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# ABUNDANCE AND DIVERSITY OF THE LABYRINTHODONTS AS A FUNCTION OF PALEOLATITUDE

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ABSTRACT. The distribution of the labyrinthodont Amphibia is found to vary with paleolatitude; although some are found in high paleolatitudes, most occurrences (80 percent) and the greatest diversity in form (as measured by the number of recorded genera) are in paleolatitudes of less than 30°. This dependence of abundance and diversity on latitude is comparable with that observed in modern amphibians. The variation with paleolatitude in the labyrinthodonts is markedly stronger in the late Carboniferous and Permian than in the Triassic; this is taken to reflect the presence of a much stronger latitudinal temperature gradient (perhaps associated with glaciation) in the Upper Paleozoic than in the early Mesozoic.

## 1. INTRODUCTION

That modern animal life is far more abundant and varied within the tropical latitudes than in others was remarked on by Wallace (1876). Since his time, examples of the correlation of organic diversity with latitude for certain animal groups have accumulated. These have been reviewed by Fischer (1960), and they strongly support Wallace's views. It is of much interest to investigate whether similar latitudinal gradients of abundance and diversity occurred in the geological past and then to compare these with the pattern observed in modern forms. In this paper, a study is made of the paleolatitudes of the labyrinthodont amphibians for the time interval late Carboniferous to Rhaetic, using the paleomagnetic data as a basis for estimating paleolatitudes.

As it is known at present, the distribution of the labyrinthodonts in time and over the Earth's surface depends on such factors as the occurrence of suitable environments for preservation and on the extent of geological exploration and study, in addition to the initial distribution of the animals themselves. Moreover, the estimates of paleolatitudes are subject to errors of the order of 10°, inherited from statistical errors in the paleomagnetic determinations. The following analysis is based on paleolatitude estimates of numerous (203)[1] occurrences in North America, Europe, Asia, and Australia so that these fluctuations will tend to be averaged out.

In general terms, the strength of this method is that it is based on comparisons between results of independent studies. On the one hand, the paleogeographical distribution of a given fossil group and its comparison with the zoogeographical distribution of the closest modern relatives may suggest that the occurrences of the members of the group were confined to a certain habitat, which in its turn was subject to a latitudinal temperature control. On the other hand, the paleolatitude estimates are based on an entirely different set of ob-

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[1] This is a reduced figure—see table 2.

servations and assumptions (sec. 4). Therefore, any strong correlation found as a result of these comparisons is likely to be significant, whereas the absence of such correlation may imply either that there is no dependence on paleolatitude or that one or more of the underlying paleoecological or paleomagnetic assumptions is incorrect.

We do not wish to maintain that the analysis that follows is in any sense a final answer to the distribution problems posed; rather we wish only to give an illustration of a type of inter-disciplinary comparison we feel is likely to be of assistance in placing the study of paleozoogeography on a more objective basis than hitherto.

## 2. THE LABYRINTHODONT AMPHIBIA

In the present study, the labyrinthodont amphibians are grouped in six orders (table 1), the first of which, from the Devonian, is not considered here.

TABLE 1

Classification of the Amphibia
(after Piveteau, 1959)

| | |
|---|---|
| Class AMPHIBIA | |
| Sub-Class APSIDOSPONDYLI | (Derived from Osteolepiform Crossopterygians *Osteolepis, Eusthenopteron*) |
| Super-Order Labyrinthodontia | |
| Order Ichthyostegalia | Upper Devonian |
| Order Rhachitomi (R) | Carboniferous to Triassic |
| Order Stereospondyli (S) | Triassic |
| Order Trematosauria (T) | Triassic |
| Order Embolomeri (E) | Carboniferous to Lower Permian |
| Order Seymouriamorpha (SM) | Upper Carboniferous to Permian |
| Super-Order Phyllospondyli | Upper Carboniferous |
| Super-Order Anura (Frogs) | Lower Triassic to Recent |
| Sub-Class URODELOMORPHA | (Derived from Porolepiform Crossopterygians *Porolepis, Holoptychius*) |
| Super-Order Lepospondyli | Carboniferous |
| Super-Order Urodela (Salamanders) | Lower Cretaceous to Recent |
| Super-Order Apoda (Caecilians) | Recent |

Representatives of the Super-Order Labyrinthodontia usually possess a relatively large, bony, low-vaulted skull and are characterized by hollow conical teeth with strongly plicate and grooved enamel, which is considered to be a reflection of their common crossopterygian ancestry.

The labyrinthodonts were chosen for the present study for the following reasons:

1. They are well-defined paleontologically, and there is a considerable fossil record covering the period of time for which many paleomagnetic data are available. They formed an important component of the vertebrate biota of the Upper Paleozoic, and their degenerate, though very large, descendants survived into the Triassic Period from which system their remains have been quite well documented. The fact that the labyrinthodonts are continuous in the

evolutionary scheme across the Paleozoic-Mesozoic boundary is particularly useful. Had a group of animals like the corals, which suffered a strong evolutional change at this time, been chosen, then it would be difficult to separate effects due to environment and those resulting from evolutionary changes in the organisms themselves.

2. By analogy with modern amphibians, they lacked a warm blood supply, and this makes it unlikely that they could have survived cold winters in the open. Moreover, their size (some Permian *Eryops* exceeded 6 feet in length, and some Triassic *Buettneriae* were 9 to 10 feet in length) and absence of digging adaptations make it improbable that they could have burrowed for the purpose of hibernation. By and large, it seems likely that they lived in warm environments, so that their occurrences when considered over their whole time span may be expected to be dependent on latitude. Thus they are a suitable group for use in conjunction with the paleomagnetic data.

3. Their remains are generally associated with deposits the characteristics of which indicate that they were laid down under warm conditions. Rock sequences in which they occur often contain red beds and evaporites (Permian and Triassic), and marine beds of comparable age in the same general region often contain thick limestones and organic reefs.

It is not intended to imply from the last two points that the labyrinthodonts were exclusively inhabitants of warm climates but only that the hypothesis that they were predominantly tropical and subtropical forms is consistent with the geological data. This is not to say that alternative hypotheses based on these same data are not possible. The purpose of taking the hypothesis just stated is that it is one that is amenable to test by independently obtained paleomagnetic data.

Table 2 lists the labyrinthodont genera on which the study is based. It is possible that a few records have been overlooked, but these would scarcely affect the results. The inevitable incompleteness of the fossil record due to lack of exploration or suitable conditions of preservation must be accepted, but it is felt that the records available at present do represent a reasonable sample of the labyrinthodont population.

The list is divided into two parts, (a) late Carboniferous and Permian genera, and (b) Triassic genera. Within each part, the genera are arranged alphabetically according to the continents, commencing with North America and working eastwards. The present geographical position of each generic occurrence is determined to the nearest degree. Records in regions for which no reliable paleomagnetic data are yet available are also listed for future reference.

## 3. THE LATITUDE SPECTRUM OF MODERN AMPHIBIA

Darlington (1957) has pointed out that in the living orders of Amphibia there is good correlation between taxonomic and ecological diversity, on the one hand, and the extent and diversity of the area occupied, on the other. Of the living Amphibia, as shown in table 1, the frogs are the nearest relatives of the labyrinthodonts. The following observations on their distribution are drawn largely from Darlington's book. Frogs, including the toads, comprise 37 families and subfamilies, about 200 or more genera, and perhaps 2000 or more

## TABLE 2

## Late Carboniferous and Permian Labyrinthodonts

Occurrence of a number in the left hand column means that unit weight has been given to this occurrence in compiling the paleolatitude histograms; the absence of a number indicates that repeat finds of the same genus have been made within 5° of arc of one another (*cf.* section 5).

Generic names are followed by letters indicating the order to which a genus belongs, namely, E = Embolomeri, R = Rhachitomi, S = Stereospondyli, SM = Seymouriamorpha, T = Trematosauria.

