Trans. Nat. Acad. Sci. & Tech. (Phils.)
1987.9:229-242

ZOOGEOGRAPHICAL AFFINITIES OF PARAMPHISTOMIDS OF RUMINANTS

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ABSTRACT

The distribution of the various species of the family Paramphistomidae is discussed.

Majority of species of the genus *Paramphistomum* occur in Asia and Europe and few are restricted to certain areas elsewhere. Previous records of some species were found to be cases of misidentifications. True records of *P. cervi* include only those in the north temperate regions. The species apparently is primarily a north temperate species and its distribution coincides with that of the intermediate host. Its introduction to south temperate areas is limited by the presence of suitable intermediate hosts as the species does not occur in South Africa and temperate parts of Australia but is now present in temperate Brazil.

The genus *Calicophoron* is predominantly African and of the 12 species, only four do not occur in Africa. All 12 species are restricted to bovidae. *C. calicophorum* is the most widespread species occurring in Asia, the USSR and Australia. *C. raja* has been recorded in 14 host genera all belonging to the bovidae, 9 of which are solely African. This species is one of the commonest in Africa but its intermediate hosts remain unknown. The species was recently identified in Cuba and was probably introduced in this country through importation of cattle and wild ruminants from Africa.

The genus *Gigantocotyle* is represented in Africa by three species and in Asia by only one. Two species occur in hippopotamus and two in ruminants. All three species of the genus *Explanatum* are Asian. Records of the presence of *E. explanatum* in Africa were cases of misidentification.

Members of the genus *Cotylophoron* occur in Africa, Asia and North and South America. Of the four African species, two were recorded outside the continent. Some earlier records of *C. cotylophorum* are also cases of misidentifications.

All 11 species of the genus *Orthocoelium* have been reported from Asia and only two species have been recorded also outside the continent. These species have probably been introduced through the zebu cattle and water buffalo from neighboring Asian countries to Australia, Kenya and Chad. All species of the genus *Leiperocotyle* and *Bilatorchis* are African and the host genera are solely African. Four paramphistomid genera characterized by the presence of pharyngeal diverticula are endemic in their occurrence as follows: *Balanorchis* in South America; *Stephanopharynx* and *Choerycotyloides* in Africa and *Olveria* in India.

Paramphistomids of ruminants probably have originated in tropical Asia. From here, they were dispersed by their hosts to several regions and in these regions evolved into genera and several species and flourished especially in

Africa where the climate is warm and a variety of ruminant hosts is present. It is believed that a land bridge existed during the late miocene between Asia and Africa and fossil records appear to suggest that families and tribes of animals invaded Africa from Asia. Despite however of extensive movements of their hosts, species of the family have not been widely dispersed by them because their establishment in new environments depends on the presence of suitable intermediate hosts.

Introduction

The superfamily Paramphistomoidae includes large assemblage of species occurring in almost all vertebrate host including mammals, birds, reptiles, amphibians and fishes. Those occurring in ruminants belong to two families, the Paramphistomidae (non-pouched amphistomes) and the Gastrothylacidae (pouched amphistomes). Generally, little is still known of the Paramphistomoidea but those occurring in ruminants are fairly known. With the recent revision of the family Paramphistomidae by the author after examination of enormous collections from various parts of the world, it is possible to discern the broad patterns of distribution and origin of the family Paramphistomidae. Gaps however still exist in certain areas. This paper deals only with those species of the family Paramphistomidae occurring in ruminants.

Materials and Methods

Specimens of Paramphistomids of ruminants were obtained from various sources. Majority of the specimens were from the collection of Dr. J. A. Dinnik; the late Dr. P.L. LeRoux, the London School of Hygiene and Tropical Medicine and the Commonwealth Institute of Helminthology (now CAB International Institute of Parasitology).

Materials were also examined from the reference collection of the British Museum (Natural History); London School of Hygiene and Tropical Medicine, University of London; Commonwealth Institute of Helminthology; Naturhistoriska Riksmuseet, Stockholm, Sweden; Musée Royal de l' Afrique Centrale, Tervuren Belgium; Instituto Oswaldo Cruz, Rió de Janeiro, Brazil; Institut für Parasitologie de Veterinärmedizinische Universität Wien, Austria and the Onderstepoort Veterinary Research Institue, Transvaal, Republic of South Africa.

