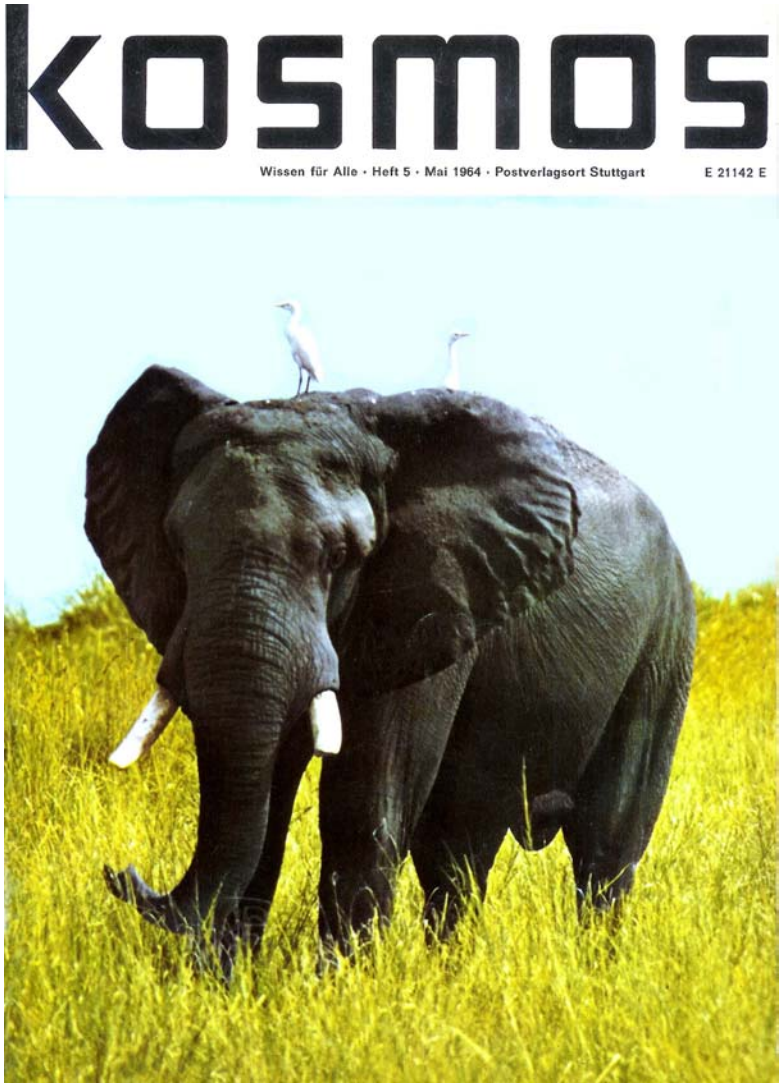

The Distribution of Proboscidea (Elephants)

Professor Dr. Erich Thenius

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When I speak here about animals with a trunk, I do not mean the tapirs or pigs, but I refer only to the elephants and their ancestors, like the *Mastodons* and *Dinotheria* which we call the Proboscidea (after the Greek: proboscis = trunk). Their main characteristic is their remarkable trunk which has been fashioned to become a "gripping" organ. That organ was not present in the geologically oldest ancestors whose skeletons stem from the deposits of the Eocene (old Tertiary) in Africa. Even though we have no "soft tissues" of those animals, their skeletal features suffice to tell the scientist just what their bodily characteristics would have been. Thus also, we are not really going to discuss much about

their distribution in historic times, but rather, we will concentrate on the development of these characteristic mammals, from their inception to their distribution in the past.

A history of the Proboscidea is necessarily a history of their distribution in time and space. Information of these animals is available from numerous fossil findings in nearly all continents. But, before we even consider the fossil history, let us take a quick look of the current distribution of elephants which is shown in Figure 1. Nowadays, there are only two species of elephants: the Indian and African elephants. They not only differ geographically but also morphologically. That is to say, they are different in their bodily form and in their anatomy in several characteristics as every attentive zoo visitor who sees them side-by-side easily observes: The small-eared Indian elephant (*Elephas maximus*) has a markedly bowed upper skull; the African cousin (*Loxodonta africana*) has longer legs and markedly larger ears. But these are merely the most obvious external differences. Many different features are found in the construction of the trunk, the number of toes, as well as other anatomic differences.

