Phylogeny of the living species of Rhinoceros

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Introduction

Terrelationships of the living rhinoceros species are disputed. Simpson (1945) separated the single-horned Rhinoceros (including both R. unicornis and R. sondaicus) in a subfamily rhinocerotinae from the double-horned Dicerorhinus, Diceros and Ceratotherium (subfamily Dicerorhininae). Pocock (1945 b) saw the relationships differently: for him Dicerorhinus (which he called Diceromeraeus) belonged in the Rhinocerinae (as he called it), separate from the two African genera which he placed in a subfamily Dicerinae. Groves (1965) followed Pocock, proposing some synapomorph features, perhaps not entirely convincingly; while Loose (1982) followed Simpson, but within the Dicerorhininae parted out two tribes, Dicerorhinini for Dicerorhinus (with the fossil Coelodonta) and cerotini for the two African genera. Guerin (1980, 1982) placed the living genera in three families: Rhinocerotinae, Dicerorhininae (to include also Coelodonta) and Dicerotinae. Finally Heissig (1973) placed them all, with a further fossil genus Stephanorhinus, in a single subfamily with no tribes.

To an extent, these differing classifications reflect their proponents' varying concerns ith fossil as much as extant members of the Rhinocerotidae. Simpson's two subfamilies are real with a number of subfamilies erected for distinctive fossil groups; the same is true of Guerin's three subfamilies, although the additional fossils considered by that author do not seem quite such a wide variety. Heissig's concern was to place all Rhinocerotidae in a phylogenetically based scheme, and he was impressed with the evident synapomorphies between the living rhinos (and their relatives) and the extinct elasmotheres; these two groups were therefore combined into a single subfamily, separated only at tribal level—hence there as no further scope for subdivision, even had such been thought desirable.

With so much disagreement, then, it seems worthwhile to attempt to draw up a list of differentiating characters within the living rhinos, and assess their phyletic status, apomorph (derived) or plesiomorph (= primitive). [Both Heissig (1981) and Guerin (1982) have cently attempted this also, but neither found himself able to come to a very definite inclusion for a number of reasons (discussed below).] When this has been done, a
Phylogeny of the living rhinos should emerge, and their admitted fossil relatives can be compared both as a test of the more narrowly based conclusions and for their own intrinsic interest. There are further problems to be considered before a cladistic analysis can be undertaken. These are, briefly, as follows:

1. The unity of the genus Rhinoceros. Of modern authors, only Heckel (1972 a, 1973, 1981) has challenged the assumption that R. unicornis and R. sondaicus are congeneric; he notes that, if they are separated, the name Euarhinoceros Grant, 1867, is available for the latter. From his cladistic analysis (1981) he concluded it was as reasonable to view them as having evolved in parallel as from a common ancestor; in particular the cheekteeth of R. unicornis would be best understood as a high-crowned specialization of the primitive Dicerorhinus type, rather than of the R. sondaicus morphology which recalls that of African rhinos in a number of characters. Earlier (1972 a) he had felt able to recognize Euarhinoceros alongside the other two Asian genera in Lower Siwalik deposits (Middle or Upper Miocene) of Pakistan.

It is true that the differences in the cheekteeth of the two single-horned rhinos are very considerable. It is also true, however, that there is variability, and that some of the features relied upon to differentiate the two by Heckel (1972 a) fall away when larger series are examined. Apart from the dentition there are characteristic differences in the skull, but the majority of these differences are reflections of the more specialized morphology of R. unicornis and/or the neotenic condition of the R. sondaicus morphology (a topic which will be detailed in a future paper). They share such a large number of clearly derived states, all those listed under Rhinoceros in Table 1, that they can be taken together in almost all respects, and their monophyly is thoroughly supported. They are henceforth treated as congeneric.

2. The generic status and interrelationships of the African rhinos. The two African species have occasionally been treated as congeneric (Ellerman et al. 1952), but the differences between them are more striking than between the two single-horned species of Asia, and their generic separation as Dicerorhinus (for D. bicornis) and Ceratotherium (for C. simum) is supported by both morphological (Cave 1962) and palaeontological grounds (House 1972). There is, none the less, no question but that they are closely related, and they are here treated as a single group with clear synapomorphy states.

3. The content of the genus Dicerorhinus. The type species, D. s. sumatrensis, is commonly considered to retain a large number of primitive character states (Groves 1965; Guerin 1980), helping to explain both why it is so difficult to classify in relation to the other two species-groups and why so many fossil species have been allocated to the genus. Guerin (1980 a) and Leakey (1982) both continue to refer the European Pleistocene and Miocene species, typified by D. etruscus, to the genus, while Kreitser (1942) and Heckel (1973, 1981) place them in a separate genus Stephanorhinus. As these latter are quite evidently a close-knit group (pace Kreitser (1942) in the case of the species hemiteocheus, and Heckel (1981) in the case of the species kirchbergensis) they are treated together here, and separate from Dicerorhinus. Other species commonly referred to Dicerorhinus are the Miocene species D. schleiermacheri (for which the generic name D. schleiermacheri, 1872 is available if required), D. sansaniensis [recently allocated to a separate genus Lartetotherium by Ginsburg (1974)], and D. leakeyi [said by its describer (House 1966) to be closely allied to sansaniensis]. The status of the latter two will be examined below. In this paper, whenever just “Dicerorhinus” is referred to, the extant D. s. sumatrensis alone is meant.

