MAMMALIAN EVOLUTION IN THE QUATERNARY OF SOUTHERN AND EASTERN ASIA

D. A. Hooijer

Rijksmuseum van Natuurlijke Historie, Leiden, Holland

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Paleontological contributions to the subject of evolution mostly refer to what is now customarily called macroevolution. The paleontologist usually has insufficient material from a particular horizon and locality to establish the variation limits of the population from which his sample was taken. Study of infraspecific variation hence is left more or less to geneticists and taxonomists. However, phylogenetic work on recent material alone has the disadvantage that the time factor cannot be used in the establishment of phylogenetic units. Paleontology introduces the time dimension, but the paleontologist is forced by the incompleteness of his material to use characters for discrimination other than those by which neozoologists distinguish between their species and subspecies. Consequently, the taxonomic literature on recent animals is of little help to him, and he has to determine whether species or subspecies of mammals that are readily distinguishable by the characters of their skin and skull can also be separated on the basis of a single tooth or (part of a) bone. This requires conscientious study of the odontology and osteology of recent material, a work which he is not always in a position to do.

The student of the Pleistocene and prehistoric fauna deals with the immediate forerunners of the animals constituting the recent fauna. Great evolutionary changes are not to be expected, and at best the student is able to trace certain trends in the evolution of the dentition or of the skeleton rarely extending beyond the limits of a species.

Previous to his researches on the Pleistocene fauna of Java, which culminated in the discovery of *Pithecanthropus erectus* (Dubois), Eug. Dubois (1891) spent some years in the Padang Highlands in central Sumatra, exploring caves yielding a mass of isolated teeth of mammals, including man. In the absence of extinct species in the Sumatran cave fauna, Dubois referred the cave deposits to the prehistoric portion of the Holocene. In Java he collected truly Pleistocene fossils as well as prehistoric teeth and bones, e.g., from the Wadjak cave and from Goea Djimbe, res. Kediri, E. Java.

As a matter of fact the Dubois collections contain many species that are still living, either on Java or on the neighboring Greater Sunda Islands. A comparison of the Pleistocene and prehistoric material with that of the recent forms reveals a certain amount of differentiation which the various forms have undergone in the course of time. In the following I shall give examples from five families, viz., the Rhinocerotidae, the Tapiridae, the Hystricidae, the Felidae, and the Pongidae.

Recent Evolution in Malaysian Rhinoceroses

Three species of rhinoceroses are still living in Asia, viz., the Indian *Rhinoceros unicornis* L., *Dicerorhinus sumatrensis* (Fischer) from Sumatra and Borneo, and *Rhinoceros sondaïcus* Desmarest from Java and Sumatra. The two latter species occur also on the continent, as far north as Bengal. Recently Deraniyagala (1946) recorded *Rh. sondaïcus* in the fossil state from Ceylon.

In the cave collection from Sumatra both *Rhinoceros sondaïcus* and *Dicerorhinus sumatrensis* were met with (Hooijer, 1946a, pp. 12–46). The former species is less abundantly represented than the latter. Isolated cave teeth of both species prove to be rather large in comparison with their recent homologues. It is remarkable that the prehistoric teeth of *Dicerorhinus sumatrensis* compare well in size with those of a large form of that species from Bengal which goes under the name *Dicerorhinus sumatrensis lasiotis* (Sclater). A single humerus of *D. sumatrensis* from prehistoric Sumatra is more than 20 per cent longer than the mean of humeri of the recent Sumatran form.

In the Pleistocene of Java we find two species of rhinoceroses, the more common of which is *Rhinoceros sondaïcus.* The fossil averages larger than the living form except in its humerus and femur which must have lengthened since the Pleistocene. The transformation of the skeleton is of the same kind as that observed in some phyla of titanotheres (Hooijer, 1946b). The Pleistocene *Rhinoceros sondaïcus* is more of a swift-moving type than the recent; it is "mediportal" in proportions like recent *D. sumatrensis,* while the recent form belongs to the "graviportal" type, exemplified by recent *Rh. unicornis.* Hunting for rhinoceroses must have been an even more dangerous occupation in the Pleistocene than it is now.

