1140 W. Orange Grove Ave., Arcadia, California, U.S.A.
Copyright 1962

DID THE CATERPILLAR EXTERMINATE THE GIANT REPTILE?

S. E. FLANDERS

University of California Citrus Research Center and Agricultural Experiment Station, Riverside, California

THE ABRUPT DISAPPEARANCE of the giant reptile during the Cretaceous period brought to an end a very successful plant-animal system. For 120 million years the reptile population had roamed over large areas of the earth, subsisting in the lush vegetation covering such areas. From the standpoint of the reptile's subsistence, plant life was unlimited. It was an apparently inexhaustible resource.

The possibility that the great reptiles disappeared as a result of malnutrition and starvation has been considered and discarded as quite untenable. That highly evolved plant-feeding animals do not normally become limited in numbers by starvation is axiomatic. Nicholson (1954) pointed out that the major influence which prevents phytophagous animals from reducing the earth's vegetation to extreme sparseness is their attack by natural enemies.

Exhaustibility of plant life, an inherent characteristic of many plant and animal relations, is rarely realized, being usually precluded through the regulation of the animal population by its natural enemies (Flanders 1959). Thus, the Cretaceous populations of the vegetarian reptiles, by serving as prey for populations of highly efficient predatory reptiles, were kept at levels well within the limits set by the amount of plant life. At the same time these predators served also to suppress the evolution of competitive types of animals of similar size such as the mammal.

The geological record of the Cretaceous period, however, reveals a series of events which may have culminated in the temporary destruction of vast amounts of plant life, a period in which the vegetarian reptiles may have been so devitalized that they either failed to reproduce or fell easy prey to their predatory relatives.

The critical events which could have led up to the disappearance of the giant reptile were: (1) the replacement of the ancient fernlike plants by phanerogamic plants; and (2) the emergence of the Lepidoptera, an insect order which with few exceptions feeds only on such plants (Imms, 1930).

The background against which these events should be visualized

is the world-wide dominance of insects both in species and in population densities, a dominance which existed throughout the Age of Reptiles and the Age of Mammals. The pre-Cretaceous insect fauna appears to have been quite similar in kind and in numbers to the post-Cretaceous insect fauna except for the lack of species which fed on flowering plants (Carpenter 1952). A number of such species were subsequently derived from the pre-Cretaceous insect orders of Coleoptera, Diptera, Hemiptera, Hymenoptera and Orthoptera, species whose immediate progenitors had presumably already acquired their natural enemies.

According to Imms (1931), it is practically certain that the Lepidoptera is pre-Tertiary in origin, highly organized individuals being represented in Eocene rocks. The paucity of insects in Cretaceous rocks is attributed to the absence in that period of suitable fresh-water deposits in which specimens could have accumulated and become fossilized.

Plant-feeding insects like other plant-feeding animals acquire natural enemies which serve to conserve the plant life upon which they subsist. The fact that the conservation of plant life is a function of the natural enemies of Lepidoptera has been demonstrated during the past sixty years by the importation and establishment in North America of the natural enemies of the caterpillar for otherwise the reduction in brown-tail moth, Nygmia phaeorrhoea (Donovan), the satin moth, Stilpnotia salicis (Linnaeus), and the larch caseberer, Coleophora laricella (Hubner) (Clausen 1956). During the past three years the writer, by using the grain moth Anagasta and its natural parasite, Exidechthis, has demonstrated in the laboratory the role of a natural enemy in the conservation of plant material. In a constant environment parasitization continuously conserved the plant material despite the presence of a persistent feeding population of Anagasta.

In nature, therefore, a community of plant-feeding animals consisting, say, of a pentatomid bug, a grasshopper, a moth caterpillar, a vole, a rabbit, and an ungulate depending on the same resource, grassland vegetation, can remain stabilized for a long period of years (Elton 1946). Such stabilization, however, consists in the total amount of plant life conserved, not in the relative abundance of the plant species involved, an abundance determined by the phytophagous animals through their effect on the competitive capacities of the plant species (Wilson 1949).