4. Other taxa referable to the lineages of living species. The genus Coelodonta is considered by Guerin (1982, 1983) to be merely the most highly evolved representative of the European “Dicerorhinus” lineage; Heckel (1981) on the other hand regards most of the resemblances as convergent; they agree, however, that the genus does align itself with the grouping that contains both the European “Dicerorhinus” (Heckel’s genus Stephanorhinus) and the living species. Paradicerorhinus of the Kenya Miocene was-plausibly referred to the Dicerorhinus lineage by its describer (House 1968). The only other fossil rhinos to be universally associated with the general grouping containing the living species are the Siwalik Gaidatherium spp. and “R.” playfairii. Colbert (1934) erected the genus Gaidatherium (for G. browni, n. sp, from the Chinti Formation of the Siwaliks; Heissig (1972 a) added a new species yardii, but reduced the genus to subgeneric rank under Rhinoceros. The species playfairii, referred to Coelodonta by Colbert (1935), was raised to generic rank as Panatherium by Khan (1971), but retained in Rhinoceros by Heissig (1972 a). In the present study a case for reference of all these taxa will be referred to by the generic names which have been awarded to them.

Material and methods

Skulls and skeletons of the five living rhinos species have been examined in collections all over the world. Most important in its coverage is the collection of the British Museum (Natural History); specimens from other collections will be mentioned and figured as appropriate. Skulls of Coelodonta and Stephanorhinus have been examined in the British Museum (Natural History); of Panatherium, in the British Museum and in the Punjab University, Chandigarh; of Lartetotherium, in the Museum National d’Histoire Naturelle, Paris, and in the Bavarian Staatsammlung für Paläontologie und Historische Geologie. Excellent descriptions and figures of further material are available in the literature, especially Guerin (1982).

The distinguishing characters of the five living species were listed and compared, by the method of Cladistic Analysis (Groves 1982). The ungroup chosen for comparative purposes was Acratherium; this was deemed most appropriate in that 1. the genus is known by a number of well preserved specimens and 2. there is no question of its phylectic distinctness. Where reference to Acratherium failed to resolve polarity in particular cases other Perissodactyls (Protherium, Ceratotherium, even living Tapiridae and Equidae) were examined and the most consistent interpretation adopted.

Results

Interrelationships of living genera

The results of the analysis, as far as concern the living rhinos, are presented in the Table. Many of the characters used are those traditionally employed to differentiate the taxa, but some are not; a few notes are required on each character.

1. Orientation of occipital crest. In Asian rhinos the occipital crest and nuchal surface slope forward — markedly so in Rhinoceros — while in African rhinos the slope is backward. Outgroup comparison indicates that both states are derived, the primitive condition being vertical.

2. Orbitonasal length in relation to orbitosurial. First used by Pocock (1945) to discriminate the two Asian genera, this measure of facial shortening unites Rhinoceros and the African genera, as pointed out by Guerin (1982).

3. Length of nasal aperture. This index, devised by Ehrlich (1972), is another indicator of the orientation of the nasals. Its nature of unusual in Rhinoceros, as pointed out by Kubik (1972), is again discerned.

4. Orientation of the nasal septum. This index, devised by Friend (1972), is another indicator of the orientation of the septum. Its nature of unusual in Rhinoceros, as pointed out by Kubik (1972), is again discerned.

5. Anterior abbreviation of the nasals characterizes the African genera, while some occur in Rhinoceros, and a few notes are required on each character.

6. Orientation of the occipital crest. This index, devised by Friend (1972), is another indicator of the orientation of the nasals. Its nature of unusual in Rhinoceros, as pointed out by Kubik (1972), is again discerned.
Table

List of synapomorph character states of living Rhinoceroses

<table>
<thead>
<tr>
<th>No.</th>
<th>Description of character state</th>
<th>Rhinoceros</th>
<th>Dicerorhinus</th>
<th>Dicerorhinus aethiopicus</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Occipital crest angle under 100°</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>2.</td>
<td>Orbital length less than orbital</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>3.</td>
<td>Nasal aperture length less than</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td>Nasal septum tends to be ossified</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>5.</td>
<td>Nasals abbreviated anteriorly</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>6.</td>
<td>Lateral nearly or quite separate from nasal</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>7.</td>
<td>Nasal notch moved back above P'</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>8.</td>
<td>Infraorbital foramen moved back above P'/M'</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>9.</td>
<td>Anterior border of orbit moved forward above P</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>10.</td>
<td>Enlarged, oblique supraorbital processes</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>11.</td>
<td>Subaural channel closed (x) or very narrow (x)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>12.</td>
<td>Vomer sharply ridged</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>13.</td>
<td>Posterior margins of pterygoid plates vertical</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>14.</td>
<td>Posterior palatine margin moved forward to M'</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>15.</td>
<td>Foramen ovale may fuse with E. lacrumer</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>16.</td>
<td>Masticatory inflated</td>
<td>XX</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>17.</td>
<td>Mandibles postorbital processes</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>18.</td>
<td>Mandibles postorbital processes</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>19.</td>
<td>Loss of bilateral symphysial ridges</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>20.</td>
<td>Inferior border of mandibular corpus convex</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>21.</td>
<td>Ascending ramus slopes forward</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>22.</td>
<td>Lingual mandibular cornet V-shaped</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>23.</td>
<td>Mandibular foramen above level of alveoli</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>24.</td>
<td>Incisor occlusion above level of that of cheekteeth</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>25.</td>
<td>Upper incisors lost</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>26.</td>
<td>E. lost</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>27.</td>
<td>F. lost</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>28.</td>
<td>Crochet developed on premolars</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>29.</td>
<td>Medial fissures developed on premolars</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>30.</td>
<td>Median valleys formed on premolars</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>31.</td>
<td>Hypocondro joined to cæsophagus on premolars</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>32.</td>
<td>Metacone rib developed on upper cheekteeth</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>33.</td>
<td>Anterior arcade on cheekteeth</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>34.</td>
<td>M' subtriangular</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>35.</td>
<td>V-shape of mandibular molar valleys</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>36.</td>
<td>Lower molar valleys of equal depth</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>37.</td>
<td>DP. retained into adult life</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>38.</td>
<td>Trudier of humerus very elongated</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>39.</td>
<td>Fibular head blunt, nasals under proximal shelf of riba</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>40.</td>
<td>Radius shortened, usually under 85% length of  humerus</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>41.</td>
<td>Metacarpal lengthened; M111 more than 60% length of radius</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>42.</td>
<td>Foreleg longer than hindleg</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total synapomorph character states</td>
<td>31</td>
<td>15</td>
<td>20</td>
</tr>
</tbody>
</table>

