Palæontology. — *The evolution of the skeleton of Rhinoceros sondaïcus Desmarest.* By D. A. HOOIJER. (Communicated by Prof. S. T. BOK.)

(Communicated at the meeting of May 25, 1946.)

In an earlier paper (HOOIJER, 1946) I described the fossil remains of *Rhinoceros sondaïcus* Desmarest from the Pleistocene of Java collected by EUG. DUBOIS some fifty years ago. I had many recent skulls and also four skeletons of the species for comparison. The fossil teeth and many of the limb and foot bones proved to be larger than the recent, with the exception of the humerus, femur and tibia which present smaller dimensions than the recent. I did not, then, especially emphasize this point, and merely stated (l.c., p. 76) that the femora might belong to some small variety. There is nothing peculiar in the fact that fossil bones and teeth of a still living species average larger than the recent; on the contrary this is a common thing to students of Pleistocene and prehistoric Mammals. Many animals have diminished in size, both on continents and on islands, since the Pleistocene, and the purpose of the present paper is to make it evident that the reduction in size may affect different parts of the skeleton to a different degree. This is shown by the rhinoceros material I have worked upon, and the explanation will be offered below.

Let us turn now to the facts. In the following table I give the observed ranges and means for the dimensions of upper toothrow and limb and foot bones of recent and fossil *Rhinoceros sondaïcus* Desmarest, extracted from my paper of 1946. Much more convenient than to compute many indices it is to follow SIMPSON (1941) in constructing ratio diagrams of the dimensions of the different bones. This principle has been fully explained by SIMPSON (l.c., pp. 23—25), but a short explanation will not be out of place here.

Rhinoceros sondaïcus Desmarest.

Length of	Recent		Fossil	
	Range	Mean	Range	Mean
pd^1—M^3	242—255	249	267—272	270
Humerus	[illegible] - 0	392	386 - 389	388
Radius	318 329	324	343—359	349
Metacarpal III	170—173	171	187	187
Femur	440—495	474	438 476	459
Tibia	323 - 335	328	320 337	330
Metatarsal III	150 155	153	165	165

First the direct measurements are converted to their logarithms, and then the differences are calculated from some one standard, for which I selected the logarithms of the means of the measurements found in the fossil specimens. They are set in a straight vertical line, the larger observations fall to the right of this line, and the smaller to the left. The more nearly the line, connecting the means of the corresponding values in some other material, approaches a vertical line, the closer the similarity in proportions throughout the parts measured. It goes without saying that this will do regardless of absolute size which is ignored here; the differences between the logarithms represent the logarithms of the ratios. Size is of no importance; I have shown that the fossil remains are doubtless specifically identical with the recent Javan rhinoceros.

A glance at fig. 1 will show that the humerus and the femur, and, to a lesser extent also the tibia, have disproportional dimensions in the recent skeletons as compared to that of their forerunner in the Pleistocene. The fossil animal had the radius, tibia and distal limb segments longer relative to humerus and femur than the recent. Why should fore arm and manus, leg and pes have become shortened in the course of time?

The explanation presents itself immediately. It is exactly the same trend of evolution observed in some phyla of the brontotheres (Titanotheres) of North America, viz., the transformation from a mediportal to a graviportal type (OSBORN, 1929, especially Chapter IX). Humerus and femur lengthen, radius, tibia, and metapodials shorten when passing from swift-moving to slow-moving animals. In our example the tibia is shortened to a lesser degree than the radius, and the metatarsal seems to abbreviate less than the metacarpal. I was desirous to know whether the other recent rhinoceroses present proportions throughout the parts of their skeleton similar either to the recent or to the fossil Javan rhinoceros or not. Skeletons of *Dicerorhinus sumatrensis* (Fischer) and *Diceros bicornis* (L.) are in the Leiden Museum, and I took the measurements of *Rhinoceros unicornis* L. from CUVIER (1822) (with a slight correction for the length of the humerus which he measured in another way than I did). The ratio diagram, with the same standard of comparison as that in fig. 1, is given in fig. 2. It shows that the proportions for *unicornis* are more like the recent *sondaïcus* than those of the African *bicornis*, which has the maxima in the fore arm and leg instead of in the proximal limb segments. *D. sumatrensis* has an especially short radius but for the rest comes nearest to the fossil *sondaïcus* in the comparative proportions of its limb segments. It must be kept in mind that these similarities in ratios imply no genetic relations but represent only parallelisms in adaptation to speed and weight.

