THE

AMERICAN NATURALIST

Vol. XL — *December, 1906* — No. 480

THE CAUSES OF EXTINCTION OF MAMMALIA

(*Concluded*)

HENRY FAIRFIELD OSBORN

Living Environment. Infectious Diseases and Insects

In his *Great Rift Valley* (p. 265) Gregory observes that the great herds of game which roamed over the steppes of South Africa are being rapidly decreased in size and number. Man no doubt has played the leading part in the annihilation of the enormous herds that once thronged Cape Colony. The fact that during the last few years the game has retreated from the Somali coast into the interior shows how easily it can be driven from a district. In South Africa, however, man's influence has probably been insignificant as compared with natural agencies, lions and disease being the leading factors in extermination. Vast herds of the wild buffalo (*Bubalus caffer*) were exterminated between 1890 and 1893 by the cattle disease (rinderpest), which also killed off the gnu and giraffe (*op. cit.*, p. 266). Gordon Cumming[1] observed, as early as 1855, that " . . . . the goat in many districts is subject to a disease called by the Boers 'brunt sickta,' or burnt sickness, owing to the animals afflicted with it exhibiting the appearance of having been burnt. It is incurable; and if the animals inflicted are not speedily killed, or put out of the way, the contagion rapidly spreads, and it is not uncommon for a farmer to lose his entire flock with it. This sad distemper also extends itself to the *feræ naturæ*. I have shot hartebeests, black wilde-

[1] *The Lion Hunter in South Africa*, London, 1855, p. 138.

beests, blesbucks, and spring-bucks, with their bodies covered with this disease. I have known seasons when the three latter animals were so generally affected by it, that the vast plains throughout which they are found were covered with hundreds of skulls and skeletons of those that had died therefrom."

Aflalo[1] in his paper "The Beasts that Perish," has discussed many of the various causes of extermination and gives disease a prominent place. Among the Carnivora there are the non-epidemic diseases, such as distemper, affecting dogs, foxes, wolves, cats, and other wild felines. The more rare and sporadic epidemics claim victims among the Carnivora wholesale. The prevalence of rabies among foxes was observed on the continent from 1830 to 1838 in Switzerland, also in Württemberg and Baden.

Carnivora are protected by their relatively non-gregarious habits. On the contrary, the more gregarious Herbivora offer much more favorable conditions for the spread of disease. Flemming in his *Animal Plagues* enumerates 86 epidemics affecting wild quadrupeds and birds. In the list are diseases affecting nearly every wild species in Europe and some in the New World, including the red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), the chamois (*Rupicapra tragus*), wild hog, also among the Carnivora, wolves, foxes, bears, among the Rodentia, the hares, rabbits, and rats. Various forms of tuberculosis account for a large percentage of death among domesticated animals. Only the goat enjoys immunity from it. Among animal plagues anthrax was formerly the most rapid and deadly, and is now perhaps the least common owing to Pasteur's discoveries. American zoölogists are familiar with the spread of disease from domesticated to non-domesticated animals, of the sheep scab, for instance, to the wild sheep (*Ovis montana*).

Insects and Infection.— In my opinion the most striking advance toward a complete theory of the causes of natural extinction has come from recent discoveries regarding the real nature of the animal diseases and how they are communicated. Only recently have we come thoroughly to understand that insects are the most

[1] The original article has not been accessible to the writer.

active means of introducing and spreading fatal diseases over great geographical areas and on a vast scale.

Moisture Favoring the Spread of Diseases Carried by Flies.—The presence of the blood protozoan parasites known as *trypanosomes,* combined with certain flies which act as disease carriers, is in many countries correlated with moist conditions. This is especially true of the disease known in India as 'surra,' [1] the history of which was first suspected by Surgeon Major Lewis in 1888.

Extermination of the Equidæ. Surra.—The wide geographical range of surra and related diseases is significant with reference to former periods in the history of the Equidæ. All authors now agree with Lewis that the disease is carried by flies and coincides with moist conditions occurring chiefly during or immediately after heavy rainfalls, though sporadic cases may occur at other seasons of the year. In the "Emergency Report on Surra" by D. E. Salmon and C. W. Stiles [2] this is described as chiefly a wet-weather disease, invariably fatal to horses and mules, occurring in other animals, such as camels and elephants, more rarely in ruminants, and transmissible to goats, sheep, and other mammals. In India it is said to affect horses, camels, and elephants (p. 18). It occurs in Burma, Persia, Tonquin, and Korea. In Africa there is the similar *nagana* or tse-tse fly disease, more accurately described below by Bruce [3] (p. 833). In Algiers, France, and Spain, the dourine or *maladie de coit* attacks the horse and ass in particular, and may be transmitted to certain other animals; it is attributed to a trypanosome, *T. equiperdum.* In the Philippines surra caused the death of 2000 army horses in six months. The intermediary is a fly, *Stomoxys calcitrans.* It was also reported (Curry, 1902) as affecting the carabao (*Bos* (*Bubalus*) *kerabau*), but according to Lingard ruminants are not particularly susceptible. An interesting note which may bear upon the *origin of colors* in certain quadrupeds is the advice to those in charge of horses in the Philippines (p. 97): "Avoid light colored animals as much

[1] Lewis, T. R. "Flagellated Organisms in the Blood of Animals." *Physiological and Pathological Researches . . . . of the late Timothy Richards Lewis,* 8vo, London, 1888.

[2] *U. S. Dept. of Agric., 1902, Bureau of Animal Industry,* bull. 42.

[3] *Science,* n. s., vol. 22, no. 558, Sept. 8, 1905, pp. 289–299.

as possible; the darker the animal the safer he appears to be from the attack of flies." In this connection we recall the dark color of the true Bovinæ. In South America the *mal de caderas* affects horses, asses, cattle, hogs, and certain other animals, and is attributed to the protozoan known as *Trypanosoma equinum*. It is distinctively a wet-weather disease, almost completely disappearing in dry seasons. Asses, swine, and water hogs are said to be affected, and horses are never known to recover. It is chronic in course, lasting from two to five months in horses, and from six to twelve in asses and mules. See Voges [1] for fuller details.

Immunity and Adaptation.— Existing conditions among the large quadrupeds of Africa are especially important because of the increasing conviction that North American conditions in the Oligocene, Miocene, and Pliocene are most closely paralleled in the great upland region of modern Africa, the central life belt as distinguished from the coast belt.

From these recent discoveries [2] it appears that *immunity from disease* is one of the most important features of animal adaptation to environment, and that conversely non-immunity has probably been one of the potent causes of diminution and extinction. T. H. Morgan [3] includes the phenomenon of immunity among the adaptive processes. He states, as his personal opinion, however, that certain of these phenomena could not be explained as due to any selective processes. Similarly Leo Loeb [4] believes that a large number of instances of acquired immunity cannot be directly explained as adaptive phenomena.

Variations in Immunity.— There are in Africa diseases fatal to both wild and domesticated animals, others fatal to domesticated animals to which wild animals are immune. Some to which all successive generations succumb; others to which immunity is acquired in the second generation or among 'natives.' Still more remarkable is the fact that both wild and domesticated

[1] "Das Mal de Caderas." *Zeitschr. f. Hyg. u. Infectionskrankh.*, vol. 39, (3) 13 März, pp. 323–372.

