

Das Vorkommen des Luchses im Böhmerwald. *Ochrana přírody*, Praha, 15, 48, 1960. — 261. VODICKA, F.: Der Karpatenhirsch und sein Stamm. Praha, 1942 (Tschechisch). — 262. VRANOVSKÝ, M.: Bericht über einen Fund des Nestes der Birkenmaus (*Sicista betulina* Pallas). *Acta Rer. Nat. Mus. Slov.*, Bratislava, 6, 67–68, 1960. — 263. WANKEL, K.: Beiträge zur Fauna der mährischen Höhlen. *Lotos*, Praha, 10, 105, 136, 201, 1860. — 264. ZÁLESKÝ, M.: Die Säugetiere der Gegend von Jindřichův Hradec (Südböhmen). *Čas. Nár. musea, odd. přírodov.*, Praha, 102, 85, 1928. — 265. ZAPLETAL, M.: On the occurrence of the brown rat, *Rattus norvegicus* Berk., under natural conditions in Czechoslovakia. *Folia zoologica, Brno*, 13, 125–134, 1964. — 266. ZEJDA, J., V. HOLISOVÁ & J. PELIKÁN: On some less common mammals of Silesia. *Přírodov. čas. slezský, Opava*, 23, 25–35, 1962. — 267. ZEJDA, J. & M. KLÍMA: Die Kleinsäuger des Naturschutzgebietes „Kubany Urwald“ (Boubín). *Folia zoologica, Brno*, 7, 292–307, 1958. — 268. ZELIZKO, J.: Heutige und jungdiluviale Verbreitung des Steppenitlisses und des Nerzes sowie verwandter Formen in der Tschechoslowakei. *Quartär*, Berlin, 1, 119–124, 1930.

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On the Rhinoceroses of South-East Asia

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With 4 Figures

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The object of this paper is to review knowledge of the distribution and taxonomy of two of the world's rarest mammals: *Rhinoceros sondaicus* (the Javan rhinoceros) and *Dicerorhinus sumatrensis* (the Sumatran rhinoceros). Together with three other species, these two forms make up the living representatives of the family Rhinocerotidae. Although the family thus consists of no more than five species, it is certain that no fewer than four well separated lines of descent are represented, and the family must be split into four genera, three of which are accordingly monotypic.

Beyond this level, a classification into subfamilies is usually employed. Certain it is that the two African genera, *Diceros* and *Ceratotherium*, differ in every conceivable adaptive feature from the Asiatic one-horned genus *Rhinoceros*, and fully merit the subfamily separation awarded to them. The position of the Asiatic two-horned genus, *Dicerorhinus*, is equivocal however. SIMPSON (1945) puts it with the African genera in a subfamily Dicerorhinidae, separating *Rhinoceros* and its extinct ancestral genus into the subfamily Rhinocerotinae (both of these names are correctly formed). On the other hand POCOCK (1944) and, by implication, CAVE (1962) prefer to align *Dicerorhinus* with the other Asiatic genus. A third course, followed by ZEUNER (1934), is to refer the genus in question to a third subfamily, separating it from both *Rhinoceros* and the African group.

It is felt by this author that, although the very primitive features of *Dicerorhinus* are liable to confuse an assessment of its relationship, the genus does in fact show sufficient progressive characters to unite it to *Rhinoceros*, and to separate it entirely from the African rhinoceroses. Such features are the enlargement of the lower tusks (canines or lateral incisors, according to different authors) to form weapons (HUBBACK, 1939:3); the tendency to develop deep folds in the hide; the less advanced reduction of body hair; the lack of backward occipital projection; the closeness of approach of the postglenoid and poststympnic processes, narrowing and even (in *Rhinoceros* and some fossil species of *Dicerorhinus*) closing the subaural canal; the processus narrow, pointed nasals; and — in outline but not in detail — the structure of processus glandis of the penis. All these features contrast strongly with the African rhinoceroses, the most marked difference being the complete abbreviation of the jaws and nasals in the latter, related to the loss of incisors and canines.

It will be as well here to remark upon the question of bodily hair. It is usually stated that in all species except *Dicerorhinus* the hair is restricted to the rims of the ears and the end of the tail. In reality, the situation is more complex. CAVE & ALLBROOK (1959:104) state that in the White Rhinoceros, *Ceratotherium simum*, hair is present but rudimentary in the follicles, and sometimes may reach almost to the surface. Hairs actually project on the summit of the nuchal eminence, and BIGALKE and HELLER are quoted to the effect that hairs can be detected in the neonate and the young up to 15¹/₂ months.

DESMAREST (1822:399) describes a young *Rhinoceros sondaicus* as having an epidermis "épais, divisé en tubercules anguleux, marqués chacun d'un petit creux au milieu, du fond duquel sort un petit poil court, roide et brun". In his description of an adult *Rhinoceros unicornis* he says, after speaking of hairs on the ears and tail, that there are "d'autres poils, mais plus rares, comme frisés et d'apparence laineuse, sur quelques parties du corps". HUBBACK (1939:2) says of *Dicerorhinus sumatrensis* "The young rhinoceros has hair but this disappears as the animal ages and only very short hairs, almost bristles, are found on most exposed parts of the mature animal". THOMAS (1901) describes just such changes as having occurred during the lifetime of "Begum", the type specimen of *Rhinoceros sumatrensis lasiotis* Sclater; the bodily hair was originally long, copious, soft and brown, and in thirty years of captivity was worn to a short, sparse, bristly black condition. SODY (1959:118-9) mentions corresponding ages changes in *Rhinoceros sondaicus*; speaking of the hexagonal scales into which the skin is divided (the "tubercules anguleux" of DESMAREST), says "Jedes Schildchen hat in der Mitte eine Vertiefung, aus der eine oder ein paar Borsten entspringen. Bei älteren Tieren sind diese an den Seiten meistens abgescheuert". In conclusion, one may accept the opinion of CAVE & ALLBROOK (1959:104) who state: "Present findings suggest than an original sparse external hairy endowment becomes reduced with age, either from the mechanical abrasion of the projecting portions of the body hairs or from natural atrophy consequent upon the development of a substantial layer of subcutaneous fat". The presence of fat in quantity is a feature of *Ceratotherium* alone; presumably therefore abrasion would be the chief or only cause of apparent hairlessness in other species.

From the absence of any mention of hair in numerous descriptions of specimens of *Diceros bicornis*, both adult and young, it may be assumed that a hairy coat in this species is either absent or very inconspicuous and sparse. Certainly the careful description of DESMAREST makes no mention of it. It may be supposed, therefore, that hair may occur on the young of most or all species, surviving into adulthood in the Asiatic forms, most noticeably in the Sumatran, and to a less striking extent in the other two (i. e. the genus *Rhinoceros*).

Besides *Rhinoceros* and *Dicerorhinus*, the subfamily Rhinocerotinae will contain at least two other genera: *Gaindatherium* and *Cœlodonta*. The former is decidedly the ancestral genus to *Rhinoceros* (COLBERT, 1936 and 1942); it shows that by the Pliocene the lines leading to the two living Asian genera had already separated. The genus *Cœlodonta* is Plio-Pleistocene in age, derived from *Dicerorhinus*; there is dispute as to the precise limits of the two genera, which show a graded series from *D. sumatrensis* — which is strangely, the most primitive member of its genus — to *C. antiquitatis*, the Pleistocene woolly rhinoceros of Europe and northern Asia. It would seem that members of this line of descent retained copious body-hair, but progressively reduced the front teeth. *Cœlodonta antiquitatis* lacked incisors and canines, but showed its affinities to *Dicerorhinus* rather than the *Diceros* line in its retention of the elongate premaxillae and nasals.

It has been mentioned above that *Dicerorhinus sumatrensis* is the most primitive living species; indeed it is a great deal more primitive than many forms long extinct

(such as the woolly rhinoceros). Features indicative of this position include (KRUMBIEGEL, 1960) its small size, hairiness, and the thinness of its simply folded skin. Otherwise its intermediate skull features sufficiently show its primitive character.

Rhinoceros sondaicus belongs to a genus showing a considerable degree of advancement over *Dicerorhinus*, mainly to do with its adaptation to a particular type of forest environment (see below); nonetheless it shares certain primitive characters with *D. sumatrensis*. The fact that these relate to visceral anatomy (FLOWER & LYDEKKER, 1891) and tooth pattern (HOOIJER, 1946) indicates that we have here a retention of a common pattern of nutrition. In the differences in dentition between the two, *D. sumatrensis* shows a certain degree of convergence with *Rhinoceros unicornis*: notably the presence of a protocone fold. One would therefore expect to find that the Sumatran rhinoceros has ecological similarities with both the species of *Rhinoceros*.

