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VERLAG PAUL PAREY · SPITALERSTRASSE 12 · HAMBURG 1

Phylogeny of the living species of Rhinoceros

By C. P. Groves

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Introduction

ıterrelationships of the living rhinoceros species are disputed. Simpson (1945) separated the ıgle-horned *Rhinoceros* (including both *R. unicornis* and *R. sondaicus*) in a subfamily hinocerotinae from the double-horned *Dicerorhinus, Diceros* and *Ceratotherium* ubfamily Dicerorhininae). Pocock (1945 b) saw the relationships differently: for him *icerorhinus* (which he called *Didermocerus*) belonged in the Rhinocerinae (as he called it), parate from the two African genera which he placed in a subfamily Dicerinae. Groves 965) followed Pocock, proposing some synapomorph features, perhaps not entirely ınvincingly; while Loose (1980) followed Simpson, but within the Dicerorhininae parated out two tribes, Dicerorhinini for *Dicerorhinus* (with the fossil *Coelodonta*) and icerotini for the two African genera. Guerin (1980, 1982) placed the living genera in three bfamilies: Rhinocerotinae, Dicerorhininae (to include also *Coelodonta*) and Dicerotinae. nally Heissig (1973) placed them all, with a further fossil genus *Stephanorhinus*, in a single ıbfamily 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 ıeval with a number of subfamilies erected for distinctive fossil groups; the same is true of uerin's three subfamilies, although the additional fossils considered by that author do not ıan quite such a wide variety. Heissig's concern was to place all Rhinocerotidae in a ıylogenetically based scheme, and he was impressed with the evident synapomorphies ıtween the living rhinos (and their relatives) and the extinct elasmotheres: these two groups ere 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 fferentiating 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 nclusion for a number of reasons (discussed below).] When this has been done, a

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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 HEISSIG (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 *Eurhinoceros* Gray, 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 specialisation 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 recognise *Eurhinoceros* 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 HEISSIG (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 specialised morphology of *R. unicornis* and/or the neotenous nature 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 *Diceros* (for *D. bicornis*) and *Ceratotherium* (for *C. simum*) is supported on both morphological (CAVE 1962) and palaeontological grounds (HOOIJER 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 synapomorph states.

3. The content of the genus *Dicerorhinus*. The genotype, *D. 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) and LOOSE (1980) both continue to refer the European Plio-Pleistocene incisorless species, typified by *D. etruscus*, to the genus, while KRETZOI (1942) and HEISSIG (1973, 1981) place them in a separate genus *Stephanorhinus*. As these latter are quite evidently a close-knit group [pace KRETZOI (1942) in the case of the species *hemitoechus*, and HEISSIG (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 *Dihoplus* Brandt, 1872 is available if required), *D. sansaniensis* [recently allocated to a separate genus *Lartetotherium* by GINSBURG (1974)], and *D. leakeyi* [said by its describer (HOOIJER 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. sumatrensis* alone is meant.

4. Other taxa referable to the lineages of living species. The genus *Coelodonta* is considered by GUERIN (1980, 1982) to be merely the most highly evolved representative of the European "Dicerorhine" lineage; HEISSIG (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 "Dicerorhines" (HEISSIG's genus *Stephanorhinus*) and the living species. *Paradiceros* of the Kenya Miocene was plausibly referred to the *Diceros* lineage by its describer (HOOIJER 1968). The only other fossil rhinos to be universally associated with the general grouping containing the living species are the Siwalik *Gaindatherium* spp. and "*R.*" *platyrhinus*. COLBERT (1934) erected the genus *Gaindatherium* for *G. browni* n. sp. from the Chinji Formation of the Siwaliks; HEISSIG (1972 a) added a new species *vidali*, but reduced the genus to subgeneric rank under *Rhinoceros*. The species *platyrhinus*, referred to *Coelodonta* by COLBERT (1935), was raised to generic rank as *Punjabitherium* by KHAN (1971), but retained in *Rhinoceros* by HEISSIG (1972 a). In the present study for ease of reference all these taxa will be referred to by the generic names wich have been awarded to them.

Material and methods

Skulls and skeletons of the five living rhinoceros 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 *Punjabitherium*, in the British Museum and in the Panjab University, Chandigarh; of *Lartetotherium*, in the Museum National d'Histoire Naturelle, Paris, and in the Bayerische Staatssammlung für Paläontologie und Historische Geologie. Excellent descriptions and figures of further material are available in the literature, especially GUERIN (1980).

The distinguishing characters of the five living species were listed and compared, by the method of Cladistic Analysis (GROVES 1982). The outgroup chosen for comparative purposes was *Aceratherium*: 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 phyletic distinctness. Where reference to *Aceratherium* failed to resolve polarity in particular instances, other Perissodactyls (*Prosantorhinus*, *Caenopus*, 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 orbitoaural. 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 WÜST (1922), is another indicator of facial shortening but does not in fact duplicate character (2). A rhino with somewhat abbreviated face can still have elongated nasals, or vice versa; and some fossil species do.

4. Ossification of the nasal septum, or Cloison, has not been recorded in African rhinos but occurs, usually to a very limited degree, in both Asian genera. POCOCK (1945 a) described some cases of unusually extensive ossification.

5. Anterior abbreviation of the nasals characterises the African genera, where they terminate anteriorly not in a point, but abruptly and broadly.