In right-hand columns, paleolatitudes are denoted + = north and – = south. Letters refer to mean northern hemisphere paleomagnetic pole positions as set out in table 3. (*q.v.*)

| | Genus | Locality | Geographical Position | | Paleolatitude | |
|---|---|---|---|---|---|---|
| 1 | *Acheloma* (R) | Texas | 34N | 99W | –14 | B |
| 2 | *Acroplous* (S) | Kansas | 39N | 97W | –10 | B |
| 3 | *Alegeinosaurus* (R) | Texas | 34N | 99W | –14 | B |
| 4 | *Archeria* (E) | Texas | 34N | 99W | –14 | B |
| 5 | *Aspidosaurus* (R) | Texas | 34N | 99W | –14 | B |
| 6 | *Broiliellus* (R) | Texas | 34N | 99W | –14 | B |
| 7 | *Broiliellus* (R) | New Mexico | 36N | 107W | –10 | B |
| 8 | *Cacops* (R) | Texas | 34N | 99W | –14 | B |
| 9 | *Chenoprosopus* (R) | New Mexico | 36N | 107W | –10 | B |
| 10 | *Dissorophus* (R) | Texas | 34N | 99W | –14 | B |
| 11 | *Eobaphetes* (E) | Kansas | 38N | 97W | –11 | B |
| 12 | *Eobrachyops* | Texas | 34N | 99W | –14 | B |
| 13 | *Eryops* (R) | Texas | 34N | 99W | –14 | B |
| 14 | *Eryops* (R) | New Mexico | 36N | 107W | –10 | B |
| 15 | *Goniocara* | Texas | 34N | 99W | –14 | B |
| 16 | *Neopteroplax* (E) | Texas | 33N | 99W | –15 | B |
| 17 | *Parioxys* (R) | Texas | 34N | 99W | –14 | B |
| 18 | *Platyhystrix* (R) | New Mexico | 36N | 107W | –10 | B |
| 19 | *Seymouria* (SM) | Texas | 34N | 99W | –14 | B |
| 20 | *Slaugenhopia* (R) | Texas | 34N | 99W | –14 | B |
| 21 | *Tersomius* (R) | Texas | 34N | 99W | –14 | B |
| 22 | *Trematops* (R) | Oklahoma | 35N | 99W | –13 | B |
| | *Trematops* (R) | Texas | 34N | 99W | –14 | B |
| 23 | *Trimerorhachis* (R) | Texas | 34N | 99W | –14 | B |
| 24 | *Waggoneria* (SM) | Texas | 34N | 99W | –14 | B |
| 25 | *Zatrachys* (R) | Texas | 34N | 99W | –14 | B |
| 26 | *Zatrachys* (R) | New Mexico | 36N | 107W | –10 | B |
| 27 | *Arkanserpeton* (R) | Arkansas | 36N | 94W | – 8 | A |
| 28 | *Baphetes* (R) | Nova Scotia | 46N | 63W | – 7 | A |
| 29 | *Anthracosaurus* (E) | Ohio | 41N | 81W | – 7 | A |
| 30 | *Colosteus* (R) | Ohio | 41N | 81W | – 7 | A |
| 31 | *Cricotus* (E) | Illinois | 40N | 88W | – 6 | A |
| 32 | *Erierpeton* (R) | Illinois | 41N | 88W | – 5 | A |
| 33 | *Erpetosaurus* (R) | Ohio | 41N | 81W | – 7 | A |
| 34 | *Eryops* (R) | Pennsylvania | 40N | 80W | – 8 | A |
| 35 | *Eumicrerpeton* (R) | Illinois | 41N | 88W | – 5 | A |
| 36 | *Eusauropleura* (SM) | Ohio | 41N | 81W | – 7 | A |
| 37 | *Leptophractus* (R) | Ohio | 41N | 81W | – 7 | A |
| 38 | *Macrerpeton* (R) | Ohio | 41N | 81W | – 7 | A |
| 39 | *Mazonerpeton* (R) | Illinois | 41N | 88W | – 5 | A |
| 40 | *Micrerpeton* (R) | Illinois | 41N | 88W | – 5 | A |
| 41 | *Mytaras* (R) | Ohio | 41N | 81W | – 7 | A |
| 42 | *Neopteroplax* (E) | Ohio | 40N | 81W | – 8 | A |
| 43 | *Pelion* (R) | Ohio | 41N | 81W | – 7 | A |
| 44 | *Platyrhinops* (R) | Ohio | 41N | 81W | – 7 | A |
| 45 | *Saurerpeton* (R) | Ohio | 41N | 81W | – 7 | A |
| 46 | *Stegops* (R) | Ohio | 41N | 81W | – 7 | A |
| 47 | *Tuditanus* (SM) | Ohio | 41N | 81W | – 7 | A |
| 48 | Unidentified | Pennsylvania | 40N | 80W | – 8 | A |

TABLE 2 (Continued)

| | Genus | Locality | Geographical Position | | Paleolatitude | |
|---|---|---|---|---|---|---|
| 49 | Unidentified | West Virginia | 40N | 81W | -11 | A |
| 50 | *Acanthostoma* (R) | Dresden | 51N | 14E | + 7 | D |
| 51 | *Actinodon* (R) | Autun | 47N | 4E | + 1 | D |
| | *Actinodon* (R) | Saar | 49N | 7E | + 4 | D |
| 52 | *Archegosaurus* (R) | Saar | 49N | 7E | + 4 | D |
| 53 | *Branchiosaurus* | Bourbon-l'Archambault | 47N | 3E | + 1 | D |
| | *Branchiosaurus* | Commentry | 46N | 3E | 0 | D |
| 54 | *Branchiosaurus* | Halle | 51N | 12E | + 6 | D |
| 55 | *Dasyceps* (R) | Kenilworth | 52N | 2W | + 1 | D |
| 56 | *Discosauriscus* (R) | Dresden | 51N | 14E | + 7 | D |
| 57 | *Leptorophus* (R) | Odernheim | 50N | 8E | + 5 | D |
| 58 | *Micromelerpeton* (R) | Odernheim | 50N | 8E | + 5 | D |
| | *Micromelerpeton* (R) | Thuringia | 50N | 10E | + 5 | D |
| 59 | *Onchiodon* (R) | Dresden | 51N | 14E | + 7 | D |
| 60 | *Pelosaurus* (R) | Rheinpfalz | 50N | 8E | + 5 | D |
| | *Pelosaurus* (R) | Sankt Wendel | 49N | 7E | + 4 | D |
| 61 | *Phaiherpeton* (SM) | Dresden | 51N | 14E | + 7 | D |
| 62 | *Protriton* (R) | Autun | 47N | 4E | + 1 | D |
| 63 | *Sclerocephalus* (R) | Rheinpfalz | 50N | 7E | + 5 | D |
| 64 | *Adenoderma* (SM) | Třemošná | 50N | 13E | + 6 | D |
| 65 | *Chelydosaurus* (R) | Brno | 49N | 17E | + 6 | D |
| 66 | *Cochleosaurus* (R) | Nýřany | 50N | 13E | + 6 | D |
| 67 | *Dawsonia* (R) | Kounová | 50N | 14E | + 6 | D |
| 68 | *Diplovertebron* (SM) | Nýřany | 50N | 13E | + 6 | D |
| 69 | *Gaudrya* (R) | Nýřany | 50N | 13E | + 6 | D |
| 70 | *Letoverpeton* (SM) | Boskovice | 50N | 17E | + 7 | D |
| 71 | *Loxomma* (R) | Nýřany | 50N | 13E | + 6 | D |
| 72 | *Lusor* (R) | Ruprechtice | 49N | 17E | + 6 | D |
| 73 | *Memonomenos* (E) | Košťálov | 49N | 17E | + 6 | D |
| | *Memonomenos* (E) | Kounová | 50N | 14E | + 6 | D |
| 74 | *Mordax* (R) | Nýřany | 50N | 13E | + 6 | D |
| 75 | *Nummulosaurus* (E) | Třemošná | 50N | 13E | + 6 | D |
| | *Onchiodon* (R) | Kounová | 50N | 14E | + 6 | D |
| | *Phaiherpeton* (SM) | Brno | 49N | 17E | + 6 | D |
| | *Phaiherpeton* (SM) | Boskovice | 50N | 17E | + 7 | D |
| | *Phaiherpeton* (SM) | Horní Kulná | 50N | 17E | + 7 | D |
| 76 | *Potamochoston* (R) | Nýřany | 50N | 13E | + 6 | D |
| 77 | *Solenodonsaurus* (SM) | Nýřany | 50N | 13E | + 6 | D |
| 78 | *Osteophorus* (R) | Klein-Neundorf | 51N | 17E | + 8 | D |
| 79 | *Archegosaurus* (R) | Inta River | 66N | 60E | +32 | D |
| 80 | *Buzulukia* (SM) | Pron'kino | 52N | 53E | +22 | D |
| 81 | *Buzulukia* (SM) | Kotlas | 62N | 47E | +26 | D |
| 82 | *Bystrowiana* | Kotlas | 62N | 47E | +26 | D |
| 83 | *Chalcosaurus* (R) | Mamadysh | 56N | 51E | +22 | D |
| | *Chalcosaurus* (R) | Chkalov | 52N | 55E | +22 | D |
| 84 | *Chorionosuchus* (SM) | Pron'kino | 52N | 53E | +22 | D |
| 85 | *Chorionosuchus* (SM) | Gorky | 56N | 44E | +22 | D |
| 86 | *Chorionosuchus* (SM) | Kotlas | 62N | 47E | +26 | D |
| 87 | *Discosauriscus* (SM) | Chkalov | 52N | 55E | +22 | D |
| 88 | *Dvinosaurus* (R) | Sokolki | 61N | 47E | +25 | D |
| 89 | *Dvinosaurus* (R) | Il'inskoe | 55N | 49E | +21 | D |
| 90 | *Dvinosaurus* (R) | Gorky | 56N | 44E | +21 | D |
| | *Dvinosaurus* (R) | Kotel'nichi | 58N | 48E | +23 | D |
| | *Dvinosaurus* (R) | Gremyachy Klyuch | 60N | 44E | +23 | D |
| | *Dvinosaurus* (R) | Maurnikovskaya | 60N | 43E | +23 | D |
| | *Dvinosaurus* (R) | Aristovo | 61N | 46E | +25 | D |
| | *Dvinosaurus* (R) | Golodaevo | 61N | 46E | +25 | D |
| | *Dvinosaurus* (R) | Zavrazh'e | 62N | 48E | +26 | D |
| | *Dvinosaurus* (R) | Mar'yushkina Sluda | 61N | 46E | +25 | D |
| | *Dvinosaurus* (R) | Porog | 61N | 46E | +25 | D |
| | *Dvinosaurus* (R) | Strizhenskaya Mts | 60N | 43E | +22 | D |