which still fails to interrupt the lacrimal-nasal contact. In African rhinos, however, the lacrimal bone is broad and square and the nasal is shortened posteriorly, so that they fail to meet except occasionally as a point, and that there is always a contact between maxilla and frontal (Fig. 1).

7. Posterior migration of the nasal notch, perhaps in part a compensation for the anterior abbreviation of the nasals, characterises African rhinos.

8. The backward migration of the infraorbital foramen again reflects facial shortening, but is not dependent on its other manifestations.

9. The anterior migration of the orbit, noticeable even in living animals, characterises the genus Rhinoceros.

10. African rhinos have a prominent supraorbital bony shelf, which is never seen in Asian skulls.

11. On the contrary, a narrow, postorbital process is developed, sometimes very prominently, in skulls of Asian rhinos, but the orbital-temporal fossa remains without a trace of bony division in Africans.

12. Closure of the subaural channel by fusion of the postglenoid and poststympanic processes occurs in all species of Rhinoceros subsequent to extreme infancy (Fig. 2 a).

Pocock (1943) recorded extreme narrowing of the channel in Dicerorhinus, and suggested that fusion might be possible in occasional examples; although I have never observed actual fusion, the narrowness of the channel stands in contrast to its relative openness in African rhinos (Figs. 2 b, c), and I infer that it could be a relic of an evolutionary stage immediately preceding the development of a genetic potentiality for fusion. Hirsch (1927 a) regards the character as of limited significance, since it was developed independently in other, unrelated rhinos (Ranzatherium); while agreeing that its evolution in parallel is intriguing, this surely does not affect the potential significance of the feature within a restricted lineage. The continued openness of the channel in Dicerorhinus, and especially in Lartetatherium in which the two processes appear actually to be pressed together but still not fused, indicates that there still has to be a genetic propensity for it; even though an appropriate mutation might arise independently.

13. Characters of the vomers are useful in differentiating the two species of Rhinoceros (Pocock 1943 b), but descriptions of the region have never been published for the other three extant species. Effectively, the bilateral fusion of the vomer to the base of the pterygoids is unique to R. unicus, and appears correlated with an extreme narrowing of the mesopterygoid fossa; but it appears not to have been noticed before that the vomer in

Fig. 1. Lacrimo-nasal relationships (juvenile specimens). Left = Rhinoceros unicus (NMV unreg.); long lacrimo-nasaluture; right = Dicerorhinus aethiopicus (NMV unreg.); trunical and maxilla insert between nasal and lacrimal.
both *Rhinoceros* species is convexly ridged, an evident derived state contrasting with the primitively smooth, rounded or flat condition seen in the other three species (Fig. 3).

14. The prezygoid plates are posteriorly extended at their free ends in *Rhinoceros*, and the posterior margins of the plates are vertical. In other extant species, preserving the primitive condition, the posterior margins slant forward from their bases towards the hamuli, which are somewhat produced backwards. The alar canals, at the bases of the posterior margins of the plates, are vertically above the hamuli in *Rhinoceros* but well posterior to them in other taxa (Fig. 4).

15. The palate is posteriorly shortened, ending opposite the first or second molars, in Asian rhinos. In the primitive condition the palate ends level with the posterior part of M₃, or the M₄ boundary.

16. The condition of Foramen Ovale in living rhinos, whether it occurs as a separate foramen or is fused with Foramen Lacerum Medium (Fig. 5), has been reported by Cave (1955). Edinger and Kelts (1954) conclude that the primitive state for perissodactyls, as for mammals generally, is its occurrence as a separate entity, but that fusion has occurred independently a number of times. There is polymorphism in *Dicerorhinus* in the character; so we must suppose that the occurrence of fusion either has remained variable since its common ancestor with *Rhinoceros* (in which it has since become fixed), or has arisen independently in the two.
Fig. 4. Shape of posterior margins of pterygoid plates. Above: a = Rhinoceros sundacutus (BM 22.10.13.1); plate margins vertical in overall direction, with alar canal vertically above hamulus; below: b = Osteo- rhinus sumatrensis (BM 21.2.8.2). Plate margins slope forward at 45°, with alar canal placed well behind hamulus.

Fig. 5. Foramen ovale and F. lacerum medium relationships. Above: a = Rhinoceros sundacutus (SAM c194); foramina confluent; below: b = Osteorhinus sumatrensis (MZS 6956), right side; foramina separate (but polymorphism occurs in this species).
22. When the symphysal region of the mandible is examined in dorsal view, the lingual contour is round, U-shaped, in Dicerorhinus and the African rhinos as apparently in the primitive condition. In Rhinoceros however the inner margins come together in a V in front (Fig. 6). It is possible that this thickened bone supports a hyper trophy of the lateral incisor roots, but there are many fossil forms in which the crowns, at least, of the lateral incisors are enlarged yet the lingual contour of the symphysis remains U-shaped.

