A dichotomous key based on cranial, mandibular and dental anatomy for identifying the skull of living rhinoceroses (Perissodactyla, Rhinocerotidae)

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Abstract

Rhinoceroses are a greatly endangered group of animals and research is rendered difficult by the scarcity of specimens available for study. Museums, in particular, often have old specimens in store for which the documentation has been lost. Correct identification of these specimens will definitely enlarge our study sample of rhinoceroses without requiring further collection in the wild. In this paper I offer an identification key for rhinoceros skulls. Though rhinoceroses have been studied for a long time, I found that no work bringing together a wealth of anatomical data with the view of a quick skeletal identification was ever published. I believe that this key will be particularly useful to identifying rhinoceros skulls of unknown provenance that may be located in provincial museums and old collections. The fast rate of disappearance of rhinoceroses makes such identifications invaluable for their study and conservation efforts. This work may be considered a large review of data available in the literature, but in the format of a key. It follows a particular taxonomic classification, and I include a classification of rhinoceroses.

Key-words: rhinoceros skull; skull anatomy; taxonomic identification; discrete characters; continuous characters

Introduction

Rhinoceroses are a greatly endangered group of animals. No less than three subspecies of the recognised six species (Groves & Grubb 2011; Groves *et al.* 2010) are thought to have disappeared in the 20th century (Groves & Grubb 2011; Rookmaaker & Groves 1978; Rookmaaker 1997), and one already in the 21st century (Brook *et al.* 2011, 2012). Four species are today critically endangered (IUCN 2015), with one, *Ceratotherium cottoni* Lydekker, 1908, having only three living individuals left (San Diego Zoo Global 2015). Their scarcity makes research into many aspects of their biology difficult due to the near impossibility of collecting wild specimens. It follows that rhinoceros material already present in lesser-known collections, or stored away in museum reserves is irreplaceable and invaluable (Gippoliti *et al.* 2013; Groves & Chakraborty 1983; Groves & Leslie 2011). In particular, small museums and private collections may house specimens of considerable importance, with specimen and its documentation often separated (Casas-Marce *et al.* 2012; Watson & Werb 2013). Nevertheless, even when full documentation has been retained, the importance of finding and correctly identifying unknown rhinoceros material in already existing museum collections cannot be overemphasised.

Here I offer a dichotomous key for the identification of extant rhinoceroses, based solely on cranial, mandibular and dental anatomy, reviewed from the literature. This key is not intended to be an evolutionary view of extant species, and thus it must not be regarded in any way as a proposed phylogeny. It merely considers taxonomic distinctions that can be made among taxa according to

modern comparative anatomy. I will not consider characters such as geographic provenance, life history traits, behaviour, or other traits external to bony anatomy of the skull.

Rhinoceros skulls are easy to distinguish from other mammalian skulls, not only for their shear large size, but also for their shape and characteristic horn. I will start off the dichotomous key with the horn or, more specifically, the number of horns, what is perhaps the most distinctive feature among rhinoceroses. Of the six extant species of rhinoceros, two have only one horn, while the four others have two. Female horns are generally smaller than those of males (Groves 1971), and they are totally absent in females of the species *Dicerorhinus sumatrensis* G. Fischer [von Waldheim], 1814 (Groves & Kurt 1972). An abnormal three-horn condition seems to occur rarely in *Diceros bicornis* Linnaeus, 1758 (Hillman-Smith & Groves 1994). Horns are often found isolated in museum reserves, but are too variable among themselves and among different species to be convincingly identified when no other information is available (but see Groves 1971); thus, characters in horns will not be used in this dichotomous key. In the absence of horns *in situ*, the number of horns can be ascertained by looking at the rugose regions of the nasals and frontal; the frontal bone being smooth in species that have only the nasal horn (Groves & Leslie 2011; Laurie *et al.* 1983).

Apart from the number of horns, another separation may be readily achieved: African species can be straightforwardly separated from Asian species, not only geographically, but also by a number of anatomical characters. For example, no rhinoceros has canine teeth, but the three Asian species have tusk-like anterior mandibular teeth that look like canines but are in fact incisors (Groves 1967b). In museum specimens, the cranium or the mandible are sometimes found without some of the teeth, which fall off during museum preparations (Groves & Leslie 2011). Nevertheless, this key will report characters relating to those anatomical parts. I confine myself as much as possible to those characters which are clearly distinct between taxa; I do not attempt to make a complete description of each taxon, and I invite interested readers to refer to the original literature for more in-depth details. This key considers skulls belonging to fully adult individuals only.