Type specimens were re-examined on loan from the above institutions and Museum für Naturkunde (Bereich Zoologisches Museum) and der Alexander von Humboldt Universität zu Berlin, German Democratic Republic; Museum d' Histoire Naturelle Geneve, Switzerland; United States National Parasite Collection, USDA, Beltsville, Maryland and American Museum of Natural History, New York, U.S.A.

Additional materials were obtained from numerous individuals in various parts of the world who kindly provided specimens on request. These are given in

the taxonomic part published as series of papers (Eduardo 1982a, c; 1983; 1984; 1985a, b, c; 1986). Specimens from the Philippines are the author's own collection.

The host and origin of all materials examined were carefully noted. For specific identification, both hand thick and microscopic sections in the frontal, sagittal and transverse planes were prepared and representative specimens of some species were examined under the scanning electron microscope. The technique of hand thick section preparation and processing specimen for scanning electron microscopy are detailed in a separate paper (Eduardo, 1982b).

Results and Discussion

To present an accurate picture of the distribution of any particular group of parasites is difficult to provide especially when there is a dearth of information and when existing information contains inaccurate records of species due to misidentifications. Such is the case of the paramphistomids of ruminants where our knowledge of their geographical distribution is far from complete, gaps exist in certain areas and the life history of many species remains unknown. The situation is confused by many previous inaccurate records including reports of species by some authors who followed synonymies which were later proved to be valid species. Some misidentifications have been established by re-examination of the original materials or analysis of the original descriptions and accompanying illustrations but others could not be verified particularly when these records are incomplete or when the original materials are no longer available for re-examination.

All nine species of the genus *Paramphistomum* are parasitic only in ruminants, the majority of which occur in Asia and Europe and few are restricted to certain areas elsewhere. The exact distribution of *Paramphistomum cervi* is difficult to assess due to many previous dubious records. Maplestone (1923) confused the situation by placing eight species as synonyms of *P. cervi* and some subsequent authors based their identifications on this synonymy. Thus, the species has been recorded in various parts of the world giving a picture of a worldwide distribution. However, seven of the eight synonyms (some now belong to other genera) are in fact valid species. Therefore previous records of *P. cervi* which followed Maplestone's synonymy could also be any of the seven valid species. Subsequent re-examination of available original materials and investigation of recent collections have shown that the distribution of the species is not worldwide as was originally thought. Fischoeder (1903) was of the opinion that the species is purely of European distribution and Näsmark (1937) strongly endorsed this view. Dinnik and Dinnik (1954) have shown that what was previously recorded as *P. cervi* in East Africa by Dinnik (1951) was actually *P. microbothrium* (now moved to the genus *Calicophoron*). Record of the species by Joyeux and Baer (1928) in Dahomey and Stunkard (1929) in the Congo was regarded by Nasmärk (1937) as dubious identifications. He considered Stunkard's material as *P. clavula* (now moved to the genus *Calicophoron*) and concluded that *P. cervi* does not exist in Africa south of the Sahara.

Swart (1954) also claimed that previous records of *P. cervi* in the Republic of South Africa were infact *P. microbothrium.* Looss (1912) stated that what he described as *"Amphistomum conicum"* (=*P. cervi*) in Egypt in 1896 was actually *P. microbothrium.* Sey did not find *P. cervi* in his examination of amphistomes from Egyptian ruminants and stated that previous records of the species in the country could be *P. microbothrium.* Round (1968) concluded that none of the records of *P. cervi* in Africa is likely to be that of the species but of related ones.

Durie (1951) has shown that previous records of *P. cervi* in Australia were erroneous and these actually consisted of two species, *Ceylonocotyle streptocoelium* (now *Orthocoelium streptocoelium*) and *Calicophoron calicophorum.* Although *P. cervi* has been recorded in the Philippines (De Jesus, 1938; Tubangui, 1947), recent collections did not reveal the presence of this species there (Eduardo and Manuel, 1975; Eduardo, 1982c). Sey (1979) did not identify *P. cervi* in his examination of several collections of amphistomes of ruminants in India and specimens labeled *"P. cervi"* presented to him by various Indian authors were in fact either *P. epiclitum* or *P. gracile.* He came to the conclusion that previous records of *P. cervi* in the subcontinent could either be one of the two other species. Caballero y Caballero, Brenes and Jimenez-Quiros (1957) recorded *P. cervi* from *Bos taurus* in San Jose, Costa Rica but their description and illustration clearly indicate that their specimen was *Calicophoron microbothrioides.*