23. The mandibular foramen is placed high, above the level of the alveolar margin, in Rhinoceros, but lower down in the other two genera. This character was first pointed out by Guérin (1982).

24. In Rhinoceros the premaxillae maintain a horizontal course, with 1° emerging from the antero-ventral surface just behind the tips; the mandibular symphysis curves upward, 1° maintaining the same orientation to occlude, with 1°. In Dicerorhinus however the premaxillae slope strongly downward, while the mandibular symphysis is horizontal; the upper and lower incisors therefore occlude in much the same way, but at or somewhat below the level of the cheekteeth. In African rhinos however, in the species, lacking front teeth, this character is of course not observable. The evidence of other perisso- dactyls, including other fossil Rhinocerotidae with the characteristic block-like 1° procumbent, occlusion (Radinisky 1969), indicates that the Rhinoceros raised upraised occlusion is derived.

25. Both upper incisors are typically lost in African rhinos, although as discussed by Hitchins (1978) two pairs may be present in rudimentary form in either jaw in Dicerorhinus bicornis, whether deciduous only (persisting into maturity) or permanent also is uncertain; Schauritz (1966) reports similar occurrences in Ceratotherium simum. They are, in any case, functionally lost and where they do occur in the ill-formed premaxillae they do not emerge from their alveoli. In both Asian genera well-formed 1° occur, with at least 1° alveoli for 1° (found in Dicerorhinus by Pocock (1944), and in my own experience they can occur in Rhinoceros also).

26. The procumbent mandibular tusks, often supposed to be canines but identified phylogenetically as 1°, by Radinsky (1969), are retained and well-developed in Asian rhinos, but lost (as discussed under the previous subheading) in African ones.

27. Small peg-like 1° are retained between the tusks-like 1° in Rhinoceros, although in R. sondaicus, they may be shed, and their alveoli sealed over, during adult life. They are never present in Dicerorhinus; indeed there would seem to be no room for them between the closely adjacent bases of the tusks. This is interesting, as the occasional presence of all four lower incisors (see 25 above) in Dicerorhinus implies that front tooth loss has proceeded independently in the two lineages.

28. With increasing molarisation a crochet, a small loph emerging from the anterior margin of the metaoph, developed in some rhinos. Its absence on the premolars as well; such fusion is very common in African forms and in Rhinoceros, but of course could not occur in Dicerorhinus where the premolars lack a crochet.

29. In all lophodont rhinos the crochet is united, at or towards the base of the crowns of the molars, with the crista (another small loph, emerging from the lingual margin of the ectoloph); with wear, this basal union reaches the occlusal surface, and a small isolated mediotessette is produced. Because of the position of this union and of crown hypsodonty, wear does not have to be very intense in Rhinoceros unicornis or in Ceratotherium simum before an occlusal mediotessette is formed on the other species such a formation is rarer, and indeed in Dicerorhinus cottoni (1982) was only a single mediotessette present, with no significant molarisation of the premolars during rhinocerotid evolution, a tendency for crista/crochet fusion developed in some groups on the premolars as well; such fusion is very common in African forms and in Rhinoceros, but of course could not occur in Dicerorhinus, where the premolars lack a crochet.

30. Primitively the entrances to the median valleys on the cheekteeth were wide, and this remains true of the molars; but on the premolars of Rhinoceros and of African rhinos the bases of protocone and hypocone have expanded so that the lingual entrance to the medi-

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Fig. 6. Contour of lingual margin of mandibular symphysis. Left: a = Rhinoceros sondaicus (BM 76.1.16.1); contour V-shaped; right: b = Dicerorhinus (BM 2.11.18.6); contour more open, U-shaped.
may become lost as a car. This has never been recorded for Dicerorhinus. It was Guerin (1982) who first pointed out that whereas in Rhinoceros and African rhinos, a complete metaloph, united at right-angles to the ectoloph, is present even on unworn premolars (as on the molars), this is not the case in Dicerorhinus in which the hypoloph is initially isolated and a metaloph is formed only with wear. In common with the previous three characters, this reflects the lesser state of molarisation of the premolars in Dicerorhinus; whether the four should really, therefore, be counted as a single character is arguable.

Asian rhinos have at least a trace of a buccal pillar on the ectoloph marking the position of the metacone, although it is weakly developed in Rhinoceros antarcticus. No such "rib" occurs in African rhinos; it may have been developed and subsequently lost, although from out-group comparison it seems much more likely that it was never developed.

The presence of an antecrochet on the molars seems to be a primitive character. It may be found, in at least rudimentary form, in living African rhinos (also on the premolars); but is never found, hence is probably lost, in the Asian species.

Hooijer (1966) pointed out that in Dicerorhinus \textit{M} is trapezoidal, due to a bulging-out at the junction of ectoloph and metaloph; he was describing an extinct species which he referred to the genus, but the character is as well seen in the extant \textit{D. sumatrensis}, and is fairly similar in living African rhinos. In \textit{Rhinoceros}, on the other hand (and, conversely, in some extinct genera such as \textit{Aceratherium}), \textit{M} is subtriangular, and quite different in shape from the other two maxillary molars.