6. The relations of the anterior facial bones appear not to have been noticed previously, but are none the less consistently different in African and Asian rhinos, wherever the sutures can be traced. In *Rhinoceros* the lacrimal intervenes between maxilla and frontal, and makes a short suture with the nasal; this is true also for *Dicerorhinus*, in which the lacrimal is somewhat expanded, constricting the postero-dorsal angle of the maxilla into a long process

Table

List of apomorph character states of living Rhinoceroses

No.	Description of character state	*Rhinoceros*	*Dicerorhinus*	*Diceros* and *Ceratotherium*
1.	Occipital crest angle under 100°	××	×	
	above 100°			×
2.	Orbitonasal length less than orbitoaural	×		×
3.	Nasal aperture length less than 45 % of orbito-condyle length	×		×
4.	Nasal septum tends to be ossified	×	×	
5.	Nasals abbreviated anteriorly			×
6.	Lacrimal nearly or quite separated from nasal			×
7.	Nasal notch moved back above $P^{2/3}$			×
8.	Infraorbital foramen moved back above P^3/M^1			×
9.	Anterior border of orbit moved forward above P^4	×		
10.	Enlarged, oblique supraorbital processes			×
11.	Postorbital processes developed	×	×	
12.	Subaural channel closed (××) or very narrow (×)	××	×	
13.	Vomer sharply ridged	×		
14.	Posterior margins of pterygoid plates vertical	×		
15.	Posterior palatine margin moved forward to $M^{1/2}$	×	×	
16.	Foramen ovale may fuse with F. lacerum	×	×	
17.	Mastoids inflated	××	×	
18.	Foramen magnum pear-shaped or triangular	×	×	
19.	Loss of bilateral symphyseal ridges			×
20.	Inferior border of mandibular corpus convex			×
21.	Ascending ramus slopes forward	×		
	backward			×
22.	Lingual mandibular contour V-shaped	×		
23.	Mandibular foramen above level of alveoli	×		
24.	Incisor occlusion above level of that of cheekteeth	×		
25.	Upper incisors lost			×
26.	I_2 lost			×
27.	I_1 lost		×	×
28.	Crochet developed on premolars	×		×
29.	Medifossettes developed on premolars	×		×
30.	Median valleys formed on premolars	×		×
31.	Hypocone joined to ectoloph on premolars	×		×
32.	Metacone rib developed on upper cheekteeth	×	×	
33.	Antecrochet lost on cheekteeth	×	×	
34.	M^3 subtriangular	×		
35.	V-shape of mandibular molar valleys	×		×
36.	Lower molar valleys of equal depth	×		
37.	DP_2 retained into adult life	×		
38.	Trochiter of humerus very elongated	×	×	
39.	Fibular head blunt, nestles under proximal "shelf" of tibia	×	×	
40.	Radius shortened, usually under 85 % length of humerus	×	×	
41.	Metacarpus lengthened: McIII more than 50 % length of radius	×	×	
42.	Foreleg longer than hindleg			×
	Total apomorph character states:	31	15	20

Shared by *Rhinoceros* and *Dicerorhinus*: 14, by *Rhinoceros* and *Diceros/Ceratotherium*: 7, by *Dicerorhinus* and *Diceros/Ceratotherium*: 1.

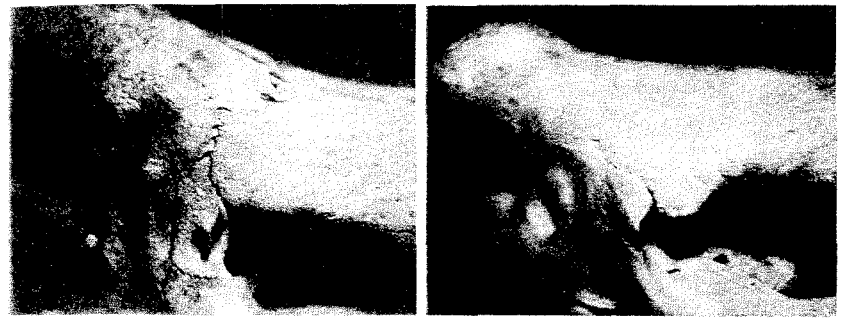

Fig. 1. Lacrimo-nasal relationships (juvenile specimens). *Left:* a = *Rhinoceros unicornis* (NMV unreg.): long lacrimo-nasal suture; *right:* b = *Diceros bicornis* (NMV unreg.): frontal and maxilla insert between nasal and lacrimal

which still fails to interrupt the lacrimo-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 orbito-temporal fossa remains without a trace of bony division in Africans.

12. Closure of the subaural channel by fusion of the postglenoid and posttympanic processes occurs in all specimens of *Rhinoceros* subsequent to extreme infancy (Fig. 2 a). Pocock (1945) 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. Heissig (1972 a) regards the character as of limited significance, since it was developed independently in other, unrelated rhinos (*Ronzotherium*); 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 *Lartetotherium* 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 vomer are useful in differentiating the two species of *Rhinoceros* (Pocock 1945 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. unicornis*, and appears correlated with an extreme narrowing of the mesopterygoid fossa; but it appears not to have been noticed before that the vomer in