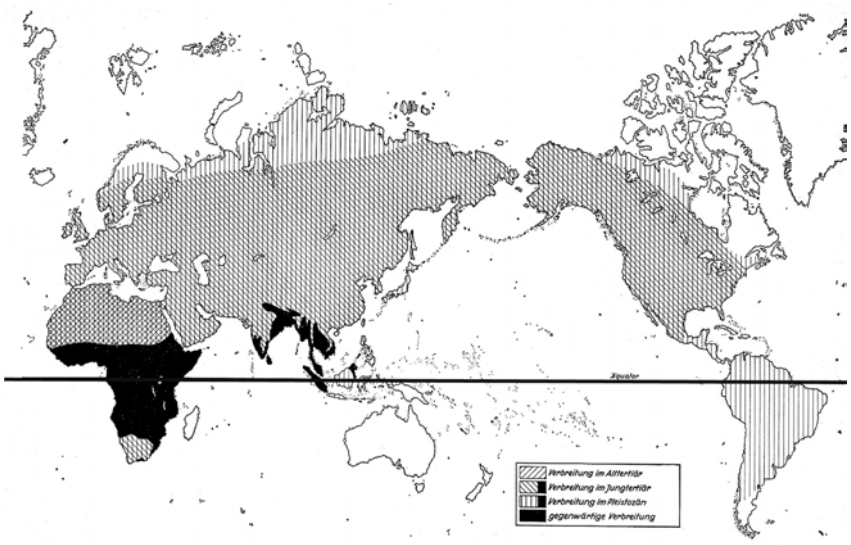


Figure 1. Distribution of Proboscidea, then and now. During the Ice-Age the animals were present on all continents, except Australia. Today, they are found only in parts of Africa and South Asia.

The current distribution of elephants is markedly reduced compared to what was true in the past. Even during historic times, as at the time of the Roman Empire, elephants were found in North and South Africa, and in southern Asia. Today the elephant of North Africa has totally disappeared and, at the Cape, it is found only in the Addobush of Port Elizabeth and the Knysa forest. Also, the once present Asian elephant (formerly in lesser Asia, Syria, Mesopotamia, Persia, India, Sumatra, Java, Borneo and southern China) has been much reduced in it distribution.

As is apparent from their taxonomic designation, the two extant species have been given generic ranks (*Elephas* and *Loxodonta*). That is to say, they are less related one to another than lion and tiger are which have the same genus rank (*Panthera or Felis*); this may be hard to comprehend for lay people. Indeed, it has to be acknowledged that the

anatomic differences between the two elephant species are considerably greater than is true of those between tiger and lion. This is the consequence of evolution, because the common ancestor of these elephants is much more distant in the past than that of lion and tiger.

Now let us consider the fossil and distributional history of all proboscidea, at least as much as we can learn from that record. The fact that, once upon a time, elephants existed in middle Europe is apparent from the numerous bones found in Europe of the Mammoth *(Mammonteus primigenius*), a distant relative of the current Asian elephant. As a cold-weather-adapted animal, the Mammoth possessed a thick coat of hair as we find it in the remains of Siberian cadavers. The gigantic (up to 5 m) long, curved tusks came quite frequently into extensive commerce from Siberia. But they were not only at home in Europe and northern Asia, they were also known in North and South America. Australia is the only continent where they have not been discovered.

But where did the Proboscidea actually originate? Their current status suggests that they originated everywhere, but what do the fossil findings tell us?

The geologically oldest proboscids are known from the Eocene in Africa, at least 50 million years ago. The absence of relevant finds in the northern hemisphere at that time suggests that they have an African origin. They are thus primarily of African descent, in contrast to many other African mammals that moved to Africa from other places. The most complete documents come from El-Fayum in Egypt; these have been described as *Moeritherium* and are named after the Moeris Lake whose last remains is the current Birket-el-Qurum. In fact, if one wants to be strictly taxonomical, the *Moeritheria* were not “proper” Proboscidea; they had neither trunk nor tusks. They were of the size of tapirs, had five toes and a relatively long tail. Even though true tusks were absent, one of the upper and lower incisors is much elongated and from these the tusks of mastodons were to develop.