The lower molar valleys are primitive \textit{U}-shaped in \textit{Dicerorhinus}, but \textit{V}-shaped like the premolars in other extant rhinos, occasionally (especially in \textit{R. sondaicus}) opening out with wear into more of a \textit{U}-shape. This character was first noticed by Guerin (1982).

Guerin (1982) also noted that the lower molar valleys may be of nearly equal depth,
or the anterior valley could be considerably deeper. The latter, implying less incorporation of the talonid into the lophid tooth structure, is probably primitive. Valleys of nearly equal depth are seen only in *Rhinoceros* among extant forms.

37. The rudimentary anterior premolar — almost certainly deciduous (Hetherington 1978) — is shed at or well before adulthood in both jaws in most living rhinos, but occasionally retained well into adult life in *Rhinoceros*. Its retention would appear to be a derived feature.

38. There are characteristic differences in the form of the processes of the proximal end of the humerus in extant rhinos (Guérin 1982). The Asian rhinos have an exceptionally elongated trochanter, so that the whole of the bicipital groove is enclosed by a pair of claw-like structures (Fig. 7).

39. Although not mentioned by Guérin (1982), inspection of articulated skeletons indicates that there is a useful character in the disposition of the proximal end of the fibula. In Asian rhinos the fibular head is short and blunt, and nestles under a shelf-like extension of the fibula. In African rhinos the fibular head is elongated, emerges proximal of the tibia's lateral condylar surface, and may even articulate with the femur, forming a small facet in the lateral condyle (Fig. 8). Although the polarity may be argued, it would seem likely that the reduced condition, as seen in Asian rhinos, is the more derived.

40. Proportions of the long bones are discussed by Guérin (1982), and I have myself measured a number of skeletons. The proximal limb segments remain primitively long in African rhinos, whereas they are shortened in the Asian forms, especially the radius which is nearly always under 85% of the length of the humerus.

41. The distal segments of the limbs on the other hand are elongated in Asian rhinos. The median metacarpal (M3III) is more than 50% of the length of the radius in Asian forms, less than this in African genera.

42. If an approximation is made to the total limb length by adding the segments (Humerus + Radius + M3III, Femur + Tibia + M3III), the total forelimb length exceeds that of the hindlimb in African rhinos; the reverse is true in *Dicerorhinus*; the two limbs in *Dicerorhinus* are about equal in length, or the hindlimb very slightly longer. As an excess in hindlimb length is general among mammals, the African rhino condition is here considered derived.

This list by no means exhausts the skeletal differences among the living species: Guérin (1982) details characters of all regions of the skeleton, and I have found also characters in the vertebral column, ulna, femur (head and third trochanter), tibia, scapula and pelvis, which it is intended to describe in detail at a future time. In all of them however the polarity is uncertain, and in some cases the influence of size differences cannot be ruled out.

Adding up the derived states of the above 42 characters (see Table), *Rhinoceros* is much the most "advanced" genus, in the sense of having many more derived states than the others; while *Dicerorhinus* is the most primitive. The two African genera share 14 derived states: the two two-horned groups (*Dicerorhinus* and the African genera) share only 1; while *Rhinoceros* and the African genera share 7. It is evident that the indicated phyletic scheme would correspond most closely to a geographic split. At the same time, there has been considerable parallelism between *Rhinoceros* and the African group, mainly in dental characters but also in overall facial shortening.

As noted above, two other attempts at a cladistic analysis have been made. Heissig (1981) uses 19 characters, some of which are actually alternative states of the same character; Guérin (1982), 13 characters. In general, both authors note extensive parallelism as well as cases of evolutionary reversal. Heissig (1981) produces two almost equally parsimonious schemes based only on the five extant species, then finds further complexities when some fossil forms are introduced; Guérin's (1982) analysis includes fossil taxa right from the start. In both analyses the choice of characters seems to be unwise: in Heissig's scheme Molariform Premolars, Skull Shortening and even "Panzerung" are listed alongside characters of the Metacone Rib and Protocone Fork; in Guérin's, Semi-Cursorial Skeleton and Hypsodonty coexist with Metacone Rib; both authors include absolute size and front tooth reduction.

In the present analysis an attempt has been made to reduce characters to their components. While Guérin (1982) notes, cogently, that reduction of the facial skeleton characterizes both *Rhinoceros* and the African rhinos, and makes this the basal synapomorphy of a common stem (separating them from *Dicerorhinus*), the distribution of nasal bone length, nasal aperture length, position of nasal notch and anterior orbital margin, and so on, suggests very strongly that facial shortening amounts to different things in the two, and has occurred independently. Again, "loss of front teeth" can be divided into loss of upper incisors, and loss of 1 and 1; *Dicerorhinus* has lost 1, but not 1 or the uppers (the only derived condition in the Table which it does not share to some degree with *Rhinoceros*), while all four incisors in both jaws are equally reduced, though they may occur, in African rhinos. Thus, incisor loss will have occurred independently and in different ways in the two.

The polarity of such characters as number of horns cannot be determined by out-group comparison; other living perissodactyls do not have horns, and small horns leave imperceptible traces on the cranial bones, and it cannot be assumed that a single horn is a halfway stage from hornlessness to having two horns. The case can only be argued a posteriori: *Dicerorhinus* has been demonstrated above to share a common stem with *Rhinoceros* yet shares the two-horned condition with the African rhinos, hence parsimony suggests that two horns are primitive, and that *Rhinoceros* is advanced in having only one. One can go from this and propose a functional correlation with the shortened, saddle-shaped dorsum cranii of *Rhinoceros*, "crowding out" the posterior horn, but this could not have been reasonably argued a priori.

