

A PROBLEM OF FAUNAL REPLACEMENT ON PERMO-TRIASSIC CONTINENTS

by PAMELA LAMPLUGH ROBINSON

Twelfth Annual Address, delivered 5 March 1969

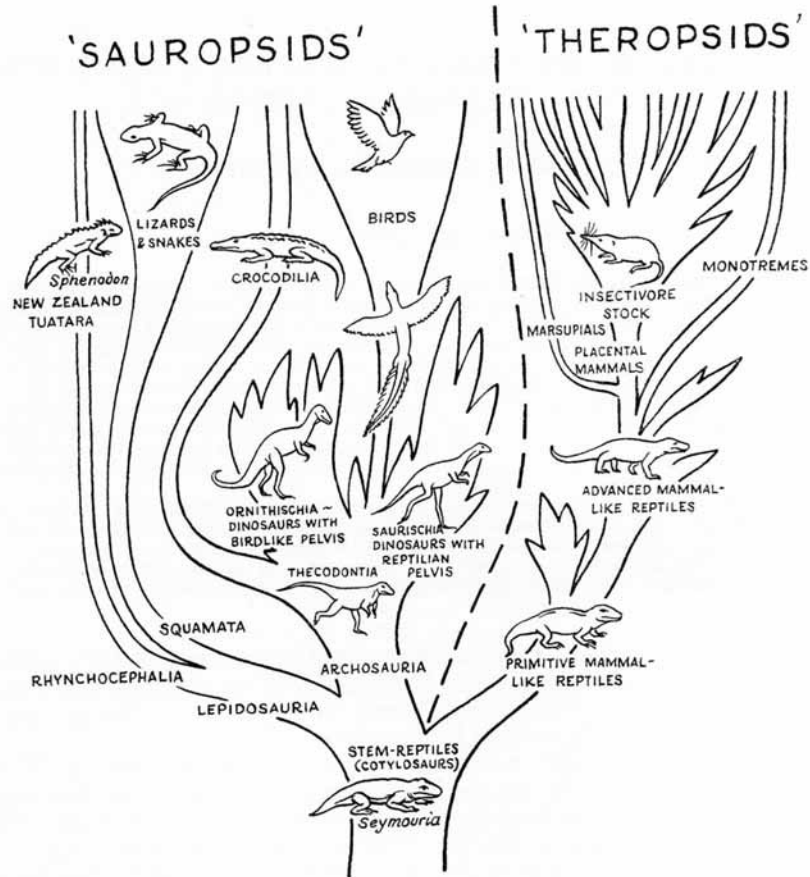
ABSTRACT. The faunal replacement of the mammal-like reptiles or theropods by the non-mammal-like reptiles or sauropsids (archosaurs and lepidosaurs) during Triassic times, is discussed. The basic physiological characters of the modern descendants of these two reptilian groups are reviewed and contrasted. It is now known that these characters have considerable, and differing, adaptive properties and affect the broad distribution of each of the two groups in the general environments of the modern world. The environments of the Upper Permian, the time when the theropod reptiles were at their peak in importance, are contrasted with those of the Upper Triassic, when the sauropsids had largely replaced the theropods. It is shown that there is a correlation between the number of genera representing theropods and sauropsids, and relative abundance of certain types of environments in the Upper Triassic and Upper Permian. It is suggested that the correlative link is to be sought in certain basic physiological characters which distinguish the theropods from the sauropsids, and affect the ease with which they adapt to certain environments.

Palaeomagnetic evidence for successive geological periods shows that most of the world's continents have tended to migrate northward across the parallels of latitude, as well as drifting apart. The relative size of land-masses, and the changing incidence of latitudes on these, have progressively changed the abundance of certain types of environment, as reflected by rock-type, in successive geological periods, offering opportunities for deployment, through their basic physiological characters, of first one major group of tetrapods, and then another.

'PROBLEMS of Triassic Vertebrates', a title suggested by the Council for this Address, is tactfully broad and generous in scope. So broad that choice is difficult, and prompts one to think about *kinds* of problems of Triassic vertebrates, as a preliminary, and an aid, in making a choice of a problem for discussion.

The first array of problems, which come to mind, are those connected with the evolutionary events of the Period, and of the preceding Permian Period. For during these two Periods reptiles became the dominant members of the land faunas of the world, and underwent a major adaptive radiation, producing the stocks from which the mammals and birds were derived (text-fig. 1). During the Permian the mammal-like reptiles became numerous and varied, and by the end of the Triassic some had progressed through all the major evolutionary changes which culminated in mammalian structure. The two most important groups of non-mammal-like (or sauropsid) reptiles, the subclasses Archosauria and Lepidosauria, originated late in the Permian, and had their first major radiation during the Triassic. The Triassic Archosauria include certain kinds of reptiles, of the order Thecodontia, which were restricted to the Period, and which represent an early adaptive radiation of archosaurs. But, in addition to the Thecodontia, Triassic Archosauria include the earliest crocodiles, and also the first members of the two orders of dinosaurs, Saurischia and Ornithischia, which were to be the most prominent, varied, and numerous members of the world's land faunas for the whole of the rest of the Mesozoic, a time interval of more than 100 million years. From some stock of ornithischians the birds were derived during Jurassic times. The Lepidosauria, originating in the late Permian as a small and inconspicuous order of

[Palaeontology, Vol. 14, Part 1, 1971, pp. 131-53.]



TEXT-FIG. 1. A 'family tree' showing the general relationships of those reptiles, and their descendants, which are here termed 'theropsids' and 'sauropsids'.

reptiles, the Eosuchia, were also represented, in the Triassic, by two orders of reptiles still in existence today, the beak-headed Rhynchocephalia, and the earliest lizards (Squamata). The snakes (Squamata) evolved later, from some stock of lizards at present unknown, and are first found in the Cretaceous. Apart from the snakes, all the main kinds of non-aerial terrestrial reptiles had appeared by the end of the Triassic, and so had the earliest mammals.

There are so many fascinating problems connected with the evolution, relationships, and structural adaptations of Triassic reptiles, that it would seem that one need look no further for a subject for discussion, indeed choice of subject already presents formidable difficulties. Yet these problems are basically similar to most of those posed by

vertebrates of any geological period from the Ordovician onwards. Their importance depends on their setting within the general framework of ideas which were first formulated in the nineteenth century, ideas concerning the evolution of animals and plants, and which were capable of demonstration from the fossil record. And the demonstration and solution of problems in the evolution of vertebrates has depended on a methodology, comparative anatomy, and embryology, which, though having its beginnings in classical times, was elaborated chiefly in the late eighteenth and nineteenth centuries.

A second set of problems concerns the use of vertebrate fossils in the stratigraphy of the continental facies of the Triassic. These problems are becoming increasingly important in the Gondwanaland continents, and in parts of Laurasia, such as China, the U.S.S.R., and North America. But, although the types of fossils used may be unfamiliar, Triassic vertebrates are sometimes abundant enough to allow subdivisions of the Triassic rock sequence and to provide the means of mapping formations across country; the type of stratigraphic problem is familiar, and the geological principles involved are well established.

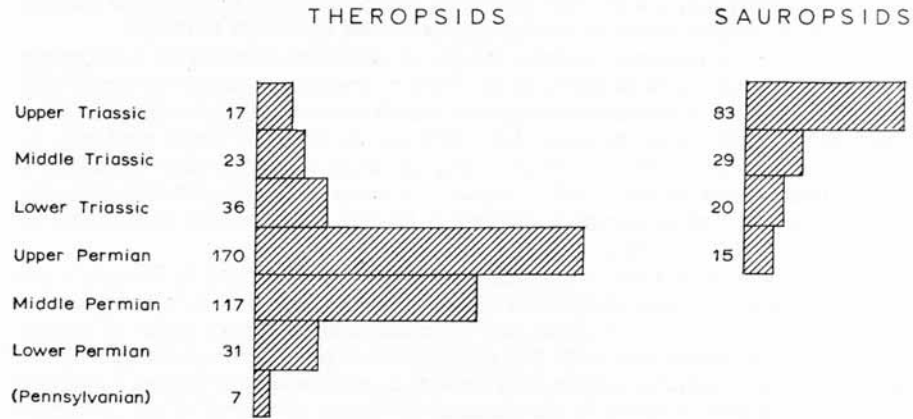
There are two other kinds of problems which are well illustrated by Triassic vertebrates. One concerns their distribution in space, their geographical distribution during the Triassic. This kind of problem can be linked with geological topics of current interest, such as continental drift. The second kind of problem is concerned with the distribution of vertebrates in time, with changes or replacements of faunas. Vertebrate faunal replacement occurred in the sequence of faunas of several of the geological systems, and is little understood. The faunal replacement illustrated by the sequence of Permian and Triassic vertebrate faunas is particularly striking, and affected stocks of major evolutionary importance. Because no satisfactory explanation of it has so far been offered, and even the methodology for doing so is not immediately apparent, this problem presents a special challenge. It will first be described, and then discussed, as the subject of this Address.