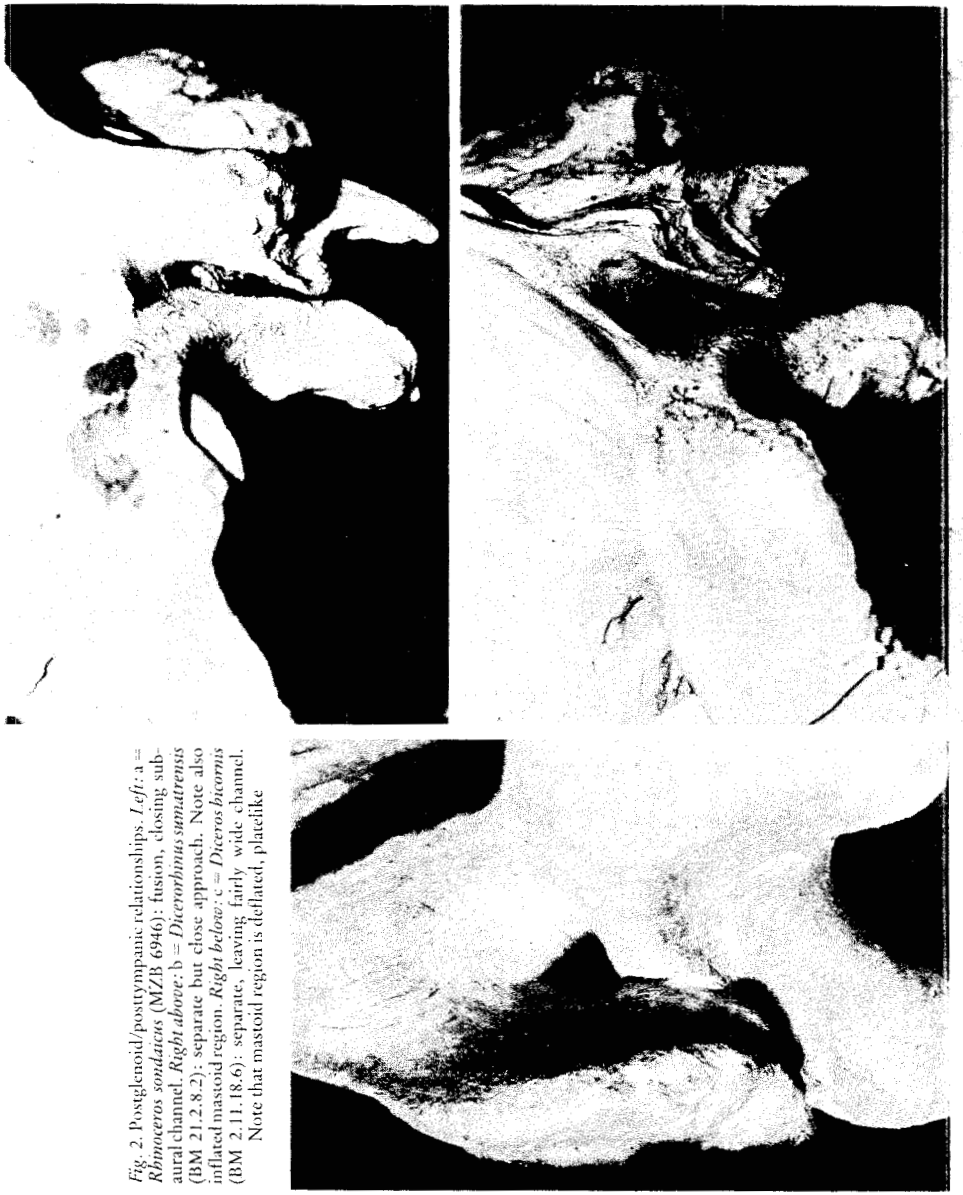

Fig. 2. Postglenoid/posttympanic relationships. *Left:* a = *Rhinoceros sondaicus* (MZB 6946): fusion, closing subaural channel. *Right above:* b = *Dicerorhinus sumatrensis* (BM 21.2.8.2): separate but close approach. Note also inflated mastoid region. *Right below:* c = *Diceros bicornis* (BM 2.11.18.6): separate, leaving fairly wide channel. Note that mastoid region is deflated, platelike

Fig. 3. Shape of vomer. *Left:* a = *Rhinoceros sondaicus* (MZB 6954): strongly ridged; *right:* b = *Dicerorhinus sumatrensis* (MZB 6956): evenly rounded

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 pterygoid 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 M^2, or the $M^{2\,3}$ 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 Kitts (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.