Both Javan and Sumatran species of rhinoceros exist — or existed until recently — in the tropical rain-forest zone of South-east Asia. The maps (figs. 1 and 2) will show both the similarities and differences in distribution pattern. The absence of both species from a given area may well reflect the little-known nature of that area, but if one has been amply recorded from a given region and the other not, it would seem to indicate that the second species really was always absent from that region. As examples of this one may cite the absence of *R. sondaicus* from Borneo, where *D. sumatrensis* was well known, and the reverse situation in Java. In neither case is the missing species known from the fossil state on that island.

Some areas need special comment.

1. Eastern Java. Locality records in western Java are so numerous that those to be included on Fig. 1 have had to be selected. But very few records occur as one travels east on the island. It seems probable that this reflects the fact that in eastern Java evergreen gives place to deciduous forest (RICHARDS, 1956).

2. Kalimantan. The scarcity of locality records from Indonesian Borneo, except along the frontiers of the Malaysian portion, is probably to be explained by the little known nature of the country, which has been very little explored.

3. Malaya. Locality records for both species occur almost entirely on the western side of the peninsula. There appears to be only one definite record of a rhinoceros east of the central highlands, this being *D. sumatrensis*, for which the records are more numerous than for *R. sondaicus* anyway. (As for the Javan species in Java, records of the Sumatran rhinoceros in Malaya are so numerous that they have had to be selected).

4. The Indo-Chinese area. It is little realised that *D. sumatrensis* is almost unknown in this area. Some records refer merely to "rhinoceroses", but wherever the species is specified it is *R. sondaicus*, except in one instance: the Sumatran rhinoceros is known from Cam Ranh, South Vietnam. However TALBOT (1960:179) says that both species were found in the Mekong valley in the 1920's. But no Sumatran rhinos appear ever to have been recorded from North Vietnam or northern Laos. According to LOCH (1939:143), Prof. Bourret was sure that both species existed in the south of Indo-China, and *sondaicus* in Tonkin. If it is true that *sumatrensis* was restricted to the south of the area, it needs to be explained; it will also make it certain that any rhinoceroses which are reported from there in the future are Javan. Also, if TALBOT (1960:205) is right that rhinos existed over the Chinese border, then these must be Javan.

5. Burma. The maps show *D. sumatrensis* distributed continuously up the coast of Burma, and up to the northernmost part, on the border with Assam. On the other hand there would seem to be a gap in the range of *R. sondaicus*: north of Kahilu

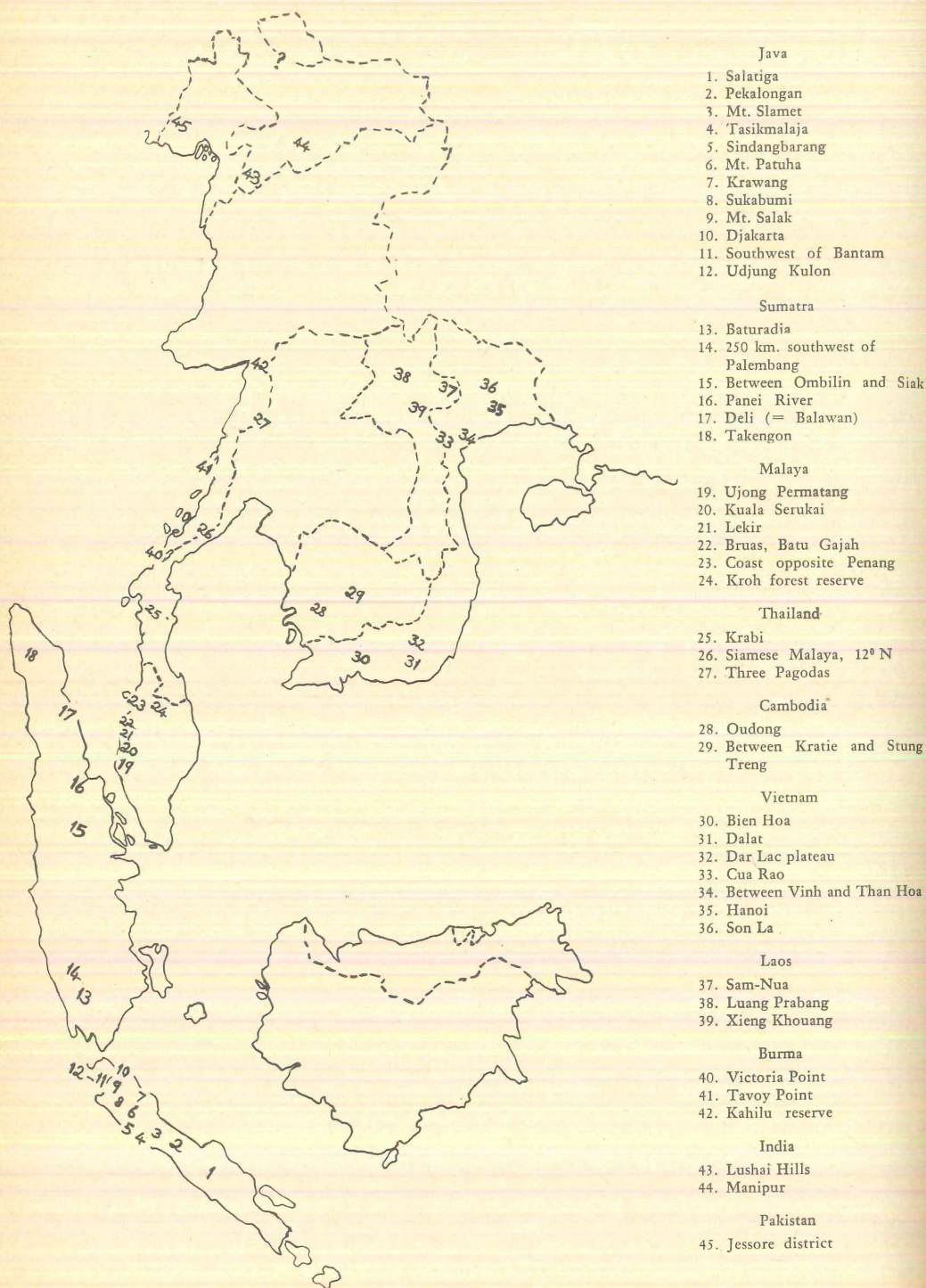


Fig. 1: Map to show the Distribution of *Rhinoceros sondaicus*: Known locality records (Sody, 1959; Talbot, 1960; Loch, 1939; and labels of Museum specimens)

- Kalimantan
1. Kapan Mts. (uncertain)
 2. Upper course of R. Boh
 3. Headwaters of R. Bahau
- Sarawak & Sabah
4. Baram River
 5. Sandakan
 6. Mt. Kinabalu
- Sumatra
7. Sumatera Selataun reserve
 8. Djambi
 9. Padang Besi
 10. Pangkalan Kampar
 11. Panci River
 12. Siboga
 13. Deli (= Balawan)
 14. Loser forest reserve
- Malaya
15. Kian Puhu
 16. Tahan River
 17. Ulu Bernam
 18. Slim River
 19. Bruas
 20. Kenas
 21. Maxwell Hill Cottage
- Thailand
22. Kanchanaburi
- Vietnam
23. Cam Ranh
- Burma
24. Victoria Point
 25. High Island, Mergui archipelago
 26. Kahilu reserve
 27. Bassein
 28. Shwe-U-Daung reserve
 29. West of Prome
 30. Mogok
 31. Chindwin Uyu district
 32. Myitkyina
 33. Putao
- India
34. Lushai Hills
 35. Manipur Hills
- Pakistan
36. Chittagong Hills
 37. Tipperah



Fig. 2: Map to show the Distribution of *Dicerorhinus sumatrensis*: Known locality records (From the same sources as Fig. 1)

there are no records until one reaches India and Pakistan — the Lushai Hills and the Sunderbunds. *D. sumatrensis* was known from the former locality but not, apparently, from the latter.

Thus the available evidence shows the two species to have had roughly equivalent distributions, but with strange gaps where one or the other was absent. These gaps, if in fact they are real, may offer clues to a puzzle: how could two large species live side by side in the same areas and avoid competition?

The solution seems to lie in the concept of ecological displacement. This concept implies that where two closely related species are sympatric, their habitats will be segregated; but where one or the other is found alone it can occupy both preferred habitats.

The evidence is conflicting as to precisely what are the differences in habitat between the two species. On the one hand we have SHORTRIDGE (1915) who says that in the Dutch East Indies he was always told that the Javan was more of a mountain animal than the Sumatran, but found that in Tenasserim their habits were similar; on the other hand we find PEACOCK (1933) who says of *R. sondaicus* "It was supposed never to ascend high into the hills, i. e. into the typical habitat of the Sumatran rhinoceros". On the whole, authors tend to confirm the opinion of PEACOCK, that the Javan rhinoceros tended to exist more on low ground. Indeed, when one plots the localities of the two onto a map showing altitudes, this tendency is revealed. It is, however, only a tendency. Both in Sumatra and in Malaya *D. sumatrensis* is known from the swampy lowlands, and most markedly of all in Borneo, which is what one would expect from the ecological displacement concept. In Java and in northern Laos one finds reports of *R. sondaicus* ascending high mountains.