THE RISE AND DECLINE OF THE MAMMAL-LIKE REPTILES

The degree to which certain lithologies become abundant only in certain geological systems almost causes one to lose faith in the principle of uniformitarianism. The Triassic, more than most geological systems, contains abundant continental sediments which are widely distributed in both hemispheres of the world, and the Permian System runs the Triassic a close second in this respect. So there is an excellent record of terrestrial vertebrates, particularly of reptiles, in the rocks of the Triassic and Permian, and this allows recognition of a problem of faunal change.

To appreciate this problem it is convenient to consider Triassic reptiles in two main groups or taxa. The mammal-like reptiles can be grouped as a taxon of 'theropsids'. The two important subclasses of non-mammal-like reptiles, the Archosauria and Lepidosauria, may be considered together as a second taxon, the 'sauropsids' (text-fig. 1). If one compares the number of genera of each taxon which have been discovered in the three main subdivisions of the Permian, and those of the Triassic, a remarkable contrast becomes evident (text-fig. 2). The theropsids, which first appeared in the late Carboniferous, became more abundant in number of genera during the Permian,

reaching their acme during the Upper Permian; thereafter they dwindled rapidly until they had become relatively rare in the Upper Triassic. The sauropsids first appeared in the Upper Permian, and in the Middle and Upper Triassic increased rapidly in number of genera, precisely at the time when the number of theropsid genera was declining.



TEXT-FIG. 2. Numbers of genera of theropsids and sauropsids found in the subdivisions of the Permian and Triassic Systems. (Source: Romer 1966.)

There is no doubt that some bias is introduced into this picture by accidents of collecting. To be aware of this one need only compare the total number of genera of both taxa from the Lower Triassic with the total from the Upper Triassic. But that this bias does not obscure or falsify the main peculiarity of the distribution of genera can be seen by comparing the total of both taxa for the Upper Permian with the total for the Upper Triassic. The totals are large in each System subdivision, yet the relative importance of the two major taxa of reptiles has been completely reversed by Upper Triassic times. In the Upper Permian the theropsids are the abundant members of the world's terrestrial faunas, but by Upper Triassic times the theropsids are relatively rare and the sauropsids have become dominant. The advanced theropsids, or early mammals, continued to be rare until the beginning of the Tertiary.

The methodology for tackling this problem is not readily apparent. If it were the case, for example, that the carnivorous theropsids of the Permian were replaced by carnivorous sauropsids during the Triassic one could turn to the methods of comparative anatomy in an attempt to discover those ways in which the sauropsids were superior, structurally, for a carnivorous role in Upper Triassic times. But during the Upper Permian the theropsids were filling all the usual roles of omnivore, carnivore, and herbivore, while by Upper Triassic times these roles were being filled by sauropsids. Moreover by Upper Triassic times the theropsids were, in structure, at their most advanced from the evolutionary point of view, being close to, or having just attained, mammalian status. Nor is it easy to invoke some peculiarity of geographical or facies

distribution to explain the problem. Excellent faunas of Upper Permian theropods are known from localities as far apart as the U.S.S.R. and South Africa, while Upper Triassic sauropsid faunas are known from nearly all the world's continents. The faunas of reptiles of both taxa come chiefly from flood-plain, lacustrine, and deltaic sediments, the fluvial facies of the Permian and Triassic.

When there is no established methodology for tackling a problem, it remains simply to wait, until clues emerge which provide an insight into some of the factors responsible, and allow suggestions to be made about possible causes. While it is certain that no one factor can alone have been responsible for the sweeping faunal change which occurred during Triassic times, some clues have presented themselves which seem to indicate some of the possible factors and causes, and these clues will now be reviewed in the order in which they emerged.

A COMPARISON OF TWO FISSURE FAUNAS FROM BRITAIN

The first clue to the problem emerges when one compares two faunas of a rather special kind which are found in Britain in some of the counties round the Bristol Channel. These are faunas obtained from fissures but it is not yet generally recognized that there are really two such faunas, distinct in age, in faunal composition, and in environmental background. The earlier of the two faunas is Upper Norian in age (Robinson 1957). At this time Britain still formed part of a North Atlantic continent, lying to the north of the Tethyan sea, and in western Britain some of the Hercynian fold-structures still projected above the adjacent lowlands as hilly regions. The hills were mainly built of Carboniferous Limestone, and their drainage was mostly underground, by systems of caverns and passages developed along joints and bedding planes by solution of the limestone. Some of the caverns were extensive, about 50 ft across, and they gradually silted up as the watertable rose in the region towards the end of Norian times, just prior to the invasion of the area by the Rhaetic seas. By Upper Triassic times the hill regions were semi-arid, and were gradually being buried in their own waste, an insolation scree of angular or sub-angular limestone debris. Vegetation cover was poor, and evaporite deposits were forming in the adjacent lowlands. The fissure sediments were swept into the underground watercourses by intermittent and rather violent rainstorms, which scoured debris from a wide area of hill-surface and sent much of it down the drain of the nearest watercourse system. This sometimes effected a rather impressive concentration of animal bones, for the fauna preserved in the Upper Norian fissure fillings consists, not of cave-dwellers, but of vertebrates living on the hill-surface near to the entrance of the watercourse. The fauna thus consists of hill-dwellers, rather than lowland forms, and its members are moderate to small in size. The composition of the fauna is interesting; there are no amphibians, no semi-aquatic reptiles, and no theropods; the fauna consists entirely of sauropsid reptiles and one small cotylosaur (procolophonid). The absence of theropods is real, for in the tons of Upper Norian fissure sediments which have been examined under a binocular microscope to date, not even a single tooth of a theropod has ever been found.

The second fissure fauna is probably mainly Liassic in age. All the fissure localities of this age are found on the small islands which remained above water after the invasion of Britain by the Rhaeto-Liassic seas, and are well exemplified by the Glamorgan area

The first clue is thus a contrast in faunas, and of the environments in which they lived. The theropods are found only in the more genial environment of the small islands of the early Liassic, they are not found in the more stringent environment which existed in late Norian times in the same area, when it was an interior continental region.

BASIC PHYSIOLOGY AND ADAPTATION TO ENVIRONMENT

A second clue to the problem of early Mesozoic faunal replacement can be found by considering certain physiological characters of the living descendants of the Upper Triassic theropods and sauropsids. These living descendants are separated by a very long time interval from their forebears of the late Palaeozoic and early Mesozoic, and

TABLE 1. Comparison of metabolic rates

	<i>Cal/kg/24 h</i>	<i>Cal/m²/24 h</i>
Rattlesnake (ectotherm)	7.7	91
Rabbit (endotherm)	44.8	619
Woodchuck (endotherm—can hibernate)	28.7	418

so it may be thought that physiological characters can hardly have any bearing on a problem so remote in time from the present. However, as will be shown, in certain basic features the physiology of the descendants of these two taxa differ markedly from one another, and within each taxon these features are common to all or nearly all. These differences must therefore have arisen at an early date, and each taxon thereafter have pursued a separate path in physiological evolution and adaptation. The modern descendants of the theropods are, of course, the mammals; those of the sauropsids are, chiefly, the lizards and snakes on the one hand, and the birds on the other. The crocodilians have been semi-aquatic in habits since Lower Jurassic times, and this has had very considerable effects on their physiology. They can no longer be regarded as truly terrestrial vertebrates physiologically, and will not be considered in this general review. Lizards and snakes (Squamata) are represented today by about 6000 species; they are the typical sauropsids or 'reptiles' of the present scene. They are not very closely related in ancestry to birds, for birds are descendants of the archosaurian sauropsids, while the modern Squamata are descended from lepidosaurian sauropsids. Yet some of the basic physiological characters of birds are so similar to those of squamates that physiologists, comparing the two groups, tend to refer to birds as 'feathered reptiles'. For present purposes therefore birds may be regarded as 'sauropsids'.

The first important generalization, which is basic to an understanding of the physiological adaptations of mammals, birds and reptiles, is that mammals and birds have a much higher basal metabolic rate (B.M.R.) than do reptiles of the same weight and active at similar temperatures. Some early figures by Benedict (quoted in Prosser and Brown 1961) still illustrate this sufficiently well by comparing a reptile, a non-hibernating mammal (rabbit) and a mammal capable of hibernation (woodchuck), each 2.5 kg in weight and with body temperatures of 37 °C (Table 1).

There are advantages and disadvantages biologically in maintaining relatively high metabolic rates. Disadvantages are that these animals must eat more frequently particularly if they are relatively small, i.e. with a large body surface relative to body weight.

The heightened metabolism puts more 'pressure' on many organs of the body such as the excretory organs, especially the kidneys. The increase in excretory activity is, at least potentially, expensive in terms of the animal's water economy. Squamates and birds excrete waste nitrogen from protein metabolism as uric acid; mammals excrete it as urea, a basic difference between living theropods and sauropsids. Urea is soluble, and requires much more water for its excretion than uric acid. However, mammals have evolved a special segment of the tubule of the kidney, the loop of Henle, which reabsorbs much of the water required for pressure filtration of the urea from the blood capillaries through the kidney capsule and into the kidney tubule. The evolution of this loop has allowed mammals to conserve much of the body water which would otherwise be expended in urea excretion. Even at their most efficient, however, mammals cannot rival birds in economy of excretory water. Molecule for molecule, twice as much nitrogen can be excreted in the form of uric acid as compared with urea, and even the most economic mammalian excretion expends more than ten times as much water in getting rid of urea wastes, compared with uric acid excretion in birds (Dawson and Bartholomew 1968). Uric acid, a relatively insoluble substance, thus provides the most effective means of disposing of waste nitrogen when water conservation is important, and is the method used by the living sauropsids, birds, and squamates.