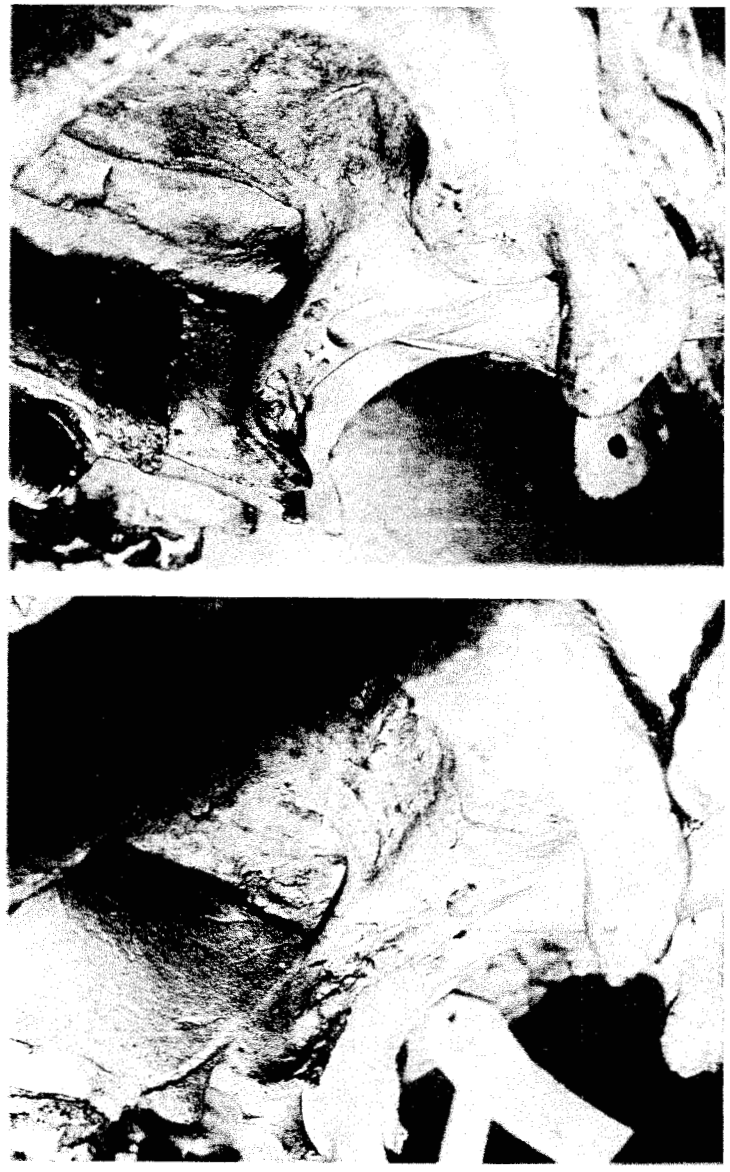

Fig. 4. Shape of posterior margins of pterygoid plates. *Above:* a = *Rhinoceros sondaicus* (BM 20.10.13.1): plate margins vertical in overall direction, with alar canal vertically above hamulus; *below:* b = *Dicerorhinus sumatrensis* (BM 21.2.8.2). Plate margins slope forward at 45°, with alar canal placed well behind hamulus

Fig. 5. Foramen ovale and F. lacerum medium relationships. *Above:* a = *Rhinoceros sondaicus* (SAM unreg.): foramina conjoint; *below:* b = *Dicerorhinus sumatrensis* (MZB 6956), right side: foramina separate (but polymorphism occurs in this species)

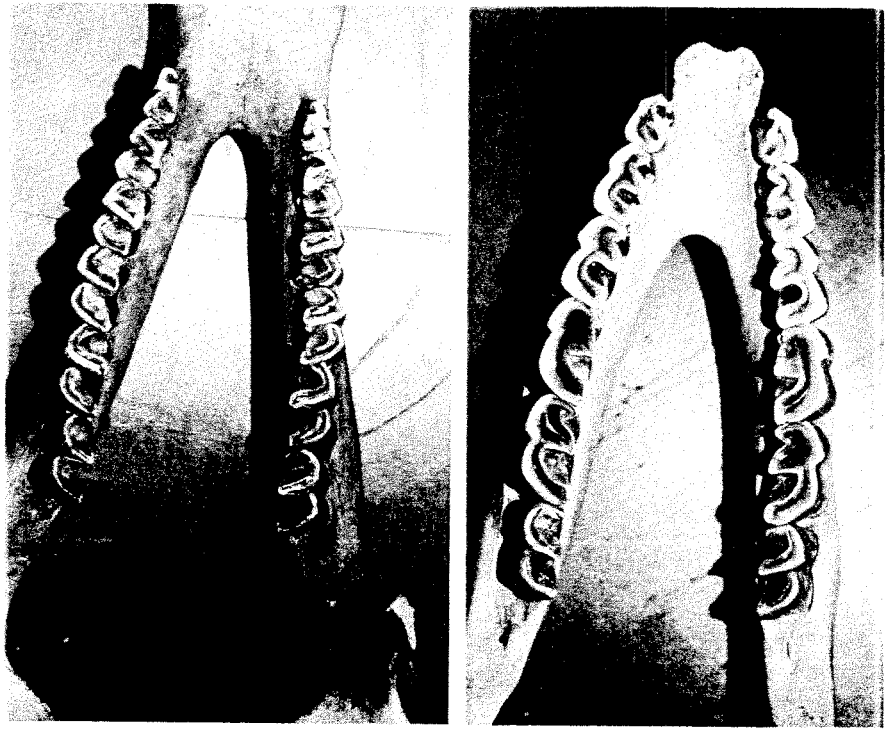

Fig. 6. Contour of lingual margin of mandibular symphysis. *Left:* a = *Rhinoceros sondaicus* (BM 76.3.30.1): contour V-shaped; *right:* b = *Diceros bicornis* (BM 2.11.18.6): contour more open, U-shaped

17. The mastoid region is inflated in all Asian rhinos, but enormously so in *Rhinoceros*, in which the occipital region is trapezoid in posterior view. [Although this affects the morphology of the auditory region (Fig. 2) it is not responsible for fusion, in which the backward extension of the postglenoid seems to play the major role.]

18. The foramen magnum is a simple oval in African rhinos, but has become triangular or pear-shaped (i. e. narrowly extended dorsally) in Asian skulls. It is possible that this is correlated with the upslanting head carriage, permitting cranial dorsiflexion without interference from the dorsal spine of the atlas vertebra; but as will be seen any correlation with character (1) breaks down when fossil forms are considered. This morphology is discussed by CHAKRABORTY (1972), and well illustrated in LOOSE (1975).