Transitional forms between *Moeritheria* and the nearly elephant-sized mastodons of the young tertiary; they were described as the *Palaeomastodonts* (Old-Mastodons). But long tusks were absent in these animals as well; they have been found only in northern Africa (Figure 2). The mastodons arrived in Europe only later, near the time of the young Tertiary and they were soon also distributed to eastern Asia. In those days, neither the Sahara nor the Red Sea existed, but the Tethys in the regions of the current Mediterranean reached to Asia. For a long time there was a connection between northern Africa and the Iberian Peninsula, *i.e.* a bridge of land between northeast Africa and Asia.

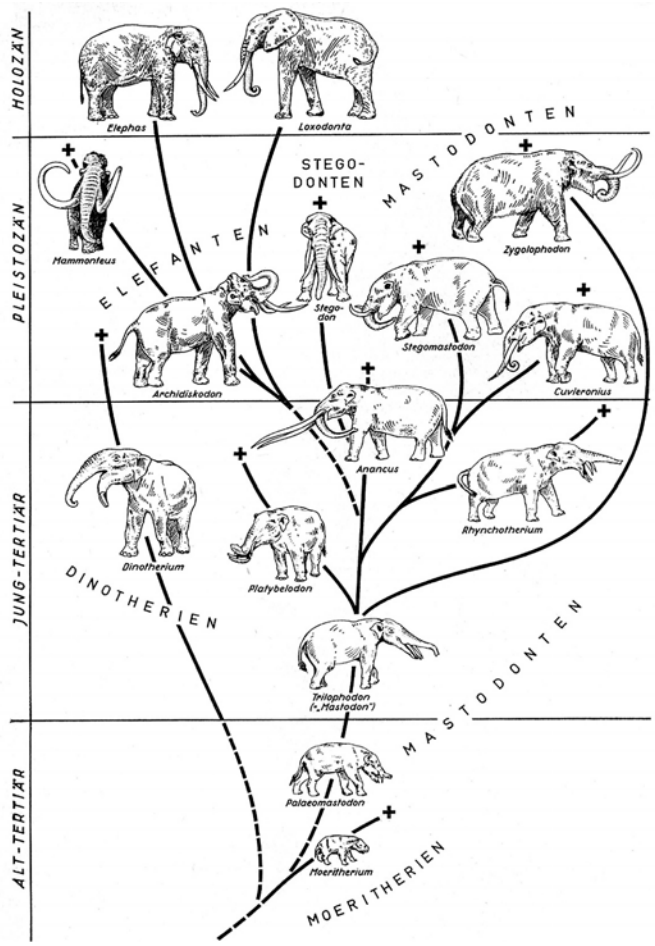


Figure 2. Overview of the Proboscidea. From the Eocene, *Moeritheria* developed the mastodons which died out at the end of the glaciation after the Stegodonts and elephants had developed during the Tertiary. Stegodonts as well as the Dinotheria became extinct during the glaciation, which is also true of most elephants then living. The sizes shown here reflect considerations by O. Abel, W.O. Dietrich, H.F. Osborn and M. Wilson.

Originally relatively small (*Trilophodon*), the mastodons developed during the Tertiary into elephant-sized Proboscidea which now also had tusks and real trunk (*Anancus*). The trunk developed probably by foreshortening of the bony mouth' portion of the skull. As the bones retracted, so did the mandible in which there were initially also tusks, until the lower tusks atrophied and, with it, the mandible of the current elephants eventuated (Figure 3). During the Miocene (young Tertiary) the mastodons went via the Bering Bridge to North America and, during the glaciation, via the land bridge to South America as well.

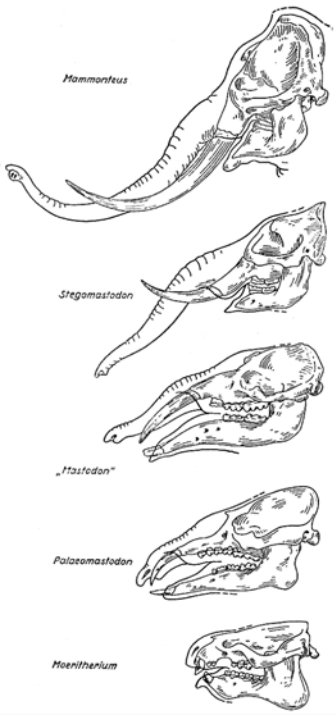


Figure 3. The development of trunk and tusks of the Proboscidea (From Thenius, 1963).

