploscapanes* Arrow, *Chalcosoma* Hope, *Beckius* Dechambre, *Eupatorus* Burmeister, *Pachyoryctes* Arrow.

Description. Clypeus mesal margin: Slightly emarginate in *Haploscapanes*, deeply emarginate in other genera. **Male cephalic horn apex:** Acuminate in all genera. **Male cephalic horn armature:** Adenticulate in some *Haploscapanes,* some *Chalcosoma* and all *Beckius, Eupatorus* and *Pachyoryctes*; denticulate in some *Haploscapanes* and some *Chalcosoma*. **Male cephalic horn length of longest-horned species:** Medium in *Haploscapanes*, long in other genera. **Male cephalic horn length of shortest-horned species:** Short in *Haploscapanes*, medium in *Eupatorus*, and long in *Chalcosoma*, *Beckius* and *Pachyoryctes*. **Female frons:** Atuberculate in *Chalcosoma*, tuberculate in other genera; tubercle mesal and large in *Pachyoryctes*, lateral and large in other genera. **Mandible incisor:** Adenticulate in all genera. **Maxillary lacinia:** Adenticulate in *Haploscapanes*, denticulate in other genera; denticles directed apically and mesally in *Beckius* and *Eupatorus*, mesally in *Chalcosoma* and apically in *Pachyoryctes*; denticles number less than four in *Chalcosoma,* four or more in *Beckius* and *Eupatorus*. **Dorsal pronotum of major males:** With paired horns, bosses or carinae that vary from mesal to lateral, except *Haploscapanes barbarossa* and *H. enermis* in which the dorsal pronotum is simply convex. **Mesal pronotum dense pilosity:** Absent in all genera. **Male anteroventrolateral pronotal apices:** Horns absent in *Haploscapanes, Chalcosoma* and *Beckius,* equivocal in *Pachyoryctes*, developed *Eupatorus*. **Male pronotal horn length of longest-horned species:** Short in *Haploscapanes* and *Pachyoryctes*, medium in *Eupatorus*, long in *Chalcosoma* and *Beckius*. **Male pronotal horn length of shortest-horned species:** Absent in *Haploscapanes,* short in *Chalcosoma, Eupatorus* and *Pachyoryctes*, long in *Beckius*. **Pronotal architecture of female:** Not seen in *Pachyoryctes*, in other genera simply convex. **Pronotal integument of male:** No anastomosing sculpture in *Chalcosoma*, *Eupatorus* and *Pachyoryctes*, some anastomosing sculpture in *Haploscapanes* and *Beckius*. **Pronotal integument of female:** Considerable anastomosing sculpture in *Haploscapanes*, *Chalcosoma, Beckius, Eupatorus* and not seen in *Pachyoryctes*. **Prolegs:** Sexually monomorphic in *Pachyoryctes*, sexually dimorphic in other genera. **Elytra of female:** Integument significantly different from male in *Chalcosoma*, essentially same as in male in *Haploscapanes, Beckius* and *Eupatorus*, not seen in *Pachyoryctes*. **Dorsal integument color:** Uniformly dark red/brown/black in *Haploscapanes* and *Pachyoryctes*, colored in *Chalcosoma*, *Beckius* and *Eupatorus*. **Dorsal pilosity:** No genera with conspicuously hirsute species. **Paramere dorsal conjunction:** Without interdigitating teeth in all genera. **Paramere apex:** Lateral contours converging inward. **Paramere apex setation:** Nearly absent, or short and inconspicuous. **Raspular complex:** Without enlarged, sclerotized spines in all genera.

Key to subtribes and genera of Dynastini

The key is based on the morphology of males that fully express the secondary sexual traits.