Advantages of a high basal metabolic rate include the possibility of maintaining a relatively high and constant internal body temperature, i.e. the condition known as endothermy. This allows the body's biochemical reactions to be run at optimum and relatively constant rates. The relatively constant and highly efficient inner environment permits the development of a large brain and well-co-ordinated nervous and sensory system, introducing learning and choice as important adaptational mechanisms, well shown in a great variety of ways by the endothermic mammals and birds.

The mechanisms for regulating body temperature are similar in birds and mammals, even though they must have evolved independently in the two groups. These mechanisms are controlled augmentation of body heat, as required, by increasing metabolic rate, and control of heat loss, as required, by varying the conductance of the body. Control of heat loss, in both birds and mammals, depends on having an outer body layer and covering whose conductance and insulation properties can be varied, and on being able to transfer unwanted body heat into a capacious heat sink, namely, an environment which is at a temperature significantly below that of the body core. The range of body core temperatures shown by mammals and birds may therefore affect their capacity to use the environment as a heat sink, or to insulate themselves from its cooling effects. The normal range of preferred, or eucritic body temperature for the major taxa of living tetrapods is given in Table 2 below, though mammals capable of hibernation have been omitted, as they are often not fully endothermic.

Evidently body core temperatures of mammals are significantly below those of birds. This means that in the hotter environments of the world mammals adapt with greater difficulty. Ambient temperatures may more readily rise above body core temperatures so that heat tends more continually to flow the wrong way, into the body, and unwanted heat can be got rid of only by evaporating water (panting or sweating). This is an 'expensive' method of keeping cool, except as a temporary measure, in hot climates where water may be short. Just how expensive it may be can be gauged from human performance; for men doing hard physical work in saturated atmospheres at 35.5 °C

sweat at rates up to 4.2 litres per hour, yet the total volume of water in a man's blood is about 4 litres (Gordon 1968). Of course some modern mammals have adapted to hot arid conditions, some desert rodents do not sweat, have evolved methods of reducing respiratory water loss, and can live without drinking water. But of those mammals which have adapted to desert life many (though not all) have done so by the 'artful dodger' method, as far as temperature regulation is concerned. They spend the day in burrows dug down to the cooler and moister substratum and emerge in the evening to feed.

TABLE 2. Temperature data on modern tetrapods

Taxon	Normal range of eccentric body temperature (°C)	Highest tolerated body temperature (°C)
AMPHIBIA (terrestrial)	0-35	37.6 (<i>Microhyla olivacea</i>)
SQUAMATA	18-44	47.0 (<i>Dipsosaurus dorsalis</i>)
BIRDS	39-43	45.0 (birds of several orders)
MAMMALS (endotherms only)	35-39	

(Sources: Bartholomew 1968, Bartholomew and Dawson 1968, Dawson and Bartholomew 1968, Mayhew 1968.)

Though the rather low body core temperatures of mammals mean that, generally speaking, they adapt with difficulty to the hotter environments, they adapt rather more easily to the colder climates than do birds, with their higher core temperatures. The fact that the difference between core and ambient temperatures is smaller in mammals means that less metabolic work, and less food, is necessary to maintain core temperatures. In cold climates, too, control of heat loss requires only the intensification of the mechanisms already evolved to regulate conductance by the outer shell of the body and its covering.

The modern sauropsid reptiles, lizards and snakes, are ectotherms. They derive from the sun, directly or indirectly, most of the heat required to maintain the body temperature at which they perform their daily activities. While active they may maintain a remarkably constant body core temperature, and do so chiefly by a pattern of behaviour. They gain body heat, when required, by basking either in the sun or in a warm part of their environment. They lose body heat when necessary, by running to the nearest local heat sink—a patch of shade, a crevice, or a burrow. Control of body posture, of heart-beat rate, panting, and exploitation of the degree of thermal variety of the environment, are used as aids in maintaining body temperatures at the preferred level, and for damping the oscillations of body temperature which would result from a simple on-off use of heater and heat sink in the environment. When inactive, the body temperature of most lizards and snakes drops to a level close to that of the ambient temperature. Ectothermy has its disadvantages, for the inner environment is optimum only when the animal is active. It also has its advantages, for the animal needs much less food than an endotherm to maintain itself. It has been calculated that, if there were a lizard as large as a man, the man would require about forty times as much food as the lizard just to maintain basal metabolic rate. As Bartholomew (1968) has remarked, though endotherms are more independent of environmental temperature than are ectotherms, they pay a high price

for this independence in terms of metabolic cost of living, for about 80–90% of their oxidative energy is used to maintain thermal homaeostasis.

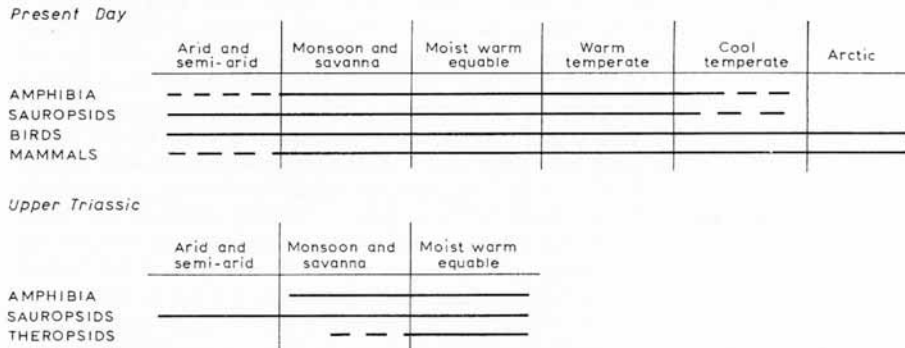
Modern lizards and snakes show a wide range of preferred or eccritic body temperatures (Table 2), and some show astonishingly high values which would be lethal to any mammal, and are close to the values at which proteins and enzymes are denatured. Modern squamates are uricotelic, and this, and the methods of body temperature maintenance and regulation, means that they adapt well to the hot arid climates, but cannot adapt to the frigid environments.

TABLE 3. Some physiological characters of 'theropsids' (mammals) and 'sauropsids' (birds and squamates)

Uricotelic	Ureotelic	
BIRDS SQUAMATES	MAMMALS	Higher B.M.R.s, typically endothermic, larger brains. Lower B.M.R.s, typically ectothermic, smaller brains.
Higher eccritic temperatures	Lower eccritic temperatures	

The basic differences in certain physiological characters of mammals, birds, and squamates are shown in Table 3 above. Mammals and birds have independently evolved endothermy, which gives them some independence from environmental temperatures, a relatively constant and optimum inner environment and hence better sensory and central nervous systems. Mammals and sauropsids differ from one another in two respects; mammals are ureotelic whereas sauropsids are uricotelic, and sauropsids have achieved higher values of eccritic temperatures than mammals. The adaptive value of these basic physiological characters of mammals, birds, and squamates is well shown by their relative numbers in the more extreme environments, deserts on the one hand and frigid climates on the other (text-fig. 4). Squamates, particularly lizards, are the

Distribution of tetrapods in certain environments



TEXT-FIG. 4. The distribution of tetrapods in certain environments at the present day, and in the Upper Triassic.

most numerous, in species and individuals, of the inhabitants of deserts, with birds next most numerous, and then mammals. Mammals have adapted best to the cold climates, some birds have done so, but squamates are absent.

ENVIRONMENTS OF THE PERMO-TRIASSIC

It is highly unlikely that theropsids were endothermic in Permo-Triassic times. As will be mentioned later, it is probable that this physiological character evolved in late Mesozoic and early Tertiary times, for it was during the early Tertiary that a general enlargement of the brain occurred in the evolution of many mammalian stocks. Birds also probably evolved endothermy in post-Jurassic times for the three known specimens of Upper Jurassic birds show that at this time birds had relatively small brains and were gliding fliers incapable of flapping flight. The theropsids and sauropsids of the Permo-Triassic were probably all ectothermic.

The differences between modern theropsids and sauropsids in certain physiological characters, such as method of nitrogen excretion, and the upper range of preferred body core temperatures, are distinctive for all the modern members of the two taxa as defined and discussed here. So it seems probable that these features evolved early in the history of the two taxa, and must be regarded as basic physiological characters which have distinguished each taxon for a long time. These characters are sufficiently different in their adaptive properties to suggest that they may have evolved against rather different environmental backgrounds and perhaps at rather different times in the history of the two taxa.

Does this throw any light on the problem of the faunal replacement of theropsids and sauropsids during the Triassic? Is it possible to suggest that at the beginning of the Triassic, a stock of early sauropsids, living in the varied and often more difficult environment of hill ranges, with a patchy water supply, greater exposure to sun, and greater scarcity of food, evolved the basic physiological adaptations which have characterized them ever since? That, armed with these new adaptations, they gradually invaded the lowland regions (from which come the greater part of the continental fossil record), where they had a selective advantage over the theropsids, whose physiological adaptations were, at that time, much poorer.