The northern Laos area is continuous with the Vietnam coastal region from which *D. sumatrensis* is known, but the apparently suitable habitat here is ignored. The reason for this remains a mystery. But very clear habitat segregation occurs in the Burma-Assam-Pakistan border area; here, the Sumatran species is known from the mountains of northern Burma but not from the swampy, low-lying Sunderbunds; the Javan form, on the other hand, shows the opposite distribution, although it does extend up to Manipur, and to the borders of Bhutan a little further west.

It was mentioned above that the nature of the forest in eastern Java appears to have prevented the Javan rhinoceros inhabiting that portion of the island to any marked extent. Similar forests, of the monophyllous, more open type, are found in a belt across the Shan States, northern Thailand and northern Laos. It is very noticeable that there are very few reports of rhinoceroses from this belt; what there are — those from northern Laos — are marginal. It is entirely possible that avoidance of this belt is the reason for the absence of the Sumatran rhinoceros from northern Indo-China: its only method of invading the area would be via the coastal strip of evergreen forest of Vietnam which, being all low-lying, would be more suitable for the Javan species; and, being a narrow corridor, would be able to support only one species, and thus form a barrier to the distribution of the other. Meanwhile *R. sondaicus* would be existing alone in the north, and habitat segregation would no longer be necessary: it would thus be able to inhabit the mountains, even overspilling slightly into the deciduous forest zone.

In this way the concept of ecological displacement can be used to explain distribution, and to aid in questions such as that posed above, of how to explain the co-existence of two large, closely related species.

It was remarked above that the habitat segregation is "only a tendency". This tendency is transgressed, it would seem, more often by *D. sumatrensis*; it was mentioned that this species is known from low-lying swampy areas in both Malaya and Sumatra. It is also known that the species is a wanderer. Wandering seems not to be

recorded of *R. sondaicus*. Indeed, the contrast of the two in this respect extends to social pattern, where the impression was given that the Sumatran species is — or was — thinly scattered and found singly, while the Javan species could and did build up large populations in a single area. The various sources quoted by SODY (1959) testify to this latter point. Thus on p. 131 he mentions the killing of 526 rhinoceroses in Java between September 1st., 1747 and January 14th., 1749. On p. 134 he quotes HORSFIELD as saying that "it lives gregarious in many parts of Java". Elsewhere in his section on Java he quotes authors who state that it is "sehr zahlreich". At the other end of the range it was „numerous in the Annamite Chain in the Forests of North-Annam and Haut-Laos" (p. 172); in 1884 it was "yet plentiful in the Sunderbans" (p. 176); and between 1860 and 1870 in Assam POLLOCK "shot there 44 to my own gun, and probably saw some 60 others slain, and lost wounded fully as many as I killed" (p. 174-5).

All this goes to show that, not only was *R. sondaicus* a very numerous species before intensive hunting began, but also it existed in large concentrations. It did not undertake the extensive wanderings of *D. sumatrensis* (see HUTCHINSON & RIPLEY, 1954), and probably lived similarly to *R. unicornis*, where wandering is the normal reproductive pattern, but takes place over much smaller areas and allows a much greater concentration of animals.

During its wide wandering, the Sumatran rhinoceros would be bound to enter a variety of habitats, and it is entirely probable that the animals seen in the swamps would be a transient element. This variety of habitats would necessitate a variety of foodstuffs — a possible explanation of the protocone fold on the cheekteeth which it shares with *R. unicornis* as opposed to *R. sondaicus*.

Over such wide areas of distribution, both species might be expected to show geographic variation; very little work has been done on this in *D. sumatrensis* and none at all in *R. sondaicus*. Too little is known of the external features of either species to build subspecies on such characters (although SCLATER 1872, and GRAY 1872 believed that this could be done). The skull and teeth must therefore form the chief, if not the only basis for intraspecific taxonomy. The teeth would seem to be of particular importance in this respect, as the frequency with which they turn up in fossil beds would enable the story of subspeciation to be carried back into the past.

Before examining geographic variation in skulls, it is necessary to investigate age variation and, if possible, sexual variation. Unfortunately most skulls to be found in museums of rhinoceroses are not sexed. A sufficient number are sexed, however, to enable it to be said with confidence that marked size difference is found in only one feature — nasal breadth: a happy result, as it not only allows for larger samples, but it also reflects the different horn sizes in the two sexes.

The skulls were divided in each species into six growth stages, using tooth eruption, as follows:

- Stage 1. First permanent molar not visible.
- Stage 2. First permanent molar erupting; no trace of second molar.
- Stage 3. Second molar erupting; second and third premolars in process of replacement.
- Stage 4. Second molar in wear; fourth premolar in process of replacement.
- Stage 5. Third molar in evidence; all milk teeth replaced.
- Stage 6. Third molar fully erupted.

This sequence of eruption corresponds in the two species under consideration. The duration of the different stages would appear to differ, however — judging from the number of specimens available for each species from each growth stage. These numbers were as follows:

| | <i>D. sumatrensis</i> | <i>R. sondaicus</i> |
|---------|-----------------------|---------------------|
| Stage 6 | 20 | 27 |
| Stage 5 | 6 | 2 |
| Stage 4 | 8 | 9 |
| Stage 3 | 7 | 3 |
| Stage 2 | 8 | 3 |
| Stage 1 | — | 2 |

This makes a total of 49 Sumatran and 46 Javan skulls. As percentages of the total number, the numbers in each stage fall out as follows:

| | <i>D. sumatrensis</i> | <i>R. sondaicus</i> | % |
|---------|-----------------------|---------------------|---|
| Stage 6 | 40.8 | 58.7 | |
| Stage 5 | 12.3 | 4.3 | |
| Stage 4 | 16.3 | 19.6 | |
| Stage 3 | 14.3 | 6.5 | |
| Stage 2 | 16.3 | 6.5 | |
| Stage 1 | 0.0 | 4.3 | |

If these figures were taken literally, it would mean that in *D. sumatrensis* the first permanent molar begins to erupt shortly after birth, i. e. Stage 1 is very short. However, a possible reason for the differing percentages of the two species becomes apparent at a glance at Table 1. Here it can be seen that there is a smooth size increase

Table 1: Mean measurements of skulls at different growth stages: *Dicerorhinus sumatrensis*

| STAGE | 6 | 5 | 4 | 3 | 2 |
|----------------------|-----------------------------|-----------|-----------|-----------|-----------|
| | 1. <i>D. s. barrissoni</i> | | | | |
| Skull length | 467.8 (5) | 460.0 (2) | 441.0 (3) | 443.0 (5) | 432.7 (3) |
| Basal length | 475.0 (6) | 480.0 (1) | 433.7 (2) | 461.7 (3) | 443.0 (3) |
| Zygomatic breadth | 264.3 (6) | 254.5 (2) | 256.3 (3) | 254.1 (5) | 251.7 (3) |
| Nasal breadth | 81.4 (5) | 76.5 (1) | 72.3 (3) | 64.1 (5) | 59.2 (2) |
| Occipital breadth | 118.0 (6) | 113.0 (2) | 109.3 (3) | 105.4 (4) | 99.0 (3) |
| Occipital height | 114.8 (5) | 122.0 (1) | 107.7 (3) | 115.0 (3) | 116.0 (3) |
| Interorbital breadth | 87.0 (6) | 89.5 (2) | 87.3 (3) | 88.5 (5) | 90.0 (3) |
| | 2. <i>D. s. sumatrensis</i> | | | | |
| Skull length | 525.8 (6) | 543.0 (2) | 498.0 (2) | 490.5 (2) | 466.8 (5) |
| Basal length | 507.0 (6) | 513.5 (2) | 490.0 (1) | 484.5 (2) | 465.2 (5) |
| Zygomatic breadth | 283.3 (6) | 294.5 (2) | 278.5 (2) | 273.5 (2) | 265.4 (5) |
| Nasal breadth | 104.0 (6) | 99.5 (2) | 76.0 (2) | 91.0 (2) | 13.3 (5) |
| Occipital breadth | 128.0 (6) | 124.5 (2) | 124.5 (2) | 114.0 (2) | 118.2 (5) |
| Occipital height | 114.0 (6) | 117.5 (2) | 110.0 (2) | 114.0 (2) | 114.3 (5) |
| Interorbital breadth | 100.0 (6) | 119.5 (2) | 101.5 (2) | 100.5 (2) | 93.9 (5) |