Methods

The dichotomous key presented here feeds largely on the existing literature containing descriptions of the anatomy of *Rhinoceros* (Chakraborty 1972; Flower 1876; Groves & Chakraborty 1983; Groves & Guérin 1980; Groves & Leslie 2011; Groves 1967b, 1982; Guérin 1980; Laurie *et al.* 1983; Pocock 1945; Rookmaaker 1980, 1983, 1997; Yan *et al.* 2014), *Dicerorhinus* (Amato *et al.* 1995; Chakraborty 1972; Flower 1876; Groves & Chakraborty 1983; Groves 1967b; Guérin 1980; Pocock 1945; Yan *et al.* 2014; Zainuddin *et al.* 1990), *Diceros* (Groves 1967a; Harley *et al.* 2005; Hillman-Smith & Groves 1994; Rookmaaker & Groves 1978; Rookmaaker 1995), and *Ceratotherium* (Groves 1975; Groves *et al.* 2010; Robinson *et al.* 2005). Surveys of all Asian species exist (Chakraborty 1972; Groves & Chakraborty 1983; Groves 1982), and broad surveys of several aspects of all rhinoceroses are also available (Amin *et al.* 2006; Groves 1971, 1983, 1997; Willerslev *et al.* 2009).

I will follow the classification of Groves and Grubb (2011), who consider *Ceratotherium cottoni* a full species (rather than a subspecies of *Ceratotherium simum*) and eight subspecies of *Diceros bicornis*. I will attempt to bring identification down to the subspecies level, and for this I will follow mostly (Groves & Grubb 2011; Groves & Kurt 1972; Groves 1982; Laurie *et al.* 1983). A taxonomic classification of the species and subspecies considered in this dichotomous key is provided next; the symbol † denotes a taxon declared extinct, extinct in the wild or technically extinct.

Classification

Ordo Perissodactyla Owen, 1848
- Familia Rhinocerotidae Gray, 1821
  - Genus *Rhinoceros* Linnaeus, 1758
    - Species *Rhinoceros unicornis* Linnaeus, 1758
    - Species *Rhinoceros sondaicus* Desmarest, 1822
      - Subspecies *Rhinoceros sondaicus annamiticus* Heude, 1892 †
      - Subspecies *Rhinoceros sondaicus inermis* Lesson, 1838 †
      - Subspecies *Rhinoceros sondaicus sondaicus* Desmarest, 1822
  - Genus *Dicerorhinus* Gloger, 1841
    - Species *Dicerorhinus sumatrensis* G. Fischer [von Waldheim], 1814
      - Subspecies *Dicerorhinus sumatrensis harrissoni* (Groves, 1965)
      - Subspecies *Dicerorhinus sumatrensis lasiotis* Buckland, 1872
      - Subspecies *Dicerorhinus sumatrensis sumatrensis* (G. Fischer [von Waldheim], 1814)
  - Genus *Ceratotherium* Gray, 1868
    - Species *Ceratotherium cottoni* (Lydekker, 1908) †
    - Species *Ceratotherium simum* (Burchell, 1817)
  - Genus *Diceros* Gray, 1821
    - Species *Diceros bicornis* Linnaeus, 1758
      - Subspecies *Diceros bicornis bicornis* (Linnaeus, 1758) †
      - Subspecies *Diceros bicornis brucii* (Lesson, 1842)
      - Subspecies *Diceros bicornis chobiensis* Zukowsky, 1965 †
      - Subspecies *Diceros bicornis ladoensis* Groves, 1967
      - Subspecies *Diceros bicornis longipes* Zukowsky, 1949
      - Subspecies *Diceros bicornis michaeli* Zukowsky, 1965
      - Subspecies *Diceros bicornis minor* (Drummond, 1876)
      - Subspecies *Diceros bicornis occidentalis* (Zukowsky, 1922)

Dichotomous Key

1 One horn (underlying bone rugose). Nasal bones anteriorly pointed. Dorsal outline of the cranium strongly concave. Occipital plane very wide, forming a flat-topped triangle in posterior view, and strongly concave, sloping anteriorly in lateral view. Occipital bone near the occipital condyle, and the condyles very prominent. Foramen magnum more or less triangular. Closure of subaural channel by union of postglenoid and posttympanic processes below the external auditory meatus. Lacrimal bridge ligamentous (not ossified). Incisors present (upper incisors block-like, mandibular incisors tusk-like. … genus ***Rhinoceros***, 2

- Two horns (underlying bone rugose). Nasal bones anteriorly truncated or pointed. Dorsal outline of the cranium not strongly concave. Occipital plane narrow and not concave. Foramen magnum not triangular. No closure of subaural channel; postglenoid and posttympanic processes not united below the external auditory meatus. Lacrimal bridge invariably ossified. Incisors present (either block and tusk-like or rudimentary) or absent. … other genera, 5