19. The mandibular incisor-premolar diastema is marked by a prominent thin ridge on either side in Asian rhinos as in other perissodactyls. The anterior shortening of the jaw in African rhinos has quite eliminated these ridges, whose occurrence therefore depends largely on symphyseal abbreviation but not on anterior dental reduction per se (Fig. 6).

20. The inferior margin of the mandibular corpus is primitively straight, marked posteriorly by a prominent angle, in Asian rhinos, but highly convex in the African species.

21. The ascending ramus is vertical in *Dicerorhinus*, preserving the primitive condition; but slopes forward in *Rhinoceros*, and markedly backward with no demarcating angle between it and the corpus in the African genera.

22. When the symphyseal 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 hypertrophy 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 GUERIN (1980).

24. In *Rhinoceros* the premaxillae maintain a horizontal course, with I^1 emerging from the antero-ventral surface just behind the tips; the mandibular symphysis curves upward, I_2 maintaining the same orientation to occlude with I^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, whereas in *Rhinoceros* they occlude above that level. In African rhinos, lacking front teeth, this character is of course not observable. The evidence of other perissodactyls, including other fossil Rhinocerotidae with the characteristic block-like I^1/procumbent I_2 occlusion (RADINSKY 1969), indicates that the *Rhinoceros* 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 *Diceros bicornis*, whether deciduous only (persisting into maturity) or permanent also is uncertain; SCHAURTE (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 I^1 occur, with at least alveoli for I^2 [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 I_2 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 I_1 are retained between the tusk-like I_2 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 *Diceros* 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 metaloph, developed in some rhinos. Its absence on the premolars of *Dicerorhinus* is therefore probably a primitive feature.

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 medifossette 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 medifossette is formed: on the other species such a formation is rarer, and indeed in *Dicerorhinus sumatrensis* GUERIN (1980) was able to find only a single case. With progressive 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-

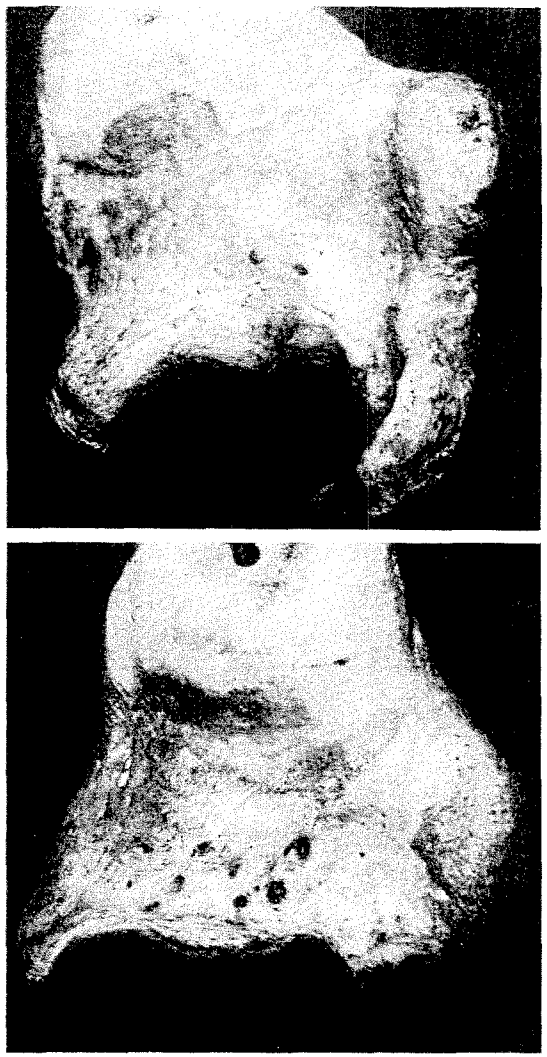

Fig. 7. Caput humeri and bicipital groove, left side, from proximal view. *Above:* a = *Rhinoceros unicornis* (BM 1950.10.18.5): long clawlike trochiter; *below:* b = *Diceros bicornis* (BM 1876.2.15.5): trochiter short, blunt

sinus may become closed with wear. This has never been recorded for *Dicerorhinus*.

31. It was GUERIN (1980) 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 hypocone 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.

32. 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 unicornis*. 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.

33. 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.

34. HOOIJER (1966) pointed out that in *Dicerorhinus* M^3 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 *D. sumatrensis*, and is fairly similar in living African rhinos. In *Rhinoceros*, on the other hand (and, convergently,