[2] *Nature*, vol. 72, no. 1872, Sept. 14, 1905, pp. 496–503. Address of Bruce, before the Section of Physiology, British Association.

[3] *Evolution and Adaptation*, New York and London, 1903.

[4] "Immunity and Adaptation." *Biol. Bull.*, August, 1905, p. 141.

'immunes' may act as reservoirs of disease organisms which through flies or ticks may be carried to non-immunes. Thus the wild ruminants of Africa among the Bovidæ especially, the buffalo (*Bos* (*Bubalus*) *caffer*), the kudu (*Strepsiceros kudu*), the wildebeeste (Connochætes) carry about in the fluid portion of their blood, without themselves suffering any harm, certain protozoan trypanosomes which are fatal when borne by flies to domesticated horses (Equidæ), dogs (Canidæ), and cattle (Bovidæ).

Thus, causes favorable either to the genesis of these disease organisms or to the acquirement of immunity, or to the propagation and distribution of flies and ticks become matters of prime interest in relation to extinction.

Tse-tse Fly Disease of Domesticated Equidæ and Bovidæ.—The nagana or tse-tse fly disease of Africa is caused by *Trypanosoma brucei* (Plimmer and Bradford); the carrier is the tse-tse fly (*Glossina morsitans*). Together this trypanosome and its host the fly render thousands of square miles of Africa uninhabitable and no horses, dogs, or cattle can venture even for a day into the 'fly country.' After all the non-immune animals of the country have been killed off and thus no longer exist as sources of infection, the tse-tse fly spreads abroad out of the 'fly country' still giving rise to the disease. This strange fact led to the discovery of the fact noted above that many of the immune wild ruminants carry the same trypanosome (*T. brucei*) in small numbers in their blood and thus act as continuous reservoirs of the infection; it is from them that the fly obtains fresh supplies of the infectious parasite. A similar parasite also lives in the blood of healthy rats.[1]

Ticks, the Rapid Spreaders of Disease among Domestic Ruminants.—The *Piroplasma parvum* is a protozoan which, unlike the trypanosome, invades the blood corpuscle; it is malignant with cattle along the greater part of the east coast of Africa causing what is known as 'east-coast fever'. The infection is usually transmitted by ticks (most frequently by the brown tick, *Rhipicephalus appendiculatus*, also by *R. simus*). Migrating or treking cattle may carry the ticks many miles a day, and thus spread the

[1] Analogous to this is the 'sleeping-sickness' disease affecting man, which has spread very rapidly from west to east Africa, carried by a fly, *Glossina palpalis*, claiming hundreds of thousands of victims.

disease rapidly over a wide area of country. The larva creeps on an infected animal, sucks some of its blood, drops off, lies among the roots of the grass, and passes its first moult becoming a nympha, then an imago, in either of which latter stages it may infect a healthy animal by creeping from the grass. The tick is very hardy and may survive with its infection for a year, but after a year or fifteen months the infected ticks are all dead and healthy cattle may enter the field without risk.

Wide Geographical Distribution.—*Piroplasma bigeminum* similarly causes the 'Texas' or 'red-water fever' of our Southern States; it is conveyed by a tick. The germs are latent and the blood of an animal which has recovered from Texas fever remains infective; thus apparently healthy cattle may infect imported susceptible cattle. Such latency has an important bearing upon the theory of natural extinction as caused by similar germs. The geographical distribution of this species of Piroplasma is very wide; first discovered in North America, it is now epidemic throughout most of South Africa. Although acquiring immunity, it is the domesticated native Bovidæ which act as reservoirs of the disease in contrast to the tse-tse fly disease in which the wild Bovidæ act as reservoirs. The further fact that the native cattle may become immune has an important theoretical bearing on the natural origin of immunity to the tse-tse fly disease on the part of the wild Bovidæ and wild Equidæ.

Ticks among Equidæ.—The biliary fever of domesticated Equidæ (horses, mules, donkeys) is conveyed by a corpuscle parasite, *Piroplasma equi*, which is spread by the red tick, *Rhipicephalus evartsi*, the infection taken in the nymphal and transferred in the adult stage. As in the case of Texas fever in cattle, so the native South African horses become immune to the disease and are said to be "salted," but equines which have recovered from the disease continue to act as reservoirs and remain as sources of infection throughout their lives. The same is true among the Carnivora of the *Piroplasma canis*, spread by the dog tick (*Hæmophysalis leachii*). The blood of recovered animals remains infective.

Extermination of Wild Ruminants.—The rinderpest or cattle disease has been the greatest destroyer of the wild African quadrupeds (compare Gregory, p. 266). It is fatal to the following forms: wild buffalo, Bos (Bubalus), the kudu (*Strepsiceros kudu*), the sable antelope (*Hippotragus niger*), the gnu (*Connochætes albojubatus* and *C. taurina*), also in the Philippines to the carabao (*Bos* (*Bubalus*) *kerabau*). It is fatal to from 90 to 100% of domesticated cattle. Unlike the diseases before considered: (1) the parasite causing rinderpest is undiscovered, (2) no *natural* immunity is known (methods of artificial immunity were discovered in 1893), (3) it is distinguished by the ease and rapidity with which it spreads in all countries, climates, and seasons, being carried even on the clothes and person of man. It therefore appears improbable (Bruce) that insects have anything to do with it. It may be due to a wind-borne bacterial organism.

This disease has been known from time immemorial in Europe and Central Asia. It is believed by some to have entered the Nile provinces of 1880, to have reached the Transvaal in 1896, and thus to have traveled the whole length of Africa in fifteen years. The spread in Africa has been largely through the wild ruminants.

By analogy we can imagine that a disease affecting the Pleistocene horses of North America may have traveled an equal distance, namely, from Texas to Patagonia, and destroyed all the South American Equidæ.

Local Distribution, Immunity. Horse Sickness.— A very important point for the naturalist is the fact that this disease is local in its distribution, prevailing in low countries and during wet seasons. The infection is not carried into the high country or during the dry season.[1] The parasite causing it is unknown, and is believed to be ultra-microscopic. It is believed to be carried in the blood because the 1,000th part of a single drop of blood injected under the skin of a healthy animal will cause death; some horses require a larger dose than others, indicating fluctuations in power of resistance or immunity. Unlike the foregoing diseases it is not

[1] The same climatic relation is true of the heart-water disease of cattle, goats, and sheep (Bovidæ), which is similar in distribution to the heart-water horse sickness and is carried by the bont-tick (*Amblyomma hebræum*), in that it dies out on the high veldt. Similarly again the *catarrhal fever of sheep* has a distribution in South Africa similar to that of horse sickness, and is probably carried by means of the same night-feeding insect.

endemic or permanent, but occurs in epidemics at intervals of from ten to twenty years. Its geographical distribution in South Africa is very wide: in Natal, Zululand, the greater part of Rhodesia, Bechuanaland, and Portuguese East Africa. Horses placed in fly-proof shelters even in exceedingly unhealthy places in no case incur the disease. The particular fly or insect carrier is still unknown. As in several of the foregoing diseases the infective power of the blood persists for years.