The result of the present study which consisted of examination of several collections from various parts of the world, both early and recent collections, also strongly indicates a limited distribution of *P. cervi.* The species was identified only in collections from some countries in Europe and from the only two samples from the yak (*Bos grunniens*) in Tibet. Recently, Velázquez-Maldonado (1976) recorded the species from cattle in Rio Grande du Sul, Brazil. The intermediate host of *P. cervi* in nature in Europe is *Planorbis planorbis* (Szidat, 1936). The distribution of this snail host includes Europe and western and northern Asia (Ellis, 1969; Frandsen personal communication). Other snails which were found experimentally to serve as intermediate hosts are *Anisus vortex, A. leucostomus, Bathyomphalus contortus, Hippeutis complanatus, Armiger crista* and *Segmentina nitida* (Kraneburg, 1977; Odening, Bockhardt and Gräfner, 1978). Since many previous records of *P. cervi* in tropical regions were found to be cases of misidentifications and true records include only those in the north temperate regions, the species apparently is primarily a north temperate species and its distribution coincides with that of the intermediate host. Its introduction to south temperate areas is limited by the presence of suitable intermediate hosts as the species does not occur in South Africa and temperate parts of Australia but is now present in temperate parts of Brazil.

Two species namely, *P. leydeni* and *P. hiberniae* which are closely related to *P. cervi* are also of European distribution. The former species has been recently recorded in Rio Grande du Sul, Brazil (Velázquez-Maldonado, 1976). The known snail hosts of both species serve also as intermediate hosts for *P. cervi, P. gracile,*

P. epiclitum, *P. ichikawai* and *P. gotoi* are primarily Asiatic species. The last two however extend to eastern Europe. *P. echikawai* also occurs in Australia, and *P. gotoi* has been recorded recently in Egypt from water buffalo (Sey, 1977). Both species and *P. gracile* have been recorded in Brazil (Velázquez-Maldonado, 1976) but the author's descriptions and illustrations clearly indicate that he was dealing with specimens of *P. leydeni* and *P. cervi*, respectively. The known intermediate host of *P. epiclitum* is *Indoplanorbis exustus* whose distribution includes India, Thailand, Malay Peninsula and Sumatra (Malek and Cheng, 1974). The record of the presence of *Cotylophoron indicum*, a species regarded here as a synonym of *P. epiclitum*, in Africa by Näsmark (1937) and Dinnik, Walker, Barnett and Brocklesby (1963) was a case of misidentification. The writer has re-examined Näsmark's material and his specimen was not of that species. Dinnik, Walker, Barnett and Brocklesby (1963) based their identification on Näsmark's description. The snail hosts of *P. ichikawai* are *Segnitilia* (now *Helicorbis*) *alphena* in Australia, *Helicorbis sujfunensis Gyraulus filiaris*, *Segmentina nitida*, *Polypylis largillieri* and *Hippeutis complanatus* in the U.S.S.R. and *Planorbis planorbis* in Hungary (Durie, 1953; Kiselev, 1967 and Sey and Vishnyakov, 1976).

Paramphistomum liorchis is so far known only in North and South America. It is mainly a parasite of the American deer belonging to the tribe Odocoeliein and its intermediate host is still not known. Only one species of the genus, *P. cephalophi* Eduardo, 1982 is so far known in Africa and it is a parasite of the black-fronted duiker (*Cephalophus nigrifrons*), whose present distribution is restricted only to Central Africa.

As judged from these records, the genus *Paramphistomum* is predominantly Euroasian and the genus has probably developed and radiated from this region. Despite extensive movements of the final hosts, species of the genus have not been widely dispersed by them because their establishment in new environment depends on the presence of suitable intermediate hosts.