Heissig (1973) made a case for uniting the group containing extant rhinos with the Elasmotheres, in a subfamily Rhinocerotinae. Within this subfamily, the tribe Elasmotherini was defined by clearly derived character states, but his tribe Rhinocerotini had only primitive states. There is, consequently, no evidence that groupings within the latter are any less diverse than one another than from the Elasmotherini. Until interrelationships are sorted out, therefore, I propose to split Heissig's tribe Rhinocerotini into two, giving both of them the same rank as the Elasmotherini. Their uniquely derived features (from the evidence of extant taxa alone) are as follows:

**Tribe Rhinocerotini.** More forward-sloping occipital crest; nasal septum tending to be ossified; postorbital processes developed; subaural channel very narrow; posterior margin of palatal moved forward to M1-1 level; foramen ovale may be fused with 1. lacrimal medium; mastoid region inflated; foramen magnum triangular or pear-shaped, pointed dorsally; metacone rib developed on upper cheekteeth; antecrochet lost; upper incisors, and loss of 1 and 1; while in *Rhinoceros* these are retained; postorbital processes developed; maxillary more symmetrical, articulated in the same way in the lower jaw. *Rhinoceros*.

**Tribe Dicerotini.** Occipital crest sloping backward; nasals anteriorly abbreviated; lacrimal nearly or quite separated from nasal; nasal notch moved back, above P2-M1; infraorbital foramen moved back, above P3-M1; enlarged supraorbital processes; mandibular symphysis abbreviated, with loss of lateral diastema ridges; convex, angle reduced; ascending ramus slopes backward; upper and lower incisors very reduced, peg-like, or more usually absent; foreleg longer than hindleg. Additionally, convergent with *Rhinoceros* in some characters of facial shortening and molarisation of premolars.

*Genera:* *Dicerorhinus*, *Ceratotherium*.
Allocation of fossil genera

Coelodonta and Stephanorhinus

For Heissig (1981), there is a clear phyletic division between Coelodonta (the Woolly Rhinoceros of the Middle and Upper Pleistocene of the temperate Old World) and Stephanorhinus, containing the other temperate-zone Plio-Pleistocene rhinos, more usually referred to Dicerorhinus. Figs. 2, 3) disagree in whether the two genera are to be allocated to the Dicerorhinus or Dicerorhinini groups, but agree in separating them into two different sublineages. He points out that Coelodonta has a reduced premaxillary cingulum, more elongated skull with backwardly inclined occipital crest, and very hyposidont cheek teeth, whereas Stephanorhinus has more modified premaxillaries; and accretes any similarities between them to convergence. Guerin (1980, 1982) takes a different viewpoint: Coelodonta emerged from within the "European dicerorhine" complex (he does not recognise the genus Stephanorhinus), and is especially related to D. crassus and D. hemitorques, and only slightly more distantly to D. mercki (Recte kirchbergensis) and D. jeannereti.

In the present study, the characters of all these taxa, taking for granted the evident homogeneity of the group Heissig calls Stephanorhinus, but keeping Coelodonta apart, were examined for indication of synapomorphy with either Rhinocerotini or Dicerorhinini. As far as Stephanorhinus is concerned there is no doubt that it shares various characters with Rhinocerotini; the nasal septum is ossified, in fact very strongly so; postorbital process are developed in the earlier forms, such as "D. jeanereti", though they tend to disappear altogether in later representatives; the subaural channel is firmly closed; the palate ends opposite M3 in earlier forms; the foramen ovale varies, but may be fused with P3; the maxillae are rather strongly inflated; the metacarpal rib is well developed; there is no antorbital; the trochohyal is elongated; the fibular head is short; the metacarpals is elongated.

In a few characters, Stephanorhinus differs from the usual Rhinocerotini morphology: the occipital crest tends to slope back, although in the earlier species it is often as vertical as in D. sumatrensis; the foramen magnum is primitively oval; the radius is elongated, more than 85% the length of the humerus, indeed sometimes nearly the same length.

The last two characters have probably both reversed in evolution, and this can be certainly demonstrated for occipital crest slope and postorbital process presence; so there is no difficulty in including the Stephanorhinus group in the Rhinocerotini. Moreover it is closer to Rhinoceros than to Dicerorhinus: the firm fusion of postglenoid and postzygomatic, the great mastoid inflation, and the strong molarisation of the premolars (with development of premaxillae, mediodentes and closed median valleys) place this group closer to Rhinoceros. It is certainly incorrect therefore, from a phylogenetic point of view, to continue to refer these species to Dicerorhinus.

Within this restricted group, however, Stephanorhinus -- including even such early species as the Pliocene "D. megarhinus" -- shows strongly autapomorphic features: very elongated nasal bones, a fully developed cloison (especially in the later species), backward movement of nasal notch, anterior orbit border and posterior margin of palate, backward slope of ascending ramus, completely molarised premolars, and total loss of incisors. It lacks the more special features of Rhinoceros such as vomer ridge, form of pterygoid plates etc.

Coelodonta only shares many of the specialisations of Stephanorhinus: elongation of nasals, cloison, incisor loss and so on; like the latter and Rhinoceros, the subaural channel is firmly closed, and the premolars have crochets and mediodentes, and closed median valleys.