D. sumatrensis is regarded by OSBORN (1898) and others as the most primitive among the living species of rhinoceroses. The subfossil humerus from Sumatra described and figured by me (HOOIJER, 1946, pp. 26—27, pl. X fig. 6) constitutes all we know of the early history of the post-cranial skeleton of the Sumatran form. When plotting this specimen against the log difference scale in the diagram, the point is seen to fall much to the right of the standard line, while the recent specimens all remain to the

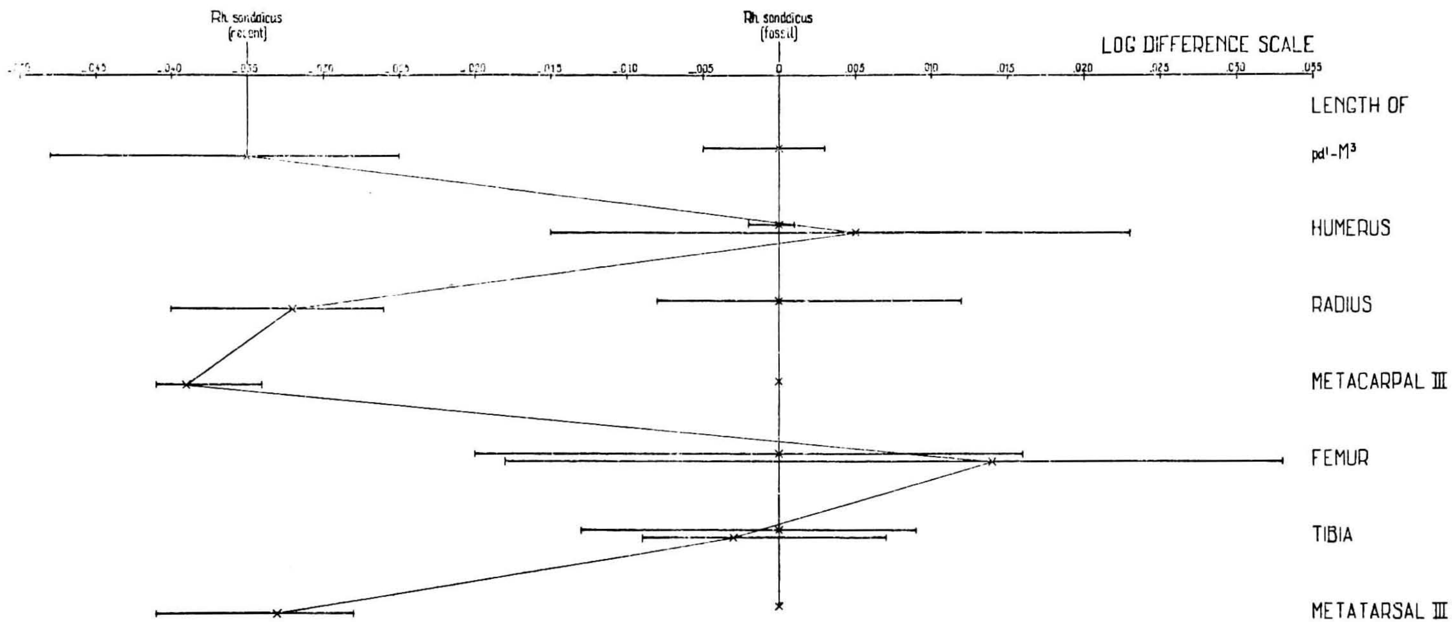

Fig. 1.

