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ANTARCTICA AS A CENTER OF ORIGIN OF BIRDS

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With the rapid evolution of reptilian forms during Triassic and Jurassic times, many reptilo-avian forms may have evolved. Two examples of such evolution have been preserved in the Jurassic sediments of Germany (*Archaeopteryx* and *Archaeornis*).

An anatomical feature, characteristic of birds, and not reported for either of these forms, is a well-developed sternum (Wetmore, 1951). Since this is an important avian characteristic, neither of these bird-like animals should be considered to be related directly to the ancestors of modern birds. Therefore, other yet undiscovered forms may be regarded as more properly comprising the Archaeornithes, and these ancestral forms may be found to have lived on the Antarctic continent at a time when that land supported a flourishing tropical vegetation and highly varied vertebrate fauna.

To explain the uniform presence of a very well-developed sternum in birds would be difficult if this structure were not already present in some ancestral reptile or amphibo-reptile. While a sternum is found in amphibians, there is no rib-sternum articulation comparable to that found in the known birds. Furthermore, the variation in rib-sternum apparatus in the reptiles is considerable and does not compare with the rib-sternum apparatus in any of the known birds. Recently, the view has been widely accepted that the carinate sternum preceded the non-carinate or ratite type of sternum. This latter view remains open to presentation of further substantiating evidences.

Since there is no apparent evidence of its presence in either *Archaeopteryx* or *Archaeornis* (Wetmore, 1951), it may be inferred that these forms are palaeontological curiosities which did not contribute to avian evolution, and that there may have been a great many other (undiscovered) unsuccessful reptilo-avian or avio-reptilian forms produced.

The occurrence of feathers in these animals may be regarded as another instance or example of paramorphogenesis and not one of convergent evolution. The capacity for flight is not restricted to birds, but is known to have been developed in reptiles and mammals as well as in birds.

It is possible that the fossil evidences of the true ancestral birds are to be found in or among the Jurassic coal deposits of Antarctica. It is likewise possible that the fossil remains of pro-mammalian forms, early Metatheria and Eutheria, are to be found in or among these same deposits.

**PALAEOGEOGRAPHICAL INFERENCES**

Most of Europe, Asia, Australia, Greenland, South America, and Antarctica are said to have had a tropical or sub-tropical climate during Jurassic time. Since the climate would have been generally favorable for the production and survival of many new land vertebrates, it may be inferred that the origin of pro- and quasi-avian and mammalian forms could have taken place in any one of these land masses.

Based on the neogeographical as well as the palaeogeographical distribution of the known orders of birds, and especially the relict orders, it is not entirely feasible to look for the center of origin in Asia or Europe, nor for that matter in either South America or Australia. While Greenland has been suggested as a center of origin, there have been too many objections to this view. Major objections to the Arctic region as a center of origin are readily found in the known distribution of birds.

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To assume that Greenland had been the center of origin for birds and mammals would make it more difficult to explain a pre-Miocene distribution of either Meta-theria or Eutheria in South America, marsupials and monotremes in New Zealand and Australia, or the post-Miocene occurrence of tinamous and rheas in South America, and emus, cassowaries and kiwis in New Zealand and Australia. On the other hand, if we were to assume the origin of early birds and mammals to have taken place in Antarctica, the subsequent occurrence of these forms in seemingly widely separated and unconnected land masses (Australia and South America) could be accounted for by assuming that land connections existed between Antarctica and South America, and between Antarctica and Australia—during or subsequent to the period of evolution of these early birds and mammals. Such land connections would have been possible with a sea level lower than at present. This could have occurred during a period of extensive glaciation or during one of the great ice ages. Pauly (1952) has reported on the occurrence of such an ice age during Mesozoic time.

![Figure 1. Probable routes of dispersal from Antarctica.](image)

(Heavy solid lines = Primary dispersal routes.)
(Heavy broken lines = Secondary dispersal routes.)

According to Pauly (1952) a large part of southeast Africa was covered by a great ice and snow mass, while Antarctica was subjected to tropical and subtropical climates, during Jurassic time.

There are still some evidences of land connections in the form of small islands between these land masses. The land bridge to South America still is quite evident (Graham's Land, South Orkney, South Shetland, and Faulkland Islands). The land bridge to Australia and New Zealand is less evident today than that with South America.

In addition to these two land bridges, there was a land connection between Australia and the Asiatic mainland. This provided an avenue for the dispersal of forms which evolved in and about Australia. Furthermore, this latter land connection accounts for the pre-Miocene distribution of some birds and possibly all mammals which occurred in the Holarctic, Ethiopian, and Oriental regions. Remnants of this land connection are readily discernible even today.
Malaya and West Borneo formed a land mass during Miocene times, while the western Malay archipelago was largely inundated (deBeaufort, 1951). Such disconnections with the formation of islands appears to account for the successful survival of many relict forms which are found in the Australasian region.