2 Basal length of the cranium always > 600 mm. Premaxilla broad and fused to maxilla. Vomer thick and its posterior part fused lateraly to pterygoids. Mesopterygoid fossa narrow, with the bases of the pterygoid wings almost touching posteriorly. Distance between opisthion and inion > 190 mm. Nasal bones forming an expanded, rounded and rugose nasal boss; nasal width rarely < 110 mm. Posterior margin of palate lacking a median projection. Maxillary toothrow length > 241 mm. Crown height of unworn M^1-M^2 58-72 mm; crowns of cheekteeth wear into a uniformly flat plane instead of ridges. Maxillary premolars and molars not shaped like the Greek letter π; crista generally well developed; crochet and crista unite with wear, cutting off an accessory valley from the medisinus; cingulum absent; protocone fold present; parastyle buttress not pronounced; ectoloph flat; M^3 triangular without metacone bulge. … species ***Rhinoceros unicornis***

- Basal length of the cranium always < 600 mm. Premaxilla narrow and unfused to maxilla (except in very old individuals). Vomer slim and its posterior part not fused laterally to pterygoids (except in very old individuals). Mesopterygoid fossa wide. Distance between opisthion and inion < 190 mm. Nasal bones narrow, smooth and not forming a nasal boss; nasal width rarely > 110 mm. Posterior margin of palate with a pronounced median projection. Maxillary toothrow length < 241 mm. Crown height of unworn M^1-M^2 46-53 mm; crowns of cheekteeth wear into ridges instead of a uniformly flat plane. Maxillary premolars and molars shaped like the Greek letter π; crista rudimentary or absent; crochet and crista almost never unite with wear; a remnant of cingulum present; protocone fold absent; parastyle buttress pronounced; ectoloph sinuous. … species ***Rhinoceros sondaicus***, 3

3 Palatine bones occupying a larger proportion of the hard palate, > 80 % of the total palate length posterior to the incisive foramina; palatine bones 50–80 % as wide as long. P^2 protoloph remaining separate from the ectoloph, apparently throughout life; anterior premolars (probably actually milk molars) shedding before maturity; crochet on the premolars usually not doubled; crista present on the premolars, absent from the molars. Mandibular corpus noticeably deepening posteriorly, its depth at M_3 167% of that at P_2. Horn absent in females. … subspecies ***Rhinoceros sondaicus inermis***

- Palatine bones occupying a smaller proportion of the hard palate, < 80 % of the total palate length posterior to the incisive foramina; palatine bones 50–80 % as wide as long. P^2 protoloph fusing with the ectoloph with wear; anterior premolars (probably actually milk molars) remaining in place for much of the animal's adult life; crochet on the premolars doubled or not doubled (usually not doubled); crista present or absent on the premolars and molars. Mandibular corpus not greatly deepening posteriorly, its depth at M_3 111–144 % of that at P_2. Horn present in females … other subspecies, 4

4 Nuchal surface more inclined anteriorly. Facial skeleton relatively low, with a comparatively deep dorsal concavity. Palatine bones 39–63 % of the total palate length posterior to the incisive foramina; palatine bones 36–66 % as wide as long. Crochet on the premolars usually not doubled; crista usually absent on the premolars, but usually present, though small, on the molars … subspecies ***Rhinoceros sondaicus annamiticus***

- Nuchal surface less inclined anteriorly. Facial skeleton relatively low, but flat or without a deep dorsal concavity. Palatine bones 44–53 % of the total palate length posterior to the incisive foramina; palatine bones > 80 % as wide as long, and usually longer. Crochet on the premolars usually doubled; crista on the premolars usually much reduced or absent, and absent on the molars … subspecies ***Rhinoceros sondaicus sondaicus***

5 Frontal horn placed some distance from nasal horn, over the eye or even posterior to eye; bases of horns not continuous. The nasal bones are anteriorly pointed. Cranium elongated anterior to orbit, shortened posteriorly. Occipital plane narrow, somewhat rectangular in posterior view, and more or less vertical in lateral view. Presence of a pair of large, block-like upper incisors, with a much smaller lateral pair (at least in young adults); mandibular central incisors lacking; lateral incisors tusk-like. The foramen magnum is pear-shaped, its dorsal rim reduced upward into a narrow prolongation. … genus ***Dicerorhinus***, species ***Dicerorhinus sumatrensis***, 6

- Frontal horn placed closer to nasal horn; bases of horns sometimes continuous. The nasal bones are much thickened, and anteriorly truncated. Cranium not elongated anterior to orbit. Occipital plane narrow, extending backward in lateral view, and overhanging the occipital condyles posteriorly. Incisors rudimentary (possibly only deciduous) or absent. Both jaws abbreviated anteriorly. The foramen magnum is more oval, flattened dorsoventrally. … … other genera, 8