1. Apex of cephalic horn acuminate (*Augosoma, Dynastes, Golofa, Haploscapanes, Eupatorus, Beckius, Pachyoryctes, Chalcosoma*) or bifurcate (*Allomyrina, Xylotrupes, Trypoxylus, Xyloscaptes, Megasoma*); if acuminate then pronotum has a medial horn (*Augosoma, Dynastes, Golofa*) or is essentially hornless (female-like *Golofa*); if essentially hornless then anterolateral pronotal integument is immaculate to punctate (*Golofa*), never cristate and distinctly anastomosing (as in *Haploscapanes*), and mandibular incisors are bidentate (with rare exceptions); lateral contours of paramere apex converging inward (Dynastina) or parallel to diverging outward (Xylotrupina) .... **2 (Dynastina MacLeay and Xylotrupina Hope)**

— Apex of cephalic horn acuminate (*Haploscapanes, Eupatorus, Beckius, Pachyoryctes, Chalcosoma*); pronotum without a medial horn (*Haploscapanes, Eupatorus, Beckius, Pachyoryctes, Chalcosoma*). or with paired more or less medial horns (*C. mollenkampi, E. birmanicus*), or with more or less lateral horns (*C. atlas, C. caucasus, Beckius*, all other *Eupatorus*), or with horn-like transverse lateral carinae (*Pachyoryctes*); if pronotum is essentially female-like, without obvious male ornaments, then anterolateral pronotal integument is anastomosing and cristate (*Haploscapanes barbarossa, H. inermis*); lateral contours of paramere apex converging inward (except *Beckius*) and apex setation absent or nearly so; mandibular incisors adenticulate .... **9 (Chalcosomina, new subtribe)**

2(1). Cephalic horn apex acuminate (*Augosoma, Dynastes, Golofa*) or bifurcate (*Megasoma*); if bifurcate then mandibular incisor denticles diverge strongly, usually at least 45°; mesal pronotal horn or boss present (*Augosoma, Dynastes*, most *Megasoma*, most *Golofa*) or absent (female-like *Megasoma* and *Golofa*); if horn or boss absent then mandibular incisor denticles diverge strongly as above (*Megasoma*) and paramere blades are on a similar plane as or below that of paramere orifice (*Megasoma, Golofa*); pronotal medial horn or medial boss usually with dense ventral pilosity; lateral contours of paramere apex converging inward; Africa, America .... **3 (Dynastina MacLeay)**

— Cephalic horn bifurcate; mandibular incisor adenticulate (*Trypoxylus, Xyloscaptes, Allomyrina, Xylotrupes florensis*) or denticulate and denticles diverge at most 30° (other *Xylotrupes*); pronotal horn lacking dense pilosity (*Xylotrupes, Trypoxylus, Xyloscaptes*) except when entire dorsal surface of body is densely hirsute (*Allomyrina*); lateral contours of paramere apex parallel or diverging outward; Asia .... **6 (Xylotrupina Hope)**

3(2). Pronotum with ventrolateral undercut carinae; mesal pronotal horn without ventral dense pilosity; anterolateral pronotal integument with anastomosing, cristate sculpture; Africa .... ***Augosoma* Burmeister**

— Pronotum without such ventrolateral carinae; mesal pronotal horn usually with ventral dense pilosity; anterolateral pronotal integument without anastomosing, cristate sculpture **4**

4(3). Cephalic horn apex bifurcated to form two lateral tines; mandibular incisor denticles usually diverge at least 45°; anterior margin of clypeus broadly emarginate, forming two widely separated denticles; America .... ***Megasoma* Kirby**

— Cephalic horn apex acuminate; mandibular incisor denticles diverge at most 30°; anterior margin of clypeus narrowly emarginate or not emarginate **5**

5(4). Relative size of mandibular incisor denticles subequal; when a pronotal horn present then angle between posterior pronotal margin and apex of pronotal horn at least 30° (may be up to 80°); in species with pronotal horn, cephalic horn has weakly to strongly serrated lateral margins; cephalic horn rarely with multiple medial denticles (*G. eacus, G. spatha*); pronotal horn without laterally paired accessory horns; America .... ***Golofa* Hope**