The finding of the extremely long humerus of *D. sumatrensis* in the prehistoric cave collection of Sumatra would suggest that the latter species evolved in a direction opposite to that in which *Rh. sondaïcus* evolved, and at a still faster rate.

Rhinoceros sondaïcus was transformed from a swift-moving to a slow-moving animal during the Quaternary; this is an established fact. It must be kept in mind, however, that the fossil bones are from various localities and perhaps not even all from the same portion of the Pleistocene. A tripartition of the Pleistocene of Java into the lower Pleistocene Djetis fauna, the middle Pleistocene Trinil fauna, and the upper Pleistocene Ngandong fauna, has been worked out in recent years by von Koenigswald (1935). *Rhinoceros sondaïcus* is known since the lower Pleistocene, and by studying the skeletal remains from each of these stages in sufficient quantities it must be possible to follow step by step the change in the limb proportions, which goes hand in hand with a gradual diminution in size.

The second species of rhinoceroses in the Pleistocene of Java is not, as might be expected, *Dicerorhinus sumatrensis,* known in the subfossil and recent state from the islands of Sumatra and Borneo, but a representative of the Indian *Rhinoceros unicornis,* viz., *Rh. unicornis kendengindicus* Dubois. The differences between the two forms are but slight, consisting in the less hypsodont teeth, more molarized premolars, and comparatively narrower metaloph of the upper molars in the fossil Javan form as compared to the recent continental form (Hooijer, 1946a, pp. 84–107). The molar from the Djetis fauna of Sangiran recorded as "? *Coelodonta*" by von Koenigswald (1934, p. 193), a photograph of which was kindly sent to me by Dr. von Koenigswald in 1946, belongs to *Rh. unicornis kendengindicus,* and I found the latter subspecies also in the Dubois collection from the middle Pleistocene of Trinil (Hooijer, 1946a, pp. 104 and 107). No upper Pleistocene remains of *kendengindicus* have been made known as yet. Since the fossil form differs from the recent in progressive as well as in primitive characters, the former cannot have been ancestral to the latter.

RECENT EVOLUTION IN TAPIRS, PORCUPINES, TIGERS, AND ORANG-UTANS

The excess in size of the subfossil teeth over their recent homologues, shown by the species of rhinoceroses referred to above, is still more evident in the tapir, *Tapirus indicus* Desmarest. The teeth from the prehistoric Sumatran caves almost invariably are larger than those of the recent form. I have described the prehistoric tapir as *Tapirus indicus intermedius* (Hooijer, 1947b) since the dimensions of the cave teeth are intermediate between those of the recent Sumatran tapir and those of the Pleistocene *Tapirus* *augustus* Matthew and Granger from Wanhsien, province of Szechwan, China. The fossil Chinese form has exactly the dimensions we should expect to find for the ancestor of the recent Sumatran tapir through the large subfossil race of the same island. The Pleistocene tapir, however, has more molarized premolars than have the subfossil and the recent, which removes the former from the ancestral line of the latter. The Pleistocene tapir from Java, however, is indistinguishable in size from the recent one of Sumatra.

The porcupines give a beautiful example of subspecific advance in the time dimension. At present there is a race of *Acanthion brachyurus* (L.) in Sumatra, viz., *A. b. longicaudum* (Marsden), that is larger than the recent Javan subspecies *A. b. javanicum* Cuvier. Fossil porcupine teeth from Java are larger than those of the recent form from Java but fall within the limits of the recent Sumatran race, and the subfossil Sumatran cave teeth again exceed the recent from the same island in size (Hooijer, 1946c). Porcupine teeth which are larger even than the subfossil Sumatran specimens are known from Pleistocene caves in southern China and Burma, but the evidence is too scanty to proclaim with a tolerable degree of certainty the Chinese fossil form as the forerunner of *Acanthion brachyurus* in the same line of descent.

