

ECOLOGICAL SUCCESSION AMONG LATE PALAEOZOIC AND MESOZOIC TETRAPODS

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ABSTRACT

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Natural selection and the development of new taxa are associated with ecological replacement and the increase in number of niches with time. Continental faunal inter-change was possible globally because of the existence of the super-continent Pangaea during much of the Upper Palaeozoic and Mesozoic. Figures of tetrapod niches vs. time and discussion of this concept for that period are presented for the first time. Four habitat divisions are used, namely marine, fresh-water, lowland and upland.

The marine habitat was colonised rather late by tetrapods and these may have been the first predators on the early bony fishes which had diversified in the Permian. The radiation of bony fishes in the Jurassic was followed by a further increase in variety of their reptilian predators. Predators seem to develop some time after the radiation of a new potential prey group.

Most early amphibians occupied fresh-water habitats in "crocodile" or "frog" niches, but from the Triassic tetrapods moved from fresh-waters and lowlands into the uplands also.

In terrestrial habitats, the replacement of mammal-like reptiles by dinosaurs is tentatively explained in terms of palaeoclimatology and thermoregulatory physiology. Ornithischians capable of dealing with tough vegetation evolved to occupy the new niches produced by the radiation of conifers in the Jurassic. The extinction of dinosaurs appears to have been connected with temperature and habitat changes.

Conclusions are supported by a summary of published opinions on the palaeoecological roles of early tetrapods.

INTRODUCTION

Fossil vertebrates are studied with two approaches: (1) the reconstruction of body form, the elucidation of phylogenies, and the construction of classifications, and (2) the interpretation of functional morphology and lifestyles of particular animals and the understanding of former ecosystems.

In recent years, palaeontologists have taken an increasing interest in the palaeoecology of different vertebrate faunas. This has become feasible only

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with increasing knowledge of presumed habitats and diets of different animals. One of the most marked features of the fossil record is extinction (Mayr, 1970, pp.372–373) caused either by a change in the environment or by the incursion of more “advanced” animals from another region. In all cases, the animals which become extinct are replaced ecologically to a large extent. Newell (1963) suggested that “ecological replacement appears to be a characteristic feature of evolution”.

THE CONCEPT OF ECOLOGICAL REPLACEMENT

A terrestrial ecosystem consists of the climate, soils, bacteria, fungi, plants and animals at any particular place (Pianka, 1974, p.4). Ecosystems are characterised by a trophic structure with food webs linking plants, primary, secondary and tertiary consumers. Different populations within an ecosystem will evolve in response to different stimuli and occasionally one population will be ousted by a “better” competitor at the same trophic level — often an immigrant (competitive exclusion: Pianka, 1974, pp. 141–142). This is particularly well documented in the case of unstable island faunas (Macarthur and Wilson, 1967), and occurs on continents, but to a lesser extent (e.g., birds introduced by man: Mayr, 1964).

For simplicity in the following discussion, “niche” is used in the community role sense of Elton (1927): “the niche of an animal means its place in the biotic environment, *its relations to food and enemies*” (Elton’s italics) and “the niche of an animal can be defined to a large extent by its size and food habits”. In many cases “niche” is used in a very broad sense equivalent to the term “adaptive zone”. I do not imply the n -dimensional niche model of Hutchinson (1957), which is based on the total range of conditions under which the individual (or population) lives and replaces itself (Pianka, 1974, pp. 185–187).

The niche of an animal may change during ontogeny (especially if there is an aquatic larval stage) and an animal’s predators may also change in such a way that, say, juveniles are subject to predation but adults are not because of their size.

Extrapolating from cases of animals arriving on islands by chance and artificial introductions, it seems probable that naturally occurring immigrations will also cause the extinction of parts of endemic continental faunas, especially if there is a change in conditions favouring the incomers. Immigrations, or range extensions, may be initiated by an increasing population or reduced food supply, by the opening up of new land connections or by an extension of favourable habitat.

Immigrants need not always cause the extinction of endemic forms. The immigrant itself may not be able to compete successfully in the new habitat and may become extinct, or the niche of immigrant and endemic species may change in some way so as to reduce competition.

Complete ecological replacement occurs when one animal comes to occupy

a niche formerly occupied by another animal. This involves local extinction of the latter. Thus, we may say, to a close approximation, that crocodiles "replaced" phytosaurs ecologically at the beginning of the Jurassic or that ornithischians replaced prosauropods as large herbivores at the end of the Triassic. Replacements will clearly occur at different times in different places and one family may take several million years to oust totally another family. The radiation of forms and development of new taxa depend largely on ecological replacement (Reig, 1970). However, the processes of extinction and ecological replacement interact and it would be difficult to decide which comes first.

Present knowledge of the temporal distribution and ecology of fossil vertebrates is scanty, but it would seem possible to speculate on possible major ecological replacements in the past. This kind of data would be best summarised in the form of a niche vs. time chart which has been done for certain North American mammals (e.g., Shotwell, 1964).

THE POSSIBILITY OF A NICHE VS. TIME CHART FOR EARLY TETRAPODS

Several authors (e.g., Osborn, 1917; Colbert, 1958; Olson, 1966, 1971a, 1976; Sill, 1974) have given information on ecological replacements among amphibians and reptiles in the Late Palaeozoic and Mesozoic. However, I have been unable to find a generalised summary of ecological replacement among early tetrapods and this is attempted here (Figs.1—3). The figures are discussed below (p. 133).

