Antarctica, Isostacy, and the Origin of Frogs

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It is a basic tenet of zoogeography that an animal group arises in and spreads from a single area, its center of origin. For larger, more inclusive groups, as the more primitive members move out from the center of origin, successively more advanced forms evolve in the center. As they in turn spread, they tend to eliminate the more primitive forms by competition. A large group that has been in existence for a long time typically shows a pattern of distribution in which the primitive species are located at the periphery of the range, in areas that the more advanced members have not yet reached or have reached only recently.

The more primitive members of many vertebrate groups are found in the southern continents, in South America, Africa south of the Sahara, and Australia. The order Testudinata (turtles) comprises two suborders. The more primitive suborder, Pleurodira, includes the side-necked turtles, which draw the head under the shell by bending the neck to the side. Of the two families of side-necked turtles, Pelomedusidae occur in South America and Africa and Chelidae in South America and Australia. Fossil pelomedusids are known from the Upper Cretaceous of North America and Europe. The suborder Cryptodira includes more advanced forms, which withdraw the head by bending the neck in a sigmoid curve. They are widely distributed in the warmer parts of the northern continents. The only cryptodires to reach Australia are the marine turtles, and cryptodires have probably been in South America and Africa only since the Miocene.

Distribution patterns similar to that shown by the turtles are found in many vertebrates. This led Matthew (1915) to postulate a Holarctic center of origin for the majority of the groups of vertebrates. Darlington, on the other hand, believes that most of the groups arose in the Old World tropics.

Some vertebrates do not conform to the distribution pattern described above and do not seem to have originated either in the Holarctic or in the Old World tropics. One such group is the frogs

(Salientia). We believe that the evidence suggests an Antarctic origin for this group.

ANTARCTICA

This continent, which caps the southern polar region and is covered with ice, seems an improbable place to seek for the origin of frogs, but certainly it was not always as it is today. Although no petroleum or gas have yet been located there, "estimates of enormous coal reserves in the Beacon sediments of the Trans-Antarctic Mountains have been made from time to time" (Warren, 1965, p. 314). The climatic conditions under which coal is formed are also capable of supporting an amphibian fauna. The Beacon Group sediments lie on a peneplain of igneus and metamorphic rocks complex and variable in both age and lithology. In the McMurdo Sound District, the sediments are estimated to range in total age from pre-Devonian to Jurassic. The formation containing *Glossopteris* (Permian) is about 700 m thick in the upper Beardmore district, a thickness unequaled in other areas so far measured. Glacial conditions were present in the late Paleozoic and also in the Jurassic.

Among fossils previously reported from the Beacon Group are Devonian freshwater fishes (Woodward, 1921) and Jurassic freshwater gastropods, fishes, and beetles (Adie, 1962). Plumstead (1964) has given a review of the plant fossils of the Beacon Group. The first amphibian material known from Antarctica is a fragment of a labyrinthodont jaw taken at Graphite Peak in the Trans-Antarctic Mountains by Peter Barrett in 1967. In 1969 Dr. E. H. Colbert and his party collected about 450 specimens of fossil vertebrate material from exposed outcrops in Coalsack Bluff just a few miles from their Beardmore Camp. Additional materials were collected during a second field season. These fossils represent in essence the *Lystrosaurus* fauna.

ISOSTACY

Seismic and gravitational studies (Bentley, 1965; Gow, 1965) indicate that the ice cover over wide-spread areas of Antarctica ranges between 2000-3000 m in thickness; in west-central East Antarctica the land is under a load of 3600 m of ice. Isostatic studies indicate that with this load part of the continent should be depressed about 1000 m.

Antarctica is at present connected with each of the three southern continents, South America, Africa, and Australia, by the following undersea ridges at depths appreciably less than 1000 m: the Scotia Ridge to South America; the Macquarie Rise to Australia; and the Atlantic-Indian Rise, the West Indian Ridge, and the South Madagascar Ridge to Africa. Of these, the Scotia Ridge appears at the surface as the Falkland Islands, South Georgia Island, the South Sandwich Islands, and the South Orkney Islands. The Macquarie Rise reaches the surface as MacQuarie Island and, on the prong that extends to New Zealand, as the Aukland Islands. The Ridge to Madagascar and South Africa appears at the surface as the Bouvet and Prince Edward Islands. These ridges are shown in Figure 1.

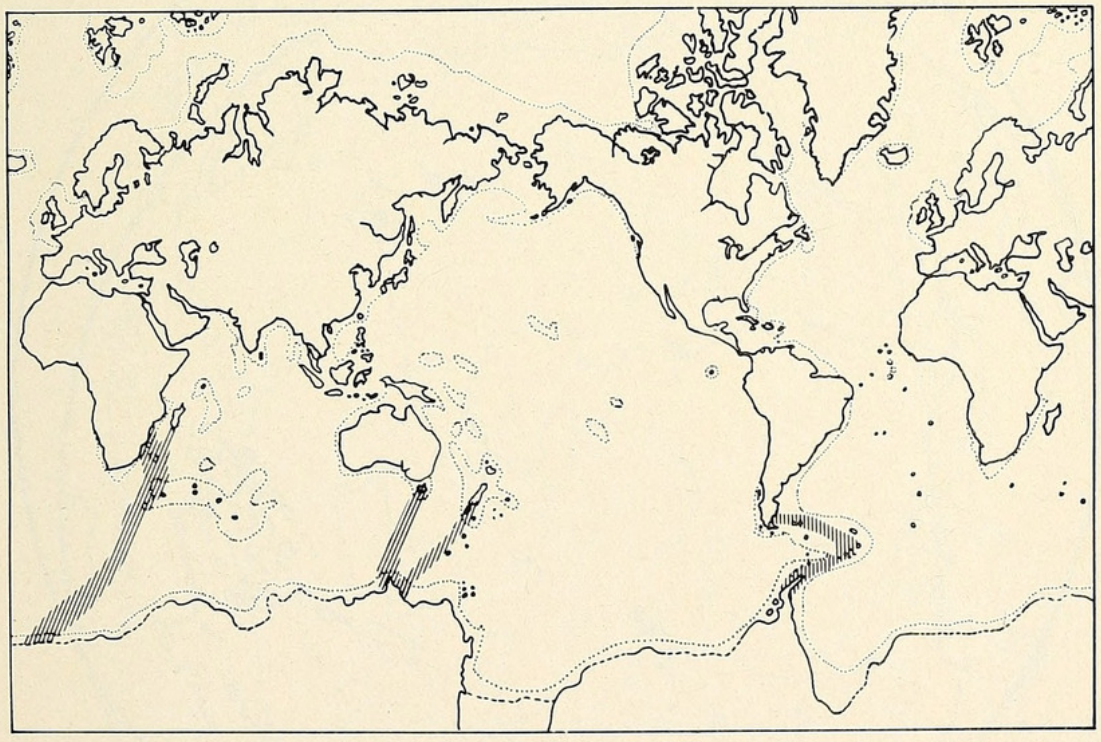

Fig. 1. Present location of undersea ridges that might, at a time of isostatic adjustment, have been emergent ridges or at least island chains that frogs would have been able to cross.