Natural Origin of Immunity.—For the student of extinction an important point to note, in connection with 'horse sickness,' is that while artificial immunity is thus far undiscovered, degrees of immunity and of natural immunity sometimes occur. Such variations in respect to immunity would in a state of Nature lead to the gradual selection of immune forms and the production of an immune race.

Summary as to Natural Extinction by Disease

To summarize these remarkable conclusions which we owe to the labors of Lewis, Koch, Theiler, Kilborne, Smith, Watkins, Pitchford, and many others, we undoubtedly have here an agency which must be seriously considered as an occasional if not a frequent cause of extinction of quadrupeds in the past. It will be noted (1) that in the case of the tse-tse fly disease the wild ruminants are the permanent though unharmed reservoirs of the infective protozoan; (2) that in Texas fever or red-water fever native immune Bovidæ are the permanent carriers of the disease organism; (3) that the 'rinderpest' appears to be in an early stage of its history as a disease in which neither domesticated nor wild Bovidæ have become naturally immune and all the Bovidæ act as reservoirs; (4) that in the east-coast fever the infective ticks survive for a year, while the permanent carriers of the infective organism are not discovered; (5) that in the biliary fever of domesticated horses, the recovered equines act as reservoirs; (6) similarly again that in 'horse sickness' of South Africa the infective power of the blood in a recovered animal persists for years.

Thus in these diseases we have all the conditions favorable for the wide distribution of insect-borne diseases which in past times may have attacked various types of quadrupeds and resulted in extermination before natural immunity was acquired.

Living Environment. Competing and Hostile Mammalia

From the struggle with physical environment, with the living plant and insect environment, we now pass to the struggle with other mammals.

In the Tertiary of North America we witness:

(*a*) the rapid multiplication of certain local or native mammals;

(*b*) the repeated introduction by migration of new mammals, coming either singly or in waves;

(*c*) the slowly or rapidly sequent extinction of certain local animals.

Even considering the disastrous effects of glaciation and of desiccation this *competition*, because it has worked more widely and over longer periods of time, has been a tremendous agency of extinction.

Competition of Lower and Higher Types.— Of marsupials in competition with rodents in Australia Spencer[1] observes: "In the case of such smaller marsupials as, for example, species of *Sminthopsis* in which the number of young produced at a birth is from eight to ten and there are at least two broods in each year it is a matter of considerable surprise that they are not much more numerous than they are. The explanation is probably associated with the fact that there is a considerable length of time during which not only does the capture of the mother result in her destruction and in that of all the young ones [by birds of prey, for example], but that during this period she is severely handicapped by not being able to reach shelter rapidly. It may perhaps be objected to this that such an animal as a rabbit is handicapped by having to carry the young ones in utero for a much longer time than the marsupial does, but anyone who has seen the well-developed, pouch young ones of a marsupial will realize how much more cumbersome a burden they are than the uterine embryos of such an animal as a wild rabbit."

[1] Spencer, Baldwin. "Through Larapinta Land, A Narrative of the Horn Expedition to Central Australia." *Report of the Horn Expedition to Central Australia*, Sept. 1896, pp. 127–128.

As regards this principle, Wallace observes: "There is good reason to believe that the most effective agent in the extinction of species is the pressure of other species, whether as enemies or merely as competitors." Lyell[1] observes: "Extension of the range of one species alters that of others. In reference to the extinction of species it is important to bear in mind, that when any region is stocked with as great a variety of animals and plants as its productive powers will enable it to support, the addition of any new species to the *permanent* numerical increase of one previously established, must always be attended either by the local extermination or the numerical decrease of some other species."

Exception must be taken to the sweeping character of these statements: First, because the *eliminating action of a change in plant life* may have been the *real* cause of extinction in several cases where competition with other mammals is the *apparent* cause. For example the extinction of the Titanotheriidæ and Elotheriidæ may have been entirely due to changes in vegetation, rather than to competition with any other Herbivora.

Second, because the survival of the opossums (Didelphiidæ) in North America shows there may be striking exceptions to this principle.

The conclusion drawn from such exceptions is that of Darwin, namely, that the *keenest competitors are the animals of most nearly similar feeding habits.* There are, however, exceptions to Darwin's conclusion also, as the following instances prove.

Destruction of Food Supply by Smaller Browsing Animals.—The enormous changes in the quadruped life of the district encircling the eastern and southern sides of the Mediterranean are popularly attributed to secular changes of climate. Haan shows, however, that evidence for secular change of climate within the historic period is insufficient or actually negative. Parts of these regions were formerly inhabited by some of the larger quadrupeds which have since disappeared through the agency of man; it is equally true that the country could not support the life of these quadrupeds at the present time. There can be little doubt that the change in soil and vegetation has been indirectly caused by

[1] Lyell, C. *Principles of Geology*, vol. 2, 1872, p. 451.

deforestation of the hills and mountains, and this has largely been the result of the unrestricted browsing of large herds of sheep and goats, which has been going on since long before the Christian era. Even now the goats can be observed in certain parts of Palestine and Greece destroying the last of the forests and killing the seedling trees. Destruction of the forests led to the washing away of the soil and to the entire unfitness of the country for the support of any of the larger Herbivora.[1]

"The mastodon, for example," observes Morris[2] "needing great quantities of herbage for its food supply, might, in cases of severe drought, succumb to the food competition of the rabbit, or some still more insignificant creature, which, spreading in vast numbers over the country, devoured the sparse herbage and left its huge competitor to starve.... Thus hosts of Herbivora may have frequently perished in consequence of an insect assault upon their food; and numerous Carnivora, thus deprived of their food, may have similarly perished."

Especially Intense on Islands.—This great change is paralleled by the influence of the goats on islands, as cited by Wallace[3] and Palmer.[4]

Palmer (*loc. cit.*) observes: "Sheep and goats when numerous are likely to cause widespread injury, particularly in forested regions. An instructive example of the damage done by goats is that on St. Helena, described by Wallace.[5] St. Helena is a mountainous island scarcely 50 square miles in extent, and its highest summits reach an elevation of 2,700 feet. At the time of its discovery, about the beginning of the sixteenth century, it is said to have been covered by a dense forest; to-day it is described as a comparatively barren rocky desert. This change has been largely brought about by goats first introduced by the Portuguese

[1] Osborn, H. F. "Preservation of the Wild Animals of North America." Address before the Boone and Crockett Club, Washington, Jan. 23, 1904, pp. 15–16.

[2] Morris, Charles. "The Extinction of Species." *Proc. Acad. Nat. Sci. Phila.*, 1895, p. 254.

[3] *Island Life*, 1880, pp. 280, 283–286.

[4] Palmer, T. S. "The Danger of Introducing Noxious Animals and Birds." *Yearbook U. S. Dept. of Agric. for 1898*, p. 89.