The genus *Calicophoron* is predominantly African and of the 12 species of the genus only four, namely *C. calicophorum*, *C. papillosum*, *C. papilligerum* and *C. microbothrioides*, do not occur in Africa. All 12 species are restricted to the Bovidae. *C. calicophorum* is the most widespread species of the genus, occurring in Asia, the U.S.S.R. and Australia. Previous records of its occurrence in Africa are doubtful and probably are misidentifications. The description and illustration of Swart (1954) for the species based on specimens from the Republic of South Africa clearly indicate that his specimens were *Calicophoron raja*. Specimens labeled *"Paramphistomum calicophorum"* from the collection of the Onderstepoort Veterinary Research Institute were examined by the writer and these were found to be *C. raja*. Despite examination of extensive collections of amphistomes from various hosts and localities in Africa, *C. calicophorum* was not identified. The known intermediate hosts of *C. calicophorum* are planorbid snails, *Pygmanisus pelorius*, *Glyptanisus* (now *Gyraulus*) *gilberti* and *Segnitilia* (now *Helicorbis*)

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alphena in Australia (Durie, 1956) and *Planorbis planorbis* and *Anisus* sp. in the U.S.S.R. (Katkov, 1973, Khaidarov, 1974). The species has probably been introduced to Australia through importation of water buffalo at various times from Indonesia and India. *Calicophoron papillosum* and *C. papilligerum* are so far known in India and the former also in Indonesia and their snail hosts are still unknown. The genus *Calicophoron* is represented by only one species, *C. microbothrioides* in North and Central America including the Carribean. The snail hosts of this species in the U.S.A. are lymnaeids, *Fossaria parva, F. modicella* and *Stagnicola cubensis. C. microbothrioides* also occurs in Eastern Europe. It has been recorded in the U.S.S.R. as "*Ceylonocotyle petrovi*" (Davydova, 1961) and has been introduced to Bulgaria through importation of cattle from the U.S.A. (Kamburov, Vasilev, Samnaliev and Kanev, 1977; Samnaliev, 1980). However, previous records of its occurrence in Albania (Erhardova, 1964) and Hungary (Kotlan 1958, 1960) were cases of misidentifications and these authors were dealing with specimens of *Calicophoron daubneyi* (Odening and Gräfner, 1979). *C. microbothrioides* has recently been recorded from cattle in the Philippines (Eduardo, Kaw and Javellana, 1987). It probably was introduced to the country through importation of cattle from the U.S.A.

The African species of *Calicophoron* are: *C. microbothrium, C. bothriophoron, C. raja, C. clavula, C. sukari, C. phillerouxi, C. daubneyi* and *C. sukumum.* Two of the above, namely *C. microbothrium* and *C. daubneyi* extend outside the continent. The former occurs in the Mediterrenean where it is the predominant species, in Portugal and in the Near East and the latter also in the Mediterrenean and Eastern Europe. The known intermediate hosts of *C. microbothrium* are bulinid snails. According to Dinnik (1965), *Bulinus truncatus* acts as the intermediate host for the species in North Africa, the Mediterrenean and the Near East and *Bulinus tropicus* and some species of the subgenus *Physopsis* in Africa south of the Sahara where these are widespread. On the other hand, the intermediate hosts of *C. daubneyi* are lymnaeid snails, *Lymnaea truncatula* in Kenya (Dinnik, 1962), *L. truncatula* and *L. peregra* in East Germany (Odening, Bockhardt and Gräfner, 1978) and *L. peregra* in Hungary (Sey, 1974). Dinnik (1962) has demonstrated experimentally that *C. daubneyi* failed to develop in bulinid snails which are intermediate hosts of *C. microbothrium*, likewise, the latter species failed to develop in *Lymnaea truncatula* which is the intermediate host of *C. daubneyi.* Sey (1974) failed to infect snails belonging to the same family as *Bulinus*, namely *Planorbis planorbis, P. spirorbis* and *Gyraulus crista* with miracidia of *C. daubneyi.* Both species appear to be strictly specific to their respective intermediate hosts. Although *C. microbothrium* has been previously recorded in Eastern Europe, i.e. Hungary (Kótlan, 1958; Sey, 1971), Bulgaria (Mereminskii and Vishnyakov, 1969; Vasilev and Samnaliev, 1974; Mikhailova, Gateva and Nedeva, 1972-73), the Balkans (Kótrla, Prokopič and Vishnyakov, 1974), recent investigations in these areas did not reveal the species but of another closely related one, *C. daubneyi* (Sey, 1974; Sey and Vishnyakov, 1976) and it is more likely that the above