There is no assurance that even if the main body of the continent did rise 1000 m to attain isostatic balance during glacier-free times its margins and the ridges would have risen an equal amount. However, had they been elevated by only one third that amount there could have been either direct land connections or island chains be-

tween Antarctica and the southern continents since the crests of the ridges rise in many places closer than this to the surface.

ORIGIN OF THE FROGS

The earliest known remains of any salientian-type animal are some footprints found in the Ecca formation in the basal Permian of South Africa. The prints are of the fore-feet and indicate the presence of an animal that swam about or groveled on the bottom. The earliest fossilized skeleton is that of *Triadobatrachus* (*Protobatrachus*) from the Lower Triassic of Madagascar. This animal

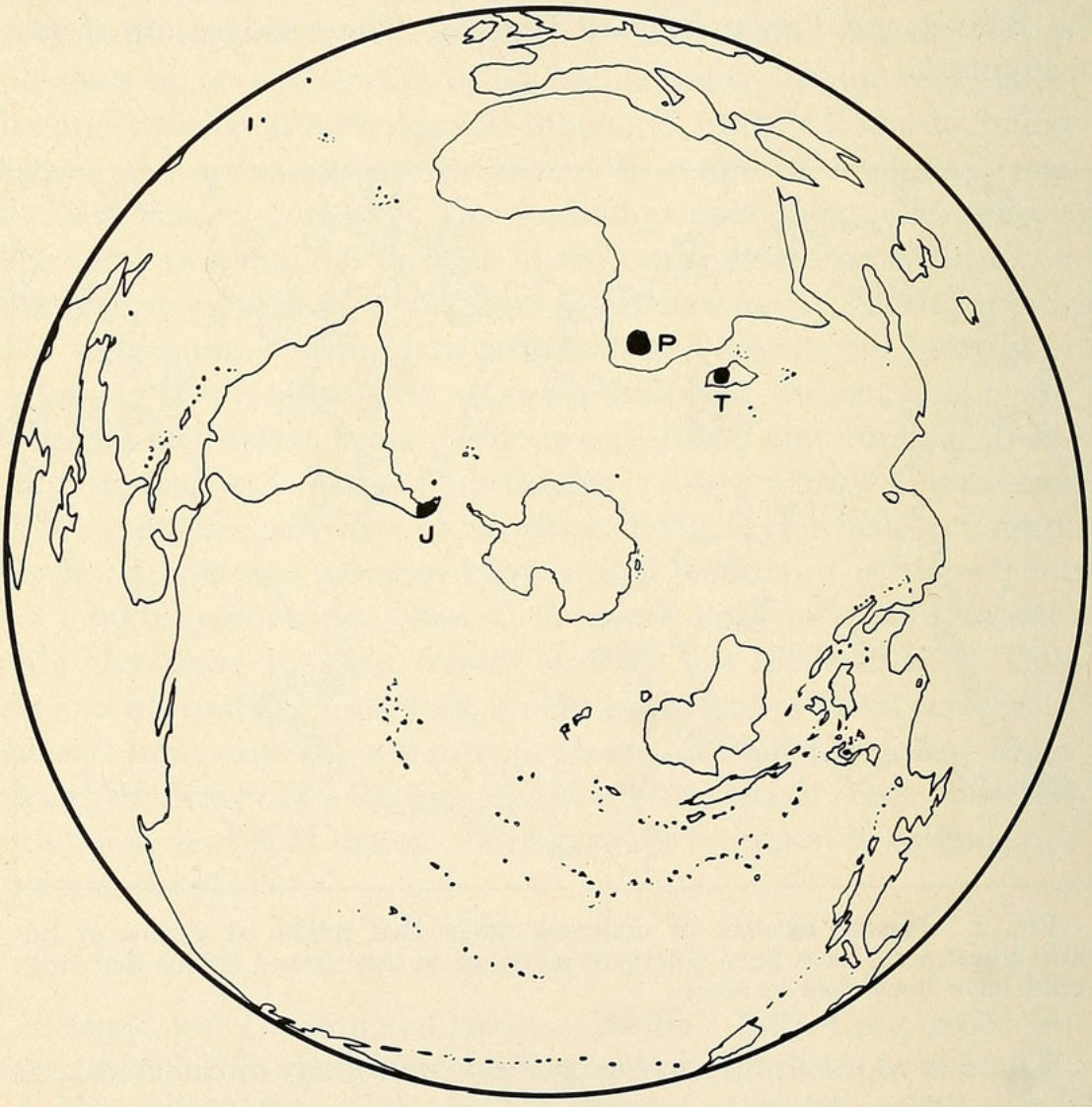

Fig. 2. Distribution of the three earliest evidences of salientians. "P" are footprints from Permian Ecca beds of South Africa; "T" represents *Triadobatrachus* from the Triassic of Madagascar; "J" is *Vieraella* from the Lower Jurassic of Patagonia. This figure and all of the following distribution maps are based on an Azimuthal Equidistant Projection, centered on the South Pole.

had a froglike skull and showed a tendency toward elongation of the hind legs. These remains indicate that the probable ancestors of the modern frogs were present in Gondwanaland.

The oldest known real frog (order Anura) is *Vieraella* from Patagonia, which shows that the basic anuran pattern had been established by the Lower Jurassic. *Notobatrachus* is from the mid-Jurassic of Patagonia. Upper Jurassic frogs are known from both North America and Europe. Figure 2 shows the distribution of the earliest salientian fossils.