This suggestion may contain some truth, but it is much too crude. It is as though one imagined the sauropsids descending from their Triassic hills inspired by some ruthless policy which spelt extinction for theropsids. But the Triassic theropsids were not 'second-class citizens'. They had had an extraordinarily successful history during the Permian, and they were to achieve even more spectacular successes in the Tertiary. Bearing in mind the basic physiological differences between the modern representatives of the two taxa, one may examine the general environments of the world's lands during the acme of each taxon, the Upper Triassic and the Upper Permian, to see whether this throws any further light on the problem.

The maps for the Upper Triassic (text-fig. 5, p. 152) show the world's continents reassembled in their pre-drift positions, on two equal area projections: the normal (and more familiar) Mollweide, and an oblique Mollweide which gives good representation of polar regions (see notes on projections given with the maps). Two supercontinents, a northern Laurasia and a southern Gondwanaland, are distinguishable, but are

connected together at their western ends, while diverging eastwards on either side of the Tethyan Gulf and Ocean. The idea for this assembly is from Tuzo Wilson (1963), who made it in the light of work done on the mid-oceanic ridges, and ideas regarding the significance of these ridges for the break-up of the fragments which now form the world's continents. Wilson's assembly has been modified here to include other lines of evidence on its character, such as that of Bullard *et al.* (1965) on the fit of the Transatlantic Continents, and palaeomagnetic evidence (especially Irving 1964). The reassembly of the continents was carried out on a globe 19 inches in diameter, and though they are not shown on the maps because of the small scale on which these are reproduced, the continental shelves were allowed for and used in making the reconstruction. It was found that the reassembly given here for the Upper Triassic satisfied and fitted all the major lines of evidence used, and which are mentioned in the notes included with the captions for the maps. The distribution of certain kinds of Upper Triassic sediments have been roughly indicated; coals, red-beds (with a qualifying letter showing, where known, whether they are fluvatile, lacustrine, or deltaic), aeolian deposits (which sometimes succeed red-beds) and the two localities at which palaeowind directions have been obtained from these deposits and evaporites (gypsum, anhydrite, and salts). It is assumed here that red-beds which are associated with fluvatile deposits often indicate heavy seasonal rainfall followed by a dry season (Van Houten 1961, 1964).

The pre-drift assembly of the world's continents has been projected in the latitude positions for the Upper Triassic, and this at once invites proper consideration of the climate of the time. To do this adequately, and discuss the effects of the supercontinents on such important features as the intertropical convergence, interior continental pressure centres, and the oceanic 'horse latitude' high pressure centres, is beyond the scope of the present study and must be considered in another paper. Only brief comments, in very general terms, can be made here. However, in considering the distribution of the warmer climates of Upper Triassic times the lack of polar ice-caps has to be borne in mind. In an ice-free world fairly hot climates would probably extend into quite high latitudes, up to about 50°, with temperate conditions at the poles.

The Upper Triassic equator more or less bisects the Tethyan Gulf, and the two great supercontinents are disposed rather symmetrically on either side of it. This suggests the possibility of an interesting aspect of the general climate of Upper Triassic times, by analogy with the profound effects, on modern climates, of the enormous landmass of Eurasia. The influence of the Asiatic landmass in causing monsoon conditions is well-known, though the causes are not quite so simple as usually indicated in many textbooks, which usually quote an explanation which really originated from Halley in 1686. But though surface air conditions are now known to be partly reinforced and partly modified by conditions aloft (Pédelaborde 1963), it remains a fact that the large Asiatic landmass profoundly affects the air at many levels, and during summer sucks in surface air from all sides. Wherever this summer air has travelled over warm seas it is drawn towards Asia as the rain-bearing winds of the summer monsoon. In winter the opposite surface conditions occur. The great cold of the central and northern parts of the Asiatic landmass builds up a surface high-pressure centre, which is reinforced above by advection of cold air from the Arctic. So surface winds blow outwards from Asia during winter, and are therefore dry. In many of the middle and lower latitude marginal regions of Asia, including much of Peninsular India, there is a dry season which may last for

six months or more with a rainfall of only a few per cent of the annual total, in strong seasonal contrast to the high rainfall of the summer months.

It is not impossible that each of the two great supercontinents of Upper Triassic times may have created monsoon conditions, though the less frigid climates of the polar regions have to be borne in mind. Winds reaching the middle and lower latitude eastern portions of Laurasia and Gondwanaland, in their respective summer seasons, may well have brought monsoon-type seasonal rains to each of these areas, local topography permitting. From each supercontinent, in their respective winter seasons, winds may have blown outwards, and have brought a dry hot season to the marginal areas of middle and lower latitudes. The conditions in the central and western parts of these two great landmasses would be rather different from those in the east, generally rather drier because most summer-season winds would have travelled over landmasses. Even here, in the centre and west, some areas would receive rain through the presence of local areas of sea, as might parts of the western selvedge of the supercontinents through onshore winds (see palaeowind direction for western North America).

These suggestions seem to be in accord with the general distribution of certain Upper Triassic lithologies which were entered on the maps (text-fig. 5) *after* the continents had been re-assembled on independent evidence. Evaporites occur chiefly in two climatic regions. They are found in the contemporary tropics, approximately between the Upper Triassic latitudes of 25° N. and 25° S., in the central and western parts of the supercontinents. The Tethyan Gulf and its environs, lying in low latitudes, and landlocked by the great supercontinents, seems to have behaved like a giant evaporating pan wherever there were suitable bays or other local physiographical conditions. The other evaporite occurrences, in Africa and South-east Asia, lie at about 40° of Upper Triassic latitude, and so can be regarded as contemporary 'horse latitude' arid zones. Aeolian deposits occur chiefly in the interior of the two supercontinents, and in Gondwanaland with its more continental polar regions, up to quite high latitudes. Red-beds occur chiefly in two zones; either in the intertropical zone (approximately 25° N.–25° S.), or in middle latitudes, especially in Gondwanaland, and not too distant from western seas and ocean, or from the Tethyan Ocean (and its Madagascan Gulf). Coals occur mainly in the eastern, peninsular parts of the two supercontinents, in middle to high latitudes, where temperatures may have been more moderate, and rainfall less strictly seasonal under the stormier influence of the belt of westerlies and polar easterlies. Of the four lithologies discussed above, three are suggestive of climates with at least a seasonal drought.

In considering the general environments available to land-dwelling vertebrates in Upper Triassic times the scale and generality of the world-map (text-fig. 5) should not be forgotten. It should not be imagined that the central and western parts of the two supercontinents were one vast monotonous desert of evaporites and windblown sand. Between these more arid areas were better-watered regions with a seasonal rainfall at least, as is shown by the details of the sedimentary record of the Upper Triassic of North America and Europe for example. But the map suggests that, except in the high latitudes of the eastern regions, environments with at least a seasonal drought were widespread over the lands of the Upper Triassic world. If, early in the Triassic, the sauropsids had evolved their basic physiological characters of uricotelism and well-controlled ectothermy, with a range of body core temperatures which in some extended to high values,

then they would have been well adapted to the environments generally prevailing over the lands of Upper Triassic times.

It may be objected that some of the world's most famous salt deposits occur in Permian rocks, at a time when theropods were widespread and abundant. But though Permian salt deposits are thick and economically important, evaporites, including gypsum, are more restricted in time and space during the Permian than during the Upper Triassic. They are also restricted in distribution during the Upper Carboniferous (Pennsylvanian), the period during which the theropods originated. During Pennsylvanian times evaporites are known chiefly from the Amazon (Manaus) basin, from the Paradox basin of Colorado-Utah and some adjoining areas, from the Sverdrup basin of Arctic Canada, from East Greenland and Spitzbergen, and from very restricted areas of central and eastern U.S.S.R. Pennsylvanian coals are widely distributed in the central parts of Laurasia, from eastern North America to the Donetz basin and beyond. In the lower Permian (Sakmarian-Artinskian) evaporites are known chiefly from Peru, perhaps from the Amazon (Manaus) basin, from parts of the Mid-Continent region of North America, from very restricted areas of North Europe (Rotliegendes), and from one or two very small areas of central U.S.S.R. In Gondwanaland glacial conditions covered very large parts of the supercontinent, and were followed by equally widespread coal formation. The Middle Permian (Kungurian-Ufimian) evaporites occur only in Laurasia, chiefly in three regions; in North America in the Mid-Continent, Lusk, and Williston basins, in North Europe in the Zechstein basin (Poland to Greenland), and in the Ural-Caspian and Aral-Black Sea region. There are no evaporites in Gondwanaland, coal formation continued to be widespread there, and red-beds are rare.

The Upper Permian was the heyday of the theropods, so a map has been prepared depicting the pre-drift assembly of continents in approximately the correct Permian latitudes, and showing the general distribution of the same kinds of rock types as those given for the Upper Triassic (text-fig. 6, see p. 152). Evaporites are very restricted in occurrence, in Laurasia only, chiefly in the Mid-Continent and Mexican basin of North America and in the Zechstein basin of North Europe.