While mastodons became extinct in the Old World during the early glaciation, those of the New World remained there until the end of the glaciation.

The tertiary mastodons were composed of numerous groups of animals. Especially divergent types were the Platybelodonts (*Platybelodon*) whose mandible was modified including the broadened tusks which were spoon-like structures. Scientists differentiate among these genera and species of mastodons (*Rhynochotherium, Curieronius, Zygolophodon*) primarily on the basis of the teeth which are not only very characteristic but they are also often found in sand deposits; this is so despite the fact that we assume that their habitus was not especially different. The cheek teeth are knobby structures that gave the name to mastodons (Mastodont = Nipple-like teeth). These teeth are principally different from those of the elephants, because the latter are based on numerous lamellae that have become fused together and which have cement substance between them. Thus develops a uniform chewing platform for the purpose of crushing and mashing the food.

At the end of the Tertiary, elephant-like forms appear in southern Asia with long tusks in the maxilla and a true trunk. Their teeth are not lamellar and thus they are not counted as "real" elephants; but these are the Stegodonts (*Stegodon*). In the past, these animals were considered to have been an original ancestor of the elephant but we now believe that they are a separate lineage that became extinct during the glaciation period. As the name suggests, their cheek teeth were made of numerous roof-like yokes. The Stegodonts distributed from the southern part of Asia to all of Asia and also to Africa. They have not yet been found in Europe and the Americas.

The Dinotheria (*Dinotherium*) are a "sterile" branch of proboscids from the young Tertiary and the Glaciations, but their origin is undetermined so far. They were restricted to the Old World and produced real giants (shoulder height to 4 meters) in the young

Tertiary. They differ from the other proboscids by absent upper tusks, two-yoked cheek teeth, and by downwards-bent mandibles with two short, strong tusks (Figure 2). The Dinotheria became extinct in Eurasia at the end of the Tertiary. Only in the tropical Africa did they survive during the Glaciations. While we lack finds of old Tertiary proboscid animals from Africa, we are certain that the Dinotheria have an African origin since they appeared simultaneously with the mastodons in Eurasia. It is of special interest that the Dinotheria did not reach the American Continent.

While the *mastodons* are characteristic for the Tertiary, the *elephants* typify the proboscid animals of the Quaternary. At the beginning of the glaciations, the new forms coexisted with the old species, but it was during the glaciation period that a new blooming of Proboscidea came about which is exemplified by the richness of many new species and their wide distribution. As cold-adapted animals, some species were distributed all over Eurasia, Africa and North America; thus, they occupied, at least in the Northern Hemisphere, a larger region than did the mastodons. But they did not get to South America. This expansion of elephants is perhaps related to the development of their cheek teeth. While the low-crowned teeth of mastodons and Dinotheria were useful for the squashing of soft plants (leaves and fruit), the high-crowned, lamellar teeth of elephants enable not only the squashing of food but also allowed the grinding of harder plant stuff such as grasses. Thus, elephants and mammoths whose lamellar teeth are the largest (27-29 for M3 = the last mandibular tooth), were able to live in new regions, like steppes and tundras.

While there is no doubt that the origin of mastodons is Africa, the original ancestry of elephants is more difficult to answer because the remnants identified are in the same strata of regions in Europe, Asia and Africa. Thus there are questions of their definitive ancestry and their original distribution. In former times, one assumed that they derived from back-migrating Stegodons, while now a derivation from mastodons seems more likely. Stegodons not only appeared simultaneously with elephants in the fossil record but they are also already specialized with respect to their dentition. In addition, it has to be noted that dwarfed elephants from the Celebes Islands became known; they still had mandibular tusks, similar to the mastodons. While it may still be too early to judge, it seems more likely that elephants originated in Africa rather than in Asia. The African elephants, geologically speaking being the older species, while the Asiatic species is the younger derivative. Both derived from *Archidiskodon*-like species which were widely distributed over Eurasia and Africa.

It is of special interest that several dwarf-elephants have become known from a number of islands. Well-known are the dwarf-elephants from Mediterranean Islands (Malta, Crete) which lived there together with hippopotami and giant tortoises. The fact that this has been recorded from several islands lets us assume that the regional restriction on islands leads to dwarfism; this notion conflicts, however, with the still extant dwarfed elephants of the Congo Rainforest.