[5] *Island Life*, 1880, pp. 283–286.

in 1513, and which multiplied so fast that in seventy-five years they existed by thousands. Browsing on the young trees and shrubs, they rapidly brought about the destruction of the vegetation which protected the steep slopes. With the disappearance of the undergrowth, began the washing of the soil by tropical rains and the destruction of the forests. In 1709 the governor reported that the timber was rapidly disappearing and that the goats should be destroyed if the forests were to be preserved. This advice was not heeded, and only a century later, in 1810, another governor reported the total destruction of the forests by the goats.

"The Santa Barbara Islands, and Santa Catalina off the coast of southern California, and the island of Guadalupe, off the Lower California coast, are utilized as ranges for goats. All these islands are dry and more or less covered with brush, but arborescent vegetation is comparatively scarce. The goats practically run wild, and already exist in considerable numbers. As yet the goats have not been on the islands long enough to cause any serious effects on the vegetation, and they may never bring about the ruin which has been wrought on St. Helena. But it is scarcely possible for the islands to be grazed by goats for an indefinite length of time without suffering serious damage."

Goats, however, do not always enjoy a monopoly of the food of islands as the case cited above from Linnæus proves.

Small Browsers in Relation to Carnivora.—In both instances cited above, unrestricted browsing and rapid multiplication of the goats have taken place under artificial conditions of protection of these animals from Carnivora. It is quite possible, however, that in certain regions under natural conditions the Carnivora themselves may have become extinct through epidemics or other causes, thus promoting the unrestricted multiplication of the smaller browsing animals so fatal to the vegetation and to the normal distribution of food supply of a country. The period during which these changes have taken place in the Orient is a comparatively short one as compared with the periods of geological time.

Application to the American Oligocene.—Thus we see that the introduction of new forms of *dissimilar feeders* may completely disturb the balance of Nature and entirely alter the character and amount of food supply or even of water supply and of competition in any given region. Rabbits exert a great influence on the food supply of the marsupial Herbivora of Australia. This factor of the browsing competition of the smaller Herbivora on islands is one which, while by no means demonstrated, is a possible cause of extinction of the larger Herbivora in larger areas and is worth considering even in relation to the sudden disappearance of the Titanotheres. For example, the extreme multiplication of the Oreodonts (Oreodon, Agriochœrus) and horses (Mesohippus), small browsers which swarmed in herds in the Middle Oligocene period in the regions of South Dakota and Nebraska, may possibly have cut off part of the food supply of the Titanotheres.

Application to the Oligocene and Miocene of Europe.—Since the introduction and unchecked increase of small browsing animals may in course of a century or a number of centuries — a comparatively short period in geological time — effect a profound influence in a country upon the forests, since sheep and goats are forest destroyers especially under the artificial conditions where the increase of these animals is unchecked, and such browsers are especially destructive of the circumscribed flora of islands, we should consider the part the smaller browsing animals may have played during the Tertiary of Europe when so many parts were archipelagic.

Dwarfed Pliocene and Pleistocene Island Life.—In the islands of Malta, Cyprus, and Crete, as recently explored by Miss Bate,[1] we have fine examples of comparatively recent insulation.

It appears probable that Cyprus became an island first, because: (1) no submerged bank connects it with the mainland, and the 200-fathom line is reached within a short distance of the coast line; (2) the terrestrial fauna and avifauna include several distinct races peculiar to the island, a fact confirmed by Kobelt from his study of the recent Mollusca. The reduced existing Cyprus fauna contains a mingling of European and North African forms, and shows the effects of deforestation in historic times. The largest animal on the island is the moufflon (*Ovis ophion*) 25 inches high at the shoulders; yet this is the *smallest* of all the wild sheep, and is related to East Persian species.

[1] Bate, Dorothea M. A. "Pleistocene Mammalia in Crete." *Geol. Mag.*, n. s., dec. 5, vol. 2, pp. 193–202, May, 1905.

The affinity of Malta to Sicily is indicated by the occurrence of two species, *Hippopotamus pentlandi* and *Elephas mnaidriensis*, in the cavern deposits of both islands. The early separation of Cyprus is indicated by the fact that *E. cypriotes* and *H. minutus* are both more primitive than the Maltese-Sicilian species. Crete also includes antelope and deer in its Pleistocene fauna.

Pleistocene Extinct Fauna of the Mediterranean Islands

	Cyprus	Malta	Sicily	Sardinia
Proboscidea, pigmy elephants	*E. cypriotes*	*E. melitensis*		*E. lamormoræ*
		E. mnaidriensis	*E. mnaidriensis*	
Artiodactyla, pigmy hippopotami	*H. minutus*	*H. pentlandi*	*H. pentlandi*	

The occurrence of these specifically different though apparently closely related races of small elephants and hippopotami in widely separated islands is an instance of independent development with some divergence from common ancestors.

Introduction of Carnivora

Striking examples of the introduction and competition of Carnivora in past and recent times are:

(1) The true Carnivora in competition with the Creodonta of Europe and North America, followed by the final extinction of the latter order in the Lower Oligocene.

(2) The true Carnivora in South America in the Middle Pliocene. At this time the Canidæ and two destructive types of Felidæ, the sabre-tooths (Machærodontinæ) and the true cats (Felinæ), suddenly appeared; they entered a faunal region which, subsequent to the extinction of the marsupial Carnivores (Thylacinidæ) in the Oligocene, had been entirely free from Carnivora.

(3) The dingo (*Canis dingo*), in the Australian mainland, followed by the extinction of the Tasmanian wolf (Thylacinus) and devil (Sarcophilus), animals which survive only in Tasmania.

(4) The mongoose (Herpestes) in various countries.

In each instance intelligence, ferocity, and facility in change of habit have played an important part. The Carnivora in relation to the balance of Nature, the food supply, the *young* of the Herbivora is our special inquiry.

Smaller Carnivora and the Balance of Nature.— T. S. Palmer[1] has given a striking summary of the influence of the mongoose:

"The common mongoose of India (*Herpestes mungo* or *H. griseus*).... is a well known destroyer of rats, lizards, and snakes, and was introduced into Jamaica....for the purpose of ridding cane fields of rats....Various remedies were tried, but apparently with little success, until in February, 1872....nine individuals of the mongoose, four males and five females, from India, were introduced. These animals increased with remarkable rapidity, and soon spread to all parts of the island, even to the tops of the highest mountains. A decrease in the number of rats was soon noticeable....The mongoose increased, and as the rats diminished, its omnivorous habits became more and more apparent. It destroyed young pigs, kids, lambs, kittens, puppies, the native 'coney' or capromys poultry, game, birds which nested on or near the ground, eggs, snakes, ground lizards, frogs, turtles' eggs, and land crabs. It was also known to eat ripe bananas, pineapples, young corn, avocado pears, sweet potatoes, cocoanuts, and other fruits. Toward the close of the second decade the mongoose, originally considered very beneficial, came to be regarded as the greatest pest ever introduced into the island. Poultry and domesticated animals suffered from its depredations, and the short-tailed capromys (*Capromys brachyurus*), which was formerly numerous became almost extinct except in some of the mountainous districts. The ground dove (*Columbigallina passerina*) and the quail dove (*Geotrygon montana*) became rare, and the introduced bobwhite, or quail, was almost exterminated. The peculiar Jamaica petrel (*Æstrelata caribbœa*), which nested in the mountains of the island, likewise became almost exterminated. Snakes, represented by at least five species, all harmless, and lizards, including about twenty species, were greatly diminished in numbers. The same thing was true of the land and fresh-water tortoises and the marine turtle (*Chelone viridis*), which formerly laid its eggs in

[1] Palmer, T. S. "The Danger of Introducing Noxious Animals and Birds." *Yearbook U. S. Dept. of Agric. for 1898*, pp. 93, 94.

abundance in the loose sand on the north coast. The destruction of insectivorous birds, snakes, and lizards was followed by an increase in several injurious insects, particularly ticks, which became a serious pest, and a Coccid moth, the larvæ of which bore into the pimento trees."