The general distribution of certain rock-facies, and their broad climatic implications, are as interesting for the Upper Permian as for the Upper Triassic. They seem to demonstrate the combined effects of latitude position, and size of land surface of the two supercontinents, as in the Upper Triassic. But in the Upper Permian the equator lies further north, and the two supercontinents are not quite so symmetrically disposed about it as in Upper Triassic times. In the Upper Permian Laurasia extends from low to high latitudes, whereas the land areas of Gondwanaland lie chiefly outside the intertropical zone in middle and high latitudes. This correlates with the restriction of evaporites to low latitude regions, and hence to Laurasia, and their occurrence, through the influence of continentality, in the central and western parts of that supercontinent. Red-beds are widespread in the intertropical zone of the central and western parts of Laurasia; they also have a restricted distribution in Gondwanaland, occurring in middle latitudes and mainly in the west (South America), not too far from western seas and ocean. Red-beds may occur as subordinate facies in Upper Permian fluvial sediments in certain other parts of Gondwanaland, such as the central parts of the Indian Peninsula (Robinson 1970). Coals occur in the middle and high latitudes of the eastern, more 'peninsular' regions of both supercontinents.

A comparison of the two maps shows clearly that rock-facies suggestive of semi-arid or arid conditions, or of seasonal drought, are much more restricted in distribution in the Upper Permian. The greater part of the land areas of Gondwanaland, nearly the whole of Asia, and the north-west part of North America, lay in middle to high latitudes. The Upper Permian world was free of glaciation, and its middle and high latitudes presumably enjoyed moderately hot to warm temperatures. The rock facies found in these latitudes suggest moderately, or even very well watered environments.

FAUNA AND ENVIRONMENT IN THREE UPPER TRIASSIC LOCALITIES

The general environments prevalent over the greater part of the lands of Upper Permian times would obviously have suited the basic physiological adaptations found in modern theropods. That these conditions suited the late Palaeozoic theropods is suggested by the very large number of genera (text-fig. 2) found in continental rocks of this age. Theropods were rare in the Upper Triassic, sauropsids were abundant, and at this time environments with at least a seasonal drought were widespread over the world's land areas. But these comparisons are of very generalized information, of total number of genera in each taxon, and of broad environmental conditions, for the whole world, at two different intervals of time. To test the implications of these generalized comparisons more particular and detailed information is needed, of actual faunas and environments at known localities, supplied by fossiliferous formations of known age. To make this test three localities have been chosen, each of which contains a rock formation and vertebrate fauna of Upper Triassic age. The three localities are situated in widely separated regions of the world, and though their fossiliferous formations all provide evidence of continental conditions, each represents a different type of continental environment. The first is the Maleri formation of the Deccan of India, the second the Lossiemouth-Findrassie formation of Elgin in eastern Scotland and the third the Ischigualasto formation of western Argentina.

The Maleri is a red-bed formation, and is chiefly built of three lithologies: thick, bright red, silty clays; poorly sorted, trough cross-bedded, whitish sandstones; and pale green, trough cross-bedded rocks consisting of small, rounded, roughly sorted pellets of lime in a sparse silty matrix. There are several kinds of red-beds (Van Houten 1961), but those lying on the world's cratons can be roughly divided into two groups: well-sorted sediments associated with evaporites, and poorly sorted sediments containing evidence of fluvial deposition. The Maleri red-beds belong to the second category, and are the sediments of a river flood-plain situated in the interior of the Indian craton. The presence of abundant iron oxide suggests that there was a hot dry season, with oxidizing conditions either favouring the formation of the iron oxides, or allowing their preservation if brought in from source areas in the hinterland. A fairly high degree of chemical mobilization in source rocks, producing the abundant iron, would require moderately high temperatures in adjoining source areas during the wet season. The peculiar lime-pellet rocks probably also indicate alternate wet and dry seasons in a fairly hot climate of monsoon type (Robinson 1964). Poorly preserved fossil wood is locally abundant in the formation, but no other plant remains are preserved as macrofossils. Shell banks of unionids occur locally in the red clays and pellet rocks (Kutty 1969).

The vertebrate fauna is listed below.

Maleri formation: vertebrate fauna

Fishes

<i>Ceratodus</i>	}	Aquatic
subholostean pleuracanth		
Amphibia	}	Semi-aquatic
metoposaur Reptiles phytosaur		
rhynchosaur aetosaur saurischian*	}	Terrestrial

(* Personal communication, from recent discoveries, by T. S. Kutty.)

Evidently the Maleri formation represents a monsoon-type climate, with fairly high year-round temperatures, and a dry season alternating with a season of abundant rainfall. That this was well-watered country, at least seasonally, is suggested by the locally abundant unionids, and by the presence of three aquatic and two semi-aquatic members of the vertebrate fauna. Probably these members of the Maleri fauna passed through the dry season in the more permanent bodies of water in the region, such as the deeper pools along watercourses.

The reptiles of the Maleri fauna are all sauropsids, theropods are completely absent. The well-known vertebrate faunas of the continental Upper Triassic of North America are not dissimilar in composition to that of the Maleri formation, and sauropsid reptiles are abundant while theropods are absent. The red-beds in which most of the North American Upper Triassic vertebrate faunas are found probably represent environments of deposition most of which were not dissimilar to that of the Maleri.

The Lossiemouth and Findrassie sandstones of Elgin, in eastern Scotland, represent a different kind of environment from that of the Maleri formation. The sandstones are mainly aeolian deposits, but they are closely associated, at the base, with fluvial sediments (Peacock *et al.* 1968). Probably this was a terrain of watercourses with very dry interchannel areas. As the water-courses shifted position on their flood-plain, their older sites and deposits were overwhelmed by the sand dunes of the semi-arid interchannel regions. These sand-dunes, blown by winds from the south, buried a sample of the local fauna which lived either near to the river banks, or in the drier interchannel regions. There are no aquatic or semi-aquatic members of the Elgin fauna, and also no theropods. The Elgin fauna consists of sauropsids, and a procolophonid reptile. Walker (1961, 1964) has made some interesting suggestions about the adaptational characters of some of the members of the Elgin reptile fauna. An armoured aetosaur (thecodont) probably lived close to the river banks, grubbing up vegetation, roots, and small invertebrates with its spatulate snout, and it may have carried a store of fat in its broad-based tail, to tide it over seasonal scarcity, much as in some desert lizards of today. The rhynchosaur may also have lived not far from the river banks, for it may have been a digger too, using its beaked snout and spatulate forked lower jaw and

perhaps also its claws, or it may have grubbed up molluscs from the river (Chatterjee 1969). Two members of the fauna which probably lived, at least partly, in the dry sandy interchannel areas are *Scleromochlus* and *Ornithosuchus*. The small *Scleromochlus* has been likened to a jerboa rat, the structure of its hind limbs suggesting jumping habits similar to those of certain modern rodents or marsupials which have become adapted to a leaping progression in sandy arid areas. *Ornithosuchus* (*Dasygnathus*) was a large saurischian carnivore, reaching a length of about 12 ft and standing about 5 ft high. Its huge skull, 18 in long, was armed with blade-like serrated teeth up to 2.5 in long, and this powerful reptile was at least partially bipedal.

The Ischigualasto formation of western Argentina is buff-coloured, greenish, or drab, and some of its sediments contain a considerable admixture of tuff. Parts of it are cross-bedded, possibly river channel deposits, but the greater part of it seemed, on brief acquaintance, to consist of extremely well-bedded layers of wide lateral extent, suggestive of lake-bottom deposits. Certain horizons contain abundant and well-preserved plant remains. The fossil vertebrates are often present as associated skeletons or skulls, little disturbed, and are present in abundance in some parts of the formation. The environment of deposition of the Ischigualasto formation has not yet received detailed study. cursory examination of the sediments suggests that this was a region with more sustained rainfall in Upper Triassic times, lacking the dry season of the Maleri environment. The Ischigualasto formation must have lain almost at the western margin of the Gondwana supercontinent, in middle latitudes. Perhaps this was a region of on-shore winds, which brought a more sustained rainfall from the western seas, and sometimes heavy falls of ash from volcanoes immediately to the west, along the Andean geosyncline, to a series of lakes surrounded by abundant vegetation and a rich and varied fauna of vertebrates. The composition of the fauna is interesting. Sauropsids are well represented by a rhynchosaur, saurischian and ornithischian dinosaurs, a sphenosuchid crocodylian, and other reptiles. But several genera of theropsids are also found abundantly in the Ischigualasto formation, and represent stocks which had been more widespread on the world's land areas in earlier Triassic times.

Knowledge of environments of deposition of fossiliferous continental formations of Upper Triassic age is still very inadequate in many cases. However, text-fig. 4 attempts to show the distribution of the major tetrapod vertebrate taxa of Upper Triassic times in the three environments just discussed, for all localities, as far as this is possible. The three environments have been designated arid and semi-arid (e.g. the Lossiemouth-Findrassie sandstones of Elgin, and the Upper Norian fissure deposits of the Bristol Channel area), monsoon and savannah (e.g. the Maleri formation of the Indian Deccan—monsoon), and moist warm equable (e.g. the Ischigualasto formation of western Argentina). In some red-bed localities, probably representing monsoon and fluvial conditions, theropsids do occur, usually as minor elements of the faunas (e.g. the upper part of the red beds of the Stormberg Series of southern Africa). Theropsids have therefore been represented as occasionally present in the monsoon-savannah environment in text-fig. 4, but as occurring mainly in formations representing more equable conditions with a less seasonal rainfall. Amphibia occur in both monsoon and equable environments but are absent from the more arid regions. Sauropsids occur in all three environments. It is interesting to compare the distribution of these taxa with that of their modern representatives in these environments (text-fig. 4).