Mean measurements of skulls at different growth stages: *Rhinoceros sondaicus sondaicus*

| STAGE | 6 | 5 | 4 | 3 | 2 | 1 |
|----------------------|------------|---------|-----------|-----------|-----------|---------|
| Skull length | 514.5 (12) | 500 (1) | 508.8 (4) | 452.0 (2) | 393.7 (3) | 338 (1) |
| Basal length | 575.8 (8) | 503 (1) | 547.3 (3) | 492.7 (3) | 433.0 (2) | 354 (1) |
| Zygomatic breadth | 347.5 (12) | 330 (1) | 342.0 (5) | 305.0 (2) | 274.0 (3) | 246 (1) |
| Occipital breadth | 296.0 (11) | 265 (1) | 281.5 (4) | 243.3 (3) | 216.3 (3) | 192 (1) |
| Occipital height | 158.8 (12) | 144 (1) | 153.8 (4) | 126.0 (2) | 110.5 (2) | 81 (1) |
| Interorbital breadth | 120.1 (12) | 114 (1) | 122.0 (5) | 119.7 (3) | 113.7 (3) | 109 (1) |

in *D. sumatrensis*, and that Stage 2 skulls are not so very much smaller than adult ones — on average, they are 90.2% of the size (Occipitonasal length) of Stage 6 skulls. On the other hand there is in *sondaicus* a sudden size increase between stages 3 and 4, and Stage 2 is only 76.5% of the size (Occipitonasal length) of Stage 6, taking all specimens into account. Thus, hunters shooting a young Sumatran rhinoceros — of

the stages represented in this series — might well have been excused for thinking that they were shooting an adult; whereas below Stage 3 a Javan rhinoceros is most clearly undersized. This being so, two things still need to be explained: (1) the small number of Stage 5 *R. sondaicus*, and (2) the absence of any Stage 1 *D. sumatrensis*. (There is however a foetus of the Sumatran species in the Cleveland Natural Science Museum, which has an Occipitonasal length of 220 mm., i. e. 41.8 % of the adult. In the catalogue this is entered as a neonate, but it seems very small for this).

The only point of tooth eruption in which the two species appear to differ concerns the Deciduous first molar. This tooth, with no permanent replacement, is very reduced in size; in *D. sumatrensis* both upper and lower are shed in stages 3 or 4; whereas in *R. sondaicus* the lower one is shed well before the upper, in Stage 4, while the upper one is often still present in stage 6, and is never shed before Stage 5.

A subspecific classification of each species may now be attempted. In the Sumatran rhinoceros, specimens of Stage 5 have been used to arrive at the figures in Table 2, the skulls of this stage being of approximately the same size as those of Stage 6 (see Table 1).

Table 2: Mean skull values for adult specimens of *Dicerorhinus sumatrensis*

| Skulls | Borneo | Sumatra | Malaya | Pegu | Burma |
|---|--------------|--------------|---------------------------|------|-------------|
| Skull length | 465.6 ± 17.2 | | 528.3 ± 20.9 | | |
| Basal length | 475.7 ± 12.0 | | 507.4 ± 16.1 | | |
| Toothrow length | 190.7 ± 10.6 | 201.3 ± 14.4 | 193.8 ± 12.3 | 208 | 219.7 ± 2.4 |
| Zygomatic breadth | 261.9 ± 13.2 | 288.6 ± 11.3 | 297.0 ± 10.8 | 282 | 294.0 ± 1.4 |
| Nasal breadth $\left. \begin{array}{l} \text{♂} \\ \text{♀} \end{array} \right\}$ | 80.0 ± 8.5 | | 125.0 ± 4.7 99.5 ± 7.8 | | |
| Occipital breadth | 116.8 ± 9.0 | 125.6 ± 8.5 | | 141 | 150.5 ± 5.0 |
| Occipital height | 116.0 ± 4.4 | 114.9 ± 3.9 | 118.7 ± 4.5 | 120 | 125.0 ± 1.4 |
| Interorbital breadth | 87.6 ± 6.5 | | 103.2 ± 8.4 | | |
| Palate-Occiput angle | 86.4 ± 2.5 | | 96.9 ± 4.2 | | |
| Occipital crest angle | 66.0 ± 2.9 | | 59.3 ± 2.6 | | |
| Foramen Magnum angle | 90.6 ± 2.7 | | 92.8 ± 7.7 | | |

In an earlier paper, the present author (GROVES, 1965) described the Bornean form of *D. sumatrensis* as a new subspecies and suggested the validity of three others, respectively from Burma, Malaya and Sumatra. In the light of the present greatly increased sample — which includes most or all specimens in museums of Western Europe (and East Berlin) and the United States — it would appear that the Malayan deme is separable from the Sumatran on average only: in the Tables 2 and 3, the figures for the two hardly ever differ even by one Standard deviation. Graphs combining two measurements added nothing to this picture (fig. 3).

A further postscript to the earlier paper by GROVES needs to be made: that in this earlier paper growth was supposed to have been completed by Stage 4. Table 1, on the enlarged sample, shows that this is incorrect: Stage 4 specimens average 94.9 % of the length of Stage 6. They have therefore been removed from the adults' sample.

In *R. sondaicus*, Occipital breadth is taken low down, at mastoid level; otherwise the skull measurements do not need explanation beyond that given in GROVES (1965). Tooth measurements were made in the manner of HOOIJER (1946), except that his upper tooth lengths were not taken, because of their inherent inaccuracy. The present author's measurements of the Leiden skulls tallied closely with those given for the same specimens by HOOIJER; accordingly, the latter author's figures for fossil teeth can be accepted without qualification.

The skull angles were in GROVES (1965) accepted as being the same as those of ZEUNER (1936); however an earlier paper by ZEUNER (1934) shows this not to be the case. None the less, the Palate-Occiput angle measures the deviation of the occipital plane from the vertical; the other two are more nearly those of ZEUNER.

In this paper the generic name *Dicerorhinus* is used instead of *Didermocerus*. It would seem that the sale catalogue of the museum of Joshua Brookes, in which the name *Didermocerus* was published, was not intended for purposes of "permanent scientific record", as the International Code of Zoological Nomenclature requires;

Table 3: Mean teeth values for adult specimens of *Dicerorhinus sumatrensis*

| Teeth | Borneo | Sumatra | Malaya | Pegu | N.Burma |
|--------------------------|---------------|---------------|--------------|------|--------------|
| P ² br. ant. | 28.7±2.1 (9) | 29.7±2.1 (11) | 29.8±0.8 (6) | 36.2 | 35.0±2.2 (3) |
| P ³ br. ant. | 39.7±1.6 (9) | 40.4±2.4 (9) | 39.9±2.4 (6) | 42.0 | 46.1±2.3 (3) |
| P ⁴ br. ant. | 48.0±2.1 (3) | 47.2±3.2 (7) | 47.2±1.6 (4) | 45.2 | 50.2±2.0 (3) |
| M ¹ br. ant. | 48.7±1.2 (11) | 48.8±2.2 (15) | 50.9±1.8 (6) | 49.6 | 54.0±2.0 (3) |
| M ¹ br. post. | 43.2±2.7 (6) | 44.1±3.0 (15) | 46.2±1.7 (4) | 43.9 | 51.0±2.5 (3) |
| M ² br. ant. | 49.3±1.4 (5) | 50.3±2.8 (10) | 52.5±2.2 (4) | 50.7 | 54.6±0.8 (3) |
| M ³ br. | 42.8±2.4 (4) | 45.6±2.6 (6) | 47.3±0.6 (3) | 47.9 | 48.3±4.5 (2) |
| P ₂ length | 22.8±2.0 (7) | 24.5±1.8 (10) | 24.8±1.8 (8) | — | 28.0±0.3 (2) |
| P ₂ breadth | 12.5±1.1 (7) | 14.7±2.0 (10) | 15.8±2.1 (6) | — | 14.5±1.7 (2) |
| P ₃ length | 29.7±2.7 (9) | 29.7±1.8 (11) | 28.2±2.6 (5) | 30.2 | 34.2±1.7 (3) |
| P ₃ breadth | 17.2±1.5 (9) | 18.0±1.2 (11) | 20.1±1.4 (5) | 20.1 | 21.8±1.7 (3) |
| P ₄ length | 32.0±2.9 (4) | 33.2±1.7 (8) | 30.1±1.8 (4) | 31.6 | 37.6±1.5 (3) |
| P ₄ breadth | 20.9±1.7 (4) | 22.9±0.8 (8) | 23.7±1.2 (3) | 22.8 | 25.5±2.5 (3) |
| M ₁ length | 38.5±3.7 (14) | 37.7±3.3 (15) | 35.7±5.3 (7) | 38.2 | 40.3±1.5 (3) |
| M ₁ breadth | 24.1±1.3 (14) | 23.4±1.5 (15) | 24.6±2.3 (6) | 27.0 | 27.7±2.4 (3) |
| M ₂ length | 40.0±3.2 (7) | 41.3±1.8 (15) | 40.0±1.2 (4) | 42.5 | 45.1±2.4 (3) |
| M ₂ breadth | 25.1±1.8 (7) | 25.1±1.9 (14) | 27.7±0.6 (3) | 28.3 | 29.3±1.2 (3) |
| M ₃ length | 40.8±2.0 (4) | 40.1±2.5 (6) | 40.4±1.4 (4) | 45.8 | 46.2±7.1 (2) |
| M ₃ breadth | 24.2±1.9 (4) | 25.5±1.3 (6) | 26.5±0.9 (3) | 30.0 | 27.7±3.9 (2) |

Subfossil Sumatran Teeth (Hooijer, 1946)

| | |
|--------------------------|--------------|
| P ² br. ant. | 30.1 (1) |
| P ³ br. ant. | 44.0 (1) |
| P ⁴ br. ant. | 53.0±1.4 (2) |
| M ¹ br. ant. | 55.8±1.0 (4) |
| M ¹ br. post. | 48.0±1.4 (4) |
| M ² br. ant. | 59.5±1.0 (4) |
| M ³ br. | 53.5±2.1 (2) |

it is therefore dropped in favour of the more widely used *Dicerorhinus*, which has always been the name employed by palaeontologists.