It lacks the extreme molarisation of the premolars seen in Stephanorhinus, and conversely the foramen magnum is pear-shaped, the premaxilla is horizontal and the radius is fairly short, three characters in which it resembles Rhinoceros. Heissig's theory of extensive parallelism between Coelodonta and Stephanorhinus may therefore be correct; at the moment, however, some parallelism with Rhinoceros (in premaxillary form) and evolutionary reversal (in foramen magnum slope and radius shortening) seen more than as the similarity to later Stephanorhinus is very striking. Indeed Guerin (1982) seems to keep the Stephanorhinus/hemitorquoise group out of Coelodonta for convenience only, and if the present phylogenetic hypothesis is substantiated the limits of Coelodonta will have to be redrawn.

Some of these problems may be clarified by detailed analysis of the rhinos from the Late Miocene and Pliocene of the American South. Two taxa, referred to Dicerorhinus and Dicerorhinus, have been distinguished at this site; but some at least of the "Dicerorhinus" characters seem to be an artefact of distortion, and the two will have to be disentangled before any progress can be made.

Punjabitherium and Gandasterium

The genus Punjabitherium was erected by Khan (1971) after the discovery of a new cranium of the Upper Siwalik species previously called Rhinoceros platyrhynchus demonstrated the presence of two pairs of upper incisors. The new genus was defined as having two horns, no cloison, subaural channel closed, backwardly inclined occiput, and hypsodont cheek teeth.

Previous Colbert (1935) included it in Coelodonta on the basis of the complexity of its cheek teeth, while Heissig (1972) retained it, by inference, in Rhinoceros. There are, consequently, three competing views of its relationships: a sister-group of Rhinoceros (especially R. unicornis), or of Coelodonta, or an isolated taxon with no close affinity to either of these.

Examination of the Chandigarh skull and of the British Museum material shows convincingly that the third view is correct: the genus Punjabitherium is valid. A paper redesciribing the available material is in preparation, but comparisons on the basis of the characters used in the present paper will be made here. The cranial characters are all those of the Rhinocerotini. Like the Rhinoceros/Stephanorhinus/Coelodonta section of the tribe, it has subaural fusion and molarised premolars with mediodentes and closed median valleys formed on the premolars. It lacks the derived states of the Coelodonta line (facial elongation, cloison, incisor loss), but resembles Rhinoceros in its ridged vomer, vertical posterior margins to the pterygoid plates, and retention of DP4 well into adult life. Beyond this, however, it does not have the dental shortening of Rhinoceros, nor the strong mastoid inflation, horizontal maxilla, or V-shaped lingual mandibular contour. The presence of a distinct frontal convexity supports Colbert's (1935) and Khan's (1971) contention that a second horn persisted. In the single available mandibular specimen, there seems to be a strong level difference in the premolar valleys. There are also some marked aprotomorph states; molarisation of the premolars has gone further than any other species of rhino, extending to P4 and even to P5 which lacks only a fully-formed protoloph but is block-shaped and scarcely smaller than P4. The molars have the peculiarity of a cisto reduced in size, the mediocineses being enclosed almost entirely by a hypotrophied recurved crotchete. The posimus is greatly elongated in each molar.

Though obviously distinct generically, Punjabitherium is somewhat closer to Rhinoceros than to any other genus. It is of interest that it occurs in the Pener Bed of the Upper Siwalik series alongside a fully evolved member of the genus Rhinoceros, R. unicornis, a very close relative of R. unicornis (and probably conspecific with it).

An earlier Siwalik rhinoceros is Gandasterium Browni from the Chini Formation (Colbert 1934). Heissig (1972) reduced the genus Gandasterium to subgeneric status under Rhinoceros and added a second species, R. (G) ? indicus, to his recently described Nagri Formation. There are two competing hypotheses of its status; that it is a direct ancestor of the genus Rhinoceros (sensu lato -- i. e. including R. sandai as well as R. unicornis) (Colbert 1934, 1935), or that it is a forebear of the restricted genus Rhinoceros (i. e. R. unicornis only), "earhinerinos sandai" having already separated from the lineage (Heissig 1972).
As described and illustrated by Colbe (1934), the type cranium of C. browni is almost precisely the reconstructed ancestral morphotype of Rhinoceros; and, indeed, of Panza-

buthierium. It has all the basic synapomorph conditions of the Rhinoceros, those of the B. Rhinoceros/Caenodontina branch of the tribe (subcutaneous, medofossitite formation, median valve closure), and of the Rhinoceros/Pantheratherium sub-branch (ridged vomer, vertical posterior margins of pyriplid plates, P, retention). It is primitive in its relatively long face, downsloping premaxilla and upturned mandibular symphysis, deter-
ned later lower molar valley levels, and large P1 alveoli. There is only one identifiable autapomorphy: the apparent loss of I1, observable in the cast of a referred mandibular fragment in the Munich collection (Fig. 9). If correctly referred, this specimen indicates that G. browni as presently known does not include the common ancestor of Rhinoceros and Panthatherium.

**Laratherium**

Among the plethora of fossil rhinos commonly referred to Dicerorhinus, as well as the Stephanorhinus group referred to above, are several other species. One of these, D. schlett-
macheri, will be the subject of a future paper. The diminutive D. steinheimensis is too incompletely known for allocation. A third European species, D. sansaniensis, is placed near the base of the Dicerorhinus line by Gürich (1982, 1982) but has been referred to a separate genus, Laratherium, by Ginsburg (1974).

The defining characters of Laratherium were: occipital crest extremely high and vertical, temporal lines closely approximated, pialetus less vaulted, orbit more rounded, zygomatic arch shorter, postcranial and paraxial processes in contact, and pyramidal plates extending past the level of the postcranial processes. Dental characters were also described.