TABLE 2 (Continued)

| | Genus | Locality | Geographical Position | | Paleolatitude | |
|---|---|---|---|---|---|---|
| 91 | *Enosuchus* (S) | Isheevo | 55N | 50E | +21 | D |
| 92 | *Gnorhimosuchus* (SM) | Kazakhstan | 50N | 67E | +27 | D |
| 93 | *Intasuchus* (R) | Inta River | 66N | 60E | +32 | D |
| 94 | *Jugosuchus* (R) | Kotlas | 62N | 47E | +26 | D |
| | *Jugosuchus* (R) | North Dvina River | 61N | 47E | +25 | D |
| 95 | *Kotlassia* (SM) | Kotlas | 62N | 47E | +26 | D |
| 96 | *Kotlassia* (SM) | Strizhenskaya Mts | 60N | 43E | +22 | D |
| 97 | *Kotlassia* (SM) | Il'inskoe | 55N | 49E | +21 | D |
| 98 | *Kotlassia* (SM) | Pron'kino | 52N | 53E | +22 | D |
| | *Kotlassia* (SM) | Gorky | 56N | 44E | +21 | D |
| 99 | *Lanthanosuchus* (SM) | Malyy Churan | 53N | 54E | +22 | D |
| 100 | *Lanthanosuchus* (SM) | Isheevo | 55N | 50E | +21 | D |
| 101 | *Melosaurus* (R) | Mesen' | 66N | 45E | +28 | D |
| 102 | *Melosaurus* (R) | Pechora | 65N | 57E | +30 | D |
| 103 | *Melosaurus* (R) | Udmurtiya | 57N | 52E | +23 | D |
| 104 | *Melosaurus* (R) | Malyy Churan | 53N | 54E | +22 | D |
| 105 | *Melosaurus* (R) | Shikhovo-Chirki | 58N | 48E | +23 | D |
| | *Melosaurus* (R) | Sterlitamak | 54N | 56E | +23 | D |
| | *Melosaurus* (R) | Kirov Province | 56N | 51E | +22 | D |
| | *Melosaurus* (R) | Chkalov | 52N | 55E | +22 | D |
| | *Melosaurus* (R) | Malaya Kinel' | 53N | 53E | +22 | D |
| | *Melosaurus* (R) | Mikhaylovsky Mine | 58N | 53E | +24 | D |
| | *Melosaurus* (R) | Akbatirovsky Mine | 56N | 50E | +23 | D |
| 106 | *Platyops* (R) | Golyusherma | 58N | 53E | +24 | D |
| 107 | *Platyops* (R) | Shikhovo-Chirki | 58N | 48E | +23 | D |
| 108 | *Platyops* (R) | Malaya Kinel' | 53N | 53E | +22 | D |
| 109 | *Platyops* (R) | Kotlovka | 56N | 52E | +22 | D |
| | *Platyops* (R) | Chkalov | 52N | 55E | +22 | D |
| | *Platyops* (R) | Mamadysh | 56N | 51E | +22 | D |
| | *Platyops* (R) | Belebey | 54N | 54E | +23 | D |
| | *Platyops* (R) | Ulema River | 55N | 49E | +21 | D |
| | *Platyops* (R) | Mesen' | 66N | 45E | +28 | D |
| | *Platyops* (R) | Vyatka River | 56N | 51E | +22 | D |
| | *Platyops* (R) | Kamskie Forest | 56N | 52E | +22 | D |
| 110 | *Rhinosaurus* (SM) | Ulyanovsk | 54N | 48E | +20 | D |
| 111 | *Syndyodosuchus* (R) | Inta River | 66N | 60E | +32 | D |
| 112 | *Tryphosuchus* (R) | Isheevo | 55N | 50E | +21 | D |
| 113 | *Tungussogyrinus* (S) | Krivlyaki | 61N | 99E | +47 | D |
| 114 | *Tungussogyrinus* (S) | Tungus Basin | 64N | 106E | +50 | D |
| 115 | *Zygosaurus* (R) | Bashkiria | 54N | 55E | +23 | D |
| 116 | *Zygosaurus* (R) | Ulema River | 55N | 49E | +21 | D |
| | *Zygosaurus* (R) | Durasovsky Mine | 53N | 55E | +22 | D |
| | *Zygosaurus* (R) | Chkalov | 52N | 55E | +22 | D |
| 117 | Unidentified | Gorodishche | 58N | 56E | +26 | D |
| 118 | ” | Dudki | 52N | 55E | +22 | D |
| 119 | ” | Yugovsky Mine | 57N | 56E | +25 | D |
| 120 | Unidentified | Goloshubina | 56N | 44E | +22 | D |
| | ” | Vyshka | 58N | 56E | +26 | D |
| | ” | Bizyaki | 56N | 53E | +22 | D |
| | ” | Vyazniki | 56N | 42E | +21 | D |
| | ” | Kraakul' | 56N | 51E | +22 | D |
| | ” | Abdi | 56N | 51E | +22 | D |
| | ” | Nizhnee Churilino | 56N | 50E | +22 | D |
| | ” | Tatarskie Kirmeni | 56N | 51E | +22 | D |
| | ” | Shebulatova | 56N | 51E | +22 | D |
| | ” | Sher'ya | 55N | 55E | +24 | D |
| | ” | Krasnaya Kadka | 55N | 52E | +22 | D |
| | Unidentified (R) | Kichkas | 52N | 54E | +22 | D |
| | Unidentified | Cheremushka | 56N | 49E | +23 | D |
| | ” | Golyusherma | 58N | 53E | +25 | D |
| | ” | Santagulov Mine | 54N | 54E | +23 | D |
| | ” | Samodurovka | 56N | 51E | +22 | D |

TABLE 2 (Continued)

| | Genus | Locality | Geographical Position | | Paleolatitude | |
|---|---|---|---|---|---|---|
| 121 | *Bothriceps* (S) | New South Wales | c.32S | 151E | c.–70 | F |
| 122 | *Trucheosaurus* (R) | Lithgow | 32S | 147E | –70 | F |
| | *Laccosaurus* (R) | Ferndale | 32S | 25E | | |
| | *Micropholis* (R) | Rhenosterberg | 31S | 25E | | |
| | *Muchocephalus* (R) | Ringsfontein | 32S | 24E | | |
| | *Phrynosuchus* | Fraserburg | 32S | 22E | | |
| | *Rhinesuchoides* (R) | Stinkfontein | 32S | 24E | | |
| | *Rhinesuchus* (R) | Seekoegat | 33S | 23E | | |
| | *Rhinesuchus* (R) | Blaauw Krantz | 33S | 22E | | |
| | *Rhineceps* (R) | Nyasaland | 11S | 34E | | |
| | "*Archegosaurus*" | Khunmu | 32N | 72E | | |
| | *Actinodon* (R) | Vihi | 32N | 72E | | |
| | *Actinodon* (R) | Zewan | 32N | 72E | | |