Carnivorous Animals Directly Hostile.— The question as to how far the mammals of prey have caused the extinction at various times of various forms of quadruped life is widely disputed. Morris[1] observes: "So far as existing evidence goes, then, it seems probable that hostile aggression, while it may have occasionally been an indirect, has rarely been the direct cause of the extinction of species." The similar opinion expressed to the writer by Dr. D. G. Elliot that no wild animal causes the extinction of another wild animal is probably true (1) of undiminished herds, (2) of cases where carnivores and quadrupeds have evolved together and, as in the case of the modern battleship, modes of defence have evolved simultaneously with modes of attack.

In this connection, however, we must consider the Carnivora as one of the causes of *final extinction* of diminished groups of animals which are struggling to maintain themselves against adverse conditions of (*a*) physical environment, droughts, or cold, (*b*) changing food supply, (*c*) competition with other quadrupeds, (*d*) epidemics.

The above opinions (of Morris and Elliot), therefore, do not hold good (3) of diminished herds, which are unable adequately to defend their young, or (4) of cases where newly introduced Carnivora find quadrupeds unprovided with adequate means of defence, as in the South American invasion from North America in the upper Pliocene.

INTERNAL CAUSES OF EXTINCTION

Environment and life (including heredity and ontogeny) are *always* reciprocal. Having considered the causes of extinction which originate in the environment let us pass to those which originate in a lack of internal adaptation and adaptability.

[1] "The Extinction of Species." *Proc. Acad. Nat. Sci. Phila.*, June, 1895, pp. 253–263.

Important Differences Between the Effects of Internal and External Causes

Summarizing the external causes we observe:

(1) That in large part they originate with cosmic changes, or with changes in the earth itself, in the elevation or depression, extension or contraction of the land and water areas. From these result progressive heat or cold under both moist and dry conditions, progressive moisture and desiccation, consequent changes of soil, vegetation, forestation, water supply. Also the introduction of new food competitors or enemies, of new insect pests and new diseases.

(2) Under these changed conditions we observe that the extinction of species and genera has repeatedly occurred on a very large scale. Secular desiccation in different periods of the Tertiary, but chiefly toward the late Pliocene, was quite as fatal as the Glacial Period.

(3) A distinctive feature of such extinction, *originating in external causes*, is that it often affects the fit and unfit alike, the adapted and inadapted; it often destroys rather than improves a fauna. This was certainly the case with the glacial extinction in North America and Europe.

(4) On the contrary, the extinction, *originating in internal causes, i. e., in relative internal fitness or unfitness*, often improves a fauna by eliminating the least adapted members.

(5) A further distinction is that external causes have usually acted locally or on certain parts of the earth's surface, leaving a part of the fauna to survive elsewhere. The elimination of the Equidæ and Proboscidia in North and South America, for example, did not hinder their survival in the Old World.

(6) Internal causes, relative inadaptation or unfitness, have, on the contrary, acted simultaneously all over the world, for example, in the elimination of the great orders of Creodonta, Amblypoda, and Condylarthra during the Eocene period.

Survival or Extinction Value of Organs

Paleontology affords positive evidence that structural or functional inadaptations have been primary causes of extinction at all times but chiefly during periods of external change.

(1) Since the publication of *The Origin of Species* naturalists have disagreed as to one of Darwin's main propositions, namely, that the struggle for existence is so intense that variations adaptive or inadaptive, no matter how slight, will tend respectively toward survival or elimination. This raises the question of the modes of evolution, of *character or organ building*, in mammals, which is treated elsewhere.

(2) Whatever may be true as to the above feature of the selection theory, there is a general consensus of opinion that *animals which present the highest adaptive combination of favorable characters, of fully formed organs, and the highest adaptability or capacity of favorable change of habit or structure, will tend to survive.*

(3) Similarly there is a consensus, from certain repeatedly observed facts in paleontology that in *varietal, specific, generic, family selection,* not only adaptive or inadaptive *combinations* of characters but also *single fully formed organs,* such as the brain, the limbs, and the teeth, have in course of time been the causes of selection or extinction, partly in connection with changes of environment, partly because inherently adaptive or inadaptive.

(4) Thus we make the generalization that in certain cases extreme bulk, extreme specialization, the development of certain dominant characters, have led to extinction; that large-brained have replaced small-brained types; that certain types of teeth or certain types of limb and foot structure have simultaneously over large parts of the world been found wanting and thus proved fatal to their possessors.

These are the general lines of thought which have been followed by many authors since Darwin first directed our attention to this subject. It is necessary, however, to look into these causes somewhat more critically since many of them have been assumed without proof.

Inadaptive Foot and Molar-Tooth Structure.— Waldemar Kowalevsky, the Russian paleontologist, was one of the pioneers in this line of reasoning. He observed in his great monograph [1]

[1] "Monograph der Gattung Anthracotherium Cuv. und Versuch einer natürlichen Classification der fossilen Hufthiere." *Palæontographica,* n. s., vol. 2, 3. (XXII.)

(1873, p. 152) the *extinction of all Artiodactyla* with an inadaptive foot structure and inadaptive grinding teeth as follows: *Upper Eocene*, Xiphodon, Anoplotherium, Diplopus; *Oligocene*, Hyopotamus, Anthracotherium, Entelodon. He pointed out that the inadaptation of the foot in these animals consisted of a mechanical defect in the manus (3d metacarpal not spreading above to articulate with the trapezium as in the 'adaptive' manus of the pig and hippopotamus, see Taf. 7), and that the inadaptation in the grinders consisted of the persistent short or brachyodont crowns, bunoselenodont and bunodont, composed of partially rounded cones. These feet being mechanically weak in the function of the carpals and metacarpals were incapable of the elongation into cannon bones — a cursorial or speed adaptation which saved the lives of the adaptively reduced Artiodactyls. These short teeth were by his theory not adapted to a supposed change of vegetation from softer herbage to harder Gramineæ. His paleozoölogical supposition that such a change of food occurred was independently confirmed by the paleobotanists Saporta and Marion. His conclusion as to extinction (which was very original at the time) has since been abundantly confirmed by subsequent observations of the extinction of all forms of quadrupeds with these inadaptive types of short-crowned grinders both in North America and in India.

This generalization is noteworthy also as bearing upon the extinction of the Titanotheres (Oligocene) and Chalicotheres (Upper Miocene) types, both of which possess short-crowned bunoselenodont molars.