There are many problems associated with an approach of this kind, some of which are: (1) no reference to local faunas; (2) definition of habitats; (3) interpretation of life styles of extinct animals; (4) taxa used; (5) no reference to relative abundance of different forms; (6) incompleteness of the fossil record; and (7) changing conditions over time. These are discussed below.

Local faunas and Pangaea

Charts of the kind presented in Figs.1—3 would be meaningless for the present-day because every continent has its own peculiar fauna. The only justification for attempting them for the Upper Palaeozoic and Mesozoic is that most of the present continents were in contact as the supercontinent Pangaea from the Late Permian to Early Cretaceous (Smith and Briden, 1977). It should be noted, however, that this does not apply to the Carboniferous and Early Permian when Gondwanaland was still separate from the northern continents.

However, although present continents were in contact, parts of these were underwater in the Mesozoic. Cox (1974) gives maps showing the approximate

positions of ancient oceans, such as Tethys, which divided Laurasia from Gondwanaland in the Cretaceous, and the Turgai Sea, which isolated eastern Asia in the Jurassic and Cretaceous. These oceans would offer barriers to free faunal interchange. The converse may also apply: areas of Mesozoic continents may have been lost underwater, whether by isostatic sinking or by subduction. Many fossil sites which could potentially give information on distribution are presumably lost.

Nevertheless, faunal interchange between nearly all parts of the world seems to have been possible during much of this period and faunal provinces cannot be defined (Charig, 1971). Similar, or identical, genera of many reptiles and amphibians are found on several present-day continents (Nopcsa, 1934; Hallam, 1967; Charig, 1971, 1973; Romer, 1972, 1973; Colbert, 1973, 1974, 1975; Cox, 1973a, b, 1974; Kalandadze, 1974). Some of the better-known examples may be summarised (data largely from Cox 1973a and Charig 1973, and abbreviations as used by Romer, 1966, p.347):

- U. Carb., pelycosaur *Archaeothyris* (NA., Eu., Reisz, 1975).
- L. Perm., fresh-water reptile *Mesosaurus* (SAf., SA.); pelycosaur *Edaphosaurus* (NA., Eu.).
- U. Perm./L. Trias., dicynodont *Lystrosaurus* (SAf., EAs., SAs., Ant., EEu. Kalandadze, 1975).
- L. Trias., cynodonts *Cynognathus* (SAf., SA.) and *Sinognathus* (EAs.); dicynodont *Kannemeyeria* (SAf., SA.); proterosuchians *Chasmatosaurus* (SAf., EAs.) and *Chasmatosuchus* (NAs.).
- U. Trias., labyrinthodonts *Metoposaurus* (NA., Eu., SAs.), *Archotosaurus* ("Parotosaurus") (NA., Eu., As., Af., SAs., Aus.); flying lizards *Kuehneosaurus* (Eu.) and *Icarosaurus* (NA., Robinson, 1967); thecodontians *Ornithosuchus* (Eu.) and *Riojasuchus* (SA.); phytosaurs. *Parasuchus* ("Paleorhinus") (NA., Eu., SAs.) and *Nicrosaurus* (NA., Eu.) (Gregory, 1969; Chatterjee, 1978); coelurosaurs *Coelophysis* (NA.), *Triassolestes* (SA.) and *Syntarsus* (SAf.); prosauropods *Archisaurus* (NA., SAf.) and *Thecodontosaurus* (Eu., SAf., Aus.) (Galton and Cluver, 1976); sauropod *Diplodocus* (NA., Eu., Anonymous, 1977); therapsid *Tritylodon* (SAf., Eu., NA., SA.).
- M. Jur., sauropod *Bothrospondylus* (Eu., Mad.).
- U. Jur., sauropods *Brachiosaurus* and *Barosaurus* (NA., EAF.) (see Addendum).
- L. Cret., ornithopods *Hypsilophodon* and *Iguanodon* (WEu., NA., NAF., Galton and Jensen, 1975).
- U. Cret., coelurosaur *Ornithomimus* (NA., As.); theropods *Tyrannosaurus* (NA.) and *Tarbosaurus* (SAs.); sauropods *Titanosaurus* (SAs., SA., WEu.); *Laplatosaurus* (SAs., SA., Mad.); *Antarctosaurus* (SAs., SA.); hadrosaurs *Thespesius* (NA., As.) and *Saurolophus* (NA., EAs.).

Cox (1973a, b, 1974) calculated coefficients of resemblance between Triassic faunas of today's continents. All values were over 40%. Charig (1973) obtained similarly high values for Cretaceous dinosaur faunas. Thus, the evidence from later Palaeozoic and Mesozoic tetrapods indicates comparatively easy faunal interchange worldwide for most of this period and future discoveries can only tend to reinforce this evidence. Although local faunas must have existed, it seems feasible to consider world faunas rather than the strictly local faunas which we know today. Early members of new groups of animals, however, probably evolved locally and detailed stratigraphic studies may reveal patterns of range expansion as they replaced old faunas.

Definition of habitats

The choice of habitat and niche divisions in the figures was somewhat arbitrary. One obvious choice was "marine". However, it tended to be difficult to ascribe particular habitats to terrestrial tetrapods. Some highly aquatic fresh-water tetrapods of the Triassic (e.g., stereospondyls and phytosaurs) and early amphibians (e.g., Ichthyostegalia, Embolomeri, Trimerorhachoidea) could readily be separated as "fresh-water". Also, large herbivores, like dicynodonts and sauropods were probably "lowland". The Upper Triassic fissure faunas of primitive lizards, rhynchosaurs, small dinosaurs and mammals are commonly termed "upland" (Tarlo, 1962; Robinson, 1967). During the Jurassic and Cretaceous, most dinosaurs could have been lowland and upland in distribution, and they are included under both divisions in the figures.