BASIC PHYSIOLOGICAL CHARACTERS AND ENVIRONMENTAL CHANGE

There is a growing awareness amongst ecologists of the nature of the links between environment and physiological adaptation in modern reptiles, birds and mammals (e.g. Brown 1968). Enough work has now been done on all three groups for one to try to discern some of the basic physiological adaptations which characterize the three groups, as has been attempted here. Some important physiological aspects such as salt balance and the regulation of the ionic composition of the body fluids have had to be omitted, partly for the sake of brevity, partly because more work is needed before any generalizations can safely be made.

For the Permo-Triassic one can discern a correlation between the relative number of genera of the two major taxa of reptiles and the types of environment which were widespread over the world's land areas. This correlation is supported by the examination of some particular faunas from specific localities. It seems reasonable to suggest that the correlation is due to different basic physiological characters in the two taxa. These differences relate particularly to the range of body core temperatures preferred in the two taxa, whether or not they were endothermic, and to the degree of conservation of body water allowed by their method of excreting nitrogen.

The wide distribution of more equable conditions of temperature and rainfall present on much of the land surface of Upper Permian times obviously suited contemporary theropsids. It is unlikely that the theropsids were endothermic at this time, but it is probable that they had the same preferences as modern forms for a range of body temperature which did not extend to such high values as those found in modern sauropsids.

It is probable that the basic physiological characters of the sauropsids, as still shown by their modern descendants, evolved as this taxon differentiated early in the Triassic. These physiological characters, of uricotelism, and the ability by some to adopt higher eccentric temperatures, allowed the Triassic sauropsids to adapt to environments with high year-round temperatures, and at least a seasonal drought. Such environments gradually increased in frequency on the world's lands during the Triassic, in the middle and low latitudes, and became especially widespread in Upper Triassic times. Some of the labyrinthodont amphibians, such as metoposaurs and capitosaurus, were able to adapt themselves to the monsoon environments of the Upper Triassic. Probably they did so in the manner of the modern Australian lungfish, which lives in Queensland's monsoon environment. This lungfish, unlike its contemporary relatives in Africa and South America, does not aestivate, but spends the dry season lurking in the larger and more permanent pools of the shrunken Murray River. The Upper Triassic labyrinthodonts were too large to aestivate, and probably adopted the same method of enduring the dry season of Upper Triassic monsoon environments. During their Permo-Triassic history the theropsids had rather rarely evolved semi-aquatic forms, perhaps only certain pelycosaurs and dicynodonts. This suggests that the theropsids had adapted very well, as truly terrestrial vertebrates, to the less stringent environments which were widespread over the later Permian and early Triassic continents, but it closed to them the method of coping with a dry season adopted by the labyrinthodont amphibia. A few very advanced theropsids ('near-mammals' and 'only-just-mammals') are found

in the environments more generally suited to sauropsids, in the late Triassic red-beds of South Africa, for example, where they occur with a fauna or archosaurs. Most of them are small forms, and, like their modern counterparts, were probably able to find, or make, microhabitats with microclimates which were tolerable for their physiological range during the more stringent seasons and times of day. Except the tritylodonts, these very advanced theropsids are rare in the red-bed facies of the Upper Triassic, as those interested in the early evolution of mammals are regretfully aware.

We know rather little of the later Mesozoic history of theropsids. This history, and also its sequel, the emergence of the theropsids from their Mesozoic eclipse in late Cretaceous and early Tertiary times, require separate discussion for adequate documentation. But though this later chapter of tetrapod history lies outside the scope of the present theme, the Triassic and Permian, certain aspects are not irrelevant to some of the main points discussed above. For brevity, these aspects can only be touched on in a tentative way, and discussion must be restricted to the northern hemisphere.

The Jurassic theropsids of Europe, known chiefly from the fissure fillings of the Liassic islands of Glamorgan and the Somersetshire Mendips, also from near shore deposits close to contemporary islands at Stonesfield, and from the Kimmeridgian coal measures of Portugal, are all very small forms. The environment of the Liassic islands has already been discussed, and probably that of the Stonesfield ones was not dissimilar, though by Upper Jurassic times the Stonesfield islands would have lain at about 20° N. latitude. The coal-measures of Portugal are suggestive of humid conditions, Kuehne (1968) has described the environment of deposition as a swamp, and the region would be at about 10–15° N. in Upper Jurassic times. All three environments are suggestive of equable and rather humid climates.

The kind of world which confronted the theropsids in the early Tertiary of the northern hemisphere was one in which the palaeo-equator was situated about 10° N. of its present position. North America had begun to drift away from Eurasia and the North Atlantic was in being. In Eurasia the north shore of Tethys took an undulatory course approximately between the 30th and 40th parallels of early Tertiary northern latitudes. The terrestrial part of Eurasia thus lay mainly in middle and high latitudes. In North America an enlarged Gulf of Mexico extended north into the present Mississippi basin, about as far north as the 35th parallel of north latitude of early Tertiary times. This enlarged Gulf was flanked on the west and north-west by a lowland tropical to subtropical savannah of broad-leaved evergreen plants (Johnson 1968). In both northern hemisphere continents, therefore, the hotter low-latitude regions were largely covered by sea, and the two main landmasses were mainly situated in middle and high latitudes. Palaeobotanists have suggested that mild climates extended into quite high latitudes (e.g. Alaska and Greenland) at this time. In the early Tertiary therefore, environmental conditions were generally very different from those of the Upper Triassic, and more similar to those of the southern hemisphere and Asia in Upper Permian times. Climates with less seasonal drought and milder temperatures than those prevalent in the Upper Triassic were widespread over the land areas of the early Tertiary northern hemisphere. These environments, by analogy with the situation in the Upper Permian, should have suited the basic physiological characters of the theropsids. In fact, the theropsids began a spectacular radiation in the early Tertiary, evolving structural

adaptations fitting them for various ecological roles in the environments offered by the main landmasses of the northern hemisphere.

During the late Palaeocene and Eocene there occurred, in many stocks of theropods, a gradual enlargement of the brain, to sizes comparable with those inherited by their later Tertiary and Quaternary representatives. In a few stocks, such as primates, increase in relative size of the brain continued later, through late Cainozoic times. It is reasonable to suppose that general increase in brain size would proceed hand in hand with improvement of the basic physiological characters of theropods, and that these included endothermy, with increase in basal metabolic rate and evolution of better thermo-regulatory mechanisms, and improvement in methods of nitrogen excretion and maintenance of electrolyte balance. Possibly cool nights or cool seasons may have been important factors in selection for improvement of thermo-regulatory mechanisms.

CONCLUSIONS

Had the problem chosen for this Address been one of phylogeny or structural adaptation of the Triassic terrestrial vertebrates, a much more solid array of facts could have been presented, facts produced by a method which has won wide acceptance over a long history of research. For the method of comparative anatomy is fairly old as a scientific discipline, so that today we have a considerable accumulation of data on which to build current researches, and the method will always be the backbone of research in vertebrate palaeontology. But there are moments of depression in which one feels that the only dynamic left in this method is that of an isolating mechanism. Too exclusive a preoccupation with comparative anatomy can bring increasing isolation from other disciplines, from geology and zoology, which ought surely to be regarded as the parent sciences of vertebrate palaeontology.

I am also uneasily aware that, in studying only the anatomy of Triassic vertebrates I am allowing a great deal of the evolution of these forms to go on, as it were, behind my back. For what lies in front of me, as material for research by the methods of comparative anatomy, is, as a rule, just the bare bones on the laboratory bench. And though, because I had an excellent teacher—Professor D. M. S. Watson, F.R.S.—I have learned to extract quite a lot of data from the bare bones, I think that the number of evolutionary problems which can be solved by such data, and the method which produces it, is limited. I believe that no amount of research on bare bones will solve the kind of problem presented by the rather wholesale and sweeping faunal change which affected the major stocks of Triassic reptiles.

To try to solve this problem I have turned from the bare bones on the laboratory bench to the sediments in which they are found, and through this to the study of environment. Yet it must be acknowledged that information on types of terrestrial environments, as obtained from the study of continental environment sediments, is still poor. The study of environment requires that some note be taken of palaeolatitudes and contemporary pole positions, and data on these is still scarce. Palaeolatitudes and pole positions have implications which require a study of the hypothesis of continental drift. The distribution of continent and ocean, and of palaeolatitude, at particular periods of time require some general knowledge of meteorology, for both factors profoundly affect the broad distribution of climate in the world. None of this knowledge of environ-

ments, whether general or particular, can help to solve problems in the evolution of terrestrial vertebrates unless some knowledge of the physiological adaptations of modern representatives is sought, and this knowledge is still in its infancy, though rapidly expanding. The paucity of data in many of these branches of the earth sciences and zoology, and their collective range, sufficiently indicate some of the hazards of this approach. To these is added the danger of too rigid interpretation of some of the data, such as the physiological adaptations of the major taxa. There will always be exceptional genera, as there are at the present day. Perhaps, in the Upper Triassic, tritylodonts were also somewhat exceptional amongst theropsids, as they are not uncommon in some of the late Triassic red-beds, and though not large forms, they are not very small either.