Inadaptation of the Titanothere Grinding Teeth.— It has since been recognized by every author who has written upon these animals that the relatively short crowns of the so called bunoselenodont or combined cone-and-crescent pattern of grinding teeth, were adapted to browsing on coarse and soft rather than fine and hard kinds of food. Thus Lucas[1] observes: "....it is easy to see from a glance at their large, simple teeth that these beasts [Titanotheres] needed an ample provision of coarse vegetation and as they seem never to have spread far beyond their birthplace,

[1] *Animals of the Past.* 8vo, New York, 1901, p. 222.

climatic change modifying even a comparatively limited area would suffice to sweep them out of existence."

In the summary of the tooth characters of the Titanotheres we have shown how Nature was apparently making an effort to develop a long or hypsodont crown by the elongation of the ectoloph on the outer side of the superior grinding teeth, and secondly how this effort was apparently futile because of the separate rise or development of the inner or cone side of the tooth and the absence of a transverse crest. Such a tooth is half hypsodont and half brachyodont. It does not favor longevity because it is soon worn off.

A *cul de sac* in evolution is an avenue from which there is no escape. This was reached in the teeth of the Titanotheres not, as in many other animals by a great sacrifice of numbers in the specialization of the teeth, but by a sacrifice of *parts*; the intermediate tubercles were lost and the internal tubercles were isolated. It is noteworthy that every animal experimenting with teeth of this kind (Anoplotheriidæ, Anthracotheriidæ, Chalicotheriidæ) became extinct; there was no further mechanical progress or perfection possible, hence the *cul de sac*. At this point an animal is at the mercy either of its competitors or of a change of vegetation. We conclude from the extinction of the large-toothed *Titanotherium ingens* that it was not the size of the teeth but the mechanical pattern which was inadaptive.

While it appears that the Titanotheres with their immense bodies were poorly equipped for the competition for food, and would have been seriously affected by any change of climate which greatly altered the general vegetation, especially if it resulted in an increase of grasses and a decrease of the softer plants, we must record the fact that the Elotheres, *with still less effective teeth,* passed through exactly such a crisis (if it occurred), that soon afterward they began a very rapid increase in size, and that they survived to a much later geological period (Lower Miocene).

Regarding the influence of the teeth as chief factors in extermination there is the strong collateral evidence for Kowalevsky's theory as described above, that since all bunoselenodont quadrupeds whether belonging to the Artiodactyla or Perissodactyla, disappeared either during the Oligocene or early Miocene period in all parts of the world, the possession of this type of tooth was the primary cause of extinction.

Of all the possible causes of extinction of the Titanotheres this seems to be the one which has the strongest collateral support. Yet the suddenness of Titanothere extinction seems to require the existence of contributory causes.

Relation of Molar-Tooth Structure to Longevity and Reproductive Power.— There is obviously a direct correlation between longevity and fertility with *hypsodontism*, or the elongation of the crowns of the grinding teeth, which enables an animal to live a great many years. Elephants, according to Darwin's calculation, although slow-breeding animals, with the aid of their extremely long-crowned teeth live 90 years and produce at least three pair of young. Horses with their long-crowned teeth, living to the age of twenty-five years and foaling every year would produce twenty-two young.

In contrast such a titanothere type as Palæosyops, with its short-crowned teeth, would live a comparatively short period and produce comparatively few young. In the long run this relation of longevity to reproduction would tend to replace the races with short-crowned teeth by those with long-crowned teeth.

Theoretically this law might be one of the means of explaining the early dying out of the short-crowned, broad-skulled genus Palæosyops, if it were not for the contradictory fact that the short-crowned Manteoceras survived and that the long-crowned Telmatherium became extinct.

Feet and Limbs.— Like the teeth, the feet of the Titanotheres were practically stationary in development. Just as the Oligocene tooth is an enlarged duplicate of the Eocene tooth, so the Oligocene titanothere foot is an enlarged duplicate of the Eocene foot.

Since the remains of these animals are found chiefly in coarse river channel deposits, there is no geological evidence that these animals suffered from a scarcity of water. The floods, however, may have been periodic with intervals of drought and it may be imagined that under changing conditions of plant life the titanothere feet and limbs were not adapted to long excursions for food enforced during the annual dryer periods, as compared with other quadrupeds. But the Titanotheres were certainly not far inferior travelers to the contemporary rhinoceroses, and were equal to the modern elephant type. This therefore may be considered as a contributory cause rather than as one of the chief causes of titanothere extinction.

THE INADAPTATION OF LARGE SIZE

There is a widespread belief, which is not borne out by the facts, that bulky animals have tended to disappear first.

Thus Owen, although as late as 1877[1] disposed to attribute the extinction of the large mammals of Australia to the agency of man, advanced the theory[2] of the disadvantages of bulky size under changed conditions. "In proportion to the bulk of a species is the difficulty of the contest which, as a living organized whole, the individual of such species has to maintain against the surrounding agencies that are ever tending to dissolve the vital bond, and subjugate the living matter to the ordinary chemical and physical forces. Any changes, therefore, in such external conditions as a species may have been originally adapted to exist in, will militate against that existence in a degree proportionate, perhaps in a geometrical ratio, to the bulk of the species. If a dry season be gradually prolonged, the large Mammal will suffer from the drought sooner than the small one; if any alteration of climate affect the quantity of vegetable food, the bulky Herbivore will first feel the effects of stinted nourishment.....The actual presence, therefore, of small species of animals in countries where larger species of the same natural families formerly existed, is not the consequence of any gradual diminution of the size of such species, but is the result of circumstances which may be illustrated by the fable of the 'oak and the reed'; the smaller and feebler animals have bent, as it were, and accommodated themselves to changes which have destroyed the larger species."

Morris[3] observes: "....One tendency, which has particularly

[1] *Researches on the Fossil Remains of the Extinct Mammals of Australia.* 4to, London, 1877, pp. ix, x.

[2] *Trans. Zool. Soc. London*, vol. 4, 1850, p. 27.

[3] Morris, Charles. "The Extinction of Species." *Proc. Acad. Nat. Sci. Phila.*, 1895, p. 254.

manifested itself in herbivorous animals, has frequently led directly to their destruction. This is the tendency to increase in size through the double influence of abundance of food and little waste of tissue through exertion. In the sluggish grass-eaters, dwelling on plains covered with rich herbage, or leaf and twig eaters in tropical forests, the nutritive agencies are in excess of those of waste, and these animals seem always to have tended to an increase in size, until those of least exertion and greatest powers of obtaining food became enormous in dimensions. An example of the same kind among the Carnivora is the Greenland whale, which, while feeding on minute forms, obtains them in enormous quantities with little muscular exertion, and has in consequence become of extraordinary dimensions. . . . "

Bulk not Intrinsically Fatal.—(1) The extinction of a large quadruped attracts more attention but we recall the fact (*a*) that the small Condylarthra became extinct before the large Amblypoda, (*b*) that many families of relatively small Artiodactyla and Perissodactyla became extinct at the same period as the very large Titanotheres; (*c*) that the relatively small Mylodon disappeared as early as the large Megatherium; (*d*) that the extinction of the mammoth in the northern hemisphere during or after the glacial epoch attracts attention because of the animal's large size, but as shown, many other quadrupeds vastly inferior in size disappeared at the same time.