The separation of purely terrestrial Mesozoic animals into lowland and upland forms seems to be generally accepted (Colbert, 1966; Robinson, 1967; Halstead, 1975; Olson, 1976). Present-day biome divisions such as tropical, temperate, polar and desert, are not normally used and would probably have been less well defined at that time.

Definition of niches

The niche divisions used are rather general for two reasons: (1) it is difficult to be absolutely certain of the diet and ecological relationships of an extinct animal, and (2) ecological replacements in the past are most easily observed at family rather than genus level, and one can seldom define the ecological role of a family more precisely than as, say, "large terrestrial predators" or "small fresh-water piscivores".

Direct evidence of diet is rather rare. Examples are cephalopod hooks and remains of fish in stomach contents and coprolites of ichthyosaurs (e.g., Pollard, 1968) and conifer needles, twigs and seeds in hadrosaurs (Kräusel, 1922). Energy-flow diagrams of well-known local faunas, such as that reproduced in Olson (1971a, p.638) (Arroyo Formation, Lower Permian of the southeastern United States), are useful in assessing the ecological positions of different animals.

It is difficult to decide upon the nature of the diet of many primitive lizard-like reptiles and early mammals because of their generalised dentitions. Thus, half a dozen contemporaneous "small omnivores" may have had diets as widely separate as those of a tyrannosaur and a brontosaur.

Taxa used

In most cases, for the sake of clarity, animals are treated in families or suborders (mainly after Romer, 1966). This is usually justifiable since all genera in a family tend to be morphologically rather similar and they prob-

ably occupied similar adaptive zones in different areas or at different times. However, some exceptions are bound to exist.

Abundance of individuals

Charts of the stratigraphic distribution of different taxa often represent relative abundance at different times with reference to the number of genera. It is clear that this does not give a measure of the actual number of individuals, which is much more important, but impossible to calculate accurately. Thus, I have not attempted to represent abundance in Figs. 1–3.

Incompleteness of the fossil record

There are many gaps among known faunas, reflecting non-fossilisation, loss to erosion or deep burial, loss to marine transgression or subduction, and reflecting the distribution of vertebrate palaeontologists (Panchen, 1970, p. 68). Especially rare and poorly known are later Triassic upland faunas of small reptiles and mammals.

Changing conditions over time

Changing climates in the Late Palaeozoic and Mesozoic played an important part in extinction and ecological replacement. The Permian appears to have had an equable climate with some swampy and arid conditions (Robinson, 1971). Arid areas progressively extended in the Triassic and there is evidence of seasonal monsoon conditions with possible droughts in some areas (Robinson, 1971, 1973). These factors seem to be connected with the gradual decline of mammal-like reptiles and their ecological replacement by archosaurs (see below, p. 136). Jurassic and Cretaceous climates seem to have been warm and wet (Barnard, 1973).

Biological changes involving, for example, changes in food sources also seem to have been important in initiating or sustaining radiations of new taxa. This leads us to consider whether the number of available niches has increased over time.

NUMBER OF NICHES OVER TIME

Two major biological radiations in the Mesozoic doubtless led to the emergence of new specialisations among reptiles. The radiation of bony fishes in Jurassic and Cretaceous seas is matched by an increase in the variety of fish-eaters. The development of new groups of tough plants in the Jurassic (see p. 136) is paralleled by a proliferation of large herbivorous dinosaur types, many of them apparently having adaptations for dealing with tough vegetation. Do these two examples represent a genuine increase in biomass of animals in existence (i.e., an increase in energy assimilated) or merely an

increase in the number of niches (with concomitant reduction in biomass of animals occupying each niche)? The question of the number of niches over time has been studied by several workers in relation to Palaeozoic benthic invertebrates in particular (reviewed by Hallam, 1977).

Various lines of geochemical and biological evidence indicate that there has been a real temporal increase in total global biomass, particularly when the land was colonised in Precambrian and/or Early Palaeozoic time (Benton, in prep.). The mechanism invoked to explain this depends on the fact that present-day green plants absorb only a very small amount of energy from the sun reaching the surface of the earth (about 1%: Pianka, 1974, pp.223—224). This percentage may have been lower in the past because of less extensive plant cover. However, biomass increase does not imply an increase in the number of niches.

Von Wahlert (1968, 1977, personal communication, 1977) suggests that the number of niches occupied or available has increased over time. Tetrapods may be considered to have developed in three stages or “layers”, namely: (1) amphibians (near water), (2) reptiles (away from water in warm conditions), and (3) mammals (colder conditions and nocturnal habits). Each layer represents the radiation of a group of animals into a new habitat or set of niches. None of these layers was present in the Lower Devonian, yet all three are present today. Von Wahlert calls this layering process *anagenesis*.

GENERAL TRENDS VISIBLE IN THE FIGURES

Figs.1—3 summarise the niches and temporal distributions of most Upper Palaeozoic and Mesozoic tetrapods. Ecological roles of most groups are given in more detail in the Appendix. The major habitat divisions used are marine, fresh-water, lowland and upland and some comments on each figure are given below.