There is a similarity between the current forest-elephants (“round eared”) and steppe elephants (“pointed ears”) of Africa and the presence during the glaciations of forest elephants (*Palaeoloxodon antiquus*) and steppe elephants (*Mammontes trogontherii* and *M. primigenius*); they also differed morphologically quite markedly but had similar original ancestors (*Archidiskodon meridionalis*). These glaciation-elephants have died out during the Holocene (Current Era). As we now know from carbon

radioactivity data, the last mammoths of Siberia and North America became extinct around 10,000 to 12,000 years ago.

It appears then that the Indian elephant is closer to the mammoth than the African species, but it is not a descendant from mammoths whose distribution was wide – all over Eurasia and North America. The form that led to the African elephant was already at home in Africa during the early glaciation period. Its representatives lived all over Africa. Only during the geological Present, when the Sahara region dried out, the Northern representative became extinct, a circumstance that was enhanced by the appearance of man.

Similar circumstances are found to be the case for the Indian elephant. Once present from West-Asia to South-China, its distribution became more and more restricted so that its current distribution is minimal compared to what it once was.

Thus, the two surviving species of elephant are the last representatives of a formerly large group of species and one can only hope that these giants of the mammals remain with us into the future.

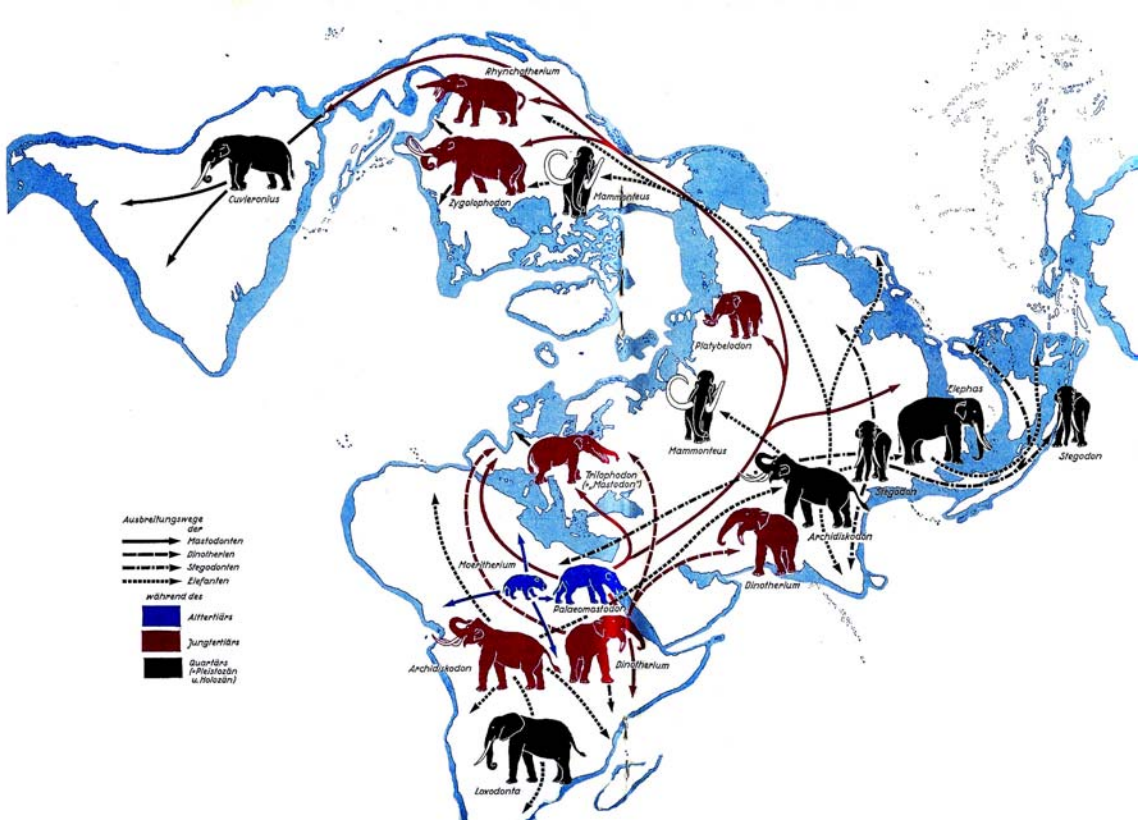
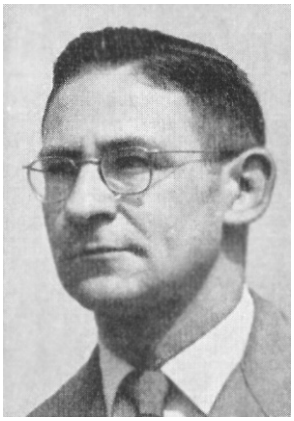