(2) The survival of animals which have been constantly increasing in size from the Eocene to the present time may be cited as proof that bulk is not a cause of elimination *per se*. The wild horses, rhinoceroses, many ruminants, bears, and probably the whales have now attained the maximum size. The African elephant is practically as large as any of the extinct species. Both the elephant and the white rhinoceros (which would have survived in large numbers but for the purely accidental interference with the order of Nature by man) are perfectly adapted in these two respects.

(3) Bulk is fatal under certain changes of environment where not correlated with an adequate feeding mechanism, with adequate defensive powers, adequate fertility, and adequate defense and care of the young.

But the *absence of these powers is almost equally fatal to small animals.*

Bulk must therefore be considered in relation to (1) disadvantage of the large amount of food required by a large animal, which is offset by the advantage that many large animals can travel long distances; (2) diminished birth rate, which is a characteristic of large animals, is a point to be noticed; as a rule, the larger the animals, the fewer the young, and the less able a species would be quickly to regain numerical strength after some widespread diminution in number; (3) by the fact that the diminished birth-rate is offset by longevity and power to protect young from enemies. "The elephant," observes Darwin, "is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair."[1]

Application to the Titanotheres.—The bulk of the Titanotheres, which exceeded that of any other land quadrupeds, excepting only the more modern elephants, may have been a serious drawback under changing conditions of vegetation; but as noted above the extinction of the huge Titanotheres was no more sudden or mysterious than that of the slender Hyracodontidæ and Lophiodontidæ, or of the Amynodontidæ—all contemporaries of the Titanotheriidæ and vastly inferior in size.

It is important to note that whereas in the elephant the diminished birth rate is offset by longevity this *was not the case* in the Titanotheres which with their very short-crowned teeth were relatively short-lived animals.

Bulk, Slow Breeding, and Variation.—The following argument by Wallace receives no support from paleontology. "There is, however, another cause for the extinction of large rather than small animals whenever an important change of conditions occurs, which has been suggested to me by a correspondent,[2] but which has not,

[1] Darwin, C. *Origin of Species*, p. 63, ed. of 1860.
[2] Mr. John Hickman of Desborough.

I believe, been adduced by Mr. Darwin or by any other writer on the subject. It is dependent on the fact, that large animals as compared with small ones are almost invariably slow breeders, and as they also necessarily exist in much smaller numbers in a given area, they offer far less materials for favourable variations than do smaller animals. In such an extreme case as that of the rabbit and elephant, the young born each year in the world are probably as some millions to one; and it is very easily conceivable that in a thousand years the former might, under pressure of rapidly changing conditions, become modified into a distinct species, while the latter, not offering enough favourable variations to effect a suitable adaptation, would become extinct."[1]

Mr. C. W. Andrews[2] has recently (1903) revived this argument that the lengthening of the time taken to attain sexual maturity may affect the rate of evolution, and under changed conditions where a rapid rate of evolution is essential may cause extinction.

"....In many Ungulates this increased longevity is indicated by various modifications of the teeth, tending to give them a longer period of wear: generally this end is attained by the increasing hypselodonty of the cheek-teeth. A necessary consequence of the longer individual life will be that in a given period fewer generations will succeed one another, and the rate of evolution of the stock will therefore be lowered in the same proportion. If now the conditions of life undergo change, the question whether a given group of animals will survive or become extinct will depend upon whether it can undergo sufficiently rapid variation to enable it to avoid getting so far out of harmony with its surroundings that further existence becomes impossible. It seems to follow then that the smaller animals, in which the generations succeed one another rapidly, will have a better chance of surviving than the larger and more slowly breeding forms, which at the same time will be still further handicapped if, as is usually the case, they are more highly specialized than the smaller forms, and therefore have a more restricted range of possible variation."

[1] Wallace, A. R. *Geographical Distribution of Animals*, vol. 1, pp. 158–159.

[2] Andrews, C. W. "Some Suggestions on Extinction." *Geol. Mag.*, dec. 4, vol. 10, no. 463, January, 1903, p. 2.

As against these purely hypothetical considerations paleontology shows that during Pliocene and Pleistocene times the slow-breeding Proboscidia evolved quite as rapidly, if not more rapidly, than the rapid-breeding Rodentia.

THE INADAPTATION OF EXTREME SPECIALIZATION

Extreme Specialization.—Specializations among the quadrupeds take many forms: the *loss of parts* which under changing conditions might be useful. In the case of the Titanotheres the diminished size of the cropping teeth, which are either degenerate or wanting, is an instance. The animals while capable of browsing were *incapable of grazing,* so far as we can infer from the general presence of well adapted paired or single cropping teeth in the surviving ruminants and horses. It may be said that the Titanotheres had lost all cropping power through the degeneration, simplification, or absence of the incisor teeth.

Survival of the Unspecialized.—This is a general but not universal principle. Cope observes:

"Agassiz and Dana pointed out this fact in taxonomy, and I expressed it as an evolutionary law under the name of the 'Doctrine of the Unspecialized.' This describes the fact that the highly developed, or specialized types of one geologic period have not been the parents of the types of succeeding periods, but that the descent has been derived from the less specialized of preceding ages. No better example of this law can be found than man himself, who preserves in his general structure the type that was prevalent during the Eocene period, adding thereto his superior brain-structure.

"The validity of this law is due to the fact that the specialized types of all periods have been generally incapable of adaptation to the changed conditions which characterized the advent of new periods. Changes of climate and food consequent on disturbances of the earth's crust have rendered existence impossible to many plants and animals, and have rendered life precarious to others. Such changes have been often especially severe in their effects on species of large size, which required food in large quantities. The results have been degeneracy or extinction. On the other hand plants and animals of unspecialized habits have survived."[1]

Dominant Characters.— Characters which have reached an extreme stage so as to demand a larger share of the sum total of bodily nutrition than their general or apparent utility justifies may be known as *dominant organs.* They appear to violate the law of economy of growth, or the maximum combination of favorable characters by the subservience of each part to the whole.

The great horns of the Titanotheres, the tooth of the narwhal, the tusks of the Babirussa, the horns of the Irish deer, Megaceros, the tusks of the mammoths, *E. primigenius, E. columbi,* and *E. imperator,* are cases in point. The tusks of the elephants, however, serve a variety of useful purposes.

Overdevelopment of such organs has long been considered among the possible causes of extinction. The overdevelopment itself has recently been explained by F. B. Loomis[2] as follows:

"The above are selected examples in which a feature once useful has been developed beyond its maximum utility. Many others equally striking might be cited, the explanation of all of which is extremely difficult unless such a factor as momentum is called in. In the light of this factor, however, a logical and apparent cause is found. Momentum also explains why a character that originated in accordance with the environment develops so rapidly, and why, when an animal had reached adjustment to its surroundings, it still goes on beyond a perfect adjustment. It may be laid down as a rule then that *a variation started along any line tends to carry that line of development to its ultimate, being driven by momentum.* If the feature is detrimental the group dies out; if, however, it is merely a minor feature it makes a handicap. A line of development may be stopped and its momentum overcome but the tendency is to keep right on."