The pyramidal, in the Paris Museum, is distorted, both posteriorly where the occiput has been pushed forward somewhat telescoping the postorbital region, and from side to side. There is fortunately a second specimen, a cranium in Munich, described by Hessig (1972); it is relatively unaffected in the areas where the Paris skull is distorted. Hooijer (1966) described Dicerorhinus laekFeedback and the type skull which I have not seen, is from the figures less distorted than that of the European species.

Although a paper fully describing the genus is in preparation, a brief note on its phylogical position is appropriate here. The genus is valid, showing primitive and autapomorphic character states and a few that recall the Rhinocerontini. The primitive features are as follows: The orbitosphenoid length is much less than the orbitosphenoid (in the Paris skull the opposite appears to be the case, but this is due to distortion). The nasals are long; the length of the aperture cannot be accurately measured, but the notch lies above P2 or P3; there is no ossification of the nasal septum. The infraorbital foramen lies above P2 or P3, the anterior border of the orbit above M1 or the M2 boundary. There are no supraorbital processes. The vomer is flat. The posterior margins of the pyriplid plates slope back at 45° and in the Munich skull do not extend as far posteriorly as in the Paris skull, which would appear to be telescoped in this region. The foramen ovalis (in the Munich skull) seems to be separate from foramen laborum. The mastoids are not at all inflated. The foramen magnum is oval. Symphyseal ridges are strongly developed. The mandibular corpus is slender and straight; there is a flaring angle; the ascending ramus is vertical. The mandibular foramen (in the types of both sansaniensis and of laek) is well below the level of the alveoli. The premaxilla slope down and the mandibular symphysis is horizontal, so that the incisors actually occlude below the level of the cheekteeth. I1 are tusk-like, I2 are present. Crocets occur on the premolars; I have seen no specimen with supernumerary teeth. Although Gürich (1982) finds that such may occur. In unworn premolars, in the Munich collection, however, the hypocion is isolated. There is no trace of a metacone rib or bulge. M1 is primitively subtrapezoid. The troctich of the humerus is short; the radius is long, 92% the length of the humerus; the metacarpus is short, about 43% the length of the radius; the hindleg is longer than the foreleg.

There are just a few characters which appear to ally Laratherium with the Rhinoceros. They are: Developed postorbital processes. The subcutaneous channel is reported to be united in the laek type (Hooijer 1966), but the figures suggest that the region in question might not be very well preserved. Additionally, processes project from the external auditory meatus in both the Paris and Munich skulls, but do not unite. The postorbital palate margin is far more posteriorly positioned; but not as far forward as in later representatives of the tribe. The antecrochete is

![Cladogram of Rhinoceroidea. Figures refer to apomorphic (derived) states, as discussed in the other lineages, but here interpreted as convergent or parallel. A is uniquely derived condition; B is derived conditions shared with one or more derived states of characters 1 and 21; 1", 12" etc. refer to normally derived states of characters 1, 12 etc.; 1", 12" to highly derived states.](image-url)
very small or absent. The form and relations of the head of the fibula are as in the Rhinocerotina. Autapomorphic characters of the genus (a couple of them convergent on *Rhinoceros*) are loss of \( \gamma \), exceptionally late shedding of DF, perhaps the low occlusion of the incisors, V-shaped inner mandibular contour (convergent with *Rhinoceros*), the curious interrelationship of the postglenoid and postzygomatic processes [seen best in the Munich skull, and well described by Haissig (1972 b); see also Fig. 10], and the absence of crest on the molars, the closure of the median valleys, the lack of a level difference between the lower molar valleys, and the highly characteristic narrow, vertical occiput.

**Conclusion**

The phylogeny of the Rhinocerotinae is reconstructed as shown in Fig. 11. The following classification of the subfamily is proposed, as the one which best reflects the phylogeny:

**Subfamily Rhinocerotinae Dollo, 1885**

- Tribe Elasmotherini Gill, 1872
  - Tribe Dicerorhinini new rank (ex-Dicerorhinus Pocock, 1945)
    - Genus: Dicerorhinus Gray, 1821
      - Catasotherium Gray, 1867
      - Paraceratherium Hooijer, 1968
  - Tribe Rhinocerotini Dollo, 1885
    - Subtribe Laratertherina nov.
      - Genus: Laratertherium Ginsburg, 1974
    - Subtribe Rhinocerotini Dollo, 1885
      - Genus: Rhinoceros Linnaeus, 1758
      - Pantheratherium Khan, 1971
      - Gauratherium Colbert, 1935
      - Stephanorhinus Krefft, 1892
      - Coelodonta Bronn, 1831
    - Subtribe Dicerorhinini new rank (ex-Dicerorhininae Simpson, 1945)
      - Genus: Dicerorhinus Gloger, 1841

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**Summary**

A cladistic analysis of the extant rhinoceous taxa and their fossil relatives shows a clear division between the Dicerorhinini and other genera: Rhinoceros, Paraceratherium, Gauratherium, Stephanorhinus, Coelodonta and Dicerorhinus, and fossil samples of *Rhinoceros* and *Dicerorhinus* alone belong to the subtribe Dicerorhinini. *Laratertherium* is a very primitive representative of the Rhinocerotinae, and forms a third subtribe.

**Zusammenfassung**

Phylogenie der lebenden Arten vom Rhinoceros

Cladistische Analyse der lebenden Rhinocerotina und ihrer fossilen Verwandten zeigt eine klare Trennung zwischen Dicerorhinini und den anderen Gattungen: Rhinoceros, Paraceratherium, Gauratherium, Stephanorhinus, Coelodonta und Dicerorhinus sind in die Rhinocerotina einzubeziehen, die