## Triassic Labyrinthodonts

| | Genus | Locality | Geographical Position | | Paleolatitude | |
|---|---|---|---|---|---|---|
| 1 | *Anaschisma* (S) | Wyoming | 43N | 109W | +16 | C |
| 2 | ? *Aphaneramma* | Arizona | 36N | 111W | +10 | C |
| 3 | *Buettneria* (S) | Texas | 32N | 102W | + 3 | C |
| 4 | *Buettneria* (S) | Arizona | 35N | 110W | + 9 | C |
| | *Buettneria* (S) | New Mexico | 36N | 107W | +10 | C |
| 5 | ? *Capitosaurus* | Arizona | 36N | 111W | +10 | C |
| 6 | *Cyclotosaurus* (S) | Arizona | 35N | 110W | + 9 | C |
| 7 | *Dictyocephalus* (S) | North Carolina | 36N | 79W | + 5 | C |
| 8 | *Eupelor* (S) | Pennsylvania | 40N | 77W | + 9 | C |
| | *Eupelor* (S) | " | 40N | 75W | + 9 | C |
| | *Eupelor* (S) | " | 40N | 76W | + 9 | C |
| 9 | *Kalamoiketor* (S) | Arizona | 35N | 110W | + 9 | C |
| 10 | *Rhadalognathus* (S) | Arizona | 35N | 110W | + 9 | C |
| 11 | *Stanocephalosaurus* (S) | Arizona | 35N | 111W | + 9 | C |
| 12 | *Hadrokkosaurus* | Arizona | 35N | 110W | + 9 | C |
| 13 | *Diadetognathus* (S) | Warwick | 52N | 2W | +17 | E |
| 14 | "*Labyrinthodon*" | Sidmouth | 51N | 3W | +16 | E |
| 15 | *Metoposaurus* (S) | ? Bristol | 51N | 3W | +16 | E |
| 16 | *Procyclotosaurus* (S) | Stafford | 53N | 2W | +18 | E |
| 17 | "*Cyclotosaurus*" (S) | Lorraine | 49N | 6E | +16 | E |
| 18 | *Mastodonsaurus* (S) | Wasselnheim | 49N | 7E | +17 | E |
| | *Mastodonsaurus* (S) | Lunéville | 49N | 7E | +17 | E |
| 19 | *Metoposaurus* (S) | Lorraine | 49N | 6E | +16 | E |
| 20 | *Plagiosaurus* (S) | Lunéville | 49N | 7E | +17 | E |
| 21 | *Plagiosuchus* (S) | Lorraine | 49N | 6E | +16 | E |
| 22 | *Xestorhytias* | Lunéville | 49N | 7E | +17 | E |
| 23 | *Capitosaurus* (S) | Benk | 50N | 12E | +19 | E |
| | *Cyclotosaurus* (S) | Stuttgart | 49N | 9E | +17 | E |
| | ? *Cyclotosaurus* (S) | Schötmar | 52N | 9E | +20 | E |
| | *Cyclotosaurus* (S) | North Baden | 49N | 9E | +17 | E |
| | *Cyclotosaurus* (S) | Pfaffenhofen | 49N | 12E | +18 | E |
| | *Cyclotosaurus* (S) | Halberstadt | 52N | 11E | +20 | E |
| 24 | *Cyclotosaurus* (S) | Ebrach | 50N | 11E | +19 | E |
| 25 | *Gerrothorax* (S) | Swabia | 49N | 10E | +17 | E |
| | *Gerrothorax* (S) | Ebrach | 50N | 11E | +19 | E |
| | *Gerrothorax* (S) | Pfaffenhofen | 49N | 12E | +18 | E |
| 26 | *Gerrothorax* (S) | Bjuv | 56N | 13E | +24 | E |
| 27 | *Hercynosaurus* (S) | Halberstadt | 52N | 11E | +20 | E |
| 28 | *Hyperokynodon* (S) | Heilbronn | 49N | 9E | +17 | E |
| 29 | "*Labyrinthodon*" | Herzogenweiler | 48N | 8E | +16 | E |
| 30 | *Mastodonsaurus* (S) | Crailsheim | 49N | 10E | +17 | E |
| | *Mastodonsaurus* (S) | Gaildorf | 49N | 10E | +17 | E |

TABLE 2 (Continued)

| | Genus | Locality | Geographical Position | | Paleolatitude | |
|---|---|---|---|---|---|---|
| 31 | *Mastodonsaurus* (S) | Halle | 51N | 12E | +20 | E |
| | *Mastodonsaurus* (S) | Hoheneck | 48N | 10E | +17 | E |
| | *Mastodonsaurus* (S) | Bavarian Alps | 48N | 12E | +17 | E |
| | *Mastodonsaurus* (S) | Markgröningen | 49N | 9E | +17 | E |
| | *Mastodonsaurus* (S) | Würzburg | 50N | 10E | +18 | E |
| | *Mastodonsaurus* (S) | Altensteig | 49N | 9E | +17 | E |
| | *Mastodonsaurus* (S) | Kappel | 49N | 8E | +17 | E |
| 32 | *Mentosaurus* (S) | Halle | 51N | 12E | +20 | E |
| 33 | *Metoposaurus* (S) | Thuringia | 52N | 11E | +20 | E |
| 34 | *Metoposaurus* (S) | South Tyrol | 47N | 13E | +17 | E |
| | *Metoposaurus* (S) | Stuttgart | 49N | 9E | +17 | E |
| | *Metoposaurus* (S) | Ebrach | 50N | 11E | +19 | E |
| 35 | *Odontosaurus* (S) | Sulzbach | 49N | 12E | +18 | E |
| 36 | *Parotosaurus* (S) | Heligoland | 54N | 8E | +21 | E |
| 37 | *Parotosaurus* (S) | Bernburg | 52N | 12E | +21 | E |
| 38 | *Plagiosaurus* (S) | Halberstadt | 52N | 11E | +20 | E |
| 39 | *Plagiosternum* (S) | Crailsheim | 49N | 10E | +17 | E |
| | *Plagiosternum* (S) | Gaildorf | 49N | 10E | +17 | E |
| | *Plagiosternum* (S) | Poppenlauer | 50N | 10E | +18 | E |
| | *Plagiosternum* (S) | Thuringia | 52N | 11E | +20 | E |
| 40 | *Plagiosuchus* (S) | Thuringia | 52N | 11E | +20 | E |
| | *Plagiosuchus* (S) | Crailsheim | 49N | 10E | +17 | E |
| | *Plagiosuchus* (S) | Gaildorf | 49N | 10E | +17 | E |
| 41 | *Sclerothorax* (R) | Queck | 51N | 9E | +19 | E |
| 42 | *Stenotosaurus* (S) | Villingen | 48N | 8E | +16 | E |
| 43 | *Trematosaurus* (T) | Kahla | 51N | 12E | +20 | E |
| | *Trematosaurus* (T) | Waldkatzenback | 49N | 9E | +17 | E |
| 44 | *Trematosaurus* (T) | Bernburg | 52N | 12E | +21 | E |
| 45 | *Trigonosternum* | Kolleda | 51N | 11E | +19 | E |
| 46 | *Parotosaurus* (S) | Gogolin | 51N | 18E | +23 | E |
| 47 | *Benthosuchus* (R) | Glinyany Ovrag | 53N | 53E | +37 | E |
| 48 | *Benthosuchus* (R) | Donskaya Luka | 48N | 43E | +31 | E |
| 49 | *Benthosuchus* (R) | Annikovo | 60N | 38E | +34 | E |
| 50 | *Benthosuchus* (R) | Sheksna | 58N | 39E | +35 | E |
| 51 | *Benthosuchus* (R) | Tikhvinskoe | 58N | 39E | +35 | E |
| | *Benthosuchus* (R) | Shumova | 58N | 41E | +35 | E |
| | *Benthosuchus* (R) | Yuza | 59N | 44E | +37 | E |
| | *Benthosuchus* (R) | Timoshin Log | 59N | 46E | +38 | E |
| | *Benthosuchus* (R) | Koshurnikovo | 59N | 51E | +38 | E |
| | *Benthosuchus* (R) | Dyn'Yu | 60N | 48E | +39 | E |
| | *Benthosuchus* (R) | Fedorovka | 60N | 50E | +39 | E |
| | *Benthosuchus* (R) | Kas'yanovskaya | 59N | 48E | +39 | E |
| | *Benthosuchus* (R) | Vakhnevo | 60N | 45E | +39 | E |
| | *Benthosuchus* (R) | Shardenga River | 60N | 44E | +39 | E |
| | *Benthosuchus* (R) | Kula | 64N | 47E | +39 | E |
| | *Benthosuchus* (R) | Mutus'ya | 65N | 47E | +40 | E |
| | *Benthosuchus* (R) | Noba | 65N | 48E | +41 | E |
| | *Benthosuchus* (R) | Tsyl'ma | 65N | 51E | +42 | E |
| | *Benthosuchus* (R) | Vybor | 65N | 48E | +41 | E |
| | Benthosuchid | Por-Iol' | 60N | 48E | +39 | E |
| | Benthosuchid | Luza | 60N | 48E | +39 | E |
| | Benthosuchid | Kudrino | 59N | 46E | +39 | E |
| | Benthosuchid | Loyma | 60N | 48E | +39 | E |
| | Benthosuchid | Podgor'e | 60N | 47E | +39 | E |
| | Benthosuchid | Podsaraitsa | 60N | 48E | +39 | E |
| | Benthosuchid | Skoba | 60N | 48E | +39 | E |
| | Benthosuchid | Slude | 60N | 46E | +39 | E |
| | Benthosuchid | Chortova Mine | 60N | 45E | +38 | E |
| 52 | ? "*Capitosaurus*" | Chkalov | 52N | 55E | +37 | E |