DISTRIBUTION OF MODERN FROGS

The modern families of frogs are divisible into four primitive

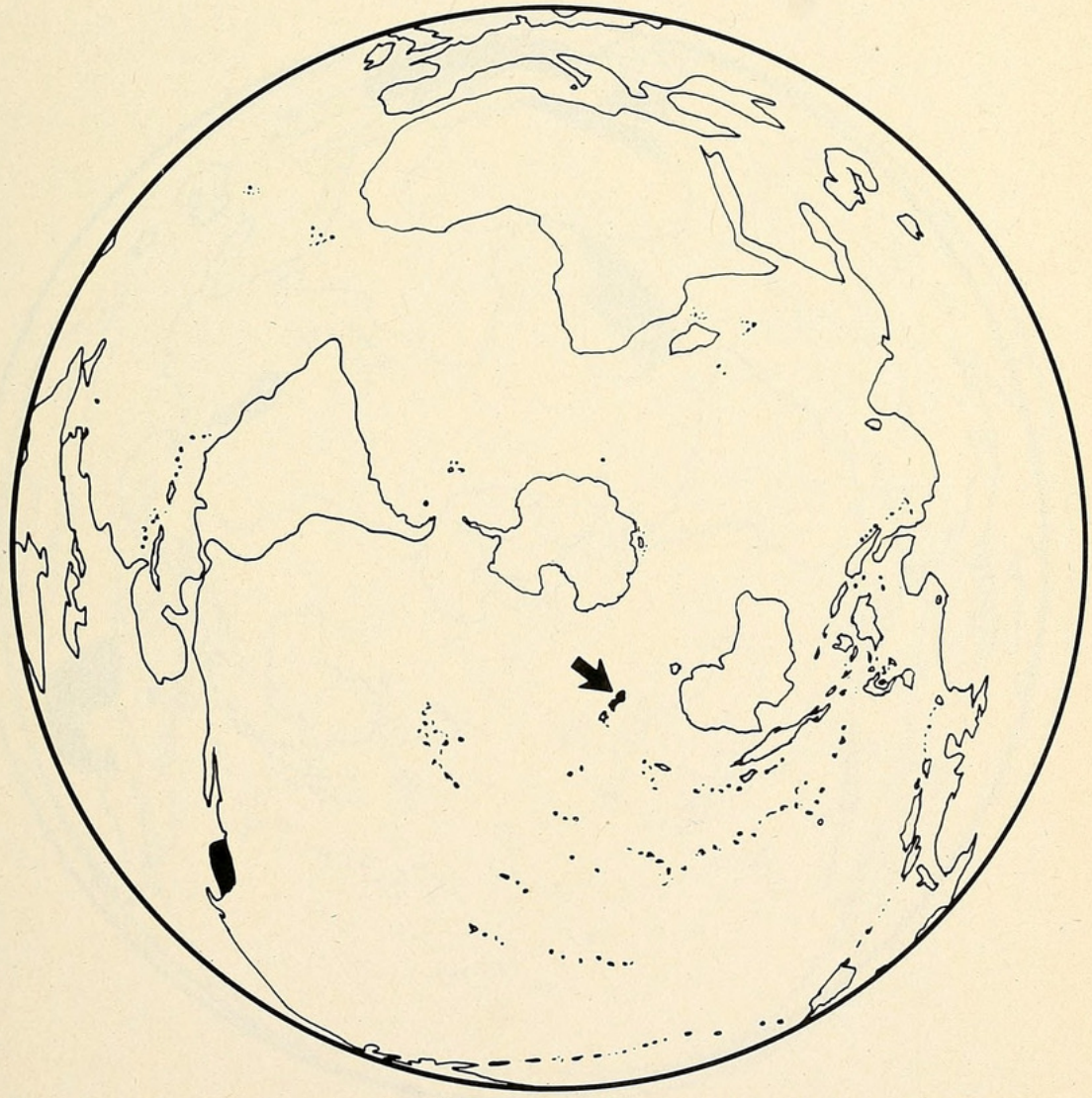

Fig. 3. Distribution of the living members of the family Ascaphidae; *Ascaphus* in the northwestern United States and *Leiolopelma* in New Zealand.

families (Ascaphidae, Discoglossidae, Rhinophrynidae, and Pipidae); one family, Pelobatidae that "unquestionably couples the more primitive with the advanced families but, none the less, is separable from both" (Griffiths, 1963, p. 271); and the more advanced families like the Hylidae, Bufonidae, Leptodactylidae, and Ranidae.

Ascaphidae. This most primitive family of living frogs is found today in two widely separated populations: *Leiopelma* in the fog-dampened ridges of New Zealand, and *Ascaphus* in the cold mountain streams of western North America (Fig. 3).

Discoglossidae. Today represented by four living genera, this family shows a typical relict distribution: *Bombina* in Europe and eastern Asia; *Discoglossus* in Europe and northern Africa; *Alytes*