Any tendency to sit in judgement on the physiological 'status' of taxa of vertebrates, because of a decline in their importance at certain periods of time, may also be unwise. The major vertebrate taxa are not 'second-class citizens' but are best regarded simply as groups of terrestrial vertebrates which possess differing arrays of basic physiological characters. These characters are subject to evolutionary change, and they interact with environment. A major factor in determining general environmental conditions is climate, which also changes.

Since mid-Mesozoic times the continents have drifted apart, but the palaeomagnetic data suggests that there has also been a general migration northward of most of the world's continents. As the continents migrated slowly northward across the parallels of latitude, first one set of environmental conditions, and then another, became widespread over the world. These changing environmental distributions offered scope for the basic physiological characters of first one major taxon and then another.

The degree to which certain lithologies become widespread only in certain geological systems has already been remarked. The tectonic factor, influencing the degree to which continents are emergent or submerged, governs the distribution of the two major environments, marine and terrestrial, and also governs local relief, and hence certain aspects of sedimentation. But climate also profoundly influences sedimentation on the continents and their shallow seas. Hence the changing incidence of latitude and landmass, and the size of the latter, are important factors, and have affected the distribution of lithologies and their relative abundance at different periods.

Being ourselves terrestrial animals we can investigate and comprehend the terrestrial environments more easily than those of the seas. The Permian and Triassic, with their abundance of terrestrial lithologies, offer excellent scope for such investigations, and have a fine sequence of terrestrial vertebrate faunas. This is another reason for choosing, as the subject for this Address, a problem of Triassic vertebrates which, I believe, requires us to relate terrestrial vertebrate faunas to their continental environments.

APPENDIX

NOTES ON THE MAPS

Projections. The problem was to obtain good representation of a very large landmass sprawling from pole to pole, and in which south polar regions contained important elements of this landmass. Interrupted projections were not considered as they usually interrupt meridionally. Hence continuous world projections remained and two of these are most commonly used in discussions of continental drift. Both are equal area world maps, one is Mollweide's projection, the other Hammer's (sometimes

known as Aitoff's), the latter being most often used (though it is occasionally referred to as Mollweide's). Both give poor representation of polar areas, as do all other variants of the oval world maps such as Denoyer's semi-elliptical, Sanson's sinusoidal, etc., and also the circular Van der Grinten. Transverse projections of these maps simply shift the poor representation or distortion to some of the 'lateral' meridional areas. Of the oblique equal area projections Breisemeister's and Bartholomew's suffer from the disadvantage of having two south (or north) polar areas and poor representation of the south polar regions. One oblique projection was found to serve very well for pre-drift assemblies, that of Fairgrieve (Close 1929).

Fairgrieve's is an oblique case of Mollweide's equal area projection, in which the great circle of the two 90° meridians is retained but, as it were, tilted on one side so that the poles are centred on the old 45° parallels. The principal meridian and the equator are similar curves but inverted in respect of each other, and both pass through the centre of the bounding ellipse.

It will be seen from the accompanying maps that this projection gives good representation of pre-drift continental assemblies except close to the northern half of the 90° E. meridian, and close to the southern half of the 90° W. meridian. Polar representation is better than in the normal Mollweide projection. The latter has, however, also been given, because it is more familiar, and can be used for comparison with other maps of pre-drift assemblies. Most of the latter are on Hammer's projection, which has curved latitude lines, except the equator, and hence gives very slightly less distortion of polar areas than Mollweide's. In projecting the pre-drift assembly on to the graticules the latitude lines are known, at least for some continents, but meridians are arbitrary. The great circle of the two 90° meridians of the graticule has been emphasized, on the oblique projection, to serve as a reference-frame for comparing the two maps, Upper Triassic and Upper Permian.

Assembly of continents. Most of the more recent assemblies of continents to pre-drift positions have been made from the viewpoint of some particular line of evidence: the fit of continental shelves and upper slopes, palaeomagnetic data for a particular rock formation and continent, mid-oceanic ridges, or special geological features. All four lines of evidence were used in making an assembly for the Upper Triassic, and the data married together remarkably well. The north polar position is 50° N., 150° E., on the present globe and the 80° S. parallel runs through the southern tip of Tasmania (Irving 1964, table 6.2, figures 6.9 and 9.40).

An assembly for the Upper Permian should differ in detail from that for the Upper Triassic, to depict major geological events and features of Upper Permian times. However, owing to shortage of time, the Upper Triassic assembly has been used for the Upper Permian, with a north polar position of 45° N. and 165° E. on the present globe. Inevitably the marriage of all data is not quite so good as for the Upper Triassic, e.g. latitude lines are correct for the east coast of North America, but not quite correct for the west coast, and Australia is about 10° of latitude too far north. It is hoped to make a better reconstruction for the Permian in a later paper, which will give a better synthesis of the evidence, especially for that portion of Gondwanaland which lies in Upper Permian high latitudes.

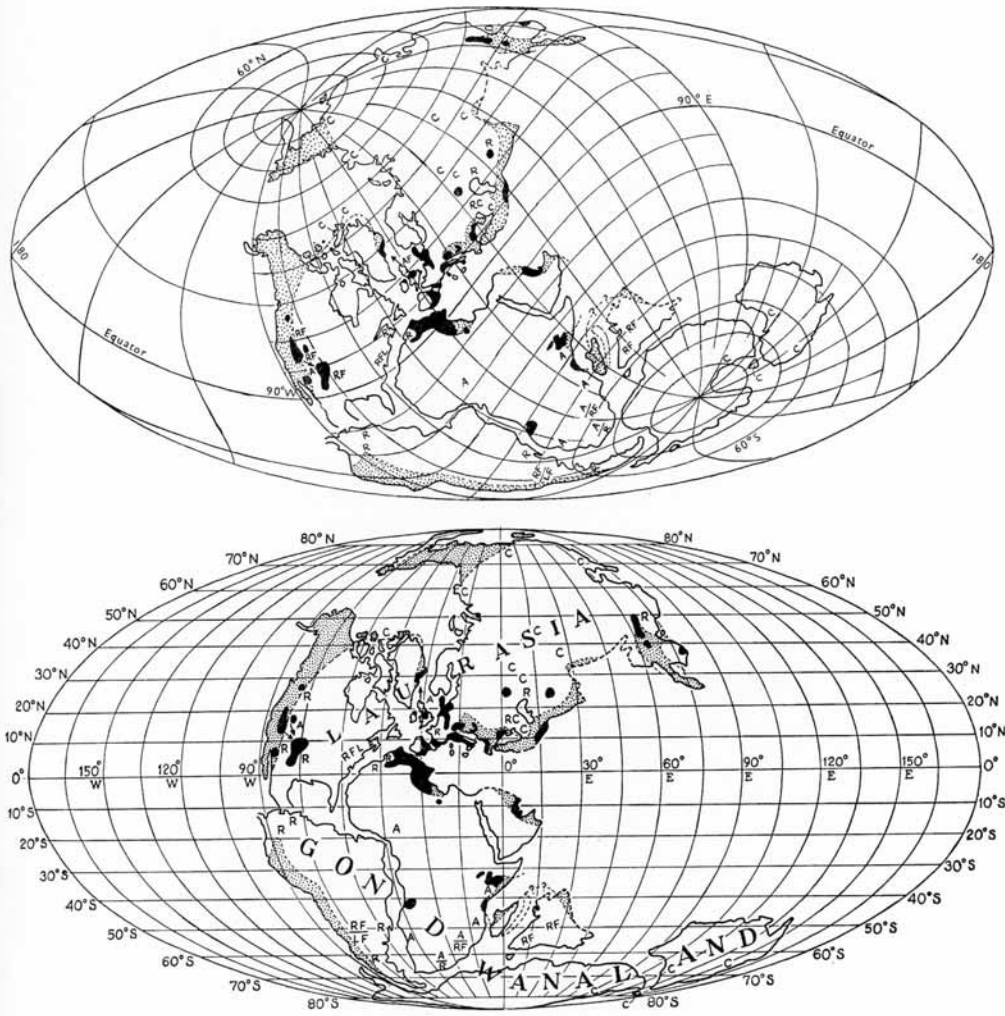
Map data sources. Evaporites: Borchert and Muir 1964, Hepple 1969, Kent 1965, Lefond 1969, Lotze 1957, 1964. Palaeowinds: Poole 1964, Opdyke 1961. Other data from standard texts, especially the *Lexicon Stratigraphique*.