On the assumption that Antarctica was the center of origin for the ancestors of present-day birds, and perhaps even for ancestral Metatheria and Eutheria, we may then attribute the occurrence of relict orders in both South America and Australia and the adjacent islands to population emigrations in these two directions along natural avenues of dispersal.

Subsequent isolation resulting from inundation of the lower land areas (deBeaufort, 1951), accompanied by the interruption of direct land connections, may have afforded conditions essential to survival and success of the isolated forms or for their continued evolution resulting in a high degree of specialization.

While South America served as the terminus for forms migrating in that direction, two major avenues for dispersal were open to those forms which migrated to Australia and thence to the Asiatic mainland. The first of these routes lies along the eastern coast of Asia to Alaska and then south along the western part of the North American continent, while the second dispersal route leads westward from Malaya across India and the Middle East to Europe on the one hand, and to Africa and Madagascar on the other hand.

These routes of dispersal appear to coincide with or approximate the marginal limits of the major zoogeographic realms (fig. 1). DeBeaufort (1951) has pointed out that the major land masses have existed since pre-Cambrian time, although there has been change in the topography and climatic conditions. This has likewise been noted by Pauly (1952).

ANATOMICAL INFERENCES

Based upon a study of the carotid artery patterns in several orders of birds (Glenny, 1940–1953 and unpublished papers), and particularly those of the Psittaciformes, there appears to be a high degree of coincidence in the distribution of carotid evolutants and the apparent routes of dispersal as noted above.

The aortic arch system affords only one source of evidence for the evolution of birds, but recent studies on parts of the skeletal system appear to further substantiate the view herein presented. Glenny and Amadon (1954), Glenny and Friedman (1954), and Glenny (195-) have reported on the reduction of the clavicles in several birds, and have found this feature to be independent of other characters, and consistent for the genus.

Classification of Bird Clavicles

Class 1+: furcula complete with hypocleidium; class 1: furcula complete, hypocleidium lacking; class 2: clavicles separate and sword-shaped, interclavicle reduced to a ligamentous bridge (pons); class 3: clavicles greatly reduced, epicleidium bone, corpus claviculi ligamentous, interclavicle ligamentous if present; class 4: clavicles entirely ligamentous, but maintaining an attachment to the clavicular face of the coracoid bone; class 5: clavicles completely absent, clavicular face of the coracoid bone lacking.

In so far as our present knowledge is concerned, among the parrots evolution from a class 1 to class 2 or class 3 clavicle occurs with greater frequency in genera in the Australian realm (9 genera) than elsewhere, and is found in more psittacine genera in the Ethiopian realm (3 genera) than in the Neotropical realm (1 genus). Three genera of the Loriinae and all of the Micropsittinae show evidence of clavicle evolution, none of the Kakatoeinae thus far studied show any reduction of the clavicles, and of the South American Psittacinae the genus Forpus alone shows evidence of a considerable reduction of the clavicles.

The Dodo (Didus cucullatus) presented a class 2 clavicle, while the Pheasant
Pigeon (*Otidiphaps nobilis*) was found to have a class 3 clavicle. Both of these birds inhabited areas not far from their presumptive center of evolution.

Of the Psittacinae, genera presenting the A-2-s carotid arrangement and some degree of clavicle reduction are *Cyanoramphus*, *Northiella*, *Platycercus*, *Poicephalus*, and to a lesser extend *Psittacus*, while genera presenting the A-1 carotid arrangement and class 3 clavicles are *Melopsittacus*, *Polytelis*, and *Agapornis*.

McDowell (1948) has shown that the classification of birds based on the bony palate results in division of the former Palaeognathae. Furthermore, he appears to present sound evidences of closer affinities between the tinamous and rheas than between the rheas and other “palaeognathous” birds. It should be noted further that in each of McDowell’s groups those forms with most similar palatal structure have or had a more nearly similar geographical distribution. The arterial arrangement-pattern and skull structure of the Apterygiformes are of a highly specialized nature (Glenny, 1942; McDowell, 1948).

The A-2-s carotid arrangement can be traced from Australia and New Zealand (*Cyanoramphus*, *Northiella*, *Psephotus*, and *Platycerus*) to New Guinea (*Psittrichas*), Madagascar (*Coracopsis*), and Africa (*Psittacus* and *Poicephalus*). All of the South American parrots have the A-2-s carotid arrangement, and except for *Forpus* the class 1 clavicle.

**NEOGEOGRAPHICAL INFERENCES**

The Sphenisciformes appear to have inhabited the southern hemisphere since their origin (Simpson, 1946), and these birds are now regarded by Wetmore (1951) to have unknown relationships with the rest of the Neornithes.