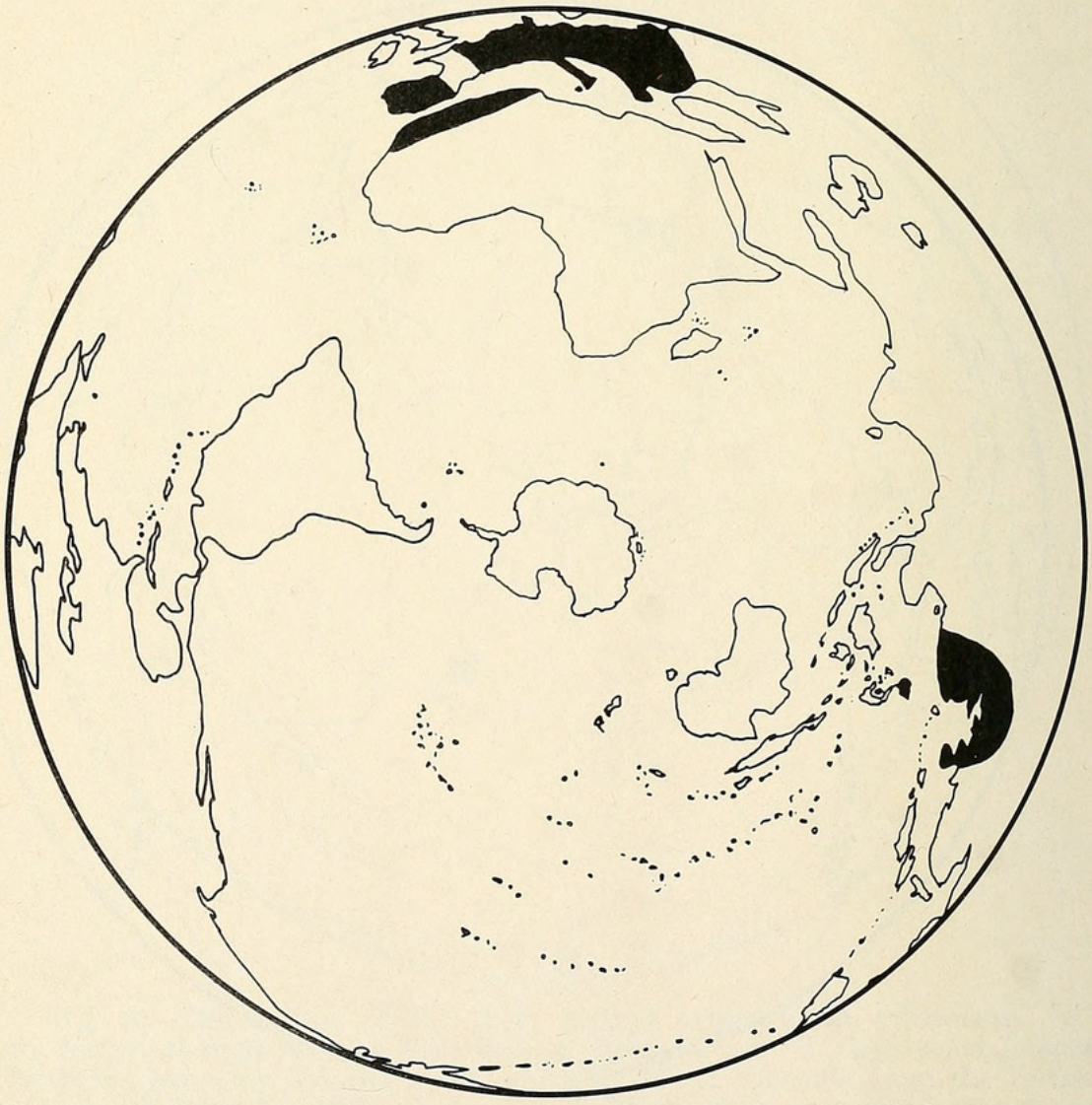

Fig. 4. Distribution of the living members of the family Discoglossidae.

in western Europe; and *Barbourula* on a single island in the Philippines (Fig. 4).

Rhinophrynidae. This family is known from a single species, *Rhinophrynus dorsalis* from the lowlands of Mexico.

Pipidae. This family of highly aquatic frogs comprises one genus from the northeastern coast of South America and three from Africa in a trans-continental belt south of the Sahara but not including southern Africa or Madagascar (Fig. 5).

Pelobatidae. The following three subfamilies of pelobatids are recognized: Pelobatinae, which includes one genus in Europe and northern Africa and another in North America; Pelodytinae (sometimes recognized as a separate family) with a single genus in Eu-

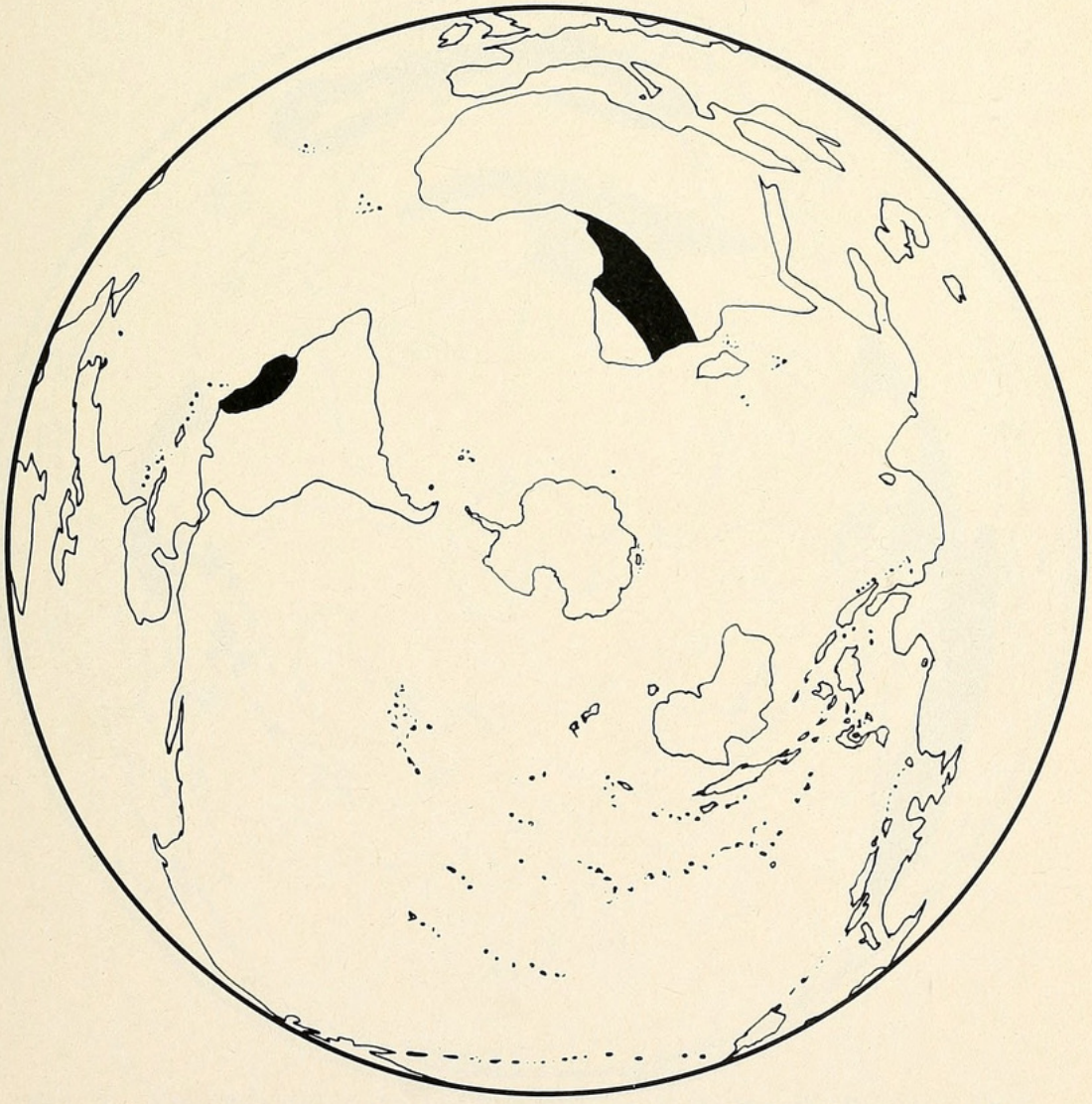

Fig. 5. Distribution of the living members of the family Pipidae.

rope; and Megophryninae with about half a dozen genera and many species in southeastern Asia and the East Indies (Fig. 6).