REFERENCES

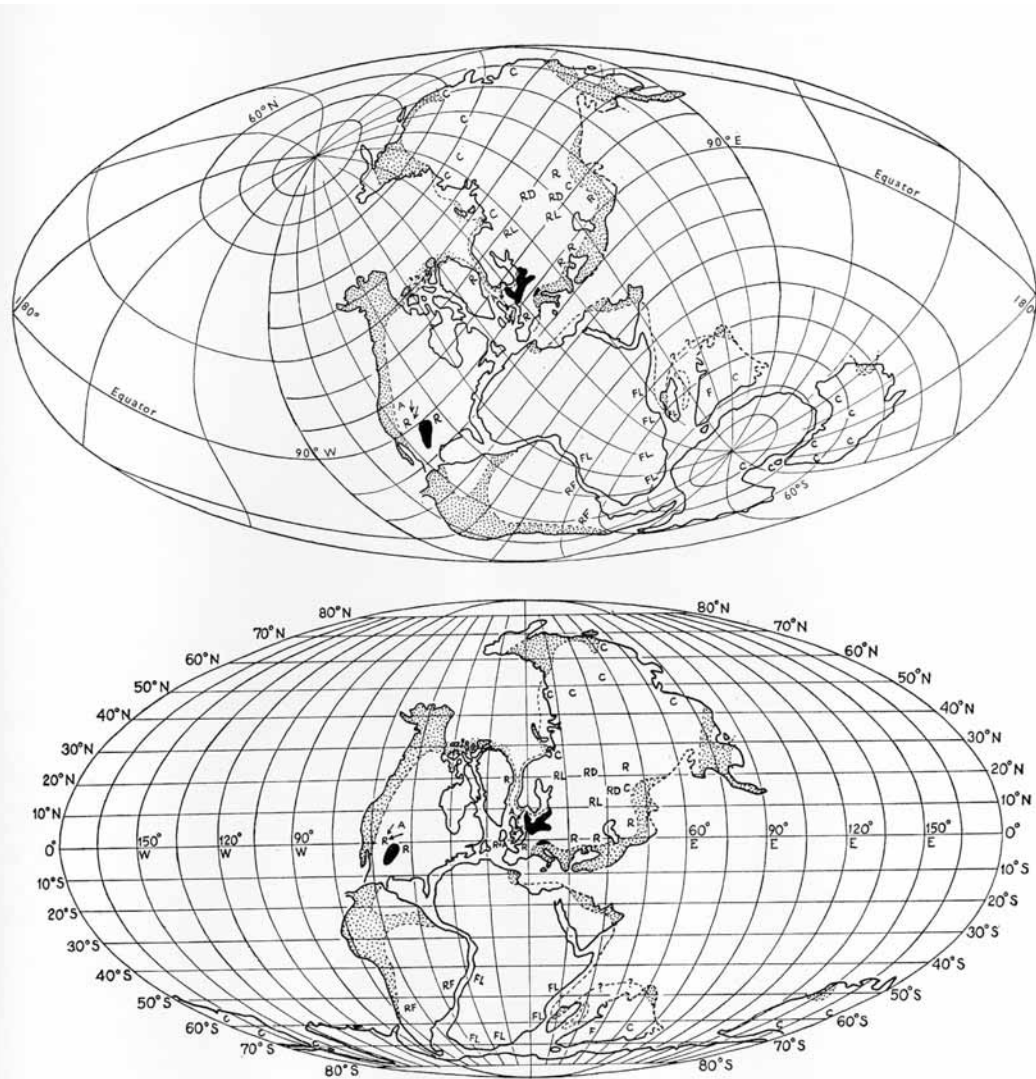
- BARTHOLOMEW, G. A. 1968. Body temperature and energy metabolism. In GORDON, M. S., *Animal function: principles and adaptations*. Macmillan.
- and DAWSON, W. R. 1968. Temperature regulation in desert mammals. In BROWN, G. W. (ed.), *Desert biology*. Academic Press.
- BORCHERT, H. and MUIR, R. O. 1964. *Salt deposits*. Van Nostrand.
- BROWN, G. W. (ed.). 1968. *Desert biology*. Academic Press.
- BULLARD, E., EVERETT, J. E., and GILBERT SMITH, A. 1965. The fit of the continents round the Atlantic. *Phil. Trans. Roy. Soc. Lond.* **A258**, 41–51.
- CHATTERJEE, S. 1969. Rhynchosaurs in time and space. *Proc. geol. Soc. Lond.* **1658**, 203–8.
- CLOSE, C. 1929. An oblique Mollweide projection of the sphere. *Geogr. Jl.*, **73**, 251–3.

- DAWSON, W. R. and BARTHOLOMEW, G. A. 1968. Temperature regulation and water economy of desert birds. In BROWN, G. W. (ed.), *Desert biology*. Academic Press.
- GORDON, M. S. 1968. Water and solute metabolism. In GORDON, M. S., *Animal function: principles and adaptations*. Macmillan.
- HALLEY, E. 1686. An historical account of trade-winds and monsoons with an attempt to assign the physical cause of the said winds. *Phil. Trans. Roy. Soc. Lond.* **16**, 153–68.
- HEPPLE, P. (ed.). 1969. *The exploration for petroleum in Europe and N. Africa*. Inst. Petrol. London.
- HOUTEN, F. B. VAN. 1961. Climatic significance of red beds. In NAIRN, A. E. M. (ed.), *Descriptive palaeoclimatology*. Interscience.
- 1964. Origin of red beds—some unsolved problems. In NAIRN, A. E. M. (ed.), *Problems of palaeoclimatology*. Interscience, Wiley.
- IRVING, E. 1964. *Palaeomagnetism*. Wiley.
- JOHNSON, A. W. 1968. The evolution of desert vegetation in western North America. In BROWN, G. W. (ed.), *Desert biology*. Academic Press.
- KENT, P. E. 1965. An evaporite basin in Southern Tanzania. In *Salt basins around Africa*. Inst. Petrol. Lond., 41–54.
- KUEHNE, W. G. 1968. Contribuição para a fauna do Kimeridgiano da Mina de Lignito Guimarães (Leiria, Portugal) I Parte History of Discovery, etc. *Mem. Serv. geol. Portugal*, **14**, (N.S.), 7–20.
- KUTTY, T. S. 1969. Some contributions to the Upper Gondwana Formations of the Pranhita-Godavari Valley, Central India. *Jl geol. Soc. India*, **10**, 33–48.
- LEFOND, S. J. 1969. *Handbook of world salt resources*. Plenum Press, N.Y.
- LOTZE, F. 1957. *Steinsalz und kalisalze*, 2nd edn., vol. 1. Gebr. Borntraeger, Berlin.
- 1964. The distribution of evaporites in space and time. In NAIRN, A. E. M. (ed.), *Problems in palaeoclimatology*. Interscience.
- MAYHEW, W. W. 1968. Biology of desert amphibians and reptiles. In BROWN, G. W. (ed.), *Desert biology*. Academic Press.
- OPDYKE, N. D. 1961. The Palaeoclimatological significance of desert sandstone. In NAIRN, A. E. M. (ed.), *Descriptive palaeoclimatology*. Interscience.
- PÉDELABORDE, P. 1963. *The Monsoon*. Methuen.
- POOLE, F. G. 1964. Palaeowinds in the western United States. In NAIRN, A. E. M. (ed.), *Problems in palaeoclimatology*. Interscience.
- PROSSER, C. L. and BROWN, F. A. 1961. *Comparative animal physiology*. Saunders.
- ROBINSON, P. L. 1957. The Mesozoic fissures of the Bristol Channel area and their vertebrate faunas. *Jl (zool.) Linn. Soc.* **43** (291) 260.
- 1964. Climates ancient and modern. In *Essays presented to P. C. Mahalanobis F.R.S.* Eka Press and Pergamon Press.
- 1970 (1967). The Indian Gondwana Formations—a review I.U.G.S. *Reviews prepared for the first Symposium on Gondwana Stratigraphy, Mar del Plata Argentina, 1967*.
- 1971 (in press). *Upper Triassic vertebrates and continental drift*.
- ROMER, A. S. 1966. *Vertebrate palaeontology*, 3rd edn. Univ. Chicago Press.
- WALKER, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis Dasygnathus* and their allies. *Phil. Trans. Roy. Soc. Lond.* **B244**, 103–204.
- 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Phil. Trans. Roy. Soc. Lond.* **B248**, 53–134.
- WILSON, J. T. 1963. Continental Drift. *Sci. Amer.* **209**, 86–100.

PAMELA L. ROBINSON
 Department of Zoology
 University College
 Gower Street
 London, W.C. 1



TEXT-FIG. 5. Maps of world palaeogeography in the Upper Triassic, the continents in their correct positions of palaeolatitude (meridians arbitrary), showing the distribution of certain rock types. Lower map on a normal Mollweide projection graticule, upper map on an oblique Mollweide projection graticule. Arrow = wind direction; stipple = major seas, full black = evaporites; A = aeolian, C = coals, D = deltaic, F = fluvatile, L = lacustrine, R = red beds.



TEXT-FIG. 6. Maps of world palaeogeography in the Upper Permian (Kazanian-Tartarian), in approximate positions of palaeolatitude (meridians arbitrary), showing the distribution of certain rock types. Lower map on a normal Mollweide projection graticule, upper map on an oblique Mollweide projection graticule. Arrow = wind direction; stipple = major seas, full black = evaporites; A = aeolian, C = coals, D = deltaic, F = fluvial, L = lacustrine, R = red beds.