Marine

It is interesting to note that tetrapods apparently did not perform any major role in the sea until the Triassic. It seems that aquatic adaptations to marine life were a secondary development in amphibians and reptiles. The predatory roles of fish-eaters at the surface, fish and cephalopod-eaters at or below the surface, and benthic mollusc-eaters were apparently all filled in the Lower Triassic, for the first time, by nothosaurs, ichthyosaurs and placodonts, respectively (Fig.1). These groups all appeared with rather advanced aquatic adaptations and their origins are obscure (Romer, 1966).

These marine reptiles may be occupying new niches. During the Devonian, large placoderms like *Dunkleosteus* were probably effective predators on smaller fish, and eurypterids seem to have been adapted to crushing the heavily armoured fish of the Middle Palaeozoic. With the extinction of agnathans and placoderms in the Carboniferous, eurypterids became extinct.

Bony fishes (palaeoniscids) replaced these primitive fish in the Permo-Carboniferous. Animals which preyed on these faster pelagic fish may not have developed until later in the Permian and they advanced particularly in the Triassic. When a group is replaced ecologically, its predators may not be able to adapt successfully to the new food source and they also may become extinct. It would take some time for animals to evolve as predators on the new group and this may explain the apparent lack of Permian marine piscivores.

The radiation of bony fishes in the Jurassic and Cretaceous has been mentioned already. Together with the radiation of ammonites and belemnites, this appears to have led to a radiation among marine reptiles: mosasaurs, geosaurs, larger pterosaurs, elasmosaurs, pliosaurs and marine birds all became fully developed late in the Mesozoic to exploit the new food sources. The larger pliosaurs may have preyed on smaller marine reptiles, thus introducing a new "top carnivore" niche in the sea.

Van Valen and Sloan (1977) suggest that the extinction of nearly all marine reptiles (except turtles) and ammonites together with replacement among Foraminifera (Percival and Fischer, 1977) at the end of the Cretaceous may have been related to a lowering in world temperatures (Lowenstam, 1964; Krassilov, 1975) together with normal, but rapid, ecological replacement.

Fresh-water

One of the main trends in Late Palaeozoic and Mesozoic tetrapod faunas was a gradual shift from lowland and fresh-water habitats to the uplands in the Triassic. Olson (1976, fig.3) illustrates this trend with reference to some Permo-Carboniferous reptiles. During the Carboniferous, several amphibian groups fulfilled a "crocodile role" as medium/large fresh-water and near-water predators and in Permo-Triassic times, several reptile groups also appear to have occupied this niche (Fig.1). After the Middle Jurassic, true crocodiles replaced all these groups, but predatory dinosaurs almost certainly chased their prey into the water also.

Fig.1. Chart of niche vs. time for the marine and fresh-water habitats of the Upper Palaeozoic and Mesozoic. Time distributions are extracted from *The Fossil Record* (Editor W. B. Harland et al., Geol. Soc. London, 1967) with some alterations from Sill (1974), Carroll (1977), Olsen and Galton (1977), McGowan (1978), etc. The classification is based largely on Romer (1966) and fuller details of niches of specific taxa will be found in the Appendix. The size categories are based on approximate lengths of animals as follows: less than 25 cm: small; 25–200 cm: medium; 2–5 m: large; over 5 m: very large. The patterns on the vertical columns represent the larger group to which the family or sub-order belongs: diagonal stripes = Amphibia; dots = Archosauria; vertical lines = Synapsida; irregular pattern = other reptiles (Anapsida, Lepidosauria, Euryapsida, Ichthyopterygia). Some smaller groups have been omitted as follows — column 4: Askeptosauria (L./M. Trias. boundary), *Tanystropheus* (M./U. Trias.), *Macrocnemia* (M./U. Trias.); column 6: *Schizomeri* (L. Carb.), *Proganosauria* (*Mesosaurus*) (L. Perm.).

During the Carboniferous and Permian there were many apparently fully aquatic, small/medium, bottom-living (?) amphibian predators which presumably fed upon invertebrates and small fish. This niche was not so clearly defined after the Triassic, being filled apparently by some chelonians, predatory fish (e.g., pike) and mammals (e.g., otter).

Many frogs and newts feed on aquatic and aerial insects. Some small Permian amphibians (Lepospondyli) may have led a similar existence, but Mesozoic tetrapods of this kind are not well known.

Lowland and upland

Another major ecological trend during the Early Mesozoic was the replacement of mammal-like reptiles by archosaurs (Figs.2,3). The earliest archosaurs were predators and they replaced carnivorous therapsids in the Lower and Middle Triassic. Early dinosaurs replaced most herbivorous therapsids in the Middle and Upper Triassic. Upper Permian and Triassic therapsids may have been primitively endothermic (Hopson, 1973) while archosaurs, and dinosaurs in particular, appear to have been ectotherms (inertial homeotherms) rather than endotherms (McNab and Auffenberg, 1976). In arid conditions (which seem to have become extensive in the Triassic (Robinson, 1971)) an ectotherm has the advantage since it can conserve water, needs to eat less than an endotherm and has a wide range of temperature tolerance. The success of dinosaurs may have been largely due to an advanced physiology, and that "advanced" state may have been ectothermy, rather than endothermy (Benton, in prep.). Similar views, expressed in slightly different terms, have been presented by Nopcsa (1934) and Robinson (1971).