6 Occiput broad and high. Very large size. Teeth proportionately very large. … subspecies ***Dicerorhinus sumatrensis lasiotis***

- Occiput narrow. … other subspecies, 7

7 Occiput narrow, high and forwardly inclined. Small size. Teeth small. … subspecies ***Dicerorhinus sumatrensis harrissoni***

- Occiput narrow and low. Large size. Teeth medium to small. … subspecies ***Dicerorhinus sumatrensis sumatrensis***

8 Frontal horn placed somewhat behind the nasal horn; bases of horns rarely continuous. Cranium extremely elongated posteriorly to orbit; occipital crest enormously prolonged posteriorly. Dorsal outline of the cranium less concave. Nasal bones broad, short and high. Antorbital process quadrangular in form. Incisors absent. Premolars occupy 43–47 % of the toothrow; protoloph and metaloph on upper premolars and molars strongly curved backward, fusing with wear; crista present on upper premolars and M^1, united early with crochet. Mandible with convex lower border; mandibular symphysis very broad and spatulate; the ascending ramus more backwardly inclined; no marked angulation at gonion. … genus ***Ceratotherium***, 9

- Frontal horn placed immediately behind the nasal horn; bases of horns sometimes continuous. Cranium not elongated; occipital crest less prolonged posteriorly. Dorsal outline of the cranium more concave. Nasals steep and hump. Antorbital process mastoid in form. Incisors absent or rudimentary. Premolars occupy 39–45 % of the toothrow; protoloph and metaloph on upper premolars and molars not strongly curved backward, rather at right angles to ectoloph; crista generally absent from molars. Mandibular symphysis narrow; mandibular corpus robust and heavy; the ascending ramus not backwardly inclined; no angular prominence. … genus ***Diceros***, species ***Diceros bicornis***, 10

9 Dorsal concavity of the cranium 33–57 mm. Maxillary toothrow 236–280 mm. … species ***Ceratotherium cottoni***

- Dorsal concavity of the cranium 55–75 mm. Maxillary toothrow 270–305 mm. … species ***Ceratotherium simum***

10 Infraorbital foramen never bifid. … several subspecies, 11

- Infraorbital foramen always or often bifid. … several subspecies, 12

11 Broad-skulled, especially across the occipital crest. Crista on the upper premolars absent or very minute. Mandibular P_1 absent. … subspecies ***Diceros bicornis ladoensis***

- Relatively broad-skulled. Crista on the upper premolars absent or very minute. Mandibular P_1 absent. … subspecies ***Diceros bicornis michaeli***

12 Crista absent on premolars. … several subspecies, 13

- Crista present on premolars (especially P^3 and P^4). … several subspecies, 15

13 Infraorbital foramen always bifid. Crochet on premolars often double. Crista on the upper premolars absent or very minute. Mandibular P_1 absent in the adults from East Africa, but retained in 60 % of those from Hluhluwe (South Africa). … subspecies ***Diceros bicornis minor***

- Crochet often double, but sometimes simple. … other subspecies, 14

14 Infraorbital foramen always bifid. Crista on the upper premolars absent or very minute. … subspecies ***Diceros bicornis chobiensis***

- Cranium much broader across the zygomata. Crista on the upper premolars absent or very minute. … subspecies ***Diceros bicornis occidentalis***

15 Infraorbital foramen always bifid. Crista present on upper premolars. Mandibular P_1 always absent in adults. … subspecies ***Diceros bicornis bicornis***

- Mandibular P_1 retained in adults… other subspecies, 16

16 Cranium very narrow across the zygomata. Infraorbital foramen often bifid. Crochet on the maxillary premolars simple, not double. Crista present on upper premolars. … subspecies ***Diceros bicornis brucii***

- Wide, square base to the horns; shorter occipital crest. Infraorbital foramen often bifid. Crochet on the maxillary premolars simple, not double. Crista present on upper premolars. … subspecies ***Diceros bicornis longipes***

Discussion and Conclusion

This paper proposes a dichotomous key for rhinoceros taxa focusing on the anatomy of the dry cranium, mandible and teeth. Many differences among rhinoceroses can be found on the cranium alone. Museums and other collections often find themselves at odds with old specimens; rarely do these specimens retain any trustworthy information regarding classification, age at death, sex, provenance, etc. This simple key provides an aid to overcome some of these shortcomings. Since museums do not always have expert zoologists available or the means to engage them, it is my hope that this dichotomous key will aid anyone with some knowledge of anatomical terminology to correctly identify species and subspecies of rhinoceroses among unlabelled or mislabelled specimens, with a minimum of time and effort. However, consultation of the original literature on apomorphic characters would be advised for a more detailed study of each rhinoceros taxon. Furthering the scientific knowledge of these animals will assuredly contribute to prevent their irreversible disappearance.

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