McDowell (1948) has emphasized the similarities in the bony palates of both the tinamous and rheas and their dissimilarities to those of the ostrich, emus, and cassowaries. These observations are of interest when considering the geographical distribution of these different birds.

The Gaviiformes and Colymbiformes are highly evolved forms possibly derived from an earlier odontognathous line which had migrated into the northern hemisphere. The resultant orders persist in the hemisphere in spite of their small number of species.

The distribution of the kiwis is a very limited one, nor is there evidence that they ever had a wide distribution.

In the Procellariiformes, the largest number of species are found to nest on islands in the southern hemisphere from about 30°S. latitude to about 65°S. latitude.

Due to the wide distribution of the Pelecaniformes, Ciconiiformes, Anseriformes, Falconiformes, Charadriiformes, Cuculiformes, and Strigiformes without any notable features in this distribution, little information is to be gained by a study of their distribution, in so far as the center of their origin and evolution is concerned. It is possible that the ancestral stocks for these orders arose in Antarctica and then spread through the major parts of the world, but at present sufficient evidence is not available to substantiate such a view.

Mayr and Amadon (1951) consider the gallinaceous birds to be of very early origin. Based on present-day distribution and certain anatomical differences, I would presume that the early galline ancestors could have had their origin and early evolution in Antarctica. The subsequent isolation and independent evolution of the Cracidae and Opisthocomidae of South America could account for some of the differences between them and their Old World allies. Likewise, isolation and the subsequent evolution of the Megapodes in the south and southwest Pacific islands could account for important differences between them and the Phasianidea. The major evolution of the Phasianidea undoubtedly took place in Asia, with a subsequent distribution throughout the Holarctic region.

Placing the Megapodidae and the Cracidae in the same super-family is somewhat misleading and taxonomically unsound. In the first place these two families do not
have the same carotid formula. The Megapodidae are characteristically unicaortid while the Cracidae are bicarotid (A-1). Any structural similarities between these two families may be due to basic characteristics found throughout the order, and achieving various levels of evolution within the different families.

In the gruiform assemblage, there are many structurally diverse families. This is suggestive of an early origin and subsequent wide divergence of early forms. The Mesoenatidae are relict species which have become quite specialized, probably as a result of their insular isolation (Glenny and Friedmann, 1954). Reduction of the clavicles and reduction or loss of the flight-function characterize the members of this family. The Turnicidae have a rather wide distribution, but the center of evolution of this family may well have been in the region of Australasia since they do not occur in the Neotropical realm. Distribution of the Gruidae indicates two avenues of dispersal from southeast Asia after an earlier evolution in the vicinity of New Guinea and Australia. The Aramidae and Psophiidae may represent the specialized descendents of early gruiform migrants from Antarctica to South America, and an ancestral ralline stock from Antarctica may have given rise to the Rallidae since the distribution of genera and species on the islands of the southern hemisphere would tend to confirm this view. The origin of the Heliornithidae likewise may have been in Antarctica, with dispersal taking place into South America and through Malaya to Africa. *Rhynochetos* is an insular relict derived from the rapidly evolving gruine stock of the Australasian region, while the Eurypygidae and Cariamidae may be relicts of early South American forms. The Otidae ancestors appear to have taken the southern dispersal route from Malaya, across India and the Middle East to Africa and Europe.

Australia and the adjacent islands appear to have been important centers of early evolution of the Columbidae (Glenny and Amadon, 1954) and certainly this region was the center for subsequent evolution of many of the Psittaciformes. The present distribution of parrots can be accounted for on the basis of their origin in and subsequent movement from Antarctica to South America and Australia and New Zealand. The occurrence of the Loriinae and the Kakatoeinae in Australia and the islands of the south and southwest Pacific tends to confirm the view that this area formed an important center for psittacine evolution. Considerable evolution of the carotid arteries has taken place in the Australasian parrots whereas there is a seemingly rigid uniformity in the carotids in the Neotropical parrots.

Two centers of early evolution and dispersal are possible in the Caprimulgiformes (Australasian and South American), although a single center in Australasia would be possible if it were followed by a world-wide dispersal.

Whether or not the families of the Apodiformes are closely allied may be a matter in question, but the origin of these birds must have been quite early in the history of the class, and probably occurred in Antarctica, since the Apodidae are found in both South America and in the Old World. The Hemiprocnidae are entirely Australasian in their present distribution, while the Trochilidae appear to have had their center of evolution and present distribution in South America and the adjacent land areas.

The trogons, relationships of which are uncertain, are found in southeast Asia and tropical America. Their distribution closely resembles that of the Heliornithidae (deBeaufort, 1951). A doubtful fossil of *Trogon gallicus* is reported from the lower Miocene of France. If this is in fact a specimen of the genus *Trogon*, then these birds had achieved a wide distribution during the Tertiary period, but have survived only in areas where the climate has proved to be more amenable to their success. Their present distribution is suggestive of an origin in Antarctica with subsequent evolution in both South America and in southeast Asia.