The recent races of the tiger, *Panthera tigris* (L.), form a continuous cline from Bengal over Sumatra and Java to Bali. In the above-mentioned order of localities they diminish in size; the Indian form is the largest, the Bali tiger the smallest. The fossils throw some light on the history of the races. In the Pleistocene of Java, as well as in the prehistoric caves of Sumatra, we find teeth and bones of the same size as those of the recent Indian form (Hooijer, 1947a). On the islands the tiger has diminished in size since the time of its immigration from the continent. The tiger underwent a similar, but less pronounced diminution of size in China, where, though smaller than the Indian, it is still larger than the insular subspecies. The Pleistocene tiger from Wanhsien in China (the locality where the large *Tapirus augustus* is from) is as large as the recent Indian subspecies. The fossil metapodials from Wanhsien, however, are decidedly more massive than those of the recent tiger; a character which the Pleistocene Chinese tiger has in common with the fossil tiger from Siberia described by Tscherski (1892). The tiger metapodials from the Javan Pleistocene are more slender than those of the Pleistocene continental tiger, demonstrating that while diminishing in general size the tiger got more slender metapodials too. In Java the tiger has undergone a greater diminution in size than on the continent, and the former was already more slender-footed than the continental forms during the Pleistocene. Racial differences already must have existed by Pleistocene times.

The last example of infraspecific evolution to be discussed here is that studied by me in the orang-utan, *Pongo pygmaeus* (Hoppius). More than three thousand teeth were collected by Dubois in the prehistoric central Sumatran caves, beyond the present range of the species which is now confined to northern Sumatra (Achin), and Borneo. The comparison of the subfossil with the recent teeth (Hooijer, 1948) shows that since the time of the deposition of the teeth in the Sumatran caves, viz., in the early Holocene, the mean of the teeth of the orang-utan has become sixteen per cent smaller. In addition, it has been possible to trace several trends in the evolution of the dentition, all stamping the prehistoric orang-utan as a more simian form than the recent, still further removed in dental structure from man in the points which differentiate the recent orang-utan dentition from that of recent man. The prehistoric males had bigger canines relative to those of the females than the recent animals. The lateral incisors were less reduced in relative size, and the anterior premolar in the lower jaw was relatively larger too. Also the excess in size of the second molar over the other molars, a typically simian feature that is also encountered during the early stages of the evolution of the hominid dentition, was much more pronounced in the prehistoric orang-utan than it is now.

The Pleistocene orang-utan from Java is indistinguishable in size from the recent form of Sumatra, while the Pleistocene form from southern China and Indo-China is decidedly larger than the subfossil form from Sumatra. Thus the Pleistocene continental form is again larger than the Javanese.

SUMMARY

From the above data the following general conclusions can be drawn:

1. Since the time of their immigration into the Greater Sunda Islands (in the late Pliocene or in the early Pleistocene) various species have undergone a gradual diminution in size, accompanied in some cases by essential changes in the structure of their limbs or feet.
2. The decrease in size during the Quaternary is more advanced in Java than it is in Sumatra. Prehistoric Sumatran forerunners of the living species may be even larger than those of the Pleistocene of Java. If, e.g., the tapir or the orang-utan could have persisted in Java up to the present, they would have become smaller than the recent Sumatran form. Neozoologists would have described them as subspecifically distinct as was done with the Javanese races of porcupine and tiger.

Thus it is evident that the subspeciation of recent species is a process that can be traced back into the Pleistocene. The recent races are the diminutive descendants of racially distinct populations that already existed in the Pleistocene. The comparatively slight amount of differentiation undergone by each of the subspecies during the Quaternary pushes the time of origin of the species back into the Pliocene. From this epoch, however, no fossils are known that can be definitely identified as belonging to any of the species dealt with above. Whether or not this is due to the incompleteness of the paleontological record is a question beyond the scope of the present discussion.

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