Ratio diagram comparing dimensions of recent and fossil teeth and bones of *Rhinoceros sondaïcus* Desmarest. The means of the proportions found in the fossil specimens are taken as the standard of comparison and are set in a straight vertical line. The observed ranges are represented as horizontal lines, with a cross at the mean value.

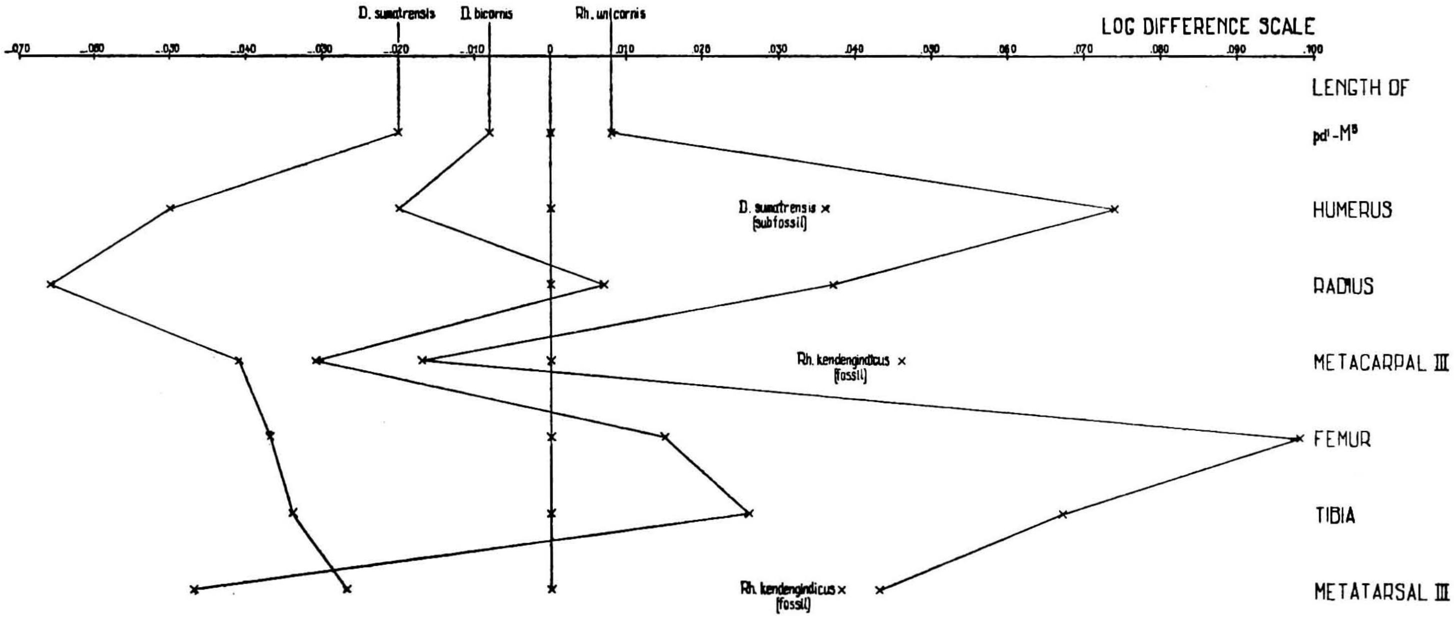

Fig. 2.

Ratio diagram comparing dimensions of *Dicerorhinus sumatrensis* (Fischer), *Diceros bicornis* (L.) and *Rhinoceros unicornis* L. Same standard of comparison as in fig. 1. Isolated crosses represent the subfossil humerus of *D. sumatrensis* (Fischer) from Sumatra and the metapodials of *Rh. kendengindicus* Dubois from the Pleistocene of Java in the Dubois Collection.

left of it. The teeth were larger too, but it is certain that the Sumatran rhino had a different story than the Javan in which latter the humerus remained of equal size or rather lengthened since the Pleistocene.