Ranidae. This is a large, modern family containing many genera and hundreds of species. It is centered in Africa, where six of the seven subfamilies occur; four of them are found no place else. One subfamily is confined to the Seychelles Islands north of Madagascar. Another extends from Africa across southern Asia to the northern coast of Australia. The subfamily Raninae includes several genera of local distribution in Africa and southern Asia and the cosmopolitan genus *Rana* which has spread from Africa through Europe, Asia, and North America and has reached the northern parts of Australia and South America. Figure 7 shows the distribution of the Ranidae except for *Rana*.

Fig. 6. Distribution of the living members of the family Pelobatidae.

Dendrobatidae. This family of three genera and about sixty species is confined to Central America and South America. It is sometimes classed as a subfamily of the Ranidae.

Rhacophoridae. This family of largely arboreal frogs is obviously derived directly from the ranids. At present it is found in Africa, southern Asia, Japan, the Philippines, the East Indies, and Madagascar. There are over a dozen genera and many species.

Microhylidae. This family is found in Africa south of the Sahara, Madagascar, southern Asia and the East Indies to New Guinea and the northern tip of Australia, and in South America. One genus ranges north to central United States and one Asian group north to Manchuria. There are about forty genera and many species. Figure 8 shows the distribution of the Microhylidae.

Fig. 7. Distribution of the living members of the family Ranidae (except *Rana*).

Phrynomeridae. This small family is confined to Africa south of the Sahara. It contains only a single genus and about half a dozen species. As the rhacophorids evolved from a ranid stock, so the phrynomerids apparently evolved from a microhylid stock.

Bufonidae. Except for the cosmopolitan genus *Bufo*, the Bufonidae are found in Africa south of the Sahara (but not Madagascar), southern Asia and the East Indies, and South America (Fig. 9). *Bufo*, with its many species, occurs on most of the major land areas of the world except Australia, New Guinea, and New Zealand.

Atelopodidae. These toads are widespread in Central and South America in the form of *Atelopus*, but the only other genus, *Brachycephalus*, is found only in eastern Brazil.

Hylidae. This large family of tree frogs includes over thirty

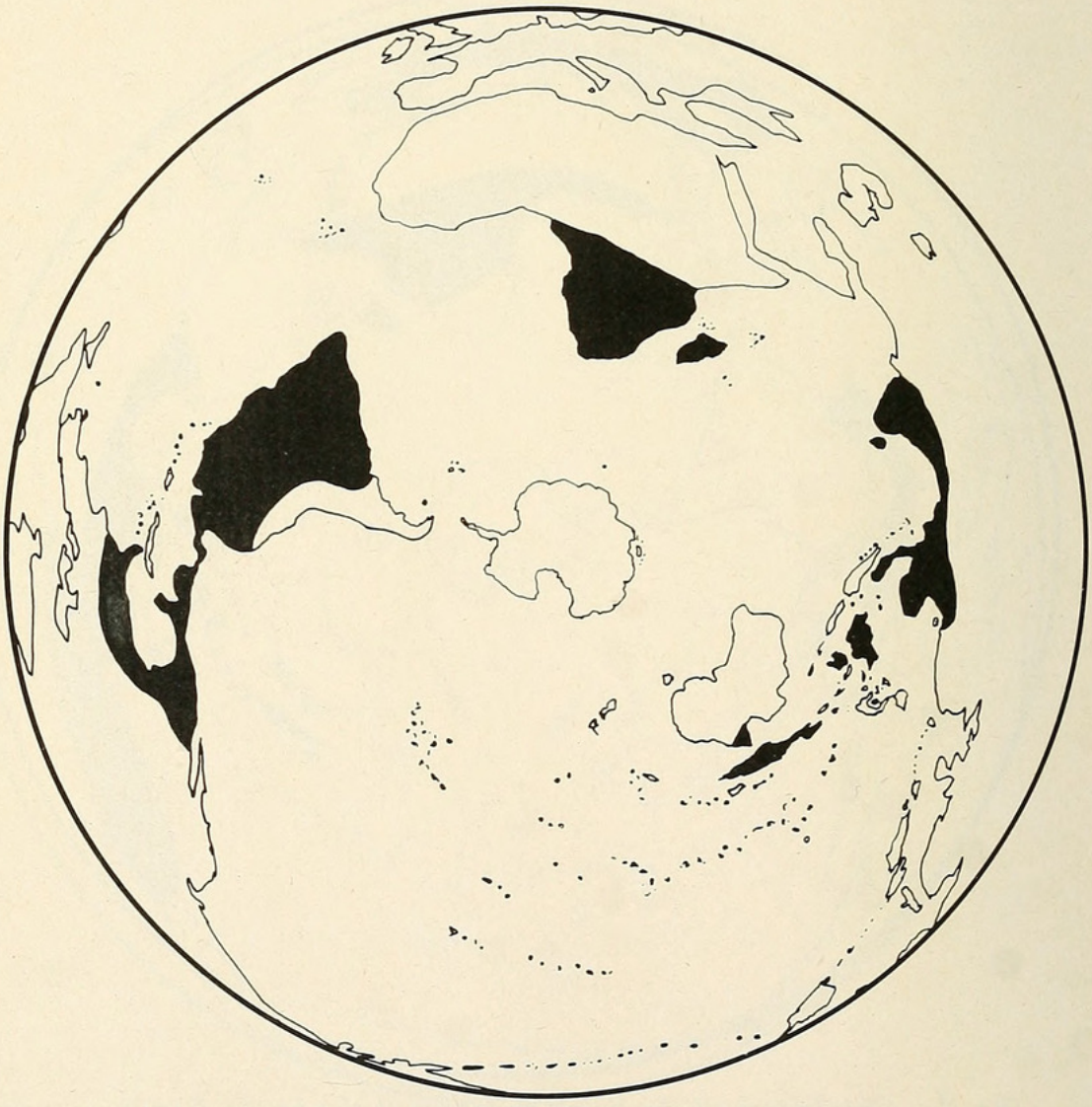

Fig. 8. Distribution of the living members of the family Microhylidae.

genera and several hundred species. Except for the genus *Hyla sensu lato,* and *Nyctimystes* of New Guinea, it is confined to the Americas from northern Argentina northward to extreme southwestern United States (Fig. 10). For the purposes of this paper, we consider the weakly defined North American genera *Pseudacris* and *Acris* to represent simply small groups of semi-specialized *Hyla.* We are not the first to so consider them (Noble, 1931). *Hyla* is widespread not only in South America but also in North America and Australia. A single variable species extends across the Palearctic Region from western Europe and North Africa to Japan.