Genus *Dicerorhinus* Gloger, 1841.

1828. *Didermocerus* Brookes, Cat. Anat. Zool. Mus. J. Brookes, London, 75. Not available: see above. *Didermocerus sumatrensis* Brookes.

1841. *Dicerorhinus* Gloger, Handbuch Naturgesch., 125. *Rhinoceros sumatrensis*.

1867. *Ceratorhinus* Gray, P. Z. S., 1021. *Rhinoceros sumatranus*.

Differs from *Rhinoceros* in the smaller size; lower canines less enlarged; orbit more centrally placed on skull; post-glenoid not fused with post-tympanic, in living form; occiput subvertical, not inclined forward, and not expanded in auditory region. Horns two, with an extensively keratinised area around their bases; nostrils overlapped su-

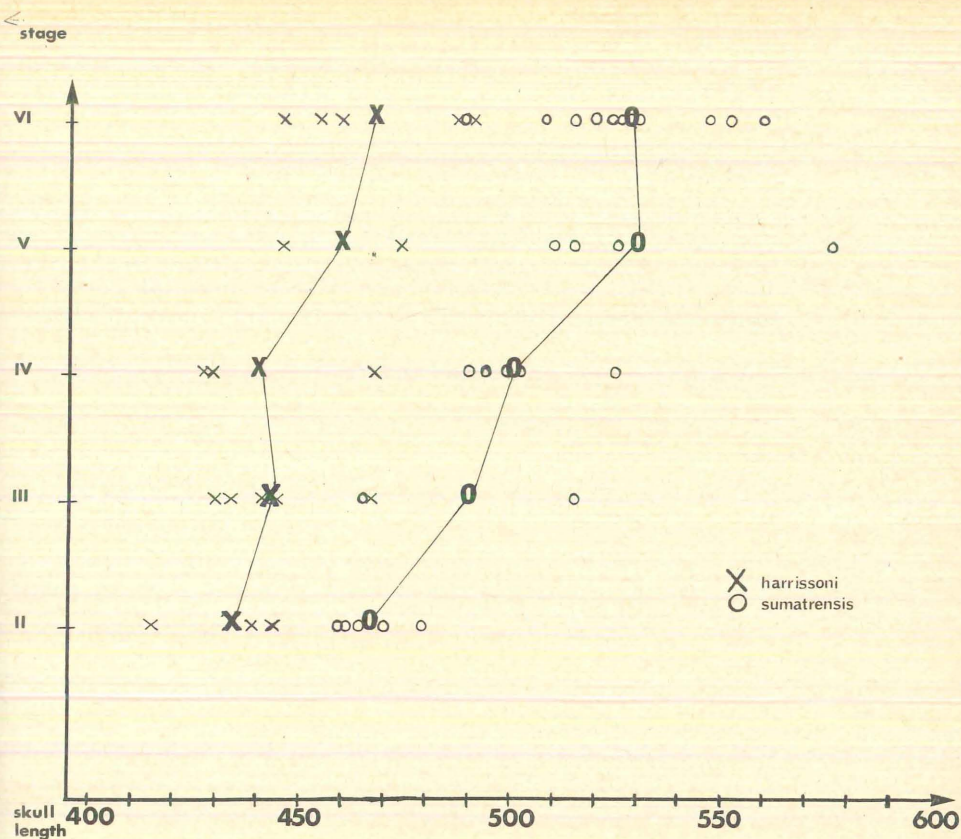


Fig. 3: Increase of skull length (occipitonasal) with growth stages.

teriorly by a horny flap; hide thinner than in other rhinoceroses, with a hairy coat which tends to be visible and apparent-throughout life; a prominent scapular skin-fold, but other folds less developed; processus glandis of penis attached at base only (CAVE, 1964).

Dicerorhinus sumatrensis Fischer, 1814.

The only living species.

Subspecies:

1. *D. s. sumatrensis* Fischer, 1814.

1814. *Rhinoceros sumatrensis* Fischer, Zoogn., 3:301. Based on BELL's (1793) Double-horned Rhinoceros of Sumatra; type locality is therefore Fort Marlborough, Bencoolen (= Bintuhan) district, Sumatra.

1820. *Rhinoceros sumatranus* Raffles, Trans. Linn. Soc., 13:268. Sumatra.

1873. *Ceratorhinus niger* Gray, Ann. Mag. N. H., 11:357 Sunghi-njong district, Malacca (SCLATER, 1876:651)

1873. *Ceratorhinus blythii* Gray, loc. cit., 360. Probably from Tenasserim. The peculiarities of the undermentioned Pegu skull would seem to make it likely that *blythii* is a synonym of the typical race.

Distribution: Sumatra and Malaya.

Diagnosis: Size large; teeth medium to small; occiput narrow, low.

The Malaccan deme differs from the Sumatran in its slightly broader zygomata, and in the comparatively broader teeth.

2. *D. s. harrissoni* Groves, 1965.

1965. *Didermocerus sumatrensis harrissoni* Groves, Säugetierk. Mitt., 13:130. Suan-Lambah, Sabah, Malaysian Borneo.

Distribution: Borneo.

Diagnosis: Size small; teeth small; occiput narrow but proportionally high, and forwardly inclined (= palate-occiput angle).

The numerous additional specimens studied since the type description have fully confirmed the distinctness of this subspecies. The largest skull, in the Cambridge Zoology Museum, has an occipitonasal length of 491 mm.

3. *D. s. lasiotis* Buckland, 1872.

1872. *Rhinoceros lasiotis* Buckland, Land and Water, 10th. August. Chittagong.

Distribution: northern Burma, into Assam and East Pakistan. The only definite localities of available specimens are Chittagong and Mogok; a further skull is labelled merely "India".

Diagnosis: Size large; teeth very large; occiput broad and high.

A skull from Pegu (B.M. 68.4.15.1) is perfectly intermediate between this race and the nominate race: teeth and occiput measurements are intermediate, but it is on the whole rather nearer to *sumatrensis* (fig. 4).

The Sumatran rhinoceros population of South Vietnam — no specimens are available — would a priori be likely to belong to the nominate race, not to *lasiotis*. In its large teeth, the present race is similar to the subfossil Sumatran race, *D. s. eugenei* Sody, 1947 (see Table 3), in which M^2 and M^3 are still larger.

Genus *Rhinoceros* Linnaeus, 1758.

1758. *Rhinoceros* Linnaeus, Syst. Nat. 10th. ed., 1:56. *Rhinoceros unicornis*.

1775. *Naricornis* Frisch, Natur-syst. vierfüß. Thiere, Tab. Gen. (N. V.) Not available (Bull. Zool. Nomencl., 1950, 4:547)

1815. *Monoceros* Rafinesque, Analyse de la Nature, 56. (N. V.) Not of Meusch, 1787 (Mollusca).

1815. *Unicornus* Rafinesque, loc. cit., Addendum, 219. (N. V.) Not of Montfort, 1810 (Mollusca).

1867. *Eurhinoceros* Gray, P. Z. S., 1009. *Rhinoceros javanicus*.

1922. *Monocerorhinus* Wüst, Centralb. f. Min. Geol. u. Pal., 650. *R. sondaicus*.

A more specialised genus than *Dicerorhinus*: lower canines more developed, occiput forwardly inclined and greatly expanded in mastoid region; post-glenoid and post-tympanic processes extensively fused below auditory meatus. Horns one — an occasional restricted keratinised area has been reported behind the true horn — and nasal region not extensively keratinised; nostrils with a flexible and rounded upper rim; hide thick, with hair-reduced and skin-folds well-developed in both scapular and pelvic regions. Processus glandis of penis attached by their whole length.

Rhinoceros sondaicus Desmarest, 1822.