Devastations of plant life by caterpillars can occur today whenever the regulating action of their natural enemies is disrupted by environmental factors. Graham (1939) reported that during a ten-year period ending in 1920 an eruption of the spruce budworm, *Choristoneura fumiferana* (Clemens), was characterized by flights of moths so numerous that in the tree tops they had the apparance of a snow storm. During this eruption the caterpillars destroyed a volume of wood

sufficient to supply all of the pulp mills then operating for a period of forty years.

The capacity of a lepidopteran in the absence of its natural enemies to reduce great areas of lush vegetation to extreme sparseness and to maintain it so thereafter was demonstrated in Australia when the caterpillars of *Cactoblastis cactorum* (Berg) imported from Argentina in 1925 destroyed within six years approximately 50 million acres of the prickly pear, *Opuntia* spp. Dodd (1929) in reporting on this devastation stated that great care had been taken not to set free any of the natural enemies of the catrpillar for otherwise the reduction in prickly pear would have been of minor proportions.

It is evident that the plant-consuming capacity of a caterpillar population could equal that of a giant reptile population and that this capacity because of the caterpillar's very short life cycle could be attained at a much greater rate. Supplementing this capacity was a power of survival much greater than that of the giant reptile, the minimum food requirements of the individual caterpillar being infinitesimal relative to that of the individual reptile.

Nevertheless, there is no reason to believe that the caterpillar and the giant reptile could not have subsisted together on the same vegetation if the caterpillar, immediately upon its Cretaceous emergence, had been subject to a regulation by natural enemies as effective as was that of the vegetarian reptile by its predatory relatives.

The theory that the caterpillar exterminated the giant reptile rests on the assumption that between the emergence of the new insect order and its accessions of regulative natural enemies there occurred a brief period in which the caterpillar population regulated the world's supply of plant food, a condition conducive to great variations in abundance of plant life and of caterpillar life, a condition characterized by "feast and famine" in which the caterpillar was able to survive but not the great reptile.

The inherent weakness of the reptile was an extraordinary need for an abundance of plant material. Only a few years of plant scarcity could have exterminated it. Hordes of caterpillars, in rapid consumption of fig and breadfruit, laurel and willow, oak and magnolia, could have so restricted the spatial distribution of the giant reptile that either its diet was inadequate or it was unable to avoid its natural enemies.

The small size of today's descendent reptiles, the vegetarian turtle, the predatory crocodile, the snake, and the lizard, is evidence of the giant reptile's elimination by starvation and predation.

The abrupt end of the Age of Reptiles during the Cretaceous period is ascribed to a newly emerged order of insects, the Lepidoptera, on the supposition that for a brief period it regulated the world's supply of plant life at starvation levels for the dependent reptiles. Thus, the giant reptiles which had survived during eons characterized by great

changes in climate, continental uplifts, and different diets may have been exterminated by the lowly caterpillar.

LITERATURE CITED

CARPENTER, F. M. 1952. Fossil insects. 1952 U.S.D.A. Year Book. pp. 14-19.

CLAUSEN, C. P. 1956. Biological control of insect pests in the continental United States. U.S.D.A. Tech. Bull. No. 113, 151 pp.

DODD, ALAN P. 1929. The progress of biological centrol of prickly pear in Australia. Commonwealth Prickly-Pear Board, Brisbane Qld. 44 pp.

ELTON, CHARLES. 1946. Competition and the structure of ecological communities. *Jour. Animal Ecol.* 15: 54-68.

FLANDERS, S. E. 1959. Biological control. *Jour. Econ. Ent.* 52: 784-5. GRAHAM, S. A. 1939. Principles of forest entomology. McGraw-Hill, N.Y.

410 pp.

1S, A. D. 1930. A general textbook of entomology. E. P. Dutton & Co., Inc., N.Y. 703 pp. IMMS, A. D.

IMMS, A. D. 1931. Recent advances in entomology. P. Blakiston's Son &

Co., Inc., Philadelphia. 374 pp.
NICHOLSON, A. J. 1954. An outline of the dynamics of animal popula-

tions. Australian Jour. Zool. 2:9-65.
WILSON, F. 1949. The entomological control of weeds. Int. U. Biol. Sci.