Early herbivorous mammal-like reptiles seem to have fed on aquatic and near-water vegetation (Olson, 1976) and many later ones grew bulky and may have had extensive digestive systems to deal with large quantities of vegetable matter of low nutritive value. Some herbivorous dinosaurs (Ornithischia) may have been able to exploit upland vegetation, and others (sauropods) had clearly found a new herbivore niche, whether they fed on swamp vegetation or high in trees (see Appendix).

The development of many new families of Coniferopsida, as well as Filicales and Bennettitales, in the Jurassic seems to have produced a radiation among ornithischians which could deal with this tough vegetation (hadrosaurs, ceratopsians). Galton (1973) suggests that the success of later ornithischians over prosauropods was largely due to the development of cheeks which prevented the loss of food while chewing.

The rise of angiosperms in the Middle to Upper Cretaceous does not seem to have led to any major radiation among reptiles. It has been suggested

Fig.2. Chart of niche vs. time for the lowland habitat of the Upper Palaeozoic and Mesozoic. See caption to Fig.1 for further details. One smaller group has been omitted — column 4: *Archaeopteryx* (U. Jur.).

CENOZOIC/ RECENT	tortoises rodents lago- morphs	cattle antelope horses	elephants rhinos hippos dino- theres	lizards birds	weasels owls	small cats dogs	lions wolves
UPPER CRETACEOUS			  				
LOWER CRETACEOUS							
UPPER JURASSIC							
MIDDLE JURASSIC							
LOWER JURASSIC							
UPPER TRIASSIC							
MIDDLE TRIASSIC							
LOWER TRIASSIC							
UPPER PERMIAN							
LOWER PERMIAN							
UPPER CARBONIFEROUS							
LOWER CARBONIFEROUS							
UPPER DEVONIAN							
"NICHE"	SMALL HERBIVORE	MEDIUM HERBIVORE	LARGE HERBIVORE	INSECTI- VORE/ OMNIVORE	SMALL PREDATOR	MEDIUM PREDATOR	LARGE PREDATOR
SIZE	S	M/L	L/VL	S	S	M	L/VL
DIET	VEGET- ATION	VEGET- ATION	VEGET- ATION	INSECTS, SMALL ANIMALS, SEEDS ETC	SMALL ANIMALS	SMALL/ MEDIUM ANIMALS	MEDIUM/ LARGE ANIMALS

LOWLAND

Swain, 1976) that the presence of hydrolysable tannins in angiosperms may have reduced the amount of palatable vegetation available to herbivores, and toxic alkaloids in flowering plants may have interfered with their physiology.

Van Valen and Sloan (1977), in a detailed study of local dinosaur extinction, show that it was not a dramatic event accompanied by the sudden death of everything that moved. They suggest that climates became cooler at the end of the Cretaceous and temperate forests developed. The cumulative effects of changing vegetation and climates appear to have led to relatively gradual rather than sudden extinction among dinosaurs. Mammal communities replaced dinosaur communities step by step over a period of 10^5 years in the area studied. It should be noted that very many theories have been presented to explain the extinction of various groups of animals at the end of the Mesozoic (Halstead, 1969), and probably several factors acted together in these events.

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APPENDIX: THE ECOLOGICAL ROLES OF EARLY TETRAPODS

This section contains a brief review of recent opinions on the niches occupied by Upper Palaeozoic and Mesozoic tetrapods. Opposing views are presented as far as possible. Unfortunately, many descriptive monographs do not give ecological information and, hitherto, very few detailed analyses of the possible life and habits of particular groups of animals have been published (but, see "Sauropoda" below). There are some gaps among therapsids in particular. The classification is based on Romer (1966).

AMPHIBIA

Labyrinthodontia

Ichthyostegalia

Lateral-line systems indicate a primarily aquatic existence. The streamlined body and flattened tail suggest good swimming ability. They probably fed on small fish (Stahl, 1974, p.211).

Temnospondyli

Rhachitomi

Loxommatoidea. "The presence of lateral lines, the long tooth row of sharp lanceolate marginate teeth . . . indicate that [loxommatids] were aquatic piscivorous predators." (Beaumont, 1977, p.92).

Fig. 3. Chart of niche vs. time for the upland habitat of the Upper Palaeozoic and Mesozoic. See caption to Fig.1 for further details. Some smaller groups have been omitted as follows — column 4: Eolacertilia (U. Trias.), Trachelosauria (U. Trias.), Scleromochlidae (U. Trias.), Trilophosauria (U. Trias. — L. Cret.); column 6: Erpetosuchidae (U. Trias.).

Edopoidea: "Primarily a water-dwelling form" (colosteid: Romer, 1969).

Trimerorhachoidea: *Trimerorhachus* was an aquatic animal "inhabiting shallow streams and ponds, and feeding upon small animals" (Colbert, 1969, p.98).

Eryopoidea: *Eryops* was a carnivorous amphibian which may have fed on fish and terrestrial animals. *Archegosaurus* was primarily aquatic and piscivorous (Colbert, 1969, p.97–98). The *Zatrachyidae* were terrestrial and had a "diet of small, fairly inactive animals" (Paton, 1975).

Trematosauroida: These are found mainly in marine beds and were probably specialised fish-eaters (Romer, 1966, p.92; Colbert, 1969, p.99; Carroll, 1977, p.412).

Stereospondyli

Capitosaurus preyed on "clumsy, heavily scaled fishes" (Colbert, 1966, p.78).