Leptodactylidae. This is another large family with hundreds of species. The geographic range covers South and Central America

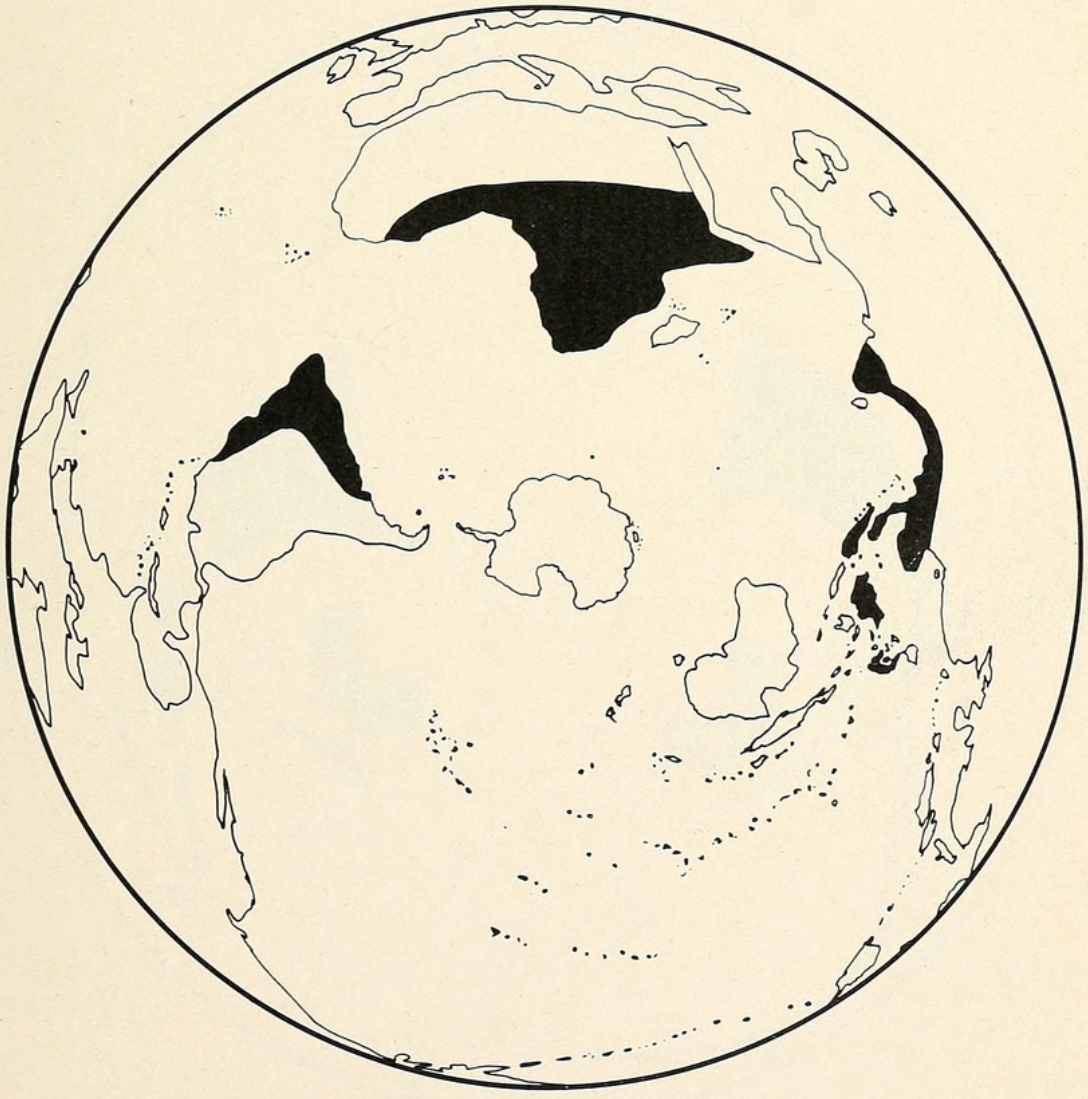

Fig. 9. Distribution of the living members of the family Bufonidae (except *Bufo*).

northward to extreme southwestern United States and Australia and New Guinea. *Heleophryne*, a little-known genus that occurs in the mountains of southern Africa, is sometimes placed in this family, but this allocation is doubted by some herpetologists. Figure 11 shows the distribution of the Leptodactylidae.

Ceratophryidae. This family includes seven genera of wide-mouthed, toadlike forms. It seems to have been derived from the Leptodactylidae and is confined to South America.

Pseudidae. Two small genera of aquatic South American frogs are placed in this family. Its relationships are obscure, but it may have been derived from the Leptodactylidae.