TABLE 2 (Continued)

| | Genus | Locality | Geographical Position | | Paleolatitude | |
|---|---|---|---|---|---|---|
| 53 | *"Capitosaurus"* | Mt Great Bogdo | 48N | 47E | +31 | E |
| | ? *Capitosaurus* (S) | Donskaya Luka | 48N | 43E | +31 | E |
| | *Capitosaurus* (S) | Koltaevo | 52N | 56E | +37 | E |
| 54 | *Mastodonsaurus* (S) | River Yushatyr | 53N | 55E | +38 | E |
| | *Mastodonsaurus* (S) | Koltaevo | 52N | 56E | +37 | E |
| 55 | *Parabenthosuchus* (R) | Dongus River | 52N | 55E | +37 | E |
| 56 | *Plagiorophus* | Koltaevo | 52N | 56E | +37 | E |
| 57 | *Rhinesuchus* (R) | Vologda | 59N | 40E | +36 | E |
| 58 | *Thoösuchus* (R) | Cheremkha | 58N | 39E | +35 | E |
| 59 | *Thoösuchus* (R) | Ples | 57N | 42E | +35 | E |
| | *Thoösuchus* (R) | Semigor'e | 57N | 42E | +35 | E |
| | *Thoösuchus* (R) | Reshma | 57N | 43E | +35 | E |
| | *Thoösuchus* (R) | Yuza | 59N | 44E | +36 | E |
| | *Thoösuchus* (R) | Zubovskoe | 59N | 46E | +37 | E |
| | *Thoösuchus* (R) | Sludka Bol'shaya | 58N | 45E | +37 | E |
| | *Thoösuchus* (R) | Vakhnevo | 60N | 45E | +38 | E |
| 60 | *Trematosaurus* (T) | Mt Great Bogdo | 48N | 47E | +31 | E |
| 61 | *Trematosuchus* (T) | Rybinsk | 58N | 39E | +35 | E |
| 62 | *Volgosaurus* (R) | Kineshma | 57N | 42E | +35 | E |
| 63 | *Volgosuchus* (R) | Kineshma | 57N | 42E | +35 | E |
| | *Volgosuchus* (R) | Krasnye Pozhni | 57N | 42E | +35 | E |
| | *Volgosuchus* (R) | Ples | 57N | 42E | +35 | E |
| 64 | *Wetlugasaurus* (R) | Khudynino | 57N | 42E | +35 | E |
| 65 | *Wetlugasaurus* (R) | Vetluga River | 58N | 46E | +37 | E |
| 66 | *Wetlugasaurus* (R) | Chërny Bor | 60N | 48E | +39 | E |
| 67 | *Wetlugasaurus* (R) | Zubovskoe | 59N | 46E | +39 | E |
| 68 | *Wetlugasaurus* (R) | Teryukhan | 60N | 51E | +39 | E |
| | *Wetlugasaurus* (R) | Kula | 64N | 47E | +40 | E |
| | *Wetlugasaurus* (R) | Chernyshata | 60N | 54E | +41 | E |
| | *Wetlugasaurus* (R) | Sausara | 62N | 51E | +42 | E |
| | *Wetlugasaurus* (R) | Usa | 65N | 51E | +43 | E |
| | *Wetlugasaurus* (R) | Reshma | 57N | 43E | +35 | E |
| | *Wetlugasaurus* (R) | Semigor'e | 57N | 42E | +35 | E |
| | *Wetlugasaurus* (R) | Sludka Bol'shaya | 58N | 45E | +37 | E |
| | *Wetlugasaurus* (R) | Tarpanka | 52N | 52E | +37 | E |
| | *Lonchorhynchus* (S) | Ostrov Russky | 43N | 132E | | |
| 69 | Unidentified (R) | Zaplavnoe | 53N | 52E | +37 | E |
| 70 | Unidentified | Koinass | 65N | 48E | +41 | E |
| | " | Aksarovo | 53N | 56E | +38 | E |
| | " | Blizhny ruchey | 65N | 48E | +41 | E |
| 71 | " | Ukhtubuzh | 59N | 45E | +37 | E |
| | " | Glinyany ovrag | 53N | 53E | +37 | E |
| | " | Markovka | 53N | 53E | +37 | E |
| | " | Pogromnaya | 53N | 52E | +37 | E |
| | " | Sukhaya Tavolzhanka | 53N | 51E | +36 | E |
| | " | S'ezzhaya | 53N | 51E | +36 | E |
| | " | Tarpanka | 52N | 52E | +35 | E |
| | " | Usmanka | 53N | 52E | +36 | E |
| | " | Yarenga | 62N | 48E | +39 | E |
| | " | Buko-Bay | 51N | 55E | +36 | E |
| 72 | *Australopelor* (S) | Lowood | 27S | 153E | –69 | G |
| 73 | *"Batrachosuchus"* (S) | Erskine Range | 18S | 124E | –49 | G |
| 74 | *"Capitosaurus"* (S) | Hobart | 43S | 147E | –79 | G |
| 75 | *"Capitosaurus"* (S) | Erskine Range | 18S | 124E | –49 | G |
| 76 | *"Mastodonsaurus"* (S) | Sydney | 34S | 151E | –71 | G |
| | *"Mastodonsaurus"* (S) | Bowral | 34S | 150E | –71 | G |
| 77 | *Paracyclotosaurus* (S) | Sydney | 34S | 151E | –71 | G |
| 78 | *"Platyceps"* (S) | Gosford | 34S | 151E | –71 | G |
| 79 | *"Rhytidosteus"* (S) | Erskine Range | 18S | 124E | –49 | G |
| 80 | *Subcyclotosaurus* (S) | Beacon Hill | 32S | 150E | –69 | G |
| 81 | *"Trematosaurus"* (T) | Erskine Range | 18S | 124E | –49 | G |

TABLE 2 (Continued)

| Genus | Locality | Geographical Position | | Paleolatitude |
|---|---|---|---|---|
| *Batrachosuchus* (S) | Aliwal North | 31S | 27E | |
| *Broomulus* (R) | Harrismith | 28S | 29E | |
| *"Capitosaurus"* (S) | Vaalbank | 33S | 22E | |
| *Cyclotosaurus* (S) | Rouxville | 30S | 27E | |
| *Kestrosaurus* (S) | Senekal | 28S | 28E | |
| *Laccocephalus* (R) | Smithfield | 30S | 26E | |
| *Laidleria* (T) | Elucwecwe | 32S | 28E | |
| *Limnoiketes* (S) | Harrismith | 28S | 29E | |
| *Lydekkerina* (R) | Harrismith | 28S | 29E | |
| *Lydekkerina* (R) | Edenburg | 30S | 26E | |
| *Microposaurus* (S) | Wonderboom | 31S | 26E | |
| *Parotosaurus* | Winaarsbaken | 33S | 22E | |
| *Ptychosphenodon* | Aliwal North | 31S | 27E | |
| *Putterillia* | Harrismith | 28S | 29E | |
| *Rhinesuchus* (R) | Beaufort West | 32S | 23E | |
| *Rhinesuchus* (R) | Spitzkop | 32S | 25E | |
| *Rhytidosteus* (S) | Beersheba | 26S | 18E | |
| *Rhytidosteus* (S) | Wonderboom | 31S | 26E | |
| *Syphonodon* (S) | Wonderboom | 31S | 26E | |
| *Trematosuchus* (T) | Queenstown | 32S | 27E | |
| *Uranocentrodon* (R) | Graaf-Reinet | 32S | 25E | |
| *Uranocentrodon* (R) | Senekal | 28S | 28E | |
| *Wetlugasaurus* (R) | Watford | 33S | 22E | |
| *Benthosuchus* (R) | Ambilobe | 13S | 49E | |
| ? *Uranocentrodon* (R) | Ranohira | 23S | 45E | |
| *Wantzosaurus* | Ambilobe | 13S | 49E | |
| *Wetlugasaurus* (R) | Ambilobe | 13S | 49E | |
| Unidentified | Ruhuhu | 10S | 35E | |
| *Aphaneramma* (T) | Spitzbergen | 78N | 17E | |
| *Boreosaurus* (R) | Spitzbergen | 78N | 17E | |
| *Cyclotosaurus* (S) | Spitzbergen | 78N | 17E | |
| *Lyrocephalus* (T) | Spitzbergen | 78N | 17E | |
| *Parotosaurus* (S) | Spitzbergen | 78N | 17E | |
| *Peltostega* (T) | Spitzbergen | 78N | 17E | |
| *Platystega* (T) | Spitzbergen | 78N | 17E | |
| *Sassenisaurus* (R) | Spitzbergen | 78N | 17E | |
| *Tertrema* (T) | Spitzbergen | 78N | 17E | |
| *Archegosaurus* (R) | Risin Spur | 32N | 72E | |
| *Brachyops* (S) | Nagpur | 21N | 79E | |
| *Gondwanosaurus* (R) | Central Provinces | 22N | 76E | |
| *Gonioglyptus* (T) | Raniganj | 26N | 87E | |
| *Gonioglyptus* (T) | Chideru | 32N | 72E | |
| *Pachygonia* (R) | Raniganj | 26N | 87E | |
| *Chigutisaurus* (S) | Las Heras | 33S | 69W | |
| *Otuminisaurus* (S) | Las Heras | 33S | 69W | |
| *Pelorocephalus* (S) | Potrerillos | 33S | 69W | |
| *"Lyrocephalus"* (S) | East Greenland | 74N | 22W | |
| *Stoschiosaurus* (S) | East Greenland | 74N | 22W | |
| *Wetlugasaurus* (R) | East Greenland | 74N | 22W | |
| Unidentified (S) | Western High-Atlas | 31N | 8W | |