The smaller of the two living species; the skull characters are given by Pocock (1945), and the tooth characters by HOOIJER (1946). Its primitive position in the genus is emphasised by COLBERT (1942).

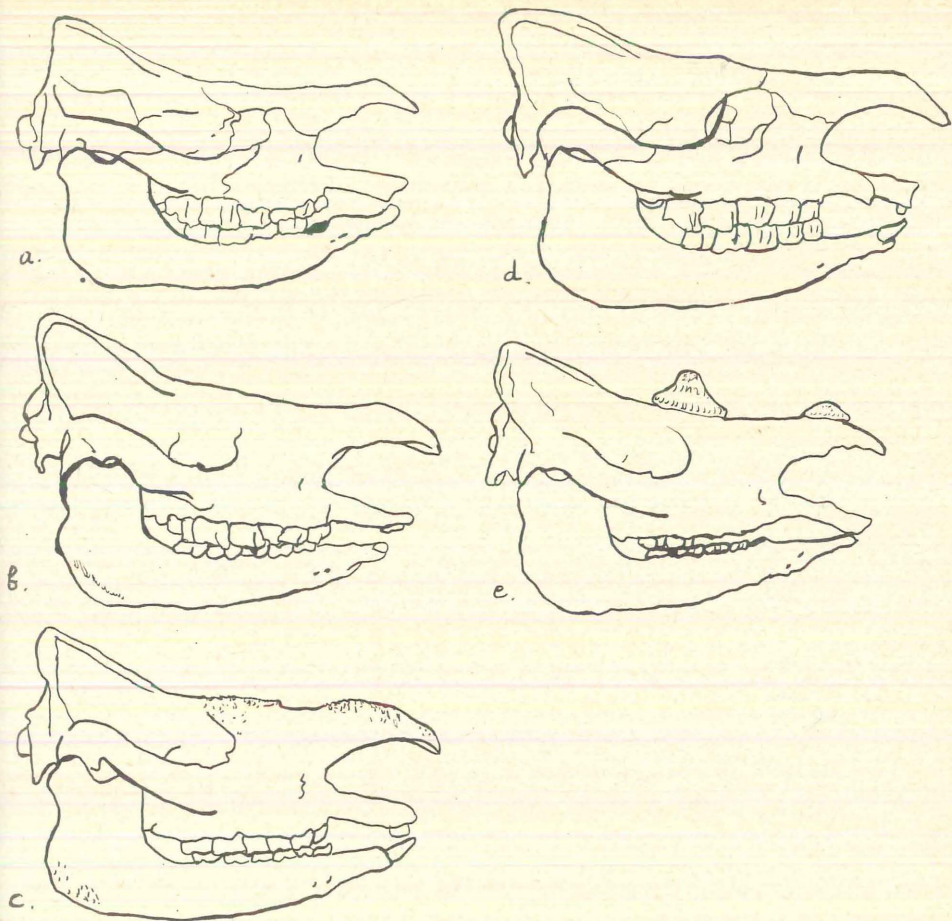


Fig. 4: Five skulls of *Dicenarhinus sumatrensis*.

a. *D.s.harrisoni*; B.M.1.8.15.1 (type). Juv., stage 4; Suan-Lambah, Sabah. Note the forward-inclined occipital surface. Occipitonasal length, 427 mm.

b. *D.s. cf. lasiotis*; B.M.68.4.15.1. Adult, from Pegu. Note the relatively long tooththrow, and the high occipital crest, inclining backward. Occipitonasal length, 525 mm.

c. *D.s.sumatrensis*; B.M.79.6.14.2. Adult, from Kian Puhu, 70 miles north of Malacca (north of Mt. Ophir). Occipitonasal length, 520 mm.

d. *D.s.sumatrensis*; B.M.1952.4.1.2. Nearly adult (stage 5), from Sumatra. The specimen agrees with (c) in the comparatively small teeth and low, backward - inclined occipital surface, but, due to its youth, shows none of the rugosity of horn bosses on nasals and frontals, or that of masseter attachment on jaw angles. Occipitonasal length, 576 mm.

e. *D.s.harrisoni*; Cambridge Zool.Mus. H.6834. Adult; Sandakan, Sabah. The Occipitonasal length of this specimen measures 491 mm., and it is the largest known skull of this race, overlapping by 3 mm. the smallest known skull of *sumatrensis* (Paris, Lab.d'Anat.Comp., A.7967, 488 mm.). It is an old skull, with all sutures closed and some teeth lost (not post-mortem) but without very marked muscular moulding. The palate-occiput angle measures 82°, and it is in every other way a typical specimen of its race, the large size notwithstanding.

Subspecies:

1. *R. s. sondaicus* Desmarest, 1822.

1822. *Rhinoceros sondaicus* Desmarest, Mammalogie, 2:399. "Sumatra"; later altered to Java (Suppl. 547).

1824. *Rhinoceros javanicus* F. Cuvier, H. N. Mamm. 4, 45:pl. 309. Java.
 1829. *Rhinoceros javanus* G. Cuvier, Règne Anim., 2nd. ed., 1:247. Java.
 1867. *Rhinoceros nasalis* Gray, P. Z. S., 1012. "Borneo": the skull of the type fits well into the sample of the typical race. Since this species is not known from Borneo, it seems the true locality must be Java.

Distribution: Java.

Diagnosis: Teeth small, occiput broad and low.

2. *R. s. floweri* Gray, 1867.

1867. *Rhinoceros floweri* Gray, P. Z. S., 1015. Sumatra.

Distribution: Sumatra.

Diagnosis: Teeth larger, especially third molars; occiput less broad, but comparatively low.

3. *R. s. inermis* Lesson, 1840.

1840. *Rhinoceros inermis* Lesson, Compl. de Buffon, 1:514. Sunderbunds.

(?) 1876. *Rhinoceros jamrachii* Sclater, Trans. Zool. Soc., 9:650. Probably Manipur district. Although this name was originated by Jamrach, the responsibility for its publication lies with Sclater.

1877. *Rhinoceros inermis* Peters, Monatsber. Ak. Berlin, 68.

Distribution: known definitely only from the Sunderbunds, the swampy, jungleclad islands of the Ganges delta.

Diagnosis: Teeth large (breadth of lower teeth greater than in *floweri*, but that of upper teeth about the same, except M^3 , which is smaller); occiput higher, narrower. It is noteworthy that the teeth from the Pleistocene of Java (*R. s. sivasondaicus* Dubois, 1890) are very similar in size to those of *R. s. inermis*, though slightly tending towards *floweri* in some measurements; the subfossil teeth from Gua Cha (Malaya) are also intermediate, while those from Sumatra are exactly like modern Sumatran teeth (see HOOIJER, 1946 and 1962).

The type of *jamrachii* is either lost or unrecognised. If the Manipur form was the same as that from the Sunderbunds, then the name *jamrachii* would be synonymous; ecologically, however, one suspects that subspecific identity with the race from Bhutan (see below) might be more likely.

Other populations of *Rhinoceros sondaicus*:

1. Malaya. The only two available skulls from Malaya resemble *floweri* except that the Basal length is very short (due to the relation between nasal and premaxilla length, rather than occipital crest direction). The breadth of M^3 is much less than in *floweri*.
2. Vietnam. The two adult skulls from Cochin China (there is also a Stage 1 skull in Paris) are smaller than others of similar age, and the Basal length is short compared to Occipitonasal, although not actually shorter than it as in Malayan skulls. The teeth are small, as in the nominate race. A stage 4 skull from Victoria Point, Tenasserim, seems intermediate between Malayan and Vietnamese skulls.
3. Bhutan. A single stage 4 skull from Moraghat, Bhutan Doors, in Copenhagen, is remarkable for its very large teeth. Its skull measurements are comparable with *R. s. inermis* of similar age.

Although a coherent picture does emerge, there are many gaps in detail, especially in *R. sondaicus*. It is now doubtful whether they can ever be filled. *D. sumatrensis* is thinly scattered over its range; *R. sondaicus* is completely exterminated except in Java and possibly Vietnam. A hundred years ago, both species (especially the former) were abundant. It seems amazing that thousands were slaughtered, both for sport and for gain, and a mere handful preserved in museums.

It is to be hoped that the new and welcome trend towards serious behavioural studies of wild mammals will very soon embrace the rhinoceros family, in particular the Asiatic species, for the only way to preserve these important and primitive creatures is to become informed on their exact way of life.

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The writer is also very greatly indebted for information on the type specimen of *Rhinoceros sumatrensis* G. Cuvier, 1817 (not Fischer's type, which is the illustration in BELL 1793), which is in the Musée d'Histoire Naturelle of La Rochelle, France, to Dr. R. Duguay and Dr. P. J. H. van Bree; and for information on other specimens, and many helpful suggestions, to Herr E. Trumler.