Centrolenidae. This small family of arboreal frogs, which we

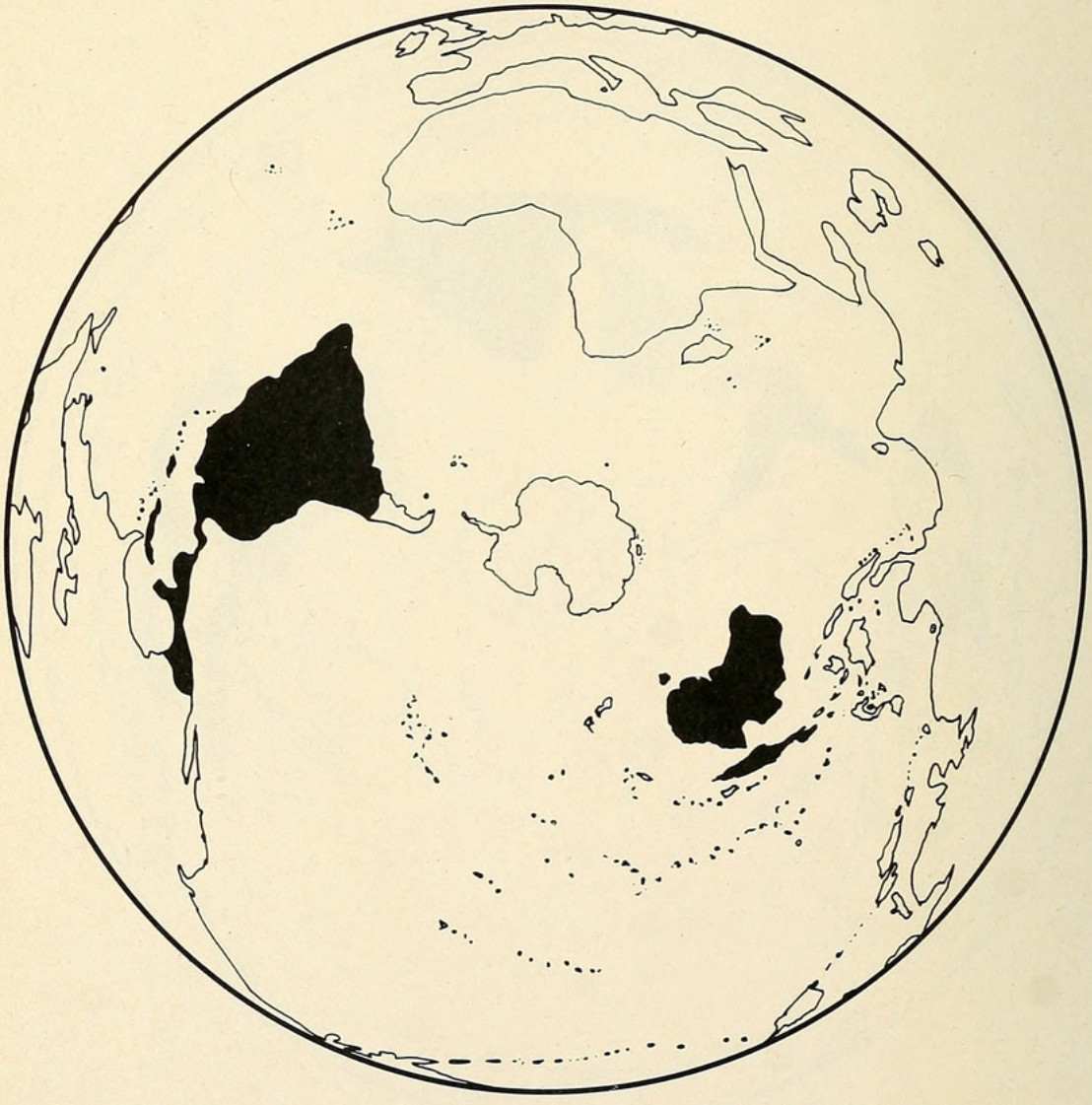

Fig. 10. Distribution of the living members of the family Hylidae (except Holarctic members of the genus *Hyla, sensu lato*).

believe to have been derived from the leptodactylids in South America, occurs only in tropical America.

DISCUSSION

As we look at the data given above, several points stand out. The oldest evidences of any frogs or froglike creatures are geographically close to Antarctica; Permian footprints in the Ecca beds of South Africa, *Triadobatrachus* from the Lower Triassic of Madagascar, and *Vieraella* from the Lower Jurassic of Patagonia.

Primitive living frogs have typical relict distributions with the Ascaphidae in western North America and New Zealand, and the Discoglossidae in Europe, North Africa, eastern Asia and the Philip-

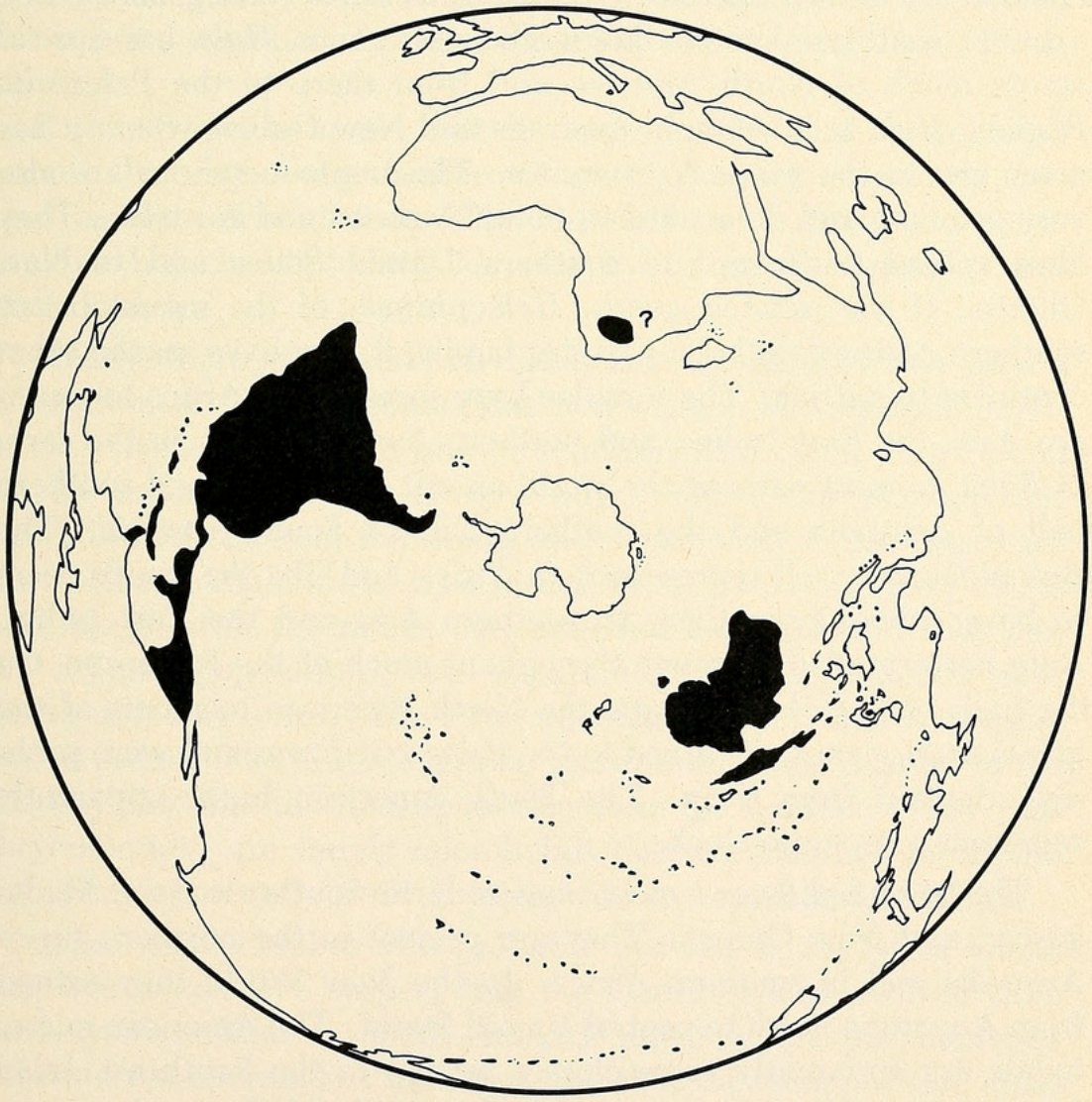

Fig. 11. Distribution of the living members of the family Leptodactylidae.