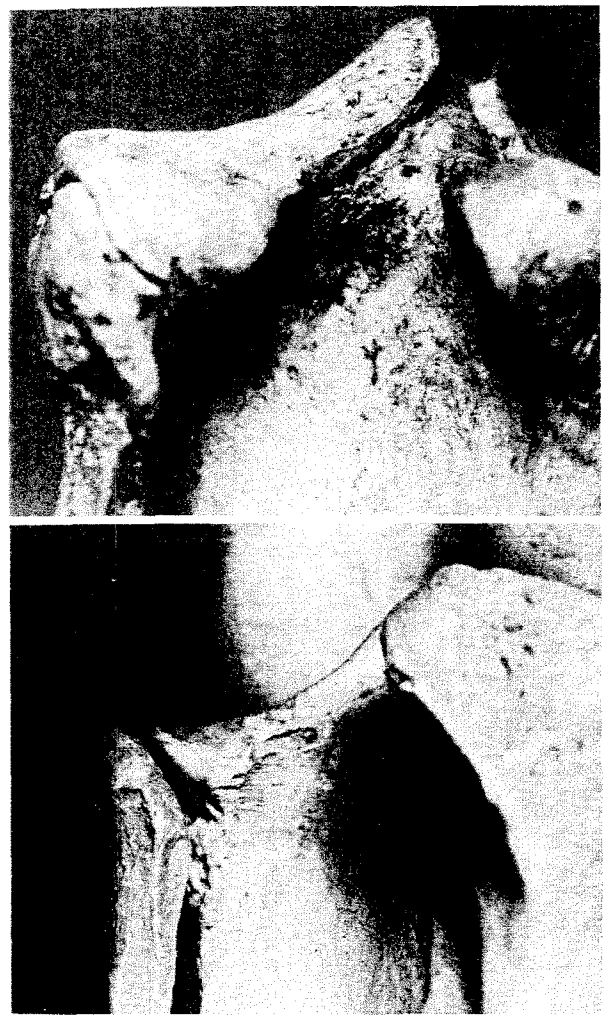

Fig. 8. Tibia-fibular relationship, left side in posterior view. *Above:* a = *Dicerorhinus sumatrensis* (BM 1894.9.24.1): head of fibula short, blunt, nestles under shelf-like protrusion of lateral articular surface of tibia; b = *Diceros bicornis* (BM 1876.2.15.5): head of fibula elongated, narrow, projects beyond edge of lateral articular surface of tibia

in some extinct genera such as *Aceratherium*), M^3 is subtriangular, and quite different in shape from the other two maxillary molars.

35. The lower molar valleys are primitively U-shaped in *Dicerorhinus*, but V-shaped like the premolars in other extant rhinos, occasionally (especially in *R. sondaicus*) opening out with wear into more of a U-shape. This character was first noticed by GUERIN (1980).

36. GUERIN (1980) 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 (HITCHINS 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 (GUERIN 1980). The Asian rhinos have an exceptionally elongated trochiter, so that the whole of the bicipital groove is enclosed by a pair of claw-like structures (Fig. 7).

39. Although not mentioned by GUERIN (1980), 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 lateral articular surface of the tibia. In African rhinos the fibular head is elongated, emerges proximad 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 GUERIN (1980), 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 (McIII) 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 + McIII; Femur + Tibia + MtIII), the total forelimb length exceeds that of the hindlimb in African rhinos; the reverse is the case in *Rhinoceros*; while in *Dicerorhinus* the two limbs 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: GUERIN (1980) details characters of all regions of the skeleton, and I have found also characters in the vertebral column, ulna, femur (head and third trochanter), talus, 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 Asian 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; GUERIN (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; GUERIN's (1982) analysis includes fossil taxa right from the start. In both analyses the choice of characters seems to be uneven: in HEISSIG's scheme Molariform Premolars, Skull Shortening and even "Panzerung" are listed alongside characters of the Metacone Rib and Protocone Fork; in GUERIN'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 GUERIN (1982) notes, cogently, that reduction of the facial skeleton characterises 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 I_1 and I_2: *Dicerorhinus* has lost I_1 but not I_2 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 on 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 Elasmotheriini 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 divergent from one another than from the Elasmotheriini. 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 Elasmotheriini. 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 palate moved forward to $M^{1/2}$ level; foramen ovale may be fused with f. lacerum medium; mastoid region inflated; foramen magnum triangular or pear-shaped, pointed dorsally; metacone rib developed on upper cheekteeth; antecrochet lost; humeral trochiter very elongated, claw-like; fibular head short, nestles under proximal end of tibia; radius usually under 85% of length of humerus; third metacarpal usually more than 50% length of radius.
Genera: *Rhinoceros*
Dicerorhinus

Tribe Dicerotini. Occipital crest sloping backward; nasals anteriorly abbreviated; lacrimal nearly or quite separated from nasal; nasal notch moved back, above P^{2-3}; infraorbital foramen moved back, above P^3–M^1; enlarged supraorbital processes; mandibular symphysis abbreviated, with loss of lateral diastema ridges; inferior border of mandible 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: *Diceros*
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*. His two alternative cladograms (1982, Figs. 2, 3) disagree in whether the two genera are to be allocated to the *Diceros* or *Dicerorhinus* groups, but agree in separating them into two different sublineages. He points out that *Coelodonta* has a reduced premolar cingulum, more elongated skull with backwardly inclined occipital crest, and very hypsodont cheekteeth, whereas *Stephanorhinus* has more molarised premolars; and ascribes 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. etruscus* and *D. hemitoechus*, and only slightly more distantly to *D. mercki* (recte *kirchbergensis*) and *D. jeanvireti*.

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 Dicerotini. As far as *Stephanorhinus* is concerned there is no doubt that it shares many features with Rhinocerotini: the nasal septum is ossified, in fact very strongly so; postorbital process are developed in the earlier forms, such as *"D." jeanvireti*, though they tend to disappear altogether in later representatives; the subaural channel is firmly closed; the palate ends opposite M^{1-2} in earlier forms; the foramen ovale varies, but may be fused with f. lacerum; the mastoids are rather strongly inflated; the metacone rib is well developed; there is no antecrochet; the trochiter is elongated; the fibular head is short; the metacarpus is elongated. In a few characters, *Stephanorhinus* does diverge from the usual Rhinocerotine morphotype: 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 been 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 posttympanic, the great mastoid inflation, and the strong molarisation of the premolars (with development of crochets, medifossettes 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 certainly 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 medifossettes, 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) seem more plausible, as the similarity to later *Stephanorhinus* is very striking. Indeed GUERIN (1980) seems to keep the *etruscus/hemitoechus* 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 site of Pikermi. Two taxa, referred to *Diceros* and *Dicerorhinus*, have been distinguished at this site; but some at least of the "*Diceros*" characters seem to be an artefact of distortion, and the two will have to be disentangled before any progress can be made.