POSTSCRIPT

Since the above was written, the author has received the measurements of skulls in the collection of the Zoological Survey of India, which were very kindly sent by Dr. B. BISWAS, Superintending Zoologist. Unfortunately only one skull has a definite locality: a female *sondaicus* skull from the lower mouth of the Chilichangpi Creek, Sunderbans, Lower Bengal, collected by Capt. CHARLING in 1879 or earlier. This skull shows measurements not very different from those given in the present Tables 4 and 5, for Bengal skulls. Occipital height is 171, rather smaller than usual for this race; breadth of M^3 is 51 mm., agreeing with the figures of Table 5, in which the Bengal skulls are shown to have this tooth intermediate in size between the large M^3 of the Sumatran race, and the small one of the Malayan skulls.

Among the skulls without locality, three show exceptionally large measurements for M^1 . These are nos. 10437, 17144 and 17685, in which this tooth measures respectively 61, 65 and 60 mm. It is highly likely that at least one or two specimens from Bhutan would be represented in the Indian collection: the large-toothed juvenile skull from Bhutan will be recalled. The possibility must be borne in mind that the three skulls above-mentioned may be from Bhutan or the Dooars area.

The *D. sumatrensis* skulls show, because of the smaller amount of individual variation and the larger subspecific differences, a better chance for classification of

Table 4: Mean skull values for adult specimens of *Rhinoceros sondaicus*

| Skulls | Java | Sumatra | Malaya | Vietnam | Bengal |
|-----------------------|-------------------|------------------|------------------|------------------|------------------|
| Skull length | 514.5 ± 19.2 (13) | 528.6 ± 18.6 (5) | 526.5 ± 21.5 (2) | 505.5 ± 27.5 (2) | 527.8 ± 16.1 (4) |
| Basal length | 575.8 ± 14.1 (9) | 578.4 ± 14.3 (5) | 506.5 ± 10.6 (2) | 525.0 ± 2.8 (2) | 567.3 ± 17.5 (3) |
| Toothrow length | 227.1 ± 8.1 (14) | 232.5 ± 4.9 (6) | 225.5 ± 7.8 (2) | 230.0 ± 2.8 (2) | 240.0 ± 5.0 (4) |
| Zygomatic breadth | 347.5 ± 13.4 (13) | 348.4 ± 15.9 (5) | 359.5 ± 2.1 (2) | 339.5 ± 3.6 (2) | 355.0 ± 4.7 (4) |
| Occipital breadth | 296.0 ± 13.5 (13) | 284.6 ± 5.8 (6) | 286.5 ± 5.0 (2) | 288.0 ± 8.5 (2) | 290.0 ± 11.3 (3) |
| Occipital height | 158.8 ± 8.1 (13) | 161.8 ± 4.1 (6) | 162.5 ± 7.8 (2) | 151.0 ± 1.4 (2) | 183.0 ± 8.5 (3) |
| Interorbital breadth | 120.1 ± 10.9 (13) | 120.6 ± 7.8 (6) | 118.5 ± 0.7 (2) | 111.5 ± 0.7 (2) | 119.0 ± 4.4 (4) |
| Palate-Occiput angle | 57.4 ± 7.2 (14) | 58.2 ± 4.0 (6) | 52.5 ± 3.5 (2) | 55.0 — (1) | — |
| Occipital crest angle | 85.7 ± 6.3 (7) | 82.0 ± 5.4 (5) | — | — | — |
| Foramen Magnum angle | 80.9 ± 7.1 (14) | 78.4 ± 5.5 (5) | 90.0 ± 2.8 (2) | 84.0 — (1) | — |

Mean values for stage four specimens of *Rhinoceros sondaicus incrimis*

| | |
|----------------------|-----------|
| Skull length | 486.5 (2) |
| Basal length | 552.5 (2) |
| Zygomatic breadth | 326.0 (2) |
| Occipital breadth | 251.5 (2) |
| Occipital height | 164.5 (2) |
| Interorbital breadth | 109.5 (2) |

Table 5: Mean teeth values for adult specimens of *Rhinoceros sondaicus*

| Teeth | Java | Sumatra | Malaya | Vietnam | Bengal | Bhutan | Java Pleistocene |
|-------------------------|----------------|----------------|----------------|----------------|----------------|----------|------------------|
| P ² br. ant. | 40.6 ± 1.6 (7) | 37.2 ± 0.8 (5) | 40.9 ± 1.4 (2) | 40.0 ± 1.4 (2) | 40.8 ± 1.2 (3) | | 41.6 ± 2.1 (7) |
| P ³ br. ant. | 51.1 ± 2.1 (8) | 50.1 ± 1.5 (5) | 53.7 (1) | 51.5 ± 1.6 (2) | 50.9 ± 1.3 (4) | | 51.7 ± 2.8 (6) |
| P ⁴ br. ant. | 54.8 ± 1.5 (8) | 55.3 ± 1.5 (6) | 57.7 (1) | 54.9 ± 1.5 (2) | 54.9 ± 1.4 (4) | | 55.8 ± 4.0 (6) |
| M ¹ br. ant. | 54.7 ± 1.5 (8) | 58.9 ± 1.3 (5) | 60.2 ± 1.4 (2) | 54.1 ± 0.7 (2) | 56.5 ± 2.1 (4) | 65.8 (1) | 57.9 ± 3.0 (8) |
| M ¹ br. post | 48.3 ± 2.0 (8) | 53.1 ± 1.7 (4) | 54.1 ± 0.7 (2) | 48.4 ± 0.3 (2) | 51.6 ± 0.7 (3) | 53.1 (1) | 53.0 ± 3.6 (3) |
| M ² br. ant. | 54.9 ± 1.3 (8) | 59.2 ± 2.3 (5) | 61.7 ± 2.1 (2) | 55.9 ± 2.0 (2) | 58.3 ± 1.9 (4) | | 58.1 ± 2.6 (12) |
| M ³ br. | 47.3 ± 2.5 (7) | 54.3 ± 2.0 (4) | 43.4 ± 1.9 (2) | 51.5 ± 2.0 (2) | 49.3 ± 1.3 (4) | | 51.9 ± 2.3 (9) |
| P ₂ length | 27.5 ± 2.5 (7) | 26.9 ± 1.7 (5) | 28.6 ± 2.7 (3) | 23.8 ± 2.4 (2) | 27.1 ± 2.7 (3) | | 27 (1) |
| P ₂ breadth | 18.1 ± 1.7 (7) | 16.9 ± 0.7 (5) | 19.5 ± 1.5 (3) | 16.3 ± 0.9 (2) | 18.6 ± 2.9 (3) | | 20 (1) |
| P ₃ length | 36.4 ± 2.1 (7) | 37.1 ± 2.2 (6) | 37.6 ± 0.9 (2) | 33.0 ± 2.3 (2) | 37.0 ± 1.2 (4) | | 34.7 ± 1.6 (3) |
| P ₃ breadth | 23.1 ± 1.7 (7) | 22.1 ± 1.4 (6) | 25.0 ± 0.3 (2) | 23.4 ± 2.0 (2) | 26.0 ± 1.1 (4) | | 25.3 ± 1.5 (3) |
| P ₄ length | 39.0 ± 1.6 (7) | 39.2 ± 1.9 (6) | 39.4 ± 1.6 (2) | 36.3 ± 3.7 (2) | 38.3 ± 1.0 (4) | | 38.0 ± 1.4 (2) |
| P ₄ breadth | 26.4 ± 2.0 (7) | 25.8 ± 1.5 (6) | 30.8 ± 3.0 (2) | 27.8 ± 1.4 (2) | 27.0 ± 2.1 (4) | | 28.0 ± 1.4 (2) |
| M ₁ length | 41.9 ± 1.9 (7) | 44.0 ± 1.7 (7) | 43.2 ± 3.6 (3) | 40.1 ± 1.8 (2) | 42.6 ± 2.2 (4) | 50.8 (1) | 42 (1) |
| M ₁ breadth | 28.1 ± 2.1 (7) | 27.8 ± 1.2 (7) | 32.1 ± 2.1 (3) | 29.0 ± 1.3 (2) | 29.2 ± 1.0 (4) | 31.1 (1) | 27.5 ± 0.7 (2) |
| M ₂ length | 45.1 ± 1.4 (7) | 45.8 ± 2.0 (7) | 47.2 ± 1.2 (3) | 45.7 ± 0.6 (2) | 46.2 ± 1.6 (4) | | 44.5 ± 1.7 (4) |
| M ₂ breadth | 29.6 ± 1.9 (7) | 28.7 ± 1.1 (7) | 33.2 ± 3.2 (3) | 31.1 ± 1.0 (2) | 30.3 ± 0.5 (4) | | 29.3 ± 1.9 (4) |
| M ₃ length | 43.5 ± 2.2 (7) | 47.6 ± 0.9 (5) | 46.0 ± 2.8 (2) | 45.7 ± 1.6 (2) | 46.5 ± 1.3 (4) | | 45.4 ± 1.9 (5) |
| M ₃ breadth | 27.1 ± 2.0 (7) | 27.0 ± 1.2 (4) | 31.8 ± 0.8 (2) | 25.3 ± 3.1 (2) | 27.4 ± 0.8 (4) | | 26.2 ± 1.5 (5) |