Distribution of the Galbulidae, Bucconidae, and Ramphastidae in South America, the Capitonidae in South America, Asia, and Africa, the Indicatoridae in Africa, and the Picidae world-wide is strongly suggestive of an Antarctica origin of
the Coraciiformes followed by the subsequent establishment of centers of evolution in the other zoogeographic realms.

The geographic isolation of the Coliiformes in Africa, without recognizable relationships to any particular order of birds remains a problem. It is possible that these birds represent the evolutants of early passerine African immigrants.

Similarity in the bony palate of the Passeres and the restricted distribution of neotropical and old world families of passerine birds is suggestive of both a common ancestry and an early separation or segregation geographically. The common origin and subsequent geographical isolation of these particular families can be accounted for on the basis of rapid evolution of diverse pro-family types in Antarctica, followed by dispersal to the adjacent land areas with or in advance of the advent of an adverse climate or with increases in strongly competitive species and rather large populations.

The influence of an adverse climate on avian and mammalian populations in Europe and in North America is most remarkable when comparing the species of these areas during the Tertiary and the Quaternary periods.

**ECOLOGICAL INFERENCES**

The process of speciation among forms with a low biotic potential usually takes place at a lower rate than among forms with a high biotic potential. This appears to hold even among populations which sustain a very high annual mortality.

Under conditions of relative isolation, a small homogeneous population may survive and undergo notable evolutionary changes. Innumerable instances of insular isolation can be offered as evidence for this rather general observation. The Kagu, Megapodidae, Mesoenatidae, and many other birds and mammals serve as simple examples of this. In larger land areas, ecological niches serve to accomplish essentially the same results. These more notable evolutionary changes may be structural, color, dietary, or physiological.

Romer (1945) has pointed out that the success of newly evolved forms is dependent upon relatively little pressure from competitive forms, but more particularly on freedom from predation by already well-established forms. Once established, a new group of organisms may survive and evolve quite rapidly in spite of other competitive forms.

An abundance of moisture and a lack of severe fluctuations in temperature—with temperatures always above freezing—are optimal conditions (deBeaufort, 1951), and optimal conditions are essential for the establishment of new and rapidly evolving forms of life.

From available information, we may infer that the climate in Antarctica was favorable for survival of both pro-avian and pro-mammalian forms. In addition, a large flora appears to have developed as evidenced by the large Jurassic coal deposits. During the same period, a large ice sheet covered a large part of Africa (Pauly, 1952). Therefore the origin of birds or mammals in Africa would appear to be out of the question during this period, particularly in as much as rapid evolution does not take place under such conditions.

Presumably competition and pressure from predation was not so severe in Antarctica during the Mesozoic Era, or shall we say that we have no evidence to show that this land mass was inhabited by the giant lizards that are reported from North America and Asia during this period. As a result, we might conclude that generally more favorable conditions existed in Antarctica for the origin and early evolution of both birds and mammals than existed in other parts of the world.

**CONCLUSIONS**

The occurrence of quasi-avian or quasi-mammalian forms on other and widely separated parts of the world cannot be held in evidence that these widely separated areas served as multiple centers of origin for either birds or mammals. Such a view
would necessitate supplanting the monophyletic origin for a polyphyletic origin of either birds or mammals. This in turn would necessitate the reconstitution of either or both groups and reassignment to their proper components. It is possible that some presumptive "mammals" are in effect quasi-mammalian forms just as *Archaeopteryx* and *Archaeornis* are to be regarded as quasi-avian forms rather than true birds.

The known distribution of the primates can be accounted for in much the same way as that given for the distribution of parrots. Likewise we can account for the wide distribution of marsupials in the same manner. Romer (1945) has pointed out that the marsupials and other small mammals of South America were subjected to much less predation prior to the land connection between North America and South America and attributes the reduction in numbers of species in South America to this factor.

The geographical distribution of the orders of birds and mammals provide us with information from which we may draw inferences with respect to the routes of dispersal of these animals. These dispersal routes appear to coincide with the marginal limits of the major zoogeographic regions.

The occurrence of trogons, swifts, parrots, marsupials, and primates in both South America and Australasia; the occurrence of tinamous, rheas, and trochilids in South America but not Australasia; and the occurrence of kiwis, emus, cassowaries, and monotremes in Australasia but non-existent in South America has yet to be satisfactorily explained on the basis of an origin in Australasia. Their origin in Antarctica, however, would make possible a natural dispersal to both Australasia and to South America and thus facilitate the explanation of some of the phenomena of vertebrate distribution. It is within the realm of possibility that the remains of many of the early birds and mammals or their ancestors still lie entombed by the snow and ice which covers the land that is Antarctica.

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