Paracyclotosaurus could walk on land and swim slowly. Its feeble dentition and large size suggest that it lay in wait for small fishes, opened its enormous mouth and engulfed its prey (Watson, 1958, pp.253–254). Brachyopids were benthonic and aquatic, possibly preying on lungfish, smaller temnospondyls and crustaceans (Cosgriff, 1974, p.104). Rhinesuchoids were medium to large semi-aquatic forms (Carroll, 1977, p.411).

Plagiosauria

Peltobatrachus was "a ponderous terrestrial amphibian" (Panchen, 1959, pp.245–246). Plagiosaurs in general "may be compared to angler fish" in the mode of jaw opening (Panchen, 1959, p.264).

Anthracosauria

Embolomeri

"The eogyrinids and anthracosaurid anthracosaurs may be pictured as large lake-dwelling carnivores" (Panchen, 1970, pp.66–67) with a piscivorous dentition. *Archeria* may even have been a filter-feeder.

Seymouriamorpha

Seymouria probably had habits like present-day salamanders, feeding on small invertebrates (cockroaches, land molluscs, worms, etc.) (Williston, 1911). *Kotlassia* had no lateral lines and had strong limbs and girdles and the adults were probably terrestrial (Bystrow, 1944, pp.412–413). Adult seymouriids were fully terrestrial and kotlasiids were aquatic (Carroll, 1977, p.415).

"Lepospondyli"

Lepospondyls "resembled modern urodeles in their size, range and adaptations" (Baird, 1965). Aistopods were snake-like and nectrideans were good swimmers (Carroll, 1977, p.417). *Diplocaulus* may have lived on the bottom of lakes and streams and fed on invertebrates (Rayner, 1971, p.467).

REPTILIA

Anapsida

Cotylosauria

Captorhinomorpha

Primitive captorhinomorphs "probably lived on small invertebrates, mainly insects or worms" (Kuhn, 1969a, p.14). The feeding patterns and general ecology of Romeriids were probably broadly similar to those of iguanid lizards (Carroll and Baird, 1972, p.350). *Limnoscelis* may have been an aquatic fish-eater.

Diadectidae: Heavily built terrestrial herbivores (Stahl, 1974, p.273).

Procolophonia

Procolophonoidea: Lizard-like insect-eaters at first, developing towards a specialised (?herbivorous) diet later (Colbert, 1946, p.265). Lower Triassic *Sclerosaurus* was a digging omnivore (Kuhn, 1969a, p.14).

Pareiasauroida: Large herbivores feeding on “bulky plant food” (Colbert, 1969, p.119) in lowland regions (Kuhn, 1969a, p.14).

Millerosauroida: “Small insect-eating reptiles” (Halstead, 1975, p.30). *Bolosaurus* was the first herbivorous reptile (Kuhn, 1969b, p.6).

Proganosauria

Mesosaurus was a fresh-water reptile possibly feeding on “tiny crustaceans” (Romer, 1966, p.116).

Lepidosauria

Eosuchia

Petrolacosaurus was purely terrestrial, possibly feeding on large insects (Peabody, 1952). *Champsosaurus* was “an aggressive predator endowed with remarkable aquatic capabilities of movement and capture of prey”. Possibly capable of diving for long periods and feeding from the bottom. Freshwater and estuarine (Erickson, 1972, p.72).

Squamata

Macrocnemia

Macrocnemus was a “scavenger and hunter of young nothosaurs” (Halstead, 1975, p.44).

Tanysitrachelia

Adult *Tanystropheus* darted their necks at fish and cephalopods (Wild, 1975). The young ate either insects (Wild, 1975) or seaweed (Cox, 1975).

Askeptosauria

Askeptosaurus was “highly specialised for a marine existence, with a long deep muscular tail and marked limb disparity” (Tarlo, 1967). Possibly fish-eaters (Romer, 1966, p.128).

Eolacertilia

Small insect-eaters (Halstead, 1975, p.29).

Sauria

Mososauridae: Mososaurs ate fish and molluscs (Romer, 1966, p.133). A large ammonite bearing tooth-marks of a young mosasaur has been described (Kauffman and Kesling, 1960).

Rhynchocephalia

“The jaws may have been used for cracking open the seeds of seed-ferns, cycads and ginkgos . . . or they may have dug in the ground for roots, but more probably they ate molluscs such as fresh-water mussels” (Halstead, 1975, p.41; Chatterjee, 1969).

Archosauria

Thecodontia

Proterosuchia

Proterosuchidae: “The proterosuchids were mostly aquatic, predaceous reptiles

living in ponds, lakes and rivers, using swimming as their main form of locomotion and preying upon other vertebrates" (Reig, 1970, p.259) such as fish and on reptiles which came down to drink (Halstead, 1975, p.26).

Erythrosuchidae: *Erythrosuchus* was "probably a slow-moving, marsh-dwelling carnivore" (Charig and Sues, 1976, p.28).

Pseudosuchia

Euparkeriidae: *Euparkeria* was an "active carnivorous animal" (Ewer, 1965, p.416) which fed upon small vertebrates and invertebrates living in upland regions.

Ornithosuchidae: *Ornithosuchus* was a "formidable carnivorous animal" with "sabre-like serrated teeth" and grasping forelimbs (Walker, 1964, p.104). The adults could prey on all large herbivores and the young on the smaller lizard-like rhychocephalians and cotylosaurs.

Rauisuchidae: These were "among the largest of the terrestrial carnivores" in the Middle and Lower Triassic (Sill, 1974, p.317).