— Relative size of mandibular incisor denticles varies from strongly positive to strongly negative; angle between posterior pronotal margin and apex of pronotal horn at most 10°; cephalic horn without serrated dorsolateral margins; with one or more dorsomedial denticles (often weak or obscure in *D. tityus*); pronotal horn with laterally paired accessory horns (except *D. satanas*); America c .... ***Dynastes* Kirby**

6(2). Plane of paramere blades strongly angled toward paramere orifice, or parameres with strong frontal notch (*X. florensis*); with two strongly sclerotized raspulae of similar structure, or if only one raspula then basal metatarsomere dorsally strongly acuminate (*X. florensis*); pronotal horn with basolateral carinae [obscure in small taxa] or, rarely, basolateral denticles (*X. florensis*); pronotal horn apex extends beyond cephalic horn apex in large species; Asia .... ***Xylotrupes* Hope**

— Plane of paramere blades essentially same as or below that of paramere orifice; with at least one sclerotized raspular spine, if two spines then they are grossly dissimilar in structure; pronotal horn without basolateral carinae or denticles; pronotal horn apex never extends to cephalic horn apex **7**

7(6). Small species, at most 40mm in total length; dorsal integument heavily hirsute; protarsal claws distinctly asymmetrical; Asia .... ***Allomyrina* Arrow**
— Large species, at least 50mm and up to 85mm in total length; dorsal integument nearly immaculate or finely hirsute; protarsal claws symmetrical or essentially so **8**
8(7). Cephalic horn very long (~ 25mm), apex divided into four lateral tines; pronotal horn short, narrow; Asia .... ***Trypoxylus* Minck**
— Cephalic horn of moderate length (~ 15mm), apex bifurcated into two lateral tines and with two lateral denticles at midlength; pronotal horn stout, short; Asia .... ***Xyloscaptes* Prell**

9(1). Pronotum with one pair of dorsolateral horns and a basomedial horn directed horizontally over base of cephalic horn; Asia .... ***Chalcosoma* Hope**
— Pronotum without horns or with one or two pairs of horns, but without a basomedial horn directed over base of cephalic horn **10**

10(9). Anterior margin of clypeus nearly entire, not forming denticles; pronotum simply convex (*H. inermis*), or with one pair of lateral bosses or incipient horns (*H. barbarossa*), or with well-developed lateral horns (*H. australicus*); anterior and basolateral pronotal integument with strong, anastomosing, cristate sculpture; dorsal integument uniformly colored, pronotum and elytra reddish brown; Asia .... ***Haploscapanes* Arrow**
— Anterior margin of clypeus strongly and narrowly emarginate, forming two conspicuous denticles; pronotum with one pair of dorsolateral horns (*Beckius*), or dorsolateral carinae (*Pachyoryctes*), or with two pairs of horns (*E. gracilicornis, E. siamensis, E. birmanicus,* most *E. hardwickei*), or one pair of basolateral horns (some *E. hardwickei*); anterior and basolateral pronotal integument sparsely punctate, without anastomosing, cristate basolateral sculpture; dorsal integument bicolored, pronotum black or nearly so, elytra reddish brown to yellowish orange **11**

11(10). Pronotum with a pair of transverse dorsolateral carinae; prothoracic legs essentially sexually monomorphic; elytra dark reddish brown; Asia .... ***Pachyoryctes* Arrow**
— Pronotum with one or two pairs of lateral horns; prothoracic legs decidedly sexually dimorphic; elytra yellowish orange or reddish brown **12**

12(11). Pronotum with two pairs of horns; Asia .... ***Eupatorus* Burmeister** (*E. gracilicornis, E. birmanicus, E. siamensis,* most *E. hardwickei*)
— Pronotum with one pair of horns **13**

13(12). Pronotal horns basolateral; lateral contours of paramere apex converging inward; Asia .... ***Eupatorus* Burmeister** (Himalayan *E. hardwickei*)
— Pronotal horns dorsolateral and with marginal spines; lateral contours of paramere apex diverging outward, nearly circular; Asia .... ***Beckius* Dechambre**

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