known species. They are very widely distributed in both hemispheres with representatives in arid and other unfavorable places as well as favorable ones, and they range farther north and south and much farther onto islands than do the caecilians and salamanders. In spite of this wide distribution, frogs occur in greatest numbers and variety of taxa in the tropics. Of the 37 families and subfamilies recognized by Darlington, 27 are confined to the tropics or nearly so and four or five others are more tropical than temperate in distribution. Of 207 genera, about 75 percent occur in the tropics, about 9 percent are north temperate, and about 16 percent south temperate. Darlington also notes that the caecilians are almost entirely tropical and that the salamanders are mostly north temperate.

## 4. ESTIMATES OF PALEOLATITUDES

The paleolatitude ($\lambda_p$) of a geological occurrence ($S$) is the distance in degrees of arc to the paleoequator at the time the occurrence originated. If the coordinates of $S$ in the present frame are ($\lambda$, $\phi$), and the coordinates of the pole of the paleogeographic axis are ($\lambda'$, $\phi'$), then

$$\sin \lambda_p = \sin \lambda \sin \lambda' + \cos \lambda \cos \lambda' \cos (\phi' - \phi) \qquad \ldots\ldots (1)$$

The paleogeographic pole position with respect to any given region may be estimated from paleomagnetic observations in that same region. The assumptions made when making these estimates are: (1) the fossil magnetism of rocks in certain favorable circumstances reflects the direction of the Earth's field at the time the rock was formed, and (2) the mean direction of samples spanning several thousand years in time corresponds to the direction of the axial geocentric dipole field.

The paleolatitude values obtained in this way may be compiled in histograms to obtain the *paleolatitude spectrum* of the occurrence (Irving and Gaskell, 1962) or displayed as maps upon which the parallels of paleolatitude are marked at suitable intervals (Creer, Irving, and Nairn, 1959); these procedures are complementary to one another, the former being useful for quantitative analysis, whereas the second gives a general picture of their distribution. In this analysis there are two points of importance. The first is that, without further assumptions, the paleomagnetic data relate *only* to the region from which the paleomagnetic samples were collected so that estimates of paleolatitude may be made only in cases where either (1) the occurrence $S$ is very close to the paleomagnetic sampling locality ($S'$), or (2) $S$ lies within a broad region that is spanned by the localities $S'$, or (3) there are good geological reasons for supposing that there has been negligible relative movement between $S$ and $S'$ since the time in question. The second point is that the data should be based on good field or laboratory evidence of magnetic stability.

The paleomagnetic pole positions used in equation (1) are given in table 3, and paleolatitude estimates for individual fossil occurrences are listed in table 2. The North American values are for late Carboniferous, Permian, and Triassic genera. In Europe and northern Asia, Stephanian, Permian, and Triassic genera are represented; in the first two cases the mean Permian pole position is used in equation (1) for calculating paleolatitude since the results from the Stephanian (Nairn, 1960) do not differ from those from Permian beds in the same region. The paleolatitudes of occurrences from India and Pakistan cannot yet be obtained since no paleomagnetic data are available from the Permian and Triassic strata of those countries. Paleolatitude values for fossil occurrences in Greenland, South Africa, and South America are not given in table 2 since the paleomagnetic data are of a preliminary nature (Bidgood and Harland, 1961; Nairn, 1960b; Creer, 1962) being unsupported by demagnetization or other stability studies; although the paleolatitudes for

TABLE 3

Paleomagnetic Data Employed

This table gives the mean northern hemisphere paleomagnetic pole positions ($\lambda'$, $\phi'$) for the periods and places under consideration. These poles have been obtained as an average of data cited in the text. The use of the letters A to G is explained in the legend to table 2.

| | Carboniferous | Permian | Triassic |
|---|---|---|---|
| North America | (A) 36N, 132E | (B) 38N, 105E | (C) 59N, 106E |
| Europe and northern Asia | * | (D) 43N, 167E | (E) 52N, 147E |
| Australia | ** | (F) 45N, 52W | (G) 53N, 28W |

* See Section 4.
** No fossil amphibians known.

the South African and South American occurrences have not been given here they have actually been calculated, as a check, using the paleomagnetic data in the references cited above, and they are found to be consistent with the results for occurrences with more firmly based paleomagnetic data.

## 5. RESULTS

Paleolatitude maps and histograms are given in figures 1, 2, and 4. In the first two the paleolatitude parallels are extended over the regions to which they are considered to apply, being based on paleomagnetic observations from these *same* regions. In compiling the histograms the value for each named occurrence in table 2 is given unit weight with the proviso that the individual occurrences of a genus are separated by more than 5° of arc; should the separation be less than 5°, then unit weight is given to each closely-grouped set. This procedure will correct for any undue weight that might otherwise be given to duplicate finds of the same genera in the same region.

*Late Carboniferous and Permian* (fig. 4, B).—The paleolatitude estimates of the North American occurrences are derived from paleomagnetic data from the Lower and Middle Permian red beds from Arizona and New Mexico (Graham, 1955; Runcorn, 1955, 1956; Doell, 1955; Collinson and Runcorn, 1960) in which the paleomagnetic directions show internal consistency and are considered stable. The paleomagnetic sample coverage is less wide than the fossil distribution, but the Permian paleomagnetic results are very similar to those obtained from both the Upper and Lower Carboniferous beds (Runcorn, 1956; Martinez and Howell, 1956; Howell and Martinez, 1957; Nairn, Frost, and Light, 1959; Du Bois, 1959) sampled in the southwestern United States and in eastern Canada, and this suggests that no substantial relative movements have occurred between the fossil occurrences and the paleomagnetic sampling areas since the Carboniferous Period. (Note in proof:—Very recent work by Roy (1963) on late Carboniferous to Permian sediments of Prince Edward Island confirms this statement.)