Stagonolepididae: "The evidence suggests that the aetosaurids were herbivorous and that the snout was used for grubbing in soft vegetation or for roots, or possibly for digging out invertebrates" (Walker, 1961, p.195). "Scavengers" (Sawin, 1947).

Phytosauria

"Their lifestyle is not basically different from that of crocodiles" (Westphal, 1976, p.118). Coprolites and stomach contents show that they ate fish and small reptiles. They had strong jaws and interdigitating teeth and could lie partially submerged in water or run on land in order to catch prey (Chatterjee, 1978).

Crocodylia

Protosuchia

Protosuchus was "well adapted for running around on the land" and there is no evidence for a fully aquatic existence (Colbert, 1969, p.238). Carnivorous.

Mesosuchia

Metriorhynchidae: Geosaurs have distinctive marine adaptations (Romer, 1966, p.143). Carnivorous.

Pterosauria

The earlier pterosaurs "seem to have been small insect-eaters" (Halstead, 1975, p.48). Most remains "have been found in saltwater deposits" and some appear to have been fish-eaters (Romer, 1966, p.144). The giant *Quetzalcoatlus* may have scavenged dinosaur carcasses like a vulture (Lawson, 1975).

Saurischia

Theropoda

Coelurosauria: "The coelurosaurs seem initially to have led a predatory existence" (Steel, 1970, p.7), feeding on small reptiles and perhaps the early small mammals (Romer, 1966, p.151). *Compsognathus corallestris*, with a paddle-like forelimb, may have lived on coral reefs, capturing prey by diving (Bidar et al., 1972). Ornithomimids appear to have "relinquished the carnivorous mode of life" (Steel, 1970, p.7) and may have made a living by robbing eggs from the nests of other dinosaurs (Romer, 1966, p.151). They may have eaten insects and other small animals (Russell, 1972, p.401).

Carnosauria: "There seems little reason to doubt that if the opportunity arose they would eat carrion; to a large extent, however, they must have been active hunters" (Steel, 1970, p.23). Herbivorous dinosaurs "presumably formed their food supply"

(Romer, 1966, p.153).

Sauropodomorpha

Prosauropoda: Anchisauridae (Thecodontosauridae): These ate flesh and included the first herbivorous dinosaurs (Halstead, 1975, p.35).

Plateosauridae: "Their ecological role was not primarily that of a carnivore although meat may have formed part of their diet" (Steel, 1970, p.53). *Plateosaurus* can be regarded "as the big herbivore of late Triassic times in Europe" (Colbert, 1966, pp.95—96).

Melanorosauridae: Large quadrupedal herbivores of the lowlands.

Sauropoda

Some recent speculations on sauropod ecology are of interest here. Steel (1970, pp.60—61) expresses the classical view: "typically semi-aquatic . . . the general consensus of opinion [is] that they were herbivorous, although molluscivorous or even carnivorous habits have been suggested . . . they must have been ponderous, slow-moving defenceless creatures on land". Bakker (1971) challenged this view, pointing out that the supposed aquatic adaptations are not very convincing and that thorax and limb structure are elephant-like and terrestrial. The long neck may have been used for grazing high in trees.

Coombs (1975) reviewed the evidence and concluded that the evidence is equivocal, but that sauropods were probably terrestrial. Hohnke (1973) speculated on blood pressures in sauropods and Seymour (1976) discussed some physiological aspects in relation to blood circulation. He showed that the high arterial blood pressures in dinosaurs were consistent with endothermy and that an aquatic sauropod could avoid "tremendous hydrostatic stresses on the cardiovascular system". If a sauropod held its neck vertically, its heart would have had to generate a tremendous pressure in order to keep the blood flowing.

Large dinosaurs were almost certainly ectothermic and homoiothermic (which could produce the impression of endothermy: Benton, in prep.). It is easy to picture a brontosaurus as some kind of enormous giraffe [e.g. Bakker's (1968) restoration of *Barosaurus*], but the physiological stresses involved may suggest different, possibly partially aquatic, habits. Tweedie (1977, pp.64, 68) suggests that terrestrial activities of brontosaurus used considerable energy and raised their internal temperatures. This additional heat may have been dissipated by resting in water, the long neck outstretched and floating.

Ornithischia

Ornithopoda

Heterodontosauridae, Fabrosauridae: Small bipedal upland herbivores with primitive dentitions (Steel, 1969, p.7; Halstead, 1975, p.38).

Hypsilophodontidae: Cursorial, non-arboreal herbivores (Galton, 1971b).

Iguanodontidae: "Primarily inhabitants of low-lying swampy or well-watered regions, where they probably ranged in herds, browsing on the succulent vegetation" (Steel, 1969, p.15).

Hadrosauridae: Active terrestrial foragers, browsing on conifers, deciduous trees and shrubs in warm subtropical lowlands (Ostrom, 1964a). However, partly aquatic [duck-like bill, webbed hand, laterally compressed tail (Morris, 1970, 1971)].

Pachycephalosauridae: Upland herbivores with feeble dentition. The thick-boned domed skull was possibly used as a battering ram in intraspecific competition as in present-day sheep and goats (Galton, 1971a).

Stegosauria

Upland herbivores with relatively feeble teeth which were suited only for a diet of

succulent plants (Swinton, 1970, pp.240—241).

Ankylosauria

"The teeth were singularly small and weak, indicating that the ankylosaurs must have fed upon soft plants" (Colbert, 1969, p.214). "Essentially upland forms" (Steel, 1969, p.52).