Figure 4. The paths of distribution of Proboscidea during the geological times of their existence (schematic). In the old Tertiary, the species were restricted to Africa. In the young Tertiary, the mastodons migrated via Eurasia to North America, and during the Glaciations, even to South America. The Dinotheria were restricted to Africa and southern Asia; they became extinct in Africa during the older periods of the Glaciation and, in Eurasia, they died out already during the older period of the Glaciation. The Stegodonts distributed themselves during the glaciations from southern Asia to Indonesia

and the Philippines, and from western Asia and Africa; they became extinct during the Pleistocene. The elephants that developed in Africa and Asia were distributed during the Glaciations well into Western Europe and northern America. (Original by author).



The author, Professor Dr. Erich Thenius.

Professor Erich Thenius has been member of "Kosmos" since 1940. Born on December 26, 1924 in Abbazia (= Opatija) in Istria, he spent his school years in Baden, near Vienna. After his studies in paleontology, zoology and geology he was promoted in Vienna in 1946 to Ph.D. Five years later he became Associate Professor of paleontology in Vienna; in 1957 he was named professor, and in 1962 Professor for mammalian paleontology and co-director of the Paleontological Institute of the University of Vienna. He concentrated his studies on the fauna of the Tertiary and Glaciation periods. He has published numerous popular articles and several books such as: the "History of the Earth" (Vienna, 1955), "Austria during the Ages" (2nd ed. Vienna, 1962), "Geology of lower Austria" (Vienna, 1962), "Fossilized Records" (Heidelberg, 1963) and, with H. Hofer, "Origin of Mammals" (Heidelberg, 1960). In the Handbook of Statisgraphic Geology, Thenius wrote on the mammalian fauna of the Tertiary. The result was his great renown that led to his becoming a "corresponding member" of the Austrian Academy of Sciences.

Translated by: K. Benirschke, November, 2004. I have also added the Figure 5 for orientation about the Geological Eras (From the British Museum of Natural History, 1961).

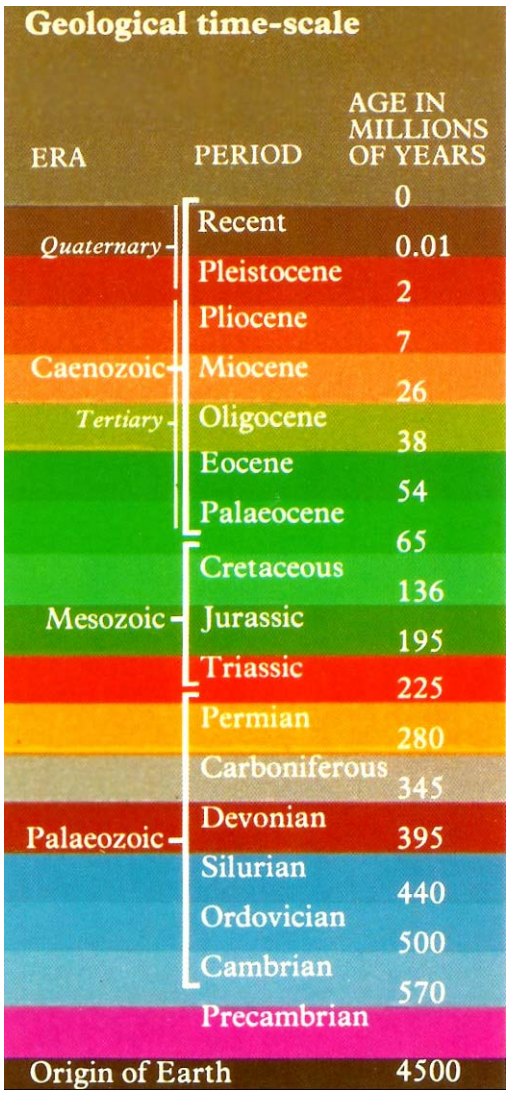


Figure 5: The Geological Eras (From the British Museum of Natural History, 1961).