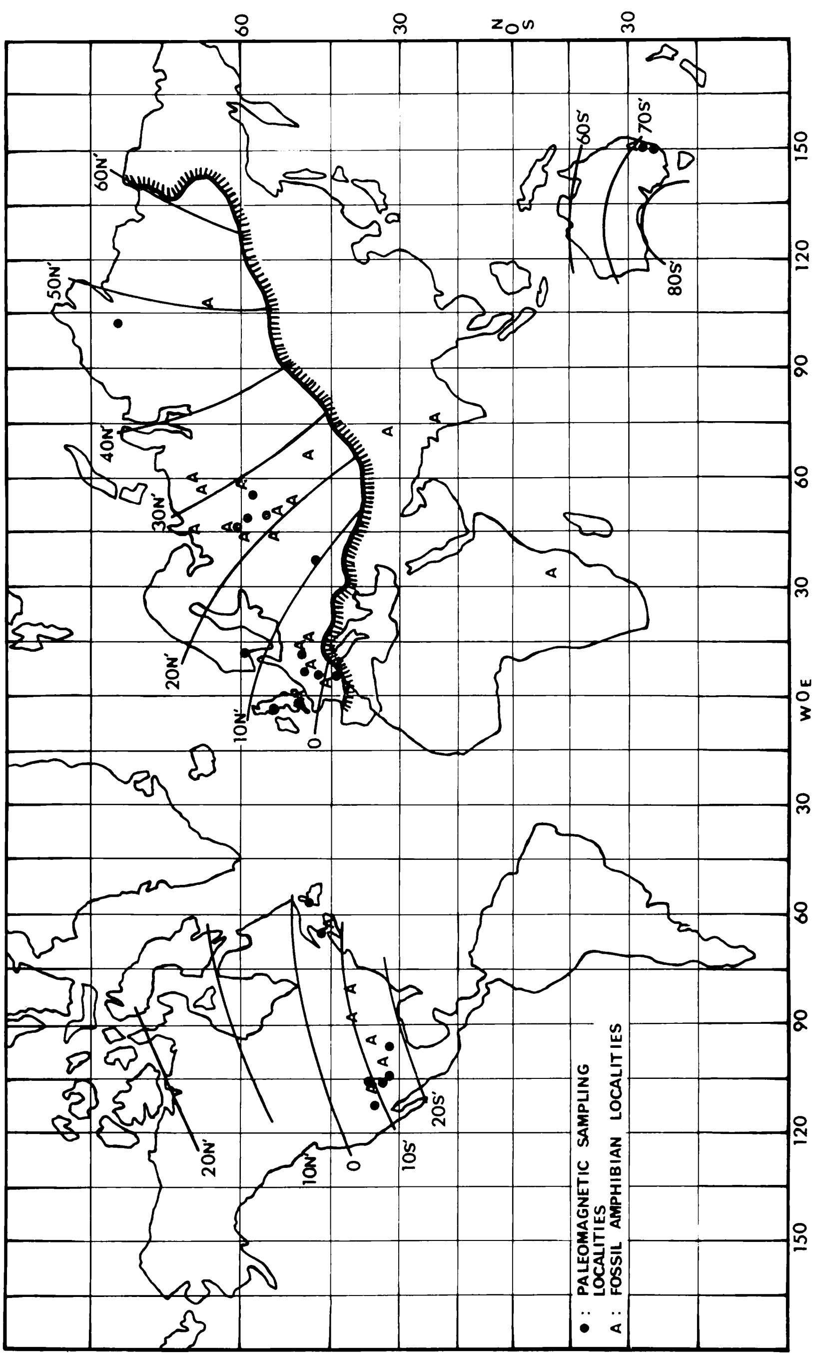

Fig. 1. Paleolatitude map for the late Carboniferous and Permian. Paleolatitude lines are drawn only for those regions for which reliable paleomagneic data are available. To avoid confusion, the fossil distribution has been indicated in a generalized fashion, but all details are recorded in table 2. The hachured line across the Europe-North Asia block is the boundary south and east of which substantial tectonic disturbance has occurred since the time in question. Letter A should appear also in southern England.

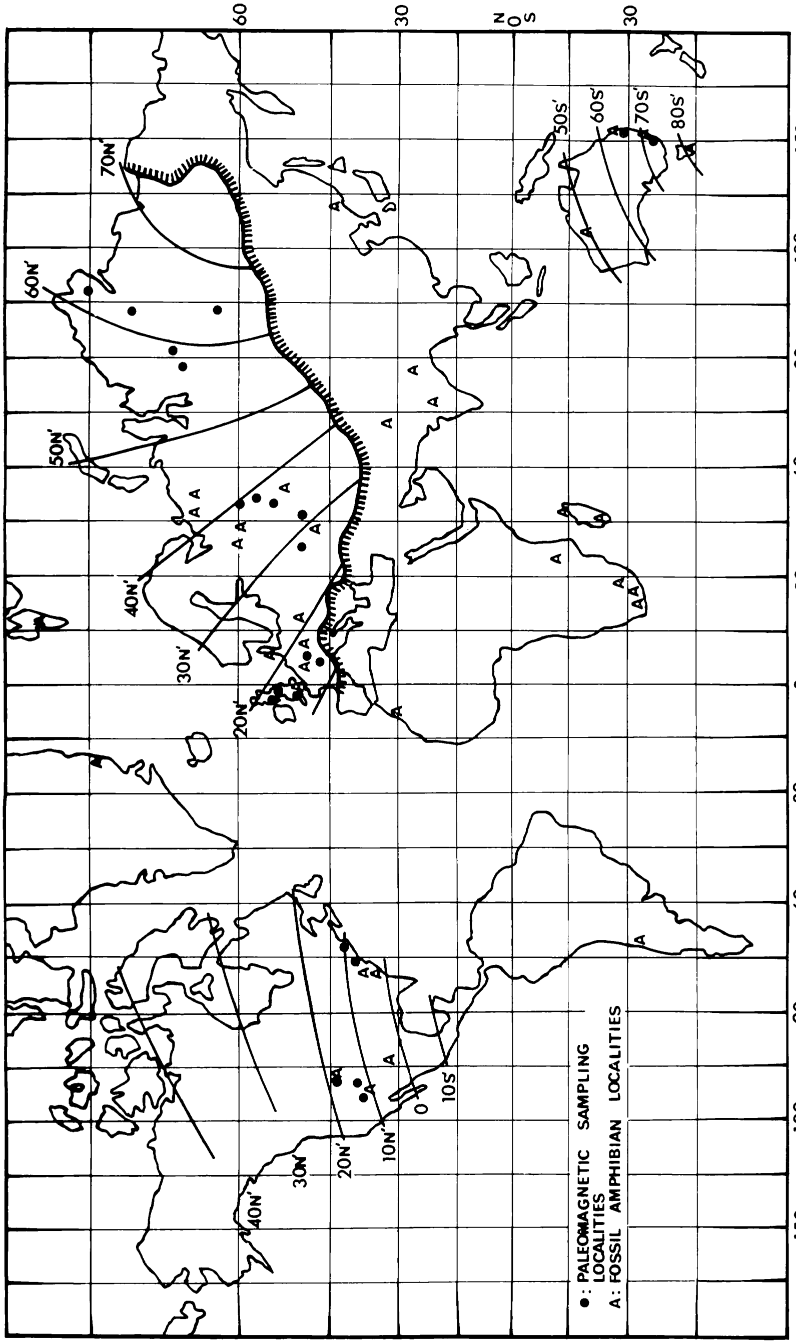

Fig. 2. Paleolatitude map for the Triassic. Legend as for figure 1.

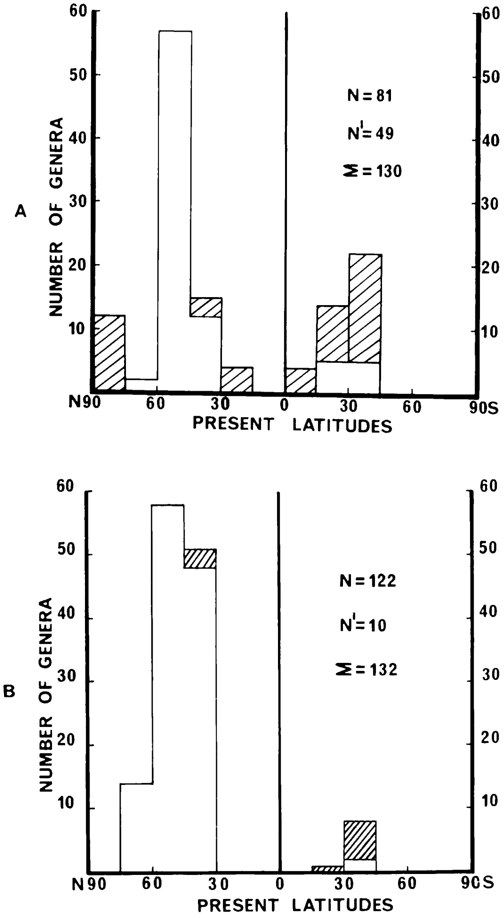

Fig. 3. Present latitude distribution of labyrinthodonts. A. Triassic occurrences; B. Late Carboniferous and Permian occurrences. The open columns represent those values for which paleolatitudes can be estimated (N); the shaded columns represent those for which the requisite paleomagnetic data are not yet available (N').

The paleomagnetism of Permian beds from Europe and Siberia has been extensively studied (Roche, 1957; Du Bois, 1957; Creer, 1957; Nairn, 1957, 1960a; Armstrong, 1957; As and Zijderveld, 1958; Khramov, 1958, quoted in Kalashnikov [1961]; Schmucker, 1959; Gusev, 1959; Everdingen, 1960; Nijenhuis, 1961). There are several instances, particularly in studies by Dutch workers, of detailed laboratory studies of magnetic stability (Everdingen, 1960). Results from sedimentary and igneous rocks varying in age from uppermost Carboniferous (Stephanian) through to uppermost Permian show good consistency, and the direction changes in the region stretching from western Europe through to northern Siberia are consistent with those of a geocentric dipole field. The fossil occurrences cover a region comparable with that of the paleomagnetic observations.