Several bones have been found associated with teeth in a cave deposit in Sarawak, Borneo. They might very well belong to *sumatrensis* (see HOOIJER, l.c., p. 10), but this is uncertain until the specimens will turn up again in the British Museum collection.

Apart from an uncertain astragalus from the Narbada beds (HOOIJER, l.c., p. 83) we know nothing about the post-cranial skeleton of *Rh. unicornis* L. in prehistoric or Pleistocene times. From Java I have described and figured two complete metapodials as belonging to a species, *Rh. kendengindicus* Dubois, which is distinguished from *unicornis* only by its less hypsodont teeth, more molariform premolars, and the upper molars being comparatively narrower posteriorly. The post-cranial remains comprise fragments of humerus and femur of the same size as recent *unicornis*, and a third metacarpal and metatarsal which are likewise larger than the corresponding bones in recent *sondaïcus*. The latter have been plotted in the diagram; they are not so much different in size as the corresponding bones in *unicornis* and fall near a single vertical line with the Sumatran humerus. It would be very interesting to know how the other parts of the skeleton of *kendengindicus* are; the teeth only indicate that the species combines progressive and primitive characters relative to *unicornis* which also dates from the Pleistocene.

Thus *sondaïcus* is the only Asiatic species of rhinoceros which is represented by a fair amount of material, which enables us to follow its history since the end of the Tertiary. The species is now very near complete extinction; probably less than seventy of this, one of the rarest and most famous of the large Mammals (HARPER, 1945, p. 381), are in existence at the present day (LOCH, 1937, p. 146). Recently COLBERT (1942) has postulated that *sondaïcus* (of which he examined only recent skulls) truly is a persisting primitive form and anatomically may be regarded as at about a lower Pleistocene or perhaps an upper Pliocene stage of development; it is, he says, a true living fossil. These conclusions are based on the comparison with skulls of the lower Pliocene genus *Gaindatherium*, of the Pleistocene *Rh. sivalensis* and *Rh. sinensis*, and of the recent *Rh. unicornis*. *Rh. sondaïcus* is shown to be intermediate in its skull characters between *Gaindatherium* and the more advanced Pleistocene and recent species of *Rhinoceros* mentioned above. COLBERT states that every distinguishing character shows an advance in the Indian rhinoceros over its expression in the Javan form, and surmises that the same holds for the post-cranial skeleton. This I am able to confirm, but matters turn out to be more complicated than first supposed.

When we trace *sondaïcus* back into the Pleistocene its limb and foot structure becomes more different from that of a graviportal type as the recent *unicornis* and is transformed to a type like *sumatrensis*, the only recent species of rhinoceros which is regarded as mediportal (OSBORN, 1929, pp. 749, 780). In its progression into the graviportal or slow-moving type *sondaïcus* is not so advanced as the recent Indian rhinoceros, as shown also in the following table of indices which I have computed to enable the direct comparison with the tables of OSBORN (l.c., pp. 735—739). Of

	Tibio-femoral	Metatarso-femoral	Radio humeral	Metacarpo-humeral
Rh. unicornis L.	67	32	83	39
Rh. sondaïcus Desm. recent	6[illegible]	32	83	44
Rh. sondaïcus Desm. fossil	72	36	90	48
D. sumatrensis (Fischer)	72	37	89	50

course this series does not represent a phylogenetic sequence but only a sequence of adaptive types.

The present contribution shows the mode of evolution known up to now only from certain series of species in successive stages to be found also within a species. Within one and the same species, for, as I have shown (HOOIJER, 1946) tooth for tooth and bone for bone the Pleistocene *Rhinoceros sondaïcus* Desmarest is identical with the living Javan rhinoceros. Should subspecific names be required, the Pleistocene form must be named *Rh. sondaïcus sivasondaicus* Dubois, and the recent *Rh. sondaïcus sondaïcus* Desmarest.

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