Punjabitherium and Gaindatherium

The genus *Punjabitherium* was erected by KHAN (1971) after the discovery of a new cranium of the Upper Siwalik species previously called *Rhinoceros platyrhinus* 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 cheekteeth. Previously COLBERT (1935) included it in *Coelodonta* on the basis of the complexity of its cheekteeth, 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 redescribing 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 medifossettes 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 DP_1 well into adult life. Beyond this, however, it does not have the facial shortening of *Rhinoceros*, nor the strong mastoid inflation, horizontal premaxillae, 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 apomorphous states: molarisation of the premolars has gone farther than any other species of rhino, extending to P^3 and even to P^2 which lacks only a fully-formed protoloph but is block-shaped and scarcely smaller than P^3. The molars have the pecularity of a crista reduced in size, the medifossette being enclosed almost entirely by a hypertrophied recurved crochet. The postsinus 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 Pinjor Beds of the Upper Siwalik series alongside a fully evolved member of the genus *Rhinoceros*, *R. sivalensis*, a very close relative of *R. unicornis* (and probably conspecific with it).

An earlier Siwalik rhinoceros is *Gaindatherium browni* from the Chinji Formation (COLBERT 1934). HEISSIG (1972) reduced the genus *Gaindatherium* to subgeneric status under *Rhinoceros* and added a second species, *R.(G.) vidali* from the succeeding 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. sondaicus* as well as *R. unicornis*) (COLBERT 1934, 1935), or that it is a forebear of the restricted genus *Rhinoceros* (i. e. *R. unicornis* only), *"Eurhinoceros" sondaicus* having already separated from the lineage (HEISSIG 1972).

Fig. 9. (left). Gaindatherium browni (PSM 1956.11.248), cast of mandibular symphysis, in anterior view (end on), to show remains of both I_2 but no trace of I_1. – *Fig. 10 (right): Lartetotherium sansaniense* (PSM unreg.), from Sandelzhausen, Middle Miocene. Temporal region, showing posttympanic closely adpressed to postglenoid but no subaural fusion

As described and illustrated by COLBERT (1934), the type cranium of *G. browni* is almost precisely the reconstructed ancestral morphotype of *Rhinoceros*; and, indeed, of *Punjabitherium*. It has all the basic synapomorph conditions of the Rhinocerotini, those of the *Rhinoceros/Coelodonta* branch of the tribe (subaural closure, medifossette formation, median valley closure), and those of the *Rhinoceros/Punjabitherium* subsection (ridged vomer, vertical posterior margins of pterygoid plates, P_1 retention). It is primitive in its relatively long face, downsloping premaxilla and upcurved mandibular symphysis, differentiated lower molar valley levels, and large I^2 alveoli. There is only one identifiable autapomorphy: the apparent loss of I_1, observable in the cast of a referred symphyseal fragment in the Munich collection (Fig. 9). If correctly referred, this specimen indicates that *Gaindatherium* as presently known does not include the common ancestor of *Rhinoceros* and *Punjabitherium*.

Lartetotherium

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. schleiermacheri*, 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 GUERIN (1980, 1982) but has been referred to a separate genus, *Larthetotherium*, by GINSBURG (1974).

The defining characters of *Larthetotherium* were: occipital crest extremely high and vertical, temporal lines closely approximated, parietals less vaulted, orbit more rounded, zygomatic arch shorter, postglenoid and paroccipital processes in contact, and pterygoid plates extending back past the level of the postglenoid processes. Dental characters were also described.

The type skull, 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 HEISSIG (1972b); though crushed dorsoventrally, it is relatively unaffected in the areas where the Paris skull is most distorted. HOOIJER (1966) described *Dicerorhinus leakeyi* as a species very close to *"D." sansaniensis*; the type skull, which I have not seen, is from the figures less distorted than either of the European specimens.

Although a paper fully describing the genus is in preparation, a brief note on its phyletic position is appropriate here. The genus is valid, showing primitive and autapomorphic

character states and a very few that recall the Rhinocerotini. The primitive features are as follows: The orbitonasal length is much less than the orbitoaural (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 P^1 or $P^{2/3}$; there is no ossification of the nasal septum. The infraorbital foramen lies above P^2 or P^3, the anterior border of the orbit above M^1 or the $M^{1/2}$ boundary. There are no supraorbital processes. The vomer is flat. The posterior margins of the pterygoid 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 ovale (in the Munich skull) seems to be separate from foramen lacerum. 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 *leakeyi*) is well below the level of the alveoli. The premaxillae slope down and the mandibular symphysis is horizontal, so that the incisors actually occlude below the level of the cheekteeth. I_2 are tusk-like, I_1 are present. Crochets occur on the premolars; I have seen no specimen with premolar medifossettes although GUERIN (1980) finds that such may occur. In unworn premolars, in the Munich collection, the hypocone is isolated. There is no trace of a metacone rib or bulge. M^3 is primitively subtrapezoid. The lower molars valleys are U-shaped. The trochiter of the humerus is short; the radius is long, 90% 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 *Lartetotherium* with the Rhinocerotini. They are: Developed postorbital processes. The subaural channel is reported to be united in the *leakeyi* type (HOOIJER 1966), but the figures suggest that the region in question might not be very well preserved: the processes touch below the external auditory meatus in both the Paris and Munich skulls, but do not unite. The posterior palate margin is forwardly positioned; but not as far forward as in later representatives of the tribe. The antecrochet is