authors were dealing with the latter species. This is supported by the fact that bulinid snails which serve as intermediate host for *C. microbothrium* do not exist in these areas, but lymnaeid snails which are intermediate hosts of *C. daubneyi* are present. In Europe, bulinid snails are distributed only in the south-western areas which include the Iberian Peninsula, southern France, Sardinia and Corsica (Haas, 1935; Mandahl-Barth, 1965). *Calicophoron raja* has been recorded in 14 host genera all belonging to the Bovidae, 9 of which are solely African. This species is one of the commonest in Africa but its intermediate host still remains unknown. Recently, the writer has identified the species in a collection of paramphistomes from cattle in Cuba. It probably has been introduced through importation of cattle or other wild ruminants from Africa and has established itself in the island due to the favourable climatic condition and presence of suitable snail host. *C. bothriophoron* has also been recorded in the neighbouring islands of Madagascar and Mauritius in domestic ruminants, it has been probably introduced from Africa through these hosts. The report of its occurrence in *Bos taurus brachycerus* in Bulgaria by Mikhailova, Gateva and Nedeva (1972-73) was a case of misidentification according to Odening and Gräfner (1979) who claimed that they were dealing with specimens of *Paramphistomum ichikawai*. *C. clavula* has been recorded in 8 host genera, all of the Bovidae, of which 5 are solely African wild ruminants. Its intermediate host in Somalia is *Bulinus abyssinicus* (Sobrero, 1962). Previous records of its occurrence in Hungary (Kótlan, 1958), Turkey (Güralp and Oguz, 1967) and Bulgaria (Mikhailova, Gateva and Nedeva, 1972-73) were misidentifications according to Odening and Gräfner (1979) and the species involved was in fact *C. daubneyi*. *C. phillerouxi* has been recorded in 8 host genera and with the exception of the genus *Bos*, all are solely African. Morphologically, the species is very closely related to *C. microbothrium* and could easily be mistaken for it. Dinnik (1961) has however demonstrated experimentally that the species does not develop in snail hosts which serve as intermediate hosts for *C. microbothrium* and *C. daubneyi*. Its known intermediate hosts are bulinid snails of the forskalii group (*Bulinus forskalii*, *B. senegalensis* and *B. cernicus*). *C. sukari* primarily occurs in domestic ruminants, but it has been recorded in *Syncerus caffer* and an unidentified antelope (Gretillat, 1964). Its known snail host is *Biomphalaria pfeifferi* and its subspecies (Dinnik, 1954; Dinnik, 1965; Dinnik and Dinnik, 1957).

From the above, the genus *Calicophoron* appears to have developed in Africa and from here radiated to other areas. It is also apparent that in species where the life cycle is known, many are highly specific to their snail hosts and their introduction to new environments is limited by the presence in nature of these intermediate hosts.

The genus *Gigantocotyle* is represented in Africa by three species, *G. gigantocotyle*, *G. duplicitestorum* and *G. symmeri* and in Asia by only one, *G. formosanum*. The first two species occur in the hippopotamus and the last two in ruminants. Round (1968) cited LeRoux (1933) to have recorded *G. formosanum* in cattle and *Kobus leche* in Zambia but this record has never been confirmed. As no additional

record of this species in Africa has appeared since then despite extensive surveys in recent years, it is more likely that LeRoux was dealing with a different species. Although existing hippopotamuses are restricted to Africa, their fossil remains were found in Eurasia from the late Pliocene and Pleistocene periods and in Madagascar from the Pleistocene.

All three species of the genus *Explanatum* are Asian, previous records of the presence of *E. explanatum* in Africa (Maplestone, 1923; Dubois, 1930; LeRoux, 1931) were misidentifications. It is clear from the illustrations of Maplestone (1923) and Dubois (1930) that they were dealing with a different species, most likely *Calicophoron raja*. Jansen, Pacenovsky and Krupicer (1974) recently reported the species from a *Damaliscus albifrons* that died in Rotterdam Zoo (although the origin of the host was not specified, it is an African host), but their illustration also clearly indicates that their specimen was *C. raja*. The known intermediate hosts of *E. explanatum* are: *Indoplanorbis exustus, Gyraulus convexiusculus* and *Lymnaea luteola f. australis* (Srivastava, 1944, Singh, 1958; Mukherjee, 1962, Agrawal, 1971). *Gyraulus convexiusculus* also serves as intermediate host for *E. bathycotyle* (Jain, 1969) in India.