Selection of Useless Dominant Organs.— Another explanation may be offered for certain male dominant characters, namely, that by sexual selection or competition between the males for females, characters are precociously or overdeveloped, which are

[1] Cope, E. D. *Primary Factors of Organic Evolution,* 1896, p. 173.

[2] Loomis, F. B. "Momentum in Variation." *Amer. Nat.,* vol. 39, 1905, p. 843.

of little use in general selection and competition with other animals. Thus in the case of horns, of tusks, and of canines, by favoring the males in which they are most strongly developed they cause an *incidence* of selection on characters which are useful in sexual selection only.

Extreme specialization in several members of the titanothere family took the form of dominance of the horns. As we have seen, the horns first appeared alike in both sexes as rudiments or small horns but gradually they became male characters, and were undoubtedly of advantage to the males in their sexual combats for the possession of the females. Thus a constant selection of the individuals with the largest horns may have been in process. This incidence or main emphasis of natural selection on characters which were useless for feeding purposes may have been the cause of the non-evolution of the teeth.

The force of this generalization is, however, weakened by the fact that in other Titanotheres, such as the genera Titanotherium and Megacerops, the horns were relatively small, yet these animals became extinct at the same time as the large-horned genera, Brontotherium and Symborodon.

Psychic or Cerebral Inadaptation

Brain.— Under temporary or prolonged changed conditions of life, intelligence and instinct are matters of first importance in relation to quickness, alertness, adaptability to new conditions. Animals differ enormously in this regard. On our western plains horses by their resourcefulness save their lives where cattle perish.

The paleontologist knows nothing of these psychic qualities, he can only judge the powers of an extinct animal by examining the intra-cranial cast which often reproduces the external form of the brain with great fidelity. The chief measure of the capacity of extinct animals is indicated by:

(1) absolute size and weight of the brain;
(2) development of the convolutions;
(3) proportionate size of the frontal lobes of the cerebrum;
(4) ratio of brain weight to body weight.

Lortet was the first to establish the law of the progressive cerebral development of the Tertiary mammals.

In 1884 Marsh briefly considered the brain question in relation to the extinction of the Titanotheres or Brontotheriidæ. He observes (p. 190): "The small brain, highly specialized characters, and huge bulk, rendered them incapable of adapting themselves to new conditions, and a change of surroundings brought extinction." Again (p. 190): "The Dinocerata, with their very diminutive brain, fixed characters, and massive frames, flourished as long as the conditions were especially favorable, but with the first geological change, they perished, and left no descendants." In discussing the brain, especially after referring to the general law of brain growth (*i. e.*, evolution) during the Tertiary period, he states:

"To this general law of brain growth two additions may now be made, which briefly stated are as follows: (1.) The brain of a mammal belonging to a vigorous race, fitted for a long survival, is larger than the average brain, of that period, in the same group. (2.) The brain of a mammal of a declining race is smaller than the average of its contemporaries of the same group."[1]

As above noted the chief advantages of brain capacity are undoubtedly in relation to adaptability of habit, resourcefulness in times of exposure, alertness in avoiding new dangers to which the young may be exposed, enterprise in seeking new habitat, qualities which should be more fully considered under the law of adaptive variation and the evolution principle of organic selection.

Arrested Variation

Brocchi on the Dying Out of Species.— An Italian geologist, Brocchi,[2] the author in 1814 of an able work on the fossil shells of the sub-Apennine hills, endeavored to imagine some regular and constant law by which species might be made to disappear from the earth gradually and in succession. The death, he suggested of a species might depend, like that of individuals, on certain peculiarities of constitution conferred upon them at their birth; and as the longevity of the one depends on a certain force of vitality,

[1] Marsh, O. C. "Dinocerata, an Extinct Order of Gigantic Mammals." *Mon. U. S. Geol. Surv.*, vol. 10, Washington, 1884, p. 59.

[2] Brocchi. *Conch. foss. subap.*, vol. 1, 1814.

which, after a period, grows weaker and weaker, so the duration of the other may be governed by the quantity of prolific power bestowed upon the species which, after a season, may decline in energy, so that the fecundity and multiplication of individuals may be gradually lessened from century to century, "until that fatal term arrives when the embryo, incapable of extending and developing itself, abandons, almost at the instant of its formation, the slender principle of life by which it was scarcely animated, and so all dies with it."[1] Lyell opposed this doctrine on the ground that there is seldom evidence of physiological deterioration in the last representatives of a species.

This idea of *self extinction*, as applied to a theoretical arrest of variation was expressed in another form by Darwin and Wallace and has been recently revived.

The Limiting of Variation.—The theoretical importance assigned to the *limiting of variation* (independently of environment) as a cause of extinction depends partly upon one's theoretical opinions as to the modes of evolution. In the citations made above from Darwin (p. 852), Wallace (p. 852) and Andrews (p. 853) the theoretical view is taken that since (1) a limitation or cessation of fortuitous variation would cut off material for improvement through selection, (2) a fixed or non-adaptable type would arise and (3) extinction would follow.

Similarly Mr. C. B. Crampton (as cited by C. W. Andrews)[2] suggests an inherent cause of extinction as follows: " . . . . In a recent paper by Mr. C. B. Crampton (*Proc. Roy. Phys. Soc. Edinburgh*, vol. xiv, p. 461) a possible inherent cause of extinction is suggested. It is impossible to do justice to this interesting paper in a short note, but the gist of the argument seems to be as follows:—In the original unicellular organism the possibilities of variation are almost infinite, but as soon as evolution along any line begins, these possibilities are restricted, and become more and more so the more highly specialized the animal is; in short, the potential variation of an organism becomes less and less as specialization advances. Furthermore, under the influence of

[1] Lyell, Charles. *Principles of Geology*, vol. 2, 11th ed., 1892, p. 270.

[2] Andrews, C. W. "Some Suggestions on Extinction." *Geol. Mag.*, dec. 4, vol. 10, no. 463, p. 1, January, 1903.

natural selection, in each generation the individuals which tend to vary in the same direction will survive, while at the same time, as already pointed out, their capacity for variation becomes more and more restricted. The consequence of this will be that the more highly specialized any stock becomes, the more the individuals composing it will come to resemble one another, until at length the same results as arise from close inter-breeding, *viz.*, weakening of the stock, and, finally, extinction, may follow."

This is purely a question of evidence and all the evidence we can muster is negative. Invertebrate paleontologists cite cases of extinction being preceded by an efflorescence of new structures.

Among the Vertebrata no evidence has been adduced of extinction being preceded by an arrest of variation, *i. e.*, of evolution. On the contrary extinction often occurs at the high tide of change and not after a prolonged period of stability.

Conclusion

The chief induction which can be made from this extensive survey of the causes of extinction seems to be this: *following the diminution in number which may arise from a chief or original cause, various other causes conspire or are cumulative in effect.* From weakening its hold upon life at one point an animal is endangered at many other points.