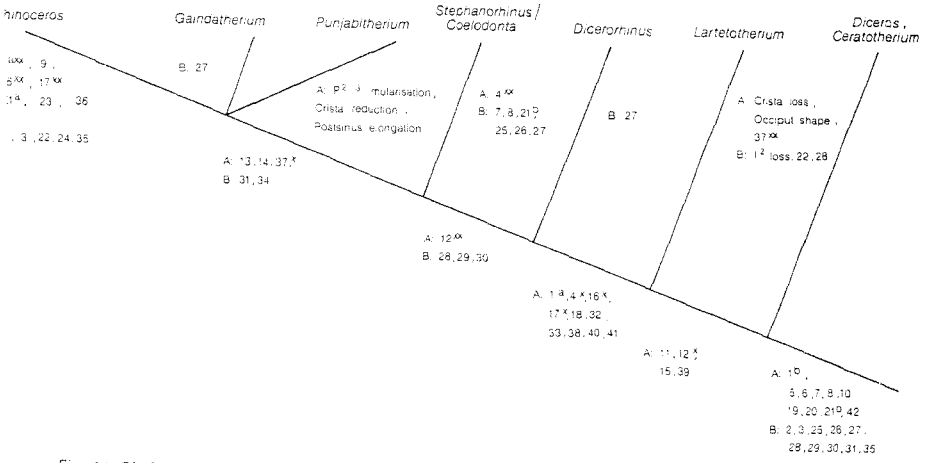

Fig. 11. Cladogram of Rhinocerotinae. Figures refer to apomorphic (derived) states, as discussed in the text and in Table 1. A = uniquely derived conditions; B = derived conditions shared with one or more other lineages, but here interpreted as convergent or parallel, $1^{a,b}$ and $21^{a,b}$ refer to the two opposite derived states of characters 1 and 21; 1^x, 12^x etc. refer to normally derived states of characters 1, 12 etc.; 1^{xx}, 12^{xx} to highly derived states

very small or absent. The form and relations of the head of the fibula are as in the Rhinocerotini. Autapomorphic characters of the genus (a couple of them convergent on *Rhinoceros*) are loss of I^2, exceptionally late shedding of DP_1, perhaps the low occlusion of the incisors, V-shaped inner mandibular contour (convergent with *Rhinoceros*), the curious interrelationship of the postglenoid and posttympanic processes [seen best in the Munich skull, and well described by HEISSIG (1972 b); see also Fig. 10]; also the absence of cristae on the molars, the closure of the median valleys, the lack of a level difference between the lower molar valleys, and the highly characteristic tall, 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 Elasmotheriini Gill, 1872
- Tribe Dicerotini new rank (ex-Dicerinae Pocock, 1945)
  - Genera: *Diceros* Gray, 1821
    Ceratotherium Gray, 1867
    Paradiceros Hooijer, 1968
- Tribe Rhinocerotini Dollo, 1885
  - Subtribe Lartetotheriina nov.
    - Genus: *Lartetotherium* Ginsburg, 1974
  - Subtribe Rhinocerotina Dollo, 1885
    - Genera: *Rhinoceros* Linnaeus, 1758
      Punjabitherium Khan, 1971
      Gaindatherium Colbert, 1934
      ?Stephanorhinus Kretzoi, 1942
      Coelodonta Bronn, 1831
  - Subtribe Dicerorhinina new rank (ex-Dicerorhininae Simpson, 1945)
    - Genus: *Dicerorhinus* Gloger, 1841

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Summary

A cladistic analysis of the extant rhinoceros taxa and their fossil relatives shows a clear division between the Dicerotini and other genera. *Rhinoceros, Punjabitherium, Gaindatherium, Stephanorhinus, Coelodonta* and *Dicerorhinus* are included in the Rhinocerotini; the first five form one subtribe (Rhinocerotina), *Dicerorhinus* alone belongs to the subtribe Dicerorhinina. *Lartetotherium* is a very primitive representative of the Rhinocerotini, and forms a third subtribe.

Zusammenfassung

Phylogenie der lebenden Arten vom Rhinoceros

Cladistische Analyse der lebenden Rhinocerotiden und ihrer fossilen Verwandten zeigt eine klare Trennung zwischen Dicerotini und den anderen Gattungen. *Rhinoceros, Punjabitherium, Gaindatherium, Stephanorhinus, Coelodonta* und *Dicerorhinus* sind in die Rhinocerotini einzubeziehen, die

ersten fünf bilden einen Untertribus (Rhinocerotina), allein *Dicerorhinus* gehört zum Untertribus Dicerorhinina. *Lartetotherium* ist ein sehr primitives Mitglied des Tribus Rhinocerotini und bildet einen dritten Untertribus.

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Author's address: Dr. COLIN P. GROVES, Department of Prehistory and Anthropology. Australian National University, P. O. Box 4, Canberra, ACT 2601, Australia