Members of the genus *Cotylophoron* occur in Africa, Asia and North and South America. Of the four African species, two were also recorded outside the continent, *C. cotylophorum* in various areas in Asia and North America and *C. fuelleborni* in the U.S.A. as *C. noveboracensis*. Some earlier records of *C. cotylophorum* however were misidentifications. *C. cotylophorum* of LeRoux (1930) in the Republic of South Africa and of Krull (1934) and Bennett (1936, 1938) in the U.S.A. were found to be *Calicophoron microbothrium* and *C. microbothrioides* respectively (Dinnik, 1965; Price and McIntosh, 1944). The writer has also examined specimens labeled *"Cotylophoron cotylophorum"* from Puerto Rico and these were found to be *Calicophoron microbothrioides. Cotylophoron panamensis* is the common species of the genus in the new world. Its distribution includes the southern states of the U.S.A., Central America and the Caribbean and northern regions of South America. Asian species of the genus include *C. bareilliense* in India and the Philippines and *C. xiangjiangense* in China. The genus does not occur in Europe and Australia despite extensive movements of animal hosts. Previous records of *Cotylophoron* species in Australia, Europe including the U.S.S.R. were misidentifications. The known intermediate host of *C. cotylophorum* in India is *Indoplanorbis exustus* (Srivastava, 1937; Sinha, 1950).

All the 11 species of the genus *Orthocoelium* have been reported from Asia and only two species have been recorded also outside the continent, *O. streptocoelium* in Australia (Durie, 1951) and the Belgian Congo (now Zaire) (Van Strydonck, 1970) and *O. scoliocoelium* in Kenya (Dinnik, 1956) and Chad (present work). This species have probably been introduced through the zebu cattle and water buffallo *(Bubalus bubalis)* from neighbouring Asian countries. Erhardova (1964) recorded *O. scoliocoelium* in Czechoslovakia but Odening and Gräfner (1979) have shown that the material was in fact *Paramphistomum ichikawai*. The known intermediate hosts of *O. streptocoelium, O. dicranocoelium* and *O. scolio-*

coelium are *Glyptanisus* (=Gyraulus) *gilberti* in Australia (Durie, 1953), *Bulinus pulchellus* in India (Jain, 1969); *Anisus natalensis* (now *Ceratophalus natalensis*) in Kenya (Dinnik, 1951) and *Bulinus pulchellus* in India; *Gyraulus convexiuaculus* in the Philippines (Mukherjee and Chauhan, 1965; Jain, 1977, Jain and Srivastava, 1969; Eduardo and Kaw, 1986 respectively).

All three species of the genus *Leiperocotyle* are African and the host genera are solely African, *L. okapi* and *L. congolense* in the Okapi *(Okapia johnstoni)* and *L. gretillati* in *Syncerus caffer*. Porter (1947) (as cited by Round, 1968) has reported an unidentified *Paramphistomum* species from a giraffe *(Giraffa camelopardalis)* that died in the London Zoo and as far as the writer is aware, this is the only record of a paramphistomid in this animal. The giraffe is related to the okapi and both belong to the same family, the Giraffidae. Although their present distribution is restricted to Africa, fossil giraffids are known from Asia in the Meiocene and Pleistocene and several groups reached eastern Europe in the Lower Pliocene (Darlington, 1963).

The monotypic genus *Bilatorchis* has so far been recorded in only two African host genera, *Kobus* and *Limnotragus*.

Among the paramphistomid genera occurring in ruminants, four are characterized by the presence of pharyngeal diverticula and because of this, they may be regarded as primitive. These genera are endemic in their occurrence as follows: *Balanorchis* (monotypic) in South America; *Stephanopharynx* (with three species but two of which are regarded here as synonyms), *Choerocotyloides* (monotypic) in Africa and *Olveria* (with two species) in India.

Paramphistomids of ruminants probably have originated in tropical Asia. From here they were dispersed by their hosts to several regions and in these regions evolved into genera and several species and flourished especially in Africa where the climate is warm. It is believed that a land bridge existed during the late Miocene between Asia and Africa and fossil records appear to suggest that families and tribes of animals invaded Africa from Asia.

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