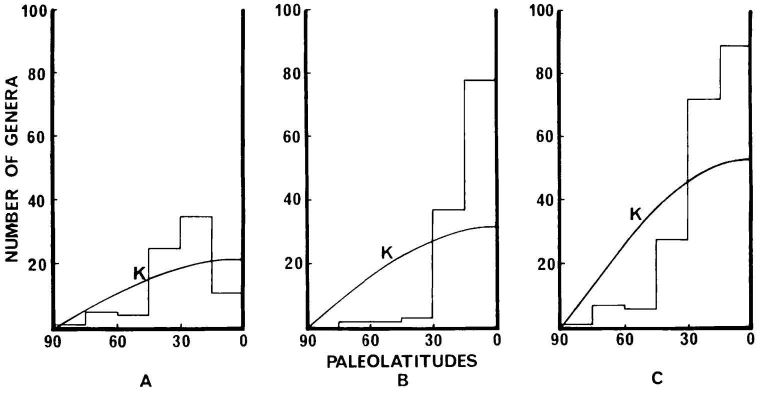

Fig. 4. Paleolatitude spectrum of the labyrinthodonts. A Triassic occurrences; B. Late Carboniferous and Permian; C. Late Carboniferous to Triassic combined. The values are plotted irrespective of sign, and the superimposed curves (K) give, for comparison, the theoretical frequency as a function of latitude expected for a uniform distribution.

Lower and Middle to Upper Permian lavas were sampled in two localities in Australia, the two labyrinthodont occurrences being close by; the paleomagnetic results are supported by detailed laboratory studies (Irving and Parry, 1963).

Viewing the latitude distribution of the late Carboniferous and Permian fossil occurrences as a whole (fig. 3, B), the values are seen to be mainly northerly, 87 percent being between 30°N and 60°N. The paleolatitude distribution is entirely different, 94 percent of the values being less than 30°. In figure 4, B the observed frequency is compared with the theoretical frequencies (curve K) expected for an ideal uniform distribution; the theoretical and observed values are quite different.

*Triassic* (fig. 4, A).—Paleomagnetic results from North America (Graham, 1955; Runcorn, 1956; Du Bois, 1957; Collinson and Runcorn, 1960; Opdyke, 1961; Irving and Banks, 1961) are derived from beds ranging in age from Lower to Upper Triassic spanning a wide region comparable to that covered by the labyrinthodont occurrences. The paleomagnetic directions show good agreement between sedimentary and igneous rocks, and in certain cases (Opdyke, 1961; Irving and Banks, 1961) laboratory studies have demonstrated high magnetic stability.

The fossil occurrences in Europe and northern Asia are well controlled by paleomagnetic surveys on rocks ranging in age from Lower to Upper Triassic and collected from localities stretching from Western Europe to the Siberian Platform (Clegg, Almond, and Stubbs, 1954; Komarov, 1957; Clegg, Deutsch, Everitt, and Stubbs, 1957; Creer, 1957, 1959; Makarova, 1959; Nairn, 1960a; Khramov, 1958; Feinberg and Dashkevitson, 1960; Deutsch and Watkins, 1961; Khramov, Kochegura, and Gusev, quoted in Kalashnikov [1961]). As in North America there is good agreement between the results from both igneous and sedimentary rocks.

The Australian paleomagnetic results are derived from beds of Lower (Irving, 1963) and Middle (Robertson, 1963) Triassic age covering the region in which labyrinthodonts occur. The paleomagnetic results show good agreement between igneous and sedimentary rocks and are based on detailed demagnetization studies.

The present distribution (fig. 3, A) shows a wide spread with most values in mid-northerly latitudes; a little over 60 percent of occurrences have reliable paleomagnetic control—a proportion substantially less than in the Permian. The paleolatitude estimates are predominantly (57 percent) in the range less than 30° with a frequency maximum between 15° and 30°, but some occurrences range up into high paleolatitudes. The divergence of observation from the ideal curve K for a uniform distribution is less strong than for the Permian and may not be significant.

*Summary.*—The above results may be summarized as follows:

1. The late Carboniferous, Permian, and Triassic groups as a whole (fig. 4, C) show a predominantly low paleolatitude distribution, 80 percent of values being less than 30°; if the distribution of occurrence had been uniform over the whole Earth then this proportion would have been only 50 percent. The theoretical frequency expected for a uniform distribution (fig. 4, C) differs from the observed frequency. This difference is thought not to be due to any inadequacy in the paleomagnetic control; there are 57 occurrences for which paleolatitudes cannot at present be estimated, and if it is assumed that as paleomagnetic work is extended it will transpire that *all* these have paleolatitudes greater than 30° (the least favorable condition for our working hypothesis), then the proportion of the total with values less than 30° is still 62 percent—substantially greater than the expected 50 percent for a uniform distribution. It therefore seems clear that the paleolatitude spectrum of these fossil amphibians is not uniform and that there is a strong tendency for the greatest number of occurrences and of genera to occur in paleolatitudes less than 30°.
2. The late Carboniferous and Permian paleolatitude distributions differ in detail from those in the Triassic, the former being grouped predominantly within 15° of the paleoequator with only two known occurrences above 60°, whereas the latter are predominantly in the range 15° to 30° with six values above 60° indicating a wider spread in the early Mesozoic as compared with the late Paleozoic.

## 6. DISCUSSION

The question of whether these paleolatitude spectra are in fact true spectra depends on the reliability of the paleomagnetic results and on the extent to which the fossil record is a true representation of the labyrinthodont distribution.

Many of the paleomagnetic data used are derived from sedimentary rocks which may be subject to an inclination error $\delta$ that will tend to make the estimated paleolatitude too low. Laboratory experiments show that sediments dispersed in water and allowed to settle produce a deposit whose magnetic inclination $I_M$ is less than that of the ambient field $I_F$ by an angle $\delta$, which is observed to be negligible when $I_F$ is near 0° or 90°, but reaches a maximum of about 25° at $I_F = 60°$ (King, 1955). No such error occurs in igneous rocks and in those cases (noted in sec. 5) where control from igneous rocks is available the agreement between results from igneous and sedimentary rocks is very good (see, for example, Opdyke, 1961). In the late Carboniferous and Permian of North America, no igneous rocks have been studied paleomagnetically, but the presence of a substantial inclination error in the sedimentary results used to calculate the paleolatitudes is unlikely since the directions of magnetization are near horizontal.

A second possible source of error is the effect of magnetic anisotropy; it is possible that prior to magnetization the rock possessed a strongly anisotropic magnetic fabric so that when magnetization occurred it was not parallel to the direction of the ambient field. In certain cases, laboratory experiments on igneous rocks have shown that the anisotropy is insufficient to affect the directions. Furthermore, the agreements noted between igneous and sedimentary rocks indicate that such effects are small since they would not be expected to have acted systematically in rocks of such widely differing origins. The evidence at present indicates that paleomagnetic errors from these sources are not substantial.

In figure 4 comparisons are made between the expectation for a uniform distribution and the observed frequency. The hypothesis tested in this way is the simplest possible and may be unrealistic since land is unlikely to have occurred with equal frequency at all paleolatitudes. The correct comparison is with the paleolatitude spectrum of land. A more complete paleomagnetic coverage for Antarctica, Africa, and South America will be needed before this can be satisfactorily estimated, although an initial attempt based on data currently available has shown that in the late Paleozoic and Triassic land occurred at all paleolatitudes between 80°N and 80°S (Irving and Briden, 1962) so that it is unlikely that the observed spectra of the labyrinthodonts arose purely from peculiarities in land distribution. But a quantitative assessment of this question cannot be made at present.

Inevitably the fossil record is incomplete. But our analysis is based on numerous data, and it would require new finds in the Permian and Triassic of Siberia and Australia comparable in richness to those of West Texas to affect in any substantial fashion the picture given here. It therefore seems to us, on the basis of evidence currently available, that the correlation of low paleolatitude with the occurrence of abundant genera in North America and Europe, and of intermediate or high paleolatitude with few or no occurrences in Siberia and Australia, is significant and is best explained by supposing that the labyrinthodonts were more diverse and more numerous in low latitudes than in high latitudes, the paleolatitude distribution as a whole (fig. 4, C) being very similar indeed to the present latitude distribution of the amphibians as enumerated by Darlington (1957). The comparative absence of occurrences in the high paleolatitude regions of Siberia and Australia is not due to the absence of suitable depositional environments; very large basins, which received much terrestrial sedimentation at these times, are found in both areas. The paleolatitude results are consistent with the view that the labyrinthodonts were, by and large, warmth-loving animals (sec. 2) and are consistent with the fact that the extensive occurrences are in beds that are themselves supposed to be indicative of warm climates.

The labyrinthodonts were not greatly affected by the large faunal changes such as affected many other forms at the end of the Paleozoic Era. Their paleolatitude distribution, however, changes, their virtual confinement to low paleolatitudes in the Permian (fig. 4, B) being replaced by a much more general distribution in the Triassic (fig. 4, A). Their restriction in the Permian may well be related to a strong latitude-temperature gradient resulting from glaciation, and their wider dispersal in the Triassic may reflect the establishment, at the beginning of the Mesozoic, of a milder, more uniform, non-glacial regime.

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