Ceratopsia

Large upland herbivores adapted to a diet of tough vegetation (fibrous cycads or palms) with shearing dentition (Ostrom, 1964b, p.33).

Subclass indet.

Araeoscelidia

The habits of *Araeoscelis* were probably not unlike those of "the more agile little lizards of the modern tropics" (Romer, 1966, p.121).

Protorosauria

Protorosaurs fed on insects and small tetrapods (Colbert, 1974, p.141).

Trilophosauria

Trilophosaurus was probably "a plant-eater, and the blade-like teeth were used for chopping vegetation" (Colbert, 1969, p.165). Others may have been small insect-eaters (Halstead, 1975, p.42).

Euryapsida

Sauropterygia

Nothosauria

Nothosaurs had jaws and teeth adapted as "fish traps" and they darted their head and neck at fish that came within range (Colbert, 1969, p.175). The "long narrow sharp teeth . . . served both to hold slippery fish and also to prevent their escape once in the mouth. Nothosaurs seem to have been land-based, even though their main food was fish . . . It may well be that the young individuals were littoral scavengers" (Tarlo, 1967).

Plesiosauria

Plesiosauroidea: Like nothosaurs, plesiosaurs darted their heads at fish (Colbert, 1969, pp.177—178).

Pliosauroida: Pliosauroids had a diet of cephalopods and fish, as well as ichthyosaurs and other plesiosaurs (Colbert, 1966, p.158; Cox, 1969, p.95).

Placodontia

Placodonts lived in the littoral seas of Tethys and may have been able to crawl on land like seals. They scraped shellfish off rocks with their front teeth and smashed them with their crushing teeth (Kuhn, 1969b, p.8).

Ichthyopterygia

Ichthyosaurs seem to have been ecological equivalents of present-day dolphins and porpoises (Romer, 1966, p.117). Stomach contents reveal belemnite hooks while fish remains are predominant in coprolites (Pollard, 1968). "Although the later ichthyosaurs were mainly cephalopod-eaters, the Triassic forms seem to have fed mainly on fish . . . One group . . . was clearly a shell-fish eater" (Tarlo, 1967).

Synapsida

Pelycosauria

Ophiacodontia

Ophiacodon and *Varanosaurus* were probably fish-eaters (Colbert, 1969, p.130; Romer, 1966, p.174). “*Eothyris* developed a highly predaceous dentition” (Romer, 1966, p.174).

Sphenacodontoidea

Sphenacodonts (e.g. *Dimetrodon*) were aggressive predators on other large vertebrates (Romer, 1966, p.175; Colbert, 1969, p.131).

Edaphosauria

Edaphosaurus probably fed on “the soft plants of the water and water margins” (Olson, 1971a, p.670). *Cotylorhynchus* had an enormous rib cage and its food was probably “of a bulky, watery nature, low in nutritive value, so that it was necessary for the animal to ingest large quantities” (Romer and Price, 1940, p.377; Olson, 1968, p.320).

Therapsida

Phthinosuchia

Carnivorous reptiles with large teeth (Chudinov, 1965, p.120).

Theriodontia

Gorgonopsia: Carnivores with “sabre teeth” for stabbing prey (Colbert, 1966, pp.54–55). They were capable of attacking fairly large animals like dicynodonts (Kemp, 1969, p.27).

Cynodontia: *Cynognathus* was an “active and aggressive predator” (Colbert, 1966, p.83). The diademodontids (gomphodonts) had broad teeth for grinding and crushing — “obviously an herbivorous side-branch of the advanced cynodont stock” (Romer, 1967).

Tritylodontoidea: Tritylodonts had a rodent-like skull and may have fed upon husked fruits or nuts or seed pods” (Colbert, 1966, p.99).

Therocephalia: “Massively built carnivores” (Romer, 1966, p.181).

Bauriamorpha: Carnivores/insectivores.

Ictidosauria: The order included both carnivores and herbivores and seems to have been restricted to terrestrial life (Olson, 1971b).

Anomodontia

Dinocephalia: Titanosuchoidea: “Large ponderous carnivores” (Colbert, 1969, p.136). Estemmosuchids have strongly worn teeth which indicates “long use and the trituration of a large quantity of plant food” (Chudinov, 1965, p.124). Anteosauridae were carnivorous, Titanosuchidae herbivorous (Boonstra, 1963b).

Tapinocephaloidea: “ponderous herbivores” (Colbert, 1969, p.136; Boonstra, 1963b).

Venyukoviamorpha: Herbivores.

Dromasauria: Probably herbivores (Boonstra, 1963a).

Dicynodontia: Dicynodonts were “apparently well-adapted herbivores” (Romer, 1966, p.183) of which *Lystrosaurus* was aquatic. *Kawingasaurus* was probably adapted to a digging mode of life (Cox, 1972). Kannemeyeriids may have been browsers feeding on fronds and leafy branches while stahleckeriids may have been grazers feeding on low grass-like herb cover (Cox, 1965).

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ADDENDUM

To the list on p. 130, add:

- M. Jur., theropod *Iliosuchus* (Eu., NA., Galton, 1976).
- U. Jur., theropods *Allosaurus*, *Ceratosaurus* (NA., Eaf.); sauropod *Apatosaurus* (NA., A Eu.); ornithopods *Camptosaurus* (NA., Eu.); *Dryosaurus* (NA., Eaf., Eu.) (Galton, 1977).