Subfossil teeth (Hooijer, 1946 & 1962)

| | Sumatra | Malaya |
|-------------------------|----------------|----------------|
| P ² br. ant. | 37 (1) | 40.0 ± 2.8 (2) |
| P ³ br. ant. | — | 49 (1) |
| P ⁴ br. ant. | 51.5 ± 0.7 (2) | 56.0 ± 1.4 (2) |
| M ¹ br. ant. | — | 57.5 ± 0.7 (2) |
| M ¹ br. post | — | 51.5 ± 0.7 (2) |
| M ² br. ant. | 60.5 ± 5.0 (2) | 58.8 ± 1.8 (2) |
| M ³ br. | 57 (1) | 52.3 ± 1.8 (2) |

specimens of unknown origin. No. 17687, if adult, will belong to *harrissoni*; nos 17689 and 17691 to *sumatrensis*; no. 17690 to *lasiotis* (this is a very certain identification: the large teeth and broad, high occiput are all seen); nos. 17686 and 17692 show the "Pegu morphology", except that the former has a strikingly short tooththrow, only 174 mm. Sincere gratitude is due to Dr. BISWAS for his kindness and courtesy in the sending of these measurements.

Summary

The present paper reviews knowledge of the taxonomy and relationships of *Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*, two species of the Oriental Fauna which are now threatened with extinction. Evidence is presented that *Dicerorhinus* belongs with the other Asiatic rhinoceroses in subfamily Rhinocerotinae. The two species overlapped in their distribution to a very large extent; where the two were sympatric, *R. sondaicus* was found in concentrations in the swampy lowlands, while *D. sumatrensis* was a solitary wanderer, inhabiting, hilly country. However, where one species occurred to the exclusion of the other, it would occupy both habitats.

Geographic variation is shown in skull and tooth measurements after taking account of growth stages and tooth eruption. A total of 49 skulls of *D. sumatrensis* and 46 of *R. sondaicus* are examined, leading to the conclusion that the former species can be divided into the three subspecies: *lasiotis* (Buckland, 1872) in Burma, Assam, and East Pakistan, *sumatrensis* (Fischer, 1814) in Malaya and Sumatra, and *harrissoni* (Groves, 1965) in Borneo. The latter can be divided into at least three: *inermis* Lesson, 1840 in the Sunderbunds, *floweri* Gray, 1867 in Sumatra and *sondaicus* Desmarest, 1822 in Java. However, the data on this species are equivocal, and are likely to remain so, as the species appears to be extinct over most of its range.

Zusammenfassung

Die vorliegende Arbeit gibt einen Überblick über die Taxonomie und die Verwandtschaft von Sumatranashorn (*Dicerorhinus sumatrensis*) und Javanashorn (*Rhinoceros sondaicus*), 2 Arten des orientalischen Faunengebietes, die nun von der völligen Ausrottung bedroht sind. Es wird aufgezeigt, daß das Sumatranashorn mit den anderen asiatischen Nashörnern in die Unterfamilie der Rhinocerotinae gehört. Die beiden Arten überschneiden sich sehr stark in ihrer Verbreitung. Wenn sie zusammen vorkommen, lebt das Javanashorn vorwiegend in sumpfigen Niederungen, das Sumatranashorn als ein Einzelwanderer im Hügelland. Dort aber, wo nur eine Art allein vorkommt, bewohnt sie beide Biotope. Es wird eine geographische Abänderung im Schädel und in den Zahnmaßen unter Berücksichtigung von Altersstadien und Zahnentwicklung aufgezeigt. Im ganzen wurden 49 Sumatranashorn- und 46 Javanashornschädel untersucht. Daraus ergab sich, daß das Sumatranashorn in 3 Unterarten aufgeteilt werden kann, und zwar *lasiotis* (Buckland, 1872) aus Nord-Burma, Assam und Ost-Pakistan, *sumatrensis* (Fischer, 1814) aus Sumatra und Malaya, und *harrissoni* (Groves, 1965) aus Borneo. Auch das Javanashorn hatte wahrscheinlich 3 Unterarten, und zwar *inermis* Lesson, 1840 im Ganges-Delta (Sunderbunds), *floweri* Gray, 1867 auf Sumatra und *sondaicus* Desmarest, 1822 auf Java. Doch sind die Unterlagen für diese Art in dieser Beziehung unzureichend und werden es auch wohl so bleiben, da die Art bereits im allergrößten Teil ihres Verbreitungsgebietes ausgerottet ist.

BELL, W.: The Double-horned Rhinoceros of Sumatra. Phil. Trans. Roy. Soc., London, 1793, 1, 3-6, 1793. — CAVE, A.: Burchell's original specimens of *Rhinoceros simus*. P. Z. S., London, 139, 691-700, 1962. — CAVE, A.: The Processus glandis in the Rhinocerotidae. P. Z. S., London, 143, 569-587, 1964. — CAVE, A. & D. ALLBROOK: The skin and nuchal eminence of the White Rhinoceros. P. Z. S., London, 132, 99-107, 1959. — COLBERT, E.: A new rhinoceros from the Siwalik beds of India. Amer. Mus. Novit., New York, No. 749, 1-13, 1934. — COLBERT, E.: Notes on the Lesser One-horned Rhinoceros, *Rhinoceros sondaicus*. 2. The position of *Rhinoceros sondaicus* in the phylogeny of the genus *Rhinoceros*. Amer. Mus. Novit., New York, No. 1207, 1-6, 1942. — DESMAREST, A.: Mammalogie, Paris, 1822. — GRAY, J.: On the dentition of the Rhinoceroses (Rhinocerotae), and on the Characters afforded by their Skulls. Ann. Mag. N. H., London, (4) 11, 357-61, 1872. — GROVES, C.: Description of a new subspecies of Rhinoceros, from Borneo, *Didermoceros sumatrensis harrissoni*. Säugetierk. Mitt., München, 13, 128-131, 1965. — HOOIJER, D.: Pleistocene and fossil rhinoceroses from the Malay Archipelago and India. Zool. Meded., Leiden, 26, 1-138, 1946. — HOOIJER, D.: *Rhinoceros sondaicus* Desmarest from the Hoabinhian of Gua Cha Rock Shelter, Kelantan. Federation Museums Journal, Singapore, 7, 23-24, 1962. — HUBBACK, T.: The Asiatic two-horned rhinoceros. J. Mamm., Baltimore, 20, 1-20, 1939. — HUTCHINSON, G. & S. RIPLEY: Gene dispersal and the ethology of the Rhinocerotidae. Evolution, Lawrence, 8, 178-9, 1954. — KRUMBIEGEL, I.: Die asiatischen Nashorne (*Dicerorhinus* Gloger und *Rhinoceros* Linné). Säugetierk. Mitt., Stuttgart, 8, 12-20, 1960. — LOCH, C.: *Rhinoceros sondaicus*: the Javan or Lesser One-horned Rhinoceros and its Geographical Distribution. J. Malay Branch Roy. Asiat. Soc., Singapore, 15, 130-149, 1937. — PEACOCK, E.: A Game book for Burma and adjoining territories. London, 1933. — POCKOCK, R.: Some Cranial and Dental Characters of the existing species of Asiatic Rhinoceroses. P. Z. S., London, 114, 437-450, 1944. — RICHARDS, P.: The tropical rain forest. Cambridge, 1957. — SCLATER, P.: (Notes by the Secretary). P. Z. S., London, 790-4, 1872. — SHORTTRIDGE, C.: The Asiatic two-horned Rhinoceros (*Rhinoceros sumatrensis*, Cuv.). J. Bombay N. H. Soc., 23, 772-4, 1915. — SIMPSON, G.: Principles of classification, and a classification of Mammals. Bull. Amer. Mus. N. H., New York, 85, 1-350, 1945. — SODY, H.: Das Javanische Nashorn, *Rhinoceros sondaicus*, historisch und biologisch. Zeit. f. Säugetierk., Berlin, 24, 109-240, 1959. — TALBOT, L.: A look at threatened species. Oryx, London, 5, 4/5, 153-293, 1960. — THOMAS, O.: On the type of *Rhinoceros lasiotis*. P. Z. S., London, 157-9, 1901. — ZEUNER, F.: Die Beziehung zwischen Schädelform und Lebensweise bei den rezenten und fossilen Nashörnern. Bericht d. naturf. Ges. Freiburg i. Br. 34, 21-80, 1934. — ZEUNER, F.: Palaeobiology and climate of the Past. Problems of Palaeontology, Moscow, 1, 199-216, 1936.

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