pines. Except for the oceanic island of New Zealand, all of these geographic points are peripheral when plotted on an Azimuthal Equidistant Projection centered on the South Pole. *Leiopelma* is the only frog on New Zealand and there is no evidence that any other frogs ever reached there. The Pelobatidae also have a disjunct distribution in North America, Europe, and Southeast Asia and the East Indies. Except for *Leiopelma*, the only primitive frogs found in the southern land masses are the completely aquatic Pipidae. Their habits may have sheltered them from competition with the more advanced, more terrestrial forms. They are peripheral ecologically.

Four of the big, modern families of frogs are centered in the southern continents and have spread northward from them. The Hylidae are most numerous in South America; several genera reach extreme southern United States and the genus *Hyla* has spread across much of North America and from there to the Palearctic Region. *Hyla* is common in Australia and New Guinea where it has given rise to the genus *Nyctimystes*. The Leptodactylidae are also very common and diversified in South America and Australia. They have spread northward to southern United States and to New Guinea. If the isolated genus, *Heleophryne*, of the mountains of southern Africa does belong to this family, it may have reached that continent by rafting. The Ranidae have spread from Africa to southern Asia, the East Indies, and northern Australia, and, in the form of *Rana*, to most parts of the world except the central and southern half of Australia and the southern half of South America. The Bufonidae are well represented in Africa and like the ranids seem to have spread from there to southern Asia and the East Indies. *Bufo* has extended its range throughout much of the Palearctic. On the basis of karyological data, the North American members of the genus *Bufo* seem to be allied to the Palearctic forms and were probably derived from them. The South American bufos apparently represent a separate stock.

The microhylids are most numerous in Southeast Asia, Madagascar, and New Guinea. They are present in the northern tip of Australia and in southern Africa. In the New World they extend from Argentina north to central United States. The American microhylids are apparently more closely related to the Southeast Asian forms than to the African ones. Parker (1934) believes the group

originated in Southeast Asia from a pro-ranid stock sometime before the close of the Mesozoic and spread from there southwestward to Africa and Madagascar, southward to New Guinea and Australia, and eastward to the Americas. He suggested that the scarcity of microhylids in Australia in contrast to their great abundance in New Guinea may result from their relatively recent arrival across the Torres Strait but that it more probably reflects the difference in climatic conditions between the two regions. If the latter alternative is correct, the microhylids may once have been more widespread in Australia when the climate was more humid and the direction of spread may have been northward to New Guinea and Southeast Asia.

Except for the relict populations of *Ascaphus*, the discoglossids, and the pelobatids, there is hardly a frog in the Holarctic Region that is not a member of one of three vigorous genera, *Hyla*, *Rana*, and *Bufo*.

It should also be noted that the large families that are centered in more than one of the southern continents are not necessarily centered in adjacent continents. The bufonids are in Africa and South America but the leptodactylids and hylids are in Australia and South America.

Finally, there are several obviously derived families that should be mentioned. The Rhacophoridae now exist in two separate populations, one in Africa and one in southern Asia. This distribution can be explained in one of two ways. Either the rhacophorids evolved in Africa from the ranids and accompanied them eastward into southern Asia and the East Indies; or, as Laurent (1951) thinks more likely, after the ranids had extended eastward and split into two disjunct populations, each separate stock independently gave rise to arboreal forms. The Rhacophoridae would then be diphyletic in origin. The Phrynomeridae stand in the same relation to the Microhylidae that the Rhacophoridae do to the Ranidae. They (the phrynomerids) are simply microhylids that are modified for climbing. They apparently evolved in and are still restricted to Africa.

Other small families also probably evolved in the place where they live today. We suspect that the Centrolenidae evolved from the Leptodactylidae in South America much as the phrynomerids did from the microhylids in Africa, and that the Atelopodidae arose from the South American Bufonidae. On the other hand, if the

Dendrobatidae are derived from the Ranidae, the ancestors of the family probably arrived in South America from West Africa by rafting. They are more similar to some of the African forms than they are to *Rana*, and *Rana* itself apparently reached South America too recently to have given rise to the distinctive dendrobatids.

CONCLUSIONS

The lines of dispersal of the major anuran stocks thus seem to point back to an Antarctic center of origin for the group. The fossil history of the frogs is not well enough documented to allow us to say much about early events in the evolutionary history of the group. If *Triadobatrachus* (order Proanura) of the very early Triassic is on or close to the line leading to the frogs, the salientian stock may have originated in the late Paleozoic. It is probable that the frogs (order Anura) evolved from the Proanura in the Triassic and that by Late Triassic or Early Jurassic times the radiation of the frogs was under way. The best known of the Upper Jurassic and Cretaceous frogs of the Holarctic Region are placed in the primitive families Discoglossidae and Pipidae, but some fragmentary remains indicate that representatives of the more advanced families were present in the northern hemisphere in the Cretacous and possibly in the Upper Jurassic.

We appeal to isostacy as an explanation for the routes by which the modern frogs spread from Antarctica rather than to continental drift because of the more or less random distribution of the major families. The Leptodactylidae and Hylidae are centered in South America and Australia, the Bufonidae in South America and Africa, the Microhylidae possibly in all three, and the Ranidae basically only in Africa. Thus while the frog families were evolving and moving out from Antarctica, this continent was from time to time variously connected with the three southern continents; with Africa but not South America and Australia, with Africa and South America but not Australia, with Australia and South America but not Africa, and also perhaps with all three at the same time. If the radiation of the frogs had taken place before the fragmentation of Gondwanaland, then it seems to us the major families should be equally distributed on all three of the southern continents. On the other hand, if continental drift began shortly before the radiation of the frogs, there was probably a closer isostatic relationship be-

tween Antarctica and the southern continents at that time than there is today.

It is to be hoped that the discovery of additional fossil material in Antarctica and the southern continents will not only elucidate the early history of the frogs but will also contribute to an understanding of the geologic history of Antarctica.

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